BEHAVIOURAL AND ENERGETIC DETERMINANTS OF INDIVIDUAL MATING SUCCESS IN MALE GREY SEALS (*Halichoerus grypus*, Fabricius 1791).

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CANDIDATE'S DECLARATION

I declare that the work recorded in this thesis is entirely my own unless otherwise stated and that it is of my own composition. No part of this work has been submitted for any other degree.

I would like to dedicate the work presented in this thesis to my grand father, Jack Swindell, a keen amateur naturalist and an inspiration to myself.

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CHAPTER 1 - INTRODUCTION

Determinants of individual male mating success

The survival abilities of an individual animal, whether in foraging skills, establishing and maintaining a suitable living space or avoiding predators and disease, can only be worthwhile if the animal succeeds in passing on its genes by reproducing. The act of reproduction is in effect the ultimate aim of all animals. Adoption of the sexual mode of reproduction by a majority of species has many profound evolutionary consequences, primarily because the "ideal" reproductive strategies of males and females can be remarkably different (Darwin 1871, Trivers 1972 and 1976, Maynard Smith 1978). In general, females expend far greater amounts of energy per gamete than males (Parker *et al.* 1972, Alexander and Borgia 1978) and also invest considerably more in post-fertilisation care to enhance the survival chances of their offspring (Trivers 1972, Wilson 1975, Greenwood and Adams 1987). This is particularly true amongst the mammals, where females nurture the embryo(s) internally and supply the offspring with milk. Thus, in many cases, the opportunities for male mammals to invest in their offspring by providing parental care is extremely limited. Also, with internal fertilisation and female gestation, the reliability of paternity for male mammals may often be reduced. Where paternity can not be assured, the evolution of paternal care for offspring is less likely (Werren *et al.* 1980, Gross and Shine 1981, Alcock 1983). Indeed, in many species males merely contribute a sample of their genes to the offspring.

A male's reproductive success is seldom limited by the number of gametes he can produce, but by the number of females' eggs he can fertilise (Trivers 1972, Greenwood 1980). In fact, each male could potentially fertilise the eggs of many, if not all, females in the population, and a male's "fitness" is a function of the number of eggs he succeeds in fertilising, with the number of female gametes available to him becoming the limiting resource. Thus, with the difficulties of providing paternal care for offspring and the problems of reliability of paternity, particularly in many mammalian species, it is often preferable, from a male's point of view at least, for him to leave a mate after fertilisation and go in search of other females. Therefore, polygynous mating systems are common amongst mammalian species.

Where receptive females form the limiting resource, males will compete for access to these females, leading to often intense intra-sexual competition (Trivers 1972). Indeed, as the potential genetic benefits for an individual male are extremely high if he can monopolise a relatively large proportion of breeding opportunities, males are often prepared to risk much to gain copulations. Males often go to extreme lengths and invest considerable energy in attempting to gain high mating success. For example, many varied and often remarkable methods are employed in order to attract or locate females, often with elaborate courtship displays and extravagant ornaments, all requiring high energy expenditure. Males will compete to succour a particular resource required by the females, such as potential nest sites or good foraging areas. More directly, males of many species compete to control groups of females, guarding them from rival males in order to secure copulations. Both territory or harem acquisition and maintenance involves considerable expense of time and effort (Trivers 1972). Thus, although males in such species invest little, if anything, in their present offspring, they are prepared to suffer high energetic costs and considerable risks in order to produce more progeny.

Winners of male-male contests are usually the more dominant individuals, whether competing directly for mates, or, for example, territories. It is generally accepted that these high ranking males are more successful in terms of mating success than more subordinate males (Trivers 1976, Howard 1978). Those males which are successful in such competition can potentially reap enormous benefits in terms of mating success. It has been demonstrated in several mammalian species that it is the more dominant males that gain above average mating success, as for example, in American bison (Lott 1979), red deer (Clutton-Brock *et al.* 1979, Gibson and Guinness 1980a, Appleby 1982), baboons (Hausfater 1975), primates in general (Cowlisham and Dunbar 1991) and Northern Elephant seals (Le Boeuf 1974, Le Boeuf and Reiter 1988). This is illustrated particularly well by McCann's work on the southern elephant seal (1981). Here, a clear dominance rank was established, at least amongst the top five ranking bulls. A good relationship between dominance and mating success was found, with the top ranking male accounting for 38 % of all observed copulations, and the top five males a massive 88 % of all copulations.

However, despite the clear benefits gained by successful males, competition can involve severe costs. Apart from the energetic costs of ornaments, displays, holding territories or harems, there can be considerable risks, such as increased exposure to possible predation, reduction in foraging time or ability, and also, the dangers from other conspecific male competitors. Often, inter-male competition can be incredibly intense, particularly where the potential benefits to successful males are very great, with male-male fights leading to serious injuries if not death. For example, from their work on red deer, Clutton-Brock *et al.* (1979) stated that some 6 % of the male population suffered serious injuries each year in intrasexual competition. Such injuries could be fatal, possibly leading to infection or increased vulnerability to predation. At the very least, they are a serious set back to the individual's future success.

Indeed it has been shown that amongst many polygynous species there is often increased male mortality, both amongst juveniles (as shown in an excellent study of sub-adult male Elephant seals, Cox 1983) and adults, whether directly due to aggression or the greater energy requirements of males in terms of growth rates and greater adult size. Males may therefore suffer more in times of food shortage (for example in red deer, the more successful stags have lower body condition during winter as measured by antler casting time, Gibson and Guinness 1980b). Competing males may also suffer less obvious costs even within a single season, particularly in species with discrete breeding seasons, where males often reduce food intake (for example, red deer, Lincoln and Guinness 1973, Gibson and Guinness 1980b), or fast during the reproductive effort such as in many polygynous pinniped species.

Though fighting ability is often a major determinant of dominance, in many species, particularly amongst the vertebrates, actual physical contact between competing males is relatively rare. Instead, often complex and elaborate ritualised threats have evolved, allowing competitors to assess their opponent(s) without risking potentially fatal injuries.

This is particularly so amongst long lived animals, where unsuccessful subordinate males have the option to defer reproductive success in one breeding season for the possibility of moving up in dominance and hence, mating success, in future seasons (Maynard-Smith and Price 1973, Parker 1974). Thus, by assessing opponents through harmless threats, such a male can avoid possibly fatal conflict early in life. As he gets older, and perhaps larger and more experienced his competitive abilities may be sufficient to gain mating opportunities. Meanwhile, subordinates may adopt alternative mating strategies, such as sneak copulations and satellite males (Cox 1983). Whilst the benefits in terms of number of copulations may not be as great as amongst dominants, these subordinates may incur lower costs, particularly by avoiding conflict with dominants.

The potential benefits of dominance in terms of lifetime reproductive success can be so great that males will invest much in order to be effective competitors. Often size is a major influence on male competitive ability (e.g. Potter *et al.* 1976, Howard 1980, Clutton-Brock *et al.* 1979, Davies and Halliday 1979, Borgia 1980, 1982, McCann 1981) and similarly for the related attributes of age (Le Boeuf 1972, 1974, Campanella and Wolf 1974, Trivers 1976, Gibson and Guinness 1980) and experience (Trivers 1972, Howard 1978). For example, Alexander *et al.* (1979) suggested that where the potential for individual males to monopolise disproportionate amounts of the available breeding opportunities is large, inter-male competition should be more intense and so lead to selection for attributes, such as larger size, that enhance a male's competitive ability. This is supported by observations of many mammal species, in particular, amongst pinnipeds. In highly polygynous species such as the elephant seals, males can be over four times the weight of females, whilst in species where the number of females a male has access to in one season is apparently more limited, there is relatively little sexual dimorphism, if any (Bartholomew 1970, Stirling 1975, Le Boeuf 1978). These differences in mating systems have been largely attributed to the breeding habitat. The topography and temporal stability of the breeding substrate largely determines the spatial and temporal distribution of oestrus females (Bartholomew 1970, Stirling 1975, Le Boeuf 1978) and therefore influences the polygyny potential (Emlen and Oring 1977). Thus, in general, island breeding species tend to be more polygynous and pagophilic species less so.

The Grey seal (*Halichoerus grypus*, Fabricius 1791) is an excellent example of species with a polygynous mating system, a discrete breeding season and where males (and females) fast during the breeding effort (Anderson *et al.* 1975, Anderson and Fedak 1985). Therefore, both males and females have no energetic input ("income" in the terms of Drent and Daan 1980), but rely solely on reserves accrued prior to the breeding season ("capital" in the terms of Drent and Daan 1980) and are suitable candidates for studies of energy expenditure during the breeding season (Anderson and Fedak 1985, 1987 a, 1987 b, Fedak and Anderson 1982, 1985, Anderson and Harwood 1985).

Grey seals are moderately dimorphic and breed both on islands and on ice, providing an excellent opportunity to examine the influences of topography on mating systems. Whilst the breeding system amongst grey seals is undoubtedly polygynous, the "degree" of polygyny and the precise form of the breeding system appears to vary between different breeding colonies. Intriguing differences in social organisation during the breeding season can be seen when comparing separate breeding populations, such as those of North Rona and Sable Island, Nova Scotia (Boness and James 1979).

General biology of the Grey seal

The Grey seal belongs to the order Pinnipedia and the family Phocidae. Grey seals occur in the temperate and sub-arctic waters of both the western and eastern Atlantic coasts. Combining recent estimates of grey seal populations gives a total world population of approximately 170 000 to 196 000 (Zwanenburg and Bowen 1990 for western Atlantic and Harwood *et al.* 1991 for eastern Atlantic populations). Over one half of the world's population, approximately 86 000, is to be found around the British Isles, of which 79 000 occur in Scottish waters (Harwood *et al.* 1991). Of these, between 55 500 and 59 000 breed in the Outer Hebrides and on the island of North Rona, which constitutes one of the largest grey seal breeding colonies in the world. Pup production on North Rona over the past six years has been estimated at between 1100 and 1500. In 1984 pup production was 1467, the following years gave estimates of 1295, 1189, 1160, 1123 and 1194 in 1989 (Sea Mammal Research Unit data).

Grey seals spend much of the year at sea; only during the annual moult and, in particular, the breeding season, do they spend appreciable amounts of time on land. The breeding season is generally during the colder months of the year, but the precise timing varies somewhat in different breeding colonies. In the UK the breeding season extends generally from the beginning of September to mid December, with colonies around the south-west coast tending to breed slightly earlier in the year whilst those on the northern and eastern coasts are somewhat later. Colonies in Ireland, the Scilly Isles, Cornwall and South Wales breed from early September through to late October with a peak of pupping in late September. In North Wales and the Hebrides the breeding period is slightly later, from early to mid September through to mid November with peak pup production during early October. On North Rona, the breeding season extends from late September to mid to late November, with peak pupping around mid October. Moving east to the Orkneys and Shetland, the seals breed from late September to the end of October, a slightly shorter breeding season. Colonies on the Isle of May and the Farnes are later still, the breeding season extending from mid October to mid December with a peak pup production in mid November. This trend is continued in the Canadian colonies which breed during late December, January and early February. The Baltic colonies have a breeding season extending from late February and throughout March (King 1983).

Despite these differences in the timing of the breeding season, the general sequence of events in the reproductive cycle is the same in all the colonies. At the onset of the breeding season the females (cows) start to come ashore at the breeding colony and tend to gather around pools of water and damper areas in the vicinity (Anderson *et al.* 1975, pers. obs). The cows give birth to a single pup and in general remain ashore, or close offshore (depending on the topography of the site), during the entire period of lactation. The incidence of twins in grey seals is very low (Spotte 1982, pers. obs.). The females fast during this period of approximately 16 to 21 days, relying on energy reserves (stored in the form of the thick layer of blubber) to survive and to provide food for their pups. The average rate of pup growth during lactation is 1.7 kg per day, whilst their mothers lose weight at approximately 3.8 kg per day. As has been found in other mammalian species (Clutton-Brock *et al.* 1981), investment in male and female pups differs somewhat (Fedak and Anderson 1985). Male pups have a earlier mean pupping date (see also Coulson and Hickling 1961), tend to be heavier at birth, gain weight at a greater rate and their mothers tend to have higher weights at parturition and lose weight at a greater rate during lactation than mothers of female pups (see also Kovacs and Lavigne 1985). The sex ratio at birth appears to be slightly skewed towards a preponderance of male pups. Boyd and Campbell (1971) found that 54 % of 2846 pups on North Rona were male (a significant deviation from parity at $p < 0.01$), a finding that has been confirmed by Anderson *et al.* (1979). After weaning the pups tend to be pushed towards the outskirts of the colony, congregating in regions largely unoccupied by adults, and may remain ashore for several weeks, finally entering the sea as their blubber reserves become depleted. The females enter oestrus shortly after weaning their pups and are mated by one or more males. The cows then return to the sea to replenish lost energy reserves and generally recuperate after the arduous breeding season. Approximately 8 to 10 days after fertilisation the blastocyst is formed; however, development is then halted and implantation delayed. The blastocyst lies dormant in the uterine horn for about 3.5 months, implantation finally occurring shortly after the annual female moult. Development proceeds for a further 8 months allowing the female to give birth at virtually the same time of year in each breeding season (the annual reproductive cycle of the grey seal is shown in Bonner 1972 and 1981).

Most females ovulate for the first time at the age of three or four years, but become pregnant for the first time in their fourth or fifth year (Boyd 1982 b). The pregnancy rate does not decline with increasing age and has been estimated at approximately 94 % at the Farnes and 83 % in the Outer Hebrides.

The differences in the timing of the breeding season are particularly intriguing, and remain to be fully explained. Coulson (1981) suggested that the actual synchrony of breeding within a colony was of greater advantage to the seals than breeding at any particular time of the year. He provided evidence that the timing of the breeding season was determined by factors which terminated the period of delayed implantation and showed that both the mean date of birth of pups on the Farne islands over a period of years, and geographical differences in date of breeding, were correlated with the sea surface temperature during the period just prior to the end of the suspended embryonic development. Thus, a lower sea temperature correlated with a later mean pupping date. Coulson also suggested that the size of a colony had a social facilitation effect, possibly modifying the termination of suspended development, such that smaller colonies had later mean pupping dates. Boyd (1984) extended this work, showing that the timing of embryonic implantation was related to female body condition. Those females showing the earliest spring increase in body condition tended to implant relatively earlier.

Further details of grey seal breeding biology and behaviour in eastern atlantic and particularly Hebridean colonies can be found in Darling (1939), Matthews (1950), Hewer (1957), Hewer and Backhouse (1959, 1960 and 1968), Boyd, Lockie and Hewer (1962), Boyd and Laws (1962), Boyd (1963), Coulson and Hickling (1964), Fogden (1968 and 1971), Bonner (1972 and 1981), Anderson, Burton and Summers (1975), Burton, Anderson and Summers (1975), Summers, Burton and Anderson (1975) and Anderson and Fedak (1985 and 1987). Similarly, descriptions of grey seal behaviour in western Atlantic colonies are given in Cameron (1967, 1969), Boness and James (1979), Boness, Anderson and Cox (1982) and Boness (1984). However, it must be noted that there appear to be some marked differences in both the behaviour and social organisation between the eastern and western Atlantic populations and within different colonies within each region (pers. obs., see Chapter 9)

Previous studies of grey seal breeding behaviour and energetics

Anderson *et al.* (1975) produced the first detailed study of breeding behaviour in an eastern Atlantic Grey seal population (on the island of North Rona). Anderson *et al.* (1975) state that a male's mating success is related to the duration of his stay on the breeding colony. They suggested that those males securing the majority of observed copulations appeared to be the more dominant individuals. However, the authors were only able to classify males loosely as dominant or subordinate. The former being those males "which held" a position on the colony "for at least a short time and copulated with one or more cows", whilst subordinates were unable to hold a position "successfully and rarely mated with cows". In respect to examining dominance and mating success relationships this is a somewhat circular argument, as dominance is defined, at least partly, by the number of copulations gained by a male and by length of stay which is also related to copulatory success. Also, as Anderson *et al.* (1975) were unable to individually mark males, their sample was limited to 30 males which could be identified by their coat patterns and scars. These were mostly the so called "dominant" males, as these remained ashore for longer, aiding identification. Only one subordinate bull was positively identified. However, the authors did conclude that the classification of males as merely dominant or subordinate was an over simplification. Anderson *et al.* (1975) concluded that male grey seals, rather than maintaining territories or harems, endeavoured to hold positions amongst the groups of females and maintain high levels of sexual activity so as to mate with as many females as possible.

Boness and James (1979), studying a western Atlantic colony (Sable Island, Nova Scotia) were able to avoid using mating success to classify male status by simply referring to males as tenured or transient. Tenure was defined as "the right to remain within the shifting population of females" and was attained by any male maintaining his position on the colony for at least two consecutive days, whilst transients failed to achieve this. The prime areas in which to establish tenure are those with the greatest concentration of females. The authors were able to show that the mating success of transients was significantly lower than that of tenured males and that tenured males were clearly dominant to transients. However, they do state that "tenured males behave as if they were equals whose status is not affected by their absolute position on the breeding ground or by their previous fighting record (rank in a dominance hierarchy)". This contrasts with the conclusion of Anderson *et al.* (1975) that some "form of hierarchy exists amongst the breeding bulls", though "not as well defined as that seen in the Northern Elephant seal (*Mirounga angustirotris* (Le Boeuf,1972))".

Subsequent studies by Anderson and Fedak (1985 and 1987 b) on the North Rona colony confirmed their belief that, at least on North Rona, Grey seal males did not form a linear hierarchy and yet were not all "of equal status". They also provided data showing that larger males lost fewer inter-male aggressive encounters and that male size (and rate of weight loss) was positively correlated with copulation frequency, implicitly suggesting that dominant males gained greater mating success. Although the authors were able to individually mark males, their observations were limited to a period of two weeks, though they were carried out during the time of greatest sexual activity.

As male grey seals fast during the breeding season and rely on energy reserves, primarily in the form of the thick layer of blubber (Anderson *et al.* 1975, Anderson and Fedak 1985, Fedak and Anderson 1985), they have a finite energy reserve for use in the annual breeding effort (Fedak and Anderson, 1985, state that the blubber can account for greater than 80 % of the energy used in reproduction). Therefore, the initial energy store and subsequent energy expenditure may indeed be an important determinant of a male's length of stay on the breeding grounds, and thus, may limit an individual's mating success as suggested by Anderson and Fedak (1985). Anderson and Fedak (1985) found a positive relationship between male weight and sexual activity and indicated that rate of weight loss was, at least in part, related to levels of sexual activity. Thus, larger males gained more copulations and experienced greater energy expenditure. Anderson and Fedak (1985) suggested that large males were able to "sustain a high level of sexual activity for long periods" and therefore were able to "out-compete smaller males, which would have to reduce their activities in order to stay for the same length of time". They also suggested that depleting body reserves to a low level in single breeding season would risk survival to the following year. In their 1987 paper (Anderson and Fedak 1987 b), the same authors concluded that "only those males which can most easily bear the high costs of an active, prolonged and successful breeding season are likely to stay for the full span". They suggested that the "finite energy reserves may act as a strong constraint on reproductive behaviour in grey seal males and selection should favour the capacity to build up body reserves".

Aims of this study

This thesis is an extension of a long term study of grey seal breeding behaviour and energetics on the island of North Rona (Scotland) conducted by the Sea Mammal Research Unit (Anderson, Burton and Summers 1975, Burton, Anderson and Summers 1975, Summers, Burton and Anderson 1975, Anderson 1978, Anderson and Fedak 1985, 1987 a, 1987 b, Fedak and Anderson 1982, 1985, Anderson and Harwood 1985).

This study examines the behaviour and energetics of individual male grey seals during the breeding season. The study examines the mating system found on North Rona, and assesses the main behavioural and/or energetic determinants of individual male mating and reproductive success.

Greenwood (1980) suggested that male reproductive success in mammals is limited by availability of potential mates rather than being resource limited. However, where the energetic costs of obtaining mates are high (for example territory or harem acquisition and maintenance) and energy resources available are finite such as in male grey seals, male mating success may also be resource limited. This thesis examines which factors influence the duration of stay on the breeding colony. Is this solely governed by a males competitive ability (dominance) or do energy reserves place limits on a male's activities during the breeding season? If so, how do male grey seals balance the potential benefits of successful breeding with the energetic costs incurred? If length of stay is the proximal determinant of mating success, what are the ultimate determinants? Using the terms provided by Greenwood (1980), two hypotheses were constructed. The first is that an individuals length of stay on the colony is determined primarily by a combination of initial energy reserves and rate of energy utilisation during the season (i.e. resource limited mating success). The second is that a male's length of stay and mating success are primarily determined by his competitive abilities (dominance status) and any effects of energetics are negligible (i.e access/mate limited mating success). Finally, there is the possibility of interactions between these two hypotheses. For example, there are potential relationships between dominance and energy reserves and expenditure, particularly if dominant males tend to be larger individuals who can, perhaps, store greater fat reserves and have differential energy requirements during the season.

This study therefore examines the relationships between dominance, length of stay and mating success in greater detail. More extensive observations and a larger sample of males than in previous studies have allowed more complete behavioural records to be collected. In an attempt to overcome the problems of arbitrarily assigning males to dichotomous classes such as tenured or transient, dominant or subordinate, a "dominance score" has been calculated, based on the outcome of inter-male aggressive encounters. This score provides each male with a relative value for dominance status which can be compared with other males and examined in relation to other behavioural data sets. Thus, it is possible to ask whether a there are clear relationships between dominance, length of stay and mating success in the male grey seal, and if so what factors determine a male's dominance status.

In an attempt to assess the relationship between observed male mating success and actual reproductive success, a pilot study involving DNA fingerprinting analyses has been conducted in collaboration with Bill Amos of the Department of Genetics, Cambridge University.

As stated above, whilst grey seals are clearly polygynous, the exact extent of polygyny appears to vary between colonies, possibly dependent largely upon habitat. This thesis presents a comparative study of the mating systems of North Rona and Sable Island, two grey seal breeding colonies with markedly different topographies. As stated by Stirling (1975) "this species offers the greatest opportunity for study of the effects of different breeding habitats on social behaviour".

CHAPTER 2 - METHODOLOGY

INTRODUCTION

This study is comprised of a combination of behavioural observations and data gathered directly from captured individuals in the study area during three breeding seasons (from mid/late September to mid/late November) in each of the years 1987, 1988 and 1989. The capture of live wild seals by the use of chemical restraint, particularly of large species, is a relatively recent practice, with constant improvements in the immobilising agent used. One of the earliest examples of studies involving immobilisation of pinnipeds by sedative drugs was that of Jewell and Smith (1965) on grey seals. They examined the effects of two analogues of succinylcholine (suxamethonium and suxethonium). Subsequent studies tended towards the use of ketamine and ketamine derivatives (Geraci 1973, Engelhardt 1977, Geraci *et al.* 1981, Trillmich 1983 and Boyd *et al.* 1990). Such techniques have been used on a number of pinniped species, for example, the Californian sea lion (Grey *et al.* 1974), Galapagos sea lions and fur seals (Trillmich 1983), Antarctic fur seals (Bester 1988, Boyd *et al.* 1990), Southern elephant seals (Baker *et al.* 1988, Bester 1988), Northern elephant seals (Grey *et al.* 1974), Harp seals (Engelhardt 1977), Harbour seals (Hammond and Elsner, 1977) and the walrus (De Master *et al.* 1981, Stirling and Sjare, 1988). Previous work of this kind on adult grey seals was conducted primarily on North Rona. Parry *et al.* (1981) report on the effects of various drugs previously used on other pinniped species. Baker and Gatesman (1985) examined the use of both carfentanil and ketamine-xylazine and Baker *et al.* (1988) discuss the effects of ketamine-diazepam on grey seals. During the three field seasons of this study, a relatively new sedative was used, Zoletil 100, the effects of which are reported in Baker *et al.* (1990). A useful review of chemical restraint of pinnipeds can be found in Gales (1989).

The capture and subsequent handling and sampling of wild seals is a somewhat specialised practice and it is vital that it is highly efficient, not only in order to gain the necessary data but also, more importantly to minimise disturbance to both the seal being worked on and to the surrounding animals. The minimisation of disturbance is an obvious aim when working with wild animals, particularly if it occurs during their one breeding attempt of the year, but it is also critical in a study such as this, where the seals caught are also those upon which behavioural observations are made. It is essential to ensure as far as possible that the relatively intrusive catching process does not unduly affect the seals' natural behaviour.

For these reasons, this chapter details the methods used to obtain the data during this study, both the behavioural observations and the catching regime, describing fully all techniques involved. In particular, a description of the drugging process is given together with a discussion of the responses of seals to the drugs applied. Also, an account of problems encountered during the course of fieldwork is given together with their solutions, where these were possible. Finally, the specific catching regime used and found to be most efficient is outlined.

Specific details of analytical methods as applied to the data collected are given in the subsequent relevant chapters.

In the comparative study of male grey seals at Sable Island, Nova Scotia, only behavioural observations were made. These utilised the same format as those employed on North Rona. The results of the Sable Island study are presented in Chapter 9.

STUDY SITE

The primary study site is located on the island of North Rona ($59^{o}06'$N, $05^{o}50'$W) which lies approximately 75.5 km NNW of Cape Wrath (Scotland). The location of North Rona is shown in Figure 2.1a and details of the island in Figure 2.1b. The island possesses a ridge, with two peaks rising to 98 and 108m, running east-west along the broadest (1.93 km), southern part of the island. The breeding colony is situated on the low northern peninsula (Fianuis), with seals occupying the vast majority of the land north of Leathad Fianuis at the height of the season. A hide was erected on the ridge over-looking Fianuis and provided an excellent vantage point from which it was possible to view almost the entire southern and central portion of the peninsula. However, the study site was limited to the most southerly part of Fianuis, covering an area of approximately 0.38 km^2 (Figure 2.1b). It is delimited on the northern side by a gulley (Geodh' a' Stoth) on the eastern shore and the remnants of a dry stone wall leading to the inlet of Sgeildige on the west. The western coast of the study site consists of vertical cliffs some 10 to 20 m in height with no possible access to or from the sea for seals. On the east, however, the coast is formed from more moderately sloping rock slabs indented by four deep and steep walled gulleys. Access to the breeding site from the sea is restricted largely to these gulleys. Southwards the study area extends up to the hide, although adult seals were rarely seen close to the hide, not because of our presence, but due to the steep slope of the ridge (between 1 in 3.5 and 1 in 1 gradient).

The vegetation on the peninsula is predominantly rough grassland and disturbed ground, particularly on the Fianuis peninsula which is colonised by annual poa grass, sea milkwort and predominantly chickweed (see Fraser-Darling 1939). However, the study area is covered mainly with grass. During the breeding season much of the vegetation is eroded by the activities of the seals, revealing bare earth and producing generally wet and muddy conditions. The study site has a variety of features, rocks, gulleys, dry stone walls and freshwater pools, some effectively permanent, others appearing only after heavy rainfalls. These are useful for pinpointing the positions of seals. A sketch map of the study site as seen from the hide is shown in Figure 2.1c. Further details of the study site

Figure 2.1 a : Map showing location of North Rona.

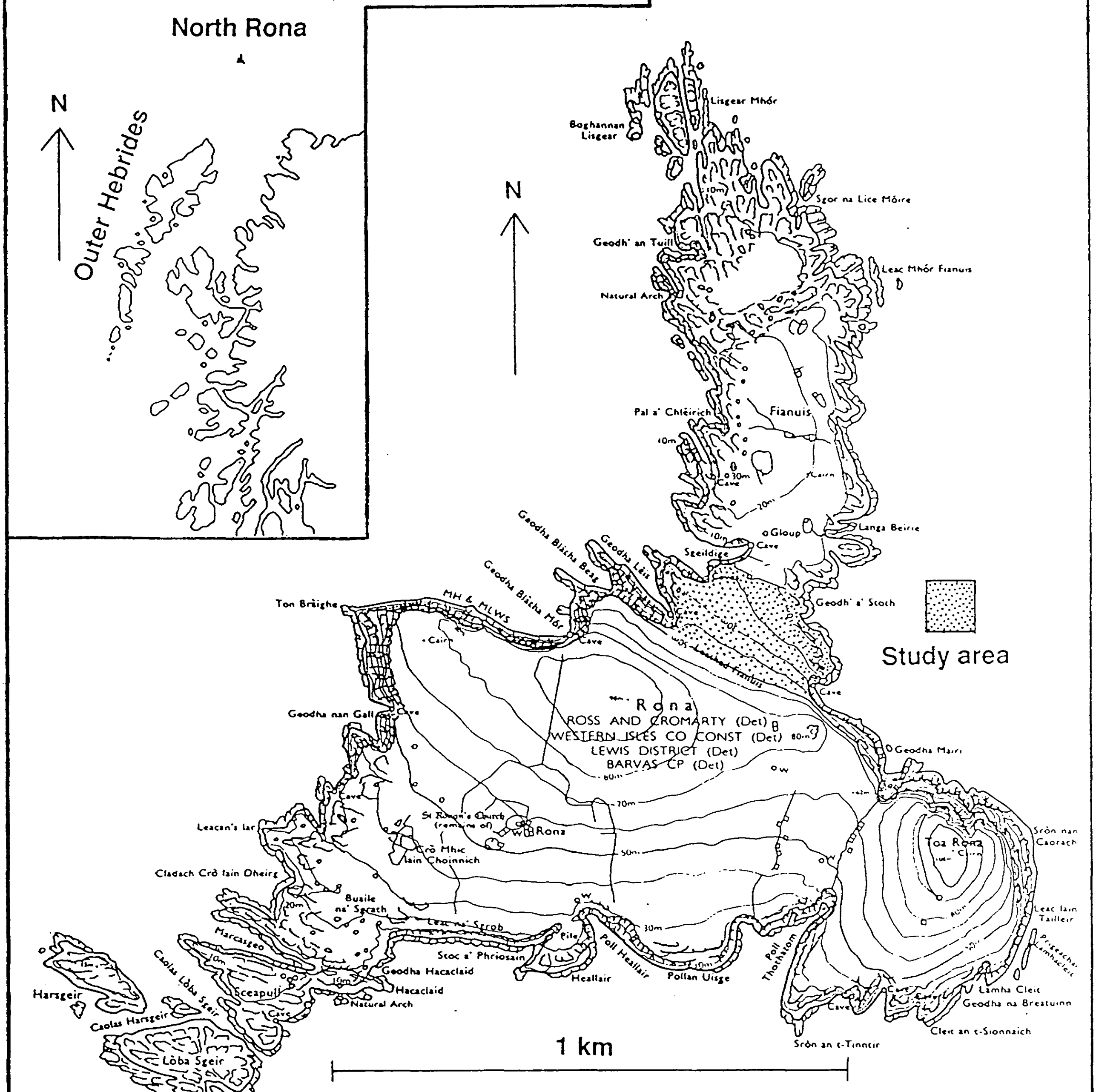
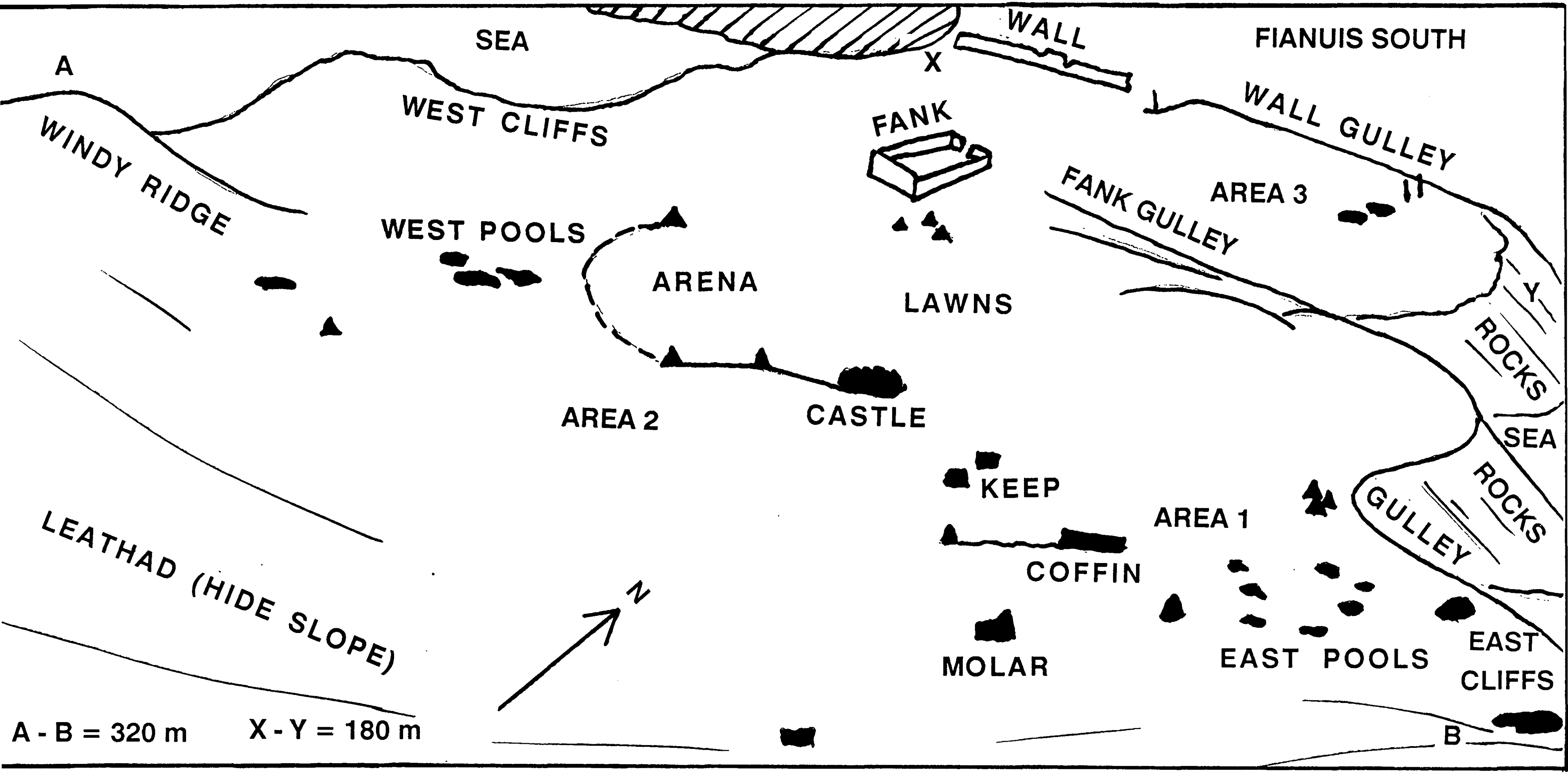


Figure 2.1 b : Map of North Rona showing location of study site.

Figure 2.1 c : Sketch map of the study area.



can be found in Bonner (1972) and Anderson, Burton and Summers (1975). Detailed descriptions of the island's topography and wildlife are given in Fraser Darling (1939 and 1952) and Atkinson (1949).

IDENTIFICATION OF INDIVIDUAL SEALS

A vast majority of the males and many of the females in the study area could be individually identified, utilising a variety of identification methods. The individual coat patterns and colouration of all males was noted in as much detail as possible and in many cases was sufficient to allow confident identification both within a single season and between successive seasons. However, it must be noted that the patterns and colours of a grey seal coat can appear markedly different when wet compared to dry and vary even under conditions of differing light quality. Thus, to be confidently identified by this means, a male must be seen ashore for some length of time and observed both wet and dry. Many males, however, were only present for very short periods (some less than one hour) and remained on the periphery of the study site close to the sea. These males were not often ashore sufficiently long to allow their coats to dry, were present on days of heavy rainfall, or were constantly washed by waves. Thus, in these cases identification could not be positive; however, these individuals engaged in very few if any behavioural interactions and were clearly itinerant males.

Many seals were marked with coloured dyes to aid identification from the hide. All seals caught were dyed and additional individuals were dyed whenever possible, for example males adjacent to seals being handled. Some of the males caught were marked with bright epoxy resin dyes in various designs and positions on their backs and flanks to enable instantaneous recognition.

All seals caught were tagged on the right hind flipper with a jumbo eartag (Rototag; Dalton Supplies Limited) each with a unique number (see Plate 2.1), unless they already possessed a tag from captures made prior to this study. Tagging involved first making a small incision through the flipper web with a sharp, clean tagging knife. The hole was then sprayed with oxytetracycline spray and the tag applied by means of tagging pliers (Dalton

Plate 2.1 : Applying a roto-tag to the hind flipper of an adult male grey seal (North Rona, 1987). The area around the tag hole is dyed purple from the application of Oxytetracycline spray.

Supplies Limited). Tags were positioned in the web between either the 2nd and 3rd or 3rd and 4th digits slightly to one side of the muscular strand running down the centre of each web and approximately the length of the tag from the edge of the web.

All adults caught were also marked by means of hot iron branding unless they had been previously branded or were not sufficiently sedated. This technique was established by Sheila Anderson and is basically similar to cattle branding. Branding irons were constructed of 5/8" steel rod, formed into letters or numbers 75 mm high and 65 broad. The handle, some 45 cm long was made of the same material. The brand consisted of a unique combination of a letter followed by a number (0 to 9) or vice-versa (see Plate 2.2). The irons were heated in a small portable forge until the irons were "cherry red" and applied for approximately 6 seconds to the flanks of the drugged seal. Thus all seals branded possess a unique letter-number combination, the same combination being displayed on either flank. All branded seals were heavily sedated at the time of branding and were also injected intramuscularly with the antibiotic Terramycin* LA (Pfizer Limited, Sandwich, Kent) at a dose rate of 1ml per 10kg of seal. This is an aqueous solution containing oxytetracycline dihydrate providing a slow release of the active component and at this dosage should provide antibiotic cover for at least four days. This proved to be highly effective in preventing infection of the brand. All seals branded were either caught again at a later stage or at least observed and none showed any signs of infection. Also, many were seen and/or caught in subsequent seasons, again showing no ill effects.

Branding is necessary as it the only method of permanently marking seals allowing firm identification of individuals year after year with the possible exception of those individuals whose coat patterns are highly distinctive. Tags can be torn off, especially in males which, when fighting, attempt to bite the hind flippers of their opponents. Similarly, dyes and epoxy resin are lost during the annual moult.

A total of 85 males and 87 females have been branded on North Rona, of which 52 males and 66 females were branded prior to this study (see Anderson and Fedak 1985). Table 2.1a shows the numbers of adult males and females branded on North Rona, during

Plate 2.2 : A recently branded (Y9) male grey seal, after having been suitably drugged (North Rona, 1987). The orange stain on the male's neck was from the dye applied in order to aid identification in the days prior to catching and branding. Photograph taken by Bruce Herod.


Y9

the course of this study and the previous studies by Anderson and Fedak.

Table 2.1 b illustrates the numbers of branded seals, males and females, observed in the years 1986 to 1989. The value in parentheses represents this number as a percentage of the total number of branded males or females available (i.e. previously branded) in each particular season. Those individuals not recorded as present may simply have not been sighted, may not have been present in that year, or may indeed be dead.

Table 2.1 c depicts the numbers of branded males, branded females and non-branded males (i.e. identified by the other means outlined above) in all possible combinations of the three seasons of this study.

From the three field seasons of this study (1987,1988 and 1989) a total of 275 males were individually identified by using the above methods, some present in only one year, others for two seasons and some present for all three seasons. Table 2.1 d shows the numbers of positively identified males present for each possible combination of the three study seasons and finally the total number of positively identified males present in each of the three seasons. Thus, for example, of the 85 males present in 1987, 52 of these were present only in this season, 11 returned also in 1988, 4 were absent in 1988 but returned in 1989 and 18 males were present in all three seasons (Chapter 4 expands on the colony attendance patterns of individual males). The values given in parentheses show the numbers of males which remained ashore long enough to interact with other seals. This was taken as an arbitrary point of ten or more separate aggressive inter-male encounters. This selection criterion allowed the calculation of a representative dominance score (see below).

Table 2.1a : Numbers of grey seals branded on North Rona each year.
NB: Brands made before 1987 were prior to the onset of this study and were conducted by the Sea Mammal Research Unit.

YEAR	No. MALES BRANDED	No. FEMALES BRANDED
PRE-1987	52	66
1987	22	15
1988	11	6
1989	0	0
TOTAL	85	87

Table 2.1b : Total number of branded seals observed in each year with percentage of available branded seals in parentheses for the three years of this study.

YEAR	No. BRANDED MALES PRESENT	No. BRANDED FEMALES PRESENT
1986	40	52
1987	32 (43.24)	55 (67.90)
1988	41 (48.24)	44 (50.57)
1989	31 (36.47)	54 (62.07)

Table 2.1c : Return rate of branded male and female grey seals and non-branded males in the study area.

YEAR(S) PRESENT	BRANDED MALES	NON-BRANDED MALES	BRANDED FEMALES
1987 only	7	28	12
1988 only	5 *	62	3
1989 only	0	96	3
1987 and 1988	7 **	4	3
1988 and 1989	13 ***	8	11
1987 and 1989	2 ****	2	13
1987, 1988 and 1989	16 *****	2	27

Notes:

* Four of these 5 branded males were also present in 1987 but not in the study area. All four of these were branded either in 1987 or prior to 1987.

** All of these males were branded prior to 1987.

*** Four of these 13 males were branded either in 1987 or prior to 1987 but were not in the study area in 1987. The remainder were all branded in 1988.

**** One of these males was branded in 1987, the other, prior to 1987.

***** One of these 16 males was not branded until 1988, but was identifiable from 1987 by his coat pattern. The remainder were branded in 1987 or prior to 1987.

Table 2.2 : Numbers of positively identified male grey seals present in the study area in each year.

YEAR(S) PRESENT	No. OF IDENTIFIED MALES
1987 only	52 (35)
1988 only	67 (60)
1989 only	102 (96)
1987 and 1988	11 (11)
1988 and 1989	21 (21)
1987 and 1989	4 (4)
1987, 1988 and 1989	18 (18)
TOTAL NUMBER OF IDENTIFIED MALES PRESENT IN EACH SEASON	
1987	85 (68)
1988	117 (110)
1989	145 (139)

NB: The values given in parentheses show the numbers of males which remained ashore long enough to interact with other seals. This was taken as an arbitrary point of ten or more separate aggressive inter-male encounters.

BEHAVIOURAL OBSERVATIONS

The study is comprised primarily of behavioural observations made from the hide. Observations were carried out during the dawn to dusk period virtually every day during each of the three breeding seasons 1987, 1988 and 1989 except on days devoted to catching seals. In 1987 the field season was slightly shorter, being approximately 7 weeks (27/9/87 to 12/11/87) but for the subsequent two years observations spanned the entire breeding season on North Rona (22/9/88 to 16/11/88 and 22/9/89 to 23/11/89). For each of the three years, 1987, 1988 and 1989 respectively, the total number of observations hours were 173.33, 194.78 and 191.42 hours. The observation regimes for each season are given in Figures 2.2 a, b and c. Relatively few days were lost due to inclement weather or logistical problems. The observation periods necessarily varied in duration and timing, generally becoming shorter as the season progressed due to diminishing daylight hours and being determined by the catching regime (which was to some extent determined by which individual seals were present, time from previous captures and minimisation of disturbance). However, in general, a reasonably even coverage of the entire season was accomplished. This was necessary to avoid biases towards certain periods of the season, particularly as the rates of activity, numbers and identities of seals alter throughout the season.

Although the limits of the study area were clearly defined, the behaviour of seals present in the adjoining area of Fianuis which interacted in any way with seals in the study site was also noted. This ensured that behavioural records of seals close to the northern border were not unduly biased by the artificial boundary.

1. Records of all observed aggressive and sexual behaviours:

During observation periods full details of all observed aggressive and sexual interactions were recorded. In 1987 all aggressive interactions between males and between males and females were noted together with detailed descriptions of the various behaviour patterns. However, in the subsequent years male-female aggression was not recorded unless directly related to a sexual interaction and detailed descriptions of

Figure 2.2 a : Observation regime - Rona 1987

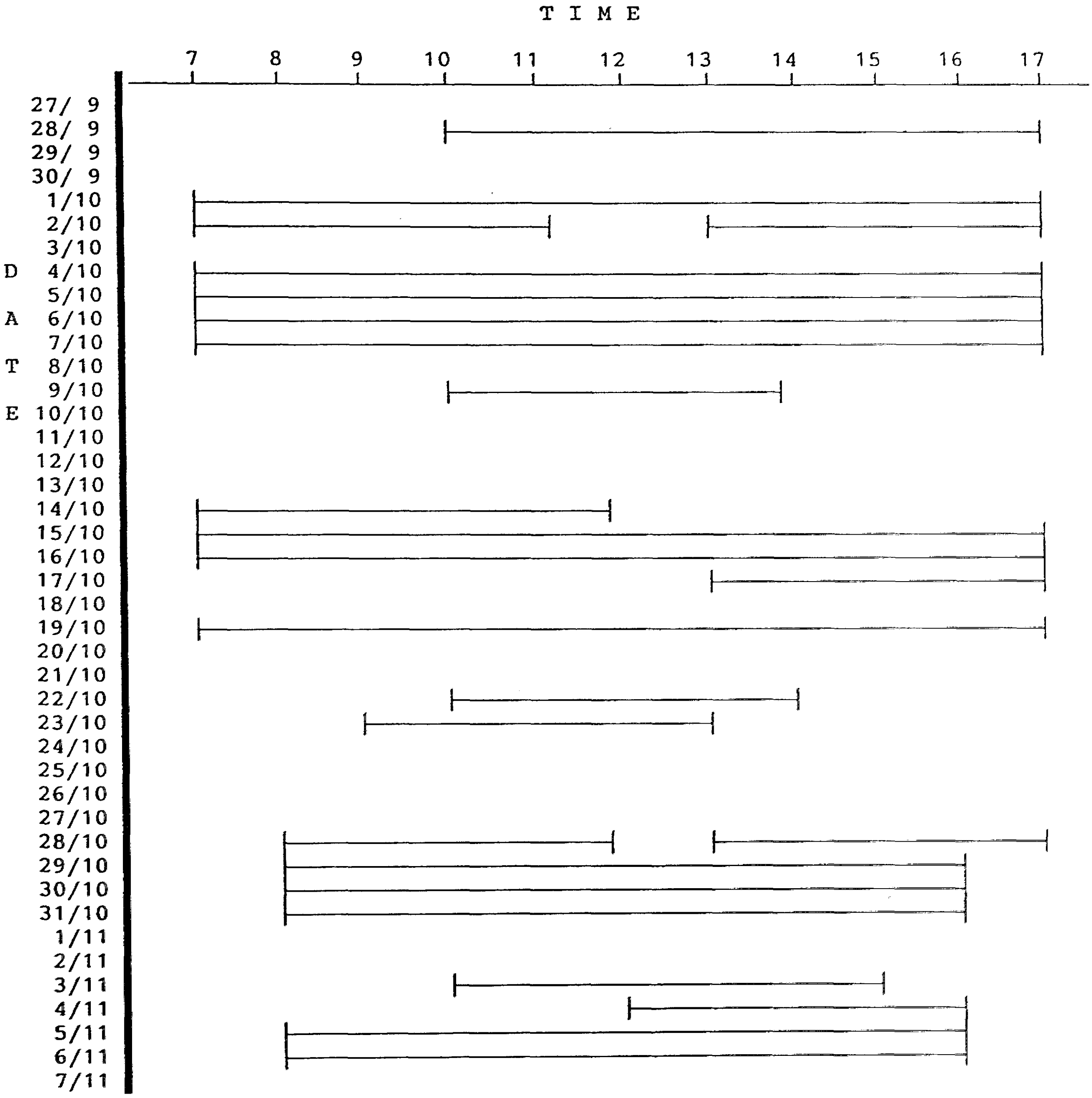


Figure 2.2 b : Observation regime - Rona 1988

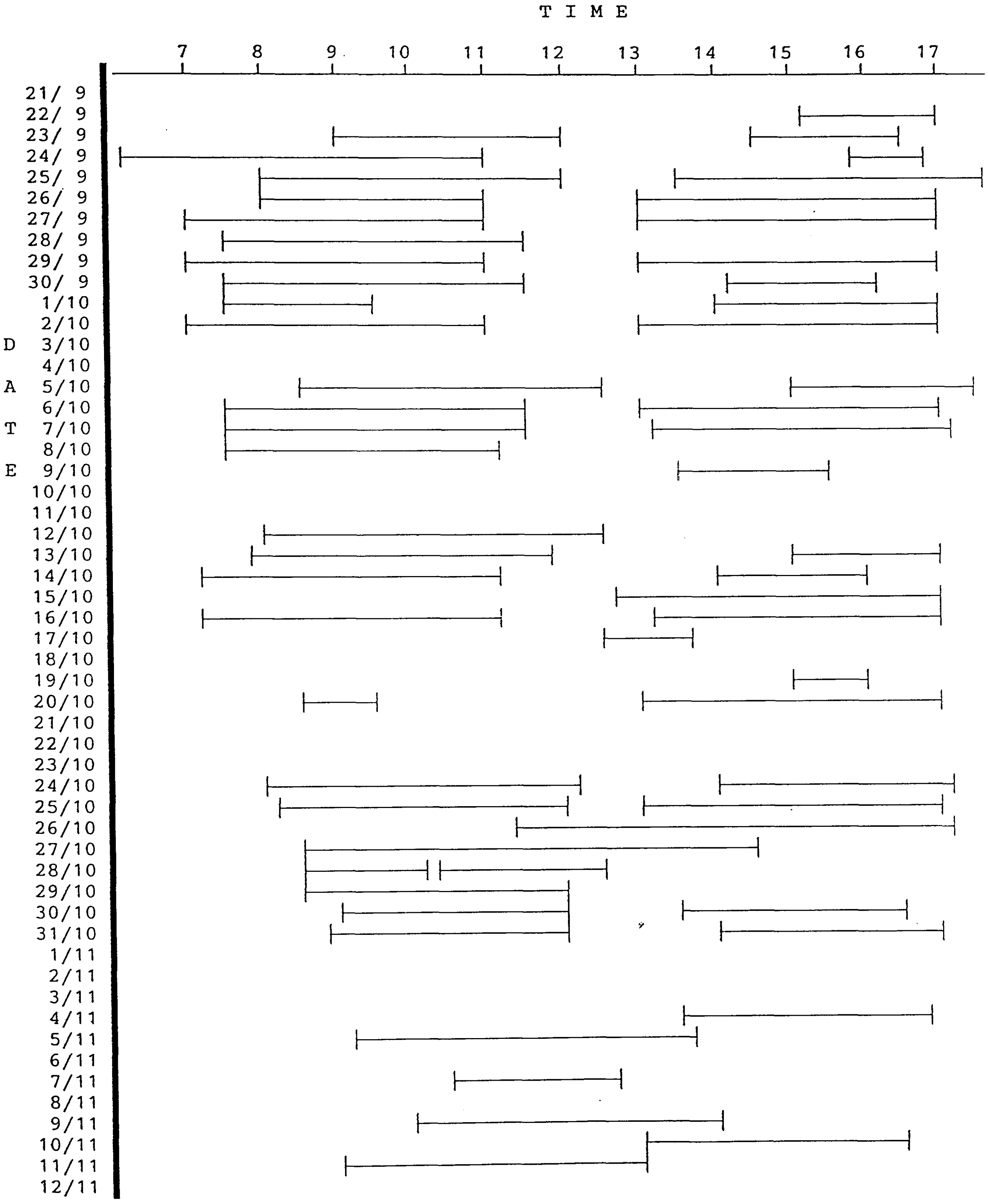
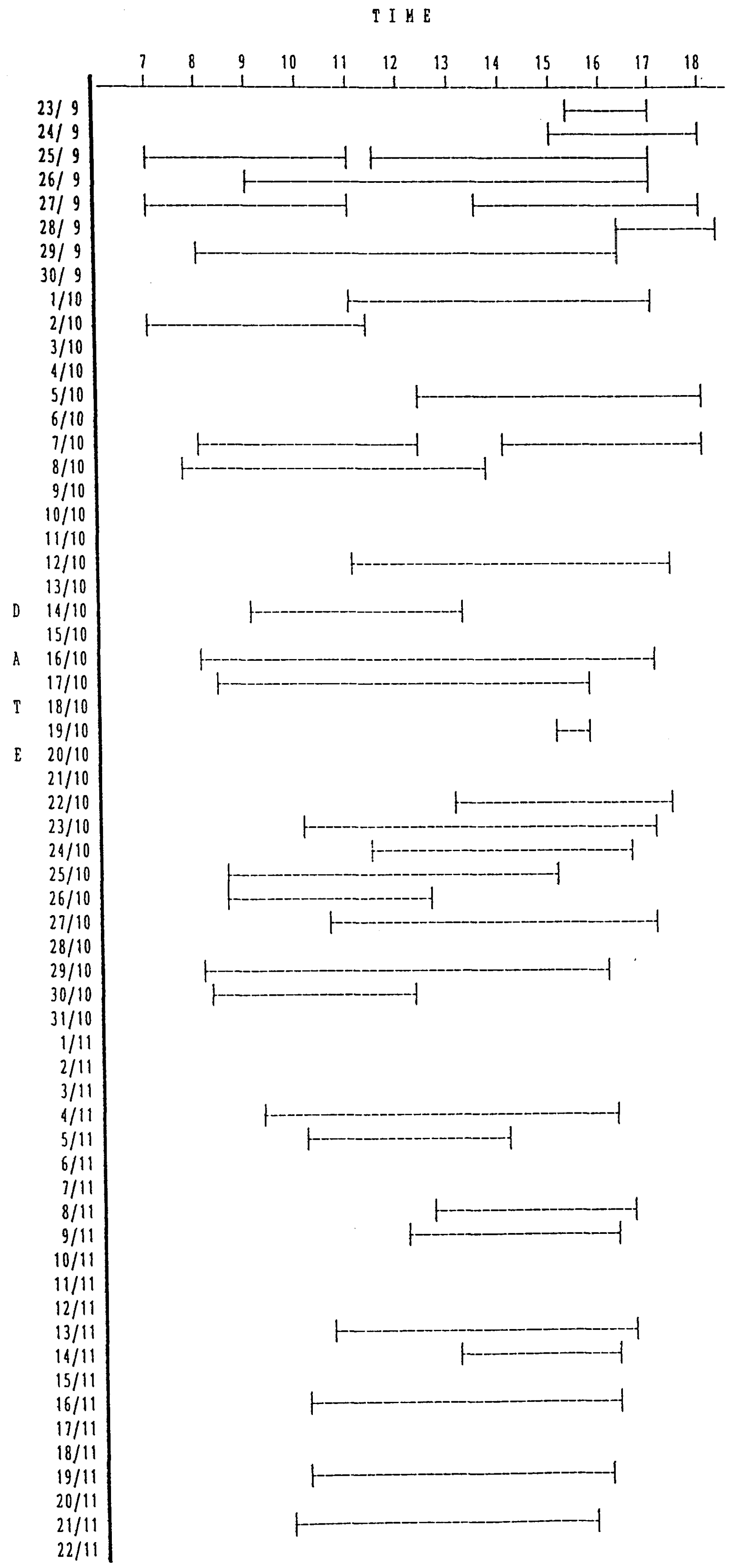


Figure 2.2 c : Observation regime - Rona 1989



behaviours were only made if an interaction was new to the observer or particularly interesting or unusual. In all years all occurrences of sexual behaviour were recorded. Records included the date and time of occurrence, initiator, duration of interaction, identity of participants and the outcome of the interaction. Times of arrival and departure of males to and from the study area were also noted. All these activities are sufficiently "attention attracting" and occur relatively infrequently allowing all such behaviours to be noted (Altmann 1974). Detailed descriptions of all observed behaviours are given in Chapter 3.

Also, gross movements of males within the study area were noted.

The records of all aggressive and sexual behaviour provided information on the frequency of occurrence, synchrony of behaviour, diurnal and seasonal patterns and the distribution of occurrences and durations of these behaviours amongst the males.

2.Scan samples:

Running concurrently with these observations during the 1988 field season, "instantaneous" scan samples of all the males in the study area were made, noting their activity category. Scans were made once every 5 minutes, for the entire observation period noting each individual's activity, whether present, absent or out of sight. The activity categories recorded are detailed in Chapter 3.

The order in which males were observed was maintained throughout each observation period to ensure a 5 minute interval between successive scan samples of each individual. Even during the peak of the season when up to 30 males were present at any one time in the study area, each round of scans could be completed in under one minute. This regime of scan samples should be adequate to yield accurate representations of the time/activity budgets of all males in the study area. Jacobsen and Wiggins (1982) found that instantaneous time (scan) sampling at intervals of 5 minutes or less provided the highest correspondence between estimated and actual total time spent in each activity in a study on captive white tailed deer (*Odocoileus virginianus*). Similarly, the results of the present study have been compared with those obtained from focal animal samples made in 1988 over periods of 4 hours during which scan samples were also made. There was no significant difference in the proportion of time spent in various activities obtained by the two methods over the same periods. The scan samples were selected as they provide detailed information on not only one or two individuals at a time but all males present and at the same time allow records of all aggressive and sexual activity to be maintained.

The scan samples allowed the estimation of time/activity budgets for individuals. The scans were also used to examine diurnal and seasonal patterns or synchrony in behaviour.

3. Census data

In addition to these behavioural observations the numbers and distribution of all seals (males, females and pups) in the study area were mapped at least once during each day. Individual identities were recorded where possible. Also, daily brand sightings were made throughout the entire island, thereby locating all branded males present, including those outside the study area on both other breeding sites and also non-breeding haul-out sites.

4. Colony attendance patterns:

Complete records of each male's presence or absence on the colony obtained from all the aforementioned behavioural observations allowed rates of aggressive and sexual behaviour per diem for each male to be calculated. This however, requires the assumption that there was no significant difference in the day and night activity levels of male grey seals. Anderson (1978) provides evidence in support of this assumption and this is discussed in detail in Chapter 5.

CATCHING SEALS

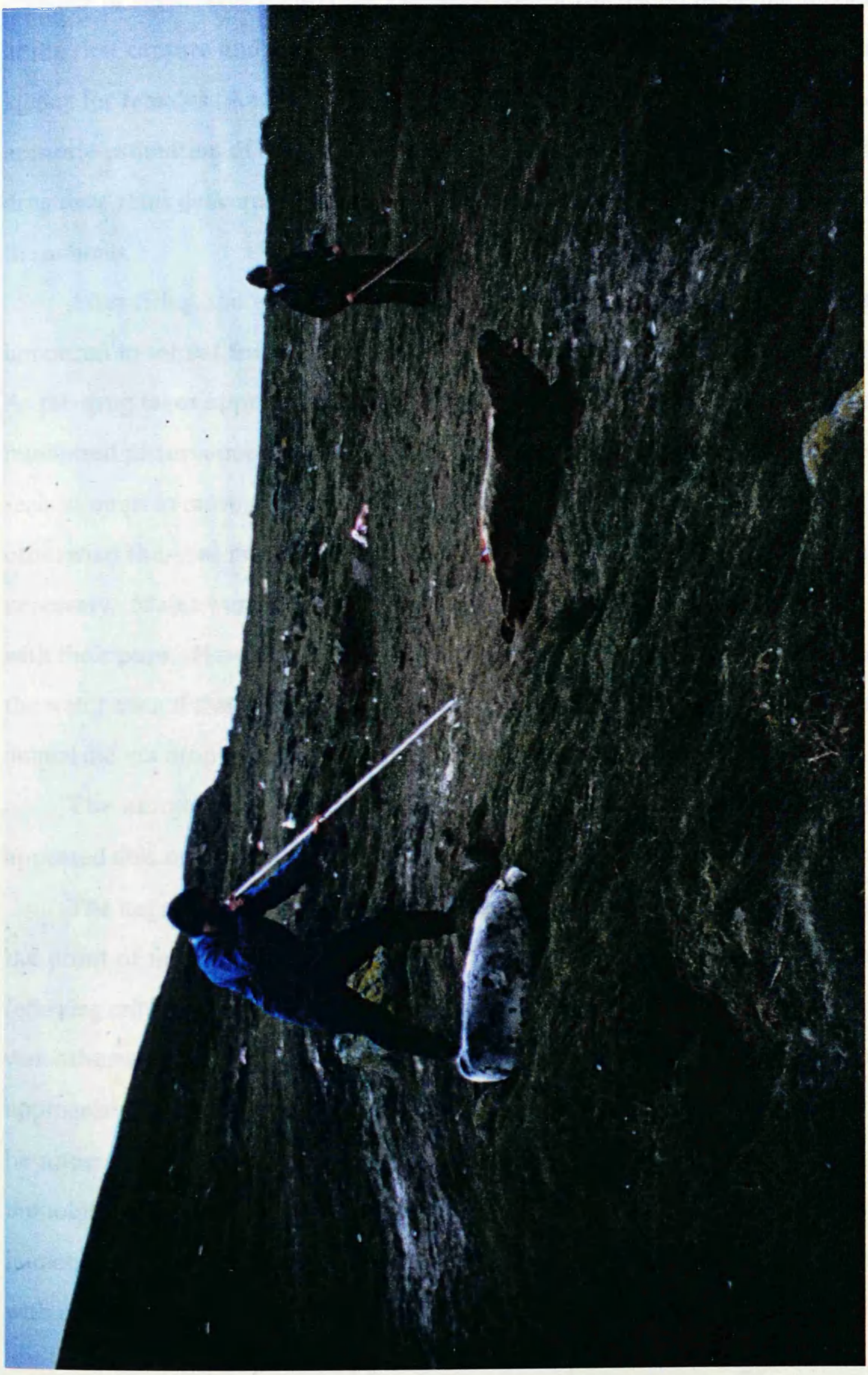
Since male grey seals fast during the breeding season, the weight loss incurred by a male is a useful indicator of energy expenditure during the breeding season. To obtain these data on individual weight changes it was necessary to capture and weigh the animals at various stages through the breeding season. This involved the immobilisation and subsequent handling of the animals. Obviously there is considerable disturbance to the seals during this process; however, the data collected are extremely important, particularly for directly assessing energy expenditure. It is vital to achieve the correct balance between the amount of data gathered in this manner and the level of disturbance, which will be reflected in the behavioural observations. Ideally, seals would be weighed and measured every week. However, it was felt that only two or three data points could be safely obtained for each seal. Only in a few cases, with males which responded particularly well to the immobilisation procedure were more than three captures made in a single season. In all captures every possible effort was made to minimise disturbance to the seals.

The following is an account of the procedures involved in catching the seals.

1. Immobilisation:

To catch a seal the animal must first be immobilised. This was achieved by carefully stalking to within a few metres of the target animal and firing a gas charged dart, loaded with a sedative drug, by means of a simple blowpipe (Parry, Anderson and Fedak ,1981, Baker, Anderson and Fedak, 1988 - see Plate 2.3). The needle used on the dart was of 5.5" length and 15 gauge. The tip of the needle was sealed with epoxy resin and a small hole drilled in the side of the needle approximately 10mm from the tip. A plastic collar covered this hole, preventing the drug from escaping. As the dart hit the seal, the plastic collar was forced up the shaft of the needle releasing the drug. During the three field seasons two different types of drug were used. In 1987 the drug used in the vast majority of the catches was a mixture of ketamine and valium (KV) in a ratio of 25:1. The recommended dose rate for grey seals was used, which is 6mg of ketamine per kg of seal (see Baker *et al.* 1988). However, in 1988 and 1989 the drug used was "Zoletil 100", which proved to be a far more effective and efficient sedative. Zoletil is a combination of tiletamine HCl and zolazepam HCl. The recommended dose rate of Zoletil for grey seals is 1 mg per kg of seal as determined by usage during the course of this study and elsewhere by the Sea Mammal Research Unit (Baker *et al.* 1990). The overall response to Zoletil appeared to be far more favourable than with the ketamine and valium mixture (see Appendix A).

Plate 2.3 : Darting a male grey seal, using the blowpipe. The red flight of the dart can be seen protruding from the male's flank (North Rona, 1987).



Dosages for the first captures of each individual were estimated by an experienced field worker remotely assessing (guessing) the target individual's weight. Subsequent captures of these seals utilised the predicted weight calculated using the recorded weight at the first capture and a mean rate of weight loss of 2.2 kg/day for adult males and 3.8 kg/day for females (Anderson and Fedak, 1985). This predicted weight allowed a more accurate estimation of drug dosage required for these subsequent captures. The actual drug dose rates delivered to the seals were calculated later using the measured weights of the animals.

After firing and visual confirmation that the dart had successfully emptied it was important to retreat from the animal, keeping low and out of sight, preferably down wind. As the drug takes approximately 10 (Zoletil) to 15 (KV) minutes to take full effect, this minimised disturbance and facilitated a good response to the sedative. However, some seals attempt to move after darting, usually heading for the sea. This had to be prevented otherwise the seal might drown and all seals were intercepted successfully where necessary. Males were more likely to "run" than females, as the cows usually remained with their pups. However, females with ready access to water often attempted to enter the water even if this was a small wallow on the study site. Care was taken to ensure the animal did not drop its head into water.

The animal's response was monitored and it was approached when reflexes appeared dull, or after the full 10 or 15 minutes were over.

The degree of immobilisation induced by the drug was rated on a scale of 1 to 5 at the point of maximum anaesthesia by an experienced observer. This scale used the following criteria; (1) the animal showed signs of uncoordinated movement but behaviour was otherwise normal, (2) less alert, head down and unwilling to locomote unless approached, (3) incapable of locomotion though head movement was possible, and could be approached and handled - this is the desired level of anaesthesia, (4) complete immobilisation with regular breathing and response to needle stimulation, (5) complete immobilisation but with irregular breathing, little or no response to needle stimulation but with corneal reflex. These criteria are similar to those used by Briggs *et al.* (1975) and

Boyd *et al.* (1989). At immobilisation level 5 apnea could occur and artificial resuscitation became necessary. Successful resuscitation was achieved in all cases of apnea by the **immediate** catheterization of the trachea with an endotracheal tube and commencing artificial respiration (as described in Baker, Anderson and Fedak, 1988 and Baker *et al.*, 1990 - see Plate 2.4). This involved placing a rubber intubation tube into the seal's trachea and ventilating the animal. Also, after commencing artificial respiration, a second member of the field party injected extradurally 5ml of the respiratory stimulant Doxapram HCl (A. H. Robbins Company Limited, Crawley, West Sussex) at a concentration of 20 mg/ml. This was repeated at 20 minute intervals until the animal revived. Throughout the resuscitation process a constant watch was maintained on the seal's reactions and in particular the colour of the gums (the only bare flesh visible), which become blue during apnea, but once resuscitation begins regain their normal pink hue. Resuscitation can take up to two hours for complete recovery. During the three field seasons a total of 17 seals became apnoeic. In one instance the seal suffered a cardiac arrest and external heart compression was required to regain the heart beat. All seals were satisfactorily revived and showed no ill effects.

Due to the hazards associated with darting and the necessity for continuous observation of drugged seals it was only possible to work on one animal at a time. This limited the number of seals that could be caught in a full day's work to around 11 or 12. However, the data collected are of limited use unless the seals were caught at least twice during the breeding season to ascertain changes in weights and measures. Table 2.3 shows the numbers of captures in each season and the number of repeat catches. A detailed discussion of the variation in responses of individual seals to immobilisation by the two drugs used is provided in Appendix A.

Plate 2.4 : Intubation of a adult male grey seal after occurrence of apnea whilst darting. As in all cases of apnea, this individual was successfully revived (North Rona, 1988). The intubation tube has been inserted into the male's trachea, and the inflatable collar of the tube has been inflated by the use of the 60 ml syringe, thus forming a tight seal around the tube in the trachea (the inflated bulb indicates that the collar is inflated). Again, the pink colouration on the male's neck was from dyes applied to aid identification.

Table 2.3: Details of seal immobilisations in each field season.

		NUMBER OF DIFFERENT INDIVIDUALS CAUGHT	
YEAR	NUMBER OF CATCHES OF EACH INDIVIDUAL	MALES	FEMALES
1987	1	17	14
	2	17	31
	3	8	0
	4	4	0
	Total No. different individuals caught	46	45
	Total No. catches	91	76
1988	1	10	5
	2	14	14
	3	5	1
	4	2	0
	Total No. different individuals caught	31	20
	Total No. catches	61	36
1989	1	4	8
	2	7	26
	3	6	0
	4	5	0
	5	1	
	Total No. different individuals caught	23	34
	Total No. catches	61	60

2.Weighing and taking standard measurements:

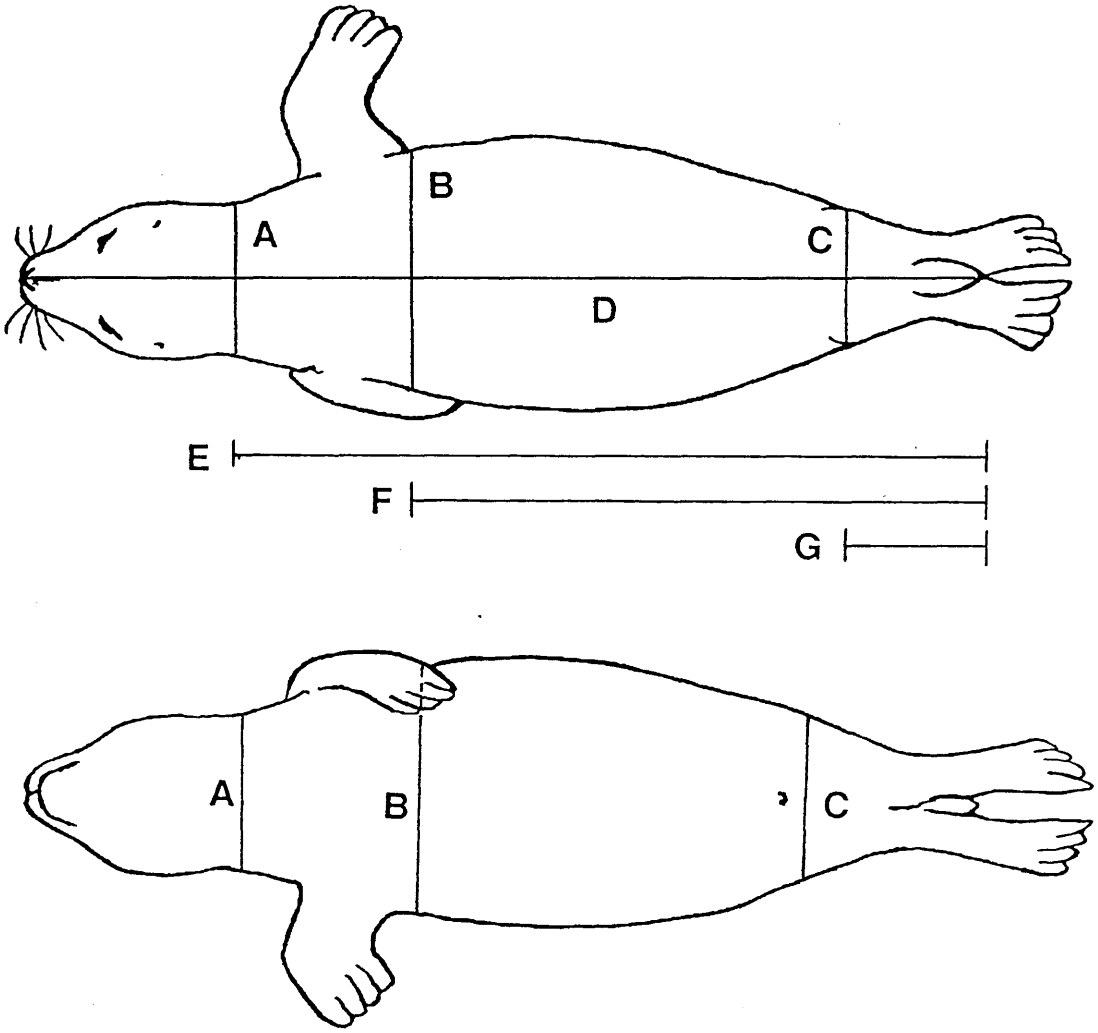
Following effective immobilisation, the seal was tied up in a "pole net" (a sturdy net with thick aluminium poles tied to two opposite sides; tying the poles together confines the seal securely in the net) and then weighed. A large lightweight aluminium tripod was erected over the seal. A "Minilift" winch (Model J, Didsbury Engineering Co. Ltd., Stockport, Cheshire) was then attached to the apex of the tripod. A load cell (strain gauge) was hooked onto the "Minilift" and the pole net hooked onto the load cell. The seal was then winched clear of the ground and the weight taken from the digital readout of the load cell (see Plate 2.5). The load cell proved to be very accurate and reliable even in the harsh field conditions of North Rona. The seal was then lowered to the ground and, if still suitably sedated, was released from the net. Standard measurements were taken as illustrated in Figure 2.3 a. During standard measurements, all seals were positioned lying on their ventral sides, as straight as possible.

There is a particularly confounding problem with measuring the nose to tail length of a seal. The seal is able to extend or retract its neck without showing much evidence externally of which state the neck is in. Therefore, from one capture to the next an individual may show either an increase or decrease in body length (Figure 2.3 b). Similarly, the neck girth alters as the length of the neck changes. To minimise these changes, all possible attempts were made to ensure that each seal was lying on its ventral surface in a straight line. However, due to the rugged nature of parts of North Rona this was not always feasible. For the reasons just outlined, other standard measurements were taken as well as the nose to tail length, in particular the axilliary to tail measurement. This is the straight line distance from the point of widest girth (the axilliary girth, generally just posterior to the fore flippers) taken at the dorsal mid-line to the tip of the outstretched tail.

These standard measurements are used to establish a model, incorporating all girth and length measurements to estimate volumes of individual males at the time of capture. This takes into account changes in body length, which are compensated for by changes in girths. These values were then compared with the weight at the time of capture in an

Plate 2.5 : Weighing an adult male grey seal (North Rona, 1987). Photograph taken by Bruce Herod.

Figure 2.3 a : Standard measurements taken from seals



A	Neck girth (NEG)
B	Axilliary girth (AXG)
C	Pelvic girth (PEG)
D	Nose to tail length (NTT)
E	Neck girth to tail length (NET)
F	Axilliary girth to tail length (AXT)
G	Pelvic girth to tail length (PET)

Figure 2.3 b : Illustration of potential hazards of measuring seals; although the seal's neck may be retracted, little sign of this may be discerned externally, particularly in a seal with much blubber.

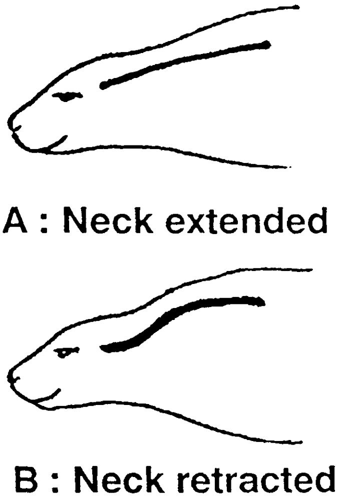
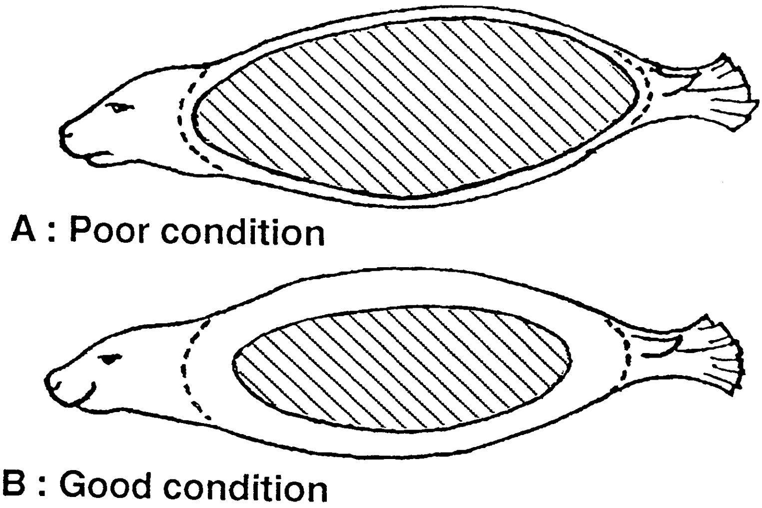


Figure 2.3 c : Illustration of the potential differences between 2 seals of the same size, and yet in different body condition (hatched area indicates lean body tissue, clear area indicates blubber). Seal B has a lower lean mass, but is in relatively "better" condition.



attempt to assess the relative body condition of males (see Chapter 5). However, to accurately assess body condition, a crucial factor is the ability to obtain accurate measures of either actual skeletal size of individuals or fat depth or preferably both.

3. Measurement of skeletal size in males:

During the course of this study, attempts were made to gain an accurate measure of the "real" size of a seal; i.e. some measure of its skeletal size. For example, two bulls of apparently the same size may in fact differ markedly in their amount of blubber reserves, one being a large seal with a thin blubber layer and so in poor condition, the other a small seal in excellent condition (see Figure 2.3 c). This obviously is of major interest in considering the potential effect of body condition on mating and/or reproductive success. For example, those with greater energy reserves may be able to maintain a position on land for longer. Attempts have been made using skull and flipper parameters to assess skeletal size, but with no success.

4. Assessing Blubber thickness/fat depth:

Attempts were made to assess blubber depth by means of an ultrasonic fat depth tester as used by Gales and Burton (1987) on the southern elephant seal. The particular model used in this study was an Ithaco fat depth measurer and pregnancy detector (Aggro-process Limited). Readings were taken at 6 points, three ventrally and three dorsally, slightly away from the mid-line to avoid the backbone. This method of determining blubber thickness proved to be extremely unreliable and very little confidence can be attributed to any of the readings. Examination of freshly dead adult grey seal carcasses revealed no correlation between fat depth measured by ultrasonic means and the real depth as determined by dissection. Whether it was the apparatus (designed for use in assessing back fat thickness in pigs) that was at fault or, some intrinsic difficulty in using this method on grey seals, is still unknown. However, it has been suggested that the presence of layers of collagen fibres in the blubber of grey seals may account the inability to assess fat depth by this means (Baker, pers. comm.).

In the 1989 field season a different technique was employed to assess body condition, the use of singly-labelled water (tritiated water - H_3O), The basic procedure used was as developed on grey seals by Reilly (Reilly 1989, Reilly and Fedak 1990). To determine an individual's body condition a known amount of H_3O was injected into the seal. This was allowed to equilibrate, a process which takes between 3 and 6 hours from the initial injection. Once equilibration was achieved a blood sample was taken. This procedure was repeated at least twice on each individual during the season, at intervals of at least one week. These two determinations of body condition were conducted slightly differently. For the first assessment the H_3O was injected remotely, using a darting system similar to that used for immobilisation. Instead of being loaded with sedative, the dart contained a known quantity of H_3O. The dart was attached by a fine cord to the field worker firing the dart. Once the dart had injected the H_3O in to the target seal the dart was recovered in order to be reweighed. Thus, for the first determination, the seal was not immobilised for the injection of the H_3O. After the 3 - 6 hour equilibration period, the seal was immobilised to gain the blood sample and the weight (all other samples outlined above were also taken at this point). For the second body condition determination the seal had to be immobilised first so that an initial blood sample could be taken to ascertain the background level of tritium (residual from the first determination). The seal was then injected extradurally with a fresh, known dose of H_3O. The syringe was flushed three times. After the 3 - 6 hour period the seal was again immobilised. It was found that a Zoletil dosage of only 80 to 90 percent of the original was necessary, particularly as the only sample required at this stage was a blood sample. During the 1989 season the initial body condition determination was made on a sample of 10 males, of which 6 were recaptured at later dates to allow for the second body condition assessment. This so called "double immobilisation" procedure is discussed further in Appendix A.

Details of the laboratory analyses of the samples collected, the calculation of total body water, total body fat, total body protein and total body energy are provided in Reilly (1989), Reilly and Fedak (1990) and in Appendix D. Details of the outcome of the labelled water technique are presented in Chapter 5.

5.Age assessment:

During the 1988 and 1989 field seasons a single lower incisor tooth was collected from each drugged seal. The teeth were extracted using a dental chisel and pliers (Cottrel Co. Ltd.). Grey seals' incisors are small, peg like teeth and are relatively easily removed. Many adults have one or more incisors, or even canines, already missing and seem to be little affected by the loss. Indeed, an extreme example is one male on Sable Island in 1990 who had no lower jaw whatsoever and only half a tongue (pers. obs.). This male was clearly in good body condition and successfully maintained a position amongst a group of females for approximately 4 weeks.

Teeth were taken upon the first capture of each seal. On subsequent captures the mouth was examined, and in all cases the wound had healed remarkably well. During these two seasons ages were gained on 33 males.

Teeth were stored in vials containing alcohol. Upon returning from field work, each incisor was sectioned along the mid-line. The annual growth rings in the cementum were counted using a binocular microscope. All ageing was conducted without the prior knowledge of which individual the tooth belonged to, and a second, independent reading was made by John Prime (of the Sea Mammal Research Unit). In all cases the readings agreed to within one year.

Further details of this ageing technique can be found in Laws (1952), Bonner (1971), Bejaminsen (1973), Prime (1978) and Fancy (1980).

6.Blood samples:

Blood samples were taken from either the hind flipper plexus (see Plate 2.6 a) or the extradural vein (see Plate 2.6 b). Blood from males, females and pups were used for DNA fingerprinting, the analysis having been carried out by Dr. Bill Amos at the Department of Genetics, Cambridge University. Details of the analytical methods employed can be found in Amos (1990) and Amos *et al.* (1991). The results of these analyses are presented in Chapter 6.

Plate 2.6 (a) : Taking blood samples from the hind flipper plexus of an adult male grey seal (North Rona, 1987).


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Plate 2.6 (b) : Taking blood samples from the extradural vein of an adult female grey seal. Photograph taken by Paddy Pomeroy.

7. Precautions taken during sampling

All sampling procedures involving invasive techniques, such as darting and sampling blood, were conducted with fresh, sterile equipment (needles, syringes etc) on every occasion and then discarded into a sharps container. All incisions and injection sites were sprayed with Oxytetracycline and all individuals branded or from which teeth were taken were injected with terramycin. All equipment reused on successive captures, such as tagging pliers, were thoroughly cleaned with Savlon in the field. All equipment used was cleaned and sterilised each evening after darting sessions.

8.Storage of samples:

All samples taken were stored in a portable gas powered freezer.

9. Optimum catching routine:

With an experienced, efficient field team of either three or four members the sampling process could be completed in 10 to 15 minutes. This gave an overall time from darting to recovery of approximately 30 to 40 minutes. Generally, two field workers were involved in the initial darting procedure, three members being required for handling the seals initially and the weighing procedure and one member taking necessary notes. The remaining samples were gathered with only two workers, freeing the remaining two to sample the pup in the case of females. The order of sampling found to be most efficient is outlined below, though it is important to be completely flexible to adjust for the unexpected.

MALES;
Darting - a 2 person operation
Netting - 2 person
Weighing - 4 person, one taking notes
remove seal from pole net if sufficiently sedated
Blood & tooth sample while the seal is still heavily sedated - 2 person
Standard measurements - 2 person, done while blood & tooth is sampled
Tag and brand - 2 person
release seal

FEMALES;

The general procedure is the same as with males except that the pup can be sampled after weighing the mother (further details of precautions taken whilst sampling females are provided in Appendix B).

NB: see Appendices A and B for discussion of some of the problems encountered when darting.

10. Responses of surrounding seals to captures:

Females near to a captured seal tended to be agitated at first but soon settled after they were able to move their pups away a few metres. The response of adjacent males varied. Generally, males with secure positions on the breeding colony remained and seemed little concerned whilst peripheral, itinerant (see Chapter 4) males would flee readily. The males holding positions amongst groups of females occasionally attempted to copulate with drugged females, and were dissuaded to prevent disturbance to the female.

It is important to note the potential effect of these captures on the seals, in particular the males. The catching procedure may have exerted an artificial selection for "tolerant" males. Males unwilling to be subjected to such disturbance would leave the study site, perhaps for elsewhere on the island. However, my observations of individual males, made prior to catching attempts, suggest that it is, to some extent, possible to predict a male's response to capture. This is based solely upon observations of the individual's status, whether he had a secure position on the colony, amongst the females or not and his general "character". From these it is possible to say whether a male will stay or flee upon the approach of field workers. This also accounts for the low numbers of itinerant, peripheral males caught, since these individuals will readily flee upon sighting a nearby human. For these reasons, strenuous efforts were made to catch these peripheral males in 1988 and 1989, involving stalking individuals along rocky shorelines.

CHAPTER 3 - DESCRIPTION OF BEHAVIOURS

INTRODUCTION

In this chapter the behavioural categories used throughout this study are defined and described. Both the durations and seasonal variation in the frequency of various behaviours are presented. The aims of this chapter are essentially to provide a qualitative and quantitative description of behaviours seen on the breeding colony as a background for more detailed analyses in subsequent chapters.

Further descriptions of grey seal breeding behaviour can be found in Darling (1939), Matthews (1950), Hewer (1957 and 1960), Hewer and Backhouse (1960), Boyd, Lockie and Hewer (1962), Boyd and Laws (1962), Boyd (1963), Cameron (1967, 1969), Fogden (1968 and 1971), Bonner (1972 and 1981), Anderson, Burton and Summers (1975), Burton, Anderson and Summers (1975), Boness and James (1979), Miller and Boness (1979), Boness, Anderson and Cox (1982), Boness (1984), Anderson and Fedak (1985), and Lawson (1991).

METHODS

The details of techniques employed in the behavioural observations are provided in Chapter 2. The duration and outcome of all sexual and aggressive interactions were noted. Thus , for each male, records of number of interactions of each type, their duration, identity and/or status of the males and/or females involved, their outcome and their date and time of occurrence were collected. In presentations of seasonal variation of aggressive and sexual activities a mean rate per male per 24 hours has been calculated. To gain these daily rates of each activity for each male, the number of observed behaviours of each type was divided by the number of hours observed on the day in question and then extrapolated to give a rate per 24 hours (this assumes no significant diurnal variation in male grey seal activity - see Chapter 5 for a discussion of this point). These 24 hour rates were then used to calculate the average rate per day per male. This yields a measure of seasonal variation in sexual and aggressive activities. The observation periods necessarily varied, generally becoming shorter as the season progressed due to diminishing daylight hours and also due to the weather, logistic demands and seal catching regimes. To minimise any effect of short sampling periods, days on which less than 4 hours observations were conducted were excluded from the analyses of seasonal trends in activities. Obviously the shorter the observation period the greater the error upon extrapolating scores to 24 hours. This is particularly so in a system such as this which contains a high level of natural variation.

All instances where attempted copulations or actual copulations were directed more than once at the same female were recorded as such, where possible. This was important as each female is certainly approached more than once by either the same or different males and most females are copulated more than once. Anderson, Burton and Summers (1975) estimated that each female may be mated up to three times by the same or different males and this is supported by observations in this study on the few marked females. For the calculation of daily frequencies of sexual activity, and individual activity budgets (see Chapter 5), all attempted copulations and actual copulations were used, whether the female in question had previously been mated or not. However, for the assessment of individual male mating success a system of first male paternity was assumed. Thus, mating success for an individual male is in fact the observed number of occasions in which he copulated with different females not previously mated (or not observed in a copulation before). This was deemed necessary as mating success is intended as a measure of an individual's reproductive success. If this convention was not adopted, potentially erroneous values for mating success would result. For example, if a single male copulated three times with the same female, recording these as different females would artificially inflate this male's mating success from one to three. Similarly, in cases where different males mate with the same female, the first male doing so has enhanced his mating success, whilst subsequent males failed to do so. Noting these repeated sexual acts was clearly possible in the case of individually marked females and also with unmarked females within a single day's observations. However, this is rather more difficult to achieve with unmarked females approached by either the same or different males on different days. Thus, this is one possible source of error in these figures, though it has been minimised wherever possible.

First male paternity was assumed as males clearly compete to gain the limited positions on the breeding colony, and it is the males that succeed in doing so that predominantly have the first opportunity to mate with oestrus females. If these males were not the successful sires, but the more peripheral males were responsible for fertilising the female, then the observed mating system would hardly be an evolutionary stable strategy (Maynard Smith and Price 1973, Maynard Smith 1974, Maynard Smith and Parker 1976, Dawkins 1976).

Dominance score (see also Appendix E):

A "dominance score" was calculated for each male involved in ten or more observed aggressive intrasexual interactions during the breeding season. The score was based on the outcome of all aggressive encounters involving a particular male. For example, the outcomes of all intrasexual encounters involving male "A" were graded with a value ranging from 1 to 7. A value of 1 represented an encounter where male "A" was the outright victor, 4 a draw and 7 where male "A" was the outright loser. A mean grade for all the encounters in each dyad in which male "A" was involved was obtained and an average of these means taken to give the final dominance score for male "A". This process was then repeated for male "B", and so on for all males in the study area. Thus, the average dominance score is 4 , the more dominant individuals (bulls that tend to win more than lose) have lower dominance scores, and more subordinate males (lose more than they win) have higher scores. This dominance score was used in preference to a simple dominance rank as not all males were present in the study area at once. The score allows all males to be compared. It is also possibly more "biologically realistic" as most males have intermediate dominance scores (close to the average score) and relatively less have particularly high or low scores (i.e. a normal distribution of dominance scores). This is perhaps a more realistic appraisal of differences in dominance between males than the standard "unit" difference between successive males in a dominance rank. Also, it is possible that most aggression occurs between the more closely matched mid ranking males, as would be predicted from the dominance score distribution.

It must be noted that accurate dominance scores could only be calculated for males observed in at least 10 inter-male aggressive interactions. For example, if a mid-ranking male has only one interaction, but a successful one, with a very subordinate male the dominance score produced would be equivalent to that of the more dominant individuals. Thus, males involved in less than 10 interactions were excluded from all analyses involving dominance score throughout this study.

This method of assigning relative dominance status to individual males is comparable to that used by Anderson and Fedak (1985) in that these authors examined the outcome of inter-male aggressive encounters to establish relative status. However, the actual computation of the dominance scores differs somewhat, particularly in the relative grading of responses to aggression. Also, far more extensive observations were made during the course of this study, enabling a more complete interaction network to be obtained.

Statistical analyses

(a) Selection criteria for cases:

For most of the parameters examined in this study, two sets of summary statistics are provided. The first includes all cases for which data are available. The second includes only cases where the individual males were involved in at least 10 inter-male aggressive interactions. This was necessary as, in Chapter 7, the inter-relationships between various parameters are examined. As such, it was necessary to ensure that individuals included in these analyses were involved in sufficient inter-male aggressive interactions to allow accurate calculation of the dominance score. Using this selection criterion removed many of those males present for only a few hours. Whilst these males may have spurious dominance scores, the remaining data gathered from these individuals, such as levels of sexual activity and colony attendance parameters are still valuable.

Hence, summary statistics and relevant analyses are provided utilising all data where possible. It is also necessary to present these data sets for only those males involved in 10 or more aggressive interactions as these are the data sets used in the final analyses in Chapters 7 and 8. This also allows examination of the effects of removing those males involved in less than 10 interactions from the data sets.

(b) Transformation of variables:

In analyses involving parametric statistics all variables were examined for normality. Histograms for each variable were produced together with statistics including skewness, standard error (S.E.) of skewness, kurtosis and S.E. of kurtosis. Both skewness and kurtosis were divided by their respective standard errors. If either of the values obtained was greater than 2.547 then the distribution of the variable was deemed to violate normality. In such cases steps were taken to transform these variables to minimise variance and the two values of skewness/SE skewness and kurtosis/SE kurtosis to below or equal to 2.547. It was found that the same variables for each year required transforming and also that the same method of transformation gave the best results (in terms of the above goals) for each year.

RESULTS

3.1. Behavioural categories used - descriptions and definitions

Listed below are detailed descriptions of the mutually exclusive categories of male behaviour recognised on the breeding colony at North Rona, and used throughout this study.

3.1.1. *Aggressive behaviours*:

(1) Alert (looking at another male) - this category includes all cases where a male was alert, and looking directly at another male.

(2) Approach to another male - the male under observation moves directly towards another male.

(3) Open mouth threat - this is a threat display, involving no physical contact between opponents, where the mouth is opened, usually in a wide gape (see Plate 3.1). The orientation of the opponents can be either directly facing each other, one seal lying perpendicular to the other or both lying parallel. The orientation of the head can either be pointing directly towards the opponent, or perpendicular to the opponent. The elevation of the head also varies, and in Anderson and Fedak (1985) the authors chose to record so called high open mouth threats and low open mouth threats separately. Here, no distinction is made between the various types of open mouth threats though the role of head elevation is discussed below. Fine behavioural details, such as relative orientation of opponents, orientation of head in respect to torso etc. are examined in detail in Lawson (1991), but here we are primarily interested in the outcome of aggressive interactions, not their intricate subtleties.

During the open mouth threat no audible sound is produced, other than a hissing and sometimes gargling sound, only audible from close quarters. However, the threat is very visual and it seems only to be performed between males in view of each other.

(4) Aggressive flippering - This involves opponents vigorously "waving" one, or both fore flippers at each other in a clearly aggressive manner (as opposed to the more gentle flippering occasionally seen in sexual interactions), often making contact with the

Plate 3.1 : Male grey seal performing open mouth threat (Sable Island, 1990).

opponent. Amongst females, a similar behaviour is seen in aggressive encounters, but involving flippering of the ground, tearing and throwing grass about.

(5) Lunge - This is an attempt at a bite but without making contact.

(6) Bite - An isolated bite (as opposed to a series of bites as would be seen in a fight). Occasionally, the bite will be accompanied by a vigorous shaking motion whilst the attacker has a grip on the opponent.

(7) Fight - A fight sequence typical of those seen on land is shown in Plates 3.2 a to o. One, or both, males will approach the other, the more dominant bull generally with his head held lower than that of the subordinate, who raises his head in a more defensive posture. Both animals will engage in open mouth threats. The fight then ensues with lunges and bites directed at each others necks and also aggressive flippering. Each male attempts to manoeuvre around to the back of his adversaries neck where they will savage the opponents neck and back (reminiscent of the mouthing of females by males in sexual encounters, though somewhat more violent in this case). The ultimate aim appears to be to reach the opponents rear end, where the hind flippers and tail are especially vulnerable. Once a male has achieved this, whilst attempting to keep his own hind flippers away from the opponent's jaws, the fight usually ends fairly rapidly. The loser attempts to retreat, though this can be hazardous. Whilst moving off forwards is the swiftest means of escape, this invariably exposes the hind flippers to yet more damage. Therefore, the loser may attempt to retreat backwards, still facing his adversary. The loser shuffles backwards, or sideways, until there is sufficient distance between the two combatants for him to turn and flee.

(8) Chase - The final category of aggressive behaviour is the chase. Chases are often seen subsequent to the initial aggressive interaction, in particular after fights, where the victor chases the loser. During a chase, one male will chase another, usually over short distances of 10 to 20 m, though occasionally up to 50 m or more. Often sequences of chases occur where one subordinate male is chased off by a dominant and flees directly towards another dominant male, only to be chased off again. This may continue, on and off, for several hours.

Plate 3.2 : Fight sequence between two adult male grey seals (Sable Island, 25/1/1990).

The action took place in the Sable Island study area around the shallow pond (see Figure 9.1 b). At 10:13 am., male 953 began to copulate with the female on the western side of the pond (shown in the foreground in Plate 3.2 a). At 10:27, shortly after completing a copulation on the eastern side of the pond (approximately 20 m from male 953), male 922 approached male 953 through the pond (Plate 3.2 a). Male 922 was the more dominant male of the pair (see Figure 9.4 b). As male 922 approached, the pair exchanged open mouth threats (Plate 3.2 b), and male 953 lost his grip on the female as she struggled. Male 922 closed in, still exchanging open mouth threats, as the female began to depart (Plate 3.2 c). The males began to fight (Plate 3.2 d) at 10:29, with male 922 on top of male 953. In Plate 3.2 e, male 922 has moved round to the left as the pair grapple. The males continued to fight, lunging at each other's necks and parrying with their fore flippers. The female returned to collect her pup (seen on the far left of Plate 3.2 f). The fight continued, whilst the female turned and moved away with her pup (Plates 3.2 g, h, i, j, k and l). Male 922 remained on the left throughout these Plates. In Plate 3.2 m the fighting has ceased (time = 10:34). Male 953 began to move away to the right (Plates 3.2 m, n, o). Male 953 eventually departed from this area, and male 922 successfully copulated with the female.

a

b

c

d

e

f

g

h

i

j

k

l

m

n

o

Rarely do individual aggressive encounters involve more than two males. Bouts of open mouth threats may occur between 3 or 4 bulls, but I have only witnessed one fight between more than two animals at once despite approximately 560 hours of observation involving over 3000 inter-male aggressive encounters. In almost all cases where a fight or chase moves towards a third male, as the third male approaches the combatants the winning male of the dyad will stop fighting or chasing and allow the third male to enter the fray.

(9) Roll - Another behaviour seen in the males is a "roll" display. This is usually seen after a fight or chase. The victor, having seen off his rival, will then roll on his back. It has been suggested that this is just a simple means of turning round in order to return from whence the seal came. However, it could possibly be a "victory roll".

3.1.2. *Sexual behaviours*:

(1) Approach - a male approaches a female, or more rarely, vice versa. This is a sub-group of general locomotion. It involves no physical contact between the male and female, except where the male "noses" the female (male and female lightly touch noses sniffing each other) and where a male investigate a females' rear end. This category is directly comparable with that of "approach" used by Boness (1984).

(2) Attempted copulation - usually an attempted copulation is initiated by the approach of a bull to a cow; very seldom do cows actively solicit the attention of a male (see also Anderson, Burton and Summers 1975). The attempted copulation begins when the male attempts to get his fore-flipper over the females back and grab her by the scruff of the neck with his jaws (an action which may have a similar pacifying effect as seen in many other mammal species - see Plate 3.3 a and b). Once he has achieved this, the male attempts to swing his rear end around to lie parallel with the female, on top of her, or by her side. This is the position in which the male attempts intromission. The cow usually responds aggressively, at least initially (see also Anderson, Burton and Summers 1975). This response seems to decline in intensity as the female approaches oestrus. If the cow's response is not too harsh and the male persists in his advance he will usually succeed in

Plate 3.3 : Copulating pair observed on North Rona.

Plates 3.3 a and b: Early in the copulation, shortly after successful intromission, showing the male gripping the females neck in his jaws and her torso with his right fore flipper.
Plate 3.3 c: Towards the end of the copulation the female becomes agitated and starts to wave her hind flippers about. As the female's struggles intensify, the males can no longer maintain his grip.
Plate 3.3 d: The female struggles, craning her neck back, to bite at the male's neck. The copulation ended shortly after this.

a

b

c

d

mating with the female. This behavioural category is comparable with that of "mount" as used by Boness (1984). A combination of this category and the approach category is equivalent to that of "pre-copulatory behaviour" used by Anderson and Fedak (1985).

(3) Copulation (see Plates 3.3 a to d) - actual copulation commences from the point of intromission. However, in many cases the male fails to maintain the copulation by, for example, falling off the female, rolling down a slope if the copulating pair are precariously balanced, or if interrupted by another seal. Most such interruptions occur early in the copulation sequence, as the male and female adjust positions. However, once settled, only interruptions from other seals disturb the mating pair. After intromission the pair lie remarkably still for most of the copulation. Such incomplete copulations are termed "unsuccessful copulations", whilst those that proceed without interruption are termed "successful copulations". A majority of copulations occur ventral to dorsal, but occasionally ventral to ventral copulations are observed.

Towards the end of the copulation the female's ventral pelvic region can be seen pulsating, possibly indicating the approximate time of ejaculation. The cow then becomes more agitated and the copulation ends shortly afterwards. The pair may lie together for a while, in some instances the male attempting to copulate again. More often, the female will move away and make her way towards the sea, a journey on which she may be accosted by other males, of which some may be successful in mating with her.

This category is directly comparable with those of "copulation" used by Boness (1984) and Anderson and Fedak (1985).

(4) Non-aggressive flippering - this is similar to the aggressive flippering, only far more gentle and sedate. It is usually directed from a female to a male, with the female lying on her side or back. This behaviour is often seen in the rare cases of female soliciting, with the female rolling and wriggling in front of the male.

3.1.3. *Other categories*:

(1) Resting - the non-active state of males, lying with eyes open or closed and head on the ground. This category includes comfort movements (adjustments of the body position and

scratching).

(2) Alert - this includes all cases where a male is clearly observant, head raised and looking around, but at a non specific target (i.e. not included in previous categories)

(3) Locomotion - this includes all locomotion not included in previous categories (e.g. chases).

(4) Out of sight - where a male is not visible from the hide and yet is known not to have departed from the study site.

3.2. Quantitative analyses of aggressive interactions

3.2.1. *Male - female aggression*:

Intersexual aggressive encounters predominantly involve either aggressive flippering, lunges, bites and/or open mouth threats. These are most often directed from the female to the more passive male. During such encounters, females will often lie on their sides waving their fore-flippers at the male. In 1987, of all the observed aggressive flippering 98.92 % occurred in intersexual encounters. Similarly 94.5 % of lunges and 86.96 % of bites occurred between females and males. Most male-female aggressive interactions are of very short duration (less than 1 minute), usually occurring upon unwelcome sexual advances by males, or if a male inadvertently moves too close to a female or her pup, such as during a male-male fight (see Boness *et al.* 1982). The females are noticeably more vocal than males during aggressive encounters (pers. obs.). Of 597 observed, non-sexual, aggressive interactions between males and females, 48 % were won by the female (i.e. the male retreated), 50 % were drawn (i.e. the interaction subsided with no clear victor) and a mere 2 % were won by the male. In subsequent seasons, details of inter-sexual aggression not directly associated with sexual activity were not recorded.

3.2.2. *Male - male aggression*:

Inter-male aggression primarily consists of open mouth threats and is predominantly a low key affair. Few aggressive encounters escalate into high intensity aggression (fights). Of the 929 inter-male aggressive encounters observed in 1987 only 5.81 % involved physical contact. A total of 909 encounters were observed in 1988, and 1513 in 1989, with only 6.71 % and 4.56 % respectively, involving physical contact.

Table 3.1 a and b summarises the statistics for mean values of total number of aggressive interactions, aggressive interactions per day and dominance score. Table 3.1 a presents these statistics for all males identified whilst 3.1 b gives values for only those males involved in 10 or more aggressive interactions.

A oneway analysis of variance with Scheffe's multiple range test was conducted on the data presented in Table 3.1.a to compare the means for each season. All data sets were transformed to approximate to normality as outlined in the methods. The mean value for total number of aggressive interactions in 1987 was significantly greater than that for 1988 at $p < 0.05$, but not at $p < 0.01$ ($F_{2,268} = 4.62$, $p = 0.011$). The mean number of aggressive interactions per day in 1989 was found to be significantly greater than that for 1988, even at $p < 0.01$ ($F_{2,256} = 7.45$, $p = 0.0007$). There was no significant difference in the mean values for dominance score ($F_{2,247} = 2.28$, $p = 0.10$).

Table 3.1.a
Summary statistics for observed aggressive activity and dominance score for all identified males on the study area.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1987	TOTAL No. A.I.s	68	19.50	27.32	25.02	3.04	1	92
	A.I.s/DAY	68	2.37	3.79	4.52	0.55	0.17	24.09
	DOMINANCE SCORE	68	4.26	4.23	1.20	0.15	1.75	6.64
1988	TOTAL No. A.I.s	92	7.50	19.53	27.70	2.89	1	118
	A.I.s/DAY	86	1.84	2.99	3.72	0.40	0.11	26.79
	DOMINANCE SCORE	87	4.64	4.60	1.25	0.13	2.49	7.00
1989	TOTAL No. A.I.s	111	9.00	26.61	42.76	4.06	1	317
	A.I.s/DAY	105	3.05	5.51	6.71	0.66	0.29	45.95
	DOMINANCE SCORE	95	4.30	4.30	1.13	0.12	1.00	7.00

Table 3.1.b

Summary statistics for observed aggressive activity and dominance score for all identified males on the study area which were involved in 10 or more inter-male aggressive encounters.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1987	TOTAL No. A.I.s	47	34.00	37.92	23.22	3.39	10	92
	A.I.s/DAY	47	2.36	3.54	4.29	0.63	0.60	24.09
	DOMINANCE SCORE	47	4.33	4.10	1.08	0.16	2.17	6.14
1988	TOTAL No. A.I.s	39	27.00	40.05	31.90	5.04	10	118
	A.I.s/DAY	39	2.83	1.89	2.80	0.45	0.61	13.97
	DOMINANCE SCORE	39	3.51	3.86	1.06	0.17	2.49	5.83
1989	TOTAL No. A.I.s	54	37.00	50.74	51.31	6.98	10	317
	A.I.s/DAY	54	2.94	5.38	7.17	0.98	0.62	45.95
	DOMINANCE SCORE	54	3.79	4.09	0.95	0.13	2.68	5.95

Again, oneway analysis of variance with Scheffe's multiple range test was used to compare the means of the variables presented in Table 3.1.b between seasons. No significant differences were found between seasons in any of the three variables (total number of aggressive interactions; $F_{2,138} = 0.95$, $p = 0.39$, aggressive interactions per day; $F_{2,137} = 3.56$, $p = 0.031$, dominance score; $F_{2,138} = 0.73$, $p = 0.48$).

Duration of inter-male fights

The mean duration of fights was approximately 3 to 3.5 minutes (1987; mean = 3.37 minutes, n = 31, S.E. = 0.70, median = 2.00, 1988; mean = 2.93, n = 27, S.E. = 0.65, median = 2.00, 1989; mean = 3.39, n = 31, S.E. = 0.63, median = 2.25). However, durations ranged from 0.5 to 15.5 minutes. In fact, the maximum recorded fight durations in the three seasons were remarkably similar, 15.5 minutes in 1987, and 15 minutes in both 1988 and 1989. The duration data for 1987 were divided into those where one male was the clear victor and those where there was no clear outcome (a draw). The average duration of fights in which there was a clear victor was 3.25 minutes (SD = 3.45 minutes, n = 25). The mean duration of fights with no clear victor was 3.87 minutes, though there is considerable variation (SD = 5.73 minutes, n = 6).

Outcome of aggressive interactions with respect to initiator

Dominant individuals obviously won relatively more aggressive interactions than more subordinate males. However, dominant males also initiated more inter-male aggressive interactions. There were significant correlations at $p < 0.001$ between dominance score and the percentage of aggressive interactions initiated (arc-sine transformed) in all three seasons (1987: R = -0.88, n = 47, 1988: R = -0.88, n = 39, 1989: R = -0.90, n = 54). Thus, males that initiate aggressive interactions tend to be the victors.

This relationship between the initiation and outcome of aggressive interactions was examined in order to assess whether it varied with the intensity of the encounter. Table 3.2 a, b and c depict the relative frequencies of victories, draws and losses of initiators of aggressive encounters for various categories of aggression for 1987, 1988 and 1989 respectively.

Table 3.2.a

Table of details of outcomes of inter-male aggression for 1987, showing number and percentage of encounters won and lost by initiator or drawn.

TYPE OF AGGRESSIVE INTERACTION	N	PERCENTAGE OF ENCOUNTERS won by initiator	drawn	lost by initiator
ALL ENCOUNTERS	929	69.5	30.0	0.5
FIGHTS	54	81.5	16.7	1.9
CHASES	467	99.6	0.4	0.0
OPEN MOUTH THREATS	396	65.7	33.6	0.8
ALL REMAINING A.I.s	12	33.3	66.7	0.0

Table 3.2.b

Table of details of outcomes of inter-male aggression for 1988, showing number and percentage of encounters won and lost by initiator or drawn.

TYPE OF AGGRESSIVE INTERACTION	N	PERCENTAGE OF ENCOUNTERS won by initiator	drawn	lost by initiator
ALL ENCOUNTERS	909	68.0	30.3	1.8
FIGHTS	61	78.7	13.1	8.2
CHASES	396	100.0	0.0	0.0
OPEN MOUTH THREATS	441	59.4	38.3	2.3
ALL REMAINING A.I.s	11	45.5	45.5	9.0

Table 3.2.c

Table of details of outcomes of inter-male aggression for 1989, showing number and percentage of encounters won and lost by initiator or drawn.

TYPE OF AGGRESSIVE INTERACTION	N	PERCENTAGE OF ENCOUNTERS		
		won by initiator	drawn	lost by initiator
ALL ENCOUNTERS	1513	56.6	42.7	0.8
FIGHTS	69	87.0	8.7	4.3
CHASES	462	100.0	0.0	0.0
OPEN MOUTH THREATS	659	58.0	41.0	1.1
ALL REMAINING A.I.s	323	19.8	79.9	0.3

It is clear that the initiator of an interaction is seldom the loser as would be expected from the clear relationships between dominance and proportion of encounters initiated. Taking all aggressive interactions into consideration, approximately two thirds of interactions are won by the initiator, one third result in draws, and only a few cases result in a loss for the initiator (between 0.4 and 1.8 percent).

An interesting pattern is observed when dividing interactions by aggression type. In low level aggression (all encounters other than fights and chases) a greater proportion of interactions are unresolved (draws). Between 30 and 40 % of open mouth threats result in a draw. In the case of "all remaining aggressive interactions" the percentage of draws rises to between 45 and 80 percent. Where interactions escalate to a fight, these are usually resolved, mostly in the favour of the initiator, with between 78 and 87 % of fights being won by the initiator. Chases almost were exclusively won by the initiator.

Seasonal variation in male-male aggression

Figures 3.1 a, b and c depict the seasonal variation in the mean rate of occurrence of inter-male fights and open mouth threats per male per 24 hours (± one standard error) for 1987, 1988 and 1989 respectively. In all three figures there are considerable fluctuations from day to day. However, general trends can be discerned. The seasonal pattern of fights (high intensity aggression) is very similar to that of open mouth threats (low intensity aggression). There is an initial peak early in the season with relatively high levels of aggression until approximately day 18 (6th of October). This is at the start of the season, when bulls start to come ashore in significant numbers. After this first peak, levels of aggression appear to decline somewhat, in particular open mouth threats. A second peak in aggression occurs approximately mid season, between approximately day 25 and 30 (13th and 18th October) in 1987 and 1988 and slightly later in 1989 (ca. 18th to 23rd October). Aggression levels then tend to decline again during the latter half of the season with a final peak in the closing days of the seasons, around day 47 (4th of November).

Figures 3.1a to c : Seasonal variation in the frequency of inter-male aggression (open mouth threats and fights) in 1987, 1988 and 1989. Values plotted are daily mean values (rate per male per 24 hours) ± standard error.

Figures 3.2a to c : Seasonal variation in the frequency of sexual activities (attempted copulations and successful copulations) in 1987, 1988 and 1989. Values plotted are daily mean values (rate per male per 24 hours) ± standard error.

Figure 3.1 a : Seasonal variation in frequency of inter-male aggression - Rona 1987

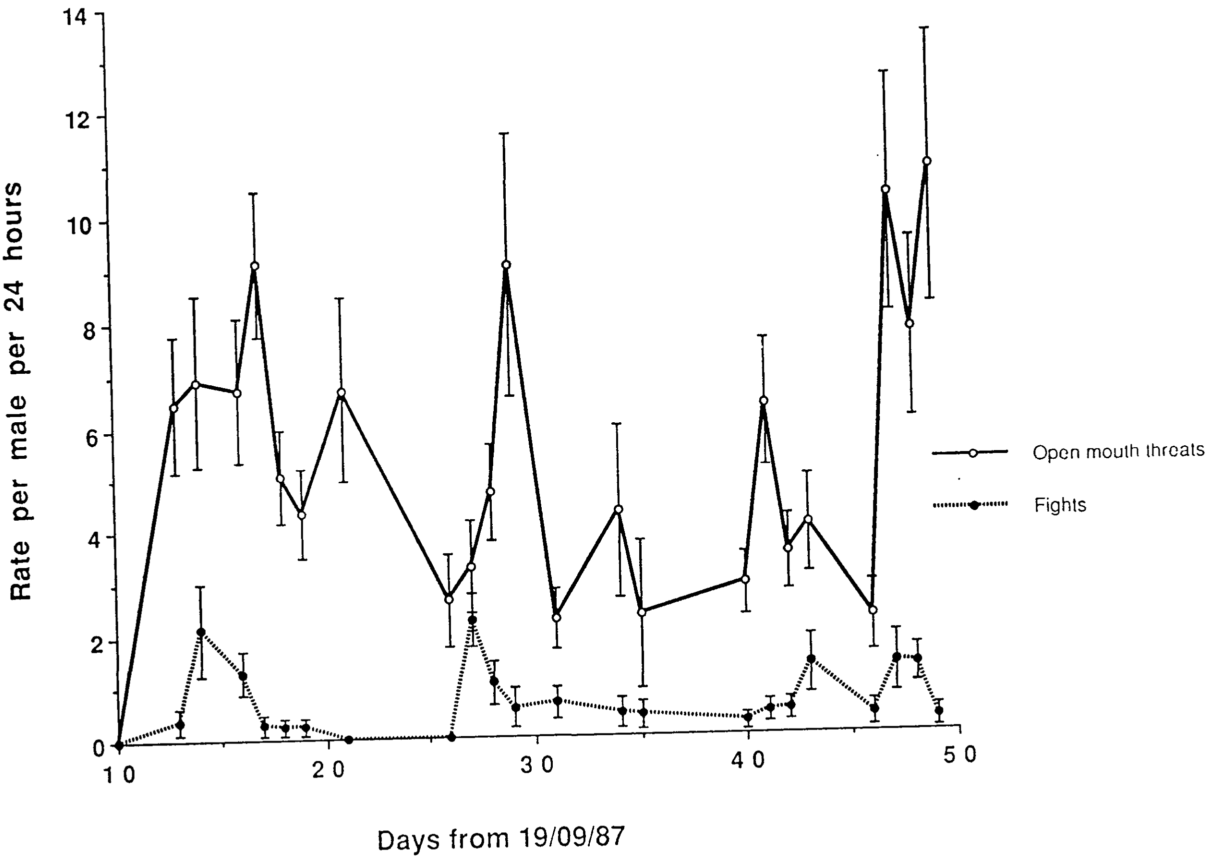


Figure 3.1 b : Seasonal variation in frequency of inter-male aggression - Rona 1988

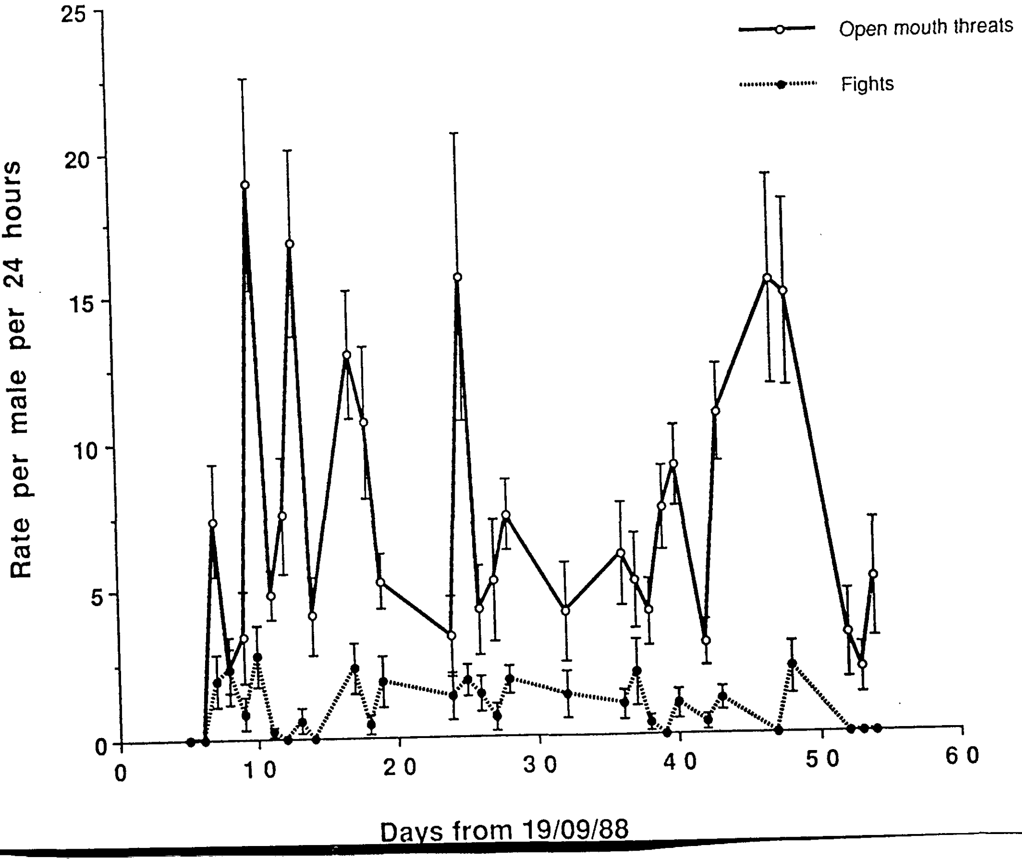


Figure 3.1 c : Seasonal variation in frequency of inter-male aggression - Rona 1989

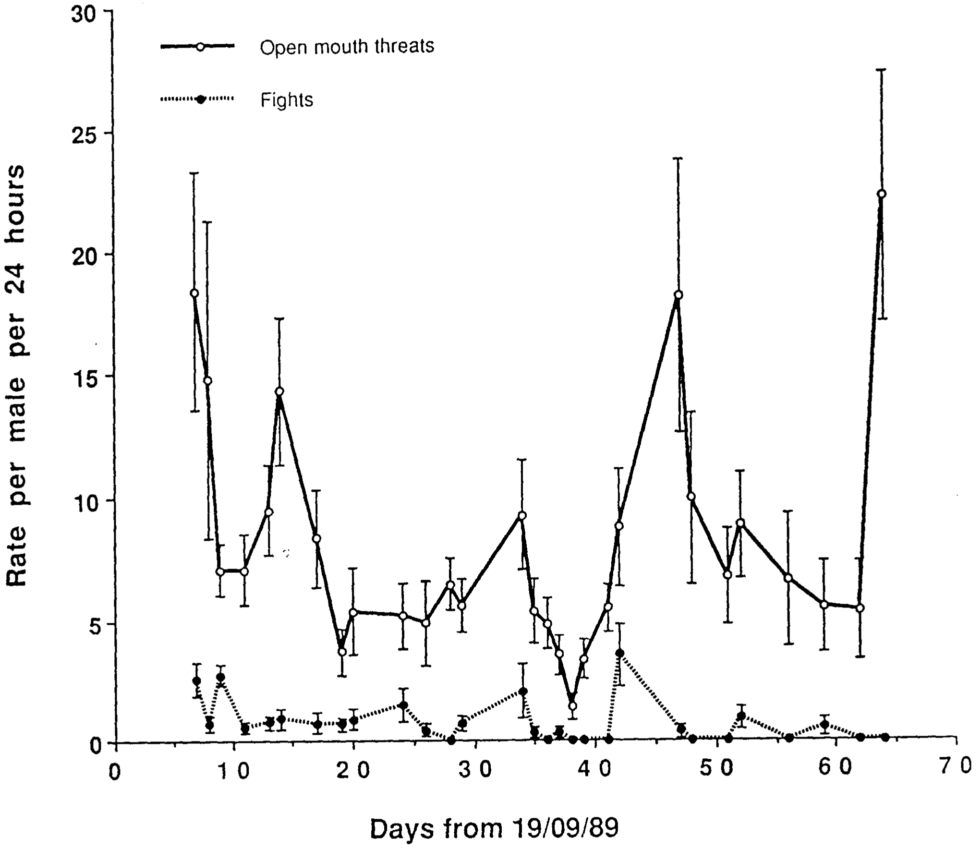


Figure 3.2 a : Seasonal variation in frequency of sexual activities - Rona 1987

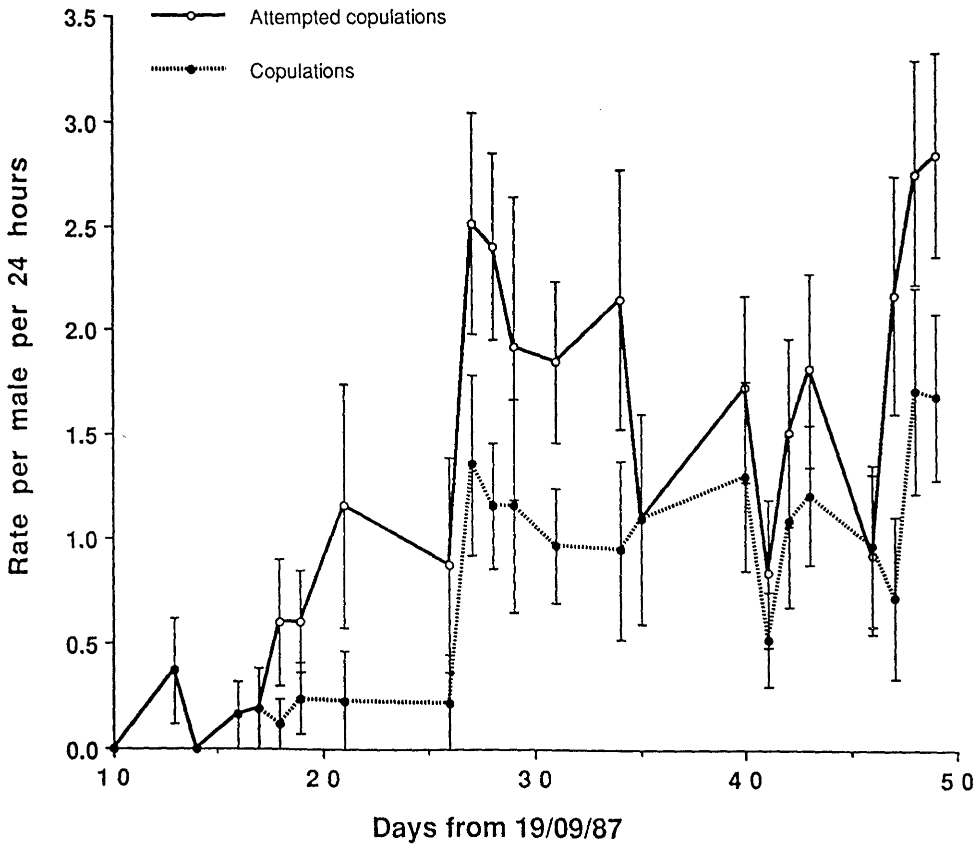


Figure 3.2 b : Seasonal variation in frequency of sexual activities - Rona 1988

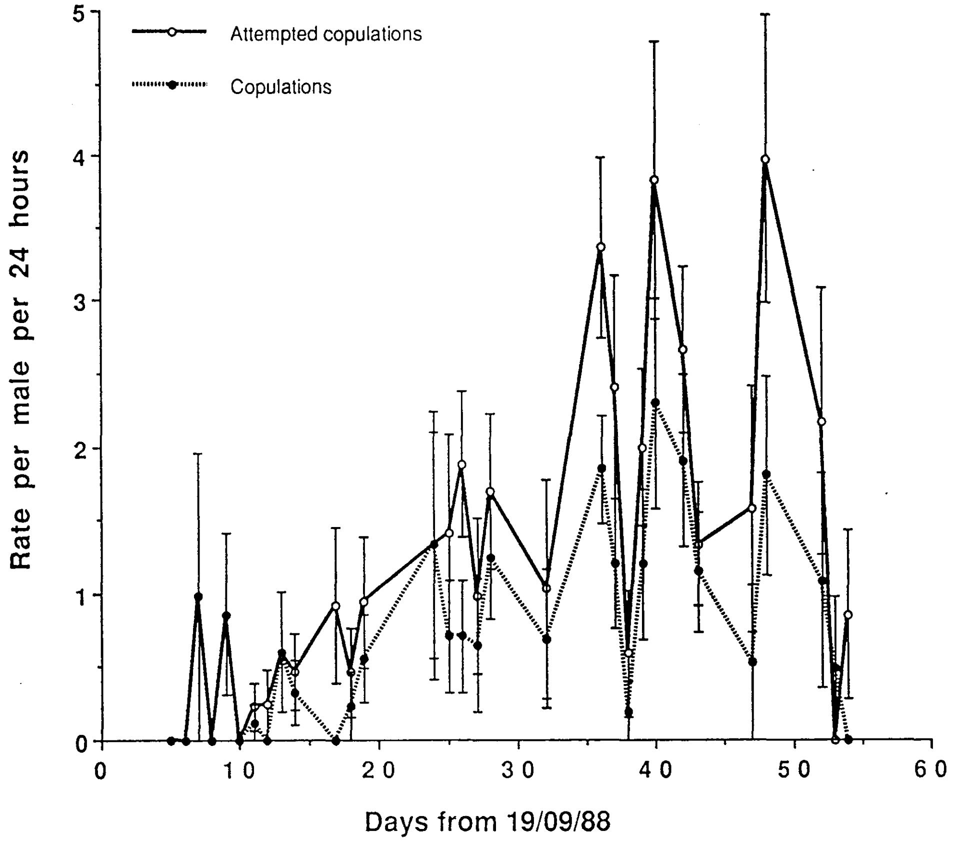
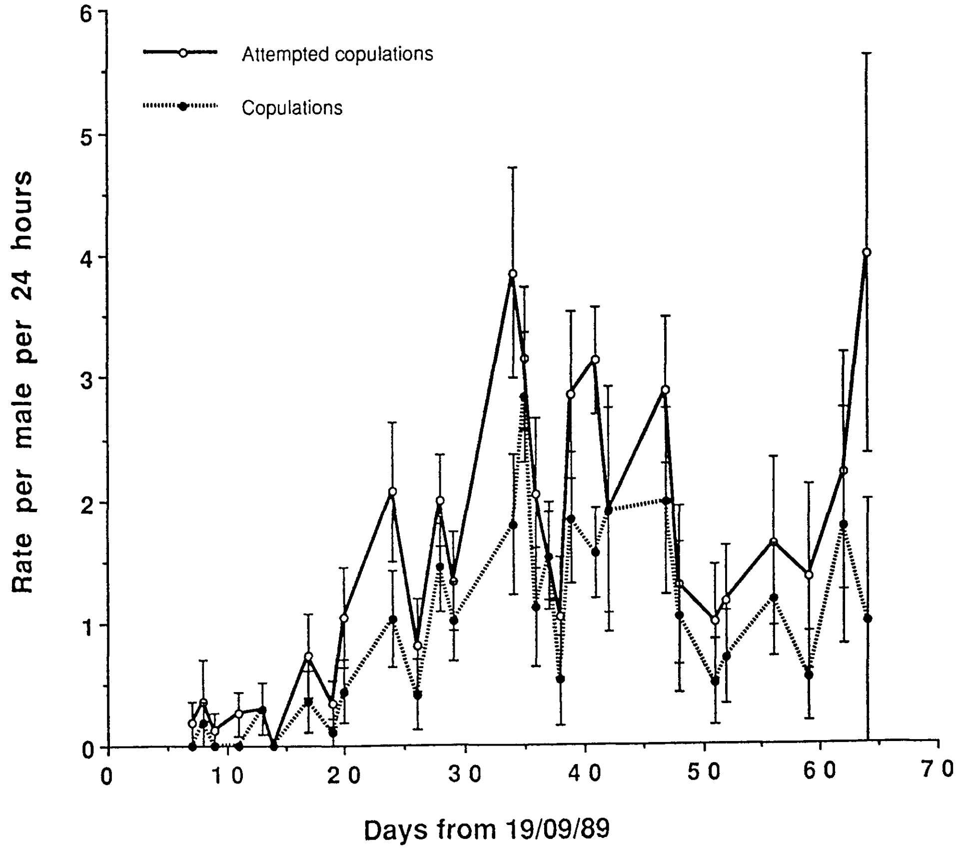


Figure 3.2 c : Seasonal variation in sexual activities - Rona 1989



3.3 Sexual behaviour

Duration of sexual activities

Table 3.3 presents the summary statistics for durations of various sexual activities in each of the three seasons. Unsuccessful copulations occur where a copulation is interrupted, either by another male or a nearby female. In several of these cases detailed observations were made concerning the nature and outcome of the interruption. These are described in detail in Chapter 6.

In 1987 A total of 125 successful copulations and 298 attempted copulations for which accurate durations were recorded were observed. Of these attempted copulations 135 (45.3 %) were successful. In 1988 a total of 83 successful copulations were observed and 213 attempted copulations of which 83 (38.97 %) were successful. In 1989 a total of 119 successful copulations were observed and 301 attempted copulations with 130 (43.19 %) of these being successful.

The data presented in Table 3.3 were transformed to approximate to normality where appropriate. The mean durations for both attempted and actual copulations were then compared between years using oneway analysis of variance with Scheffe's multiple range test. There was no significant difference in durations of either successful or unsuccessful attempted copulations between years (successful; $F_{2, 345} = 0.70$, $p < 0.50$, unsuccessful; $F_{2, 461} = 0.43$, $p < 0.65$). Similarly, there was no difference in the durations of either successful or unsuccessful copulations between years (successful; $F_{2, 324} = 0.41$, 0.67, unsuccessful; $F_{2, 19} = 1.79$, $p < 0.19$).

Whilst the durations of successful copulations ranged from 5 minutes to 65 minutes, the similarity of the median durations in all years is quite remarkable (see Table 3.3). Also, these values are very similar to the mean duration quoted by Boness and James (1979) of 20 minutes. However, since the durations for successful copulations in all years were not found to be normally distributed around the mean, the median value is a more correct measure of central tendency. Whether this is so in Boness and James' results cannot be said.

Table 3.3: Summary statistics for durations of sexual activities recorded in each of the three field seasons.

				DURATION (minutes)				
YEAR	ACTIVITY	OUTCOME	n	median	mean	standard error	min.	max.
1987	ATTEMPTED COPULATION	SUCCESSFUL	135	3.28	4.34	0.25	0.62	16.50
	ATTEMPTED COPULATION	UNSUCCESSFUL	163	3.42	4.14	0.27	0.20	21.00
	COPULATION	SUCCESSFUL	125	19.47	21.28	0.82	7.87	57.50
	COPULATION	UNSUCCESSFUL	15	7.25	7.54	1.01	2.25	17.00
1988	ATTEMPTED COPULATION	SUCCESSFUL	83	4.00	4.64	0.32	1.00	15.00
	ATTEMPTED COPULATION	UNSUCCESSFUL	130	3.00	3.79	0.27	0.20	19.00
	COPULATION	SUCCESSFUL	83	18.00	20.13	1.14	5.00	57.00
	COPULATION	UNSUCCESSFUL	4	4.00	4.25	1.11	2.00	7.00
1989	ATTEMPTED COPULATION	SUCCESSFUL	130	3.00	4.15	0.25	0.50	16.50
	ATTEMPTED COPULATION	UNSUCCESSFUL	171	3.00	3.96	0.24	0.29	15.00
	COPULATION	SUCCESSFUL	119	19.00	20.49	0.85	7.00	65.00
	COPULATION	UNSUCCESSFUL	3	5.00	5.00	0.00	5.00	5.00

As there was no significant difference in durations of successful and unsuccessful attempted copulations between years, data were combined for all three seasons. There was a significant difference between the durations of successful and unsuccessful copulations (Mann Whitney - U test; $z = -2.99$, $p < 0.003$, $n_1 = 348$, $n_2 = 464$) with successful attempts having longer durations.

The same process was applied to the durations of successful and unsuccessful copulations. The durations of successful copulations were significantly longer than unsuccessful copulations (Mann Whitney - U test: $z = -7.21$, $p < 0.001$, $n_1 = 327$, $n_2 = 22$). However, it must be noted that the sample size of unsuccessful copulations was very small compared to that of successful copulations (see Table 3.3).

2. Seasonal variation in sexual activity

Figures 3.2 a, b and c illustrate the changes in the mean rates of sexual activities (attempted copulations, both successful and unsuccessful, and successful copulations) per male per 24 hours (± one standard error) throughout the breeding seasons of 1987, 1988 and 1989 respectively. The values are expressed as average rates per male per 24 hours with standard errors. The difference between the line for attempted copulations and that for successful copulations represents the number of unsuccessful attempted copulations.

As can be seen in all three figures the standard deviation about the mean remains relatively high throughout each season

The results for 1988 (Figure 3.2 b) show noticeably more variation than those for 1987 and 1989. These later two show more similarities in seasonal fluctuations with an initial peak of both attempted copulations and successful copulations mid-season and a final peak, with considerably greater variation, at the close of the season.

DISCUSSION

Intersexual aggression amongst the grey seals of North Rona predominantly results in either a female victory, or a draw. This is quite remarkable, considering the clear size advantage males have over females. However, it is noticeable that these inter-sexual aggressive encounters are invariably short, with most aggression directed from the female to the male (see Boness *et al.* 1982). The males rarely retaliate, and soon retreat. It is difficult to say whether this constitutes social dominance of females over males, rather that there is little, if any, reason for a male with a secure position on the breeding colony to antagonise unreceptive females around him. The perceived goals of male and female may differ markedly, whilst the female will be intent on defending her pup, the male will perhaps only be assessing the female's receptivity, and an aggressive response on the part of the female is a clear "no". Indeed, if males insisted on winning these "petty quarrels", apart from potential injury, there is a risk of females moving away and possibly abandoning their pups. Thus, the male would lose mating opportunities, and, due to site fidelity, possibly cause the death of pups he sired in the previous season. More peripheral males without secured positions on the colony seldom get the opportunity to approach females on Rona, and in most cases are rebuffed by the female. Occasionally, males will attempt a forced copulation with a female, receptive or not, the outcome appears to depend upon the size advantage of the male, allowing him to pin the female down, and the topography. In uneven terrain, a male is often unable to restrain a struggling female. These circumstances are usually observed when a female is departing from the colony, enduring the attentions of many peripheral males.

There was no clear evidence of female incitation of inter-male aggression as found in Northern elephant seals (Cox and Le Boeuf 1977); in fact approaches to females by males rarely attracted the attention of surrounding males. Indeed, on many occasions, a male would approach a female with a second, more dominant male lying close by (within 10 m). Apart from a cursory glance at the approaching male, the dominant individual largely ignored the intruder. Invariably, the first male's approach to the female was rebuffed by the female. Similarly, very few sexual interactions were interupted by a second male, irrespective of the behaviour of the female (see Chapter 6), thus, it appears that either female incitation of inter-male competition does not occur, or that few males have the opportunity to compete over individual females in the centre of the breeding colony. These aspects of mating behaviour are discussed further in Chapter 6.

In general, the level of inter-male aggression at North Rona is low, with mean daily rates per male of between 3.0 and 5.5 aggressive interactions per male per 24 hours. This gives an hourly rate of between 0.13 and 0.23 interaction per male. Similarly, Anderson, Burton and Summers (1975) stated that the levels of male aggression on North Rona were low when compared with the intense territorial aggresion and displays of some otariids (Bartholomew and Hoel, 1953). Also, a vast majority of the inter-male aggressive interactions observed on Rona are low level threats, with only 4.6 % to 6.7% of interactions involving physical contact. These values are comparable with McCann's results for the Southern elephant seal (1981) where the figure was 4 percent.

In these relatively rare fights, the attacking of the rear end is interesting in comparison with behaviours seen in some other phocid species. For example, in Weddell seals (*Leptonychotes weddelli*), where bulls fight in the water, males attempt to inflict damage on the opponents penile area (pers. comm. W.N.Bonner). This is also seen in species of other groups, for example, the European otter, *Lutra lutra* (pers. comm. J.Watts). This is obviously the "best" way to inflict maximum damage on a breeding competitor, and these rear end attacks in grey seal bulls may, in part, be a legacy of a more aquatic, ice-breeding past.

Protracted fights occur when both combatants are very closely matched dominant males, with no clear difference in head elevation i.e. neither male adopts a subordinate role at the onset of the encounter. These fights usually continue until both animals are exhausted, often with no clear victor. Clutton Brock *et al.* (1979 and 1982) show that fights between rutting stags are longer when both combatants are harem holders, than if one is a solitary stag.

It is interesting that the maximum duration of a single fight was so similar in all three seasons (i.e. 15 to 15.5 minutes). In all these cases, no clear victor was established, both males becoming exhausted, resting and finally both retreating to their original positions.

In examining the outcome of inter-male encounters with respect to which male initiated the fracas, we see that overall, the initiator prevails in a vast majority of the encounters. This is not entirely surprising, as dominant males initiate more inter-male aggressive encounters. However, if we compare the results for the separated categories of low intensity and high intensity encounters, then the pattern is somewhat different. In the case of low intensity aggression a far greater proportion of encounters are unresolved, whereas in high intensity fights the initiator is victorious in the vast majority of cases. In low intensity interactions, neither male, but in particular the initiator has invested much time or effort, thus as long as the initiator does not lose, the threat has played its part as a warning. Thus, either the opponent retreats or the status quo is maintained. Therefore, outright victory is not particularly vital (as suggested by Anderson and Fedak 1985). However, in the case of persistent opponents, it may be necessary to escalate the interaction. Once a fight is initiated, the energetic investment and potential damage will be considerable. Thus, males will not initiate a high intensity interaction unless they are confident of victory, or the potential threat of the opponent is very great. Lott (1979), found that amongst mature male American bison (*Bison bison*) 88 % of all inter-male aggressive interactions were won by the initiator. However, Lott also found that when the interaction escalated from threats to fighting, initiators were no more likely to win than recipients.

Although still small, a greater percentage of fights are lost by the initiator than low intensity interactions. This is because escalated interactions occur particularly where two males are fairly equally matched, and neither will back down after mere threats. Thus, the potential for the initiator losing the interaction is greater than in low intensity interactions. Thus, the risk of fighting is not just potential physical injury, but a greater chance of losing too.

The striking similarity in the median durations of successful copulations, despite a wide range is remarkable. Also the similar figures given by Boness and James (1979) for the Sable Island breeding group, part of a separate population with a marked difference in mean sizes of both males and females and some differences in behaviour and social organisation at the colony indicates the consistency of this most important of behaviours and confirms the validity of observations made on North Rona.

The Figures depicting seasonal variation in sexual activity are difficult to interpret due to the high variance around the mean throughout the season. This high variance may be explained by a combination of the following factors;

(1) the observation periods necessarily varied, generally becoming shorter as the season progressed due to diminishing daylight hours and also due to the weather, logistic demands and seal catching regimes. To minimise this effect, days on which less than 4 hours observations were conducted were excluded from the analyses. Obviously the shorter the observation period the greater the error upon extrapolating scores to 24 hours.

(2) at the start and end of the season fewer males are present so reducing the sample size and thereby introducing more potential sampling error effects,

(3) with the obvious variation and high daily fluctuation in the mean values, the periods where no observations where made due to seal catching commitments (sometimes extending up to 4 successive days) must obviously be viewed with extreme caution,

(4) there is high variation in individual daily rates of sexual activity naturally in a polygynous system such as this where some males are very successful, whilst others consistently get no attempts at copulation throughout the entire season. Thus, individual differences in competitive ability contribute to the observed variation.

Despite this high variation a few basic conclusions can be drawn. At the start of the season there is relatively little sexual activity of any kind. This is not surprising as animals have only just started to arrive at the colony and the first pups are only just being born. During the first two weeks (approximately 22nd of September to the 6th of October) sexual activity occurs sporadically and at a low level. Also, the rates of both attempted copulations and successful copulations maintain a close parity, that is, there are few unsuccessful attempted copulations. This represents sexual acts directed to the few, earliest arriving females (arriving prior to the start of observations) who are either in or entering oestrus at this point. The males involved are the few males that secure positions on the breeding colony very early in the season; these may be more experienced males (and, indeed, females), hence the low proportion of unsuccessful attempts (see Chapter 4 for further discussion of early arriving males). In the 3rd week of the season (6th to 13th of October) we see the first significant rise in sexual activity. As the start of the season (and observations) is deemed to be when females start to come ashore in significant numbers and the first pups are born, this period (the 3rd week) reflects the time when the first substantial numbers of females will be coming into oestrus (see also Anderson, Burton and Summers, 1975). The approximate time between parturition and the onset of oestrus is between 16 and 21 days. This would then appear to be the trigger for greater sexual activity by the greater numbers of males ashore at this time. The levels of both attempted copulations and successful copulations remain high from this point to the close of the season, despite considerable daily fluctuations. It is during this period (approximately from the 14th of October to the 5th of November) that a vast majority of copulations occur. In general, throughout the season, the pattern of successful copulations follows that of the attempted copulations though with no apparent pattern for the precise rates of unsuccessful copulations. All three years show, to some extent, a mid season peak in copulations and attempted copulations and also, a second peak towards the end of the season. This final peak occurs at a time of rapidly diminishing female numbers and when many males, tenured for much of the season, are departing. This allows many transient males to enter the study site and attempt to copulate wherever possible. This may account for both the particularly high variation at this late stage and the relatively high numbers of unsuccessful copulations. The overall pattern of sexual activity through the season is similar to that presented by Anderson, Burton and Summers (1975) although they present the data as a 24 hour rate calculated on a weekly basis and do not compute rates of sexual activity for individual males and so provide no measures of variation about the mean values.

If then, most of the successful copulations occur in the 3 weeks from the 14th of October to the 5th of November, why do some males arrive at the colony some 3 weeks prior to this period? If energy stores are essential to success and yet limited, are these males particularly well endowed with blubber reserves? Are these males more experienced males, that are able to undergo prolonged fasting and yet maintain their early established position on the colony? These and other question will be addressed in Chapter 7.

The apparently higher variances in seasonal rates in 1988 than in 1987 or 1989 may be due to the lower numbers of females present. Thus, in 1988 the females were less dispersed, a majority being able to congregate around the favoured sites (see Chapter 4) and thus allowing fewer males to monopolise these females. Thus, a smaller proportion of the males present gain copulations. Individual variation in mating success, and hence measures of the degree of polygyny at North Rona will be examined in detail in Chapter 6.

Examining the seasonal variation in open mouth threats and fights in relation to seasonal fluctuations in sexual activity highlights similar trends in all three seasons. Despite the considerable daily fluctuation and high variation about the means, it is possible to discern a mid season rise in aggressive activity. In each year this corresponds with the more dramatic increase in sexual activity as the first females come into oestrus. Although aggression levels remain reasonably high, a final peak in aggression occurs towards the close of the season, again corresponding with increases in sexual activity. Thus, it appears that both aggressive and sexual activity are intensified during this latter half of the season. The availability of oestrus females and the relatively low sex ratio during this period (see Chapter 4) mean relatively more males per receptive female. Hence the increase in both aggressive and sexual activity. Clutton-Brock *et al.* (1979 and 1982) similarly discovered that fighting amongst stags varied with the potential benefits. The frequency and the duration of fights and the number of injuries sustained all peaked during the period of peak conceptions. However, on Rona, the particularly high levels of inter-male aggression evident at the start of the season cannot be related to the availability of oestrus females, nor the sex ratio, which is at its most skewed in the early part of the season. This is, perhaps, associated with the establishment and/or re-affirmation of male positions and status on the breeding grounds.

CHAPTER 4 - COLONISATION, COLONY ATTENDANCE PATTERNS AND SEAL DISTRIBUTION

INTRODUCTION

In any study of mating systems it is vital to assess both the spatial and temporal distributions of males and females throughout the breeding period. Several studies have shown that the distribution of individuals can be a major influence on mating system organisation (Bartholomew 1970, Stirling 1975, Le Boeuf 1978). In particular, such aspects as the degree of monopolisation of females by individual males and, therefore, variation in individual male mating success are affected by female distribution (Emlen and Oring 1977). This has been shown to occur in Pinnipeds, where in many cases the topography of the breeding colony appears to be an important determinant of the distribution of females (Hewer 1960, Boyd *et al.* 1962, Anderson, Burton and Summers 1975). The distribution of oestrus females, both spatially in terms of the degree of clumping, distribution and size of groups of females and temporally (the degree of synchronisation of oestrus) all affect the "polygyny potential" within a breeding group (Emlen and Oring 1977) and can therefore be a major determinant of mating systems and individual male mating success (Le Boeuf 1978, 1991). Topography has both a direct influence on male distributions and behaviour (Anderson and Harwood 1985, pers. obs.) and an indirect effect exerted via the female distribution.

Previous studies of male grey seal behaviour during the breeding season have classified individual males into broad categories, for example territorial and non-territorial or resident and non-resident (Fraser-Darling 1939, Hewer 1957 and 1960, Hewer and Backhouse 1968, Cameron 1967 and 1969). More recently Boness and James (1979), studying a western Atlantic colony (Sable Island, Nova Scotia), classified male status by simply referring to males as tenured or transient. Tenure was loosely defined as "the right to remain within the shifting population of females" and was attained by any male maintaining his position on the colony for at least two consecutive days. Males unable to gain tenure were known as "transients". This has been the generally accepted view of mating strategies amongst grey seals, with the breeding bulls being broadly divided into these two exclusive categories (Anderson *et al.* 1975, Anderson and Fedak 1985). The creation of a dichotomy from what is likely to be a continuum will only provide a broad picture of the relative attributes of males in these classifications.

The first quantitative studies of male grey seal breeding behaviour at North Rona (Anderson, Burton and Summers 1975) found that an individual's length of stay on the breeding colony was highly correlated with his observed mating success. Although these authors still used the term "tenured" and "transient" they were able to assess individual lengths of stay of 30 identified males and their copulatory success. This relationship between time ashore and mating success was confirmed in subsequent studies (Anderson and Fedak 1985). Obviously males that are able to remain on the breeding colony will potentially have access to more oestrus females. However, length of stay may only be the proximate determinant of individual mating success. It is therefore necessary to examine which factors influence a male's ability to remain ashore.

In this study the ability to identify individuals together with detailed observation of behaviour and position made throughout each breeding season allowed complete records of attendance of individual males to be made. Therefore, in this study, there is no need for arbitrary classifications of males into groups and attendance can be treated as a continuous variable.

Colony attendance parameters are clearly a major influence on both the mating system and individual male mating success. This chapter examines individual colony attendance parameters and provides the details of patterns of colonisation of the study area, distribution and numbers of males and females during the three breeding seasons of this study. The relationships between colony attendance parameters and individual male mating success and potential determinants of length of stay are examined in Chapter 7.

METHODS

Details of the methodology employed are provided in Chapter 2. Data on colony attendance patterns were obtained from daily censuses of the study area (see Chapter 2) providing maps showing the distribution of all males females and pups in the study area together with the identities of known individuals. Also, brand sightings (see Chapter 2) made throughout the island, at least once every two days, provided information on gross movements of branded males. The behavioural observations allowed individual lengths of stay on the study site and arrival and departure dates of males to be determined.

It must be noted that on the occasions where observations could not be made, due to weather or seal catching commitments, males present in the study area prior to and after the gap in observations were assumed to have been present throughout. Those males present prior to the cessation of observations, but absent upon resumption of observations, were assumed to have departed immediately after the suspension of observations. Thus, for these males, length of stay is a minimum estimate.

The daily maps of the study area were made from the hide. Therefore there is a problem of perspective, which is compounded by the rough terrain and the fact that the ground slopes steeply away from the hide northwards through the study area. Thus, it was difficult to accurately assess distances between individuals from these maps, though in the field a rough estimate could be gained by using the number of "seal lengths" (approximately 2 m) between individuals.

From the number of males and females present in the study area each day, a daily sex ratio was calculated. From these daily sex ratios mean values were computed for each season. Also, a male turnover rate was calculated form the number and identity of males present each day. The turnover rate for day X was calculated as the percentage of males present on day X that were also present on day X-1. Thus, a low proportion indicates a relatively high turnover of males, whilst a high percentage indicates little change in the identities of males present from one day to the next.

Both arrival date and departure date were measured as the number of days from the 19th of September. Hence a male arriving on the 19th of September had an arrival date of 1, and male arriving on the 20th had an arrival date of 2, etc. The 19th of September was chosen as this was the earliest date on which observations commenced in any of the three seasons. This also allows the comparison of arrival and departure dates between years, although it must be remembered that the observation periods varied between years, in particular, 1987 when observations commenced relatively late. In the following seasons, I endeavoured to arrive at the colony as early in the season as possible and remain for as long as possible.

Length of stay was measured in number of days.

As in Chapter 3, summary statistics for colony attendance parameters are presented in two formats. The first includes data from all identified males, whilst the second excludes males involved in less than 10 inter-male aggressive interactions. This has been done for the same reasons as presented in Chapter 3.

Again, for all parametric statistical analyses data were examined for normality. Data sets that produced non-normal distributions were transformed to approximate to normality using the same criteria as in Chapter 3.

RESULTS

4.1. Seal Numbers

Figures 4.1 a, b and c summarise the records of numbers of bulls, cows and pups present in the study area throughout the breeding seasons of 1987, 1988 and 1989 respectively. The general pattern is similar in all three seasons of this study and also similar to data presented by Anderson, Burton and Summers (1975) for the 1972 breeding season on North Rona. Note that the duration of the study period in 1987 was slightly shorter than the other two years with the first and last weeks of the breeding season being missed (for further discussion of changes in seal numbers during the breeding season at North Rona, see Anderson *et al.* 1975 and Summers *et al.* 1975).

Females:

Pregnant females were present in the study area prior to the onset of observations in

Figure 4.1 a : Seal Numbers - Rona 1987

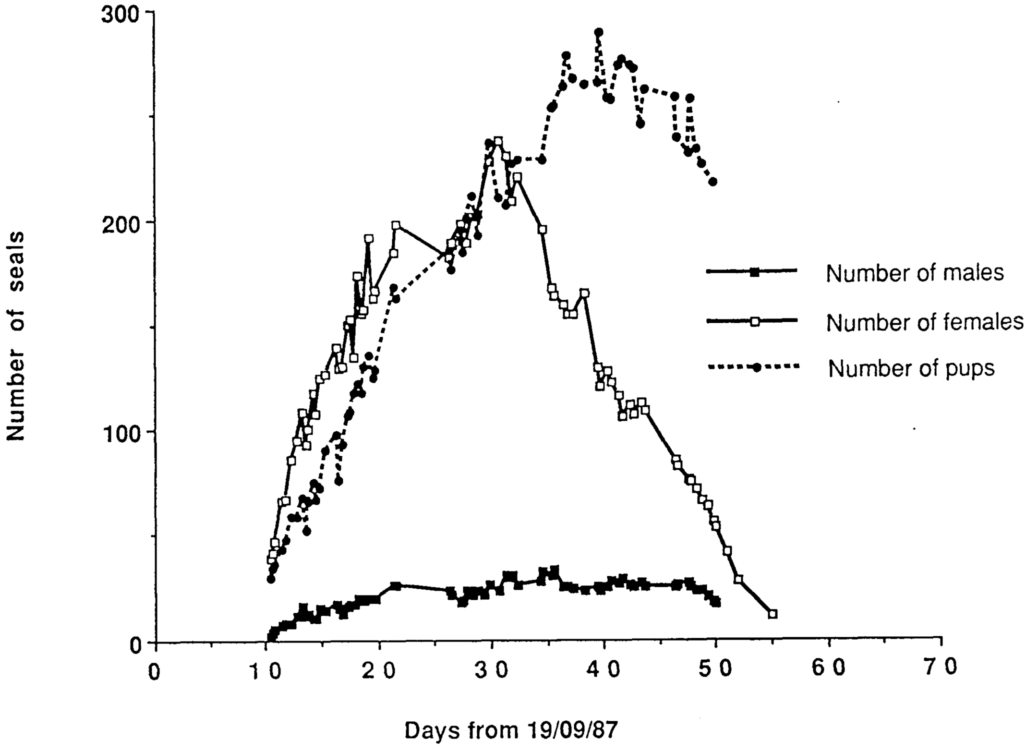


Figure 4.1 b : Seal numbers - Rona 1988

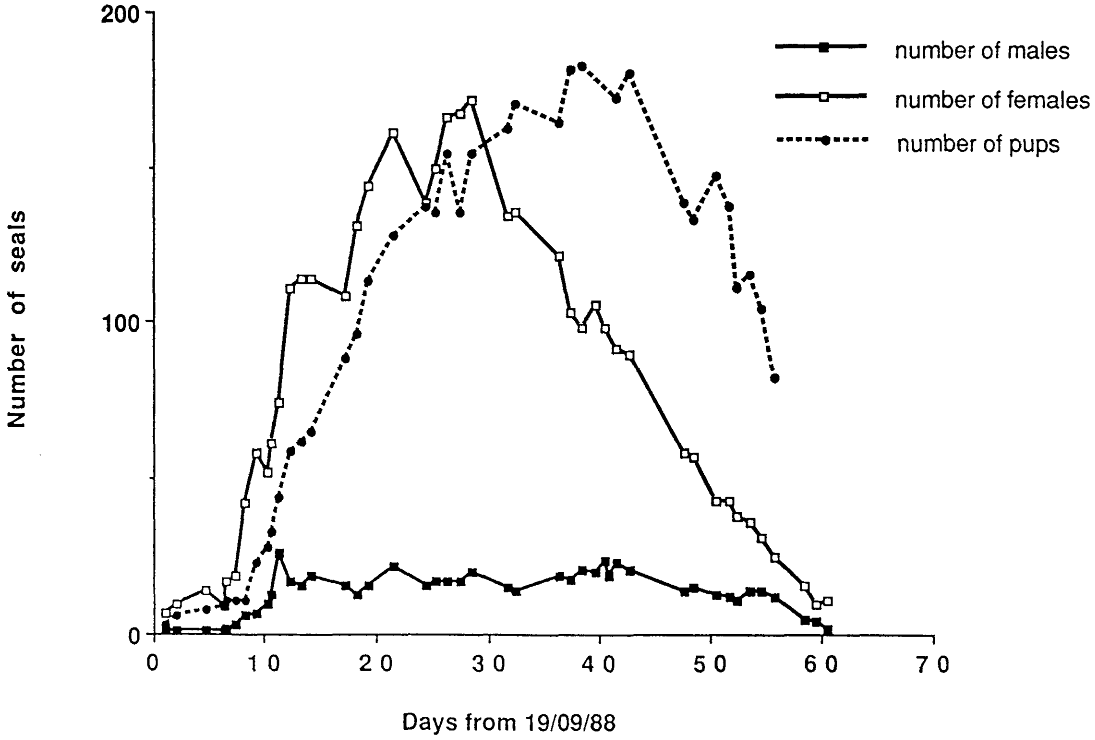


Figure 4.1 c : Seal numbers - Rona 1989

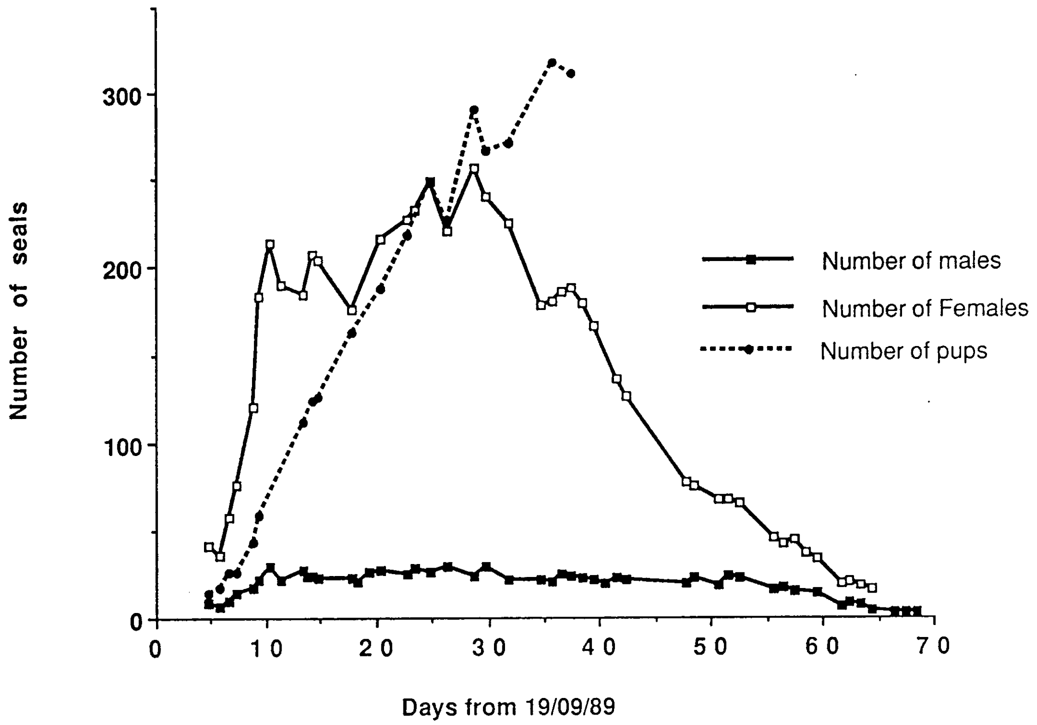


Figure 4.2 a : Variation in sex ratio - Rona 1987

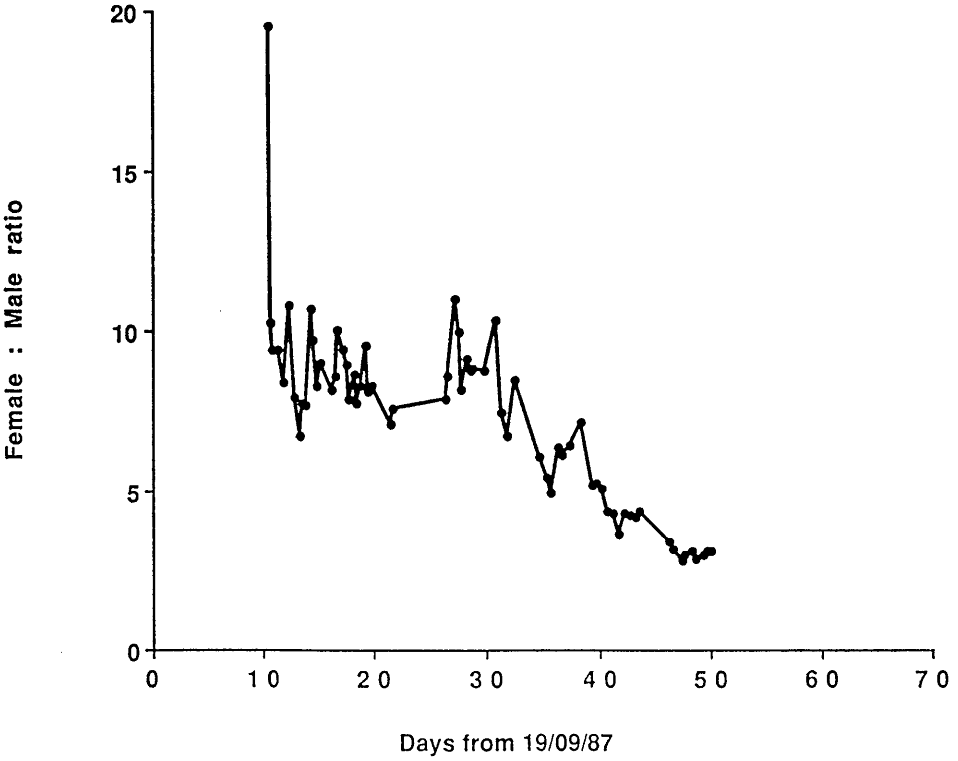


Figure 4.2 b : Variation in sex ratio - Rona 1988

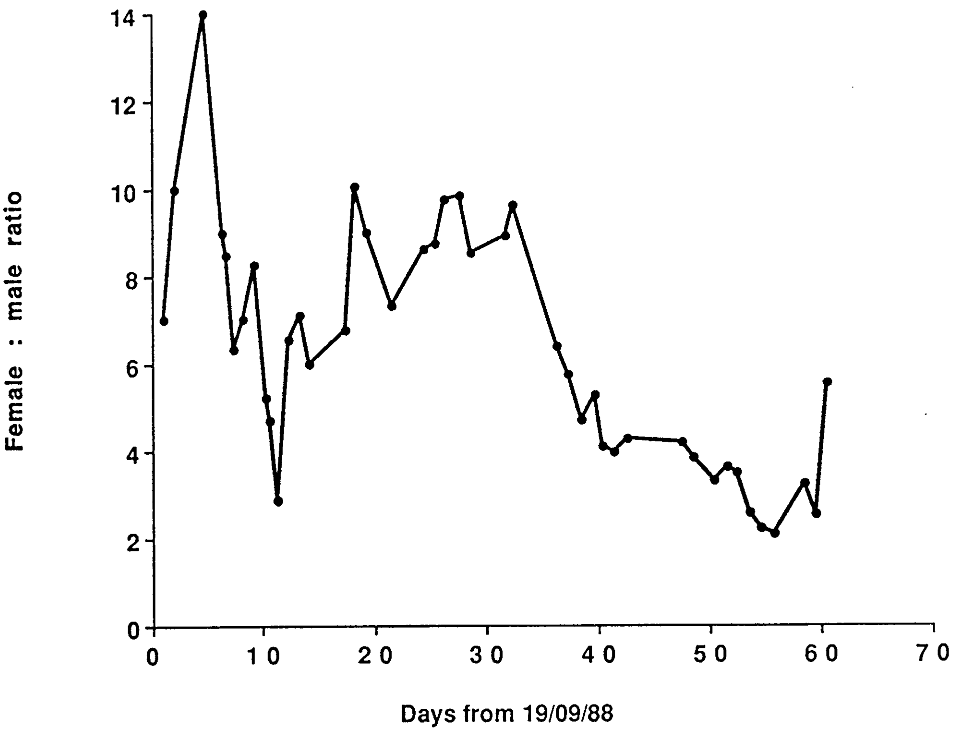
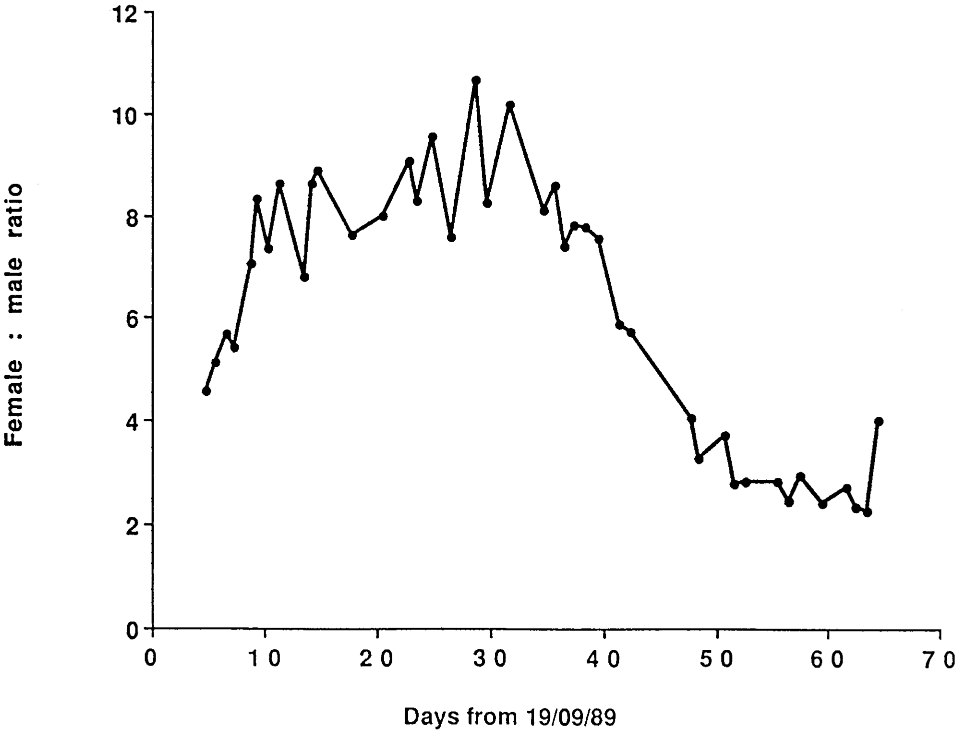


Figure 4.2 c : Variation in sex ratio - Rona 1989



all of the three years, but only in low numbers. In 1988, the year in which the earliest observations were made, a total of 7 females, 3 pups and one male (identity 012, brand X6) were present on the 19th of September. In general females started to gather at the colony in reasonable numbers towards the end of September. As increasing numbers of females came ashore to give birth, the number of cows in the study area rose rapidly. In 1989 (Figure 4.1c) the initial rise in female numbers was noticeably more rapid than in the previous two seasons. This sharp increase in numbers was due to the arrival of many pregnant females over a period of 3 to 4 days in the area between the Fank gulley and the Wall gulley (see Figure 2.1 c, Chapter 2). These females gathered in a large, but dense group (see Figure 4.4 c II, section 4.4 below). Between days 10 and 20 this group dispersed, some females spreading to other parts of the study area to give birth, others remained and pupped in this area, whilst many departed to other parts of the island. All three seasons show this initial rise followed by a slight decline in female numbers around day 20 (8th of October). The numbers of females then continues to rise. A similar temporary drop in female numbers early in the season was found by Anderson, Burton and Summers (1975). The period of lactation was taken as being between 16 and 21 days (Matthews 1950, Coulson 1959, Hewer 1957, Bonner 1972, Anderson, Burton and Summers 1975, see also Chapter 1); therefore, it is not until 2 to 3 weeks into the season that the rate of increase in female numbers begins to decline as the earliest arriving cows are mated and leave the colony. Peak numbers were reached at the mid point of the season around day 30 (approximately from the 16th to the 19th of October) in all three years. The peak numbers of females were 237, 171 and 256 in 1987, 1988 and 1989 respectively. There were fewer females present throughout the season of 1988 than in the other two years. After the peak numbers were attained, the number of departing females exceeded the number of new arrivals and a steep decline ensued. Although the occasional arrival still occurred even into November, the vast majority of females were departing by this time, and by mid November the number of cows had declined to less than 20.

Pups:

The number of pups was obviously less than the number of cows early in the season. The increase in numbers followed closely that of the females as effectively each female produced one pup. However, as the pups remained ashore for several weeks after weaning their numbers soon rose above those of females. The rate of increase was reasonably constant during the first half of the season as the influx of pregnant females continued at a high rate. However, as the number of cows giving birth declined, the increase in pup numbers eventually ceased, reaching a peak about 10 to 14 days after the maximum number of females. A contributory factor to the cessation of increase in pup numbers was the departure of pups born very early in the season. Pups are very mobile once weaned, being forced by aggression from adults to the outskirts of the colony and areas not favoured by breeding adults. This accounts for the fluctuations in pup numbers and the eventual drop in numbers together with departure of the older pups.

Males:

Males were seen on the study site from the start of the observations, but only at low numbers (see Figures 4.1 a, b and c). Males arrived at the study site throughout the very early stages of the season, but generally only remained ashore when the first pups were born (Hewer 1957, 1960, Anderson, Burton and Summers 1975, Boness and James 1979, McCann 1981, pers. obs.). Within a few days the number of males reaches a level close to the maximum achieved all season. The numbers fluctuated markedly, but the overall trend in all three years was one of an initial rise in numbers followed by reasonably consistent numbers until the end of the season. The subsequent rate of decline in numbers was also low until the close of the season when numbers dropped off more rapidly. The maximum numbers of males present on any single day were 33, 24, and 29 in 1987, 1988 and 1989 respectively. As with the females, the numbers of males present throughout 1988 were less than in 1987 or 1989.

4.2. Sex ratios

As can be seen from Figures 4.1a, b and c, relatively few males gained access to the breeding colony compared to the number of females present at any one time. Figures 4.2a, b and c show the ratio of females to males that were present in the study area during the seasons 1987, 1988 and 1989 respectively. It must be noted that these figures represent the sex ratio of only those animals on land in the study area. Throughout most of each season additional males could be seen offshore, thus the sex ratio shown here can be taken effectively as an apparent operational sex ratio. However, whether all those males ashore are actively involved in mating or not will be discussed later (see Chapter 6 and Chapter 7).

The sex ratio fluctuated considerably, particularly early in the season, when few individuals were present, thus, the arrival or departure of a single male produced large changes in the sex ratio. However, some general trends can be discerned. Again the pattern is similar to that presented by Anderson, Burton and Summers (1975).

All years showed initially high numbers of females relative to males. A secondary peak was seen in mid-season (approximately the 18th of October) in 1987 and 1988, though for 1989 this forms the highest observed sex ratio. Most importantly, the lowest sex ratios occurred in the latter half of the season in all three years. Finally, in the extended study periods of 1988 and 1989 a rise in sex ratio was observed at the end of the season. Whether this occurred in 1987 or not cannot be said as observations ceased before this point.

The mean sex ratio for the entire season in each year was approximately 1 male to 6 or 7 females (1 : 7.2 in 1987, 1 : 6.3 in 1988 and 1 : 6.2 in 1989). However, the mean sex ratios of around 1 male to 7 females may be somewhat misleading as receptive female are not present until approximately 2 weeks into the season. It is noticeable that the sex ratio declines markedly in the latter half of the season when a majority of sexual activity occurs (see Chapter 3). Thus, a more accurate estimate of the true operational sex ratio might be achieved by computing a mean value from the point at which receptive females are available. Thus, mean sex ratios were re-calculated from the date on which the first

Figure 4.3 a : Male turnover rate - Rona 1987

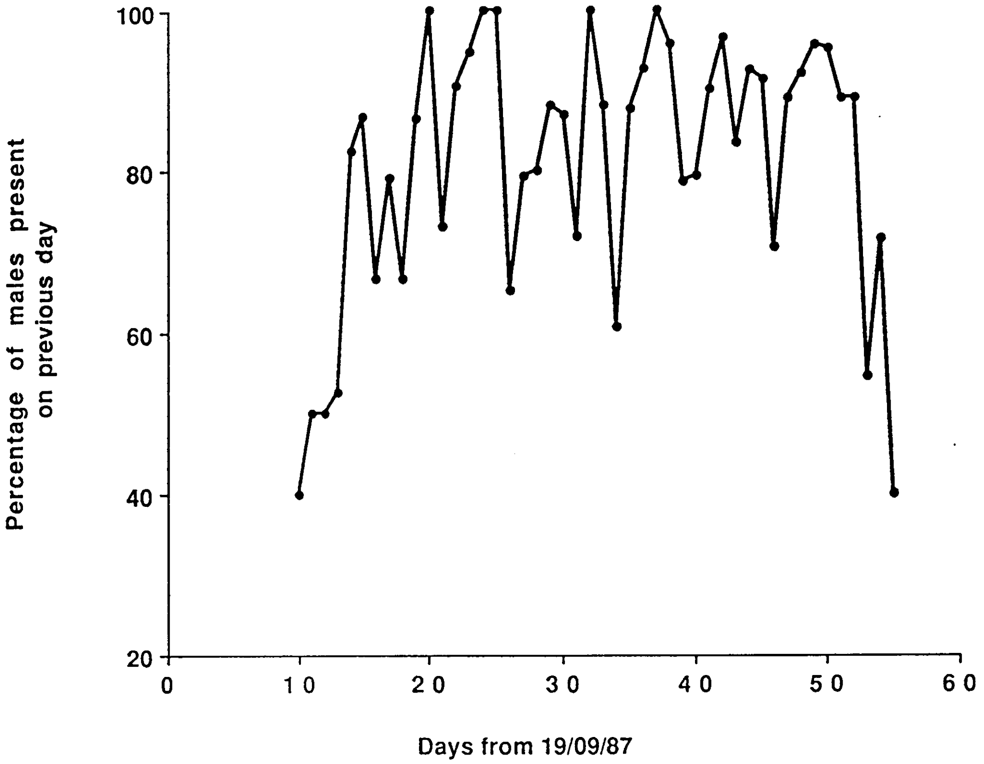


Figure 4.3 b : Male turnover rate - Rona 1988

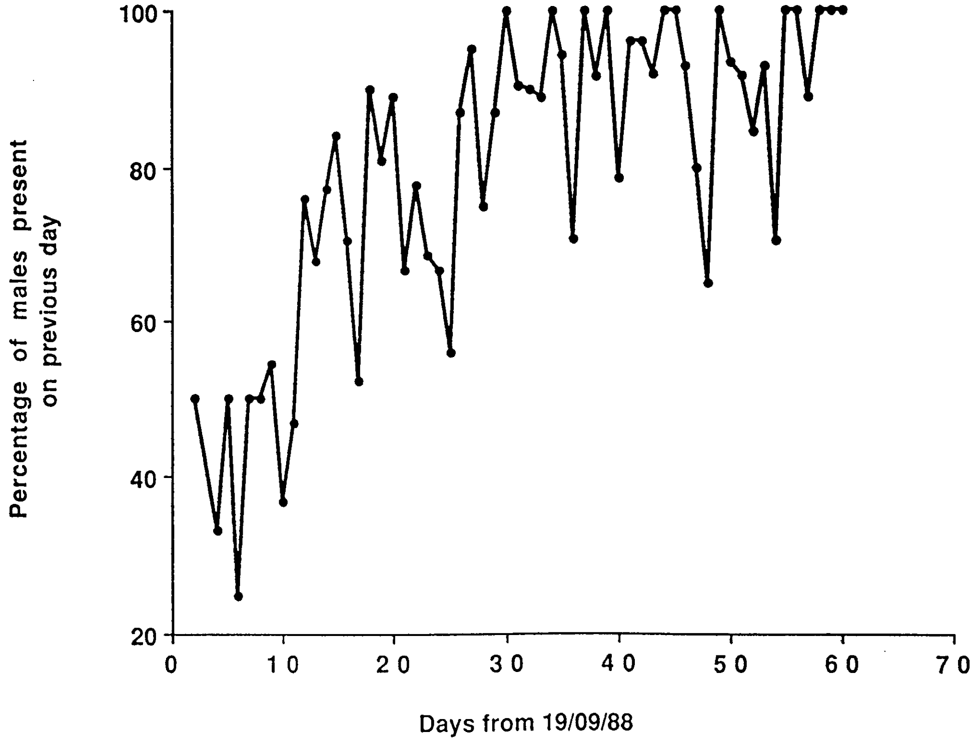
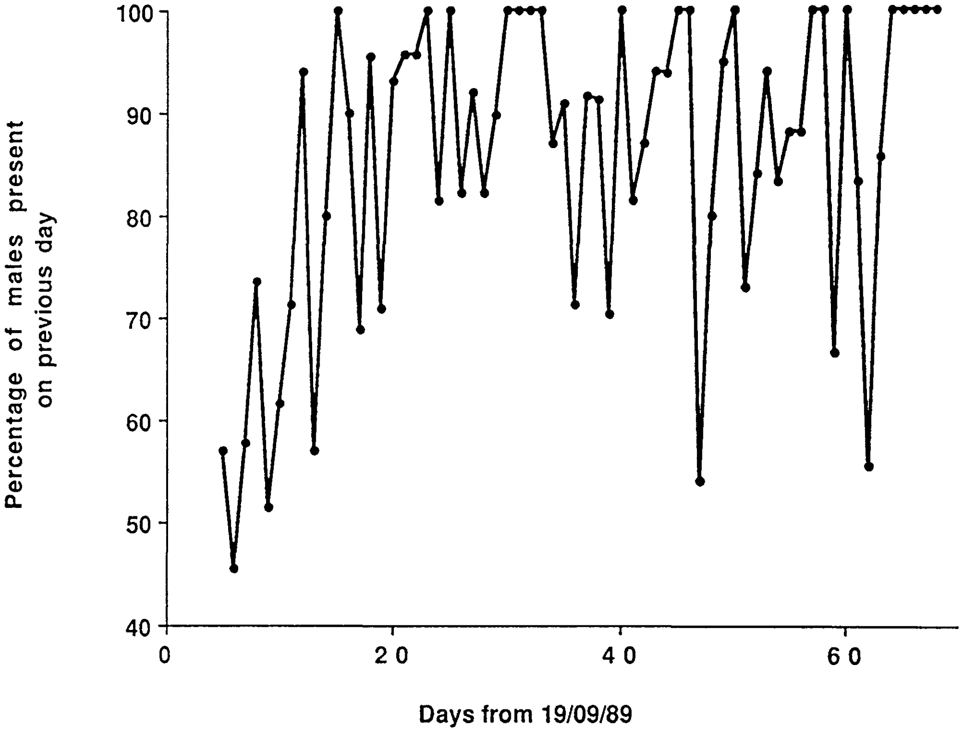


Figure 4.3 c : Male turnover rate - Rona 1989



successful copulation was observed in each of the three seasons. This produced mean sex ratios of 1 male : 6.2 females in 1987, 1 : 5.6 in 1988 and 1 : 5.8 in 1989.

4.3. Male turnover rates

Figures 4.3 a, b and c illustrate the relative turnover rates of males during the seasons of 1987, 1988 and 1989 respectively. This turnover rate is expressed as the proportion of males present in the study area on any given day that were also present on the previous day (see methods).

Again there was considerable fluctuation from day to day, but a clear general trend exists and was consistent in all three years.

The percentage of males present on the previous day was low at the start of the season indicating a high rate of male turnover. The percentage then rose during the 2nd and 3rd weeks of the season and remained fairly consistently high throughout the remainder of the season. This shows a low turnover of males during this period. Towards the end of the season, the fluctuations in turnover rate tend to increase, indicating a greater exchange of males. In 1987, the turnover rate declines at the end of the observations (day 50 to 55). Whether this would have remained at a low level or not cannot be said.

4.4. Distribution of seals

The series of maps shown in Figure 4.4 illustrate key points in the colonisation of the colony throughout each breeding season. These maps depict the relative distributions of breeding females and the positions of males. Branded females are shown and all males have an individual 3 digit identification code. Any male brands are shown in parentheses.

These maps also show the patterns of colonisation in each year and give an indication of the positions of individual males. Figure 2.1 c in Chapter 2 gives the locations of named features in the study area that are used below and a scale for these maps. It must be noted that these maps were made from the hide, with the associated

Figure 4.4 a: Maps showing changes seal distribution in the study area during the 1987 season on Rona.

Notes: see Figure 2.1 c for details of study area.
Males are denoted by blue dots, each with the relevant male identity code (and brand where appropriate).
Females are denoted by red dots.

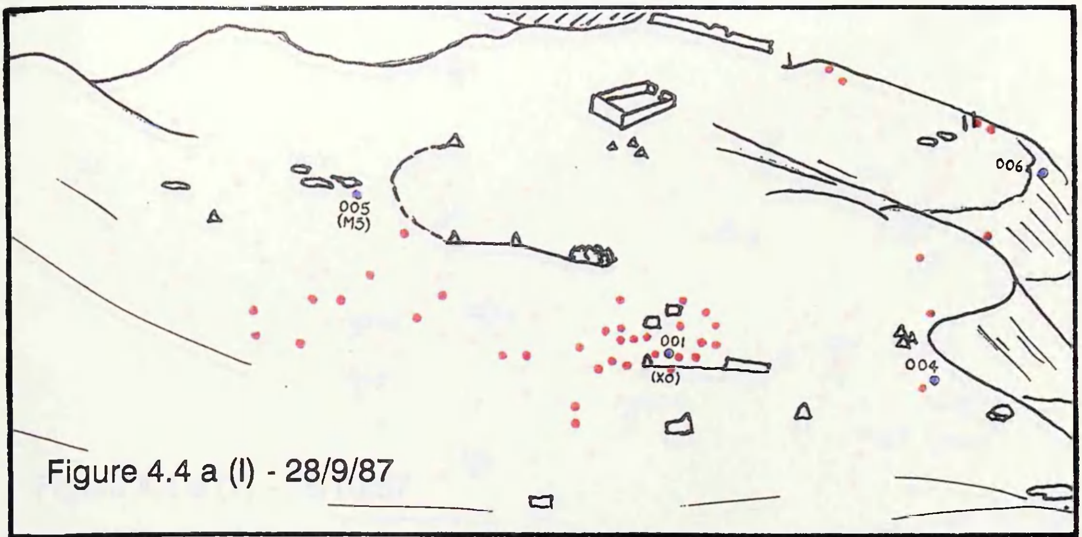


Figure 4.4 a (I) - 28/9/87

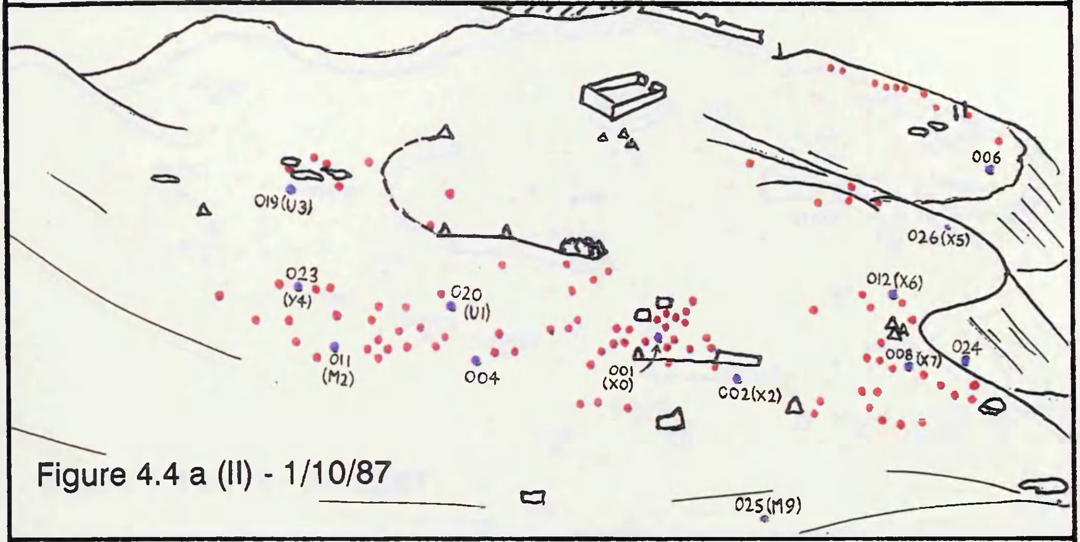


Figure 4.4 a (II) - 1/10/87

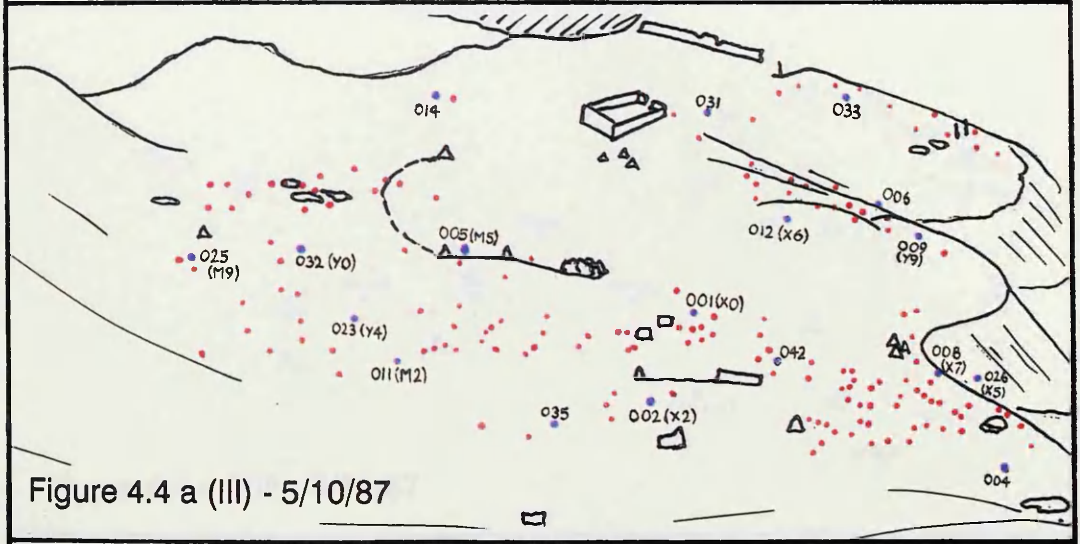


Figure 4.4 a (III) - 5/10/87

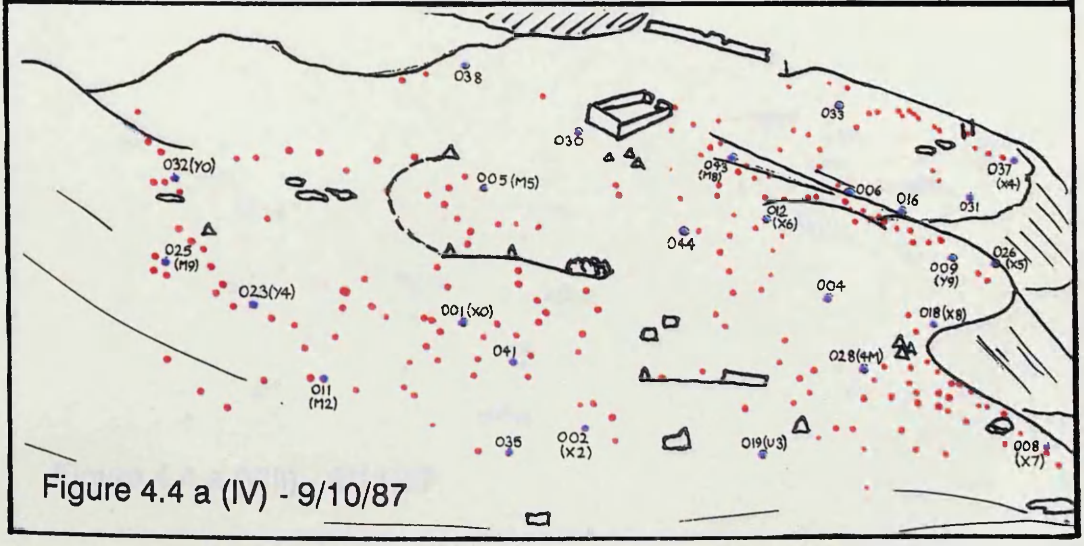


Figure 4.4 a (IV) - 9/10/87

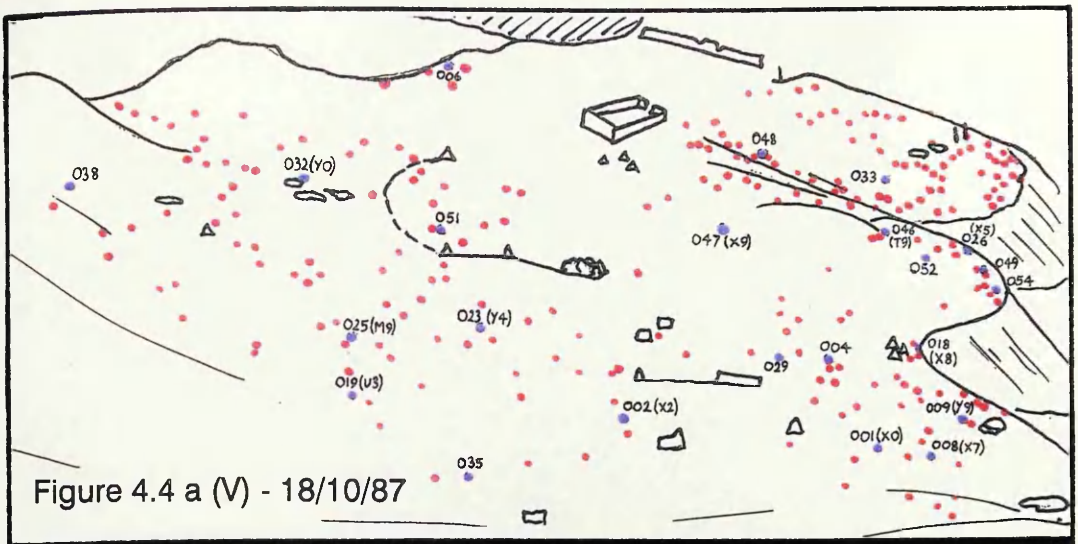


Figure 4.4 a (V) - 18/10/87

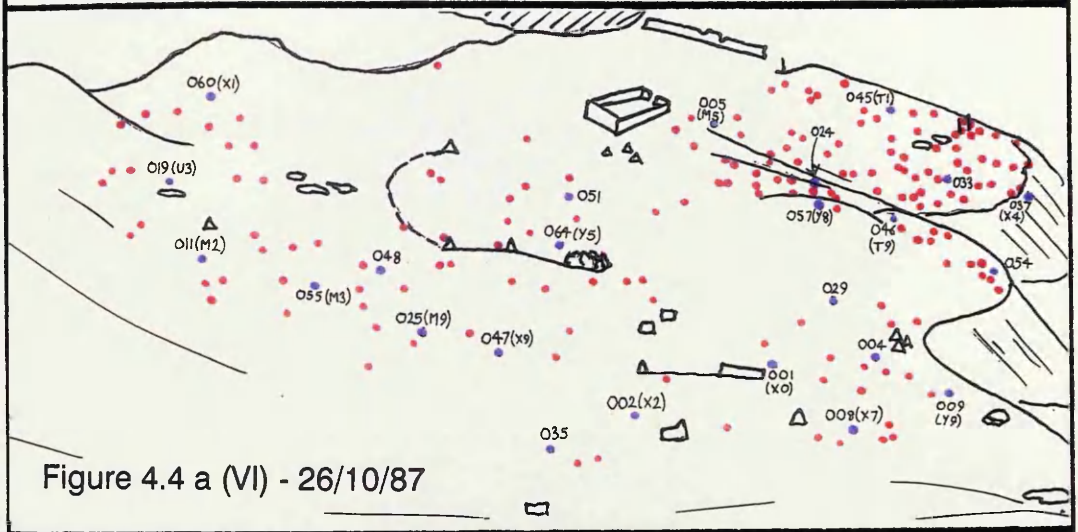


Figure 4.4 a (VI) - 26/10/87

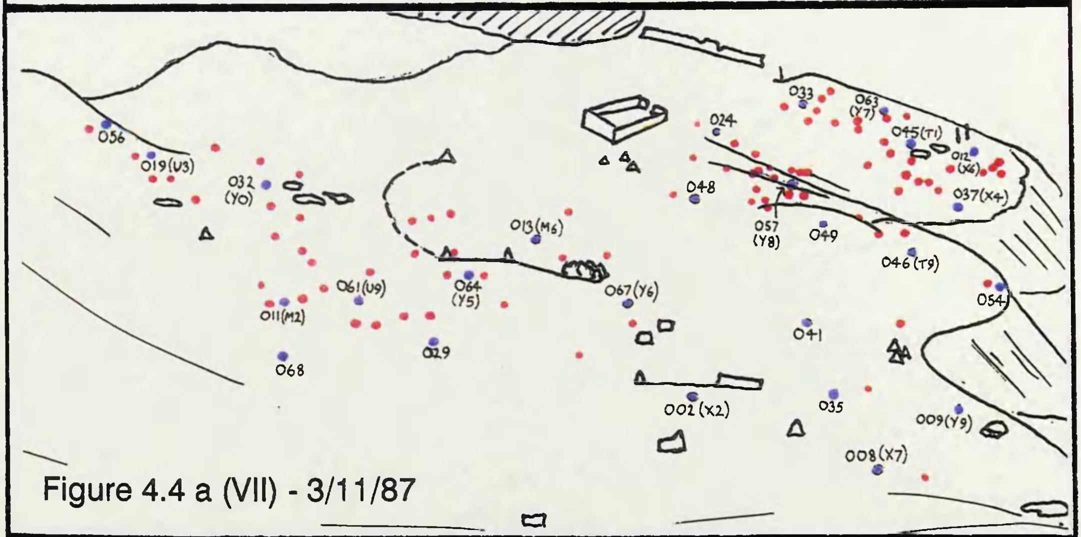


Figure 4.4 a (VII) - 3/11/87

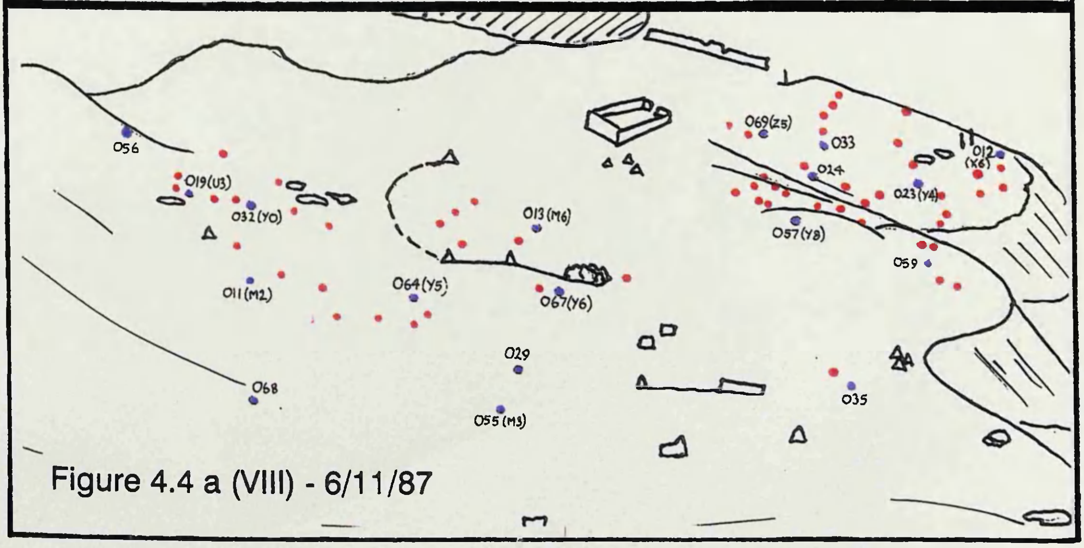


Figure 4.4 a (VIII) - 6/11/87

Figure 4.4 b: Maps showing changes seal distribution in the study area during the 1988 season on Rona.

Notes: see Figure 2.1 c for details of study area.
Males are denoted by blue dots, each with the relevant male identity code (and brand where appropriate).
Females are denoted by red dots.

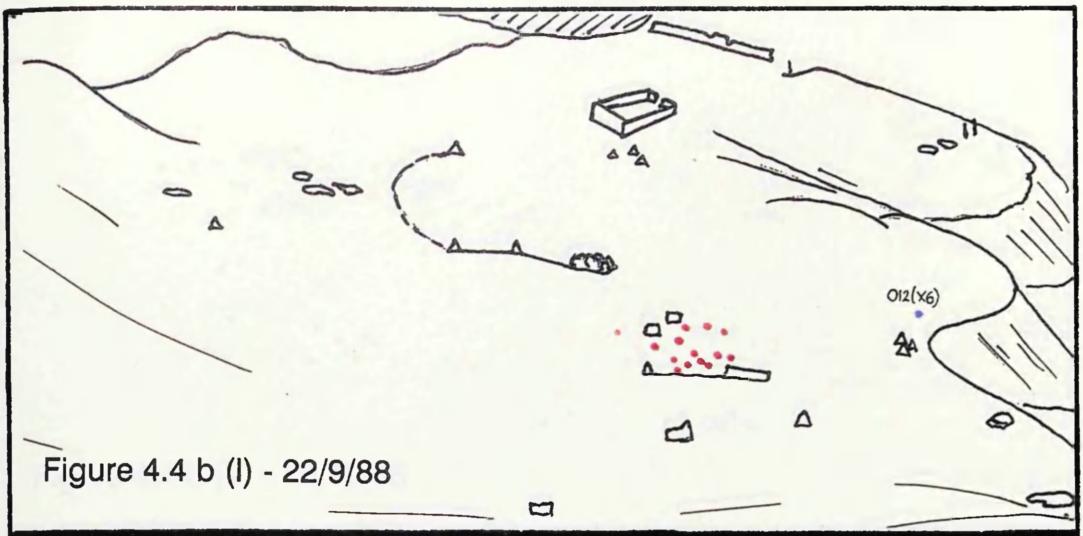


Figure 4.4 b (I) - 22/9/88

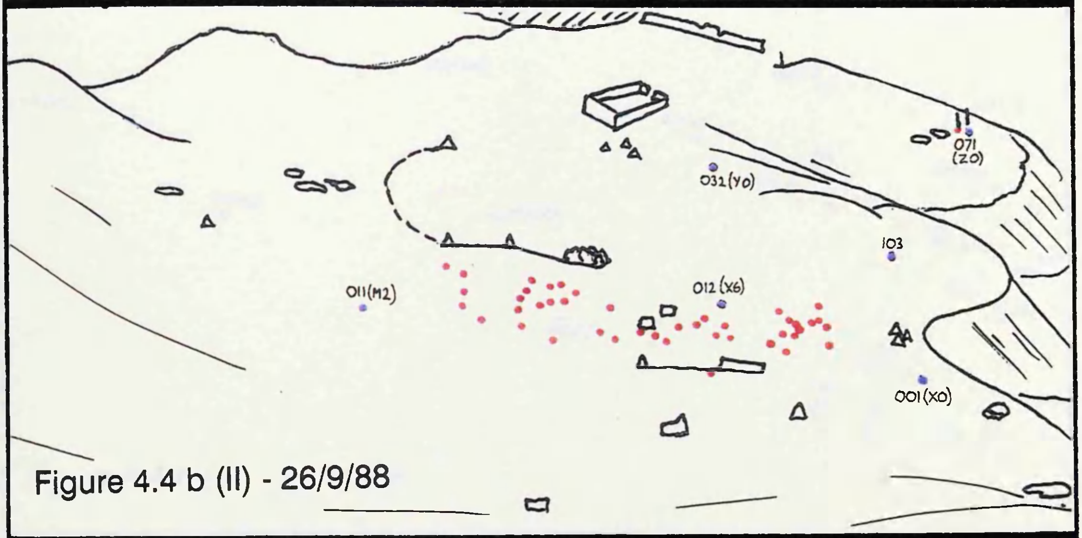


Figure 4.4 b (II) - 26/9/88

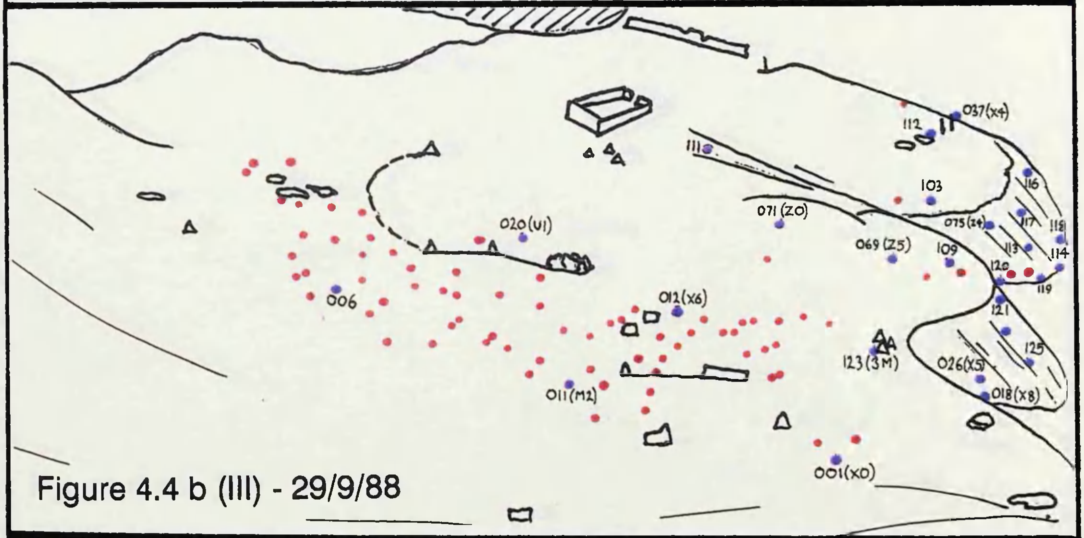


Figure 4.4 b (III) - 29/9/88

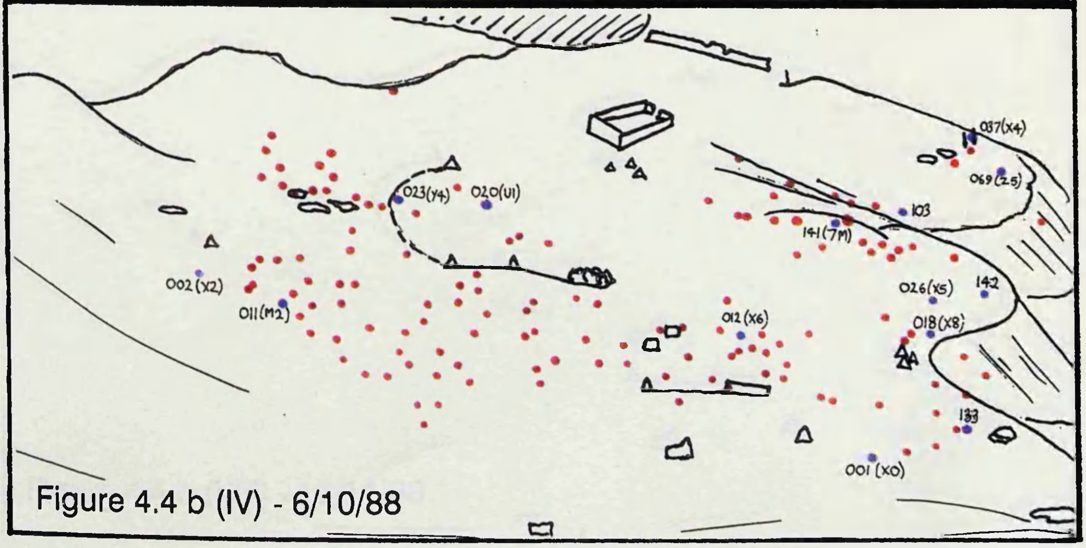


Figure 4.4 b (IV) - 6/10/88

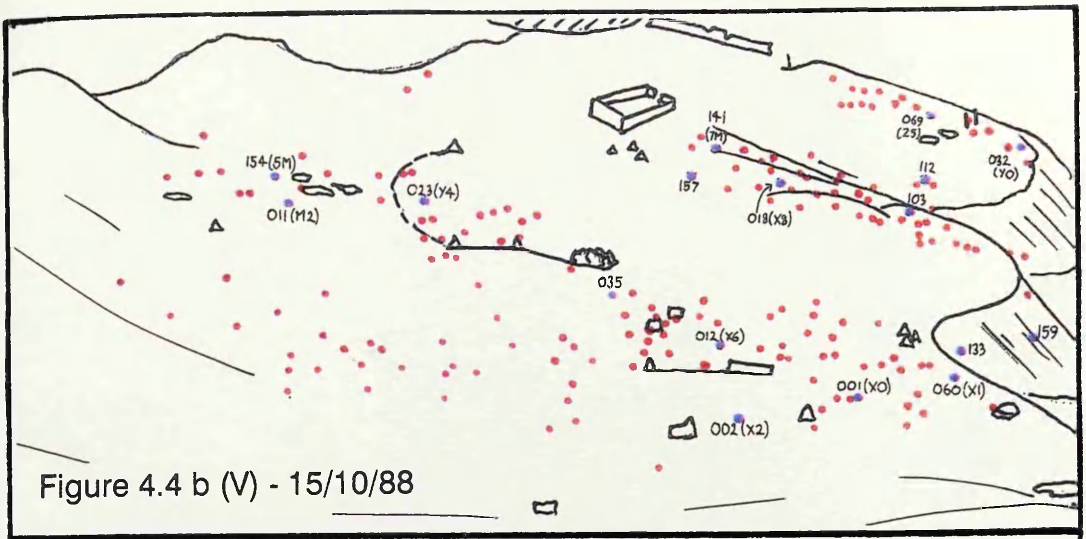


Figure 4.4 b (V) - 15/10/88

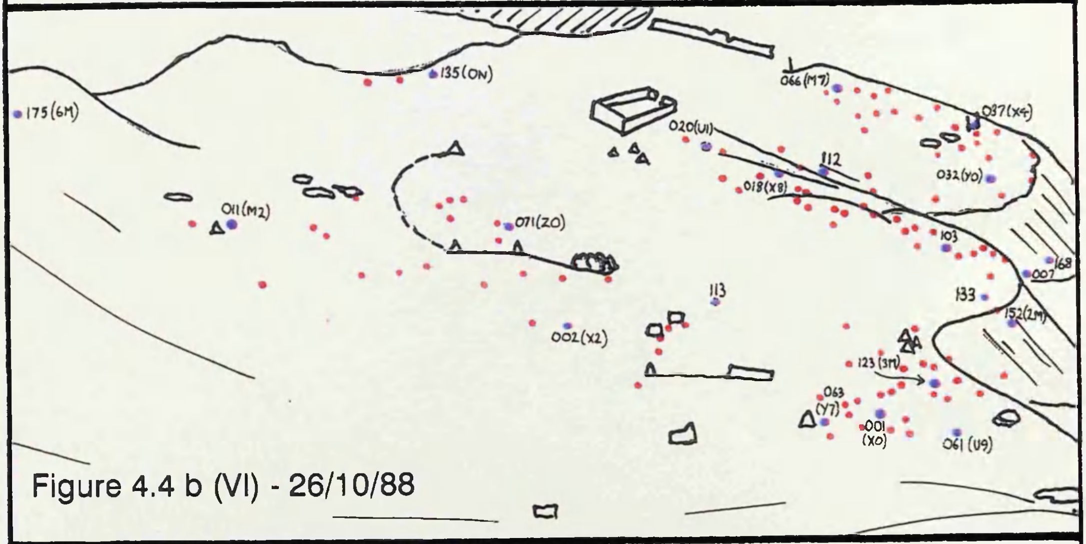


Figure 4.4 b (VI) - 26/10/88

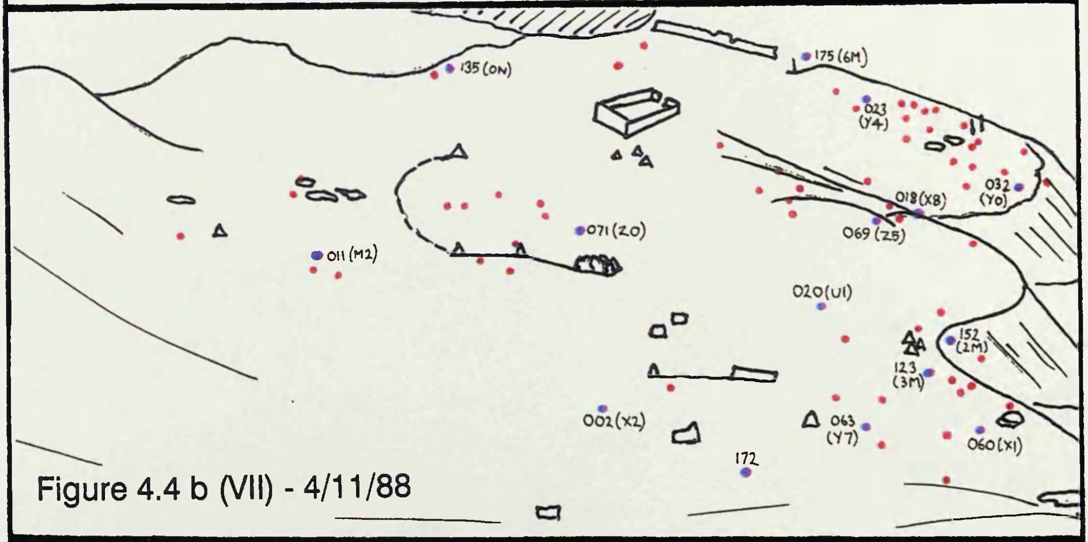


Figure 4.4 b (VII) - 4/11/88

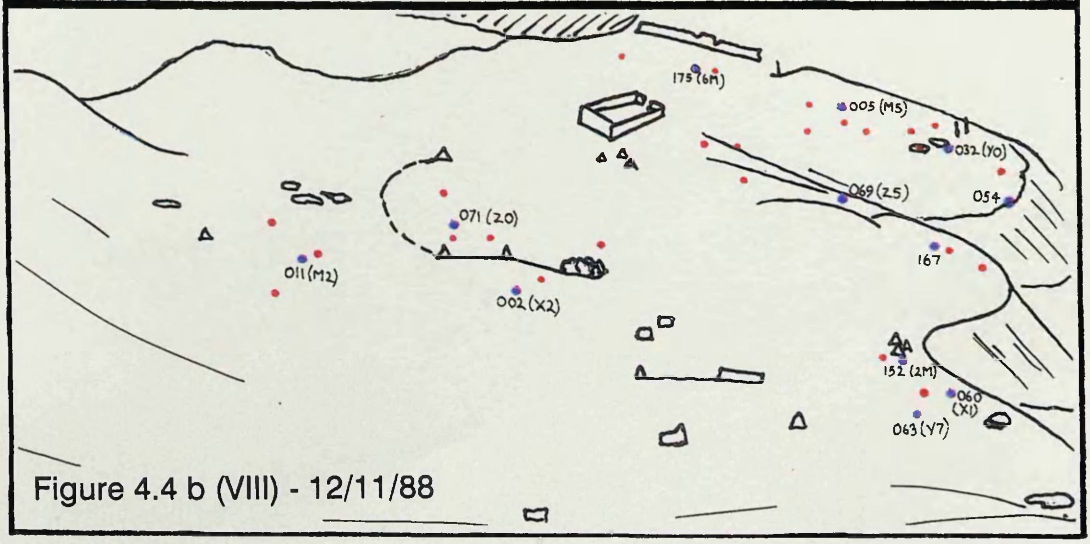


Figure 4.4 b (VIII) - 12/11/88

Figure 4.4 c: Maps showing changes seal distribution in the study area during the 1989 season on Rona.

Notes: see Figure 2.1 c for details of study area.
Males are denoted by blue dots, each with the relevant male identity code (and brand where appropriate).
Females are denoted by red dots.

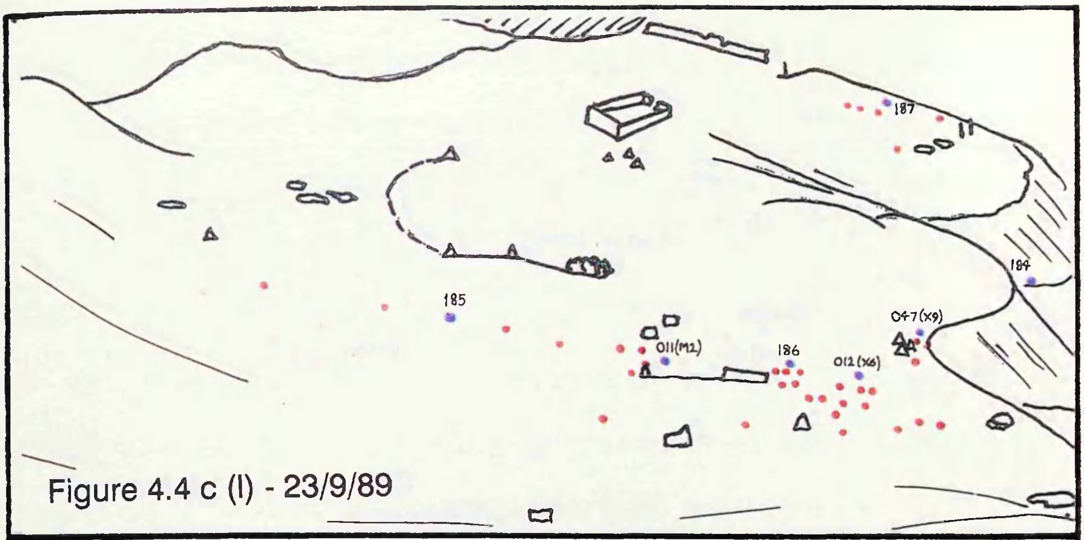


Figure 4.4 c (I) - 23/9/89

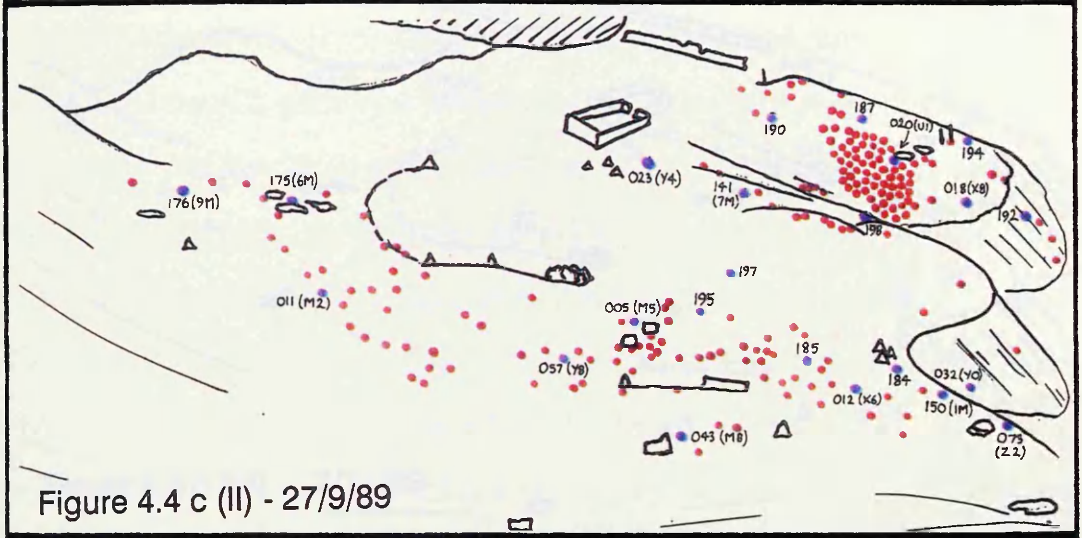


Figure 4.4 c (II) - 27/9/89

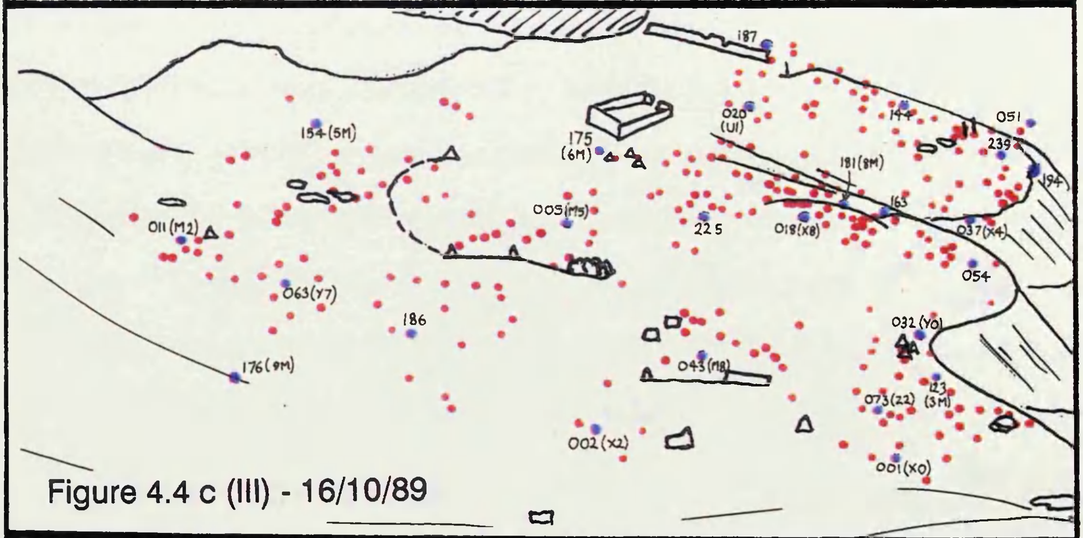


Figure 4.4 c (III) - 16/10/89

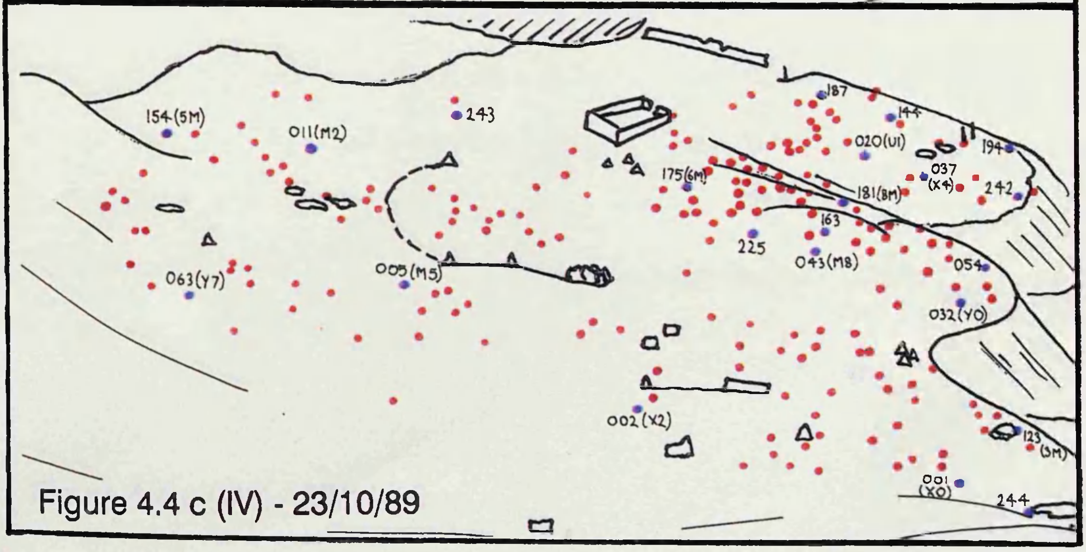


Figure 4.4 c (IV) - 23/10/89

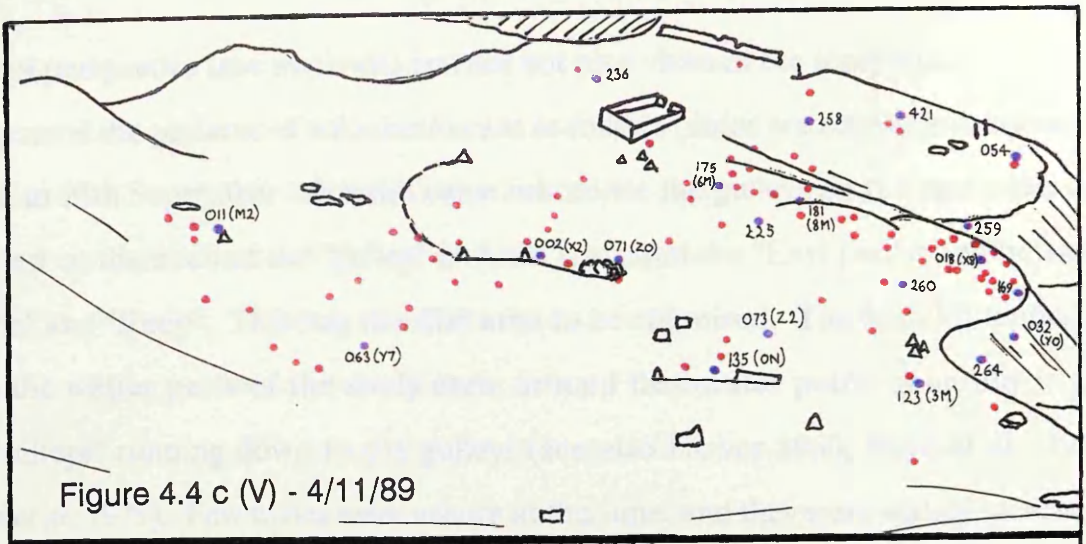


Figure 4.4 c (V) - 4/11/89

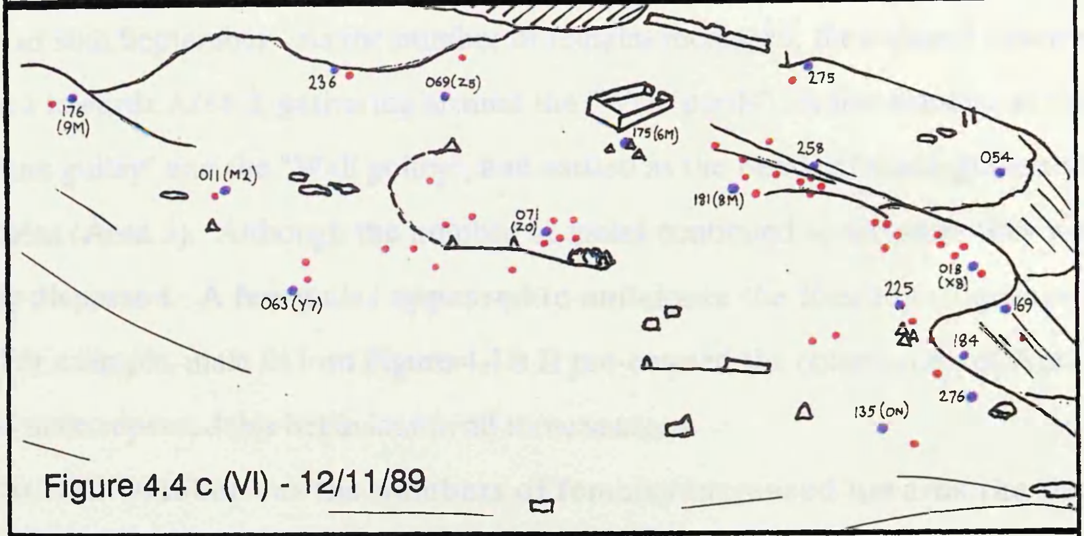


Figure 4.4 c (VI) - 12/11/89

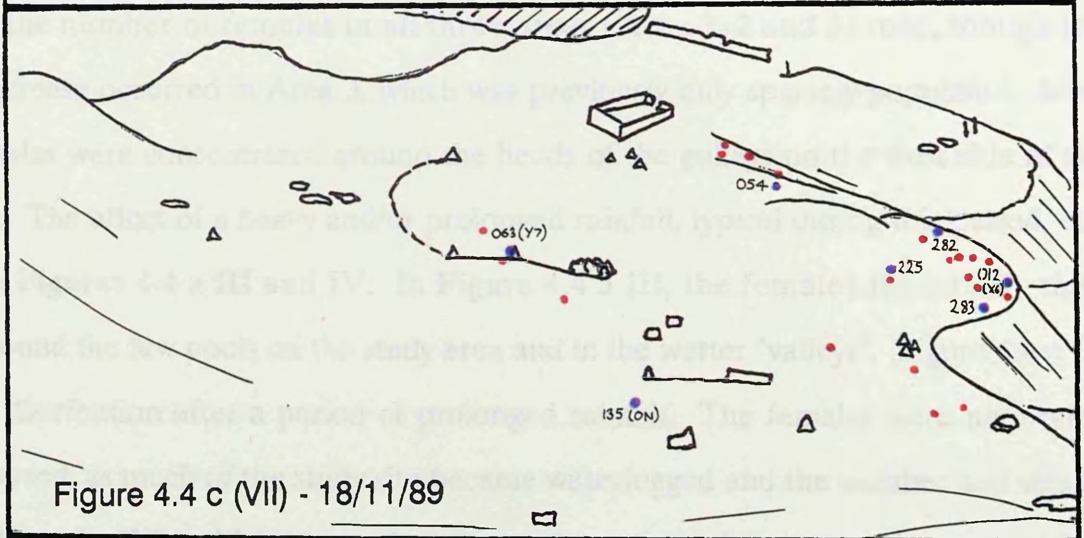


Figure 4.4 c (VII) - 18/11/89

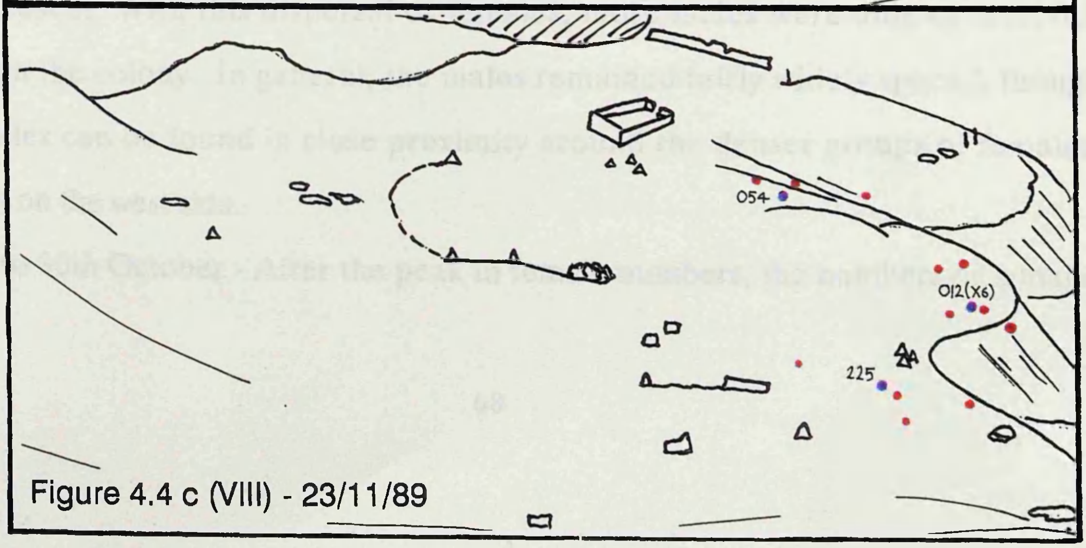


Figure 4.4 c (VIII) - 23/11/89

problems of perspective (see methods) and are not plan views of the study site.

In general the patterns of colonisation are as follows (dates are only approximate);

19th to 25th September - females came ashore via the gulleys on the east coast and congregated at the head of the "gulley" in Area 1, around the "East pools" and between the "Coffin" and "Keep". This was the first area to be colonised. The females tended to gather in the wetter parts of the study area, around freshwater pools, generally in the shallow "valleys" running down to the gulleys (see also Hewer 1960, Boyd *et al.* 1962, Anderson *et al.* 1975). Few males were ashore at this time, and they were widely spaced.

26th to 30th September - As the number of females increased, they spread westward from Area 1 towards Area 2, gathering around the "West pools". A few females arrived via the "Fank gulley" and the "Wall gulley", and settled at the heads of these gulleys and between them (Area 3). Although the number of males continued to increase, they were still widely dispersed. A few males appeared to anticipate the location of groups of females. For example, male 011 on Figure 4.4 b II pre-empted the colonisation of Area 2. In fact, this male repeated this behaviour in all three seasons.

1st to 20th October - as the numbers of females increased towards the peak numbers, the number of females in all three areas (Area 1, 2 and 3) rose, though the greatest increase occurred in Area 3, which was previously only sparsely populated. Most of the females were concentrated around the heads of the gulleys on the west side of the study area. The effect of a heavy and/or prolonged rainfall, typical during this period, can be seen in Figures 4.4 a III and IV. In Figure 4.4 a III, the females form fairly tight clusters around the few pools on the study area and in the wetter "valleys". Figure 4.4 a IV shows the distribution after a period of prolonged rainfall. The females were noticeably more dispersed, as much of the study site became waterlogged and the number and size of pools increased. With this dispersal of females, more males were able to establish positions on the colony. In general, the males remained fairly widely spaced, though several males can be found in close proximity around the denser groups of females, particularly on the west side.

21st to 30th October - After the peak in female numbers, the numbers of females present declined throughout the study area. However, this decline was greatest in those areas that were colonised first (i.e. Area 1, followed by Area 2). As females departed, the spacing between remaining females increases slightly, with much of the study area waterlogged, there was less need for females to aggregate around a few pools. The male numbers did not decline, and their distribution remained largely unaltered. However, the number of females around each male decreased.

31st October to 10th November - The numbers of females continued to decline, and Area 3 started to empty more rapidly. Many males remained, but often with only one female nearby. These males "consorted" with these single females, remaining with them until the females came into oestrus, were mated and departed. Many males were to be found in areas with no females. These males soon departed or moved to areas with females. The concentration of males around the few remaining groups of females increased during this period. Towards the end of this period, the number of males started to decline, as individuals returned to the sea.

11th November to end of observations - Both the numbers of females and males continued to decline throughout the study area. Those males which held the larger groups of females in the previous period, now only have a one or two females nearby. Some "new" males appeared late in the season, attempting to gain copulations with the few remaining females. In the extended study period of 1989, the last map (Figure 4.4 c IX) shows the situation at the close of the season, with only 12 females and 3 males present. All 3 of these males had held positions amongst large groups of females for much of the season.

The general pattern of colonisation described above is very similar to that presented by Anderson, Burton and Summers (1975). However, there are a few points of interest particularly worth noting. The lower numbers of males and females throughout the 1988 season are evident when comparing these maps. Also in 1988 (Figure 4.4 b III) an example of the presence of many peripheral males can be seen. In this figure, there are many males hauled out on the rocks along the west side of the study area. These peripheral males remain only for very short periods. The number of males on these rocks varies considerably, dependent upon the tidal state, which determines the area of rocks available. It is noticeable throughout these figures that very few females are to be found on these rocks. Females generally give birth well above the high tide mark on North Rona, this forms the actual breeding area. Thus, the males hauled out on the tidal rocks are not strictly within the breeding colony. In 1989, a large and dense group of pregnant females gathered in Area 3 early in the season (Figure 4.4 c II). These females have been mentioned above (section 4.1). These females gradually dispersed as can be seen in Figures 4.4 c III and V. A similar aggregation of pregnant females occurred in the previous two seasons, though these were close to, but outside, the study area, in Fianuis South (see Figure 2.1 b and c, Chapter 2).

4.5. Length of stay of males on the breeding colony

Though the numbers of males remained reasonably constant for much of the season, the actual lengths of stays, dates of arrivals and departures for individual males varied considerably. Tables 4.1 a and b show summary statistics for length of stay, date of arrival to the study area and date of departure from the study area. Table 4.1a gives these statistics for all identified males in the study area in each season. Table 4.1b gives statistics only for those males involved in at least 10 inter-male aggressive encounters. Although the data on colony attendance is accurate for males involved in few inter-male aggressive encounters, the calculation of dominance score (see Chapter 3) is unreliable when a male is involved in few aggressive encounters. Hence, in subsequent comparisons of data sets, only those males involved in 10 or more inter-male encounters are included. Thus, the summary statistics for colony attendance parameters are presented in this format. Those males involved in few aggressive encounters tend to be those individuals present for very short periods.

Table 4.1a

Statistics illustrating length of stay, arrival date and departure date of all identified males (n) on the study area in each breeding season.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1987	No. DAYS ASHORE	85	6.00	11.73	12.61	1.37	0.12	42.50
	ARRIVAL DATE	68	20.00	25.34	14.21	1.72	9.00	55.00
	DEPARTURE DATE	72	47.00	42.43	12.50	1.47	9.00	55.00
1988	No. DAYS ASHORE	117	2.00	9.44	13.83	1.28	0.25	54.00
	ARRIVAL DATE	117	14.00	19.26	13.03	1.21	1.00	54.00
	DEPARTURE DATE	114	28.00	31.27	16.96	1.59	5.00	60.00
1989	No. DAYS ASHORE	139	1.23	8.03	12.79	1.09	0.16	49.61
	ARRIVAL DATE	150	14.00	23.66	18.04	1.47	4.00	63.00
	DEPARTURE DATE	150	40.00	36.29	19.08	1.56	5.00	68.00

Notes:(these apply to both Table 4.1a and b)

No. DAYS ASHORE - this represents a measure of the length of stay in terms of entire days spent in the study area. In 1987 the total number of days on which censuses and/or observations were made was 47. In 1988 this total was 60 days and in 1989 the value was 65 days.

ARRIVAL DATE - for each male present a value was given denoting the day upon which he arrived, a value of 1 representing the 19th of September (the earliest date on which observations were made in any of the three years), 2 representing the 20th of September etc, etc.

DEPARTURE DATE - each male received a number recording the day on which he was last sighted on the study area using the same numbering system as for arrival date.

Table 4.1b

Statistics illustrating length of stay of all identified males on the study area which were involved in 10 or more separate inter-male aggressive encounters in each breeding season.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1987	No. DAYS ASHORE	47	16.00	18.47	12.12	1.77	0.50	42.50
	ARRIVAL DATE	47	19.00	21.79	9.84	1.44	9.00	47.00
	DEPARTURE DATE	47	49.00	45.23	9.61	1.40	16.00	55.00
1988	No. DAYS ASHORE	39	18.00	21.13	15.29	2.45	1.00	54.00
	ARRIVAL DATE	39	11.00	16.82	11.79	1.89	1.00	43.00
	DEPARTURE DATE	39	48.00	43.31	14.41	2.31	12.00	60.00
1989	No. DAYS ASHORE	54	14.66	18.40	15.17	2.06	0.46	49.61
	ARRIVAL DATE	54	9.50	15.15	12.25	1.67	4.00	47.00
	DEPARTURE DATE	54	45.00	41.87	17.83	2.43	7.00	68.00

The actual amount of time spent on land by each male during the entire breeding period can vary from a matter of hours to almost the entire season. There is considerable variation in lengths of stay, with a standard deviation of 13 to 14 days in each year. In fact, the standard deviation is greater than the mean length of stay when all identified males are included (Table 4.1a). All distributions of lengths of stay were highly skewed, with a preponderance of males remaining for very short periods, hence the median values are a more accurate measure of average lengths of stay.

The vast majority of the males have relatively short stays. In 1987, 45.9% of the males were ashore in the study area for less than a tenth of the breeding season, 78.8% of bulls remaining ashore for less than half the season. In contrast, only 1.2% of the males stayed for greater than 90% of the season. In 1988 the figures 70.9% staying for less than 10% of the season, 85.5% for less than half the season and 1.7% for greater than 90 % of the season. For 1989, 71.9% of males remained ashore for under 10% of the season, 89.2% for less than half the season and none were present for more than 90% of the season.

The variables presented in Table 4.1 a and b were transformed to approximate to normality prior to statistical analyses (see methods and Chapter 3). A comparison by oneway analysis of variance, with Scheffe's multiple range test, of the mean values of each variable in Table 4.1a revealed no significant difference between years in either length of stay ($F_{2,337} = 4.67$, $p = 0.011$) or arrival date ($F_{2,332} = 4.13$, $p = 0.017$) despite differences in the study periods. However, the 1987 departure date was significantly later than that for 1988 or 1989 ($F_{2,333} = 11.92$, $p < 0.000$). This is most probably due to the later onset of observations in 1987, missing the very early part of the season. During this period, with relatively higher male turnover, many males come ashore and depart after only a brief stay. Thus, in 1987, many of these males would have been missed.

The same analyses on data in Table 4.1b showed no significant differences between years in any of the three variables (length of stay; $F_{2,137} = 0.35$, $p = 0.707$, arrival date; $F_{2,137} = 4.51$, $p = 0.013$, departure date; $F_{2,137} = 0.67$, $p = 0.512$), suggesting that the differences observed in Table 4.1 a were due to the differing number of short stay males observed at the start of each season. As observations commenced relatively later in 1987 than the other two seasons, few of these short stay males were observed, giving an inflated mean and median length of stay in Table 4.1a, and a significantly later mean departure date. Exclusion of males with less than 10 aggressive encounters, removed many of these short stay males and thus removed the differences in mean length of stay and departure date despite the differences in observation period between each season.

The relative variation about the mean arrival and departure dates for males involved in at least 10 inter-male aggressive encounters were compared by calculating coefficients of variation ((s/x)x100)) with associated standard errors and confidence limits. Standard errors (SE) for the coefficients of variation (CV) were calculated using one of the following formulae;

(1) where $CV < 15$: $SE = CV/(\sqrt{2n})$

(2) where $CV > 15$: $SE = (CV/(\sqrt{2n})) \times \sqrt{(1+(CV/100)^2)}$

Confidence limits were assigned by multiplying the standard 2 sample $t_{99}(n-1)$ values with the calculated standard errors. Table 4.1 c presents these values for each season.

In all three years the relative variation around the mean values of departure date were significantly less than for arrival date ($p < 0.01$). Thus, departure dates for individual males tended to be more synchronous than arrival dates.

4.6. Male positions and movements

Table 4.2 summarises the number of males identified each year that were sighted at other breeding sites on North Rona as well as the study site. Also, sightings on non-breeding haul-out sites are noted. Locations of alternative breeding sites can be found in the maps presented in Chapter 2.

The numbers of branded males present in the study area each season were 48, 42 and 40 in 1987, 1988 and 1989 respectively. In each year, 11 of these individuals, were also sighted in other parts of the colony. Fianuis South, the area adjacent to the northern boundary of the study site, was found to be the main additional site utilised by seals from

Table 4.1c

Coefficients of variation with standard errors and 95 % confidence limits for arrival and departure dates of males in the study area which were involved in 10 or more separate inter-male aggressive encounters in each breeding season. df = degrees of freedom (n-1).

YEAR	VARIABLE	df	coefficient of variation %	standard error	99% confidence limit
1987	ARRIVAL DATE	46	45.16	5.11	13.73
	DEPARTURE DATE	46	21.25	2.24	6.02
1988	ARRIVAL DATE	38	70.10	9.70	26.30
	DEPARTURE DATE	38	33.27	3.97	10.76
1989	ARRIVAL DATE	53	80.86	10.01	26.75
	DEPARTURE DATE	53	42.58	4.90	13.09

Table 4.2
The numbers of males identified on the study area which were present in other parts of the North Rona breeding colony in each of the three years.

BREEDING SITES VISITED					NUMBER OF MALES			
SA	FS	FC	FN	SC	1987	1988	1989	TOTAL
X	X				5	5	2 *5	12
X	X	X	X *		1	0	1	2
X	X		X *		1	1	2 *3	4
X		X			0	0	2	2
X		X	X		2	0	0	2
X			X *		1	5 *2	3 *5	9
X				X *	1 *1	0	0	1
X	X			X *	0	0	1 *4	1
			TOTAL		11	11	11	33

Notes:

SA - Study Area
FS - Fianuis South
FC - Fianuis Central
FN - Fianuis North
SC - Sceapull
* - Sighted on a non-breeding haul-out.

*1 - this male departed from the study area immediately after being caught. He was sighted on the non-breeding haul-out of Sceapull 5 days later and had returned to his original position in the study after a further 4 days.

*2 - 3 of these 5 males were sighted offshore on non-breeding haul-out sites in Fianuis North at the end of the breeding season after departing from the study area.

*3 - one of these males was sighted in the Fianuis North breeding area at the onset of the season. The following day he was present in the study area and remained there until the close of the season.

*4 - this male departed from the study area in mid-season after being caught. He was sighted 3 days later on the non-breeding haul-out of Sceapull. The following day he had re-established the same position on the study site.

*5 - All these males were sighted on non-breeding haul-outs in Fianuis North at the end of the season.

the study area. All males present in both the study area and Fianuis South were individuals who held positions around this boundary.

A majority of these gross movements of males occurred either at the start or close of the season. In particular, males moved to non-breeding haul-out sites around the island on termination of their stay on the breeding colony. Of the 33 males sighted on other sites as well as the study area, 7 were sighted only at non-breeding haul-outs in addition to the study site, whilst another 7 individuals were sighted at other breeding sites and non-breeding haul-outs in addition to the study site. Two males left the study area after being caught, but both returned to their original sites.

DISCUSSION

The general pattern of changes in female and pup numbers through the season is very similar in all three years. Records for previous years on Rona and other breeding colonies also reflect this pattern (Anderson, Burton and Summers 1975, Boness and James 1979). However, whilst the seasonal changes in male numbers recorded in this study are similar to those given by Anderson, Burton and Summers (1975) for North Rona, they are markedly different to those recorded for some other colonies, most notably Sable Island (see Chapter 9 for a detailed consideration of this point).

The mean sex ratios for each year are similar to the average ratio given by Anderson, Burton and Summers (1975) of 1:7.5, and as these authors pointed out, these figures agree with those predicted by Hewer's (1964) life table for grey seals. However, it must be noted that they are considerably different to those for Sable Island (Boness and James 1979) where the mean operational sex ratio at the time of peak adult numbers is 1 male to 1.3 females compared to 1 : 9 (Anderson, Burton and Summers 1975) or 1 : 10.3 (1987), 1 : 8.6 (1988) and 1 : 10.6 (1989) in the present study (see Chapter 9).

As stated in the results the overall mean sex ratio of approximately 1 male to 7 females may be somewhat misleading as receptive females are not present until approximately 2 weeks into the season. It is noticeable that the sex ratio declines markedly in the latter half of the season when a majority of sexual activity occurs (Chapter 3). Thus, a more accurate estimate of the true operational sex ratio might be that calculated from the time of the first observed successful copulation in each season. These mean ratios range between 1 : 5.6 (1988) and 1 : 6.2 (1987). These values indicate a lower number of females per male than suggested by the overall mean ratio.

The initially high male turnover between successive days reflects the general turmoil of the early weeks of the season. During this period many males will visit the study area, some will depart almost immediately, perhaps to return later, others will attempt to establish positions with varying degrees of success. Even once a position has been established, a male may be removed by a later arrival during this period. Anderson, Burton and Summers (1975) also suggest greater male movement and exchange during the early part of the season, stating that "towards the end of week 2 bulls took up more or less constant positions". In 1987 much of this early period was missed, thus many males staying for only short periods were not observed, and this accounts for many of the slight discrepancies of 1987 data compared to the other years, in particular the longer mean length of stay and later mean departure date and the lower number of males observed during this first season. This also explains the relatively lower percentage of males present for less than 10% of the breeding season in this year. After this initial period, the turnover rate is remarkably low, and although new males do continue to arrive, very few are able to establish permanent positions on the study site.

The variation in length of stay for females is much less than for males, generally each female remains ashore for the period of lactation (Anderson, Burton and Summers 1975). However, the mean duration of stay for males is similar to that given by several authors for the mean duration of lactation in the female (Matthews 1950 and Coulson 1959 give values of 18 days, Hewer 1957; 16 days and Bonner 1972; between 16 and 21 days). Similarly, Anderson, Burton and Summers (1975) estimate the mean length of stay for females to be between 13 and 19 days.

The range of lengths of stay for males in this study was from a few hours to 54 days. Anderson, Burton and Summers (1975) give a range of male stays from 6 to 57 days. Whilst the upper limit agrees closely with that found in the present study, the lower value differs markedly. This may be because more of the short stay males could be identified in this study as Anderson *et al.* (1975) were only able to identify 30 males. These authors present a mean length of stay of 18.79 days. This is somewhat higher than the values presented here for all males, which range between 8 and 12 days. However, on removing those males involved in less than 10 inter-male aggressive interactions, the mean lengths of stay lie between 15 and 18 days, closer to the figure given by Anderson *et al.* (1975). The maximum recorded length of stay is particularly interesting. Anderson *et al.* (1975) state that the entire breeding season on North Rona, from the first birth to the departure of the last adult female, spanned 74 days. If the mean duration of lactation (i.e. 18 days from parturition to oestrus) is subtracted from these 74 days, the time over which oestrus females were present is approximately 56 days, remarkably close to the maximum recorded male length of stay. This will be discussed further in Chapter 7.

In general, it appears that the males will remain in just one breeding site in the colony. Relatively few males apparently venture to other breeding sites within a single season. However, this may be a somewhat biased sample as only those males which are able to come ashore in the study area are identified. Males which approach the study area by sea but are unable to come ashore may be more likely to try elsewhere on the colony. The main site outside the study area to which study males moved was Fianuis South. Seals can move freely from the study site to Fianuis South overland (see Figure 2.1 b, Chapter 2) and frequent exchange occurs particularly amongst seals located around this artificial boundary. Fewer bulls were seen in more distant areas as well as the study site. Many of these are to be seen on non-breeding haul-out sites around the periphery of the island towards the close of the breeding season. These areas cannot easily be reached by moving overland and require the seal to enter the sea when travelling to or from the study area.

As suggested earlier, the current division of breeding males into tenured and transients (Boness and James 1979) may be too rigid. From the results presented in this chapter it is clear that some males do establish central positions amongst high densities of females, remaining ashore for long periods and therefore gaining access to many potential mates. Conversely, some males have only peripheral positions, short stays, and apparently little access to females. However, there is a complete range of behaviour patterns between these two extremes.

In this study, it was possible to record actual total lengths of stay of individuals. Thus, we can attempt to assess the exact relationships of colony attendance to other variables, such as mating success, dominance and energy expenditure and dispense with categorical classifications of males determined by fairly arbitrary divisions. These relationships are examined in detail in Chapter 7.

From this point, the terms "tenured" and transient" as defined by Boness and James

(1979) will not be used, except where comparisons to previous work are made. All males who came ashore onto the study site above the high tide mark and were within the area occupied by breeding females will be termed as having secured a position on the colony, irrespective of how long or short the stay was. Of these males, some will have secured positions amongst a group of one or more females and will be referred to as having established a position on amongst a group of females. A male with a single female will be termed as "consorting" with the female as this behaviour is particularly interesting. Towards the close of the season, the few females remaining ashore tend to be rather more dispersed, this prevents males from monopolising many females and consequently relatively more males gain positions by females, often consorting with a single female. In consorting, the male is particularly attentive and follows the female closely until she is receptive. After copulation one or both of the "pair" departs.

Those males who are able to come ashore, but fail to gain positions amongst groups of females are constantly on the move, being chased by other males or even females, and generally resting only when away from other adults will be termed itinerant males. These males may rest at times, or more accurately, be allowed to rest, but always away from females. Itinerant males may eventually establish a position amongst a group of females, though a majority return to the sea without such success. Conversely, males which previously held positions amongst groups of females may become itinerant.

Males hauling out on the sea washed rocks, but failing to enter the breeding colony proper will be described as peripheral males. Of those males failing even to come ashore, little can be said, as no data are available on these individuals.

The behaviour of the females is strongly influenced by the topography of North Rona, in particular, the distribution of water (Hewer 1960, Boyd *et al.* 1962, Anderson, Burton and Summers 1975, pers. obs.) and the limited access to the breeding sites (Anderson, Burton and Summers 1975, pers. obs.). Females must move considerable distances on shore to find suitable sites for pupping. The distance from the breeding site to the sea, the restricted access and the sheer numbers of seals means that females tend to remain with their pups throughout the entire period of lactation and do not "commute" from the sea to feed their pups as seen in some beach breeding grey seal colonies. For example, Pilgrims Haven on the Isle of May (pers. obs.). At Pilgrims Haven the easy access to seals along the entire beach allows females to "commute" from the waters of the shallow cove to feed their pups lying on the beach. This is also facilitated by the small area of the site, therefore, restricting the numbers of seals. Thus, cows can leave their pups for reasonably long periods and still relocate their offspring with ease. The surrounding cliffs prevent seals moving further onto the island at this site. If cows were to "commute" on North Rona, the probability of becoming reunited with their pups would be remarkably low, with the distances from the sea, the tendency for unattended pups to wander, and the sheer number of seals on the colony. These differences in female behaviour have profound effects on the behaviour of the males. At Pilgrims Haven males compete in the water in an attempt to monopolise the shallows of the cove. Most of the matings occur in the water and bulls are rarely seen on the beach (pers. obs). On Rona the system is far more complex, with many bulls gaining positions amongst the females, but yet more failing to do so. Copulations occur predominantly on land but also in the water.

The actual distribution of females on the breeding site is also largely determined by topography (Bartholomew 1970, Le Boeuf 1978) and the tendency for females to gather around areas of standing water on the breeding colony (Hewer 1960, Boyd *et al.* 1962, Anderson, Burton and Summers 1975). This causes considerable clumping of females in the flatter, wetter areas. After heavy rainfalls, when many temporary pools appear, the distribution is dramatically altered, the females becoming somewhat more dispersed (see also Figure 2 from Anderson, Burton and Summers 1975).

Males arrive at the colony shortly after the females, but only when the first pups are born do the first males remain ashore (Anderson, Burton and Summers 1975). Males attempt to secure positions amongst the groups of females on the breeding colony, rather than strict territories (defined as a geographically fixed area, in which an individual maintains exclusive access by means of aggression, threat and/or advertisement). The prime areas to establish positions are those with the greatest concentrations of females.

Therefore, the distribution of males is primarily determined by the distribution of females. This clumping of females allows certain males to monopolise a disproportionate amount of breeding opportunities leading to a polygynous mating system. The monopolisation of groups of females by a small proportion of the male population, together with the peculiar topography of North Rona lead to male exclusion and the strongly biased operational sex ratio. As access to the breeding colony is restricted to the narrow gulleys, peripheral males tend to gather in these gulleys, prevented from access to the colony by males with previously established positions. This "backlog" of males in the gulleys further limits access to other males arriving from the sea.

It is clear from the maps presented in this chapter that, not only the distribution of females, but also the sequence of colonisation of various parts of the study area is remarkably consistent in successive years. Thus, the positions of groups of females is to some extent predictable. This may explain why males arrive at the colony and compete for positions up to two weeks prior to the availability of oestrus females.

This chapter has described the details of colony attendance patterns of both females and individual males. Subsequent chapters will examine what these males do during their stay on the breeding grounds (Chapters 5 and 6) and assess relationships between behavioural and energetic components of male grey seal activity during the breeding season (Chapter 7).

CHAPTER 5 - ACTIVITY BUDGETS, WEIGHT PARAMETERS AND AGE

INTRODUCTION

Male grey seals fast throughout the breeding season. They rely primarily on energy stored in the form of the thick sub-cutaneous layer of fat - the blubber. Various authors (e.g. Harwood 1976, McCann 1983, Anderson and Harwood 1985) have suggested that the length of stay on the breeding colony for male grey seals and their activity levels during their stay are constrained by their ability to meet energetic demands, which are influenced by the condition each male is able to attain prior to the breeding season and his subsequent rate of energy expenditure during the breeding season.

Several authors have presented general data concerning weights and ages of grey seals (e.g. Bonner 1972, King 1963 and 1983) particularly from British waters, though relatively little detailed information exists concerning the western Atlantic population (Mansfield 1979). These authors presented data based on samples of dead seals collected by a variety of methods, such as during culls and from nets. These data may not be totally representative, for example seals caught in nets may be aberrant individuals. Often data from culls yield only overall impressions of grey seal morphometrics, in many cases data being collected throughout the year. In species such as the grey seal, where individuals undergo marked seasonal changes in condition, particularly during the breeding season, more accurate information is required, preferably following known individuals over a time series rather than sampling the population, for example by culls at the start and end of the season. This obviously necessitates the capture and marking of individuals and their subsequent release. This is also a more desirable technique in terms of ethics, as it does not require the death of individuals. More recent studies have provided such data, recording changes in both male and female grey seal weights and standard measurements during the breeding season (Anderson and Fedak 1985, 1987a, 1987b, Fedak and Anderson 1982, 1985). These studies have addressed directly the question of energy constraints during the breeding season, providing data from live wild seals as part of a long term investigation into energetics of grey seal females (Fedak and Anderson 1982) and males (Anderson and Fedak 1985). These studies utilise weight data gained directly from live seals in conjunction with behavioural observations. The recent development of labelled water techniques has allowed the assessment of changes in actual body condition of individual seals during the breeding season (Reilly 1989, Reilly and Fedak 1990). The present study forms a continuation of this research and utilising this methodology examines the energy expenditure of identified male grey seals. These data are then compared with the far more extensive behavioural observations, in order to examine potential energetic constraints of individual male mating success (see Chapter 7).

The aim of this chapter is to describe how male grey seals apportion their time during the breeding season, assess the variation in male weights at the onset and at the end of the season, and also examine differences in the energy expenditure of known individuals during the breeding season as measured by rates of weight loss and labelled water techniques. This chapter also examines the age structure of males caught at Rona.

METHODS

Activity Budgets

Throughout all observation periods of 1988 instantaneous scan samples were conducted. The details of this methodology are provided in chapter 2. Anderson (1978) provided evidence that there was no significant difference in grey seal behaviour patterns during daylight or darkness. For an animal which is most vulnerable on land it makes sense for seals to maximise their activities during the breeding season by utilising all the hours of the day. Similarly, Boness (1984) found no effect of time of day on activity budgets of male grey seals breeding on Sable Island (Canada). Therefore, it has been assumed in the present study that data collected during daylight hours are a representative sample of behaviour throughout both day and night. This has enabled us to calculate daily values for time budgets and examine seasonal variation.

These scan samples were used to calculate the percentage of time spent in each activity category by each identified male throughout the entire season. The individual activity budgets were then amalgamated in order to gain mean and median values and the associated variation for percentage of time spent in each activity. Activity budgets were also computed for individual males on a daily basis in order to examine seasonal variations in activity, again using mean values. Finally, individual activity budgets were computed on an hourly time scale, for example activity budgets between 7.00 a.m. and 8.00.a.m. This allowed the examination of activity budgets for diurnal patterns, again using mean values. Thus, analyses of these scan samples provided detailed information on the proportion of time in each activity, and on both diurnal and seasonal changes in activity budgets during the breeding season.

It is important to note that not all males were present for equal lengths of time nor during the same portion of the breeding season (see Chapter 4). The results presented in this chapter represent the proportion of time in each activity category during each males stay on the study area as, clearly, observations could not be made upon departure to the sea.

In all statistical analyses the percentages of time spent in each activity category were arc-sine transformed as appropriate.

There have been several studies providing activity budgets of male grey seals at various breeding colonies. Harwood (1976) provides activity budgets for seals breeding at the Monach Isles. Anderson and Harwood (1985) provide a comparative study of both the Monachs and North Rona and include data presented initially by Boness (1984) for male grey seals breeding at Sable island. It must be noted that the methodology differs somewhat in these studies and to that employed in this study. Harwood (1976) made scan samples every 15 minutes and was unable to individually identify all individuals. Anderson and Harwood (1985) used a sampling regime of scans at 10 minute intervals and again were unable to individually identify all seals. The mean percentage of animals engaged in a particular behaviour during a sampling period was used as an estimate of the percentage of time spent in that activity by an individual. Boness (1984), however, made scan samples at 25 second intervals for 20 minute periods four times a day. As in the present study he was able to identify all individuals. However, Boness still presented his summary results as simply the percentage of scans recording each activity category. In the present study, scans were made at 5 minute intervals (see Jacobsen and Wiggins 1982) throughout the entire day's observation period and throughout the breeding season. All males were individually identified, and thus activity budgets for each male were produced. The summary statistics presented in this chapter represent the average of the observed values for each male. Also, we excluded males with relatively few scans (less than 180), thus eliminating potentially erroneous results (see below), a process which the previous authors were unable to do.

Weight and age data

Details of the seal immobilisation technique are provided in Chapter 2 together with descriptions of weighing and measuring individuals.

Similarly, details of the aging technique are provided in Chapter 2.

From the direct measurements of the weight of individual males, various parameters were computed, utilising a combination of both weight data and behavioural data. The weight parameters calculated and used throughout this study were as follows;

1. Weight on day one (kg) - the arbitrary date of 19th September was selected as a useful point prior to the onset of each breeding season at which to make comparisons of individuals weights both within and between seasons at a standard time. This date was designated as day one. Weight on day one was obtained by using each individuals' daily rate of weight loss to extrapolate back from their weight on first capture to the predicted weight on 19th September. This requires that rate of weight loss is assumed to be reasonably linear throughout the season. Evidence supporting this assumption is provided in Anderson and Fedak (1985) and in this chapter utilising repeated weighings of known individuals involved in this study.

2. Arrival weight (kg) - predicted weight of each individual on their date of arrival, again computed using individuals rates of weight loss and weight on first capture and observed date of arrival.

3. Departure weight (kg) - predicted weight of each individual on their date of departure

again using rate of weight loss to extrapolate to departure weight from weight at last capture and observed departure date.

4. Total percentage weight lost (%) - a measure of total percentage weight lost by each individual during their stay on the study site. Departure weight is expressed as a percentage of arrival weight.

5. Rate of weight loss (-kg/day) - mean daily rate of weight loss for each individual expressed in negative values. This was calculated from actual weights obtained for individuals on at least two days during each season. For males caught more than twice in a single season, an average rate was obtained by determining the regression slope of relationship between weight and date for each individual. Whilst this may not be strictly comparable with the rate for males only caught twice in a season, it is the best estimate and utilises all the available data.

6. Specific rate of weight loss - a proportional daily rate of weight loss, adjusting for arrival weights of individuals, calculated from the following formula;

$$S = (100 \times (\mathrm{Ln}(W2) - \mathrm{Ln}(W1)) / (D2 - D1))$$

where;
S = specific rate of weight loss
W1 = weight on first capture
W2 = weight on subsequent capture
D1 = date of first capture
D2 = date of subsequent capture

This gives the percentage decrease in weight per day for each male, thus accounting for differences in males' arrival weights.

Specific rate of weight loss was calculated using all available weight data for each individual, thus, males caught more than twice in a season were given an average specific rate of weight loss. The remaining calculations, i.e. weight on day one, arrival weight, departure weight and total percentage weight lost were all calculated on the basis of a constant rate of weight loss for individuals within each season.

In all three years, all weight parameters other than departure weight displayed normal distributions. Thus, in subsequent statistical analyses only departure weight was transformed to approximate to normality. This was achieved by calculating the Log_{10} of departure weight. Also, as total weight loss is expressed as a percentage, this was arc-sine transformed for statistical analyses. The frequency distribution of ages was also normal in all three seasons.

RESULTS

5.1. Activity Budgets

5.1.1. *Selection of a minimum number of scans for each male*

Due to the differing colony attendance patterns of individual males, some individuals were recorded on very few scans. This may produce unrealistic time budgets for these bulls. Therefore, initial analyses involved the determination of a minimum number of scans required to provide accurate representations of male grey seal activity budgets. This was achieved by examining the relationships between the number of scans made and the proportion of time spent in each activity category. Figures 5.1 a to m illustrate some of these relationships (n = 55 males). As can be seen, for most variables, at low scan numbers there is considerable scatter between individuals in the proportions of time spent in various activities. Despite this scatter, a majority of activity categories showed a significant correlation (either positive or negative) with the number of scans if these low scan numbers were included. However, the graphs all appear to level off, and the estimated proportion of time in a given activity becomes independent of number of scans at higher scan numbers. Further examinations of the relationships between the number of scans and the proportion of time in each activity category were conducted excluding all cases with scan numbers lower than 12 (1 hour's observation time), 24, 36, 48 etc. up to 240 scans (20 hours). The minimum number of scans at which no significant correlation was found with any activity category was 180 scans (15 hours of observation). It is evident from the figures (Figures 5.1 a - m) that this is indeed the scan number at which most of the graphs level off. Thus in all analyses where appropriate, only individuals which were observed on at least 180 scan samples are used.

Figures 5.1a to m: Plots of the percentage of time estimated in various activi categories for individual males against the number of scans made for thos individuals.

Figure 5.1 a

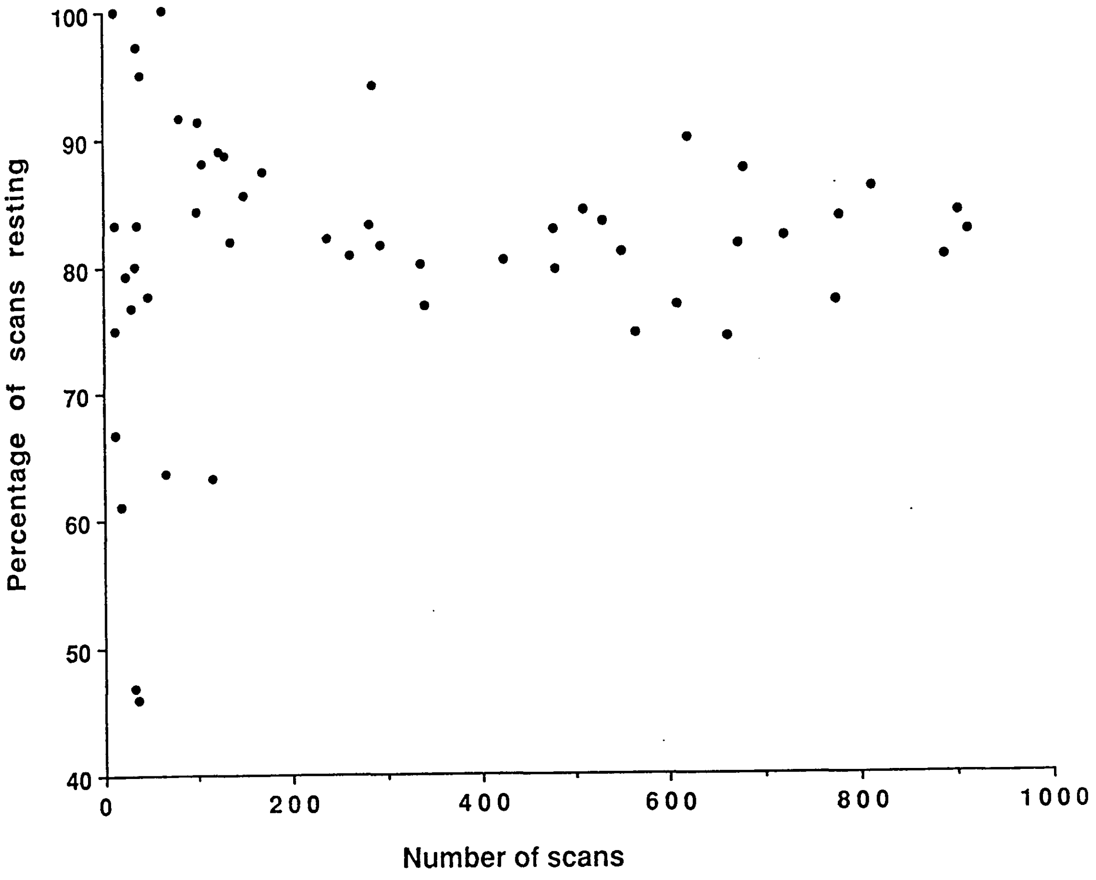
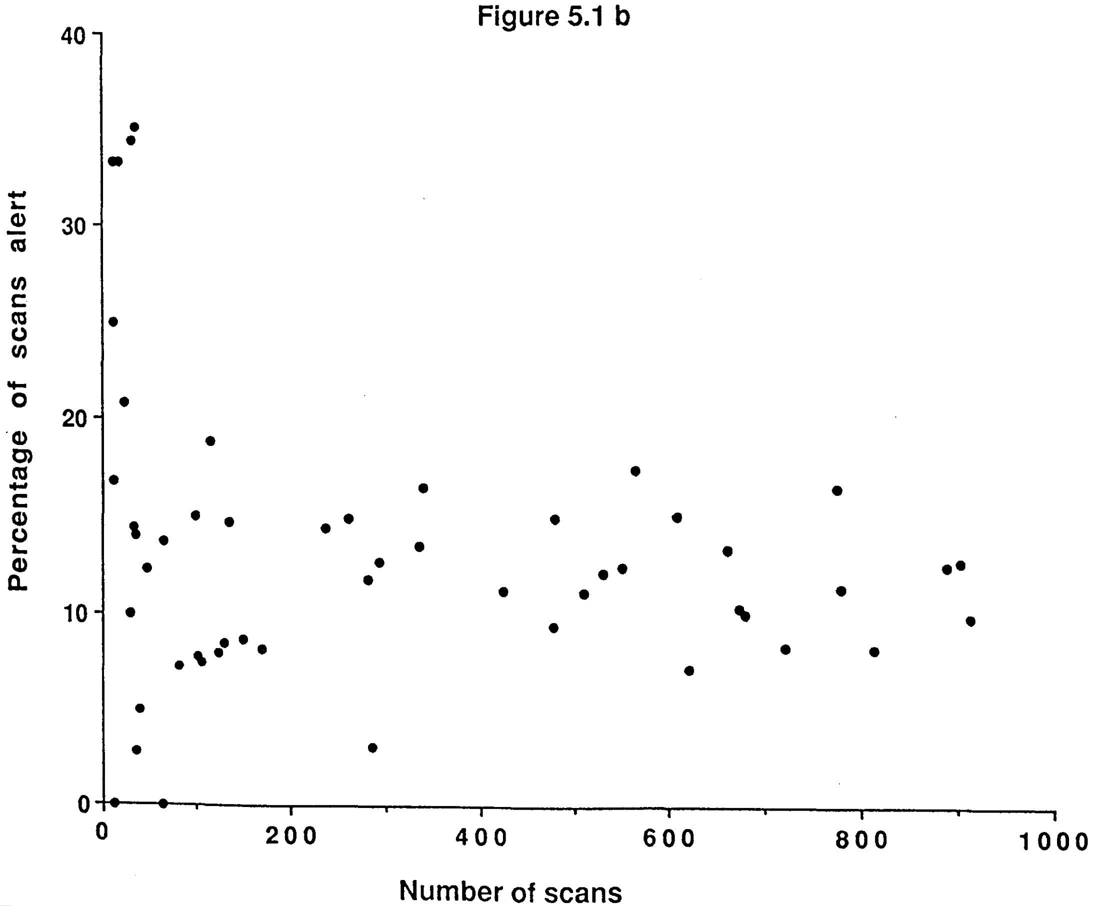


Figure 5.1 b



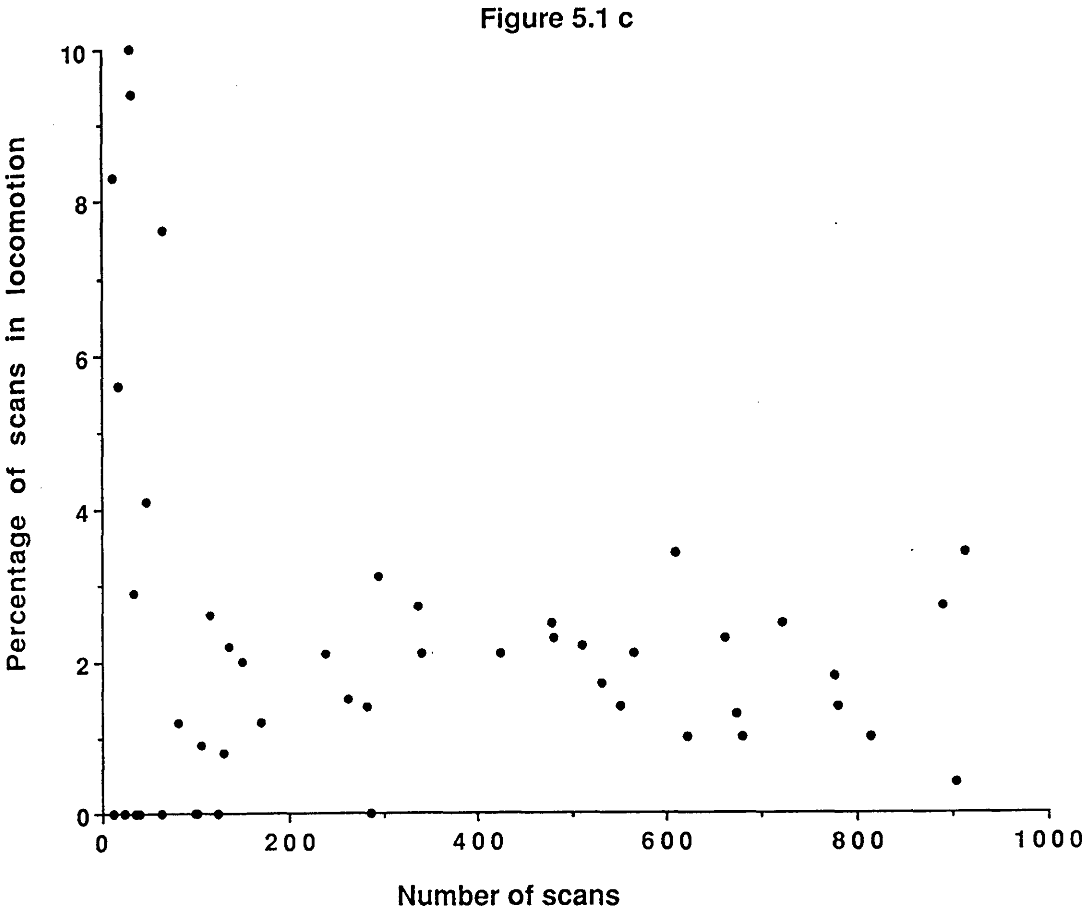


Figure 5.1 c
Percentage of scans in locomotion
0
2
4
6
8
10
0
200
400
600
800
1000
Number of scans

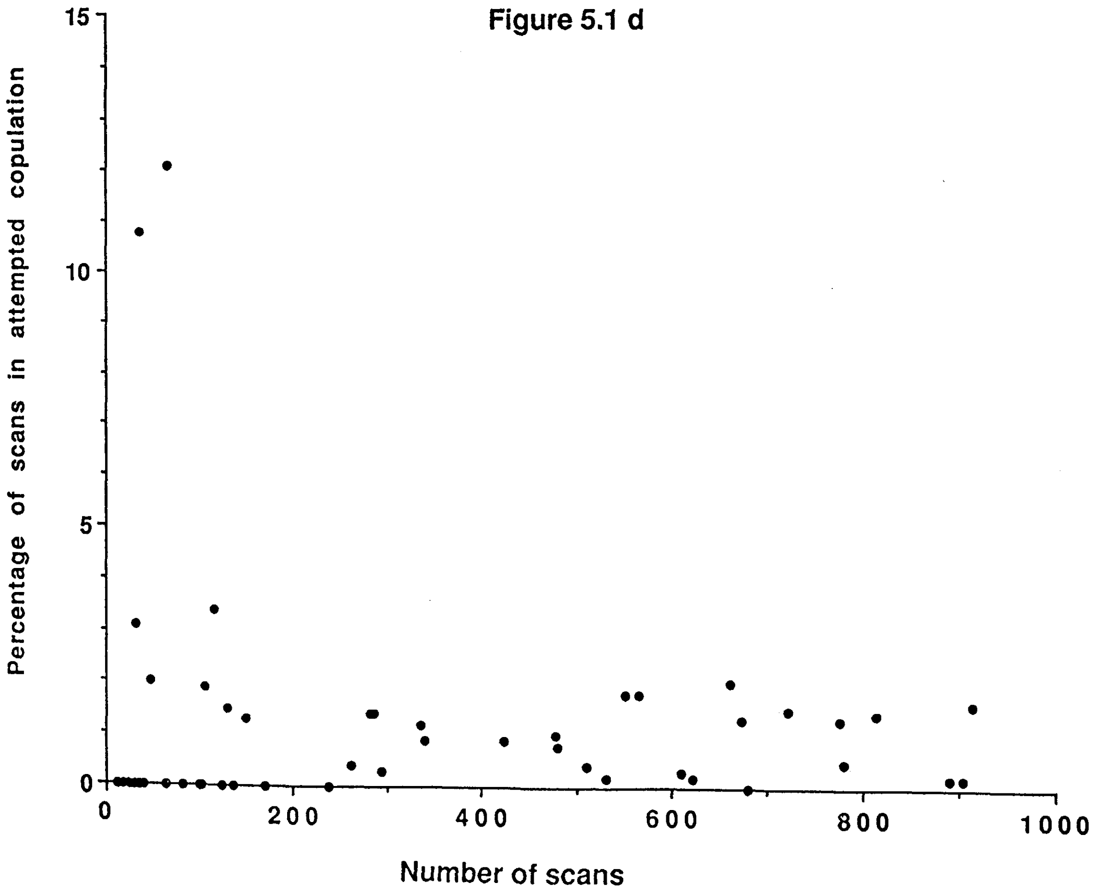


Figure 5.1 d
Percentage of scans in attempted copulation
0
5
10
15
0
200
400
600
800
1000
Number of scans

Figure 5.1 e

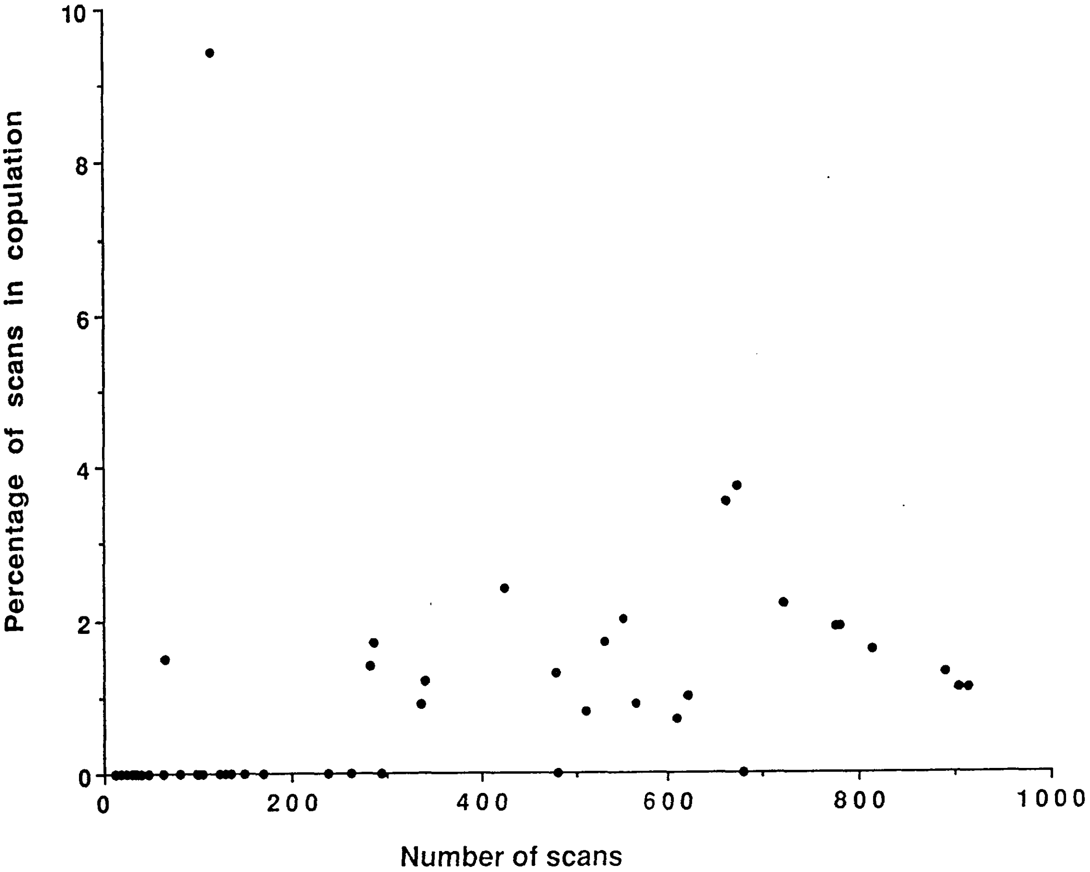


Figure 5.1 f

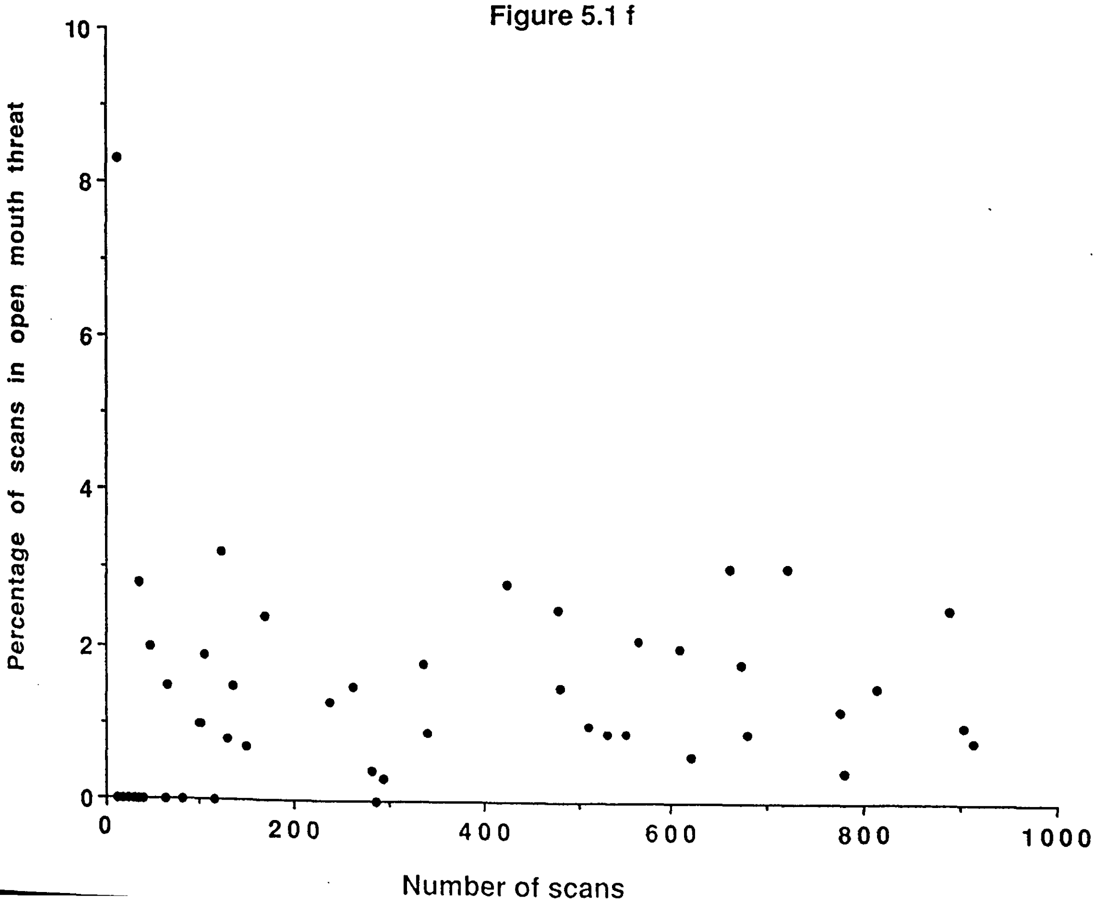


Figure 5.1 g

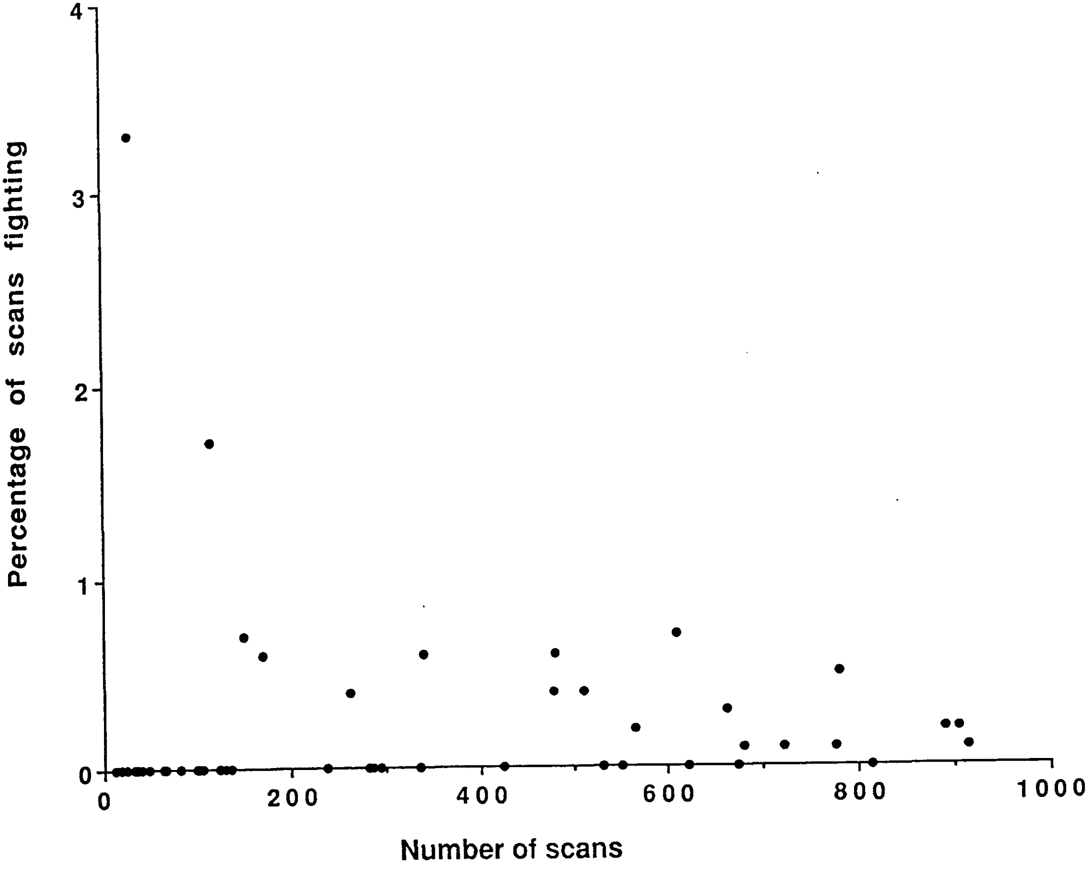


Figure 5.1 h

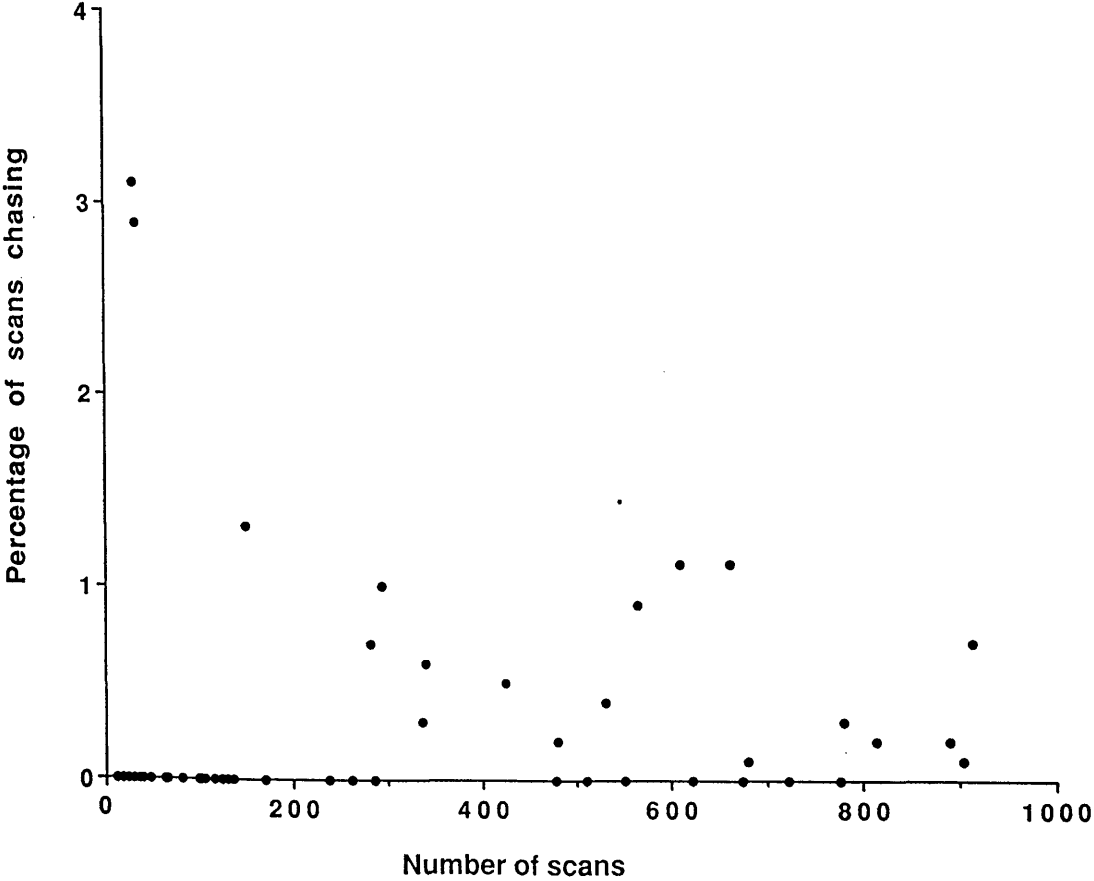


Figure 5.1 i

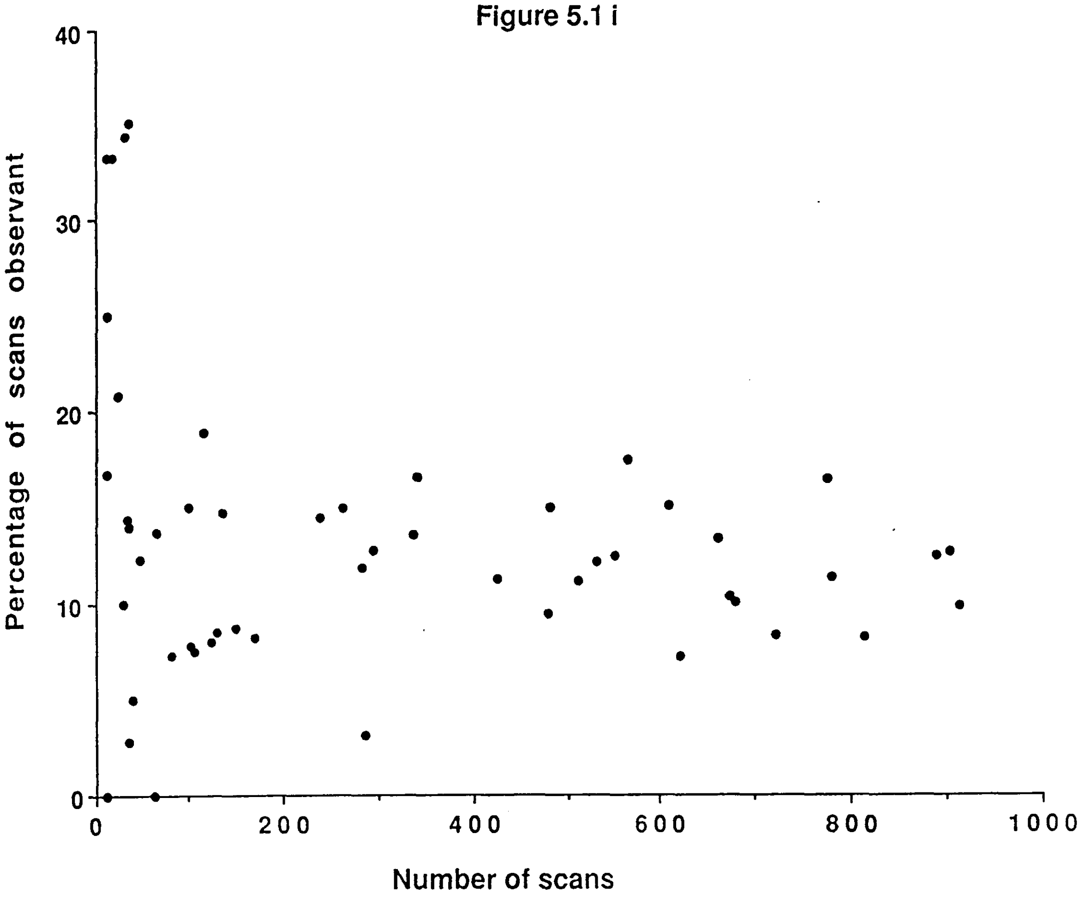


Figure 5.1 j

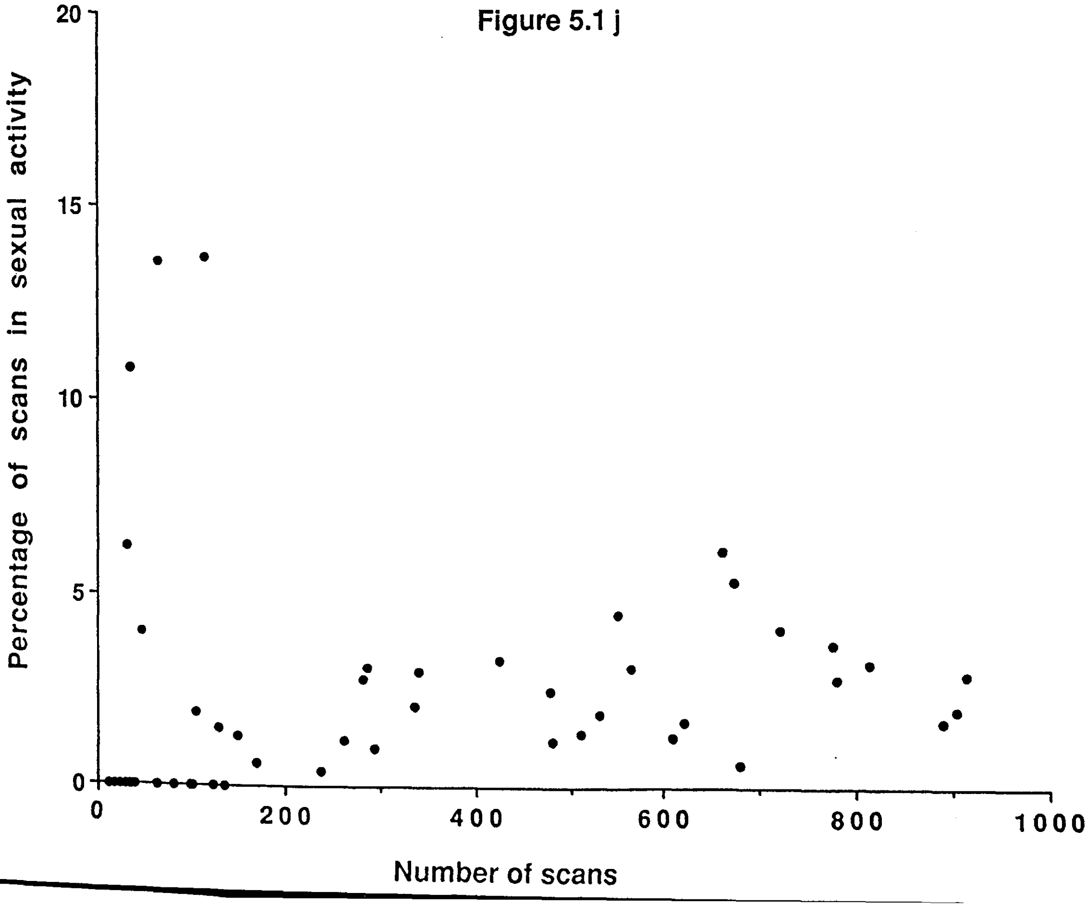


Figure 5.1 k

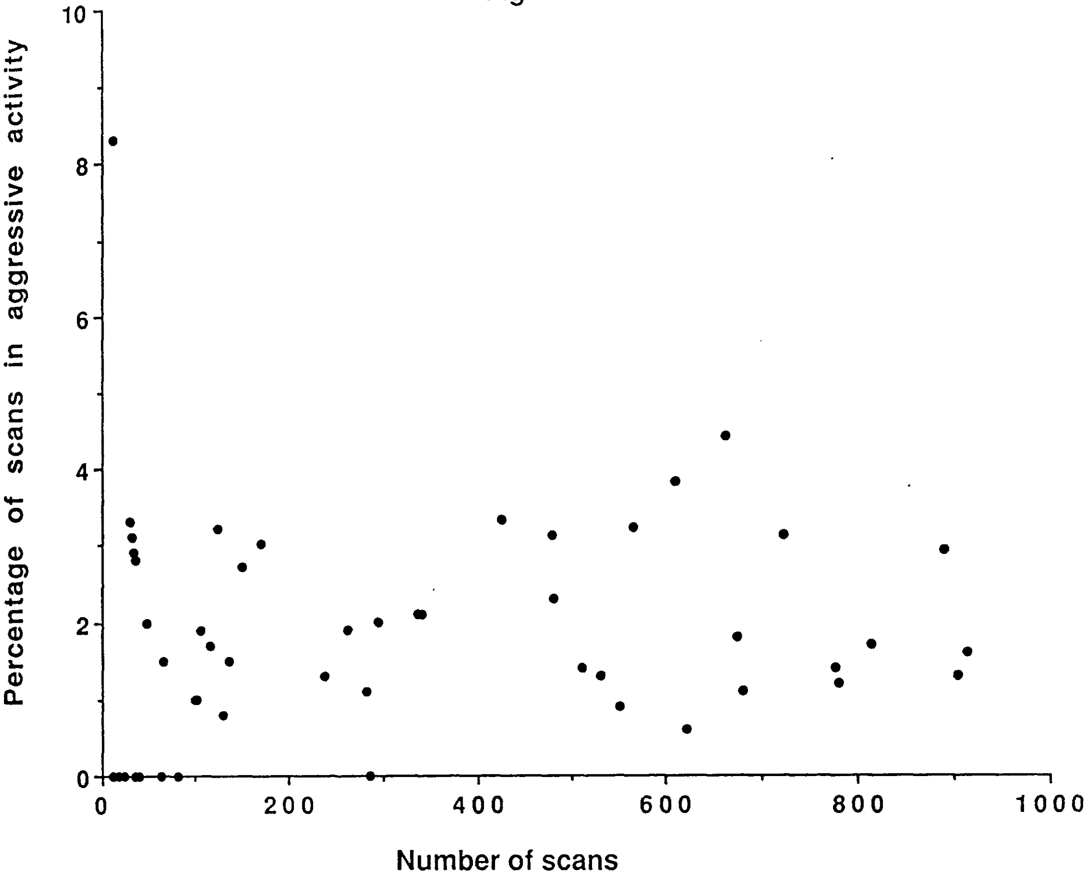


Figure 5.1 l

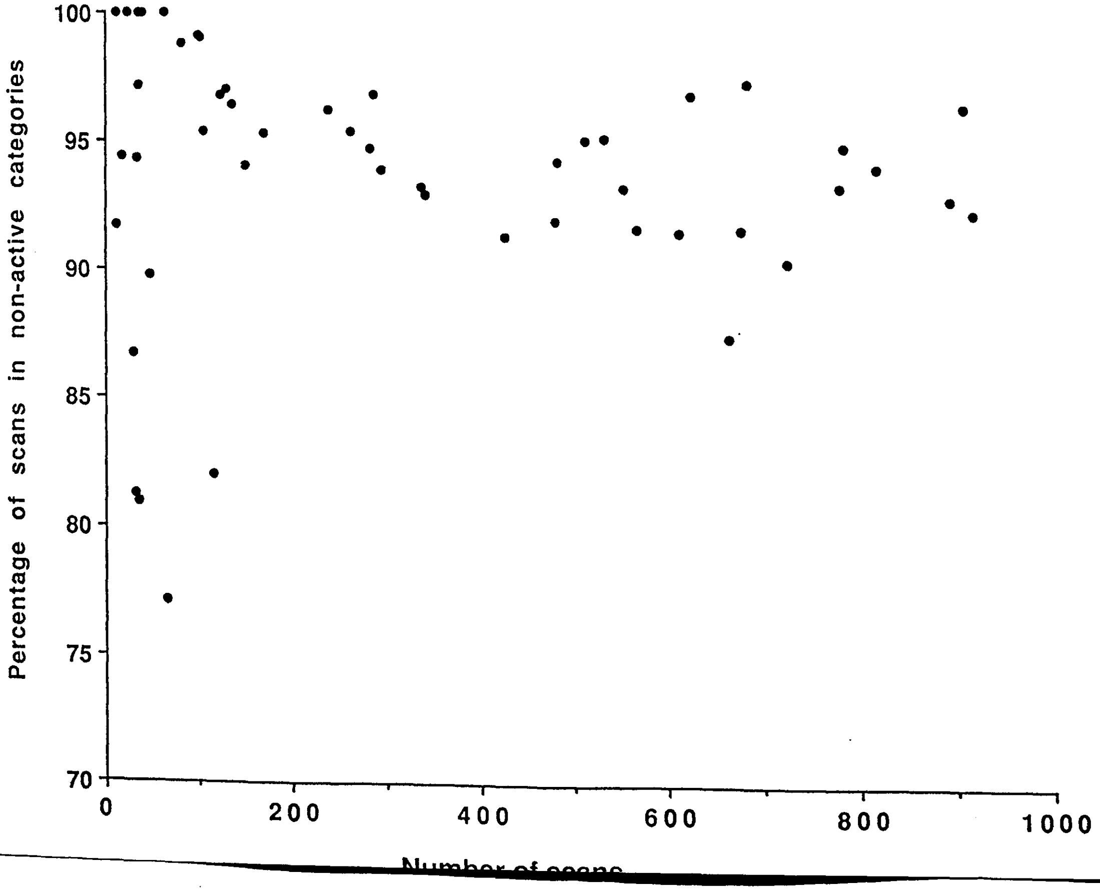
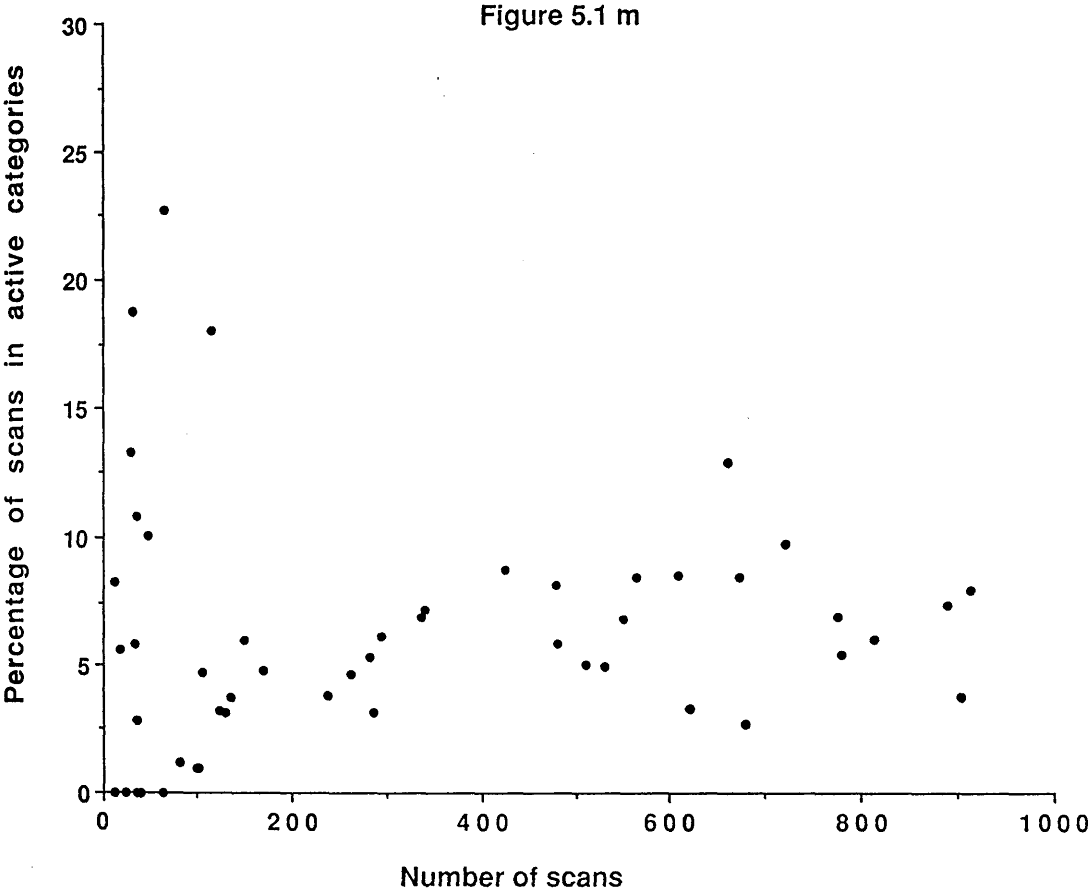


Figure 5.1 m


Percentage of scans in active categories
30
25
20
15
10
5
0
0
200
400
600
800
1000
Number of scans

5.1.2. *Gross activity budgets*

Table 5.1 shows summary statistics for the proportion of time spent in each behaviour category utilising a whole season's data for 1988. The data are based upon mean and median values of time spent in each category from the total activity budgets of all males observed. Only males which were observed in at least 180 scans were included. A total of 17940 scans were made during 1988, of which 14630 were used to gain the statistics in Table 5.1 by selecting only males observed in at least 180 scans.

Table 5.1 therefore, represents an overview of male activity patterns for a whole season. It must be noted that not every male was present for either the same duration or during the same part of the season and some seasonal changes in activity patterns may occur.

Table 5.1 shows statistics for each separate activity category and also composite (combined) categories. All categories are mutually exclusive with the exception of the combined categories. These are constructed in the following manner; Observant - this includes all categories involving being alert, namely "alert" and "looking at other males". Sexual - this encompasses all categories pertaining to sexual behaviour, i.e. "approach to female", "attempted copulation", "copulation" and "non-aggressive flippering". Aggressive - this combines all categories of aggressive behaviour, i.e. "looking at male", "approach to male", "open mouth threat", "lunge/bite/flippering", "fight" and "chase". The Non-active category encompasses all activity categories deemed to involve little energy expenditure i.e. "resting" and the observant category. The Active category includes all activities assumed to be energetically expensive i.e. aggression and sex, locomotion and rolling. Hence the combined categories of sexual and aggressive activities are mutually exclusive as are the categories of active and non-active. The observant category is exclusive of sexual activities but not aggressive activities.

The data presented in Table 5.1 were examined for Pearson correlations between the time spent in the independent categories of behaviour using the arc-sine transformed data. Inevitably, the proportion of time spent in each category is inter-correlated to some extent and many obvious correlations were produced, for example, as resting constitutes such a large proportion of the inactive phase, there was a strong positive correlation between these two categories. However, some interesting and possibly unexpected correlations and lack of correlations were produced. Sample size in all correlations was 26.

The proportion of time spent in resting was negatively correlated at $p < 0.01$ (with the exception of fighting, with which resting was correlated at $p < 0.05$ but not at $p < 0.01$) with all activity categories other than sexual activities. There were no significant correlations with any of the categories of sexual activities, nor with the combined category for sex ($r = -0.21$, $p = 0.295$).

In fact, there were no correlations between any of the sexual activities and any other type of single activity category, other than a positive correlation between attempted copulation and copulation ($r = +0.62$, $p = 0.001$). Thus, males which spent more time in attempted copulation also spent more time in actual copulation. However, males spending more time in aggression, whilst spending less time resting, do not spend significantly more or less time in sexual activity ($r = +0.14$, $p = 0.485$).

There was a significant positive correlation between amount of time in locomotion and being observant ($r = +0.59$, $p = 0.002$). Similarly, locomotion was positively correlated with time spent in aggressive activity ($r = +0.77$, $p < 0.001$) but not with sexual activity ($r = -0.11$, $p = 0.594$). The most likely interpretation of this is that males involved in more aggression tend to be those that are more observant and move around more.

Table 5.1 Summary statistics for activity budgets. Mean and median values are shown for the proportion of time spent in each type of activity and various groups of activities. Only males recorded in at least 180 scans are used in the calculation of these statistics. These values represent mean percentage of time in each category over the entire season (1988).

ACTIVITY	n	median	mean	standard deviation	min.	max.
RESTING	26	81.60	81.69	4.36	74.10	93.70
ALERT	26	12.15	11.86	3.17	3.10	17.30
LOCOMOTION	26	2.10	1.90	0.85	0.00	3.40
SEXUAL ACTIVITIES						
APPROACH TO FEMALE	26	0.35	0.36	0.26	0.00	0.90
ATTEMPTED COPULATION	26	0.90	0.89	0.63	0.00	2.00
COPULATION	26	1.25	1.32	0.98	0.00	3.70
NON-AGGRESSIVE FLIPPERING	26	0.00	0.01	0.03	0.00	0.20
AGGRESSIVE ACTIVITIES						
ALERT - LOOKING AT MALE	26	0.00	0.00	0.00	0.00	0.00
APPROACH TO MALE	26	0.00	0.00	0.00	0.00	0.00
OPEN MOUTH THREAT	26	1.25	1.41	0.85	0.00	3.00
LUNGE/BITE/FLIPPERING	26	0.00	0.04	0.14	0.00	0.70
FIGHT	26	0.10	0.19	0.23	0.00	0.70
CHASE	26	0.20	0.32	0.38	0.00	1.10
ROLL	26	0.00	0.004	0.02	0.00	0.10
COMBINED CATEGORIES						
OBSERVANT	26	12.15	11.86	3.17	3.10	17.30
SEXUAL	26	2.65	2.57	1.41	0.40	6.10
AGGRESSIVE	26	1.75	1.96	1.05	0.00	4.40
NON-ACTIVE	26	93.55	93.55	2.31	87.30	97.20
ACTIVE	26	6.45	6.44	2.33	2.70	12.80
NUMBER OF SCANS/MALE	26	558.50	562.69	212.37	238.00	914.00

5.1.3. *Diurnal variation in activity*

Graphs 5.2 a to i illustrate the diurnal variation in each activity category. These were computed by determining the percentage of time spent in each activity category by each male during successive hours. A mean value for all males was then calculated together with standard errors. Only males recorded on at least 180 scans within each hour were used in the analysis.

Although there may be an indication of a lull in activity around midday, with a corresponding increase in resting, these results show no significant diurnal variation in any activity category during the hours of observation (daylight hours). There is no consistent trend throughout the day, though all these graphs show considerable variation around the mean values. This agrees with studies by Anderson (1978) and Boness (1984). The extreme variability hides any trend in daily activity. Whilst mean values for all males present show no significant trend, it is possible that individual males may show some degree of daily pattern, but that these patterns differ between males. It was not possible to examine males individually in this respect. It would be necessary to examine an individual's activity pattern on successive days, or, for example, on a weekly basis in order to ascertain any consistent trend for that individual. Few males were observed in sufficient scans to allow this analysis. It would require focal animal samples on a reasonable sample of males in order to examine this.

Cameron (1970) stated that whilst there was no effect of daylight hours on daily patterns of seals there was relationship with tidal state. This was however based on observations of grey seals hauled out on beaches around Nova Scotia and Gulf of St. Lawrence (Canada). On Rona, during the breeding season males and females come far inland, well above the high tide mark and no tidal rhythm was evident (see also Anderson 1978). The tidal cycle may influence the behaviour of peripheral males, which haul out on the rocky shores of the study area. However, these individuals were not included in the analyses, either because they could not be observed from the hide, or, being peripheral males, were not observed on sufficient scans. Those individuals securing positions in the colony were generally present for sufficient time to be recorded in 180 scans.

Figures 5.2a to i: Diurnal variation in activity categories. Mean values (± standard errors) for estimated percentage of time in various activity categories on an hourly basis. Only males recorded on at least 180 scans within each hour were included in the analyses. Sample sizes (number of males) are given in Figure 5.2a.

Figure 5.2 a : Diurnal variation in resting

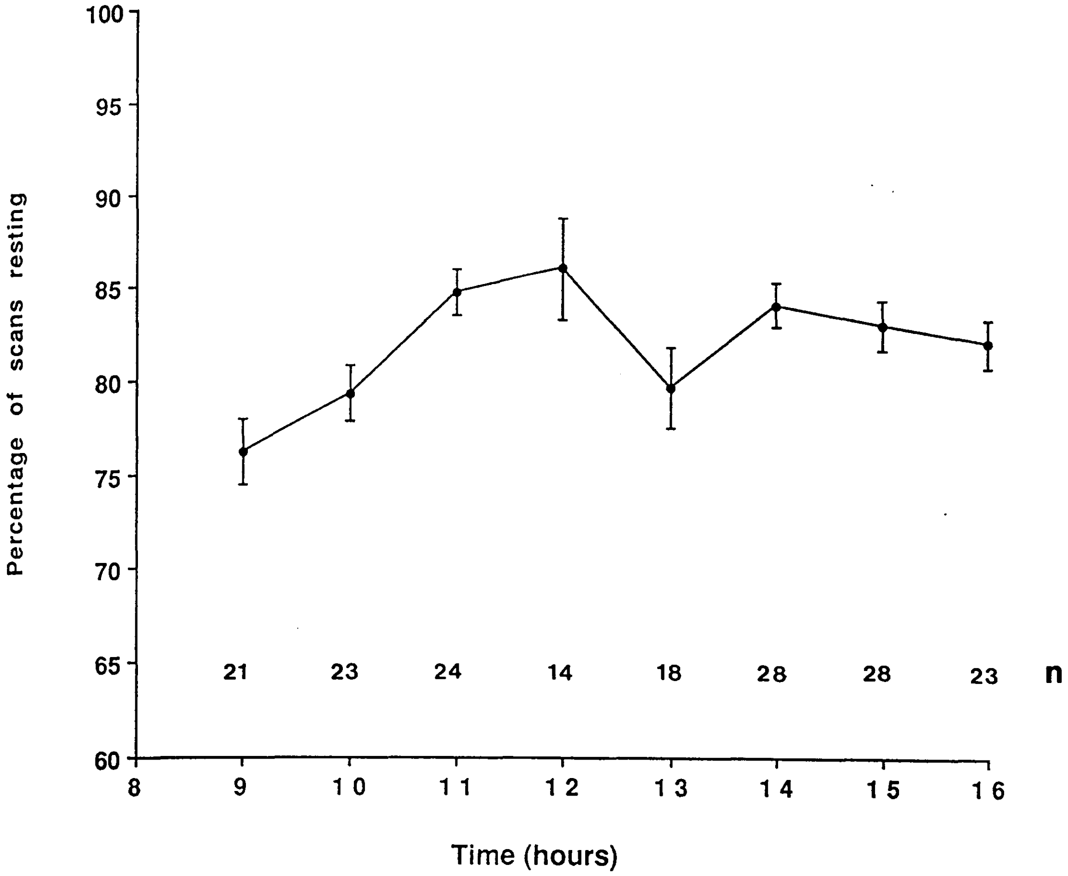


Figure 5.2 b : Diurnal variation in alert

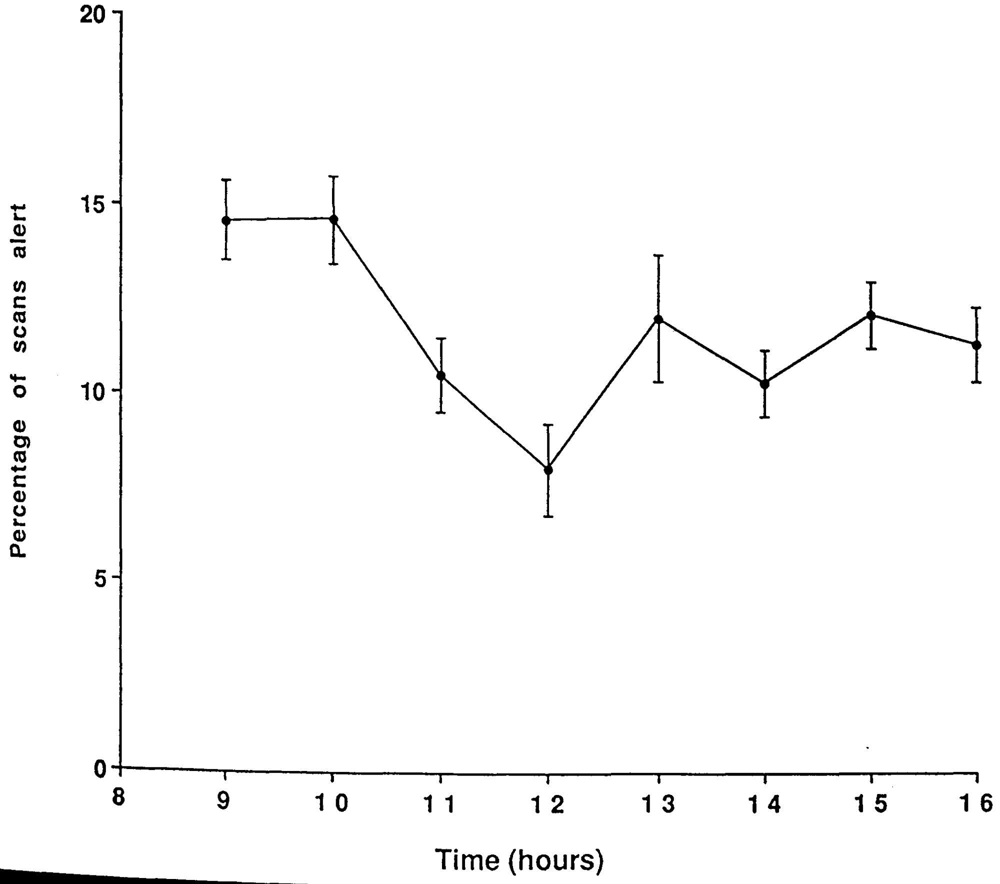


Figure 5.2 c : Diurnal variation in locomotion

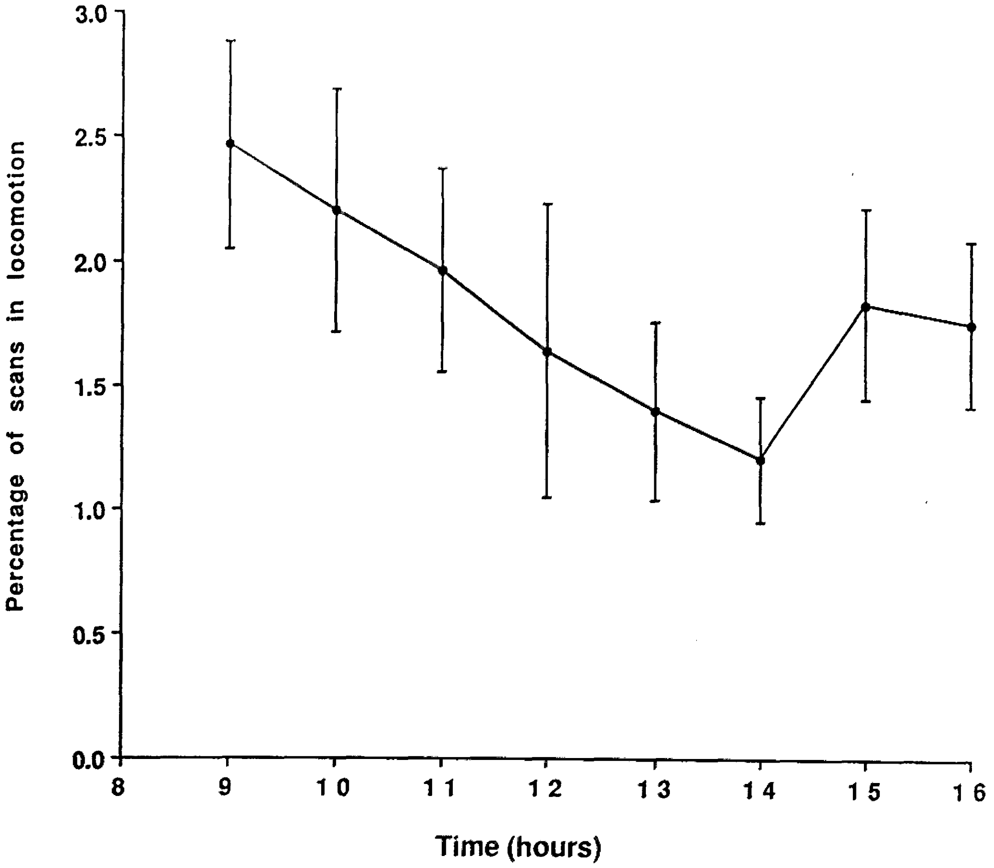


Figure 5.2 d : Diurnal variation in approaches to females

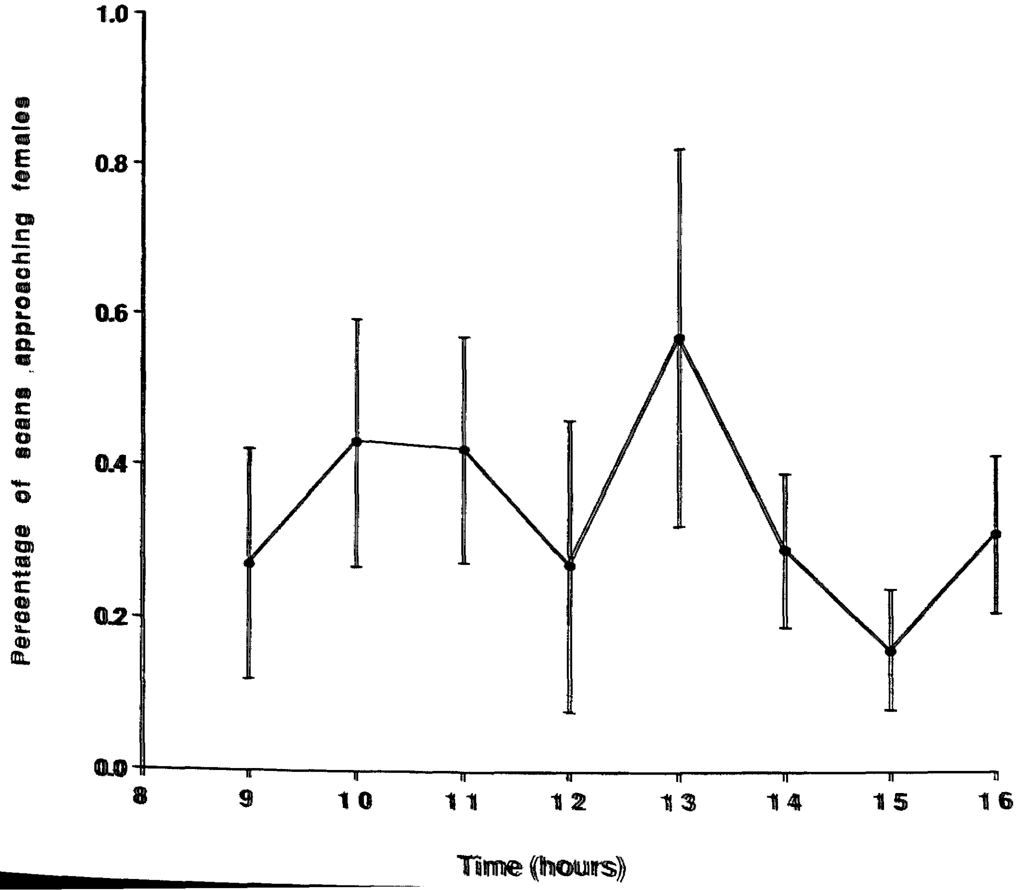


Figure 5.2 e : Diurnal variation in attempted copulation

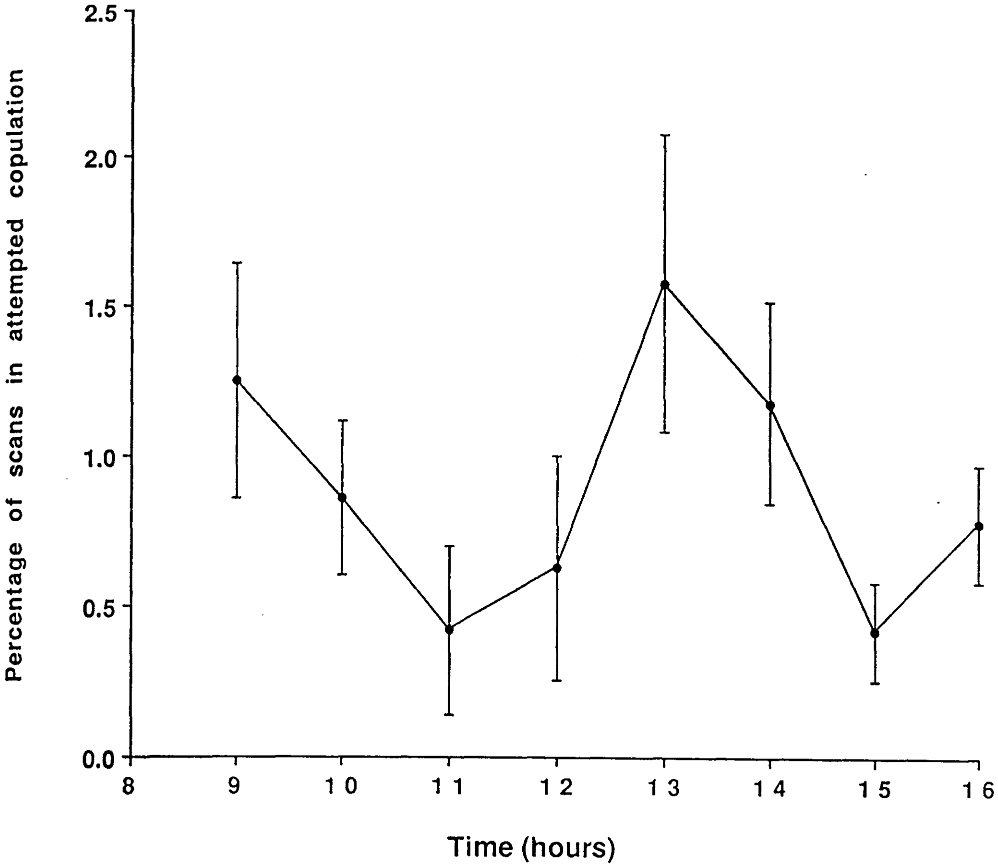


Figure 5.2 f : Diurnal variation in copulation

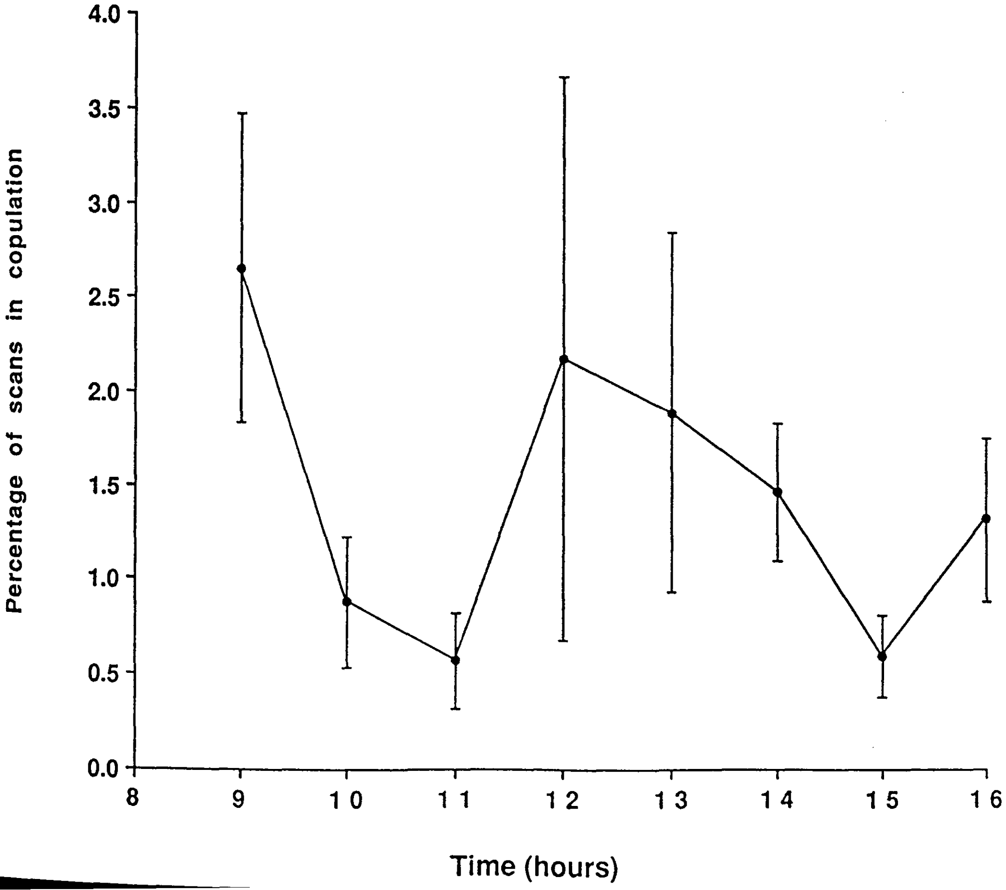


Figure 5.2 g : Diurnal variation in open mouth threat

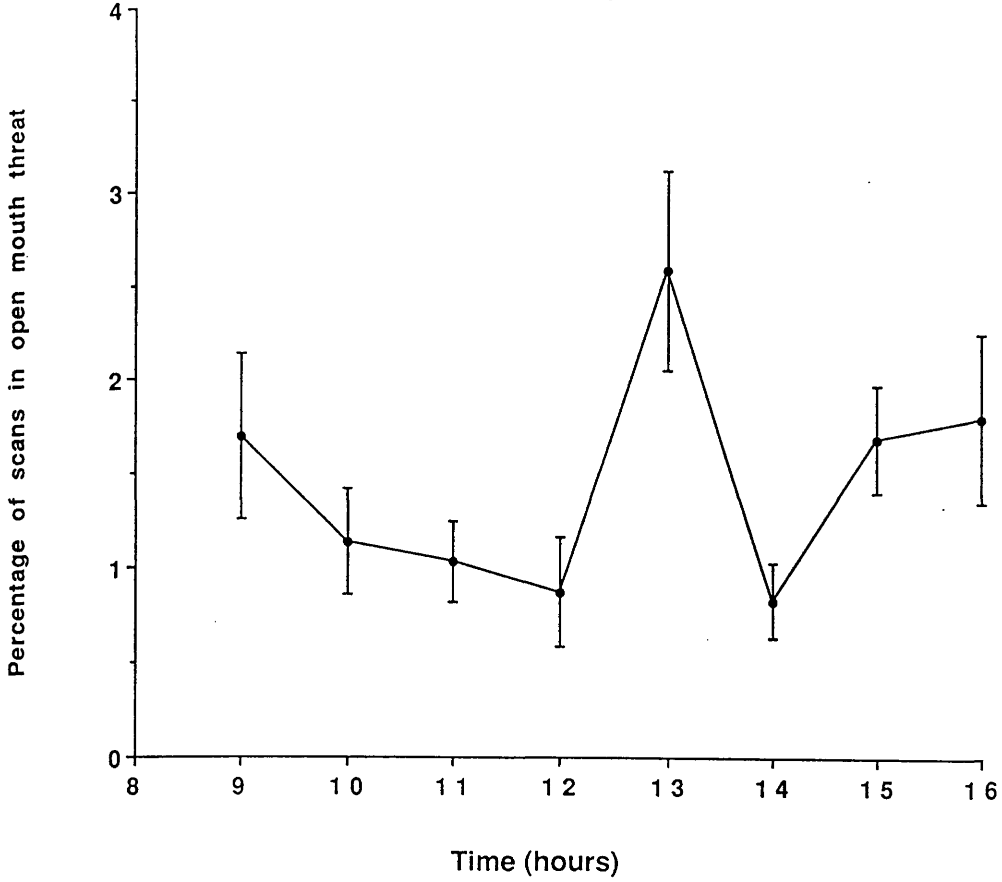


Figure 5.2 h : Diurnal variation in fighting

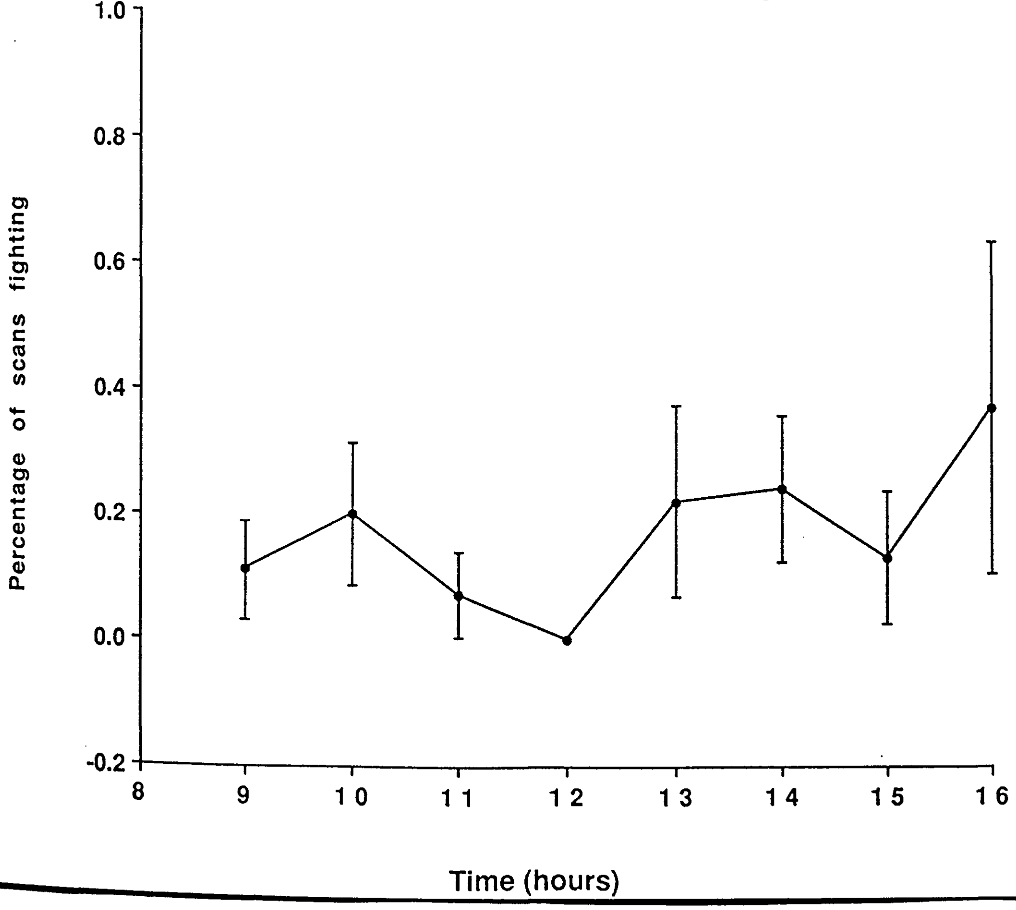
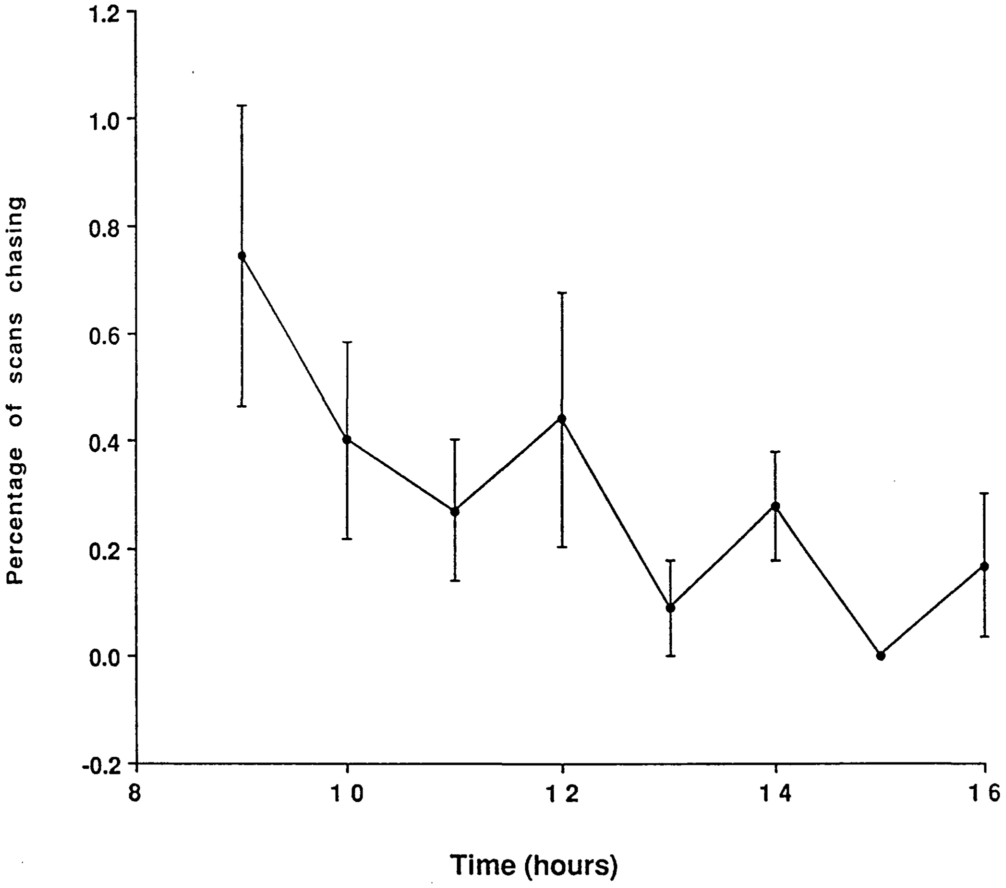


Figure 5.2 i : Diurnal variation in chasing



5.1.4. *Seasonal variation in activity*

Graphs 5.3 a to i illustrate seasonal variation in the various activity categories. Again, there is no obvious trend and variation about the mean is extreme. Whilst there is no discernible change in proportion of time spent in the various activity categories there are important trends in the frequency of activities, in particular aggressive and sexual activity (see Chapter 3). This appears somewhat contradictory as there is no detectable change in the mean durations of the main activities during the season. However, a possible explanation lies in the increased numbers of subordinate and peripheral males ashore later in the season. During the latter half of the season, the greater number of males (and females) present will tend towards increased frequencies of activities, in particular sexual and aggressive activity (see Chapter 3). The presence of relatively more subordinate males during this period, which generally partake in many short aggressive interactions and few sexual interactions, may bias the mean percentage of time spent in these categories and contribute to the high variation observed.

5.2. Weight and age data

5.2.1. *Rates of weight loss*

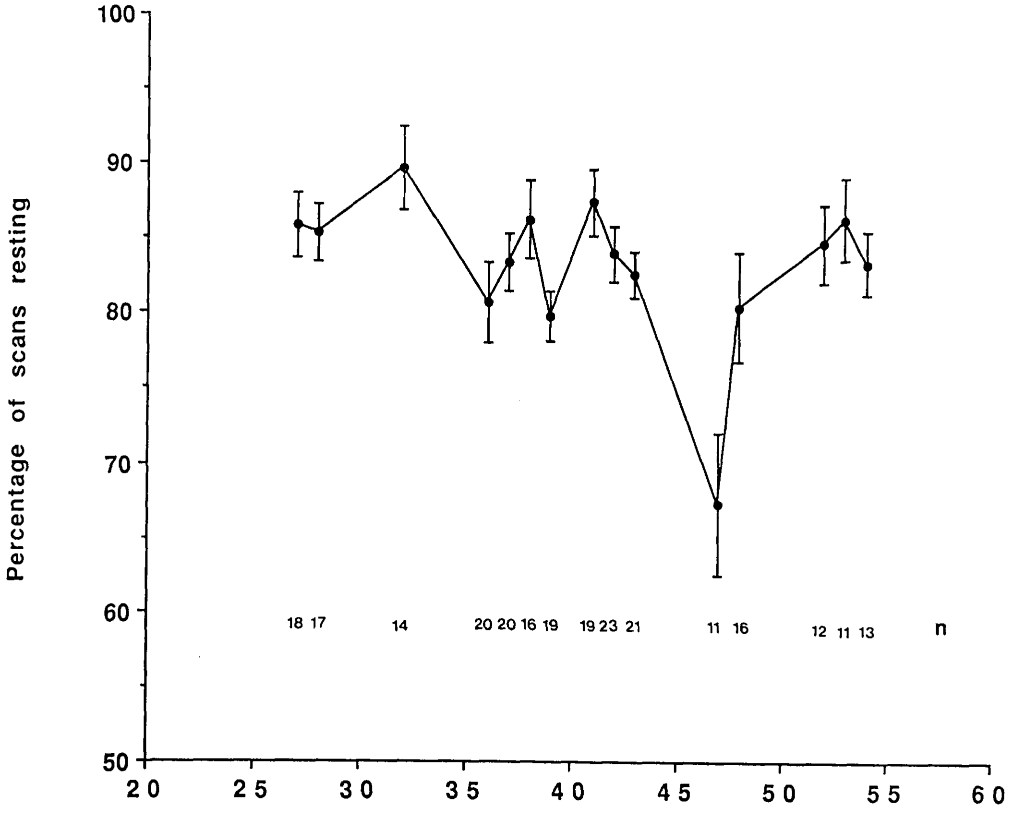
Several males were caught and weighed on more than two occasions in each season. From these we were able to examine fluctuations in the rate of weight loss of individuals during the breeding season. These are presented in Figures 5.4 a, b and c, representing 1987, 1988 and 1989 respectively.

In general the rate of weight loss appears to be reasonably linear throughout each season. There is certainly no consistent trend across all individuals, some males show a greater rate of weight loss early in the season compared to later, whilst others show the opposite pattern. Most however, do not deviate markedly from a linear weight loss regime.

The mean rates of weight loss ranged between 1.87 and 2.12 kg/day (see Table 5.2 a). Combining data from all three years the mean value is 1.99 kg/day (SE = 0.07, n = 59). The mean values for specific rate of weight loss ranged between 0.91 and 1.03. The

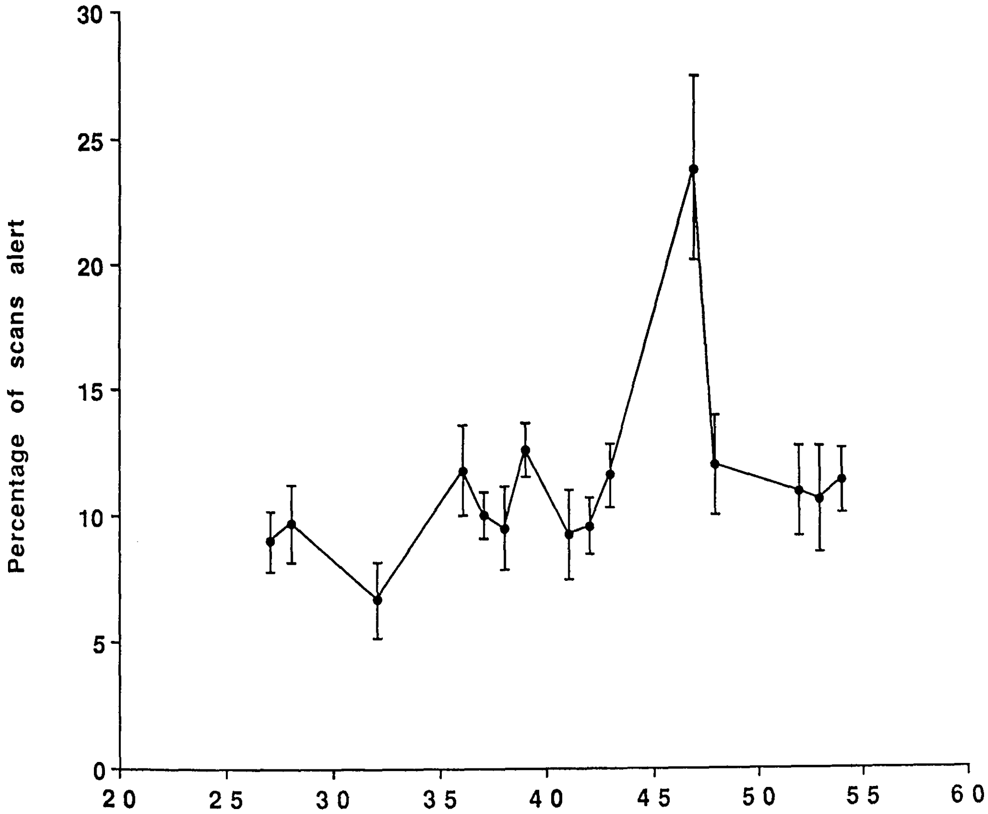
Figures 5.3a to i: Seasonal variation in activity categories. Mean values (± standard errors) for estimated percentage of time in various activity categories on a daily basis. Sample sizes (number of males) are given in Figure 5.3a.

Figure 5.3 a : Seasonal variation in resting



Days from 19/09/88

Figure 5.3 b : Seasonal variation in alert



Days from 19/09/88

Figure 5.3 c : Seasonal variation in locomotion

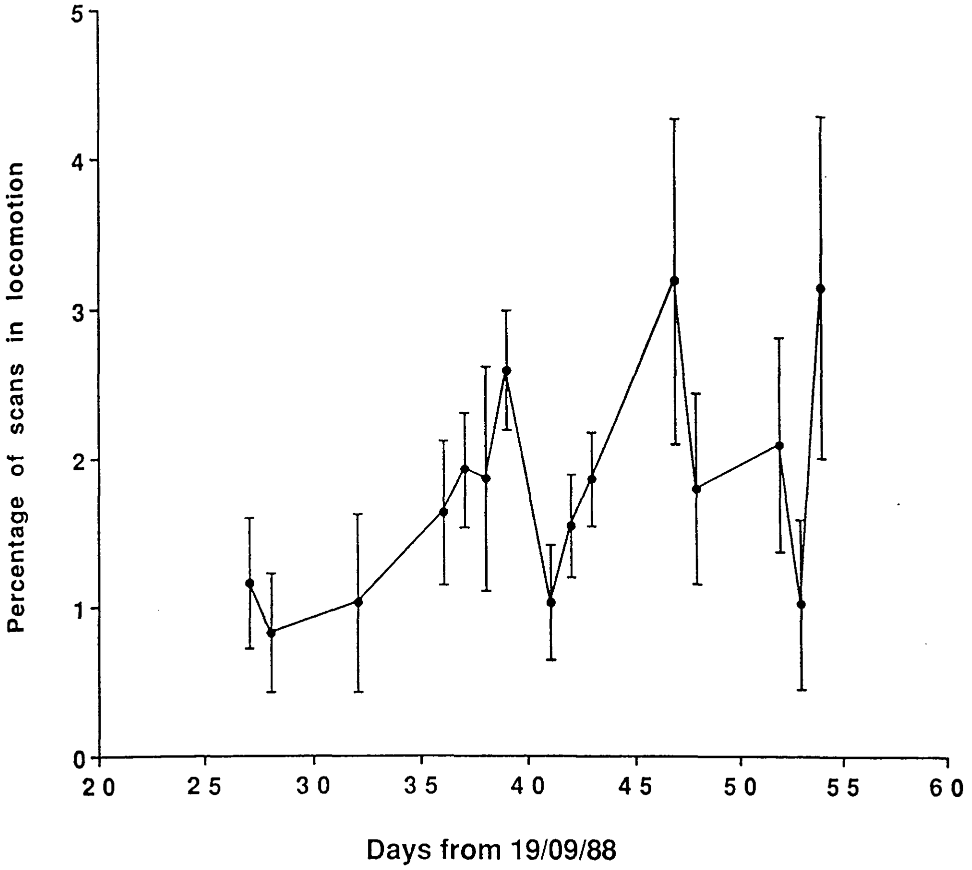


Figure 5.3 d : Seasonal variation in approaches to females

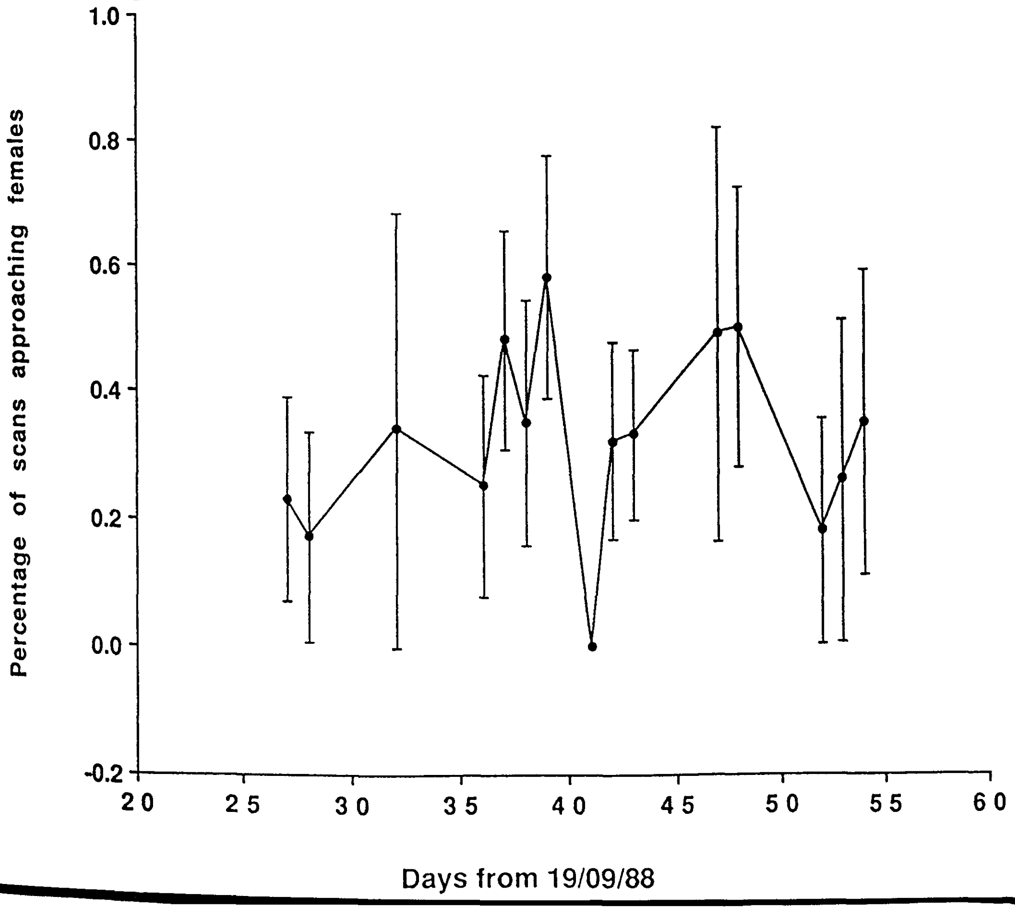


Figure 5.3 e : Seasonal variation in attempted copulation

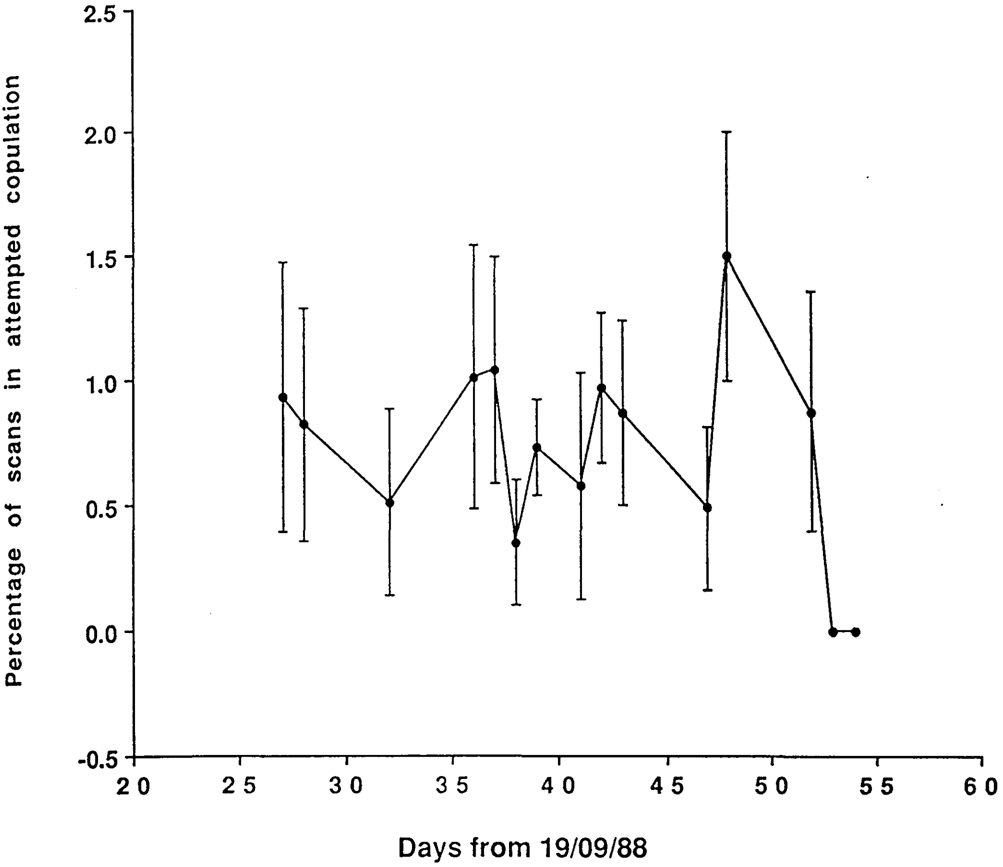


Figure 5.3 f : Seasonal variation in copulation

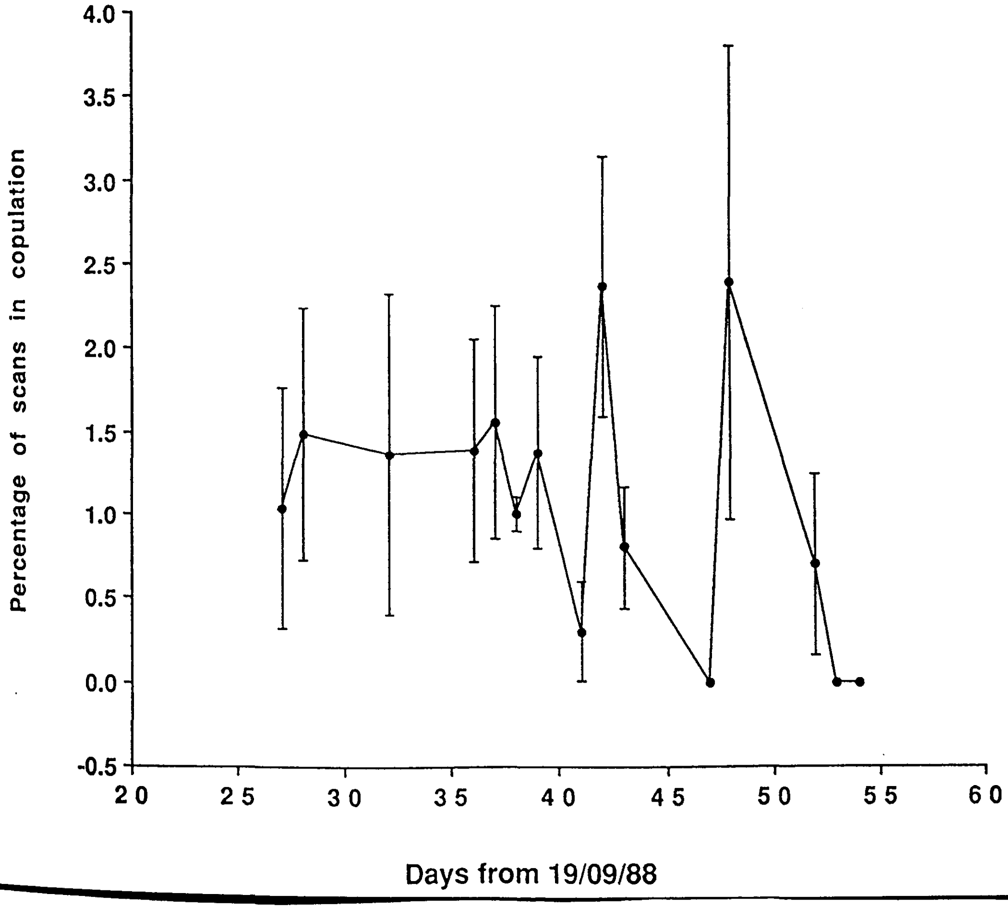


Figure 5.3 g : Seasonal variation in open mouth threats

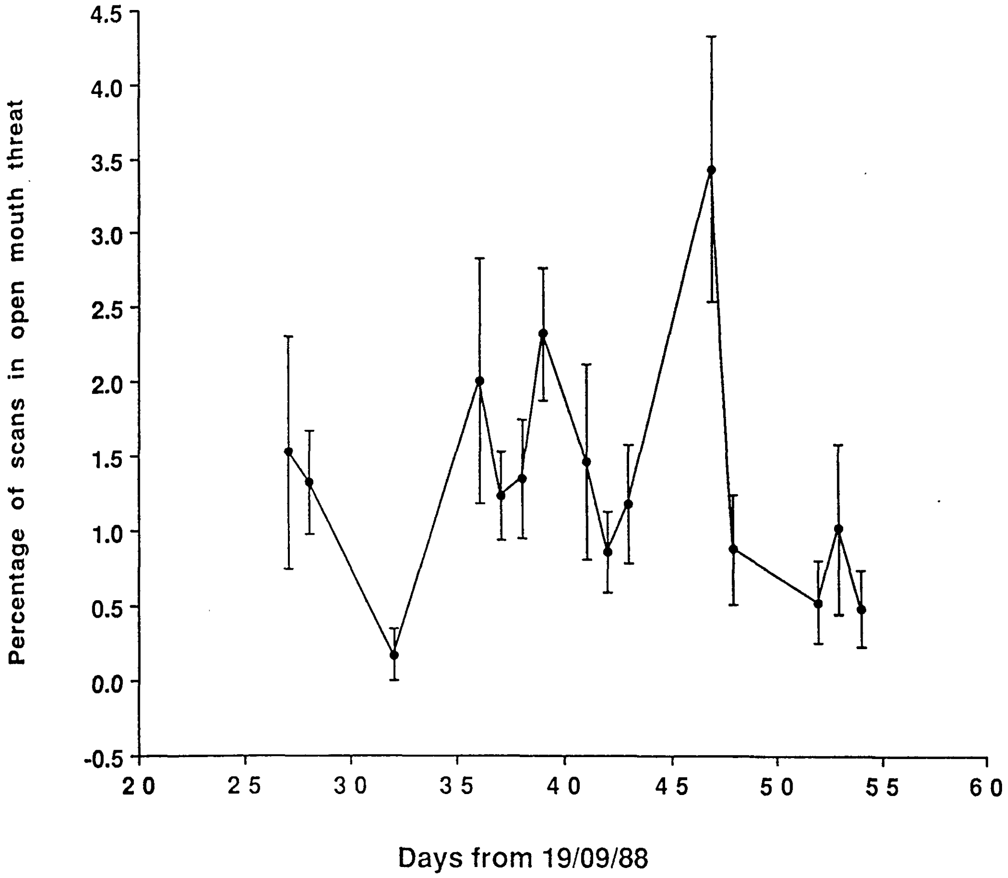


Figure 5.3 h : Seasonal variation in fighting

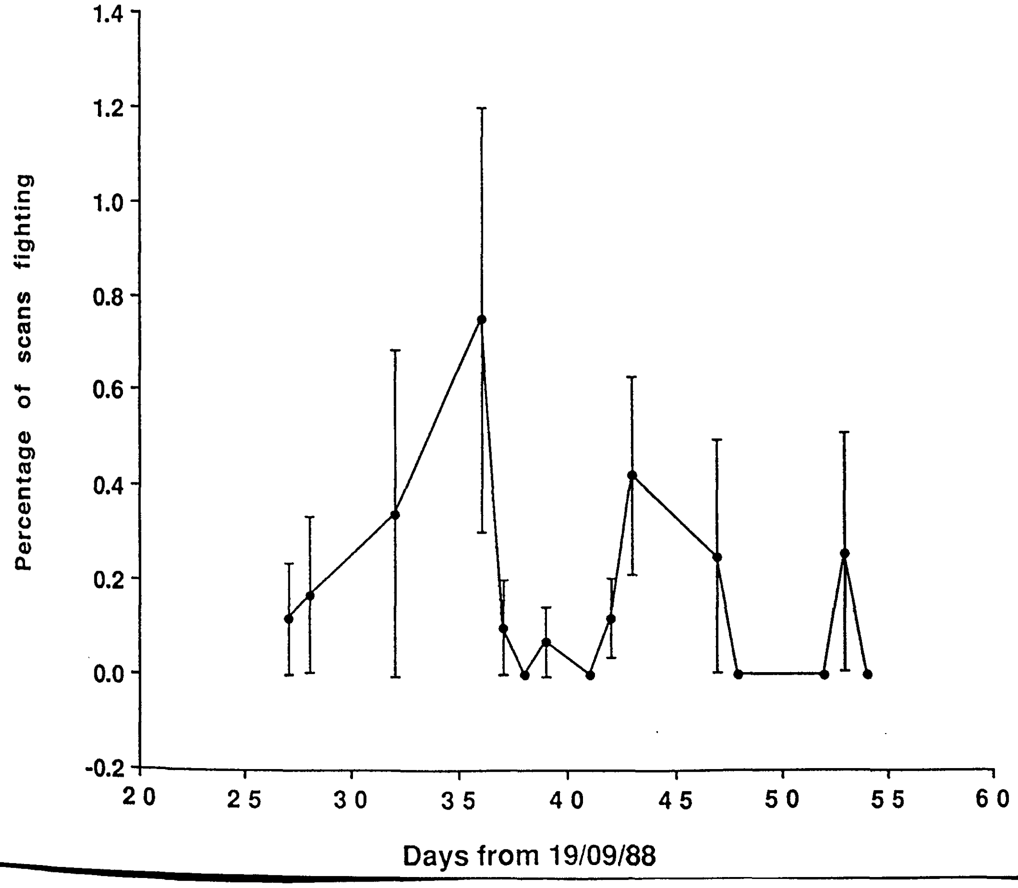
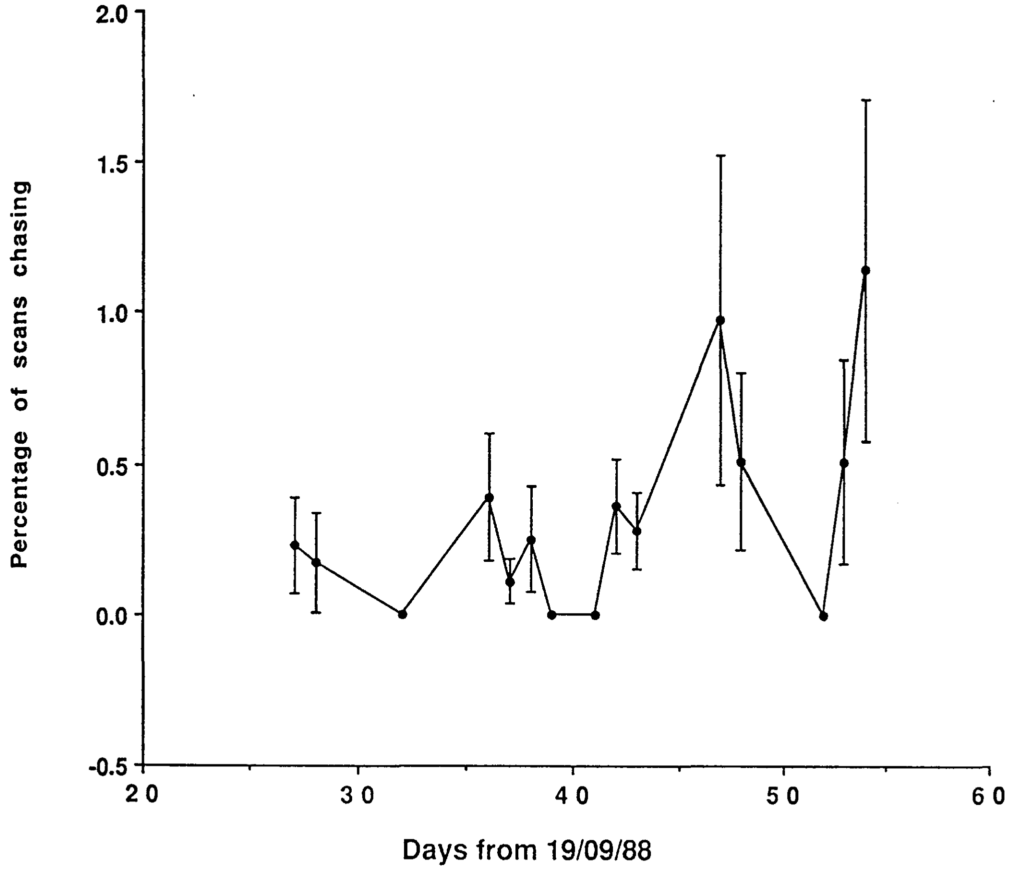


Figure 5.3 i : Seasonal variation in chasing



Figures 5.4a to c: Plots of individual rates of weight loss for Rona 1987, 1988 and 1989. Individual 3 digit male identity codes are given.

Figure 5.4 a : Rates of weight loss - Rona 1987

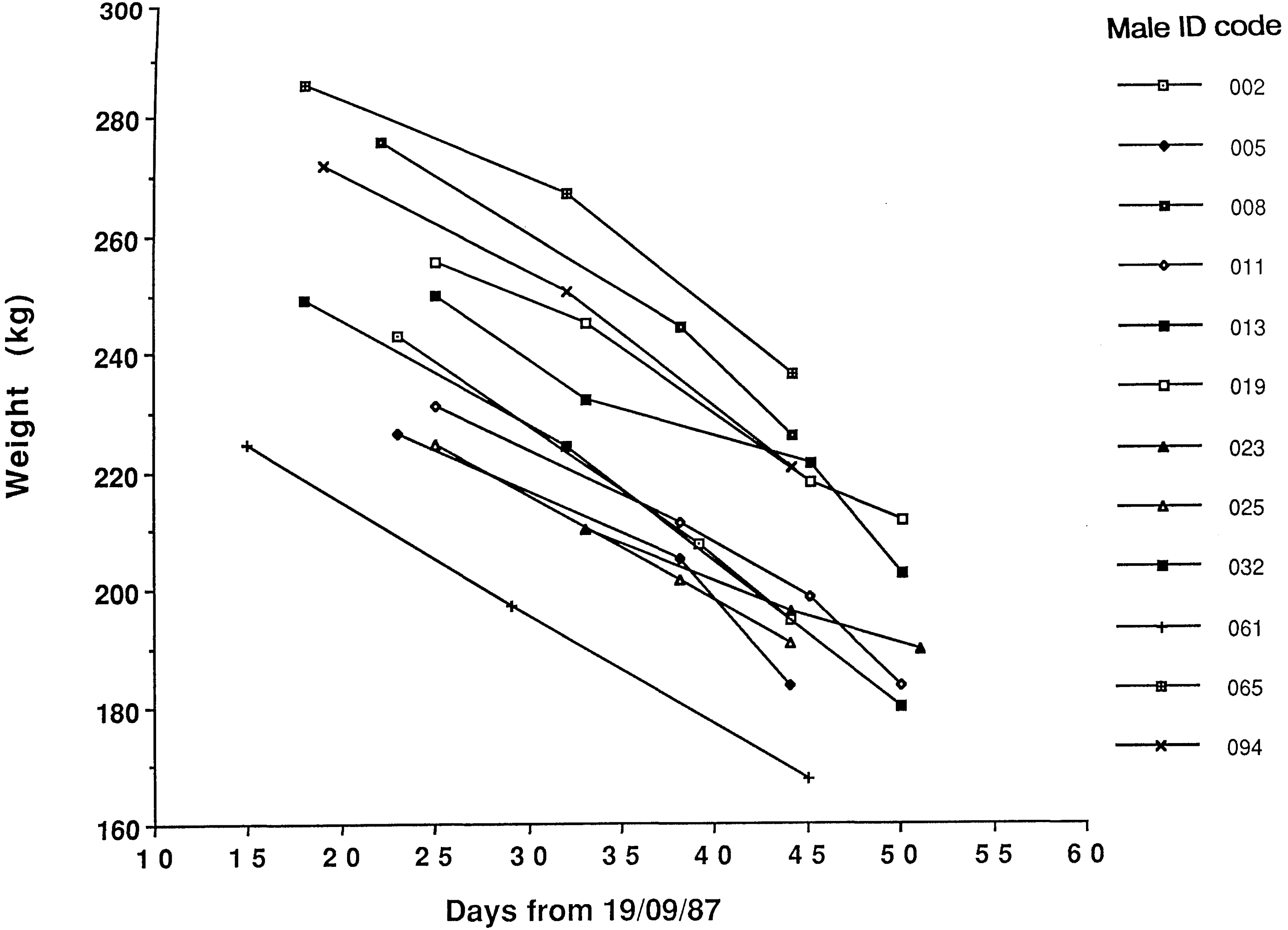


Figure 5.4 b : Rates of weight loss - Rona 1988

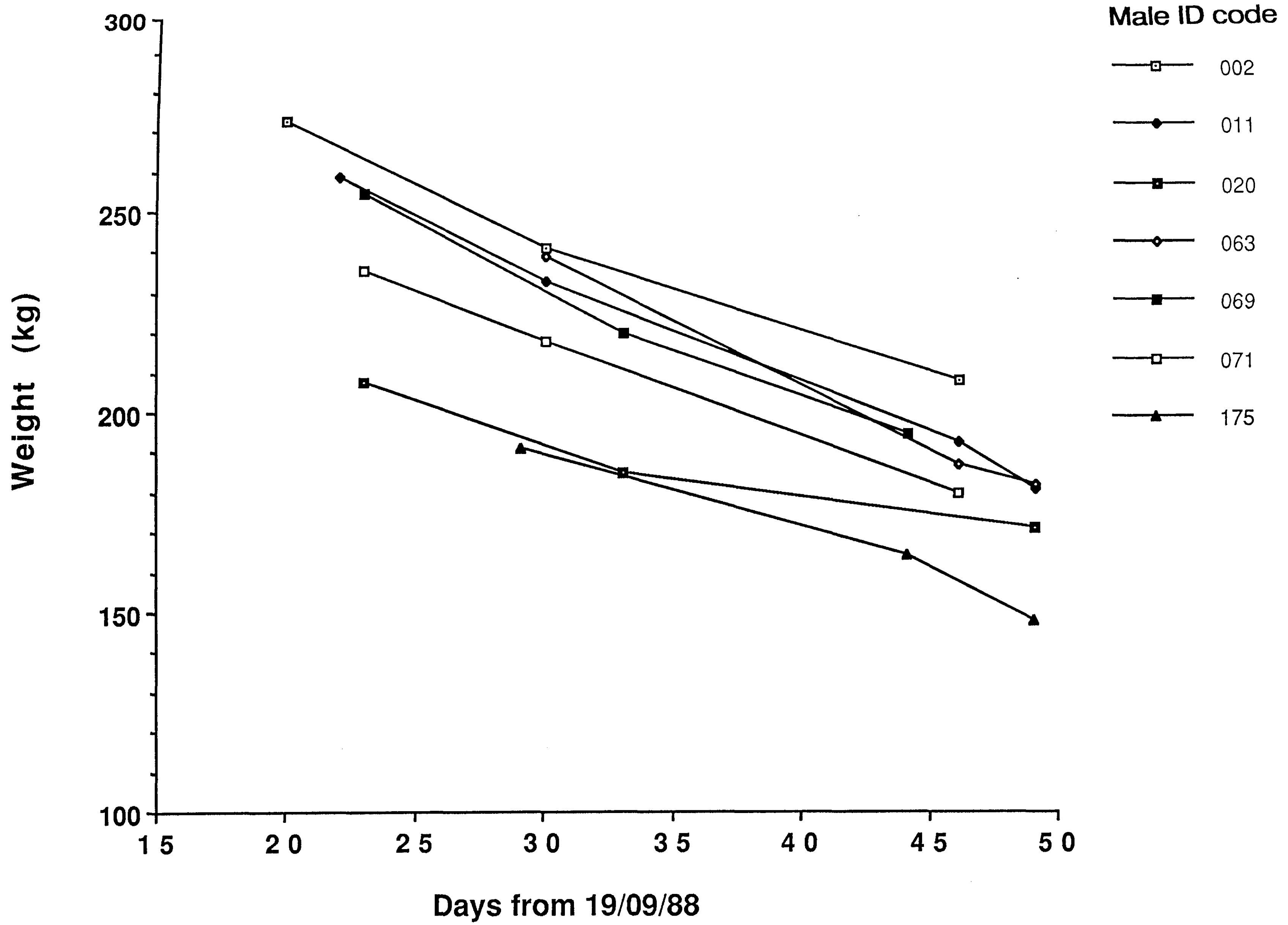
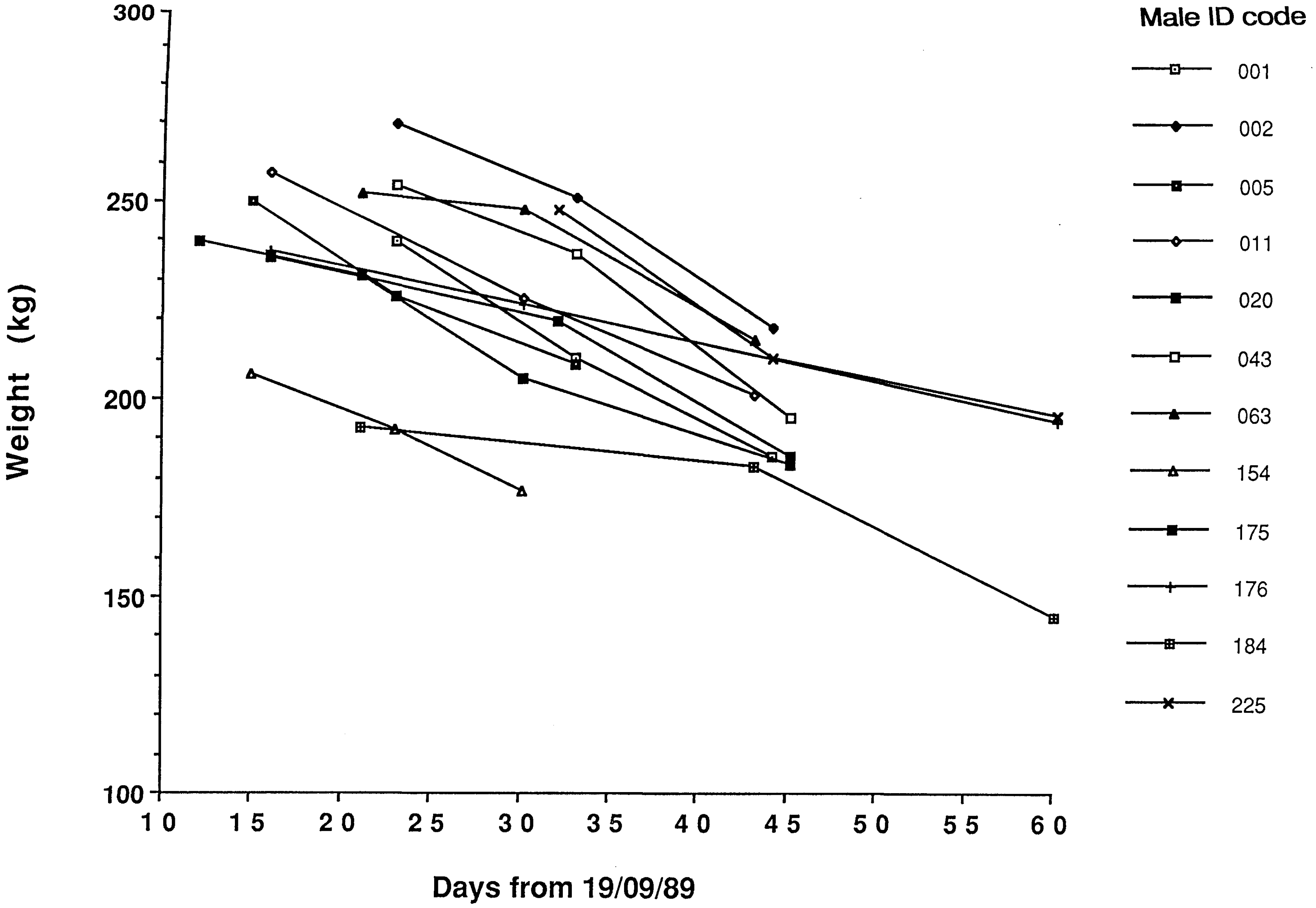


Figure 5.4 c : Rates of weight loss - Rona 1989



overall mean value was 0.95. The relative variation about the mean values for both absolute and specific rates of weight loss were compared by computing coefficients of variation and appropriate standard errors (S.E) for each parameter in each of the three years (see Chapter 4 for the formulae used). Using the data presented in Table 5.2 a, no significant differences were found in the variation about the mean values in any of the three seasons. Within each year, all absolute rate of weight loss coefficients of variation overlapped within one standard error with the coefficient for specific rate of weight loss and vice versa (see Table 5.2 c). Similarly. no difference was found between the variation about the mean of the two weight loss measures upon using the data for study area males only (Table 5.2 b).

Individual variation in rates of absolute and specific weight loss are examined in relation to behavioural and other energetic parameters in Chapter 7.

Table 5.2a

Summary statistics for weight parameters and age for all males caught during each breeding season. Units are as stated in the methods.

YEAR	VARIABLE	n	median	mean	S.D.	S.E.	min.	max.
1987	Wt ON DAY 1	19	287.30	287.46	21.07	4.83	251.50	324.19
	ARRIVAL Wt (a)	19	251.27	256.14	20.48	4.70	228.43	297.67
	DEPARTURE Wt (b)	19	185.78	187.50	14.53	3.33	161.98	213.68
	a/b x 100(%)	19	73.05	73.34	4.44	1.02	66.92	82.44
	RATE Wt LOSS	19	-1.85	-1.87	0.30	0.07	-1.15	-2.50
	SPECIFIC Wt LOSS RATE	19	0.92	0.91	0.18	0.04	0.55	1.25
	AGE (yrs)	17	11.00	11.65	3.06	0.74	8	19
1988	Wt ON DAY 1	21	280.24	286.83	42.27	9.22	187.54	337.31
	ARRIVAL Wt (a)	21	256.41	260.82	44.53	9.72	161.80	327.32
	DEPARTURE Wt (b)	21	167.67	172.23	34.78	7.59	111.70	288.46
	a/b x 100(%)	21	65.99	66.96	12.45	2.72	44.96	91.91
	RATE Wt LOSS	21	-2.37	-2.12	0.72	0.16	-0.56	-3.08
	SPECIFIC Wt LOSS RATE	21	1.07	1.03	0.35	0.08	0.26	1.55
	AGE (yrs)	28	12.00	11.93	3.01	0.57	7	20
1989	Wt ON DAY 1	19	289.95	283.46	46.25	10.61	206.20	399.75
	ARRIVAL Wt (a)	19	253.12	256.34	45.25	10.38	198.36	388.55
	DEPARTURE Wt (b)	19	182.24	180.91	26.01	5.97	142.45	256.80
	a/b x 100(%)	19	71.46	71.11	5.68	1.30	61.88	84.03
	RATE Wt LOSS	19	-1.93	-1.97	0.58	0.13	-0.78	-2.80
	SPECIFIC Wt LOSS RATE	19	0.91	0.91	0.26	0.06	0.39	1.48
	AGE (yrs)	31	13.00	12.68	3.02	0.54	8	21

Table 5.2b

Summary statistics for weight parameters and age for all males caught in the study area during each breeding season and for which behavioural observations were also recorded. Units are as stated in the methods.

YEAR	VARIABLE	n	median	mean	S.D.	S.E.	min.	max.
1987	Wt ON DAY 1	14	291.75	286.71	20.19	5.40	251.50	324.19
	ARRIVAL Wt (a)	14	252.84	255.98	20.68	5.53	228.43	297.67
	DEPARTURE Wt (b)	14	184.45	185.08	14.37	3.84	161.98	213.68
	a/b x 100(%)	14	71.53	72.44	4.35	1.16	66.92	79.06
	RATE Wt LOSS	14	-1.88	-1.91	0.35	0.09	-1.15	-2.50
	SPECIFIC Wt LOSS RATE	14	0.96	0.95	0.19	0.05	0.55	1.25
	AGE (yrs)	13	11.00	11.31	2.56	0.71	8	16
1988	Wt ON DAY 1	16	287.95	293.38	35.92	8.98	238.05	336.76
	ARRIVAL Wt (a)	16	258.04	265.66	37.11	9.28	191.80	317.09
	DEPARTURE Wt (b)	16	167.37	167.95	24.25	6.06	111.70	206.23
	a/b x 100(%)	16	63.28	64.04	11.30	2.82	44.96	91.91
	RATE Wt LOSS	16	-2.42	-2.29	0.71	0.18	-0.56	-3.08
	SPECIFIC Wt LOSS RATE	16	1.22	1.11	0.33	0.08	0.26	1.55
	AGE (yrs)	20	10.50	11.15	2.74	0.61	7	17
1989	Wt ON DAY 1	16	281.78	271.91	36.78	9.20	206.20	325.47
	ARRIVAL Wt (a)	16	249.38	249.71	30.87	7.72	200.20	294.70
	DEPARTURE Wt (b)	16	180.42	174.92	17.28	4.32	142.45	195.96
	a/b x 100(%)	16	70.65	70.39	4.95	1.24	61.88	78.99
	RATE Wt LOSS	16	-1.80	-1.86	0.56	0.14	-0.78	-2.70
	SPECIFIC Wt LOSS RATE	16	0.91	0.91	0.28	0.07	0.39	1.48
	AGE (yrs)	26	12.50	12.42	2.73	0.54	8	18

Table 5.2c

Comparison of coefficients of variation for absolute and specific rates of weight loss, for each of the three breeding seasons on Rona.

YEAR	VARIABLE	df	coefficient of variation	S.E.
1987	RATE Wt LOSS	18	16.04	2.63
	SPECIFIC Wt LOSS RATE	18	19.78	3.27
1988	RATE Wt LOSS	20	33.96	5.53
	SPECIFIC Wt LOSS RATE	20	33.98	5.53
1989	RATE Wt LOSS	18	29.44	4.98
	SPECIFIC Wt LOSS RATE	18	28.57	4.82

Table 5.2d

Comparison of coefficients of variation for arrival and departure weights, for each of the three breeding seasons on Rona.

YEAR	VARIABLE	df	coefficient of variation	S.E.
1987	ARRIVAL Wt.	18	8.00	1.30
	DEPARTURE Wt	18	7.76	1.26
1988	ARRIVAL Wt.	20	17.07	2.67
	DEPARTURE Wt	20	20.19	3.18
1989	ARRIVAL Wt.	18	17.65	2.90
	DEPARTURE Wt	18	14.38	2.35

5.2.2. *Weight parameters and age*

Table 5.2 a and b present the summary statistics for all weight parameters and age. Table 5.2 a is based on all data collected in each season, including males outside the study area, whilst Table 5.2 b is based solely upon study area males.

The arrival weights of males ranged between 161.8 kg and 388.5 kg, a 2.4 fold difference. The mean values were 256.14 kg (SE = 4.7, n = 19), 260.82 kg (SE = 9.72, n = 21) and 256.34 kg (SE = 10.38, n = 19) for 1987, 1988 and 1989 respectively. Again, combining all three seasons' data a mean of 257.87 kg (SE = 4.97, n = 59) is obtained. The mean values for departure weight ranged between 172.23 kg and 187.50 kg. The overall mean value was 180.21 kg. The relative variation about the mean values for both arrival and departure weight were compared by computing coefficients of variation and appropriate standard errors (S.E) as above. Using the data presented in Table 5.2 a, no significant differences were found in the variation about the mean values in any of the three seasons. As with the rates of weight loss, all starting weight coefficients of variation overlapped within one standard error with the coefficient for departure weight and vice versa (see Table 5.2 d). Similarly. no difference was found between the variation about the mean of arrival and departure weights upon using the data for study area males only (Table 5.2 b).

The data presented in Table 5.2 a were entered in a oneway analysis of variance (with Scheffe's Multiple Range test) in order to compare the mean values of each variable between years. There was no significant difference in the mean values of any of the seven variables between the three seasons; weight on day one - $F_{2,56} = 0.06$, $p = 0.941$, arrival weight - $F_{2,56} = 0.10$, $p = 0.910$, departure weight - $F_{2,56} = 2.45$, $p = 0.100$, departure weight expressed as a percentage of the arrival weight - $F_{2,56} = 2.15$, $p = 0.126$, rate of weight loss - $F_{2,56} = 0.83$, $p = 0.440$, specific rate of weight loss - $F_{2,56} = 1.25$, $p = 0.294$ and age - $F_{2,73} = 0.78$, $p = 0.462$.

The data presented in Table 5.2 b were also entered in a oneway analysis of variance in order to compare the mean values of each variable between years. Again, there was no significant difference in the mean values of any of the seven variables between the three seasons; weight on day one - $F_{2,43} = 1.84$, $p = 0.171$, arrival weight - $F_{2,43} = 1.10$, $p = 0.344$, departure weight - $F_{2,43} = 3.02$, $p = 0.059$, departure weight expressed as a percentage of the arrival weight - $F_{2,43} = 3.95$, $p = 0.027$, rate of weight loss - $F_{2,43} = 2.70$, $p = 0.079$, specific rate of weight loss - $F_{2,43} = 2.49$, $p = 0.095$ and age - $F_{2,56} = 1.48$, $p = 0.237$.

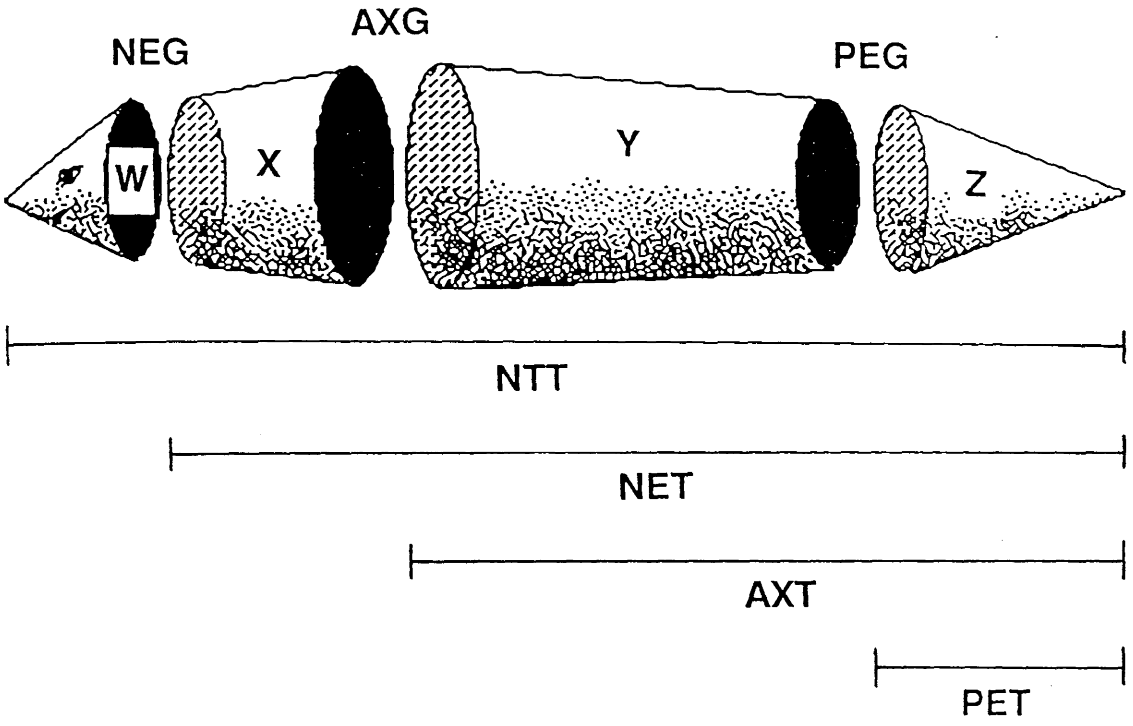
The relationships between the various weight parameters and age are examined in detail in Chapter 7. Also Chapter 7 provides analyses of weight and age data in relation to the various behavioural parameters gathered.

5.3. Lengths and girths

The length of a seal, measured in the same posture, should not change during the breeding season, whilst the girth will diminish as the individual loses weight. The problems in attaining accurate and repeatable length measurements has been discussed in Chapter 2.

In an attempt to overcome the problems of variation in length measurements, the total volume of a seal has been computed. Given that males are unable to "telescope" their spines, if a male has retracted or extended his neck during measurements an accompanying change in girth (neck girth) should be produced. Thus, a male measured twice at the same time, firstly with a retracted neck, should have a relatively large neck girth compared to a subsequent measurement made with the neck extended. To examine this, all the length and girth measurements made on an individual at a single catch were combined to produce an estimated volume. This was then compared with the weight of the seal recorded on that same capture. The formula used to calculate volume involved the determination of radii for each girth measurement (using the girth as the circumference), and then in conjunction with length measurements calculating the volume of a series of cones and truncated cones (see Figure 5.5). The formula used was as follows;

Figure 5.5 : Calculation of the estimated volume of a seal (see text)



Measurements made (see Chapter 2);
NB: All measurements are in cm.

Girth measures:

Neck girth (NEG)
Axilliary girth (AXG)
Pelvic girth (PEG)

Length measures:

Nose to tail (NTT)
Neck to tail (NET) - from the point where NEG was measured
Axilliary to tail (AXT) - from the point where AXG was measured
Pelvic to tail (PET) - from the point where PEG was measured

Calculation of radii:

General formula = Circumference/(2π)

Neck radius (NR) = NEG/(2π)
Axilliary radius (AR) = AXG/(2π)
Pelvic radius (PR) = PEG/(2π)

Calculation of heights of cones W and Z:

Height of cone W (HW) = NTT-NET
Height of cone Z (HZ) = PET

Calculation of heights of truncated cones X and Y:

Height of Truncated cone X (HX) = NET-AXT
Height of truncated cone Y (HY) = AXT-PET

Calculation of volumes of cones W and Z:

Volume of cone W (VW) = $(1/3) \times \pi \times (NR^2) \times HW$
Volume of cone Z (VZ) = $(1/3) \times \pi \times (PR^2) \times HZ$

Calculation of volumes of truncated cones X and Y:

Vol. of truncated cone X (VX) = $(\pi \times (AR^2) \times (HX/2)) + (\pi \times (NR^2) \times (HX/2))$
Vol. of truncated cone Y (VY) = $(\pi \times (AR^2) \times (HY/2)) + (\pi \times (PR^2) \times (HY/2))$

Calculation of total volume:

Total Volume in cm^3 = VW + VZ + VX + VY

Hence total volume for each male at each capture was computed. In each of the three seasons, the frequency distributions of total volume and weight were normal. The total volume was then plotted against measured weight for each season and Pearson correlation coefficients determined (see Figures 5.6 a, b and c). In all three years, total volume was very highly correlated with weight (see Table 5.3). It is instructive to compare these correlations with those of the individual length and girth measurements plotted against weight. In all three seasons NTT and NET were correlated with weight at $p < 0.01$, whilst AXT was correlated with weight in 1987 and 1988 (at $p < 0.01$), but not 1989 ($p = 0.051$). All correlations were positive. The strongest correlation was that of NET with weight in 1989 ($r = 0.85$, $n = 55$, $p < 0.001$) whilst the remaining Pearson correlation coefficients lay between $r = 0.36$ and 0.70. The girth measurements generally provided stronger correlations with weight. All three girths (NEG, AXG and PEG) correlated significantly and positively with weight at $p < 0.01$. The strongest correlation was between AXG and weight in 1987 ($r = 0.92$, $n = 89$, $p < 0.001$), whilst the weakest was that of NEG in 1989 ($r = 0.43$, $n = 55$, $p = 0.001$). The remaining correlation coefficients ranged between $r = 0.70$ and 0.87. The sample sizes, obviously, were the same as for total volume. Thus, the computation of total volume has indeed enhanced the correlation between standard measurements and weight.

From Figures 5.6 a, b and c, it is evident that there is an extremely close relationship between volume and weight, with remarkably little scatter around the regression slopes. Perhaps this is not entirely unexpected, however, considering the difficulties of obtaining repeatable length and girth measures, these relationships demonstrate that the calculation of total volume is a potential means of negating these problems.

What further use could these relationships be? Although total volume does not provide a measure of skeletal size of individuals, it may be possible to gain an index of an individuals body condition from these data. The relative proportions of fat to lean tissue will vary amongst individuals. Hence, the overall density of individuals will also vary. As density is a function of mass and volume ($D = M/V$) the deviation of an individual from the regression line (i.e. the residual) may be an index of relative condition. If weight forms the vertical (y) axis and volume the horizontal (x) axis then; males with positive residuals will be in relatively poor condition, i.e. proportionately more lean tissue, hence, a relatively high weight for their volume, whilst males with a negative residual will be in relatively good condition, i.e. proportionately more fat, hence, a relatively low weight for their volume. In order to make comparisons between individuals it would be necessary to

Table 5.3
Results of correlations between total volume and weight of individual males in the study area during each breeding season.

YEAR	n	df *	r	p	INTERCEPT (S.E.)	SLOPE (S.E.)
1987	89	46	0.97	< 0.0001	39.13 (5.43)	0.00087 (0.00002)
1988	61	31	0.94	< 0.0001	26.63 (8.48)	0.00100 (0.00005)
1989	55	23	0.96	< 0.0001	47.27 (6.71)	0.00093 (0.00004)

* df = degrees of freedom. As the data presented in Figures 5.6a, b and c contain some repeated (serial) weighings of the same individual, the number of individuals has been used for degrees of freedom rather than the total number of weighings (n).

Table 5.4 Summary of the ranges of individual mean lengths (NTT, NET and AXT) for each season, the ranges of standard deviations and, in parentheses, the standard deviation expressed as a percentage of the range of mean values. NTT, NET, AXT defined as above.

YEAR	LENGTH	Range of mean length (cm)	Range of standard deviations in cm (% of range of mean lengths)
1987	NTT	185.3 - 210.5	0.00 - 17.35 (0.00 - 68.93 %)
	NET	146.8 - 176.0	0.00 - 14.73 (0.00 - 50.36 %)
	AXT	110.3 - 137.0	0.00 - 9.90 (0.00 - 37.12 %)
1988	NTT	175.0 - 206.5	0.71 - 14.14 (2.25 - 44.89 %)
	NET	142.0 - 165.5	0.71 - 10.61 (3.02 - 45.15 %)
	AXT	108.0 - 127.5	1.41 - 13.44 (7.23 - 68.92 %)
1989	NTT	182.0 - 210.3	0.71 - 10.61 (2.50 - 37.45 %)
	NET	147.0 - 175.3	0.00 - 10.02 (0.00 - 35.37 %)
	AXT	114.0 - 130.5	0.00 - 8.14 (0.00 - 49.33 %)

Figure 5.6 a : Plot of estimated volume against actual weight - Rona 1987

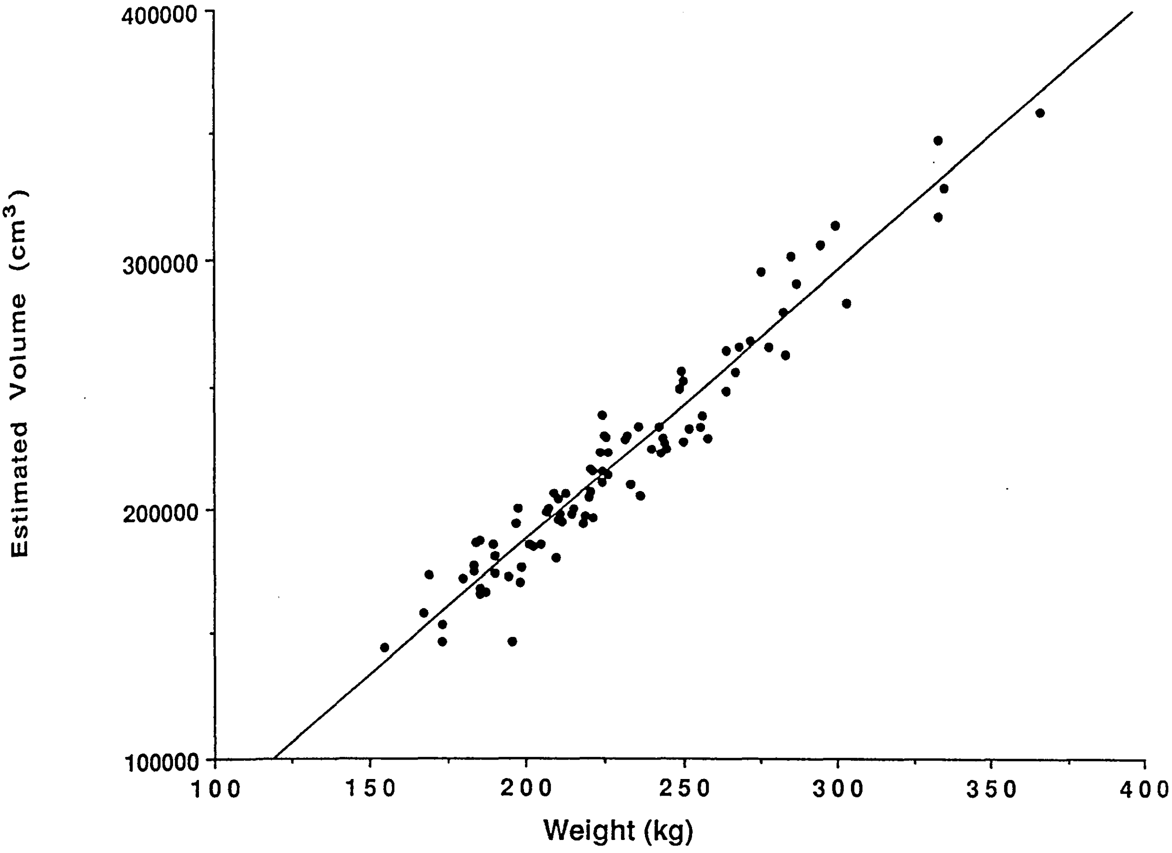


Figure 5.6 b : Plot of estimated volume against actual weight - Rona 1988

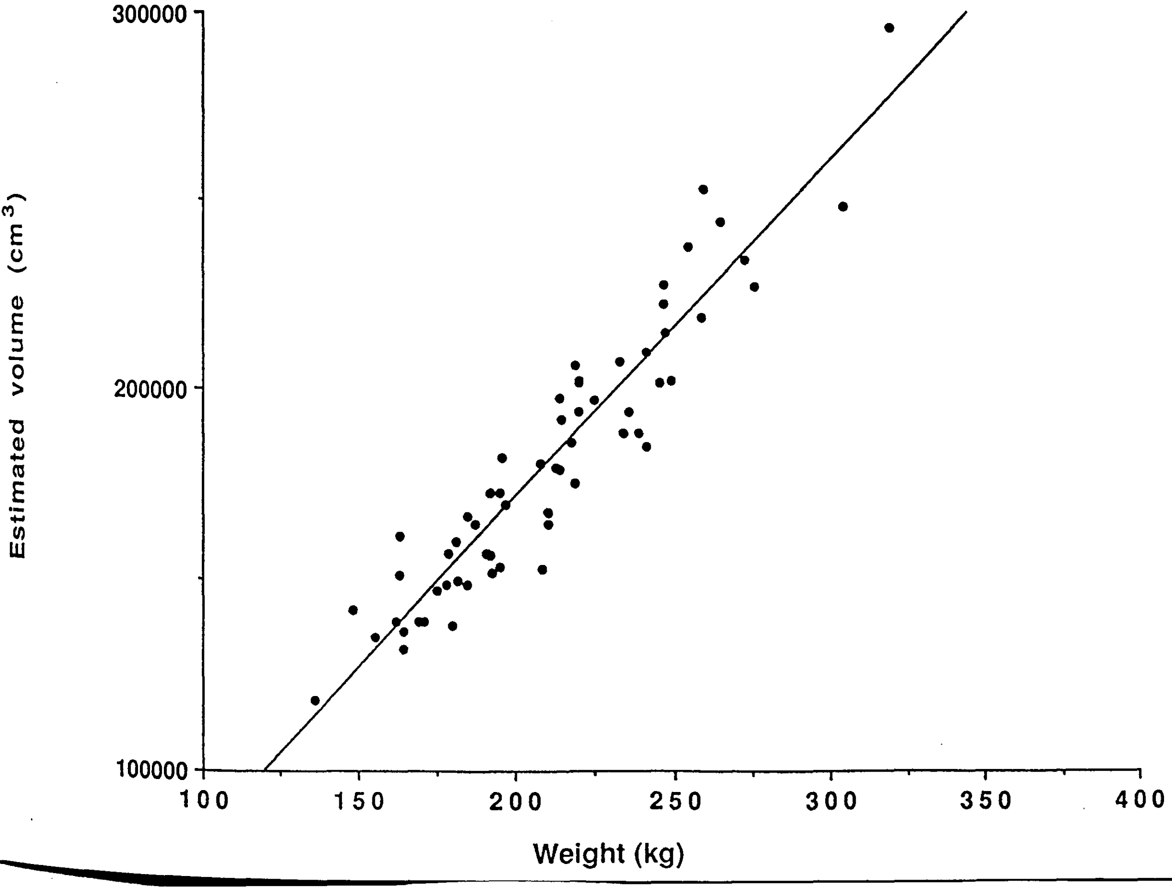
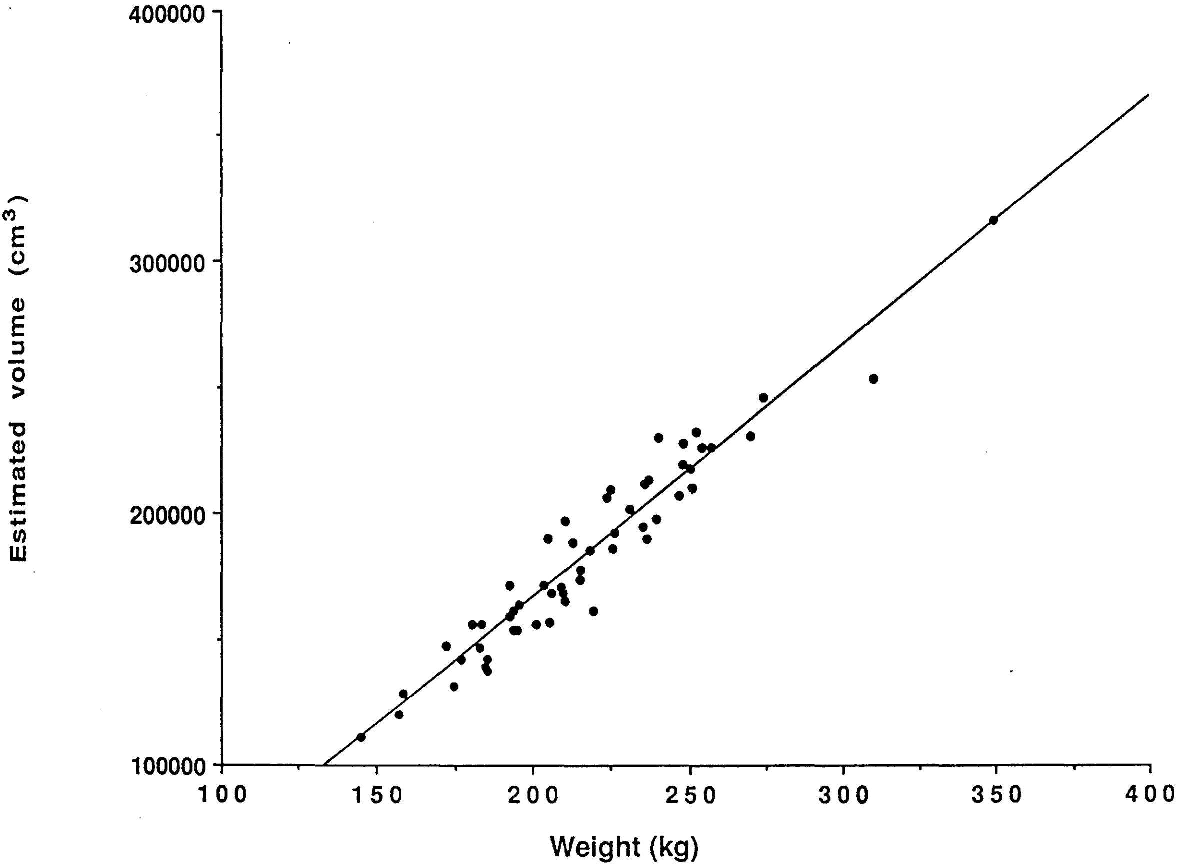


Figure 5.6 c : Plot of estimated volume against actual weight - Rona 1989



gather a series of weights and measures on each male, and extrapolate their individual regression lines back to some comparable point in time (e.g. arrival date). However, whether what little scatter there is can be attributed to some real biological difference such as condition, or is merely a product of the sampling method cannot be discerned. It is possible that the observed scatter is a product of inaccurate measurements, for example where a male shifts position between the measurement of nose to tail length and neck girth.

This method of computing an individual's weight from estimated volume as determined by standard measurements may be particularly useful in field situations where it is impracticable to carry heavy and bulky weighing equipment. For example, catching seals on offshore haul out sites outside the breeding season, the only equipment required for estimating volume and therefore weight would be two tape measures. However, for the purposes of this study, the direct weight measurements are used.

Bearing in mind the problems of attaining accurate, repeatable length measurements of individuals, a mean value for each length measurement have been calculated for each individual caught on more than one occasion. Table 5.4 gives the range of individual mean lengths (NTT, NET and AXT) for each season and the range of standard deviations. Only males measured on more than one occasion were included. It is evident from Table 5.4 that the standard deviation of the mean lengths of some individuals are rather large, in some instances being equivalent to 68 % of the range of mean lengths. This obviously makes comparisons between individuals in respect to the relationships of length with the other variables collected in this study somewhat unreliable.

In an attempt to overcome this unreliability, only individuals whose standard deviation was equal to or less than 10 % of the range in mean lengths were selected. These were then compared with other parameters, such as dominance, length of stay etc, though, obviously, the sample size was considerably reduced. The relationships of mean nose to tail (NTT), neck to tail (NET) and axilliary to tail (AXT) lengths with the other variables collected in this study are discussed in Chapter 7.

5.4. Labelled water (H_3O) analyses;

Only 9 males in total were sampled by this method (during 1989 - see Chapter 2). Of these, 6 were sampled at two points during the breeding season separated by at least 3 weeks. Hence, a total of 15 samples were taken. For each individual at each sampling point, the parameters total body fat in kg (TBFkg), total body protein in kg (TBPkg) and total body energy in MJ (TBGE) were computed using the equations derived by Reilly (1990) and detailed in Appendix D. The estimated weights of fat and protein were also converted into percentages of the individuals weight at time of sampling (TBF% and TBP% respectively). These variables were then plotted against weight in order to examine the relationships between fat, protein and energy content and weight. For each sample, duplicates were produced. Of the 15 samples, only one deviated markedly between duplicates (male 154 on 11/10/89). The remaining samples all had closely corresponding duplicates. All plots showed the same pattern, which is demonstrated in the plots of TBFkg and TBF% with body weight (Figure 5.7 a and b). The results obtained were rather eccentric, however, the pattern is quite intriguing. Of the six males sampled at two points, 4 show very similar rates of decreasing fat content with decreasing weight (males 001, 002, 063 and 175). Similarly, both duplicates of the single sample of male 043 and one of the duplicates of male 154 lie on the line formed by the aforementioned samples. Excluding all the other samples for the moment, this appears to form an ordered and rather provocative relationship, suggesting a linear relationship between body weight and fat content. However, it must be remembered that these data are not truly independent, being sequential measures of 4 individuals. Also, the elevation of the apparent slope is rather high. The absolute values for estimated fat content range from approximately 212 kg of fat in a 269.5 kg seal to 108 kg of fat in a 183.5 kg seal. As percentages, this gives a fat content of between 78.7 % and 58.9 % (Figure 5.7 b). Even the lower of these two values is considerably higher than the maximum estimated fat content of 50 % (Fedak and Anderson 1985), whilst the upper estimate is simply ridiculous! Assuming that this is a true relationship, but somewhat elevated, it is still impossible to say whether the error is consistent throughout all weights, or if there is some

Figure 5.7 a : Plot of actual body weight against estimated fat content (kg)

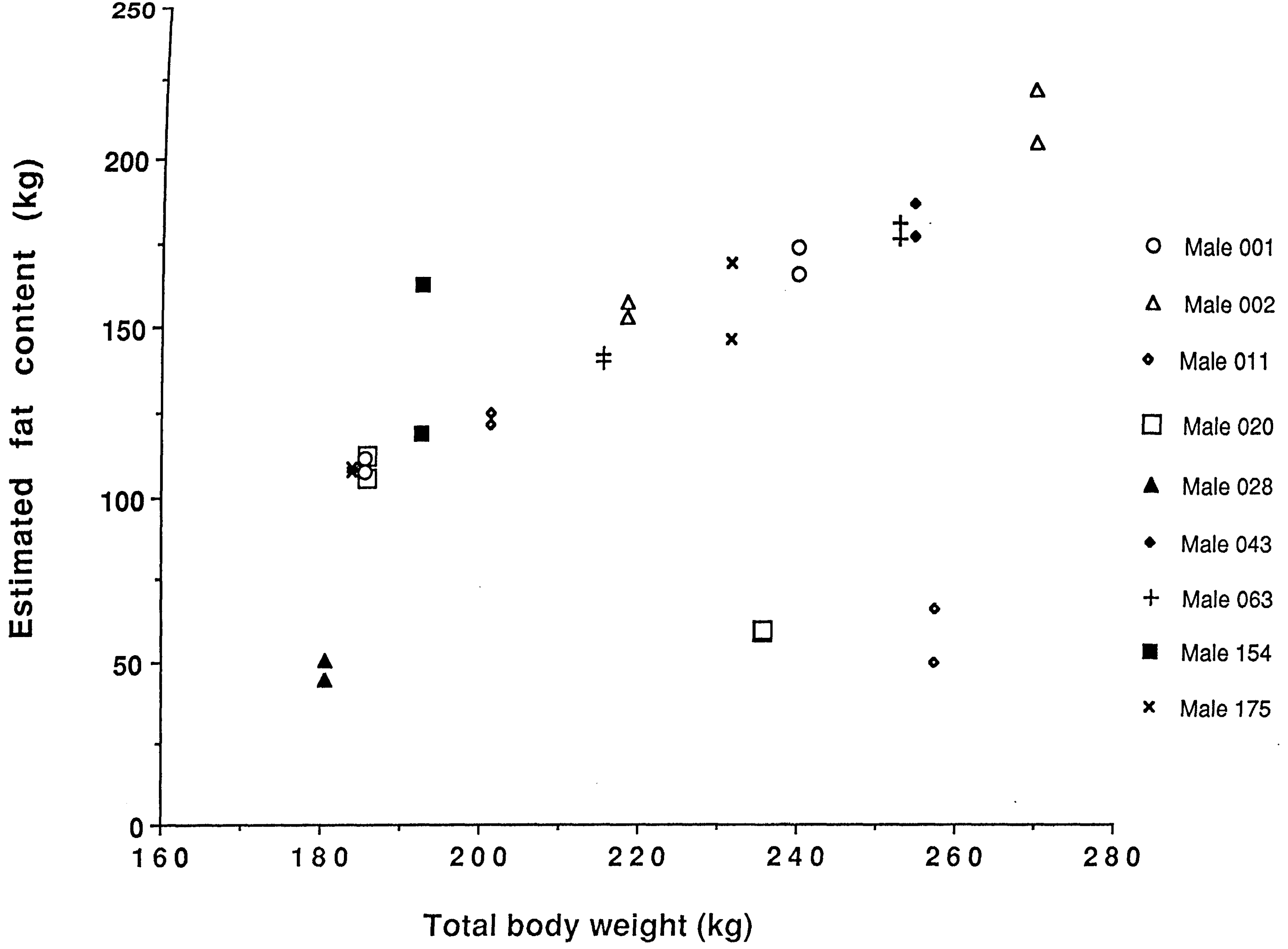
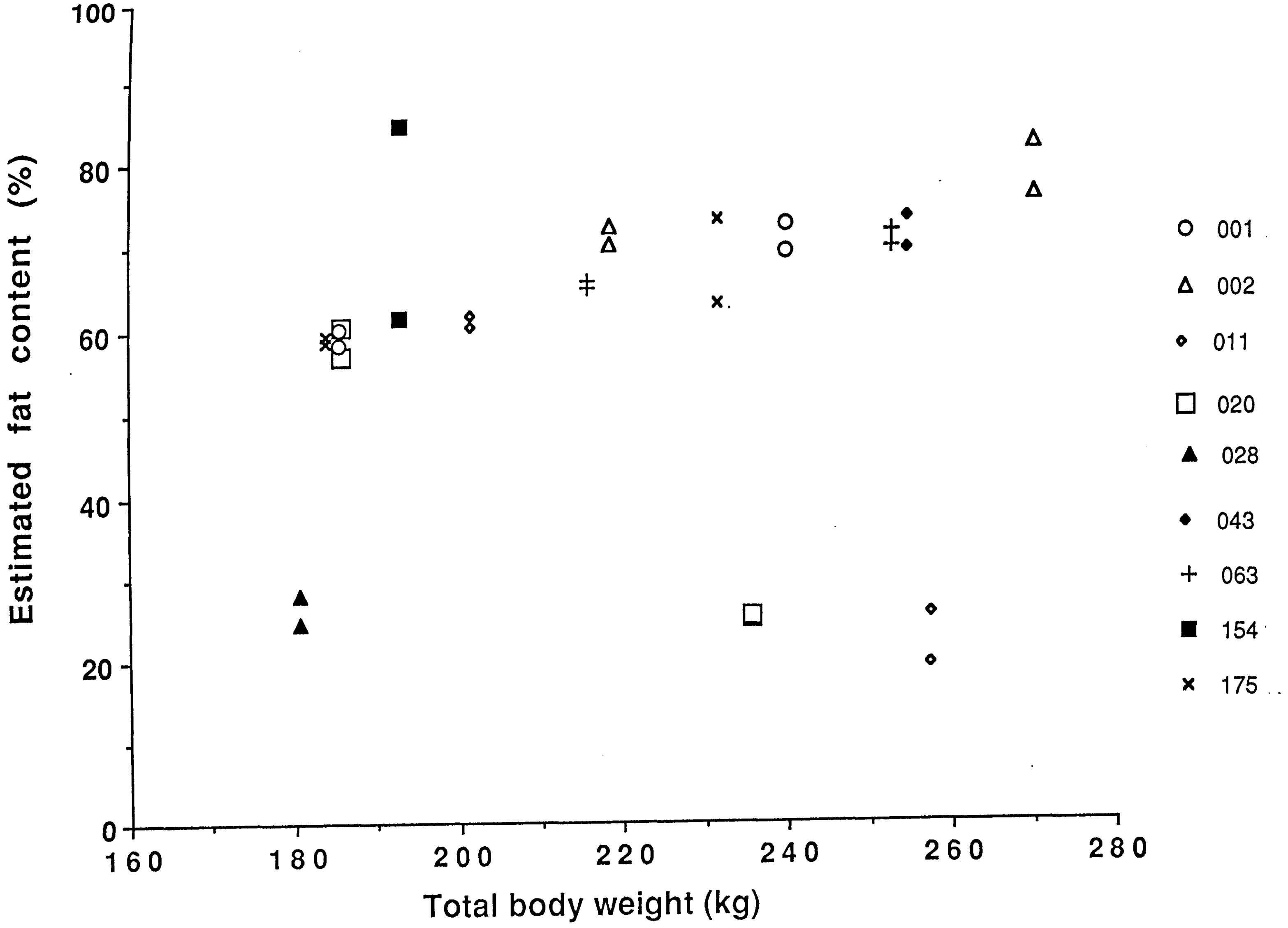


Figure 5.7 b : Plot of actual body weight against estimated percentage fat content



systematic error, whereby the error increases with increasing weight and therefore alters the slope of the relationship. A further problem is encountered when one considers the remaining samples which have so far been ignored. The single sample for male 028 does not conform to this supposed relationship at all. However, the most bizarre results are to be found in the first samples of the doubly sampled males 011 and 020. These apparently increased their absolute fat content as their overall weight diminished during the season! Again, this result is somewhat inconceivable. However, it is interesting to note that the second samples of these two males do lie on the line of the supposed relationship.

With these problems, it is impossible to discern whether there is in fact a real relationship between fat content and total body weight. It may be that there is, however, whether the slope of such a relationship is such that relative fat content increases with increasing weight or is a constant proportion of body weight cannot be said. If the slope of the supposed relationship in Figure 5.7 b is correct (ignoring the elevation), then it would indicate that relative fat content only increases slightly with increasing body weight, and would perhaps be predictable from body weight.

What the cause(s) are of these anomalous results is impossible to say. The field and laboratory techniques (see Chapter 2) were rigorously and carefully applied and subsequent retrospective detailed examination of both the field and laboratory techniques has revealed only one plausible source of error. In the first sampling of an individual, the labelled water was injected remotely, in the same manner as the usual immobilising agent for seal captures (see Chapter 2 for methodology). As it is impossible to guarantee the depth of penetration of the dart as it hits the seal it is possible that on occasions where penetration was shallow, the resistance of the surrounding blubber forced some of the labelled water out of the seal along the sides of the needle, or when the needle was withdrawn. This was in fact observed on one occasion, and as an unknown quantity of labelled water had entered the seal this individual was not used for body condition analyses. Conversely, all second samples on individuals required background blood samples to be taken prior to the injection of a fresh dose of labelled water. Hence, on these occasions all individuals were immobilised prior to injection of the labelled water, thus, the injection was made intravenously, directly into the extradural vein, allowing the syringe to be fully flushed. This is obviously a more accurate method of injecting labelled water. Can this problem explain the results obtained? If less injectate entered the seal than was believed, the estimate of H_30 space would be artificially elevated. This would lead to an elevated estimate of total body water (%) and hence to an underestimate of percentage fat (TBF%). Similarly an underestimate of TBGE and an overestimate of TBP would result. Thus, this could perhaps explain the very low TBFkg and TBF% of males 011 and 020 on the first sample and that of male 028. However, it cannot explain the generally elevated values of TBFkg and TBF% seen in the other samples. Thus, those samples that deviate from the supposed relationship are explicable, but the problem of the elevation of the relationship remains unresolved. As such these results may be rather tantalising, and may tempt one to say there is a relationship between fat content and body weight, but considering the evident errors, these results are not interpretable in a biologically meaningful way. However, they are sufficient to warrant a repeat of this work, preferably not employing the remote darting method.

DISCUSSION

As we were unable to use the labelled water analyses to estimate percentage of fat and rates of fat loss in individuals, the rate of weight loss, both absolute and proportional form the basis of the energetics studies. Similarly, as no skeletal measures could be obtained, we cannot assess the relative body conditions of males. However, as males fast during the breeding season and rely primarily on their blubber reserves to provide energy, the rates of weight loss are still valuable tools for assessing energy expenditure. With estimates of arrival weight it is possible to examine the relationships between an individuals arrival weight, his subsequent rate of weight loss, his length of stay on the breeding grounds and his performance during the stay. Whether length of stay is determined by a combination of arrival weight and subsequent weight loss (absolute or proportional), or whether males depart upon reaching a certain threshold weight or upon losing a certain percentage of their arrival weight will be examined in Chapter 7. Similarly, the influence of activity levels upon energy expenditure and therefore, perhaps length of stay shall be examined in Chapter 7.

The overall mean rate of weight loss was 1.99 kg/day. Anderson and Fedak (1985) give mean values of 2.3 kg/day (SD = 0.079) for data collected in 1980 and 2.1 kg/day (SD = 0.095) for 1981. Unfortunately they do not give the sample sizes. The reason for their slightly greater values may be that they have included weight data for males throughout the entire breeding colony and not just from the study area as is the case in the present study. It appears that the more northerly portions of the Fianuis peninsula become occupied first at the onset of the breeding season, and the study area, somewhat later. It is possible that larger males gain the positions in the north of Fianuis, and heavier males may be subject to greater absolute rates of weight loss (see Chapter 7). Thus, Anderson and Fedak's mean values would indeed be slightly greater than those presented here.

There is surprisingly little variation between these values for rates of weight loss and, from animals weighed more than twice, it appears that weight loss is reasonably constant throughout the breeding season (see also Anderson and Fedak 1985).

The overall mean arrival weight of 257.87 kg is comparable with those presented by

Anderson and Fedak (1985). Their mean "initial weights" were 235 kg (SE = 7 kg) for 1980 and 245 kg (SE = 7 kg) for 1981, though again the sample sizes are not given. However, it must be noted that this measure of "initial weight" as used by Anderson and Fedak is slightly different. Anderson and Fedak used simply the weight of the animal on the first day it was weighed. Here, the weight has been extrapolated back to the first day on which the male was sighted on the study site using the rate of weight loss. Thus, understandably, the values presented by Anderson and Fedak are slightly lower than those presented here. Fedak and Anderson (1985) quote a mean arrival weight for males on Rona as 257 kg, which agrees strongly with the overall mean calculated above.

Several new variables were computed from the weight data gathered in this study. Weight on day one was used in an attempt to compare estimated weights of males on an arbitrary date at the onset of the season. However, even using an estimated weight on a hypothetical day one may not be particularly accurate as each individual male may cease foraging prior to the breeding season at different times and then experience differing rates of weight loss. There may in fact be no particular date at which weights of individual males are directly comparable. Actual arrival date may remain as the best point of comparison, if the timing of a male's arrival is determined by when he "deems" himself "ready" for the colony. However, there may not be such an element of "free choice", for example, if the presence of more dominant individuals prevents a male from coming ashore.

The calculation of a departure weight allowed the estimation of total percentage weight lost during each individuals stay at the colony. The mean values for this variable range between 66.96 % (in 1988) and 73.34 % (in 1987). These agree with previous estimates of maximum percentage weight lost of 40% (Fedak and Anderson 1985). However, the minimum value for 1988, only 44.96 % of arrival weight remaining upon departure, is rather unrealistic, though it is the only computed value so low, the remaining cases yielding realistic values, generally between 60 and 70 percent. These parameters allow examination of the hypothesis that males depart from the colony upon reaching a threshold weight, or threshold proportion of their arrival weight (see Chapter 7).

The range of ages of males active on the colony (i.e. those we caught) extended from 7 to 21 years. Harwood and Prime (1978), Boness and James (1979) and Boyd (1982 a) suggested that only males of greater than about 10 years of age were seen on the colony, however, Anderson et al (1975) record the presence of a 7 year old branded male ashore on North Rona in 1972. The data collected here suggests that, younger males can indeed gain positions on the colony.

It must be noted that this may be a somewhat biased sample, as the males caught are those that stay. Males on the periphery of the colony or those remaining ashore for very short periods are not caught. Therefore, the sample effectively represents those males termed by Boness and James as "tenured" males. From the observations it is clear that "transient" males do come ashore throughout the season, but usually only stay for short periods and are unable to establish a position. The few that secure and maintain a position on the breeding colony then become possible candidates for capture. Thus, at present weight change data and age data can only be used with regards to males adopting the "tenured" mating strategy.

A similar cautionary note must be made concerning the activity budgets. Unlike previous authors, the present study only utilises data for individuals observed on at least 180 scans, some 15 hours of observations. This is effectively two day's observations. This therefore restricts to data to males present for at least two days i.e. so called "tenured" males, those individuals which are able to secure a position on the colony for at least a short period. Thus, the "transients" are excluded from the analyses, although scan samples were made on these individuals, they are too few and yield potentially erroneous results.

As mentioned previously, earlier studies providing activity budgets of male grey seals at various breeding colonies (Harwood 1976, Anderson and Harwood 1985, Boness 1984) adopted somewhat different methods in calculation of percentage time in the various activities. However, despite the differences in methodology it is still instructive to make comparisons.

The most striking feature of the activity budget presented in this chapter is the large proportion of time that male grey seals spend resting. This is consistent with data presented by various other authors for grey seals during the breeding season. Harwood (1976) gives a value of 87.5 % for combined time resting on the beach, at sea and immersed. Anderson and Harwood (1985) give a value of 72.1 % for resting amongst North Rona males, though combining their resting, scratching and adjusting position categories would be more comparable to the category of resting used in this chapter. This would yield a mean proportion of 74.6 percent. Boness (1984) gives a value of 88.8 % of time spent resting for Sable Island males.

The main difference between the colony at the Monachs and those of Rona and Sable is that males at the former site spend a considerable amount of time in the sea (a mean value of 59.1 % of daylight hours).

In all these studies a majority of the non-resting time was spent alert. Relatively small proportions of time were devoted to sexual and aggressive activities. A majority of the aggressive activity was low level threats (open mouth threats), presumably requiring little energy expenditure. High energy aggression such as fights or chases occupied little of the activity budget (see also Chapter 3). Of the sexual activity, copulation accounted for most of the time, as the mean duration of copulations are much greater than that of attempted copulations (see Chapter 3).

Comparison with the activity budget presented by Harwood (1976) for the Monachs, reveals that the Rona males spent more time being alert (11.86 % compared to 6.65 %). If alertness is viewed as an anti-predator device, as suggested by Harwood, this difference may be due either to differing predation risks or to the differing sex ratios at the two colonies. It appears to be unlikely to be the former, as the Monach colony is essentially beach breeding, whilst the breeding colony on Rona is predominantly inland. As breeding colonies tend to be predator free islands (Bartholomew 1970), the greatest risk of predators lies in the surrounding waters. Thus, one would expect more vigilance on the Monachs. However, there are few seal predators in UK waters, the most likely being killer whales, which have only very rarely been sighted at seal breeding colonies. In terms of the operational sex ratios, with more males being excluded on Rona, each male ashore may devote more time to being alert. An alternative explanation may be that levels of vigilance are related to levels of aggression at the two colonies, and indeed Rona does exhibit slightly more aggression than the Monachs (1.96 % compared to 1.88 %).

The Rona males devote a greater proportion of time to sexual activities, both attempted copulations (0.89 % compared to 0.31 %) and copulation (1.32 % compared to 0.91 %). Again due to the differing sex ratios at the two colonies, there are relatively more females per male on Rona than on the Monachs.

Comparison with the activity budgets for Rona and the Monachs presented by Anderson and Harwood (1985) appears to confuse the issue somewhat. The authors present new data for North Rona, and the same data as presented in Harwood (1976) for the Monachs. However, the Rona data was only collected during the middle of the season, thus the authors have taken only those samples made at the Monachs over a comparable period. Hence, these data may not be strictly comparable with the activity budget data presented here. Both Rona and Monach data provided by Anderson and Harwood give higher values of alert than in the present study (14.9 % and 18.0 % respectively compared with 11.86). Similarly, their values for total aggressive activity are higher than those in the present study (3.4 % and 5.1 % respectively compared with 1.75 %). The same is true of time spent in copulation, 2.9 % and 2.5 % for Rona and the Monachs respectively as presented by Anderson and Harwood, whilst the value for the present study is only 1.32 percent. This may be an artefact of selecting samples made during the mid portion of the season, when numbers of both males and females are at their highest and a majority of sexual activity occurs.

The method used by Boness (1984) on Sable island is more directly comparable with my own data. Similarly the behavioural categories used by Boness are largely the same as those in this chapter. The Sable males spent slightly more time being alert than those of Rona (12.0 % compared to 11.86 %) and more time in locomotion (2.1 % compared to 1.9 %). However, the main differences appear in the proportion of time spent in aggressive and sexual behaviours. The Sable males spent considerably more time in aggression than those of Rona (6.3 % compared to 1.96 %). Most of this disparity is due to differences in the time devoted to open mouth threats (4.9 % compared to 1.41 %), whilst the amount of time devoted to fights is remarkably similar (0.2 % and 0.19 %). In terms of total sexual activity, Sable males had the largest proportion of time (2.8 % compared to 2.57 %). However, examining the individual activity categories this difference was wholly due to a greater proportion of time spent approaching females at Sable (1.3 % compared to 0.36 %). The amount of time devoted to attempted copulations was very similar at the two sites (0.9 % at Sable, 0.89 % on Rona), whilst the Sable males actually spent less time in copulation than those of Rona (0.6 % compared to 1.32 %). This difference existed despite the remarkable similarity in mean copulation duration at the two sites (see Chapter 3). Again, this may be due to the differing sex ratios at the two sites, with more females per male at Rona. A further and more detailed comparison of Sable Island and North Rona is presented in Chapter 10, utilising data from both sites gathered during the course of this study.

The particularly interesting aspect of the correlations between the activity categories in the activity budget presented in this chapter is the lack of correlation between time spent resting and sexual activity. In contrast, aggressive activity is significantly and negatively correlated with resting. Thus, in terms of conserving energy, it may be advantageous for males to minimise aggressive activity wherever possible. This may account for the relatively low levels of aggressive activity on the colony, in particular the low occurrence of high energy aggression (fights and chases). This may also be responsible for males deferring to females in a vast majority of inter-sexual aggression (see Chapter 3).

This chapter has examined only the mean values of the activity budget. The main advantage of being able to identify all individuals is utilised in Chapter 7, where the time budgets of individuals are examined in respect to the other variables collected during this study, such as mating success, dominance, colony attendance and weight parameters.

CHAPTER 6 - MATING AND REPRODUCTIVE SUCCESS

INTRODUCTION

The mating systems of pinnipeds appear to range from close to monogamy, or at least very "low level" polygynous systems, to extreme forms of polygyny. In using the term "low level" polygyny I am implying that there is relatively little variation in the mating and/or reproductive success of males and that the maximum number of copulations attainable by any one male is severely restricted. For example, Boness *et al.* (1988) describe the mating system of hooded seals (*Cystophora cristata*) as polygynous, a system facilitated by the spatial pattern of the seals during the breeding season. However, with most of the groups of females consisting of between 2 and 5 animals, and a relatively high degree of synchronisation of oestrus, the extent to which individual males can monopolise mating opportunities, either by simultaneous or serial polygyny, is rather limited. Although very little information is available, it would appear that several other pinniped species have similar "low level" polygynous systems. Le Boeuf (1978) lists the bearded seal (*Erignathus barbatus*), ringed seal (*Pusa hispida*), Baikal seal (*Phoca sibirica*), Caspian seal (*Phoca caspica*), harp seal (*Pagophilus groenlandicus*), ribbon seal (*Histriophoca fasciata*), crabeater seal (*Lobodon carcinophagus*), leopard seal (*Hydrurga leptonyx*) and the Ross seal (*Ommatophoca rossi*) as potential candidates for such low level polygyny. These species generally breed on either pack or fast ice with the females being relatively widely dispersed during the breeding season, so limiting the extent of polygyny. Also, these species exhibit relatively little sexual dimorphism, a trait typically associated with less polygynous systems.

At the other end of the spectrum is the extreme polygyny found amongst the sea lions (Otariinae), fur seals (Arctocephalinae) and within the phocids, the classic example of the much studied elephant seals, *Mirounga* spp. (Le Boeuf and Peterson 1969, Le Boeuf 1972 and 1974, McCann 1981 and 1983, Le Boeuf and Reiter 1988). All these pinnipeds described as highly polygynous are all land breeders (usually island breeders) and consequently more is known about their breeding habits. These animals exhibit traits typically associated with such organisation; marked sexual dimorphism especially in size, high levels of inter-male aggression, monopolisation of females (and therefore copulations by very few males leading to vast differences in the mating success of individual males), defence of discrete harems by clearly dominant bulls together with a variety of displays and threats from males in order to maintain their position (Le Boeuf 1978, Le Boeuf and Reiter 1988, McCann 1981).

However, the "degree" of polygyny and the precise form of the breeding system may vary, not only amongst different pinniped species, but also, between separate breeding populations of the same species. This is particularly so where the different populations breed on widely differing substrates. The grey seal is a prime example of this (Stirling 1975), with populations breeding on ice, sand or islands. Intriguing differences in the social organisation during the breeding season can be seen when comparing separate breeding populations, such as those of North Rona and Sable Island, Nova Scotia (Boness and James 1979). The most noticeable of these is the strikingly different sex ratios on the breeding sites, referred to in Chapter 4. As discussed in Chapter 4, the topography, as determined by the substrate of the site, has a great influence upon the distribution of females and, therefore, males (a detailed comparison of Sable Island and North Rona is provided in Chapter 9). Traditionally, such differences in social organisation have been assumed to indicate differences in the relative degree of polygyny at the various colonies (Boness and James 1979, Anderson and Fedak 1985).

Whilst the breeding organisation of the grey seals is clearly one of polygyny (Anderson, Burton and Summers 1975, Boness and James 1979, Anderson and Fedak 1985 and 1987 b), the exact degree of polygyny may vary, not only within different parts of the colony, but also from year to year. Therefore, prior to any attempt to assess the potential determinants of mating and/or reproductive success of individual males, it is essential to establish the degree of polygyny exhibited at the study site of North Rona in each of the breeding seasons of this study. In this chapter, various measures of the "degree of polygyny" are calculated in order to allow comparison of the three seasons and also to compare with similar measures for other breeding colonies (see Chapter 9) and other species (see Chapter 10).

A further problem, which has always been present in studies of this type, is that of using individual mating success as an indicator of individual reproductive success. As seals are active during the night (Anderson, 1978), many copulations could not be observed. Also, in a species such as the grey seal, where each female may be copulated approximately 3 times in a single season (Anderson, Burton and Summers 1975), determining which male is the sire of a pup born a year later can be difficult. For the purposes of this study, a system of first male paternity has been assumed for mating success, for reasons detailed in Chapter 3. However, it would be preferable to be able to test this assumption rigorously. The recent development of DNA fingerprinting techniques (Jeffreys, Wilson and Thein, 1985, Burke 1989) may provide a suitable opportunity to assess the paternity of pups born on North Rona. During the three seasons of this study, a pilot project has been undertaken in an attempt to assess the relationship between observed mating success and actual reproductive success as determined by DNA fingerprinting.

This chapter describes the nature of the observed variation in male grey seal mating success and attempts to assess the relationship between individual mating and reproductive success. The examination of potential determinants of an individual's mating and/or reproductive success is dealt with in Chapter 7.

METHODS

See also Chapter 2 for general review of methods used.

Behavioural observations - to assess mating success:

Behavioural observations were conducted virtually every day during the breeding season for as long as possible, often dawn till dusk (see Chapter 2). To gain a measure of the mating success of individual males, records were made of all observed sexual activity using the categories described in Chapter 3. The identity of participants was noted. For males this involved noting the precise individual identification number as described in Chapter 2. For females this included noting the brand if the animal was branded but also, whether the female was branded or not, the presence or absence of a pup, together with the pup age class, or, indeed, if the female was pregnant (i.e. female status). Females without pups were classified into two groups, either "fat" or "thin". The former were pregnant females the latter had either weaned or lost their pups or were non-parous. The difference in size and shape of these two classes of females was dramatic and they could not be confused. Also, they exhibit certain behavioural differences. The duration and outcome of all sexual interactions were noted. Thus , for each male we have records of number of sexual interactions of each type, their duration, identity and/or status of the females involved, their outcome and their date and time of occurrence.

To estimate mean daily rates of copulations for each male the number of observed copulations in which a particular male was involved was divided by the number of hours for which he was observed on the day in question and then extrapolated to give a rate per 24 hours (this assumes no significant diurnal variation in male grey seal activity - see Chapter 5). The daily rates for each male were then averaged to give a mean daily rate of copulations for individuals. These individual 24 hour rates were also used to calculate an average rate per day per male. This yields a measure of seasonal variation in the frequency of copulations (see Chapter 3).

As stated in Chapter 3, all instances where attempted copulations or actual copulations were directed more than once at the same female were recorded, where possible. This was important as each female is certainly approached more than once by either the same or different males and most females are copulated with more than once. Anderson, Burton and Summers (1975) estimated that each female may be mated up to three times by the same or different males and this is supported by observations in this study on the few marked females. For the calculation of daily frequencies of sexual activity (e.g. copulations per day) all attempted copulations and actual copulations were used, whether the female in question had previously been mated or not. However, for the assessment of individual male mating success a system of first male paternity was assumed. Thus, mating success for an individual male is in fact the observed number of occasions in which he copulated with different females not previously mated (or not observed in a copulation before). This was deemed necessary as mating success is intended as a measure of an individual's reproductive success. If this convention was not adopted, potentially erroneous values for mating success would result. For example, if a single male copulated three times with the same female, recording these as different females would artificially inflate this male's mating success from one to three. Similarly, in cases where different males mate with the same female, the first male doing so has enhanced his mating success, whilst subsequent males failed to do so. Noting these repeated sexual acts was clearly possible in the case of individually marked females and also with unmarked females within a single day's observations. However, this is rather more difficult to achieve with unmarked females approached by either the same or different males on different days. Thus, this is one possible source of error in these figures, though it has been minimised wherever possible.

As stated in Chapter 3, first male paternity was assumed as males clearly compete to gain the limited positions on the breeding colony, and it is the males that succeed in doing so that predominantly have the first opportunity to mate with oestrus females. If these males were not the successful sires, but the more peripheral males were responsible for fertilising the females, then the observed mating system would hardly be an evolutionary stable strategy (Maynard Smith and Price 1973, Maynard Smith 1974, Maynard Smith and Parker 1976, Dawkins 1976).

Detection of female reproductive state by males:

Variation in the frequency of all attempted copulations, whether successful or not, were examined in relation to female reproductive status to assess the possibility that males are able to discern when females are reproductively receptive (in oestrus). In all observed attempted copulations it was noted whether the female was accompanied by a pup or not and, if so, the pup's birth date (if known) or its age class. The age of a pup was classified as one of five developmental stages, defined by certain physical features (see Radford, Summers and Young 1978). The age class can be discerned easily from the hide to give a rough estimate of a pups age. As females enter oestrus around the time of weaning, the age of a female's pup can be used as an indication of the mother's reproductive state. Therefore, the older the pup the closer the mother is to oestrus.

In cases where a sexual interaction was interrupted by a third individual, again the identity of this animal and the outcome of the interruption was noted.

DNA finger-printing - to asses individual reproductive success:

Samples of blood were taken from all individuals caught (see chapter 2). From each seal caught a single non-heparinised 10ml vacutainer was taken and split into two bijou pots (5ml), one containing 1ml of saturated salt solution, the other 1ml of DMSO solution, both acting as preservation agents. These samples were then placed in a freezer as soon as possible. After each field season the sample were then used in DNA fingerprinting analysis to ascertain paternity of all pups sampled. These analyses were conducted by Bill Amos (Genetics Department, Cambridge University) and details of the methodology can be found in Amos (1990) and Amos *et al.* (1991).

Statistical analyses:

(a) Selection criteria for cases:

As in previous chapters two sets of summary statistics are provided for each parameter measured. The first includes all cases for which data are available. The second includes only cases where the individual males were involved in at least 10 inter-male aggressive interactions. Again, this was necessary as, in Chapter 7, the inter-relationships between various parameters are examined. As such, it was necessary to ensure that individuals included in these analyses were involved in sufficient inter-male aggressive interactions to allow accurate calculation of the dominance score (see Chapter 3). Whilst these excluded males may have spurious dominance scores, the remaining data gathered from these individuals, such as levels of sexual activity and observed mating success are still valuable. Hence, summary statistics and relevant analyses are provided utilising all data where possible. It is also necessary to present these data sets for only those males involved in 10 or more aggressive interactions as these are the data sets used in the final analyses in Chapter 7 and 8. This also allows examination of the effects of removing those males involved in less than 10 interactions from the data sets.

(b) Transformation of variables;

In analyses involving parametric statistics all variables were examined for normality. Histograms for each variable were produced together with statistics including skewness, S.E. skewness, kurtosis and S.E. kurtosis. Both skewness and kurtosis were divided by their respective standard errors. If either of the values obtained was greater than 2.547 then the distribution of the variable was deemed to violate normality. In such cases steps were taken to transform these variables to minimise variance and the two values of skewness/SE skewness and kurtosis/SE kurtosis to below or equal to 2.547. It was found that the same variables for each year required transforming and also that the same method of transformation gave the best results (in terms of the above goals) for each year.

(c) Measures of the "degree of polygyny";

Several statistical techniques were employed in order to assess the relative degree of polygyny observed in each of the three seasons on Rona. The first measure of the variability of success was the standardised variance of mating success ($I = s^2/x^2$) as described in Wade and Arnold (1980) and Arnold and Wade (1984 a and b) and discussed in Clutton-Brock (1988). This measure has been utilised in several important studies of mating and/or reproductive success in various species (Clutton-Brock 1988, Boness 1991), and so allows comparison with a broad range of species (see Chapter 10).

Secondly, an index of dispersion was calculated in order to quantify the dispersion pattern of the distributions of mating success. The index used was Green's coefficient $(((s^2/x) - 1)/(\Sigma X - 1))$. This measure was selected as it takes into account sample size and as such is a more robust test (Krebs 1989). However, no sampling distributions are available for this index, therefore, confidence limits could not be assigned.

In order to assess whether there were in fact any significant differences in the "degree of polygyny" in each season a further analysis was conducted. For each year, the cumulative percentage of copulations accounted for by each successive 10 % of identified males (ranked in order of decreasing mating success) present in the study area was plotted. The curve obtained for each season was statistically compared with that of each other season by Kolmogorov Smirnov 2 sample tests.

In all of these tests, data for all identified males in each of the three seasons were utilised. The potential hazards of such measures of "degree of polygyny" are discussed in Chapter 10.

RESULTS

6.1. Individual variation in mating success

Figures 6.1 a, b and c show the frequency distributions of observed copulations amongst the males in the study area for 1987, 1988 and 1989 respectively. It must be noted that these graphs represent only observed copulations and not estimates of individuals total mating success for the entire season. However, the observation regimes were sufficiently uniform throughout the entire season to prevent biases occurring due to more intensive observations at any particular point of the season, and thus the relative rankings are probably accurate.

In 1987, of the 85 males which were present, at different times and for varying lengths of time in the study area, slightly less than half (47.06 %) gained at least one observed copulation. A total of 129 successful copulations were observed. The top ranking bull (in terms of mating success) accounted for 8.53 % of all observed copulations and the top 5 males accounted for 29.46 percent. In 1988, only 27 (23.08 %) of the 117 males present gained copulations. The top ranking male gained 8.41 % of the 107 observed copulations and the top 5 males accounted for 38.32 %. In 1989, 44 (30.35 %) of the 145 males present secured observed copulations. The top male accounted for 10.46 % of the 153 observed copulations and the top 5 bulls accounted for 35.29 %.

Figures 6.2 a, b and c show the frequency distributions of "copulations per day" for each male present in 1987, 1988 and 1989 respectively. These values are derived from the number of observed copulations for each male divided by each individuals length of stay in days for that year.

Tables 6.1a and b provide summary statistics for observed mating success and the daily copulation rate for male present in the study area in each year. Table 6.1a includes all identified males in the study area, whilst Table 6.1b gives statistics for only those males involved in ten or more inter-male aggressive encounters.

A oneway analysis of variance (with Scheffe's Multiple Range test) was conducted on the data presented in Table 6.1a. The data were transformed to approximate to normality where appropriate, as detailed in the methods. There was no significant difference in the mean numbers of observed copulations in each of the three years, ($F_{2,344} = 1.83$, $p = 0.16$). Similarly, there was no significant difference in copulation rate between years ($F_{2,344} = 2.91$, $p = 0.06$).

Also, the data from Table 6.1b showed no significant differences between years in either mating success or copulation rate for those males involved in ten or more inter-male aggressive encounters (observed mating success; $F_{2,137} = 0.08$, $p = 0.92$, copulation rate; $F_{2,137} = 0.39$, $p = 0.68$).

Figure 6.1 a : Variation in male mating success - Rona 1987

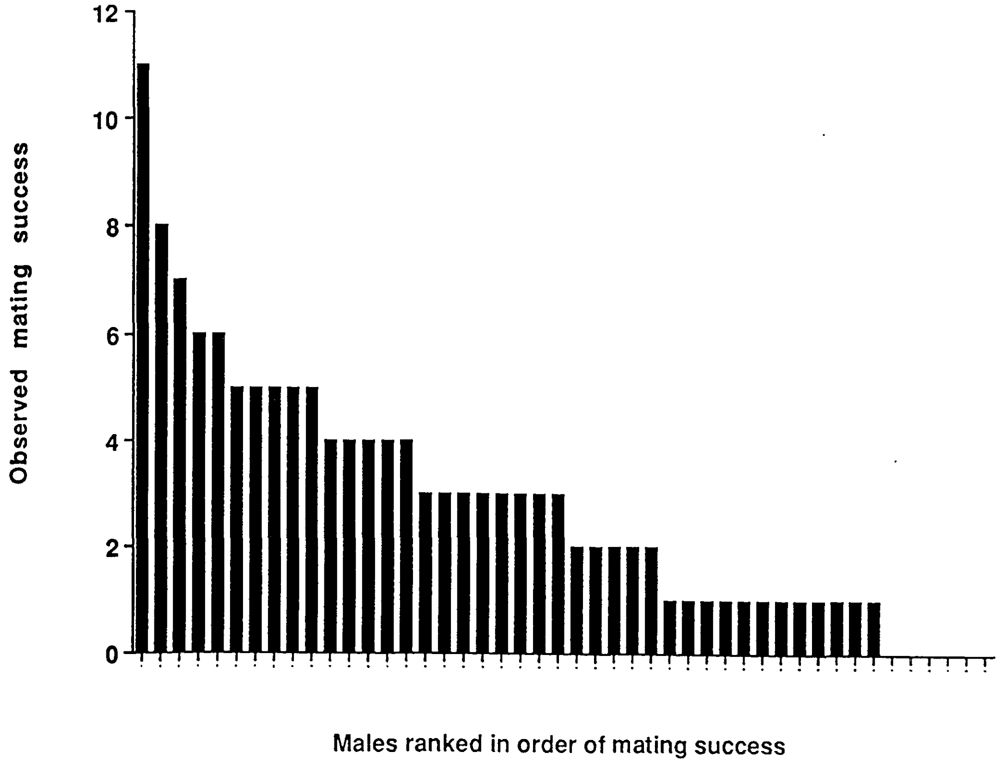


Figure 6.1 b : Variation in male mating success - Rona 1988

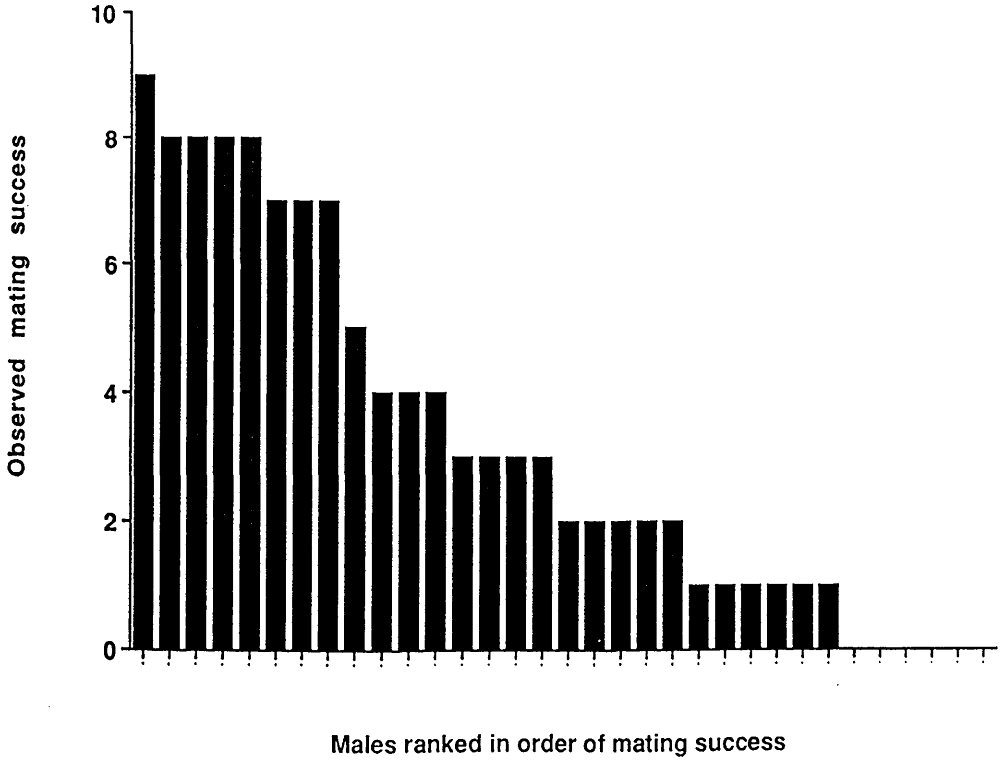


Figure 6.1 c : Variation in male mating success - Rona 1989

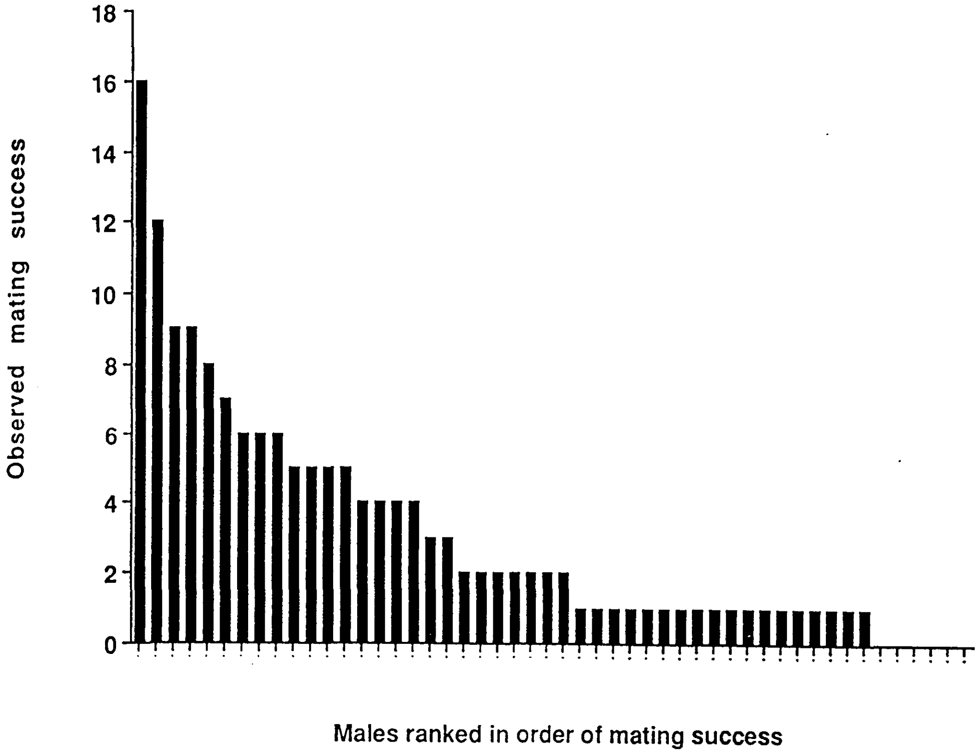


Figure 6.2 : Comparison of the relative degrees of polygyny observed on Rona

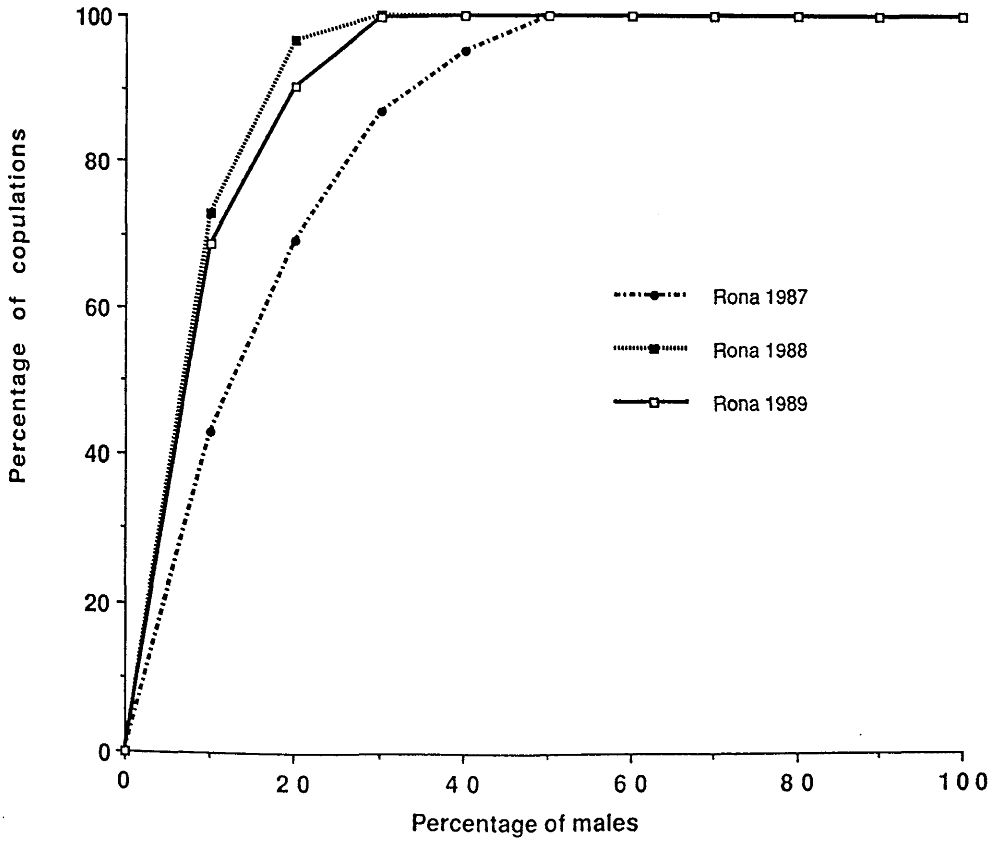


Table 6.1a

Summary statistics for observed mating success and copulations per day (copulation rate) for all identified males on the study area in each breeding season.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1987	MATING SUCCESS	85	0.00	1.52	2.23	0.24	0	11
	COPULATION RATE	85	0.00	0.11	0.24	0.03	0.00	2.0
1988	MATING SUCCESS	117	0.00	0.92	2.12	0.20	0	9
	COPULATION RATE	117	0.00	0.35	0.08	0.01	0.00	0.50
1989	MATING SUCCESS	145	0.00	1.06	2.43	0.20	0	16
	COPULATION RATE	145	0.00	0.11	0.36	0.03	0.00	3.02

Table 6.1b

Summary statistics for observed mating success and copulations per day (copulation rate) for all identified males on the study area which were involved in 10 or more inter-male aggressive encounters in each breeding season.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1987	MATING SUCCESS	47	2.00	2.47	2.54	0.37	0	11
	COPULATION RATE	47	0.10	0.12	0.12	0.02	0.00	0.46
1988	MATING SUCCESS	39	2.00	2.72	2.95	0.47	0	9
	COPULATION RATE	39	0.08	0.10	0.11	0.18	0.00	0.50
1989	MATING SUCCESS	54	1.00	2.65	3.42	0.47	0	6
	COPULATION RATE	54	0.10	0.14	0.28	0.38	0	2.00

6.2. DNA Fingerprinting results - determination of Paternity

Although blood samples were collected from females and pups in all three seasons, only those collected in 1988 and 1989 can be used in conjunction with behavioural and energetics parameters gathered during this study. Pups born, and sampled in 1988 or 1989, were sired in 1987 and 1988 respectively, those born in 1987 were sired in 1986, prior to this study. Henceforth, all reference to any particular breeding season will pertain only to the year in which a pup was sired. Obviously, fingerprints could be obtained from males sampled in any of the three seasons.

The number of males and female-pup pairs sampled during this study was severely limited by the need to minimise disturbance to individuals that were the focus of behavioural observations. With this precarious balance between disturbance and sample size in mind, it was deemed wise to err on the cautious side of minimising disturbance. As the behavioural observations form the main body of this study whilst the DNA fingerprinting was more of a pilot project, it was considered ill-advised to jeopardise these observations in an attempt to enhance sample sizes of captured individuals. In any case, measures of weight loss and paternity would be of little use if taken from a highly disturbed group of seals.

A total of 70 males have been fingerprinted, and these have been compared with the fingerprints of 46 mother-pup pairs where the pup was sired in either 1987 or 1988. Of these 46 cases, 26 cases (56.5 %) resulted in the exclusion of all 70 sampled males (i.e. father is unknown, but not one of the 70 sampled males). Of the remaining 20 cases, 9 were assigned a list of potential sires ranging between 5 and 9 potential fathers where paternity could not be ascribed to a single male (Group 1). In only 11 cases could paternity be assigned to a single male (Group 2). These cases were examined in relation to behavioural observations made during the year in which the pup was sired. In order to attempt a preliminary assessment of the extent to which observations of mating behaviour are a reliable indicator of reproductive success, records of the proximity of identified males to branded females were made in the daily census of the study site. These records were then compared with the paternity data. Similarly, any records of sexual interactions between identified males and marked females were examined in order to assess the degree of agreement with the paternity data. However, of these last two groups, where paternity has been assigned either to a list of males (Group 1), or a single male (Group 2), several cases could not be used in the context of this study for various reasons (see below). A breakdown of the cases in these two groups is provided below;

Group 1 - Paternity assigned to a list of potential sires;
(NB: Males were considered to be in close proximity to females if they were within a circle with a radius 10 m, centred on the female)

Total number of cases = 9, of these;

2 cases - the female of the mother-pup pair was not branded (and therefore not blood sampled) until the year the pup was born, hence these females were not recorded in observations in the year the pup was sired. Therefore, no data are available on the proximity and/or interaction of males with these females.

1 case - the female was branded, but not sighted in the year the pup was sired, hence this female was not recorded in observations during the year the pup was sired. Therefore, no data are available on the proximity and/or interaction of males with this female.

4 cases - these females were branded and sighted in the year that the pup was sired, **and** at least one of the males assigned as potential sires was sighted in close proximity (< 10m) to the female in the year the pup was sired.

2 cases - these females were branded and sighted in the year that the pup was sired, **but** none of the males assigned as potential sires were sighted in close proximity to the female in the year the pup was sired.

Group 2 - Paternity assigned to one male only;

Total number of cases = 11, of these;

1 case - where the male assigned as the sire, died (body was recovered and brand identified) in the year before the pup was sired! Also, the female was not branded until the year in which the pup was born, hence, this female was not recorded in observations during the year the pup was sired. Therefore, no data are available on the proximity and/or interaction of males with this female.

1 case - the female was branded, but not sighted in the year the pup was sired, hence this female was not recorded in observations during the year the pup was sired. Therefore, no data are available on the proximity and/or interaction of males with this female.

1 case - the male was not branded in the year the pup was sired, hence this male was not recorded in observations during the year the pup was sired. Therefore, no data are available on the proximity and/or interaction of this male with the mother of the pup.

1 case - where both male and female were identified in the year the pup was sired, **but** the male was not recorded in close proximity (< 10m) to the female and/or involved in sexual interaction with the female. However, this male was situated at the head of the gulley which was the females most probable route of departure from the colony on weaning her pup.

7 cases - where both male and female were identified in the year the pup was sired, **and** the male was recorded in close proximity (< 10m) to the female and/or involved in sexual interaction with the female. In one of these cases, the male was actually sighted in successful copulation with the female.

Therefore, in Group 1, 6 cases were accompanied by behavioural observations. In 4 of these cases, at least one of the potential sires could be identified from the behavioural observations. In Group 2, a total of 8 cases were accompanied by behavioural observations. In 7 of these 8 cases, paternity was assigned to a male that was clearly a potential sire in terms of the behavioural observations.

It is impossible to draw any firm conclusions from this limited data set, concerning whether paternity analyses corroborates or contradicts the records of observed mating success. This is compounded by the fact that very few copulations were observed between identified and sampled males and females that were marked prior to the copulation and sampled along with their pups in the following season (1 observed in 1987, and 3 in 1988). However, it is encouraging that in Group 2, 7 cases of the 8 assigned paternities (for which behavioural observations are available) were ascribed to males that were observed interacting with the female. Only one case attributed paternity to a male that was not observed interacting with the female. Considering that observations were limited by available light to a maximum of about 8 hours in a single day (i.e. one third of the day) it is entirely possible that this male could have copulated with the female outside the observation periods. Similarly, in Group 1, of the six cases where observations were made, 4 cases provided at least one male in the list of potential sires which was sighted interacting with the female. In the remaining 2 cases none of the potential sires were observed with the female. Again, the limited observation periods could explain this.

In the 26 cases that none of the 70 sampled males were assigned paternity it is again difficult to draw conclusions. Of these 70 males, only 48 were males sighted in the study area at any time. In total 275 males were identified throughout the three breeding seasons, hence only a small proportion were fingerprinted in total (25.45 %), and the proportion that were study area males is even smaller (17.45 %). Thus, there were many, identified but unsampled, males available (and observed in close proximity to and/or interacting with branded females) to be potential sires of the pups where no paternity has been assigned.

Similarly, only a small proportion of females were sampled. This, together with the contagious distribution of females on the study site (see Chapter 4) and variation in the size of female groups, makes extrapolation of these paternity results rather hazardous. A further confounding factor is that each male tends to operate in only a small part of the breeding colony, with movement between the various parts of the colony being rare (see Chapter 4). Hence, even if the sample size of assigned paternities was much greater, it would be impossible to extrapolate the individual success rates to encompass a predicted measure of an individual's success based on the number of females present in the colony. Such extrapolation would require detailed measures of female distribution and turnover, and the "home ranges" (area of operation) of identified males within this matrix of females.

One of the most intriguing results of this paternity analysis is the siring of a pup by a dead male! Obviously, this is somewhat improbable. How do we explain this result? The DNA fingerprint analyses do appear to confirm previous data on site fidelity of females (Anderson, pers.comm., Sea Mammal Research Unit data) and males (pers. obs., see Chapter 8). There is therefore a relatively high probability that in successive breeding seasons the same male may mate with the same female. Thus, there is the potential to produce full-siblings (brothers). It may be that the dead male had such a brother, who was in fact the sire of the pup but was not sampled. Thus, the closest matching fingerprint would be that of the deceased brother. Hence the erroneous result. If this is the case, then serious doubt must be cast upon the remaining assigned paternities. Alternatively, it may simply have been a case of a miss-labelled sample, though the sample was taken in 1986, prior to the onset of this study, so whether this is the case cannot be said.

However, assuming that the remaining cases are valid, is it possible to discern any behavioural and/or energetic parameters peculiar to these males when compared to nearby rival males which failed to inseminate the female in question? Only those cases where both paternity has been assigned, and behavioural and proximity data have been recorded can be examined in detail. Of the eight cases in Group 2 where both male and female were sighted during the season in which the pup was sired, only 5 cases involved individuals located in the study area. Hence, detailed behavioural data are only available for males in these 5 cases. The main behavioural and energetics parameters of the male that was assigned paternity in these cases was compared with those of other males observed in close proximity (< 10m) to the female towards the end of her lactation period (i.e. around oestrus). Table 6.2 lists the values of these parameters for each male assigned paternity in these 5 cases and their nearby "rivals". Table 6.2 also gives the number of days for which each male was sighted in the proximity of the female during her stay on the colony.

Table 6.2 Details of the main behavioural and energetics parameters of males assigned paternity and those sighted nearby the female at the time of oestrus. The male that was assigned paternity is listed first in bold type, followed by a list of potential, nearby rivals. X = number of days for which each male was sighted in the proximity of the female, during her stay on the colony. Length of stay is presented in number of days, arrival date as the number of days from the 19th of September, mating success as the total number of observed copulations, age in years, arrival weight in kg and rate of weight loss in kg per day.

FEMALE BRAND = B2 YEAR PUP SIRED = 1987

MALE I.D.	X	LENGTH OF STAY	ARRIVAL DATE	DOMINANCE SCORE	TOTAL MATING SUCCESS	AGE	ARRIVAL WEIGHT	RATE OF OF Wt. LOSS	SPECIFIC RATE OF Wt. LOSS
060	4	7.50	27	4.490	0	9	-	-	-
051	8	19.50	19	3.244	2	-	-	-	-
064	1	15.67	29	4.500	4	10	-	-	-

FEMALE BRAND = 3A YEAR PUP SIRED = 1988

MALE I.D.	X	LENGTH OF STAY	ARRIVAL DATE	DOMINANCE SCORE	TOTAL MATING SUCCESS	AGE	ARRIVAL WEIGHT	RATE OF OF Wt. LOSS	SPECIFIC RATE OF Wt. LOSS
060	2	15.00	25	3.752	3	10	256.41	-1.57	0.68
063	13	31.00	28	2.492	8	12	245.50	-3.08	1.22
152	7	21.00	21	3.775	3	8	280.69	-2.35	0.90

FEMALE BRAND = J3 YEAR PUP SIRED = 1988

MALE I.D.	X	LENGTH OF STAY	ARRIVAL DATE	DOMINANCE SCORE	TOTAL MATING SUCCESS	AGE	ARRIVAL WEIGHT	RATE OF OF Wt. LOSS	SPECIFIC RATE OF Wt. LOSS
069	11	47.00	10	2.857	8	9	303.52	-2.84	1.28
005	1	18.00	28	3.143	0	10	222.37	-0.56	0.26
020	5	32.00	11	5.162	2	9	237.70	-1.21	0.91
032	5	41.50	7	3.279	4	-	317.09	-2.81	1.25
037	9	18.00	2	2.964	3	-	-	-	-
112	3	24.00	10	3.406	2	-	-	-	-

FEMALE BRAND = N8 YEAR PUP SIRED = 1988

MALE I.D.	X	LENGTH OF STAY	ARRIVAL DATE	DOMINANCE SCORE	TOTAL MATING SUCCESS	AGE	ARRIVAL WEIGHT	RATE OF OF Wt. LOSS	SPECIFIC RATE OF Wt. LOSS
001	16	38.00	1	3.110	8	16	315.00	-3.00	1.27
002	2	47.33	11	3.901	4	9	304.00	-2.42	1.07
060	3	15.00	25	3.752	3	10	256.41	-1.57	0.68
073	1	14.00	7	5.619	2	9	-	-	-
133	5	24.00	13	2.812	3	-	-	-	-

FEMALE BRAND = 2A YEAR PUP SIRED = 1988

MALE I.D.	X	LENGTH OF STAY	ARRIVAL DATE	DOMINANCE SCORE	TOTAL MATING SUCCESS	AGE	ARRIVAL WEIGHT	RATE OF OF Wt. LOSS	SPECIFIC RATE OF Wt. LOSS
069	0	47.00	10	2.857	8	9	303.52	-2.84	1.28
002	4	47.33	11	3.901	4	9	304.00	-2.42	1.07
011	5	54.00	6	2.499	7	12	313.63	-2.78	1.54
071	19	41.66	8	3.198	4	12	248.66	-2.42	1.16
176	1	5.50	40	4.857	0	9	-	-	-

With so few cases of assigned paternity and accompanying behavioural data sets, it is difficult, if not impossible to draw any firm conclusions about these data, particularly in relation to the other parameters gathered during this study. There is no consistent pattern, in any of the measured variables, differentiating the male which sired the pup to those rivals which failed to do so. This is not surprising; the effects of opportunity and interactions with other males and females at the time the female was receptive would have considerable influence on which male copulates with a particular female. For example, in only 1 of the 5 cases above is the successful male the most dominant whilst in the remaining 3 cases he is the second most dominant. It may be the case that the most dominant males in these 3 cases were "otherwise occupied" while the successful male copulated with the female, for example, fighting with other males or copulating with some other, unsampled, female.

6.3. Assessing the degree of polygyny

In an attempt to classify the degree of polygyny observed in each of the three seasons on Rona various measures of the variability of mating success were calculated (see methods).

The standardised variance ($I = s^2/x^2$) for the distributions of observed mating success were 2.15, 5.31 and 5.26 in 1987, 1988 and 1989 respectively. These values suggest that the relative variation in mating success was greatest in 1988, though as similar level of variation existed in 1989. The value for 1987 is approximately half those of the other two seasons. From the same data sets, Green's coefficients ($((s^2/x) - 1)/(\Sigma X - 1)$) were calculated in order to quantify the dispersion pattern of the distributions of mating success. The respective values for 1987, 1988 and 1989 were 0.018, 0.037 and 0.030. These coefficients show the same pattern as did the standardised variances, indicating that the distribution for 1988 is the most aggregated when considering the sample size. Again, the values for 1988 and 1989 are similar, whilst that for 1987 is considerably lower. However, there is no sampling distribution available for Green's coefficient, so confidence limits could not be assigned.

In order to assess whether there were any significant differences in the "degree of polygyny" in each season a further analysis was conducted. For each year, the cumulative percentage of copulations accounted for by each successive 10 % of identified males (ranked in order of decreasing mating success) present in the study area was plotted (see Figure 6.2). The curve obtained for each season was statistically compared with that of each other season by Kolmogorov Smirnov 2 sample tests. There were no significant differences between any of the pairwise comparisons. The greatest difference was found between 1987 and 1988 ($z = 0.64$, $n = 236$, $p = 0.808$) as would be expected from Figure 6.2. The comparison of 1987 and 1989 yielded values of $z = 0.43$, $n = 282$, $p = 0.993$, whilst 1988 and 1989 showed little difference ($z = 0.21$, $n = 260$, $p = 1.00$). The deviation of the curve for 1987 from those of 1988 and 1989 is most probably due to the late onset of observations. Thus, many males arriving early, but remaining only a short time were not observed. This also accounts for the relatively low values of standardised variance and Green's coefficient for 1987.

These values will be compared with those for Sable Island in Chapter 9.

6.4.Detection of female reproductive state by males

Figures 6.4 a, b and c show the distribution of attempted copulations, whether successful (leading to intromission) or not, directed by males towards females with pups of each age class. In all three years significantly more attempted copulations were directed towards females with older pups (Chi square tests; 1987: $\text{chi}^2 = 11.68$ at 2 degrees of freedom, $p < 0.01$, 1988: $\text{chi}^2 = 14.88$ at 2 degrees of freedom, $p < 0.001$, 1989: $\text{chi}^2 = 14.53$ at 3 degrees of freedom, $p < 0.01$).

These figures also give the probability of these attempted copulations being successful (the proportion of successful attempts). All three years show significantly greater chances of success with females of older pups.

The pattern of the distributions are very similar in both 1987 and 1988, with vastly more attempted copulations directed towards mothers with stage 5 pups. Also, the chances of success are greatly enhanced by attempting to copulate with mothers of stage 4 or 5 pups. Though in both these years the probability of success declines slightly from

Figure 6.3 a : Distribution of attempted copulations and probability of success against pup age - Rona 1987

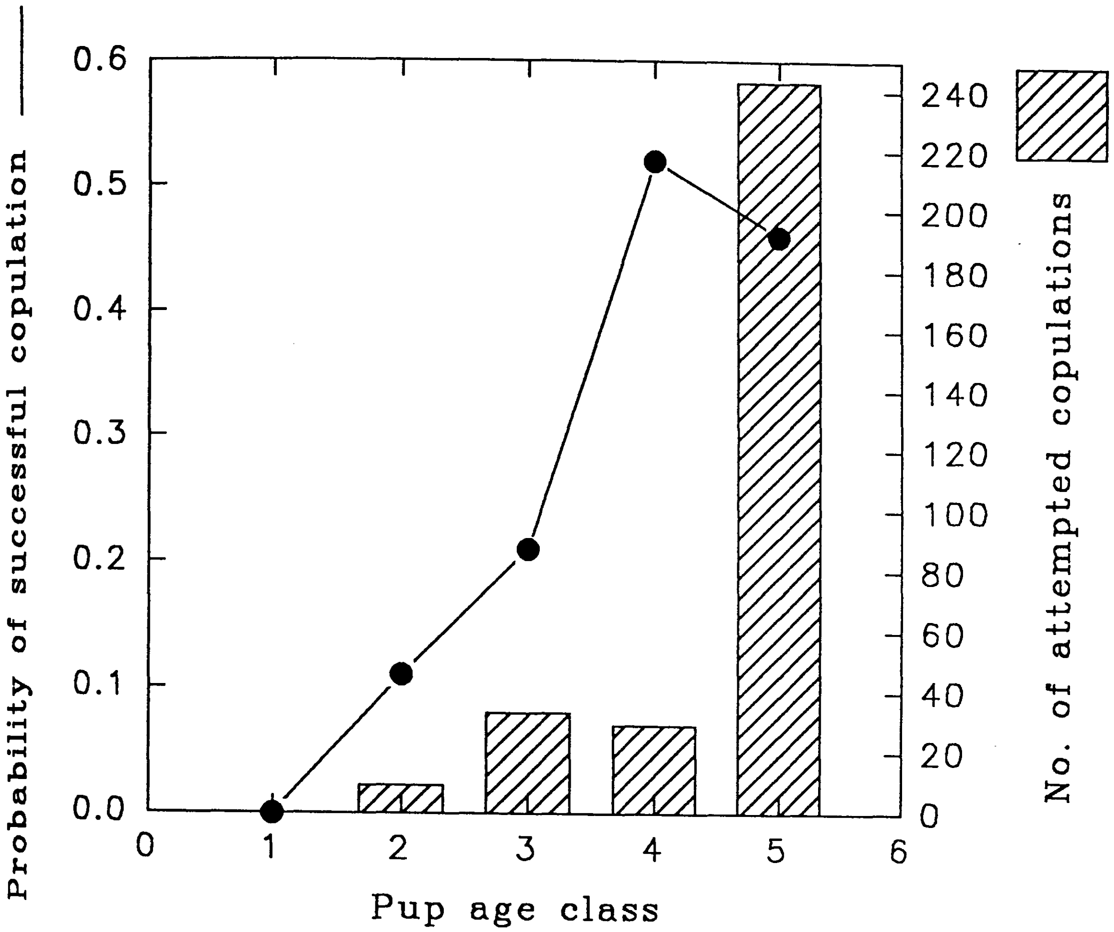


Figure 6.3 b : Distribution of attempted copulations and probability of success against pup age – Rona 1988

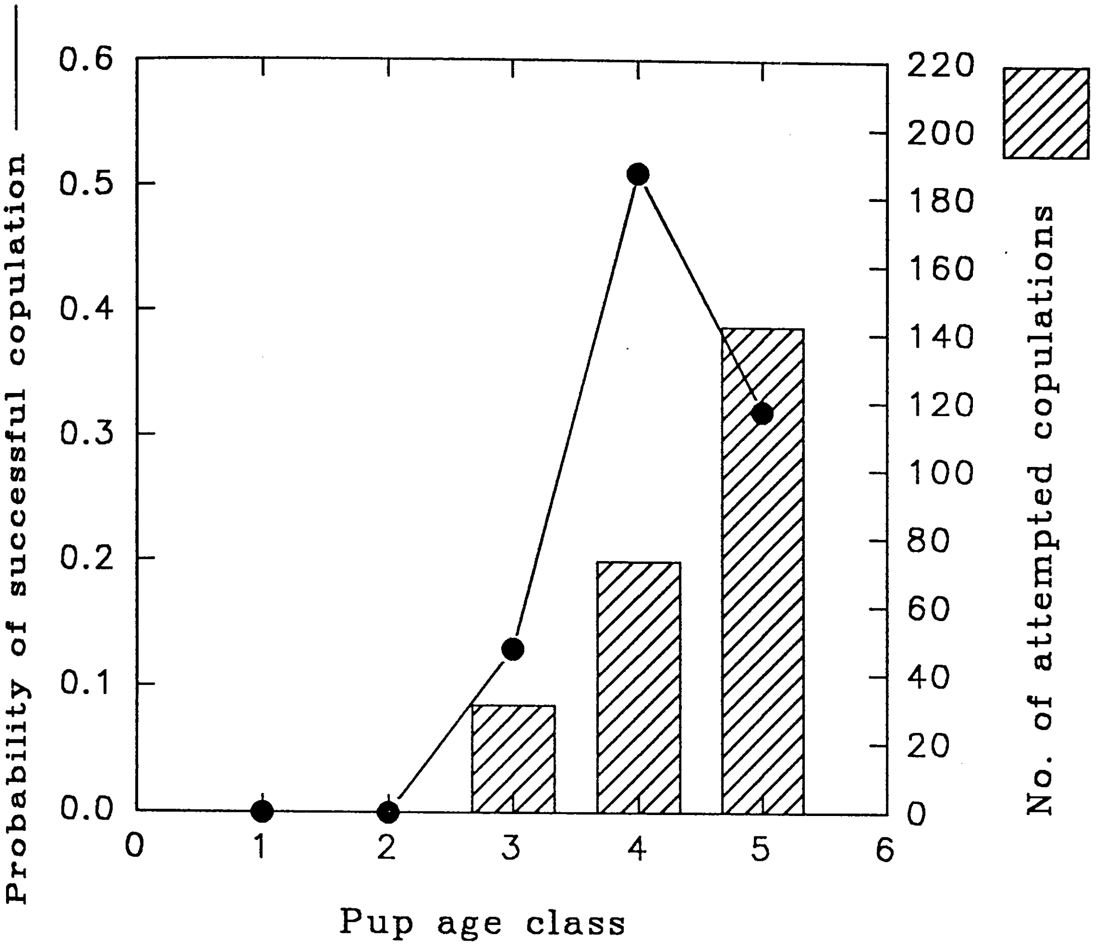
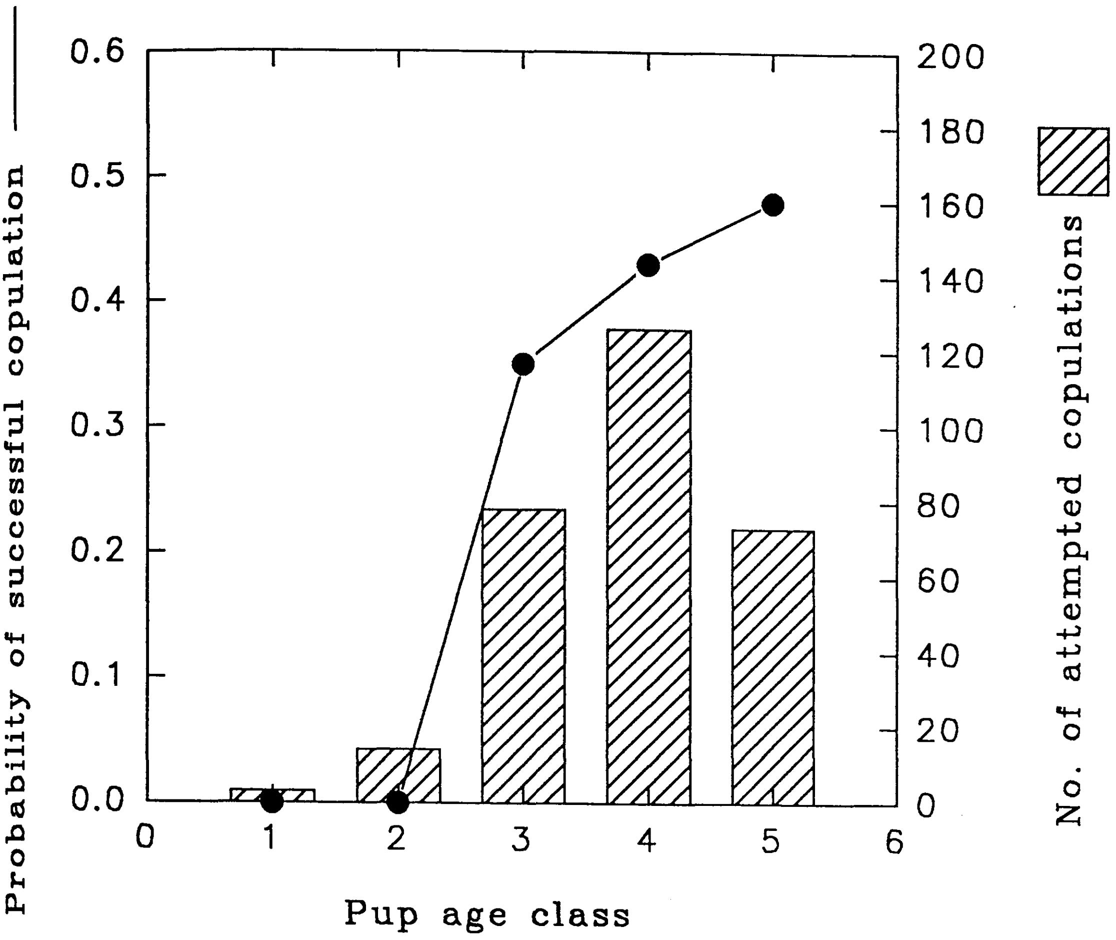


Figure 6.3 c : Distribution of attempted copulations and probability of success against pup age – Rona 1989



stage 4 to stage 5. In 1989 the opposite pattern occurs. Whilst still clear that mothers of older pups receive more attempts and provide greater success, the peak in attempted copulations occurs with stage 4 pups and the greatest degree of success with stage 5 pups.

6.5. Interrupted sexual acts

Tables 6.3a and b show the number of approaches to females, attempted copulations and copulations, which were interrupted by other males in all three years. In 1987 and 1988 (Table 6.3a) the interruptions are divided into two categories, one where the interruptions were successful, the other unsuccessful interruptions. A successful interruption was deemed to have occurred when the interrupting male succeeded in preventing the male involved in the sexual encounter from completing that particular behaviour. This basically took two forms. The first is where the interrupter succeeded in displacing the initial male by some aggressive encounter, effectively "chasing" the initial male off. The second occurred where the interrupter approached the initial male who was engaged in sexual behaviour, and upon being noticed was then "chased off" by the initial male who in doing so ended his sexual interaction. These two categories were recorded separately during 1989 (Table 6.3b) and hence the slightly different table format for this year. An unsuccessful interruption occurred when the intruding male failed to end the sexual interaction by either of the means outlined above.

In total, very few interruptions occurred at all considering the number of attempted copulations and copulations observed. Of these few interruptions, however, a vast majority were successful at the level of approach and attempted copulation whilst approximately half the interrupted copulations were successful. In 1989 however, all interruptions of copulations were successful.

These results were assessed with a chi-squared test. To examine the relative proportions of successful and unsuccessful interruptions data from all three years were combined in order to produce expected frequencies greater than 5. The analysis revealed a slight departure from the expected results ($chi^2 = 7.59$, degrees of freedom = 2, $p < 0.05$ but > 0.01). Examining the individual components of the chi value suggests that fewer approaches were unsuccessfully interrupted than expected and more copulations were unsuccessfully interrupted than expected. The remaining groups all approximated to the expected values.

A second chi-squared analysis was conducted on the successful interruptions of 1989, comparing those interruptions where the male involved in the sexual act chased off the intruder with those cases where the intruder chased off the males involved with the female. This revealed a strongly significant departure from the expected values ($chi^2 = 17.28$, degrees of freedom = 2, $p < 0.001$). Again, examining the components of the chi^2 score, suggests that for approaches fewer interruptions than expected involved the initial male chasing off the intruder and relatively more than expected involved the intruder chasing off the initial male. In the case of attempted copulations, more cases than expected involved the initial male chasing away the intruder whilst fewer than expected involved the intruder chasing off the initial male. The distribution of interrupted copulations between these two categories approximated to the expected scores. However, it must be noted that two of the six cells in this chi-squared test had expected values less than 5. None of the cells could realistically be combined.

Table 6.3a

Table showing occurrence of forms of interrupted sexual acts in 1987 and 1988.

YEAR	SEXUAL ACTIVITY	OUTCOME OF INTERACTION	
		SUCCESSFUL	UNSUCCESSFUL
1987	APPROACH TO FEMALE	7	1
	ATTEMPTED COPULATION	13	3
	COPULATION	2	3
1988	APPROACH TO FEMALE	15	2
	ATTEMPTED COPULATION	11	4
	COPULATION	2	2

Table 6.3b

Table showing occurrence of forms of interrupted sexual acts in 1989.

SEXUAL ACTIVITY	OUTCOME OF INTERACTION		
	SUCCESSFUL INTERRUPTION		UNSUCCESSFUL
	♂ involved in sexual act leaves to chase off the interrupter	interrupter chases off ♂ involved in sexual act	
APPROACH TO FEMALE	1	17	0
ATTEMPTED COPULATION	12	4	2
COPULATION	2	2	0

DISCUSSION

Rather fewer attempted copulations and copulations were observed in 1988 than in both 1987 and 1989, despite the 1988 field season being longer than that of 1987, though not of 1989. This is because considerably fewer females were present in the study area in 1988 than in either of the other seasons (see Chapter 4). By far the most sexual acts were observed in 1989 which had similar numbers of females to 1987 and a longer field season. In 1988 the females were less dispersed (see Chapter 4), a majority being able to congregate around the favoured sites and thus allowing fewer males to monopolise these females. Thus, a smaller proportion of the males present gain copulations. This is seen in the percentage of males that gain observed copulations, which is the lowest of the three years (25.55 % compared with 47.06 % in 1987 and 30.35 % in 1989). However, it must be noted that the value for 1987 may be somewhat artificially inflated as this was a shorter field season, effectively missing the first and last weeks of the breeding period which have higher turnover rates of males, with many males appearing for only short periods and gaining no or low mating success.

Despite these differences in the yearly percentages of males gaining observed copulations, it is clear that in any one year a vast majority of males present fail to secure copulations. In Anderson, Burton and Summers' 1975 paper, the top three males accounted for 35.6 % of all observed copulations. The top three males in each of the seasons 1987 to 1989 gained 20.2, 23.4 and 24.2 % of the observed copulations respectively. Again, this difference may be due to the greater number of short stay males identified in this study. Despite the differing observation periods, numbers of identified males present and the number of observed copulations, no significant difference was found in measures of the relative degree of polygyny between the three study seasons.

However, whilst clearly polygynous, the mating system on North Rona should be put in context by a comparison with the "classic" example of extreme polygyny amongst phocids, the elephant seals. Whilst clear sexual dimorphism exists in grey seals, the difference pales in comparison to that found in the elephant seals. In the southern elephant seal (*Mirounga leonina*) males can be up to 4 times the weight of females (King

1983). Similarly, the differential reproductive success between individual males does not appear to be so great. In the Southern elephant seal, the top ranking bull may account for up to 38 % of observed copulations, with the top 5 bulls monopolising an impressive 88 % (McCann 1981). This compares with figures ranging from 8.41 to 10.46 % for the top male, and 29.46 to 38.32 % for the top 5 male grey seals on North Rona.

Comparing the measures of the "degree of polygyny" exhibited at North Rona, there is remarkable similarity in both the standardised variances and Green's coefficients for 1988 and 1989. The lower values in 1987 are explicable, and have been attributed to the late onset of observations in this first season. Thus, many males arriving early, but remaining only a short time were not observed. These males generally have low or zero mating success, as not only is their time ashore brief, but there are few oestrus females available during this early part of the season (see Chapter 3 and 4). Despite this, there was in fact no significant difference in the relative "degrees of polygyny" between any of the three seasons when analysed by Kolmogorov Smirnov tests. These measures of the variability of male mating success are compared with those of a second grey seal breeding colony (Sable Island, Nova Scotia) in Chapter 9. Both the Rona and Sable values will then be compared to similar measures for a number of pinniped species and several non-pinniped species in Chapter 10.

It must be noted that these measures of variation in male mating success only include males that actually succeed in getting ashore for however long or short a time, and that there are perhaps many other males that fail to do even this. Indeed, on Rona, as well as the males which gain some time on the study site, many more can be seen in the water around the periphery of the colony and apparently never manage to enter the breeding colony. From Hewer's life table of the grey seal (Hewer 1964), only 28 % of the mature males participate in reproduction in a single year. Therefore, it is clear that relatively few males are actively involved in reproduction each year, and even less enjoy high mating success. This obviously raises the question; what factors determine which males gain high mating success? This will be assessed in Chapter 7.

Added to the fact that a few males are able to monopolise a disproportionate amount of the observed copulations in any given year are the differing abilities of individuals to either enhance or maintain their success, or lack of, in successive years. This aspect is examined in Chapter 8.

The attempt at examining the relationships between mating success and reproductive success by DNA fingerprint analyses has proved rather inconclusive in this respect, due primarily to the small sample sizes. The analyses did not clearly contradict the mating success data, nor did they unequivocally support it. Similarly, it was impossible to discern any consistent traits about those males who sired the pup which distinguished them from nearby rivals which failed to do so.

Opinion is somewhat divided as to whether male grey seals can detect a female's reproductive state and, if so, how? Anderson, Burton and Summers (1975) state that "bulls do not investigate individual cows to determine their sexual state before attempting to copulate, but once oestrus cows are present on the colony males will approach any females in their vicinity". Boness and James (1979) accept that males are able to diagnose a cow's condition prior to mounting her, but were unable to elucidate how the bulls achieve this. However, they do state that, "as in other phocids, the bulls do not investigate the cow's perineum, or any other part of her anatomy, before trying to mount her". In contrast, McCann (1981) describes a behaviour termed "heading" amongst Southern elephant seals (*Mirounga leonina*). Here the bull "lays his head on the female, sometimes sniffs her back and might also mouth her neck and back". The author suggests that depending upon the female's response the male will then attempt to copulate with her, move on to examine other cows or simply stop and rest. McCann also observed that "heading" was not shown amongst lower ranking (younger) bulls and suggests that this behaviour may have to be learned. Similarly, Cox (1983) provides evidence that subordinate, subadult male northern elephant seals (*Mirounga angustirostris*) are more likely to attempt copulations with non-oestrus females than more dominant bulls.

On North Rona certain field observations may suggest that male grey seals are indeed able to detect females' reproductive state. I have witnessed male grey seals performing a similar behaviour to that known as "heading" in elephant seals, with bulls clearly investigating a female's hind quarters. Other, more circumstantial evidence includes several instances where a clearly subordinate male approaches a female within close proximity to a resting dominant bull with a secure position amongst the females. The subordinate male then attempts to copulate with the female and is clearly seen by the dominant bull. However, the latter makes no attempt to remove the intruder, in fact, often returning to resting, completely ignoring the other male! The subsequent attempted copulation is unsuccessful. Thus, perhaps the dominant male is somehow aware that the female is unreceptive, and so the subordinate male is merely wasting time and energy and represents no threat to the dominant bull.

However, more substantial evidence is seen in Figures 6.3a, b and c. Here males show a clear preference for attempting copulations with females with older pups, that is, females which are in, or approaching, oestrus. Therefore, it does seem that male grey seals are indeed able to assess female reproductive state prior to attempting to copulate, although the method of detection remains unclear. The most probable methods being either olfactory or behavioural and morphological changes in the females, or a combination of these. Unlike McCann's work on southern elephant seals (1981), no difference was found in the ability of dominant and subordinate males to assess female receptivity. However, this may be because only males of a limited dominance range gain access to females, perhaps very young males (less than about 8 years) would have more difficulty in detecting oestrus? Also shown in Figures 6.4 a, b and c is the probability of attempted copulations being successful (i.e. leading to intromission). The chances of a successful attempted copulation are greatly increased with mothers of older pups, that is, with females in or near oestrus. Thus, having the ability to detect oestrus is a major advantage, as males can then conserve considerable amounts of time and energy by only directing copulation attempts at receptive females.

The slightly lower probability of success for group 5 females in 1987 and 1988 is because this class includes some females whose pups were abandoned or died at an early age, therefore these cows may not be in oestrus. In contrast, during the 1989 observations, these females were recorded as a separate category.

The few attempted copulations directed towards mothers with stage 1 and 2 pups were generally either young and/or subordinate, itinerant males, possibly relatively inexperienced at detecting oestrus females, or perhaps acting out of frustration or even simply "practising".

The number of observed interrupted sexual acts is surprisingly few. A vast majority occur at the stages of either approaching a females or attempted copulation. This is because at these stages the male performing the sexual interaction is not committed to a copulation and is free either to escape from an intruder or to deal with the intruder. However, when intromission has occurred the male would be somewhat more reluctant to depart from the female. Indeed in these instances, the male usually gives open mouth threats in an attempt to dissuade the intruder. However, the sample size is too small to form any firm conclusions about this.

In this chapter, the individual variation in mating success has been quantified and examined in detail. The mating system of the grey seal is polygynous, and exhibits the typically high variance in male mating success with only a few males monopolising a large proportion of the copulations. What, then are the determinants of individual male mating success?

CHAPTER 7 - DETERMINANTS OF INDIVIDUAL MALE MATING SUCCESS

INTRODUCTION

In the preceeding chapters I have defined and examined several factors influencing grey seal social organisation during the breeding season at North Rona. Particular reference has been made to quantitative aspects of the social organisation of males, and especially the nature and degree of polygyny in this population (see Chapter 6). In this chapter, the complex inter-relations between these variables within each breeding season is now examined in order to assess the main behavioural and/or energetic determinants of individual male mating success.

These analyses will be presented in the subsequent sub-sections of this chapter. However, it is first necessary to detail the analytical methodology used throughout this chapter. Details of data collection have already been provided in Chapter 2.

METHODS

1.Data

In all of the three study seasons data have been gathered for each individually identified male for some or all of the following variables;

BEHAVIOURAL PARAMETERS;

1. Mating success - the total number of observed first copulations made by each male with different females (as described in Chapter 6) during their entire stay in the study area.
2. Copulations per day - the mean rate of copulations per day for each male has been calculated from the observed rates. All successful copulations with any females have been included.
3. Total number of inter-male aggressive interactions - all observed inter male aggressive encounters in which each male was involved.
4. Number of inter-male aggressive interactions per day - mean daily rate of inter-male aggression for each male has been calculated from the observed rates.
5. Dominance score - a calculated value representing each individual male's relative

dominance (see Chapter 3 for method of calculation).

6. Age - age in years (see Chapter 2 for details of methodology).

7. Prior experience - a measure of each individuals previous experience utilising the number of days each individual had spent ashore in previous breeding seasons. This was obtained from Sea Mammal Research Unit brand sighting records prior to 1987 and data collected during this study. Obviously this measure is somewhat limited , in that only males branded prior to 1987 have known histories before the onset of this study, and even these are only known from when they were branded.

WEIGHT PARAMETERS;

8. Weight on day one (kg) - the arbitrary date of 19th September was selected as a useful point prior to the onset of each breeding season at which to make comparisons of individuals weights both within and between seasons at a standard time. Weight on day one was obtained by using each individuals' daily rate of weight loss to extrapolate back from their weight on first capture to the predicted weight on 19th September. This assumes constant weight loss for individuals within each season (see Chapter 5).

9. Arrival weight (kg) - predicted weight of each individual on their date of arrival, again computed using individuals rates of weight loss and weight on first capture and observed date of arrival.

10. Departure weight (kg) - predicted weight of each individual on their date of departure again using rate of weight loss to extrapolate to departure weight from weight at last capture and observed departure date.

11. Total percentage weight lost (%) - a measure of total percentage weight lost by each individual during their stay on the study site. Departure weight is expressed as a percentage of arrival weight.

12. Rate of weight loss (-kg/day) - mean daily rate of weight loss for each individual expressed in negative values.

13. Specific rate of weight loss - a proportional daily rate of weight loss, adjusting for arrival weights of individuals, calculated from the following formula;

$$S = (100 \times (\mathrm{Ln}(W2) - \mathrm{Ln}(W1)) / (D2 - D1))$$

where;
S = specific rate of weight loss
W1 = weight on first capture
W2 = weight on subsequent capture
D1 = date of first capture
D2 = date of subsequent capture

COLONY ATTENDANCE PARAMETERS;

14. Arrival date - date of arrival to the study area

15. Departure date - final date of departure from the study site. Both this and arrival date are expressed as integers, a value of 1 representing arrival on the earliest date on which observations were made in any of the three years (19th September), a value of 2 representing arrival on the following day etc. Thus, late arrivals have high values for arrival date, and males that depart early have relatively low values for departure date.

16. Length of stay - number of days spent ashore in the study area, or in the immediately adjoining area of Fianuis South.

The summary statistics (mean, median, standard errors, range etc.) of each of these parameters have been described in the previous chapters (Chapters 3 to 6).

2. Methods of analysis

(a) Selection criteria for cases:

For all statistical analyses only cases with greater than or equal to 10 total inter-male aggressive interactions were included. This ensured that individuals included in the analyses were involved in sufficient interactions for the data to show the male's status sufficiently accurately. Using this selection criterion removed many of those males present for only a few hours, for whom spurious results were often produced, particularly in the calculation of dominance score. For example, one successful interaction with a very subordinate male would have produced a dominance score equivalent to that of the more dominant individuals.

(b) Transformation of variables;

Initially, all variables were examined for normality. Histograms for each variable were produced together with statistics including skewness, S.E. skewness, kurtosis and S.E. kurtosis. Both skewness and kurtosis were divided by their respective standard errors. If either of the values obtained was greater than 2.547 then the distribution of the variable was deemed to violate normality. In such cases steps were taken to transform these variables to minimise variance and to reduce the two values of skewness/SE skewness and kurtosis/SE kurtosis to below or equal to 2.547. It was found that the same variables for each year required transforming and also that the same method of transformation gave the best results (in terms of the above goals) for each year.

Below is a list of variables used, the transformations used and the variable abbreviations. The list is for no specific year, as the same procedure was used for all years.

Total No. of inter-male aggressive interactions - Log10(x)
Total No. of observed copulations (mating success) - Log10(x+1)
Copulations per day - SQ root(x)
No. aggressive interactions per day - Log10(x)
Arrival date at colony - SQ root(x)
Weight on date of departure - Log10(x)
Departure weight as %age of arrival weight - Arcsin transformation
Prior experience - SQ root(x)
length of stay - Log10(x)

Variables requiring no transformation;

Dominance score
Rate of weight loss (both absolute and specific rates)
Weight on day one
Arrival weight
Age
Departure date

(c) Relationships between variables within each season;

The transformed data were examined for relationships between pairs of variables within each of the three seasons. This was done primarily by two means. Potential non-linear relationships were assessed by production of scattergrams. Plots of all relationships between pairs of variables (transformed where necessary) were examined to ensure linear relationships and checked for wayward outliers. Any apparently aberrant cases were examined for potential data input errors. If such cases were found to be valid data they were retained.

However, much of the analyses involved the production of Pearson correlation matrices for each of the three seasons based upon the transformed data. These matrices for 1987, 1988 and 1989 are presented in Appendix C. With so many variables, it is not surprising that many significant correlations were produced, there being a high potential for the production of spurious correlations by chance. Therefore, it was necessary to operate some form of selection procedure in order to assess which were the meaningful relationships. This was achieved by two complementary methods. Firstly, it was more appropriate to be rather conservative and so correlations were deemed robust only if p was less than 0.01. The second method relied on the consistency of the nature of the relationship between two variables in all three seasons. In previous chapters it has been shown that there is no or little difference in the mean and/or median values of the main variables in successive seasons. Similarly, the patterns on colony attendance, colonisation, seal distribution, numbers through the season, seasonal changes in male turnover, sex-ratio, sexual and aggressive activity are all remarkably similar in each of the three years. Therefore, we can reasonably assume that the males, and indeed the females, are behaving in general, the same in each year. Therfore, relationships between pairs of variables which are repeated in all three years can be attributed a greater degree of validity. This analysis was accomplished by analysis of covariance. This enabled relationships between pairs of variables which **DID NOT** significantly differ in slope and/or elevation in all 3 years to be distinguished. Both slope and elevation were tested at $p < 0.05$ significance levels, as the analyses were directed toward finding relationships that were similar, this p value was a more stringent test, excluding cases which would have been deemed not significantly different at $p < 0.01$. These were then compared with the Pearson correlation matrix to establish those which had significant correlations in all 3 years. Those relationships which showed significant correlations in at least two seasons, with no significant difference in slope in all three seasons though significantly differing elevations were also examined as potentially interesting relationships. The nature of these relationships was consistent even if the baseline differed between years. The following list is a summary of the results (*** indicates significant correlations in all 3 years whilst ** indicates significant correlations in 2 of the three years all at $p < 0.01$);

RELATIONSHIPS WITH NO SIGNIFICANT DIFFERENCE IN SLOPE OR ELEVATION:

MATING SUCCESS - LENGTH OF STAY ***
MATING SUCCESS - TOTAL No AGGRESSIVE INTERACTIONS***
MATING SUCCESS - DOMINANCE ***
MATING SUCCESS - DEPARTURE DATE ***
MATING SUCCESS - AGGRESSIVE INTERACTIONS PER DAY **
LENGTH OF STAY - DOMINANCE ***
DEPARTURE DATE - LENGTH OF STAY ***
ARRIVAL DATE - LENGTH OF STAY **
TOTAL No. AGGRESSIVE INTERACTIONS - ARRIVAL DATE ***
COPULATIONS PER DAY - DEPARTURE DATE **
ARRIVAL DATE - WEIGHT ON DAY ONE ***
SPECIFIC RATE OF WEIGHT LOSS - RATE OF WEIGHT LOSS ***
RATE OF WEIGHT LOSS - WEIGHT ON DAY ONE **

RELATIONSHIPS WITH NO SIGNIFICANT DIFFERENCE IN SLOPE, BUT SIGNIFICANT DIFFERENCES IN ELEVATION:

AGGRESSIVE INTERACTIONS PER DAY - LENGTH OF STAY ***
AGGRESSIVE INTERACTIONS PER DAY - DOMINANCE ***
AGGRESSIVE INTERACTIONS PER DAY - DEPARTURE DATE ***
ARRIVAL DATE - ARRIVAL WEIGHT **
DEPARTURE WEIGHT - ARRIVAL WEIGHT **
TOTAL PERCENTAGE WEIGHT LOST - ARRIVAL WEIGHT **

RELATIONSHIPS TESTED WHICH SHOWED SIGNIFICANTLY DIFFERING SLOPES

MATING SUCCESS - COPULATIONS PER DAY ***
TOTAL PERCENTAGE WEIGHT LOST - SPECIFIC RATE OF WEIGHT LOSS**

By the above methods it was possible to determine the most robust relationships. Many of these variables were indeed highly significantly correlated in all three years, and only these were used in subsequent analyses. It remains difficult to determine whether there was a causal link between two variables, or indeed whether a common relationship with some third variable was mediating the relationship. In order to assess the main determinants of each dependent variable, where appropriate, a further analytical method was employed.

(d) Multi-variate analyses;

Using a stepwise regression procedure, multiple linear regression models were developed for each dependent variable utilising only those independent variables deemed to be truly independent (for example, the mean daily rate of copulations is in effect a composite of total mating success and the length of stay in days, hence, neither length of stay nor total mating success were used as independent variables in the model describing copulations per day) or logical putative causal factors (for example, it is intuitively illogical to propose that the departure date could be a determinant of dominance, however, the reverse is indeed plausible). Those variables deemed suitable were then entered as independents. If any particular variable reduced the sample size to extremely low numbers, these were excluded (eg. AGE in 1987, n = 7). To enhance sample size, limiting variables were removed if there was no significant correlation between these and the dependent as shown by a Pearson correlation matrix (these usually included measures of weight and age).

Following statistical advice (Dr McClaren, Glasgow University Statistics Department) a second regression technique was employed as a further test of the strength of the observed relationships. For each model, the independent variable entered on the first step was then used as the dependent in a "reverse multiple regression". In this, the dependent variable of the original model is included as an independent variable along with those others used in the original model. If the original dependent variable (now an independent) is entered in the first step of this "reverse multiple regression" then greater reliability can be placed on the relationship between these two variables. For example, initially the dependent variable "Y" is regressed on the independent variables "x","z" and "w". Suppose "x" is entered in the first step. In the "reverse regression", "X" becomes the dependent and the independents are "y", "z" and "w". If "y" is then entered on the first step then greater credence can be given to the relationship between "X" and "y".

All regressions were conducted using SPSSX. In all regressions the p values for inclusion were 0.01, and default values for exclusion and tolerance were used (0.1 and 0.01 respectively).

NOTE;

AGE is not used in any multiple regression analysis in 1987 as inclusion of this variable reduces the sample size to only 7 !

RESULTS

The results are presented in the following sub-sections (7.1 to 7.8). Finally, in section 7.8, we utilise the same analytical procedures to assess the primary determinants of individual male mating success.

These analyses were used to produce the final flow diagram, presented in the discussion to this chapter, describing the relationships between factors affecting mating success.

7.1 - WEIGHT PARAMETERS

Male grey seals fast during the breeding season and rely on energy reserves, primarily in the form of the thick layer of blubber, accrued prior to the breeding period (Boness and James 1979, Boness 1984, Anderson and Fedak 1985). Fedak and Anderson (1985) state that the blubber can account for more than 80 % of the energy used in reproduction; therefore, the weight loss incurred by a male is a useful indication of his energy expenditure.

1. Weight on date of arrival:

As can be seen from the three correlation matrices in Appendix C, other than the expected correlations with weight on day one in each year, weight on date of arrival showed no consistent relationship with any other variable. However, in certain cases this lack of correlation is particularly interesting.

Males that were heavier upon arrival did not necessarily gain greater mating success or copulations per day (Figures 7.1.1 a, b and c). Whilst there was a good relationship in 1989 (Figure 7.1.1 c), this was not the case in the other two years (Figures 7.1.1 a and b).

Similarly, arrival weight showed no consistent relationship with dominance score (Figures 7.1.2 a, b and c), heavier males were not necessarily the more dominant individuals. There was also no clear relationship in any of the three seasons between the arrival weight and age of an individual (Figures 7.1.3 a, b and c).

There was also no significant correlation (at $p < 0.01$) in any year between arrival weight and subsequent rate of weight loss. Thus, heavier males did not necessarily suffer greater absolute rates of weight loss. Similarly, there is no relationship between arrival weight and proportional weight loss rate (see Appendix C). Thus, heavier males did not lose proportionately more or less weight per day.

There were also no consistent correlations between arrival weight and colony attendance parameters. Surprisingly, there were no correlations in any year between arrival weight and arrival date. Thus, males that arrived early in the season were not

Figure 7.1.1 a : Plot of Log10 (mating success) against arrival weight - Rona 1987

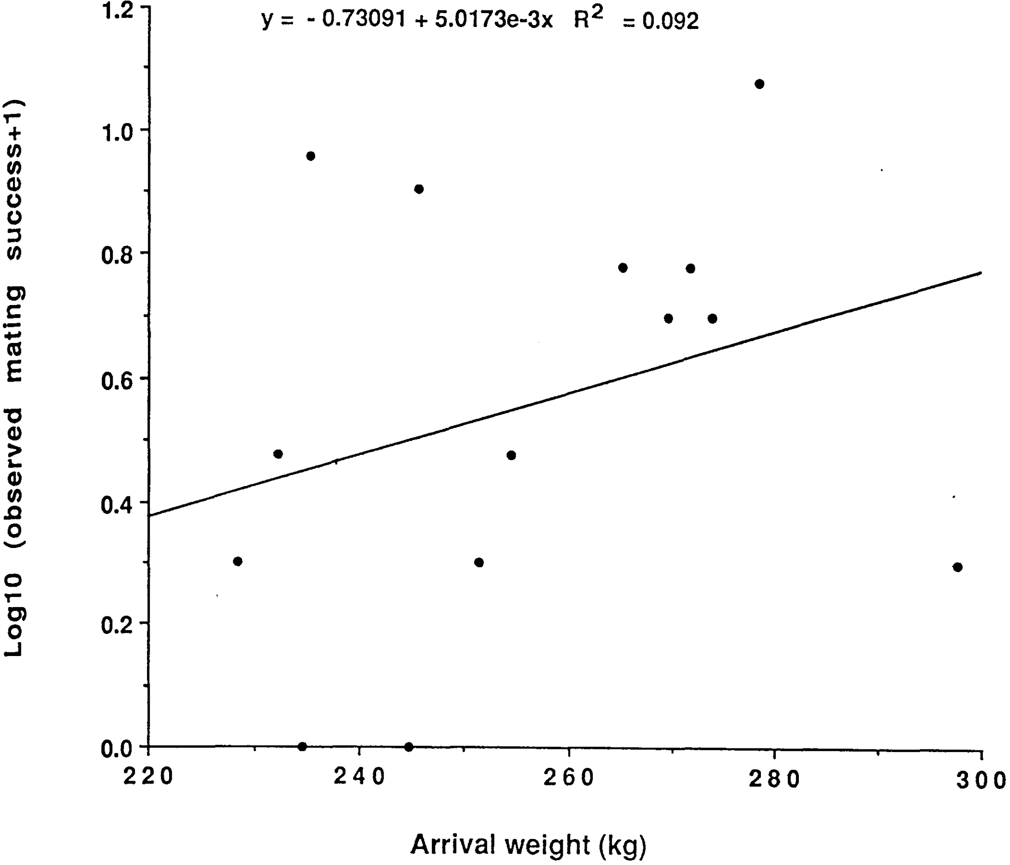


Figure 7.1.1 b : Plot of Log10 (mating success) against arrival weight - Rona 1988

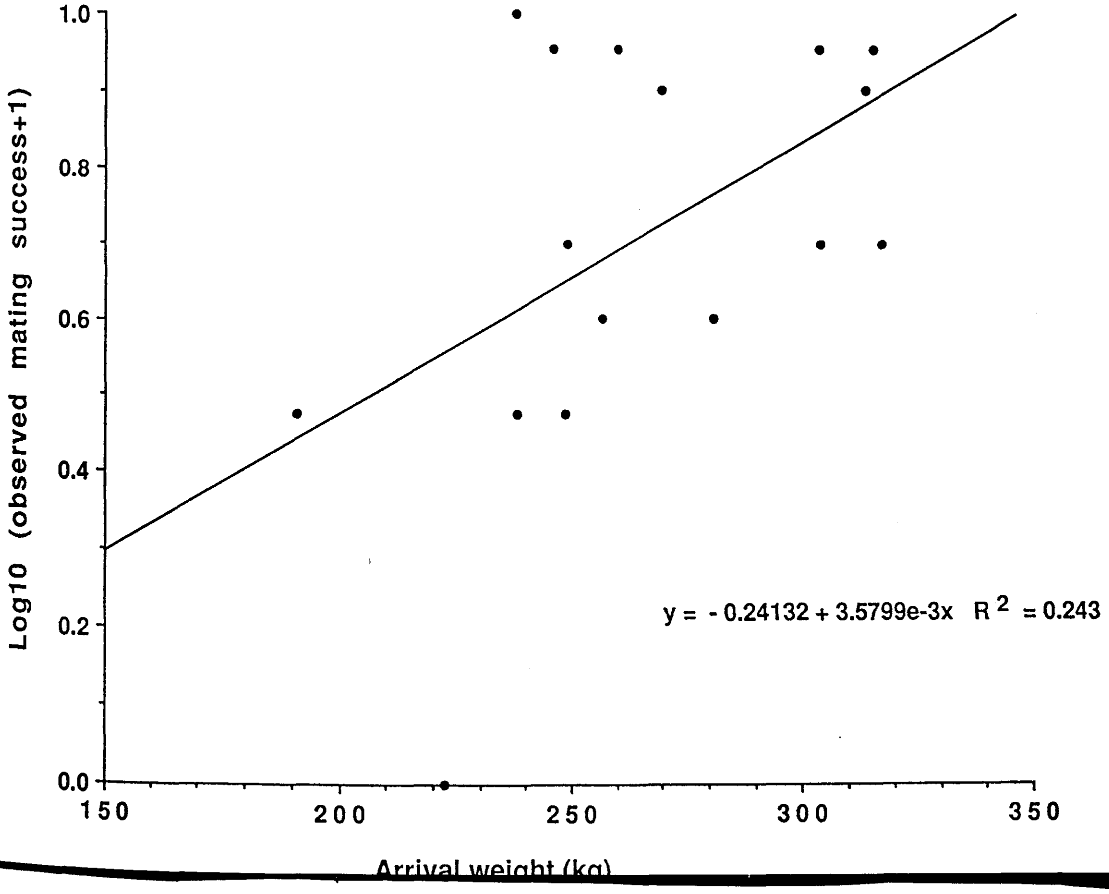


Figure 7.1.1 c : Plot of mating success against arrival weight - Rona 1989

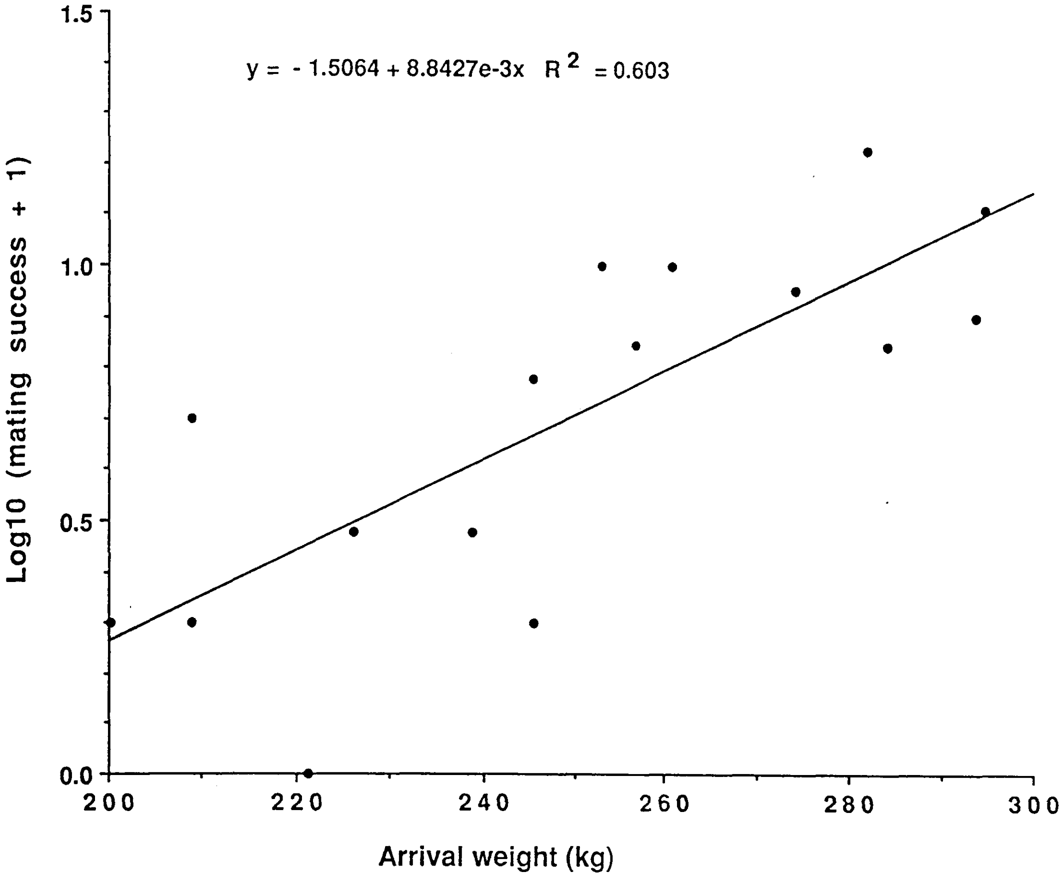


Figure 7.1.2 a : Plot of Dominance score against arrival weight - Rona 1987

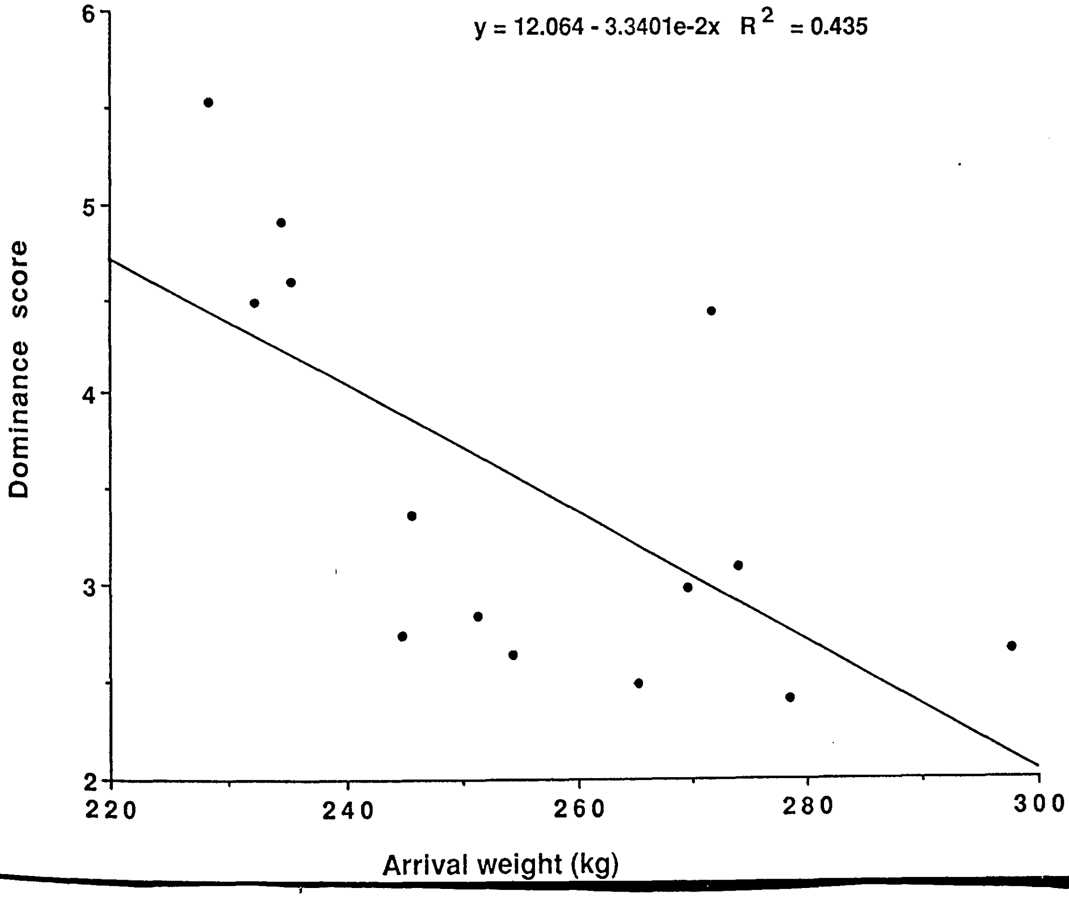


Figure 7.1.2 b : Plot of Dominance score against arrival weight - Rona 1988

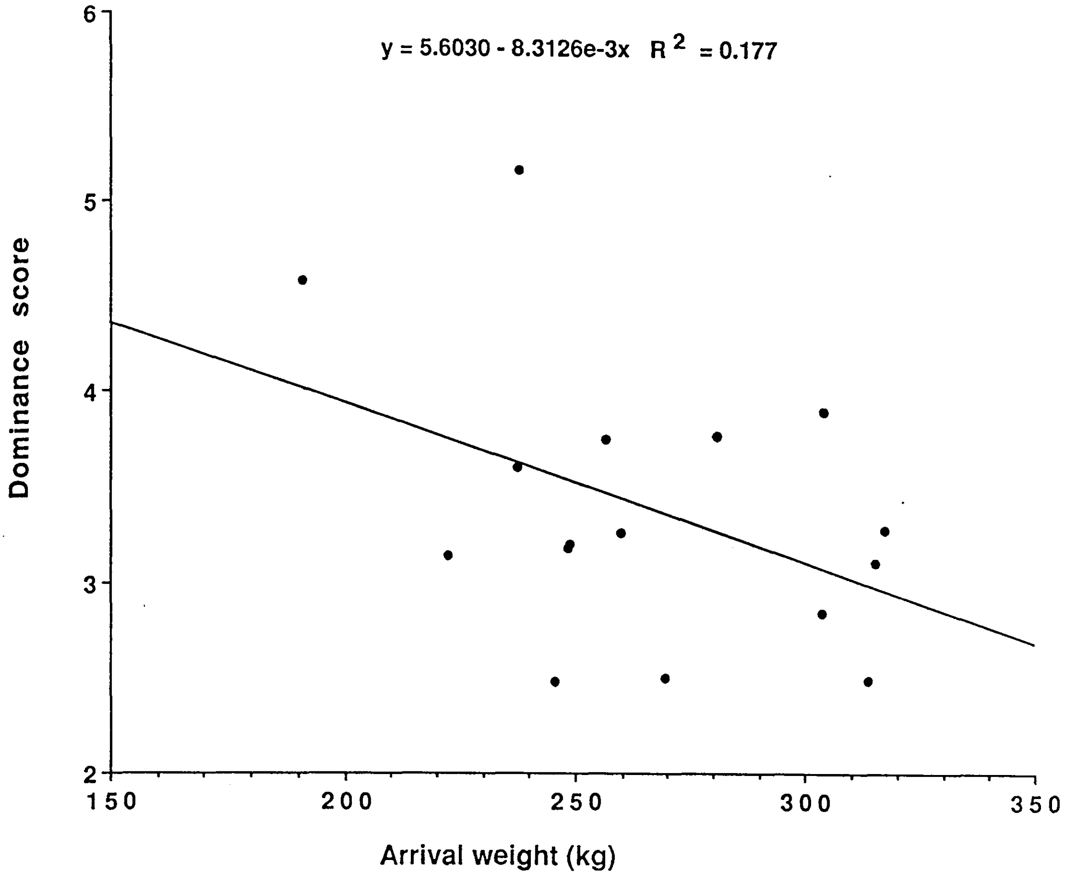


Figure 7.1.2 c : Plot of Dominance score against arrival weight - Rona 1989

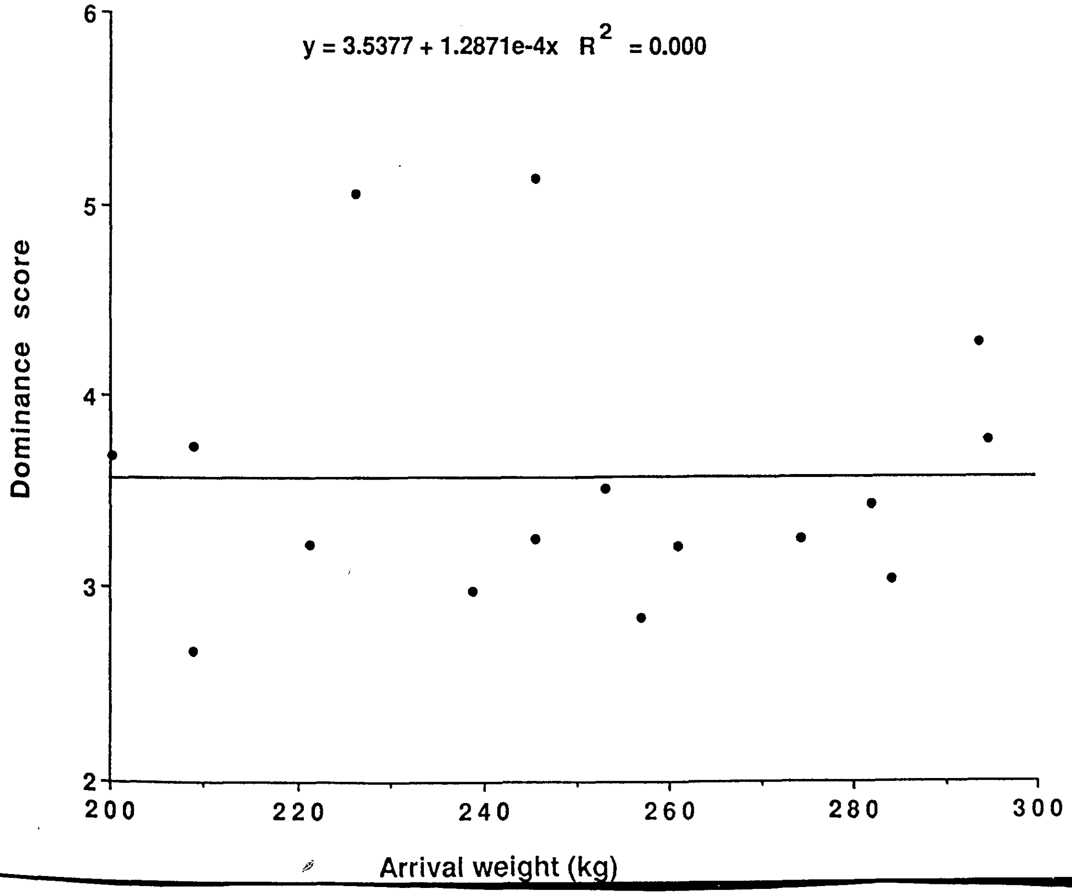


Figure 7.1.3 a : Plot of arrival weight against age - Rona 1987

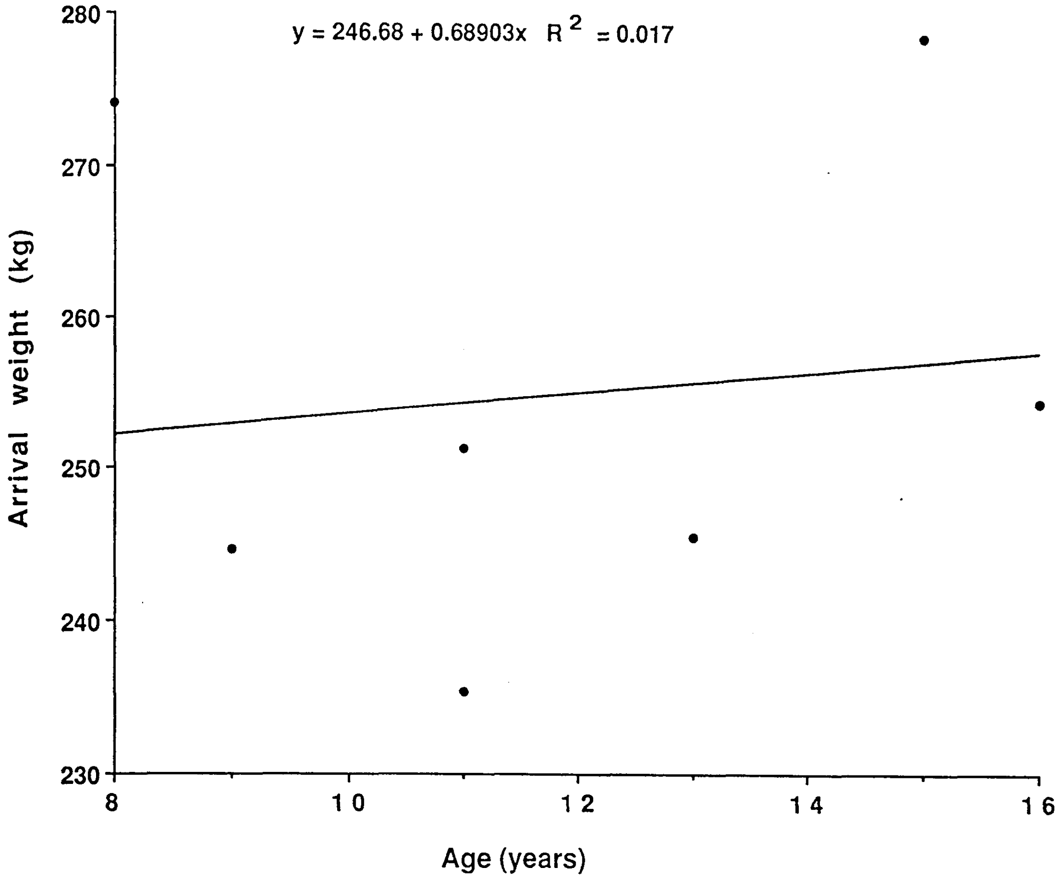


Figure 7.1.3 b : Plot of arrival weight against age - Rona 1988

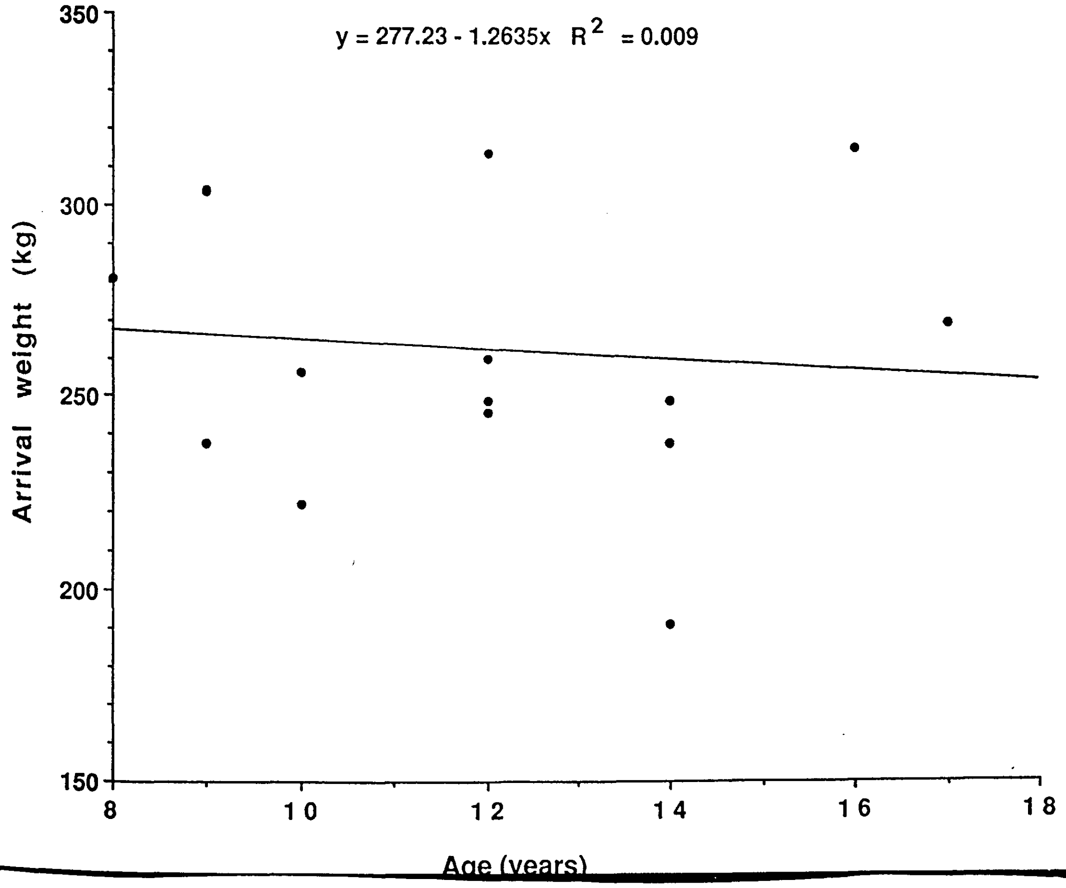
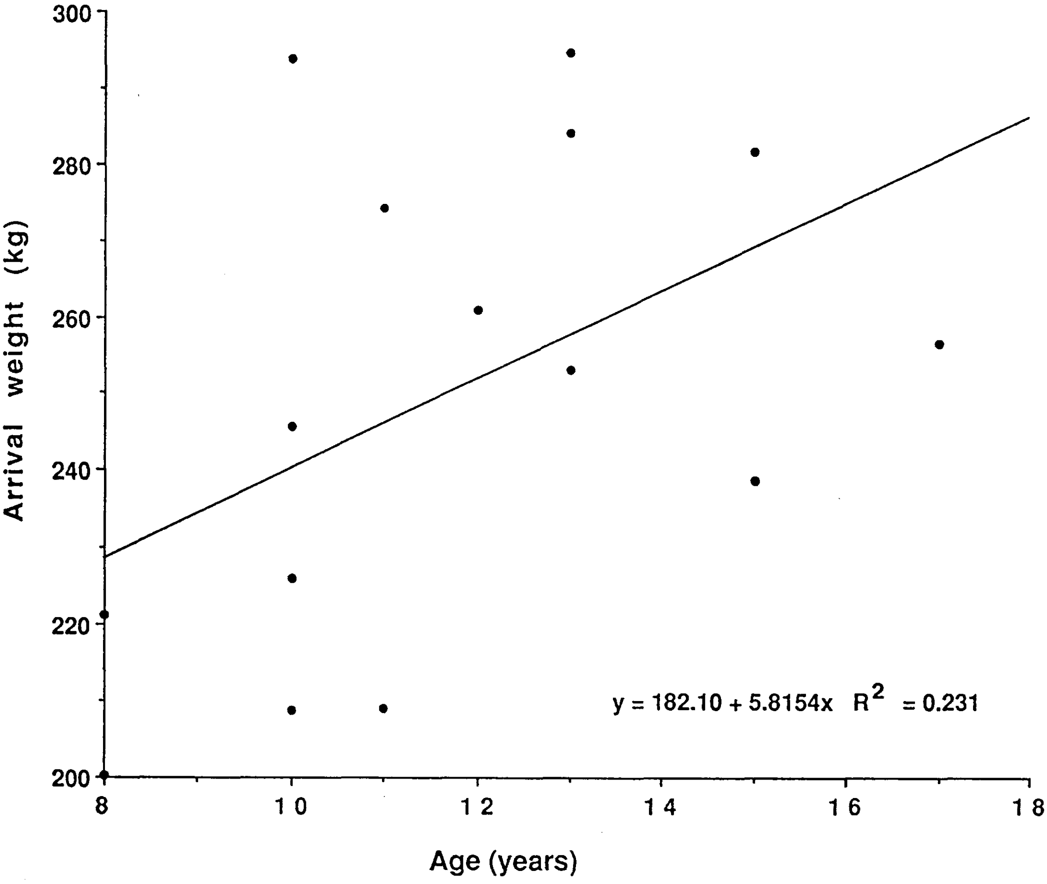


Figure 7.1.3 c : Plot of arrival weight against age - Rona 1989



necessarily heavier males, or conversely, heavier males did not necessarily arrive earlier than lighter males. Similarly, there was no relationship between arrival weight and departure date in any of the three seasons and no consistent correlation between arrival weight and length of stay. Heavier males did not remain ashore for significantly longer than lighter males, nor did they depart at a later date.

As would be expected from the foregoing, the multiple regression analyses (Table 7.1.1) show that none of the potential determinants of arrival weight are entered in the procedure, thus we have no accurate predictor of male arrival weight.

Table 7.1.1

Table summarising results of multiple stepwise regression model developed for arrival weight.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - ARRIVAL WEIGHT n = 14			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE ARRIVAL DATE		NO SIGNIFICANT RESULTS		

1988	DEPENDENT VARIABLE - ARRIVAL WEIGHT n = 15			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
AGE DOMINANCE SCORE ARRIVAL DATE		NO SIGNIFICANT RESULTS		

1989	DEPENDENT VARIABLE - ARRIVAL WEIGHT n = 16			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
AGE DOMINANCE SCORE ARRIVAL DATE		NO SIGNIFICANT RESULTS		

Notes;

Independents not used;

The remaining variables were not deemed plausible determinants of arrival weight. All the remaining variables measure occurrences post arrival, and as such are unlikely to influence starting weight.
NB both rate of weight loss and arrival date were used to extrapolate from the first weighing of the males to an estimated weight on date of arrival, thus arrival date may not be truly independent. Dominance may be the only possible determinant of arrival weight measured (other than age which is not used in the 1987 analyses).

2. Weight on day one (19th September):

As would be expected, weight on day one was highly correlated with arrival weight in all three seasons. As with arrival weight, there were no consistent correlations between weight on day one and measures of mating success, dominance, age or colony attendance parameters. The only noticeable difference was a significant correlation with rate of weight loss, though not with proportional weight loss, in two of the three seasons. This, however, was most probably due to the fact that an individuals weight on day one is calculated using that individuals rate of weight loss.

Multiple regression analysis using the same independents as for arrival weight again produced no predictors for weight on day one.

3. Weight on date of departure:

Again, departure weight showed no consistent significant correlation with any other variable. It is particularly interesting that there was no consistent relationship with either rate of weight loss or proportional weight loss. Similarly, there was no correlation with departure date or length of stay in any of the three years. Thus, males did not leave the breeding grounds upon reaching a certain threshold weight. This raises the question, did they depart upon loss of a certain proportion of their weight?

4. Departure weight as a percentage of the arrival weight:

In fact, there was no consistent relationship between percentage weight lost and any other variable measured (although there is a significant negative correlation in two of the three seasons with proportional rate of weight loss). Of particular interest is the lack of correlation with departure date and length of stay. Therefore, males do not appear to depart from the colony upon being reduced to a certain threshold proportion of their arrival weight.

5. Rate of weight loss:

At $p < 0.01$ rate of weight loss showed no consistent correlation with any other variable other than proportional rate of weight loss as would be expected. Note that there was a consistent correlation at $p < 0.05$ with dominance score (1987: $r = +0.55$, $n = 14$, $p = 0.044$, 1988: $r = +0.52$, $n = 16$, $p = 0.039$, 1989: $r = +0.53$, $n = 16$, $p = 0.035$). Thus, there was some tendency for more dominant individuals to experience a greater rate of weight loss. Analysis of covariance revealed no significant differences between the three seasons in either the slope or elevation of these relationships.

The correlations with weight on day one are outlined above.

There was no consistent correlation between rate of weight loss and either of the two measures of daily rates of high energy activities, copulations per day and aggressive interactions per day.

Of particular interest is the lack of correlations between rate of weight loss and any of the measures of colony attendance, especially departure date and length of stay. It would appear that an individual male's rate of weight loss does not in itself determine how long a male can remain ashore and energy expenditure places no severe limits on length of stay.

It is possible that length of stay may be determined by a combination of factors, for example initial condition and subsequent rate of weight loss. Such possibilities are tested later in multiple regression procedures (see Chapter 7.2, length of stay).

Assessing determinants of rate of weight loss by multiple regression models (Table 7.1.2) revealed no predictors for 1987 or 1989, however, in 1988, the rate of sexual activity (copulations per day) was entered, and was verified in the reverse regression.

6. Proportional rate of weight loss;

As with the absolute rate of weight loss, this measure of energy expenditure showed no consistent relationship with any other variable (other than rate of weight loss). There was no correlation at all with dominance score, age, rates of sexual or aggressive activity or colony attendance patterns. However, there were significant negative correlations in two of the three seasons with total percent weight lost.

Multiple regression analysis utilising the same independents as for rate of weight loss revealed no predictors of proportional weight loss in any of the three seasons.

Table 7.1.2
Table summarising results of multiple stepwise regression model developed for rate of weight loss. Results of the reverse regression where applicable, are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - RATE OF WEIGHT LOSS n = 14			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE ARRIVAL WEIGHT COPULATIONS/DAY AGGRESSION/DAY		NO SIGNIFICANT RESULTS		

1988	DEPENDENT VARIABLE - RATE OF WEIGHT LOSS n = 16			
INDEPENDENT VARIABLES	X	R^2	SIGNIFICANCE OF F	ADJUSTED R^2
DOMINANCE SCORE				
ARRIVAL WEIGHT				
COPULATIONS/DAY	1	0.44028	0.0051	0.40030
AGGRESSION/DAY				
REVERSE REGRESSION : DEPENDENT - COPULATIONS/DAY				
RATE OF Wt. LOSS	1	0.44028	0.0051	0.40030
DOMINANCE SCORE				
ARRIVAL WEIGHT				
AGGRESSION/DAY				

1989	DEPENDENT VARIABLE - RATE OF WEIGHT LOSS n = 16			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE		NO SIGNIFICANT RESULTS		
ARRIVAL WEIGHT				
COPULATIONS/DAY				
AGGRESSION/DAY				
AGE				

Notes;

Independents not used;

Age - although a potential determinant of rate of weight loss, there is no correlation between these two variables in any of the three years, thus, in the models for both 1987 and 1988 age has been removed in order to increase N.

Mating success and total number of inter-male aggressive encounters are both totals for the entire season, aggression per day and copulations per day are used as measures of aggression and sexual activity instead, as these are expressed as daily rates as is rate of weight loss.

Length of stay, arrival date and departure date are assumed not to influence rate of weight loss as weight loss is a measure of energy expenditure and no seasonal trend in weight loss has been found (see Chapter 5).

Departure weight, total weight lost and departure date are values gathered at the end of a male's stay and as such cannot affect his rate of weight loss during the stay.

7.2 - COLONY ATTENDANCE PARAMETERS.

See section 7.1 for details of relationships between colony attendance and weight parameters.

1. Arrival date;

Arrival date showed no consistent correlation at $p < 0.01$ with any variable other than total number of aggressive encounters (1987: $r = -0.48$, $n = 47$, $p = 0.001$, 1988: $r = -0.64$, $n = 39$, $p < 0.001$, 1989: $r = -0.45$, $n = 54$, $p = 0.001$). This relationship showed no significant difference in either slope or elevation between the three seasons as assessed by analysis of covariance. The negative correlation indicates that males arriving relatively early in the season experienced a greater total number of aggressive encounters, as would be expected.

The only other correlation of note was the negative correlation with length of stay, significant at $p < 0.01$ in 1987 and 1988 and at $p < 0.05$ in 1989 (1987: $r = -0.57$, $n = 47$, $p < 0.001$, 1988: $r = -0.57$, $n = 39$, $p = 0.001$, 1989: $r = -0.31$, $n = 54$, $p = 0.024$). This appears to be a reasonably obvious relationship, those males that arrived earlier had greater opportunity to remain ashore for longer as more of the season lay ahead of them.

Other interesting points are the lack of correlations with either dominance, age or starting weight. Dominant males did not necessarily arrive early at the colony, nor did older males or heavier males. There was no relationship between arrival date and departure date as the length of stay varied so dramatically between individuals.

Multiple regression analysis provided no significant predictor of arrival date in any of the three seasons (Table 7.2.1).

Table 7.2.1
Table summarising results of multiple stepwise regression model developed for arrival date.
X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - ARRIVAL DATE n = 14			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE ARRIVAL WEIGHT		NO SIGNIFICANT RESULTS		

1988	DEPENDENT VARIABLE - ARRIVAL DATE n = 16			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE ARRIVAL WEIGHT AGE		NO SIGNIFICANT RESULTS		

1989	DEPENDENT VARIABLE - ARRIVAL DATE n = 16			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE ARRIVAL WEIGHT AGE		NO SIGNIFICANT RESULTS		

Notes;

Independents not used;
All the remaining variables are parameters which occur post-arrival and are thus unlikely to affect arrival date. Rate of weight loss could conceivably influence arrival date if males were "aware" of their rate of weight loss or possible expenditure compared to reserves and were thus able to adjust arrival accordingly, however, rate of weight loss does not correlate (Pearson's) with arrival date in any of the 3 years.
NB Arrival weight may not be truly independent of arrival date, as the latter is used in the computation of arrival weight. Also, if a relationship exists between arrival weight and arrival date the direction of causality is unclear, it may be that heavier males do indeed arrive earlier, or that the observed relationship is simply a result of the calculation of arrival weight. For example, if all males are losing weight from the start of the breeding season whether they are on the breeding grounds or not, then those that arrive earlier will automatically have higher arrival weights.

2. Departure date;

Unlike arrival date, departure date provided many interesting significant and consistent correlations. Foremost of these was the positive correlation with mating success (1987: $r = +0.43$, $n = 47$, $p = 0.002$, 1988: $r = +0.54$, $n = 39$, $p < 0.001$, 1989: $r = +0.60$, $n = 54$, $p < 0.001$). Under analysis of covariance no significant difference was found between years in either slope or elevation of this relationship. Males that departed later in the season gained greater total mating success. Alternatively, one could interpret this as males that gained greater mating success tended to depart later. Similarly, departure date was strongly ($p < 0.01$) and positively correlated with copulations per day in 1988 and 1989, and was correlated at $p < 0.05$ in 1987 (1987: $r = +0.30$, $n = 47$, $p = 0.044$, 1988: $r = +0.49$, $n = 39$, $p = 0.002$, 1989: $r = +0.40$, $n = 54$, $p = 0.003$). Analysis of covariance revealed no significant difference between seasons in either slope or elevation. Thus, the relationship with total mating success is not simply a consequence of greater opportunity for copulations. Males departing relatively late were those that gained greater copulations per day, or, males with high copulation rates appear to delay departure.

Although later departing males were not necessarily involved in greater numbers of aggressive encounters in total, interestingly they do have significantly lower numbers of aggressive encounters per day. This correlation exists in all three seasons at $p < 0.01$ (1987: $r = -0.61$, $n = 47$, $p < 0.001$, 1988: $r = -0.59$, $n = 39$, $p < 0.001$, 1989: $r = -0.59$, $n = 54$, $p < 0.001$). Analysis of covariance revealed no significant difference between years in slope but significantly different elevations at $p < 0.05$.

Dominance score, though not consistently significant at $p < 0.01$, was significantly and negatively correlated with departure date at $p < 0.05$ in all three years and at $p < 0.01$ in 1987 (1987: $r = -0.47$, $n = 47$, $p = 0.001$, 1988: $r = -0.33$, $n = 39$, $p = 0.042$, 1989: $r = -0.33$, $n = 54$, $p = 0.014$). Analysis of covariance found no significant difference in slope or elevation of these relationships. Thus, dominant males, whilst not necessarily arriving early may depart relatively late.

There were no correlations between departure date and any of the weight parameters (see Chapter 7.1 for details), hence, these were excluded in subsequent multiple regression analyses.

Unlike arrival date, there was a very strong positive correlation at $p < 0.01$ between departure date and length of stay in all three seasons (1987: $r = +0.57$, $n = 47$, $p < 0.001$, 1988: $r = +0.62$, $n = 39$, $p < 0.001$, 1989: $r = +0.65$, $n = 54$, $p < 0.001$). Analysis of covariance showed no significant difference between years in either slope or elevation of this relationship. Thus, whilst arrival date may exert some effect upon length of stay, it appears that departure date exerts a greater influence. This will be examined in a multiple regression model (see below - length of stay).

Multiple regression models (Table 7.2.2) revealed length of stay to be the primary predictor of departure date in all years. Arrival date was entered on the second step in all three seasons. In all three reverse regressions, departure date was entered, but only in the third step.

Table 7.2.2

Table summarising results of multiple stepwise regression model developed for departure date. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - DEPARTURE DATE n = 47			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.34588	< 0.0001	0.33135
TOTAL No. A.I.s				
MATING SUCCESS				
DOMINANCE SCORE				
ARRIVAL DATE	2	0.26671	< 0.0001	0.59499
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
DEPARTURE DATE	3	0.16119	< 0.0001	0.81247
ARRIVAL DATE	2	0.16332	< 0.0001	0.64822
MATING SUCCESS	4	0.03491	0.0024	0.84624
TOTAL No. A.I.s				
DOMINANCE SCORE	1	0.50020	< 0.0001	0.48909

Notes;

Independents not used;

Age and weight parameters have been excluded despite being potential determinants as none of these correlate with departure date and none are entered if included in the regression (i.e. arrival date and length of stay are still entered). Removal of these increased N from 14 to 47 in 1987, 15 to 39 in 1988 and from 16 to 54 in 1989.
Copulations and aggressive interactions are not included as these are mean daily rates, sexual and aggressive behaviour are represented by total mating success and aggressive interactions.

1988	DEPENDENT VARIABLE - DEPARTURE DATE n = 39			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.41146	< 0.0001	0.39556
TOTAL No. A.I.s				
MATING SUCCESS				
DOMINANCE SCORE				
ARRIVAL DATE	2	0.34366	< 0.0001	0.74152
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
DEPARTURE DATE	3	0.05589	0.0019	0.81103
ARRIVAL DATE				
MATING SUCCESS	1	0.70250	< 0.0001	0.69472
TOTAL No. A.I.s	2	0.06731	0.0025	0.75728
DOMINANCE SCORE				

1989	DEPENDENT VARIABLE - DEPARTURE DATE n = 54			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.46413	< 0.0001	0.45382
TOTAL No. A.I.s				
MATING SUCCESS				
DOMINANCE SCORE				
ARRIVAL DATE	2	0.19772	< 0.0001	0.64859
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
DEPARTURE DATE	3	0.03867	0.0042	0.77242
ARRIVAL DATE	5	0.02564	0.0061	0.83490
MATING SUCCESS	1	0.60161	< 0.0001	0.59394
TOTAL No. A.I.s	2	0.14502	< 0.0001	0.73669
DOMINANCE SCORE	4	0.03954	0.0017	0.481054

3. Length of stay in the study area (days);

Of all the colony attendance parameters, length of stay appears to be the most important in many aspects.

As would be expected, there was a very strong positive and highly significant ($p < 0.01$) correlation between length of stay and mating success in all three seasons (1987: $r = +0.69$, $n = 47$, $p < 0.001$, 1988: $r = +0.84$, $n = 39$, $p < 0.001$, 1989: $r = +0.78$, $n = 54$, $p < 0.001$ - see Figures 7.2.1 a, b and c). Analysis of covariance revealed no significant difference between years in either the slope or elevation of these relationships. It is clear form these results that those males able to maintain a position on the colony for long periods gained greater overall mating success.

Similarly, length of stay was highly correlated with total number of aggressive encounters (1987: $r = +0.57$, $n = 47$, $p < 0.001$, 1988: $r = +0.80$, $n = 39$, $p < 0.001$, 1989: $r = +0.76$, $n = 54$, $p < 0.001$). Males that remained ashore for longer were, not surprisingly, involved in significantly more aggressive interactions. Again, analysis of covariance reveals no significant difference in slope or elevation between years.

However, whilst there was no consistent relationship between length of stay and daily copulation rate, there was a consistent negative correlation at $p < 0.01$ between stay and aggression rates (1987: $r = -0.64$, $n = 47$, $p < 0.001$, 1988: $r = -0.47$, $n = 39$, $p = 0.003$, 1989: $r = -0.63$, $n = 54$, $p < 0.001$). Analysis of covariance revealed no significant difference between years in slope, but a significant difference in elevation for this relationship. Males that were ashore for longer, although being involved in more aggressive encounters in total are in fact involved in less aggression per day.

Length of stay was significantly correlated at $p < 0.01$ with dominance score in all three seasons (1987: $r = -0.71$, $n = 47$, $p < 0.001$, 1988: $r = -0.44$, $n = 39$, $p = 0.006$, 1989: $r = -0.60$, $n = 54$, $p < 0.001$ - see Figures 7.2.2 a, b and c). Analysis of covariance reveals no significant difference between years in either slope or elevation of these relationships. Thus, more dominant individuals were able to maintain a position on the colony for significantly longer than more subordinate individuals.

The lack of relationships between length of stay and weight parameters are detailed

Figure 7.2.1 a : Plot of mating success against stay - Rona 1987

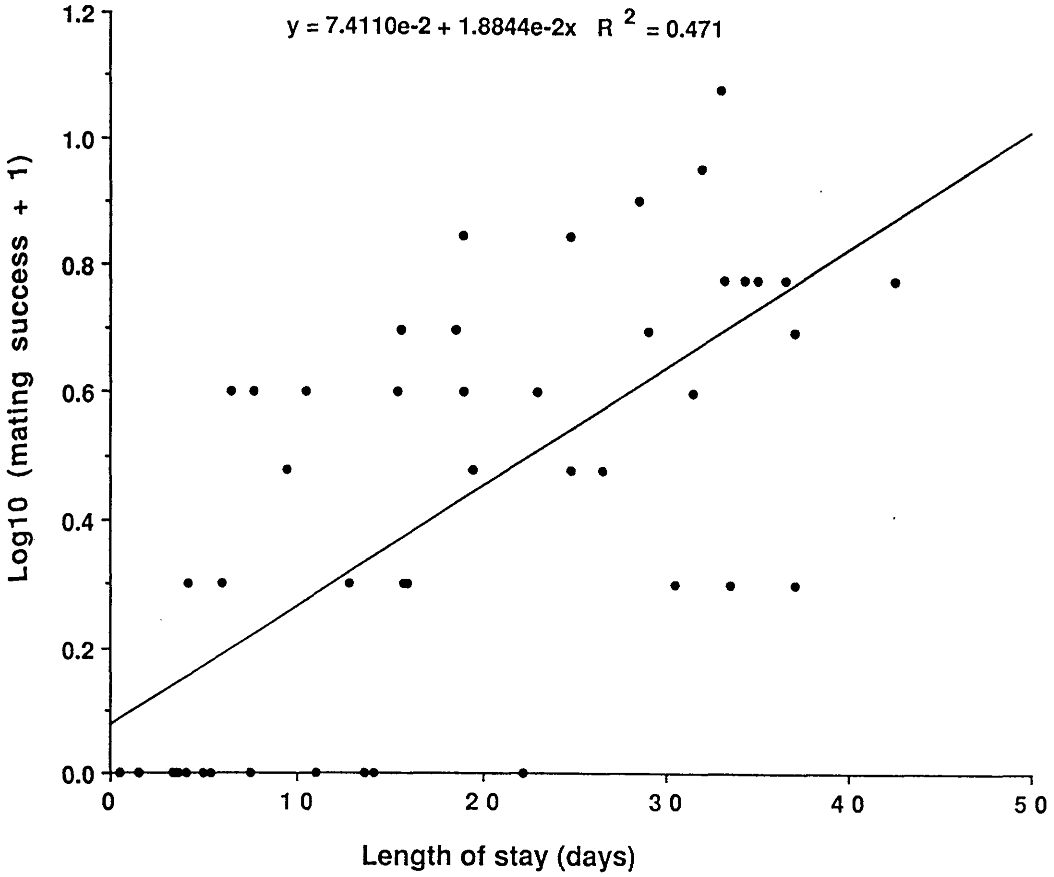


Figure 7.2.1 b : Plot of mating success against stay - Rona 1988

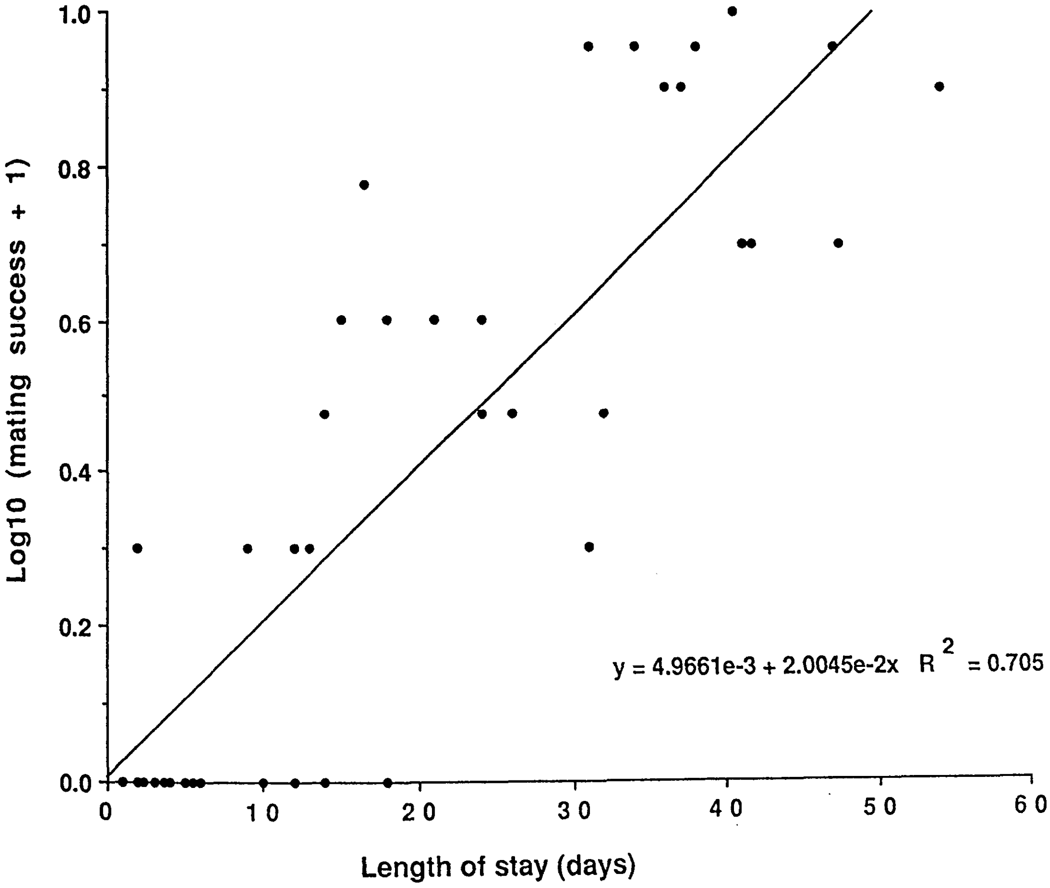


Figure 7.2.1 c : Plot of mating success against stay - Rona 1989

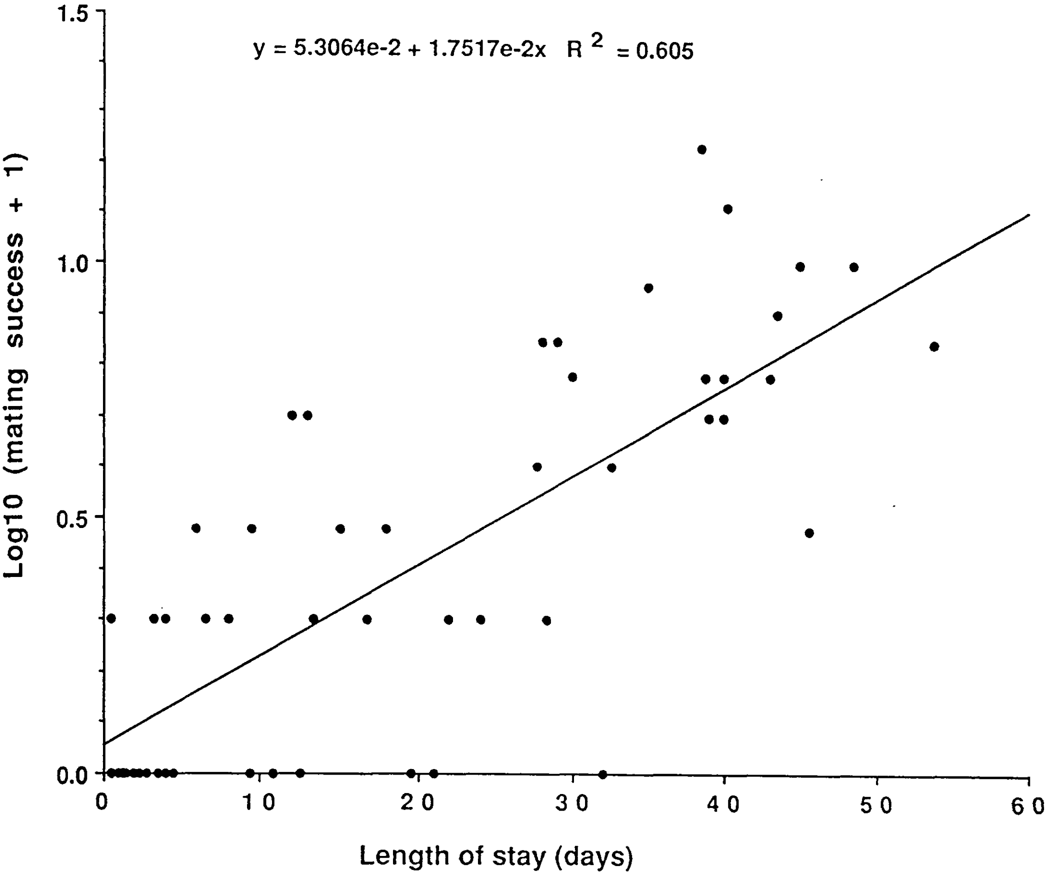


Figure 7.2.2 a : Plot of length of stay against dominance score - Rona 1987

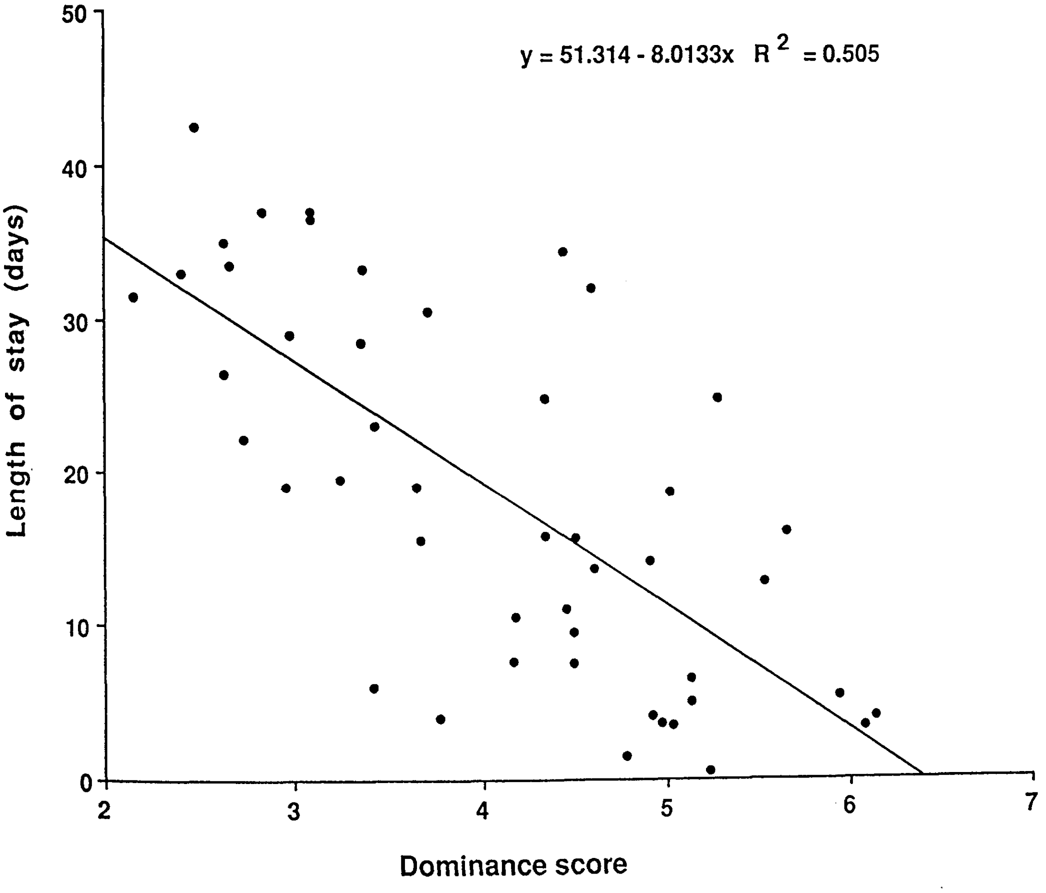


Figure 7.2.2 b : Plot of stay against dominance score - Rona 1988

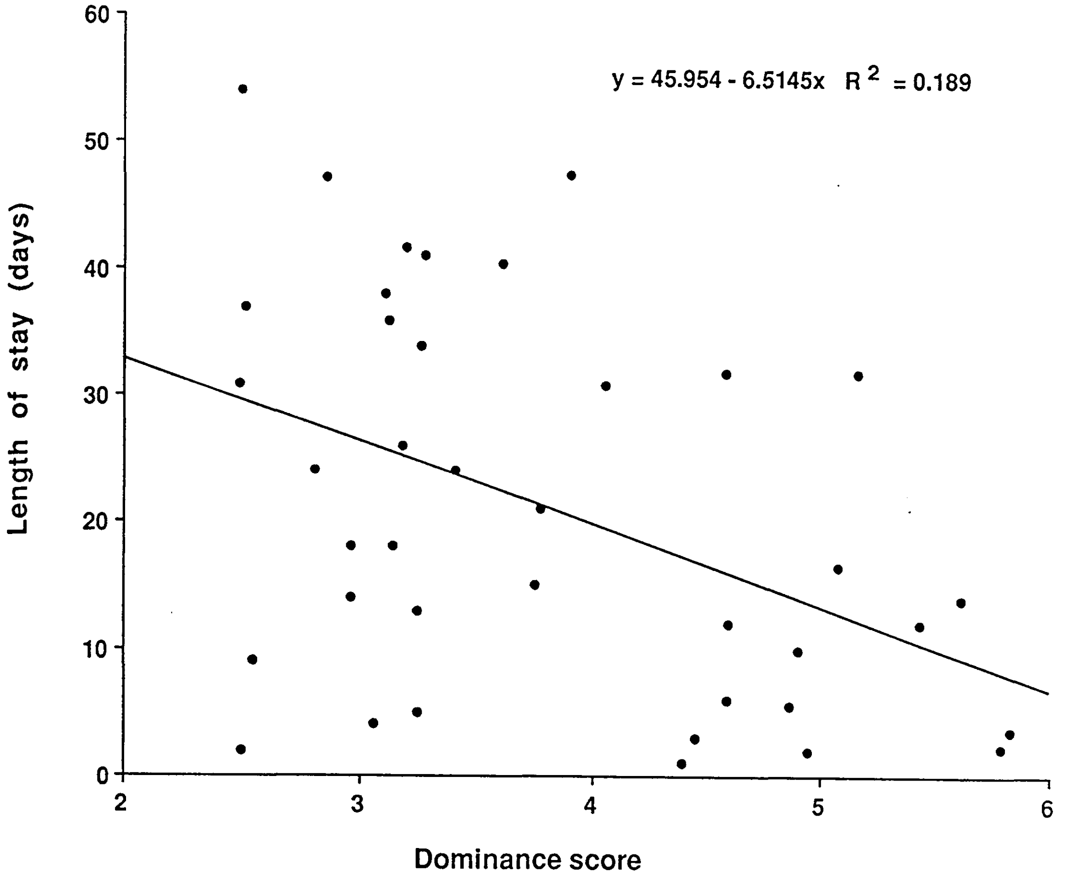
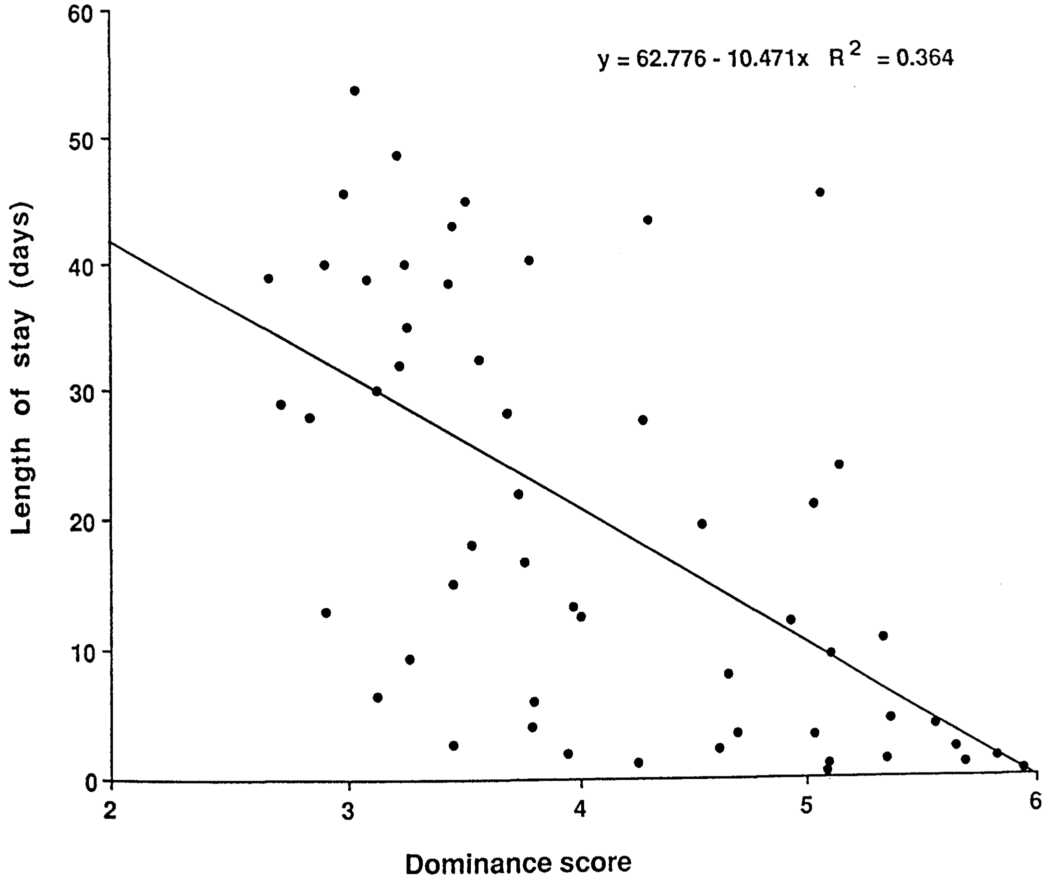


Figure 7.2.2 c : Plot of stay against dominance score - Rona 1989



in chapter 7.1.

Correlations between length of stay and both arrival and departure date were discussed above.

Multiple regression models developed for length of stay (Table 7.2.3) revealed that the main behavioural determinant of stay was dominance. This was entered first in 1987, excluded in 1988 and entered third in 1989. In all three years both arrival date and departure date were entered. Departure date was entered prior to arrival date in 2 of the years. In all three regression models the reverse regression confirmed the initial regressions.

Table 7.2.3

Table summarising results of multiple stepwise regression model developed for length of stay. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - LENGTH OF STAY n = 47			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE	1	0.50020	< 0.0001	0.48909
ARRIVAL DATE	2	0.16332	< 0.0001	0.64822
DEPARTURE DATE	3	0.16119	< 0.0001	0.81247
REVERSE REGRESSION - DEPENDENT = DOMINANCE SCORE				
LENGTH OF STAY	1	0.50020	< 0.0001	0.48909
ARRIVAL DATE				
DEPARTURE DATE				

1988	DEPENDENT VARIABLE - LENGTH OF STAY n = 39			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE				
ARRIVAL DATE	2	0.39568	< 0.0001	0.79643
DEPARTURE DATE	1	0.41146	< 0.0001	0.39556
REVERSE REGRESSION - DEPENDENT = DEPARTURE DATE				
LENGTH OF STAY	1	0.41146	< 0.0001	0.39556
ARRIVAL DATE	2	0.34366	< 0.0001	0.74152
DOMINANCE SCORE				

1989	DEPENDENT VARIABLE - LENGTH OF STAY n = 54			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE	3	0.11038	< 0.0001	0.77194
ARRIVAL DATE	2	0.21034	< 0.0001	0.66170
DEPARTURE DATE	1	0.46413	< 0.0001	0.45382
REVERSE REGRESSION - DEPENDENT = DEPARTURE DATE				
LENGTH OF STAY	1	0.46413	< 0.0001	0.45382
ARRIVAL DATE	2	0.19772	< 0.0001	0.64859
DOMINANCE SCORE				

Notes;

Independents not used;

Age - although a potential determinant, this has been excluded as it shows no correlation with length of stay in any year, and allows N to be increased.
Weight parameters - In 1987 these were not included as only arrival weight correlates with length of stay in this year and none are entered when included (the same independent variables are entered as above). On removal of weight parameters N is increased from 14 to 47.
In 1988 weight parameters are also excluded as although arrival weight, total percentage weight loss and rate of weight loss do have significant correlations with length of stay at $p < 0.05$), none are entered when included in the model. On removal of weight parameters N is increased from 16 to 39.
In 1989, weight parameters are again excluded as only total percentage weight loss correlates with length of stay and none are entered when included in the model. On removal of weight parameters N is increased from 16 to 54.
Total aggressive interactions and mating success are assumed not to be determinants of length of stay, but are themselves determined by length of stay.
Aggressive encounters and copulations per day are not determinants of stay (both are daily rates).

7.3 - DOMINANCE AND AGGRESSION

1. Dominance score:

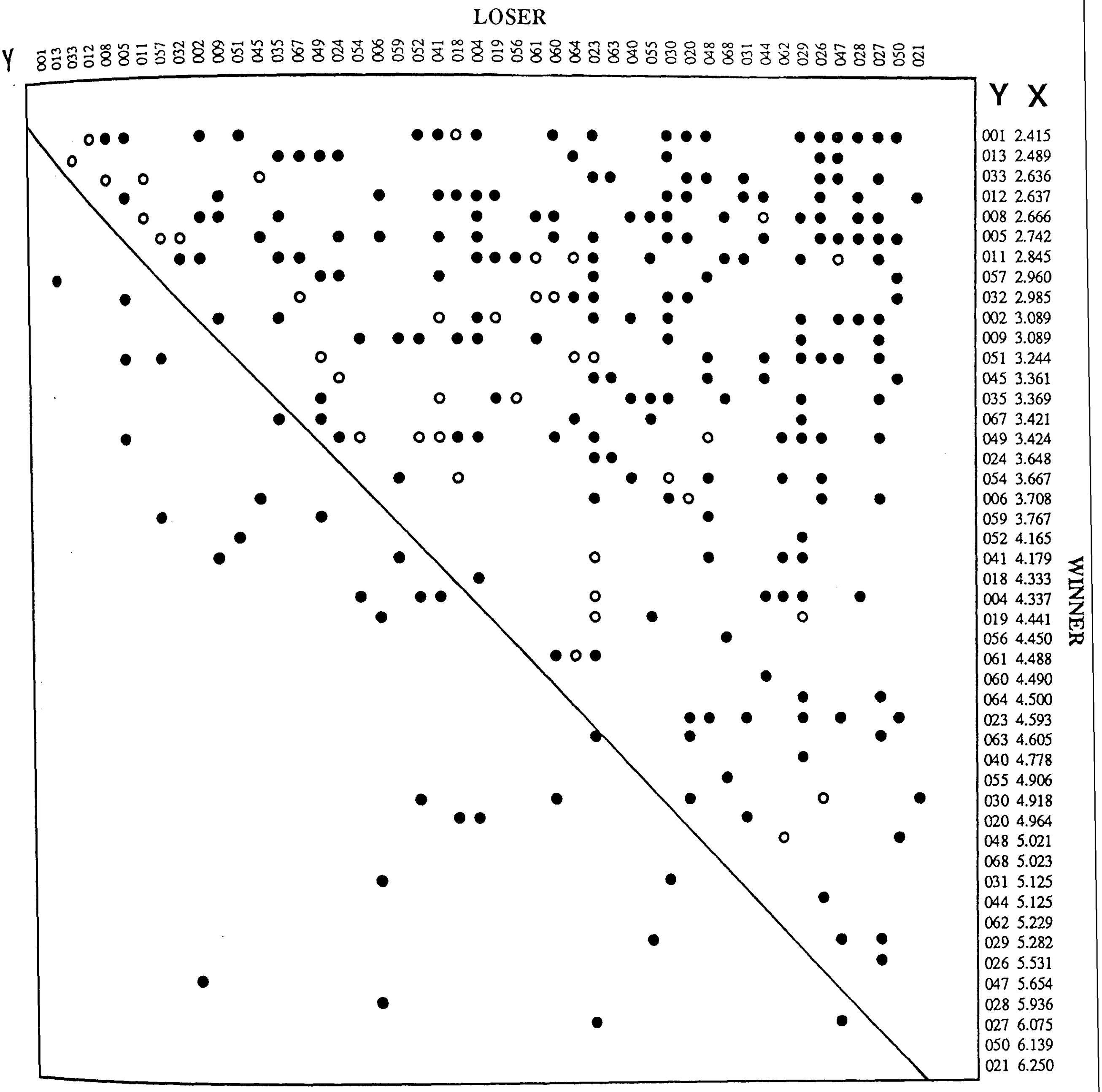
As detailed in Chapter 3, a dominance score was calculated for each male on the basis of the outcome of inter-male aggressive interactions. Using this dominance score the males were arranged in order of dominance. This revealed quite a close approximation to a linear hierarchy, bearing in mind that not all males were present simultaneously (see Figures 7.3.1 a, b and c) with 89.5 % of cases above or on the diagonal in 1987, 93.5 % in 1988 and 90.0 % in 1989. This contrasts with the earlier work of Anderson and Fedak (1985) who suggested from rather more limited data that no linear hierarchy existed amongst male grey seals on Rona. However, as stated by the authors, a major problem was that each male only interacted with relatively few others. Similarly, Boness and James (1979) stated that whilst tenured bulls were clearly the more dominant males, they were all of equal status. With the more extensive observations of the present study, males have been observed in encounters with more opponents, giving a more complete interaction network.

The dominance score calculated showed many interesting and consistent correlations. The foremost of these were the relationships with mating success and length of stay. In all three years, dominant individuals gained significantly greater mating success (at $p < 0.01$) than more subordinate individuals (1987: $r = -0.51$, $n = 47$, $p < 0.001$, 1988: $r = -0.48$, $n = 39$, $p = 0.002$, 1989: $r = - 0.56$, $n = 54$, $p < 0.001$). Analysis of covariance revealed no significant difference between seasons in either the slope or elevation of these relationships.

Similarly, there was an strong correlation between length of stay and dominance in all three seasons again significant at $p < 0.01$ (see section 7.2). Analysis of covariance showed no significant differences in either slope or elevation. Thus, more dominant individuals remained ashore for significantly longer than more subordinate males.

Dominant individuals, although gaining greater overall mating success did not necessarily have greater daily rates of copulation. Copulation rate per day was highly

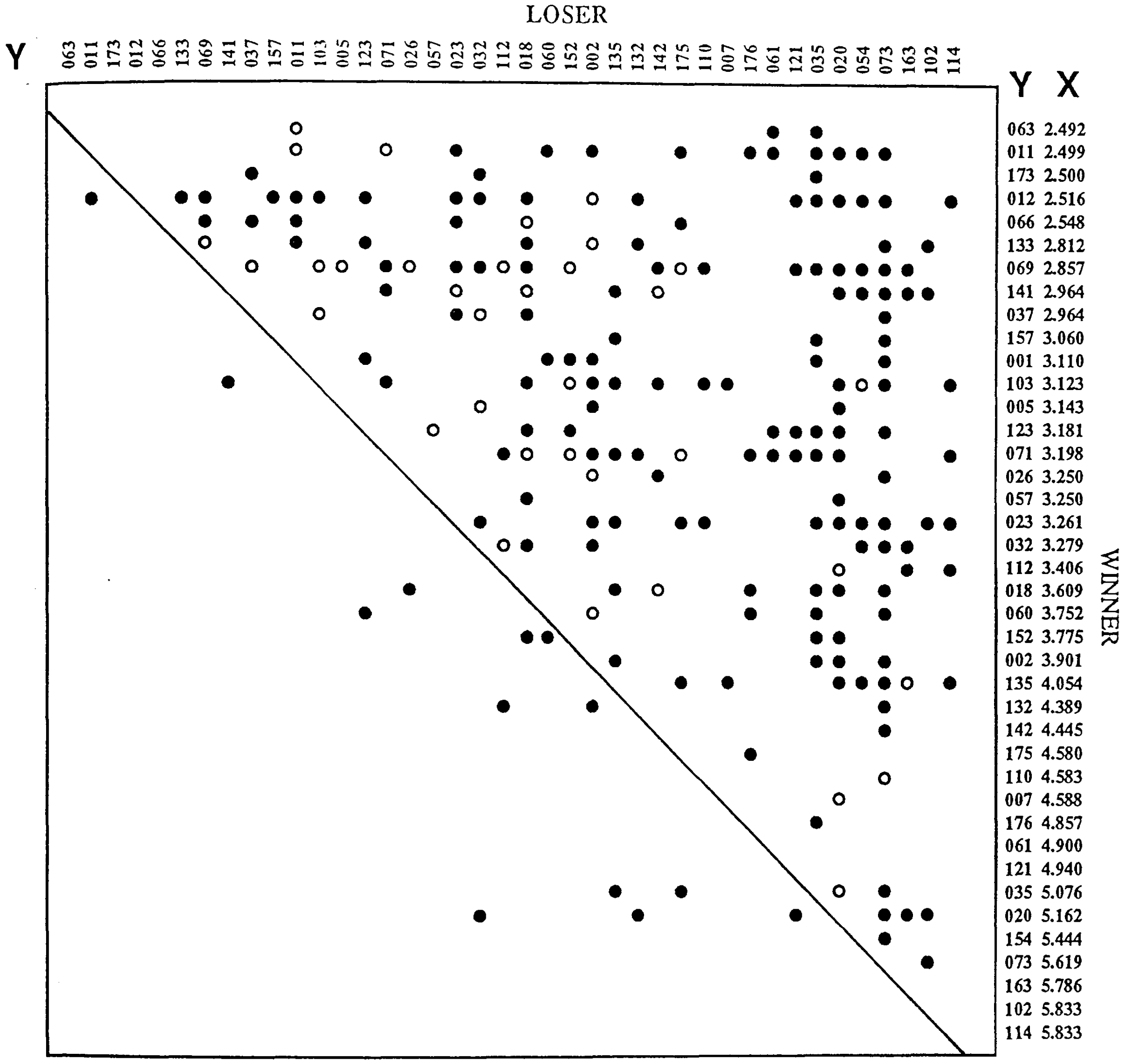
Figure 7.3.1 a : Mean outcome of inter-male aggressive encounters between all observed dyads. Males are arranged in order of decreasing dominance. Full circles indicate victory, open circles indicate draws. Rona 1987.



X = Dominance score

Y = Male identity code

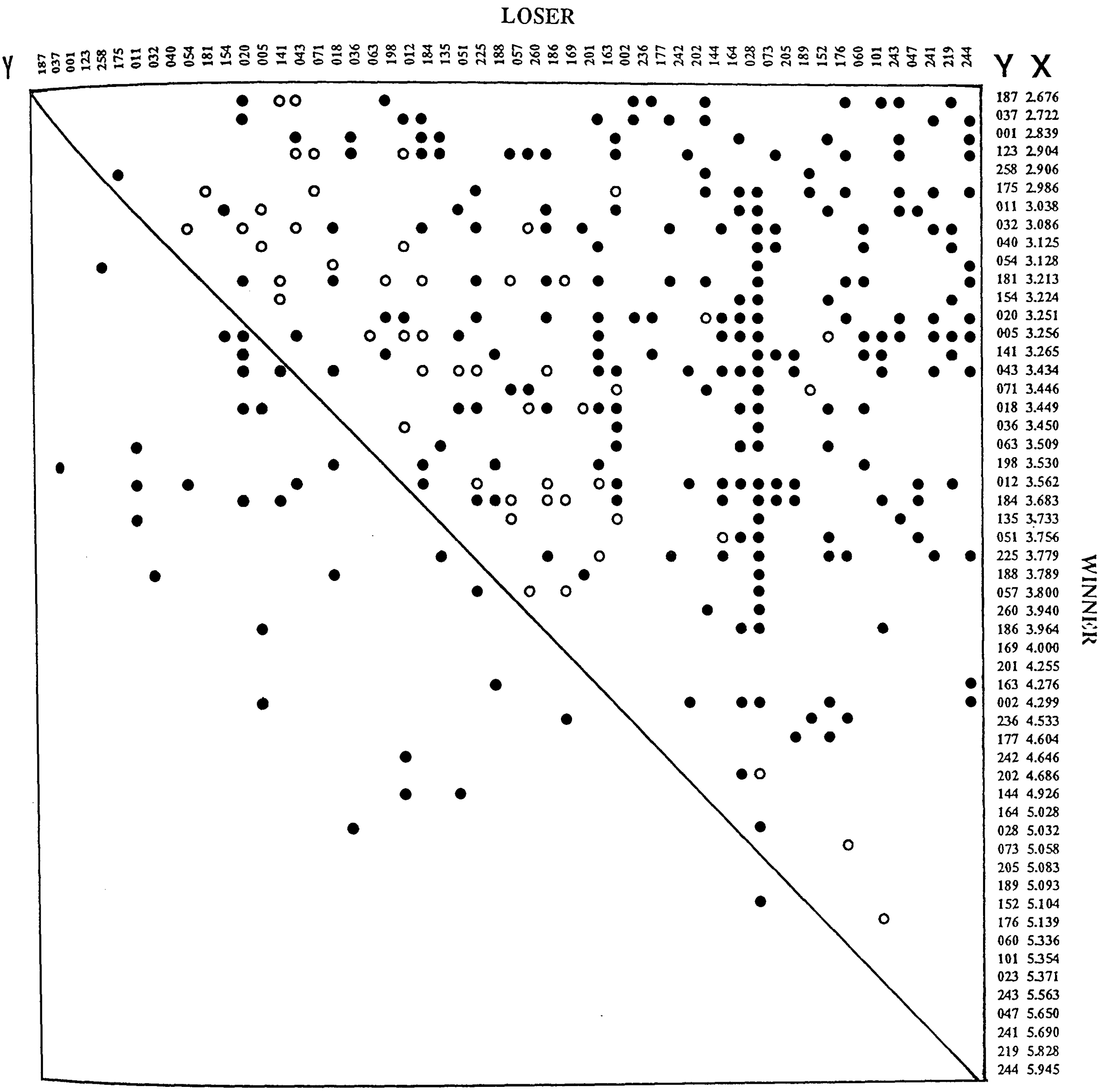
Figure 7.3.1 b : Mean outcome of inter-male aggressive encounters between all observed dyads. Males are arranged in order of decreasing dominance. Full circles indicate victory, open circles indicate draws. Rona 1988.



X = Dominance score

Y = Male identity code

Figure 7.3.1 c : Mean outcome of inter-male aggressive encounters between all observed dyads. Males are arranged in order of decreasing dominance. Full circles indicate victory, open circles indicate draws. Rona 1989.



X = Dominance score

Y = Male identity code

correlated with dominance in 1988 at $p < 0.01$, but only at $p < 0.05$ in 1987 and not at all in 1989. Thus there is no consistent trend.

However, there was a strong and consistent relationship between dominance and daily rate of aggressive activity (1987: $r = +0.48$, $n = 47$, $p = 0.001$, 1988: $r = + 0.45$, $n = 39$, $p = 0.004$, 1989: $r = +0.59$, $n = 54$, $p < 0.001$). This relationship, when tested by analysis of covariance revealed no significant difference in slope, but significantly differing elevations. The positive relationship reveals that dominant individuals tended to be involved in less aggression per day than subordinates. In contrast the relationship with total aggressive activity was negative, indicating that dominants are involved in more aggression in total; however, this relationship is only significant in 1989 at $p < 0.01$. This is most likely mediated through the relationship with length of stay (see section 7.2).

There was no relationship at $p < 0.01$ between dominance and age in any of the three years (see Figures 7.3.2 a, b and c). In 1988 a negative correlation exists at $p < 0.05$, indicating that more dominant individuals tended to be older males; however, even this significance level is not repeated in any other season.

Similarly surprising was the lack of correlation between dominance and measures of initial weight (see section 7.1). There were no consistent correlations at $p < 0.01$ with any of the weight parameters. However, it is worth noting that, at $p < 0.05$, there was a consistent correlation between dominance and rate of weight loss, indicating a possibility that more dominant males may suffer a greater energy cost (see section 7.1).

There was no consistent correlation between dominance and arrival date, dominant males did not necessarily arrive early at the colony. However, there was a consistent relationship with departure date, dominant males tending to depart relatively later (see section 7.2).

Multiple regression procedures revealed no significant predictors of dominance from the variables deemed plausible determinants (Table 7.3.1).

Figure 7.3.2 a : Plot of Dominance score against age - Rona 1987

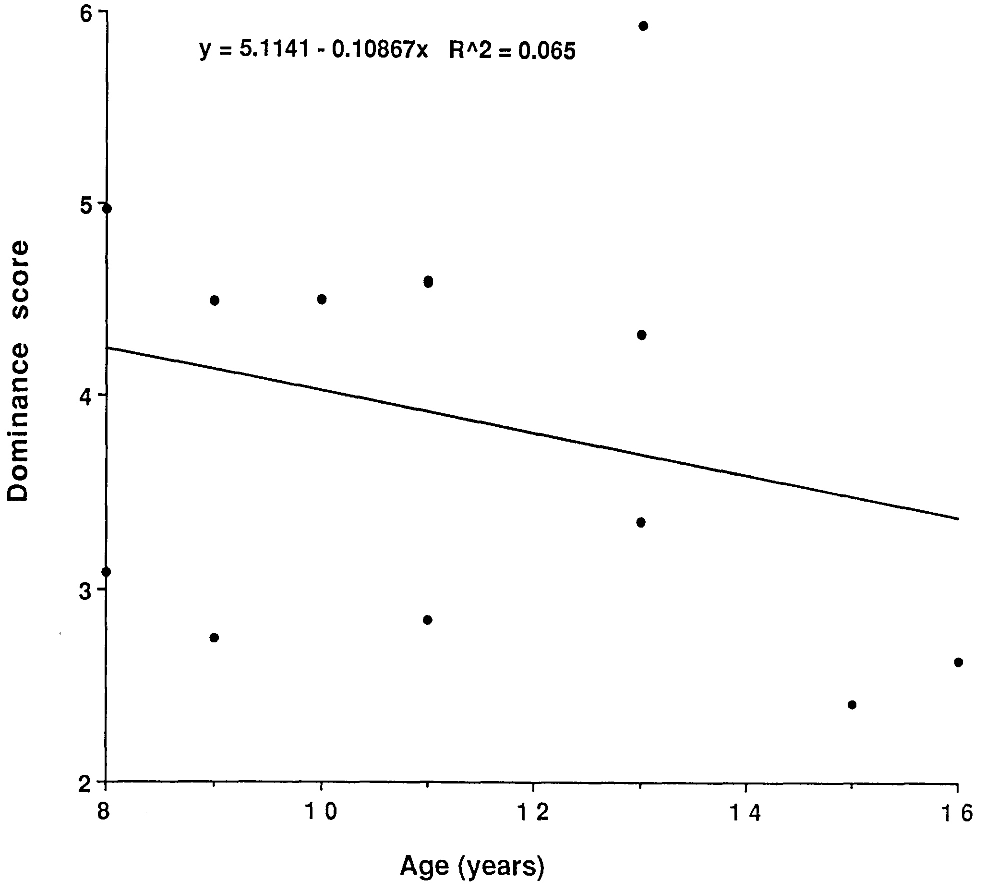


Figure 7.3.2 b : Plot of Dominance score against age - Rona 1988

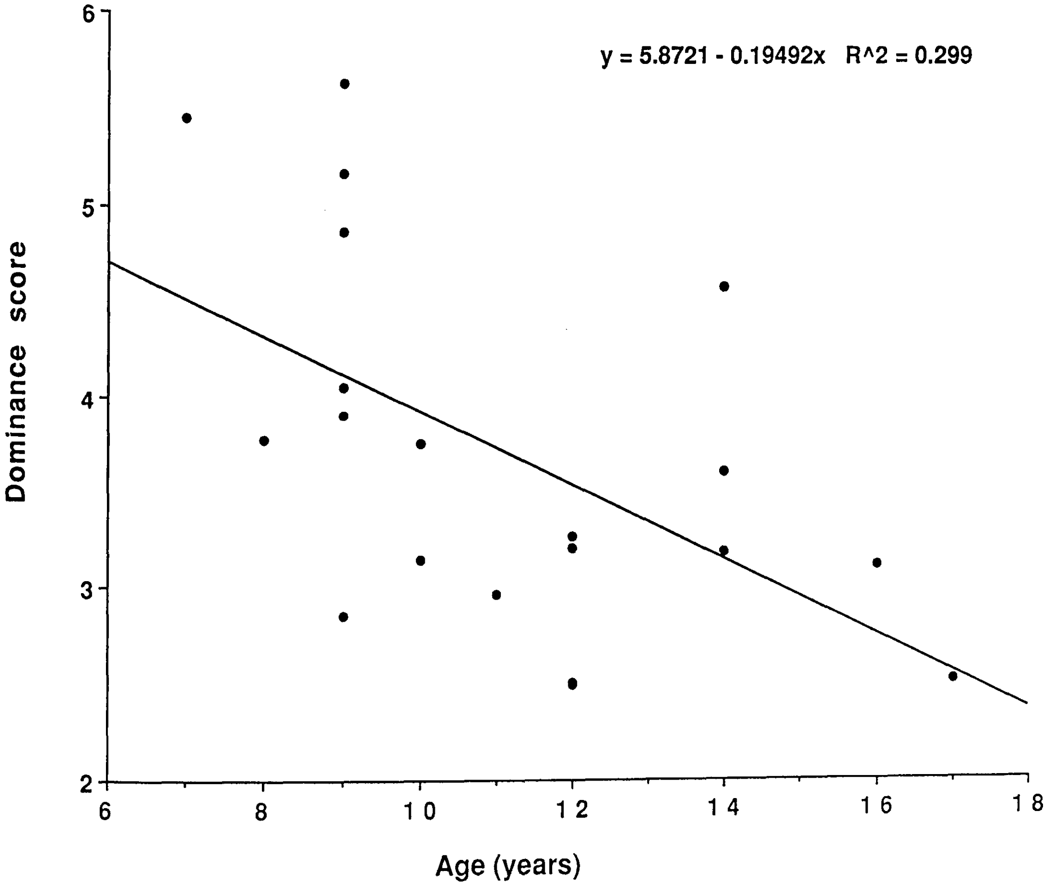


Figure 7.3.2 c : Plot of Dominance score against age - Rona 1989

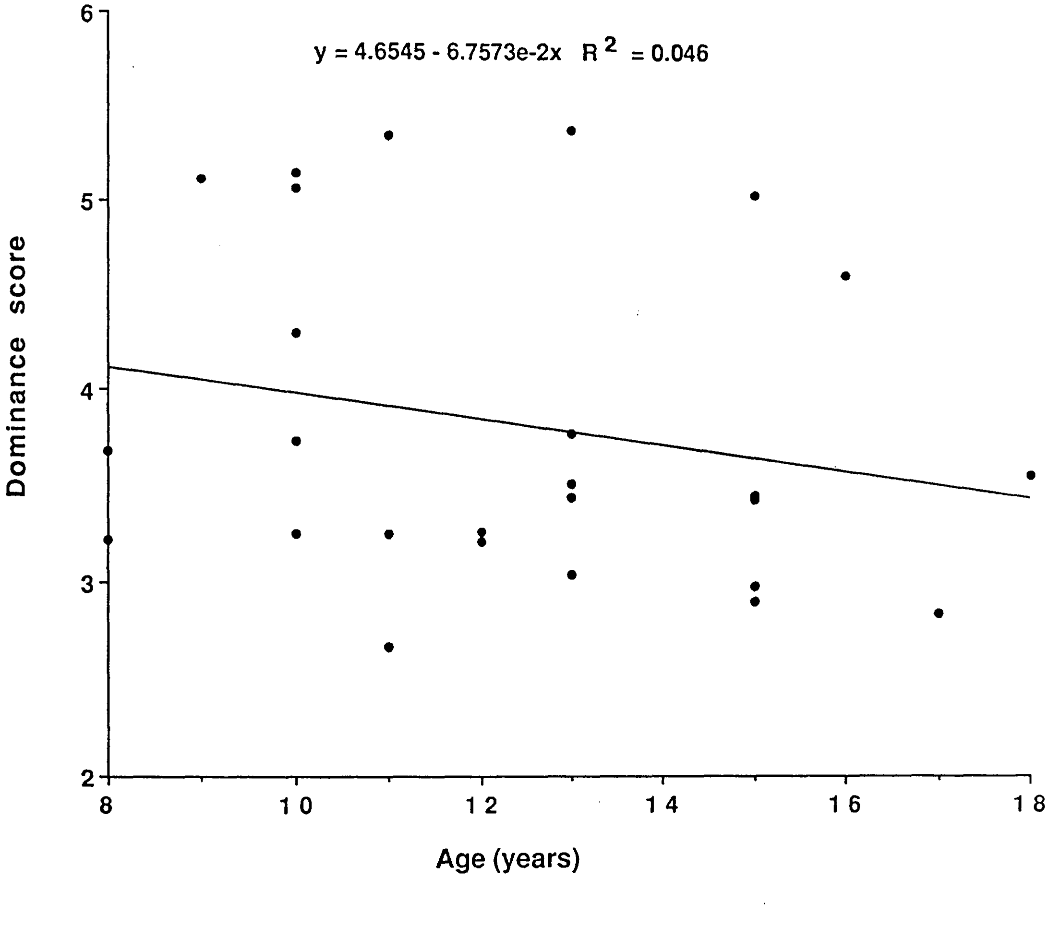


Table 7.3.1

Table summarising results of multiple stepwise regression model developed for Dominance score.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - DOMINANCE SCORE n = 14			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
ARRIVAL DATE ARRIVAL WEIGHT		NO SIGNIFICANT RESULTS		

1988	DEPENDENT VARIABLE - DOMINANCE SCORE n = 15			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
ARRIVAL DATE ARRIVAL WEIGHT AGE		NO SIGNIFICANT RESULTS		

1989	DEPENDENT VARIABLE - DOMINANCE SCORE n = 16			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
ARRIVAL DATE ARRIVAL WEIGHT AGE		NO SIGNIFICANT RESULTS		

Notes;

Independents not used;
None of other variables were deemed plausible putative determinants of dominance.
Length of stay, total aggressive interactions and mating success, rate of weight loss, weight on departure, departure date, rates of aggression and copulations and total percentage weight loss may all be affected by dominance but are unlikely to contribute towards it.
NB Even arrival date and arrival weight may not be true determinants of dominance, it is more plausible that an animals' dominance status would affect the arrival date and perhaps also the starting weight (a more dominant individual can gain access to better food resources and so gain more blubber reserves in any single season and possibly have greater lean body mass through an enhanced growth rate compared to other male members of his cohort)

2. Total number of aggressive inter-male encounters

Total number of inter-male aggressive encounters was highly correlated with total mating success in all three seasons (1987: $r = +0.46$, $n = 47$, $p < 0.001$, 1988: $r = +0.75$, $n = 39$, $p < 0.001$, 1989: $r = +0.60$, $n = 54$, $p < 0.001$). Analysis of covariance reveals no significant difference in slope or elevation in any of the three years. However, as total aggression was also highly correlated with length of stay in all three seasons, as is mating success, this relationship may be mediated via the length of stay. This will be tested by use of multiple regression procedures. Again, analysis of covariance reveals no significant difference between years in the nature of the relationship between aggression and length of stay.

The only remaining consistent correlation of total aggression was with arrival date (see Chapter 7.2)

Table 7.3.3 presents the results of the multiple regression procedure applied to number of inter-male aggressive encounters. The primary determinant in all three seasons was length of stay, with arrival date being entered on the second step in 1988 and 1989 and appearing to have some effect independently of length of stay. Notably, mating success was not entered in any of the initial regressions.

The total number of aggressive encounters was not entered in the reverse regression for 1987, and only entered on the second step in the remaining two years.

Daily rate of inter-male aggressive activity

As with total aggressive activity, this measure of daily rate of aggression exhibits few consistent correlations. These were with dominance (see Chapter 7.3), arrival date and length of stay (see Chapter 7.2).

Multiple regression analyses revealed that departure date was the main predictor of rates of aggression in 1987 and 1988. In 1989 dominance was entered first, followed by departure date (Table 7.3.4). In all three years the reverse regression confirmed the results of the initial regression.

Table 7.3.3

Table summarising results of multiple stepwise regression model developed for total number of inter-male aggressive interactions. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - TOTAL NUMBER OF A.I.s n = 47			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.31843	< 0.0001	0.30329
MATING SUCCESS				
ARRIVAL DATE				
DEPARTURE DATE				
DOMINANCE SCORE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
TOTAL No. A.I.s				
MATING SUCCESS	4	0.03491	0.0024	0.84624
ARRIVAL DATE	2	0.16332	< 0.0001	0.64822
DEPARTURE DATE	3	0.16119	< 0.0001	0.81247
DOMINANCE SCORE	1	0.50020	< 0.0001	0.48909

Notes;

Independents not used;

Age - although a potential determinant of total aggressive interactions, age shows no correlation with aggression levels and is not entered in the model if included in the analysis. Therefore age has been excluded in order to increase N.
Arrival weight is not included as there is no correlation with number of aggressive interactions despite being a potential determinant, exclusion again increases N in all three years.
Departure weight and total percentage weight loss are not included as these parameters occur post departure and can have no influence on number of aggressive interactions.
Rate of weight loss, aggression and copulations per day - these are daily rates whereas total aggressive interactions represents overall season data.

1988	DEPENDENT VARIABLE - TOTAL NUMBER OF A.I.s n = 39			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.64191	< 0.0001	0.63223
MATING SUCCESS				
ARRIVAL DATE	2	0.07836	0.0031	0.70473
DEPARTURE DATE				
DOMINANCE SCORE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
TOTAL No. A.I.s	2	0.06731	0.0025	0.75728
MATING SUCCESS	1	0.70250	< 0.0001	0.69472
ARRIVAL DATE				
DEPARTURE DATE	3	0.05589	0.0019	0.81103
DOMINANCE SCORE				

1989	DEPENDENT VARIABLE - TOTAL NUMBER OF A.I.s n = 54			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.59007	< 0.0001	0.58219
MATING SUCCESS				
ARRIVAL DATE	2	0.06369	0.0035	0.64018
DEPARTURE DATE				
DOMINANCE SCORE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
TOTAL No. A.I.s	2	0.14502	< 0.0001	0.73669
MATING SUCCESS	1	0.60161	< 0.0001	0.59394
ARRIVAL DATE	5	0.02564	0.0061	0.83490
DEPARTURE DATE	3	0.03867	0.0042	0.77242
DOMINANCE SCORE	4	0.03954	0.0017	0.81054

Table 7.3.4

Table summarising results of multiple stepwise regression model developed for daily rate of inter-male aggressive interactions. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - No. AGGRESSIVE INTERACTIONS/DAY n = 47			
INDEPENDENT VARIABLES	X	R^2	SIGNIFICANCE OF F	ADJUSTED R^2
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE	1	0.37140	< 0.0001	0.35743
COPULATIONS/DAY				
REVERSE REGRESSION - DEPENDENT = DEPARTURE DATE				
AGGRESSION/DAY	1	0.37140	< 0.0001	0.35743
DOMINANCE SCORE				
ARRIVAL DATE				
COPULATIONS/DAY				

1988	DEPENDENT VARIABLE - No. AGGRESSIVE INTERACTIONS/DAY n = 39			
INDEPENDENT VARIABLES	X	R^2	SIGNIFICANCE OF F	ADJUSTED R^2
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE	1	0.35231	0.0001	0.33481
COPULATIONS/DAY				
REVERSE REGRESSION - DEPENDENT = DEPARTURE DATE				
AGGRESSION/DAY	1	0.35231	0.0001	0.33481
DOMINANCE SCORE				
ARRIVAL DATE				
COPULATIONS/DAY	2	0.14180	0.0031	0.46601

1989	DEPENDENT VARIABLE - No. AGGRESSIVE INTERACTIONS/DAY n = 54			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE	1	0.35016	< 0.0001	0.33766
ARRIVAL DATE				
DEPARTURE DATE	2	0.17313	0.0001	0.50459
COPULATIONS/DAY				
REVERSE REGRESSION - DEPENDENT = DOMINANCE SCORE				
AGGRESSION/DAY	1	0.35016	< 0.0001	0.33766
DEPARTURE DATE				
ARRIVAL DATE				
COPULATIONS/DAY				

Notes;

Independents not used;

Age - although a potential determinant, age does not correlate with number of aggressive interactions per day and is not entered if included in the regression. Therefore, it has been excluded in order to increase N.
Arrival weight - although this is a potential determinant, it shows no correlation with aggressive encounters per day and is not entered when included in the regression analysis. Therefore, it has been removed to increase N.
Rate of weight loss - this is not deemed a plausible determinant of daily aggression rates, it is more probable that aggression per day would be a determinant of rate of weight loss.
Length of stay and total number of aggressive interactions are not included as they are not truly independent of aggression per day. Even when included, neither are entered.
Total mating success - this is replaced by copulations per day as a measure of sexual activity, this being a daily rate like aggression per day.
Departure weight and total percentage weight loss - both show males' condition at departure and so can have no effect upon rates of aggression prior to that.

7.4. - EXPERIENCE

The measure used for estimating experience is a summation of the number of days spent ashore in the breeding colony at North Rona in previous years. This data was gathered prior to 1987 from brand sighting records (SMRU), thus, information could only be obtained on branded males. From 1987 onwards detailed records of all study area males were maintained.

The sample sizes for the measure of prior experience were relatively low for the first two seasons, in particular 1987. With limited knowledge of presence or absence of males prior to this study perhaps the values for prior experience in 1987 and possibly 1988 also, are somewhat inaccurate. The values for 1989 may be rather more useful, with at least two years detailed information prior to this season. This may explain why there were no correlations between prior experience in 1987 or 1988, whereas several relationships exist in 1989. As such these data cannot be treated in the same manner as correlations between the remaining variables, but must be viewed with some caution.

In 1989, strong ($p < 0.01$, $n = 36$) positive correlations exist between prior experience and both mating success ($r = +0.55$) and total number of aggressive encounters ($r = +0.52$). However, prior experience was also very highly correlated with length of stay ($r = +0.61$), more experienced males remaining ashore for significantly longer. Thus the relationships with sex and aggression may be mediated via length of stay. Also, the measure of experience is number of days ashore in previous years, thus the relationship with length of stay is merely stating that males which tended to remain ashore for long periods in either 1987 or 1988, or both tend to remain ashore for long periods in 1989.

The only other correlation at $p < 0.01$ was with dominance ($r = -0.43$), more dominant males tended to be the more experienced males, alternatively, more dominant individuals gained more experience - or more accurately stay for longer as shown in section 7.3.

Perhaps surprisingly there is no correlation between age and prior experience measured in this way.

7.5. - AGE

The method of age determination is detailed in Chapter 2. The range of ages obtained for males present in the colony extended from 6 to 21 years (see Chapter 5).

As detailed in sections 7.1 through 7.4 there were surprisingly few correlations between age and any of the remaining variables and no consistent correlations at even $p < 0.05$.

Perhaps one would anticipate a form of inverted U shape relationship between age and for example mating success and dominance, however this is not the case (see Figures supplied in previous sections of Chapter 7).

7.6 - BODY LENGTH

The relationships of mean nose to tail (NTT), neck to tail (NET) and axilliary to tail (AXT) lengths with the other measured variables were examined. As stated in Chapter 5, there was considerable variation in the repeated measures of individual male lengths for reasons detailed in Chapter 2. In an attempt to overcome this unreliability, only individuals who had been measured on at least two occasions and whose standard deviation in length was equal to or less than 10 % of the range in mean lengths were selected. These were then compared with other parameters, such as dominance, length of stay etc. However, it was found that the sample sizes were severely reduced, all being below 10 cases. Thus, cases with standard deviations equal to or less than 20 % of the range of mean values were selected. The sample sizes in 1987 were 13 for NTT, 19 for NET and 16 for AXT. In 1988, the respective sample sizes were 12, 10 and 6, whilst in 1989 they were 11, 10 and 5.

There were no consistent correlations between any of the length measures used (NTT, NET and AXT) and any of the remaining variables. The only correlation existing in two of the three seasons, was that between NET and weight on day one (1988: $r = +0.81$, $p = 0.004$, 1989: $r = +0.75$, $p = 0.012$).

7.7 - ACTIVITY BUDGETS

Chapter 5 examined the overall mean values for percentage of time spent in the various activity categories. In this section the activity budget of each individual male (recorded on at least 180 scans) is compared with the other variables collected during 1988. This is achieved by Pearson correlations on the normalised data and using arc-sine transformations on the activity budget data.

1. Relationships with weight parameters and age:

Both weight on day one and arrival weight were significantly and positively correlated with percentage of time spent in copulation (weight on day one; $r = +0.57$, $n = 16$, $p = 0.022$, arrival weight; $r = +0.63$, $n = 16$, $p = 0.009$). However, these weight parameters were not significantly correlated with the composite category of percentage of time spent in sexual activity (weight on day one; $r = +0.38$, $n = 16$, $p = 0.148$, arrival weight; $r = +0.44$, $n = 16$, $p = 0.089$). Both weight on day one and arrival weight showed no other significant correlation, thus, heavier males do not spend a greater or lower proportion of time in aggressive activities, nor do they spent significantly more or less time resting (weight on day one; $r = -0.16$, $n= 16$, $p = 0.554$, arrival weight; $r = +0.13$, $n = 16$, $p = 0.963$). Similarly, heavier males do not spend a significantly greater or lower proportion of time in the active category.

Both departure weight and total percentage weight lost show no significant correlations with any of the activity categories, even at $p < 0.05$. Thus, the percentage weight loss during an individuals' stay on the colony is not related to his activity levels.

Examining the measures of daily energy expenditure, absolute and proportional rates of weight loss, there are few significant correlations. Absolute rate of weight loss does not significantly correlate with either percentage of time active or inactive ($r = -0.03$, $n = 16$, $p = 0.927$). Similarly, there is no significant relationship with percentage of time spent resting ($r = -0.18$, $n = 16$, $p = 0.512$). Therefore, males that spend proportionately more time resting do not necessarily have a lower absolute rate of weight loss, nor do more active males have a higher rate of weight loss. Rate of weight loss exhibits no significant correlations with measures of time spent in aggressive activities. In fact, the only significant correlation is with percentage of time in copulation (r = -0.62, n = 16, p = 0.011). Thus, males that devote a greater proportion of their activity budgets to copulation tend to have greater rates of weight loss. However, there is no significant correlation with the composite category of all sexual behaviour (r = -0.49, n = 16, p = 0.053).

Proportional rate of weight loss showed no significant correlations with any of the activity categories. There was no significant relationship with time spent in copulation (r = +0.21, n = 16, p = 0.431). Similarly, more active males did not suffer a greater proportional rate of weight loss (r = -0.16, n = 16, p = 0.561).

Age showed no significant correlation with any activity category other than fighting (r = -0.55, n = 16, p = 0.027). Thus, older males appear to spend a lower proportion of time in fighting, though not in aggression overall.

2. Relationships with colony attendance parameters:

Early arriving males spent a significantly lower proportion of time being alert (r = +0.58, n = 25, p = 0.002) and a greater proportion of time in sexual activities (r = -0.48, n = 25, p = 0.016), especially in copulation (r = -0.70, n = 25, p = 0.000).

Departure date showed no significant correlations with any of the activity categories.

Of particular interest was the lack of relationship between length of stay and the percentage of time spent resting (r = +0.31, n = 25, p = 0.13) or being active (r = -0.05, n = 25, p = 0.797). Thus, males that remained ashore for longer did not spend significantly more time resting, nor were more active males confined to relatively short stays. However, males that stayed for longer did spend significantly more time in copulation (r = +0.47, n = 25, p = 0.018) though not in attempted copulation (r = +0.17, n = 25, p = 0.41). Length of stay showed no other significant correlations, thus, males remaining ashore for longer did not spend more or less time in aggressive activity (r = -0.27, n = 25, p = 0.18).

3. Relationships with dominance and aggression:

Both total number of aggressive encounters and aggression per day showed no significant correlation with any activity category.

Dominant individuals spent a significantly greater proportion of time in copulation ($r = -0.47$, $n = 25$, $p = 0.017$) than more subordinate males. However, dominance score was not significantly correlated with any other variable. Thus, dominant males did not spend more or less time resting ($r = -0.22$, $n = 25$, $p = 0.292$), nor are they more alert ($r = +0.22$, $n = 25$, $p = 0.285$), nor do they spend significantly more or less time in locomotion ($r = +0.25$, $n = 25$, $p =0.221$.

4. Relationships with mating success:

Mating success was significantly, and not unexpectedly, correlated with both proportion of time spent in attempted copulation ($r = +0.56$, $n = 25$, $p = 0.003$) and in copulation ($r = +0.82$, $n = 25$, $p < 0.001$). Thus, males gaining greater overall mating success spent significantly more time in both attempted copulation and actual copulation. However, mating success exhibits no other significant correlation with the remaining activity categories. Thus, more successful males do not necessarily spend more time resting ($r = +0.10$, $n = 25$, $p = 0.637$), nor are more active males the most successful ones ($r = +0.29$, $n = 25$, $p = 0.161$).

7.8 - MATING SUCCESS

In the previous sections of Chapter 7 details of relationships between the many variables collected have been presented. Several of these have been shown to be highly correlated with mating success and/or daily copulation rates. This section examines which of these variables is the main predictor of individual male mating success.

The same multiple regression procedure is utilised as detailed in the methods section of Chapter 7. Only relationships which are highly significant and consistent in all three seasons are selected (analysis of covariance). Finally a flow diagram is constructed summarising these results.

Table 7.8.1 details all bivariate correlations with mating success. These are described in detail in the relevant previous sections of Chapter 7.

Table 7.8.2 shows the multiple regression models produced for mating success. In all three seasons length of stay was the primary predictor, explaining up to 70 % of the variation in mating success. In no year is total number of aggressive interactions entered, thus it appears that the relationship between mating success and total aggressive encounters is indeed mediated via length of stay. In two of the three reverse regressions mating success is entered in the first step, confirming the results of the initial regressions. In 1987, dominance is entered first in the reverse regression, with mating success entered on the fourth step.

Table 7.8.3 provides a model for the daily rate of copulations. In 2 of the three seasons, departure date was entered as the main determinant of copulation rate. In both these cases copulations per day were entered on the second step in the reverse regressions, with daily aggression rate being entered on the first step.

Table 7.8.1

Table showing relationships of mating success with other variables in each of the three study years. Analyses are Pearson correlations, only cases with at least 10 inter-male aggressive encounters have been used. Bold type denotes significance at 0.05 > p > 0.01, bold type with * denotes significance at p < 0.01.

VARIABLE	1987			1988			1989		
	R	n	p	R	n	p	R	n	p
COPULATIONS/DAY	**+0.88**	**47**	**0.000***	**+0.85**	**39**	**0.000***	**+0.66**	**54**	**0.000***
TOTAL No. A.I.s	**+0.46**	**47**	**0.001***	**+0.75**	**39**	**0.000***	**+0.60**	**54**	**0.000***
A.I.s / DAY	**-0.45**	**47**	**0.001***	**-0.34**	**39**	**0.032**	**-0.51**	**54**	**0.000***
DOMINANCE SCORE	**-0.51**	**47**	**0.000***	**-0.48**	**39**	**0.002***	**-0.56**	**54**	**0.000***
AGE	+0.37	13	0.216	**+0.52**	**16**	**0.017**	+0.19	26	0.361
PRIOR EXPERIENCE	-0.36	10	0.299	+0.18	19	0.456	**+0.55**	**36**	**0.001***
WEIGHT PARAMETERS									
Wt. ON DAY 1	+0.10	14	0.738	+0.50	16	0.051	**+0.64**	**16**	**0.008***
Wt. ON ARRIVAL	+0.30	14	0.291	+0.49	16	0.052	**+0.78**	**16**	**0.000***
Wt. ON DEPARTURE	+0.28	14	0.336	-0.19	16	0.476	**+0.55**	**16**	**0.028**
TOTAL % Wt. LOST	-0.06	14	0.834	**-0.66**	**16**	**0.005***	**-0.58**	**16**	**0.019**
RATE OF Wt. LOSS	+0.05	14	0.872	**-0.77**	**16**	**0.001***	-0.43	16	0.099
SPECIFIC RATE OF Wt. LOSS	-0.44	14	0.112	**+0.59**	**16**	**0.017**	+0.10	16	0.699
COLONY ATTENDANCE PARAMETERS									
ARRIVAL DATE	**-0.30**	**47**	**0.038**	**-0.51**	**39**	**0.001***	-0.08	54	0.554
DEPARTURE DATE	**+0.43**	**47**	**0.002***	**+0.54**	**39**	**0.000***	**+0.60**	**54**	**0.000***
STAY (DAYS)	**+0.69**	**47**	**0.000***	**+0.84**	**39**	**0.000***	**+0.78**	**54**	**0.000***

Table 7.8.2

Table summarising results of multiple stepwise regression model developed for mating success. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - MATING SUCCESS n = 47			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.48215	< 0.0001	0.47064
TOTAL No. A.I.s				
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
MATING SUCCESS	4	0.03491	0.0024	0.84624
TOTAL No. A.I.s				
DOMINANCE SCORE	1	0.50020	< 0.0001	0.48909
ARRIVAL DATE	2	0.16332	< 0.0001	0.64822
DEPARTURE DATE	3	0.16119	< 0.0001	0.81247

1988	DEPENDENT VARIABLE - MATING SUCCESS n = 39			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.70275	< 0.0001	0.69472
TOTAL No. A.I.s				
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
MATING SUCCESS	1	0.70275	< 0.0001	0.69472
TOTAL No. A.I.s	2	0.06731	0.0025	0.75728
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE	3	0.05589	0.0019	0.81103

1989	DEPENDENT VARIABLE - MATING SUCCESS n = 54			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.60161	< 0.0001	0.59394
TOTAL No. A.I.s				
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
MATING SUCCESS	1	0.60161	< 0.0001	0.59394
TOTAL No. A.I.s	2	0.14502	< 0.0001	0.73669
DOMINANCE SCORE	4	0.03954	0.0017	0.81054
ARRIVAL DATE	5	0.02564	0.0061	0.83490
DEPARTURE DATE	3	0.03867	0.0042	0.77242

Notes;

Independents not used;

Age - although this is a potential determinant of mating success, it shows no significant correlation with mating success (at $p < 0.01$) in any of the three seasons. Therefore, age has been removed to increase N.
Weight parameters - In 1987 none of these showed significant correlations with mating success, thus, although these are potential determinants of mating success, they have been removed in order to increase N.
In 1988 the weight parameters rate of weight loss and total percentage weight loss do correlate significantly with mating success at $p < 0.01$ these correlations only occur in 1988. Also, if included in the analyses, non of these weight parameters are entered in the model (length of stay remains the sole entry). Therefore, these variables have been removed to increase N.
In 1989 the weight parameters are again excluded. Although both weight on day one and arrival weight do correlate with mating success in this year (at $p < 0.01$) this relationship is not repeated in any other year. Also, if included in the analyses, non of these weight parameters are entered (length of stay remains the sole entry). Therefore, these variables have been removed to increase N.
Copulations per day - not truly independent of mating success.
Aggression per day like copulations per day, is a daily rate, not an overall measure for the entire season as is mating success. Also, aggression per day showed no significant, consistent correlations with mating success.

Table 7.8.3

Table summarising results of multiple stepwise regression model developed for copulations per day. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1987	DEPENDENT VARIABLE - COPULATIONS PER DAY n = 47			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE ARRIVAL DATE DEPARTURE DATE AGGRESSION/DAY		NO SIGNIFICANT RESULTS		

1988	DEPENDENT VARIABLE - COPULATIONS PER DAY n = 39			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE	1	0.23978	0.0016	0.21923
AGGRESSION/DAY				
REVERSE REGRESSION - DEPENDENT = DEPARTURE DATE				
COPULATIONS/DAY	2	0.14180	0.0031	0.46601
DOMINANCE SCORE				
ARRIVAL DATE				
AGGRESSION/DAY	1	0.35231	0.0001	0.33481

1989	DEPENDENT VARIABLE - COPULATIONS PER DAY n = 54			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE				
ARRIVAL DATE				
DEPARTURE DATE	1	0.16141	0.0026	0.14529
AGGRESSION/DAY				
REVERSE REGRESSION - DEPENDENT = DEPARTURE DATE				
COPULATIONS/DAY	2	0.11977	0.0014	0.44573
DOMINANCE SCORE				
ARRIVAL DATE				
AGGRESSION/DAY	1	0.34687	< 0.0001	0.33431

Notes;

Independents not used;

Age - although this is a potential determinant it does not correlate with copulations per day in any of the three seasons and if included in the regression, age is not entered. Therefore, age is excluded to increase N.
Arrival weight - although this is a potential determinant of copulations per day, there is no correlation between these two variables in 1987 and 1988, hence it was removed in order to increase N. In 1989 arrival weight does significantly correlate with copulations per day but is not entered in the model if included in the regression procedure.
Rate of weight loss - this was not deemed a potential determinant of copulations per day, it appears more likely that copulation rate may be a determinant of weight loss rate.
Length of stay - this is not truly independent of copulations per day.
Total aggressive interactions - aggressive behaviour is represented by aggression per day, which expresses this parameter as a mean daily rate, as is copulations per day.
Departure weight and total percentage weight loss - both of these parameters represent conditions at departure and are unlikely to affect copulation rate.

DISCUSSION

Determinants of male mating success:

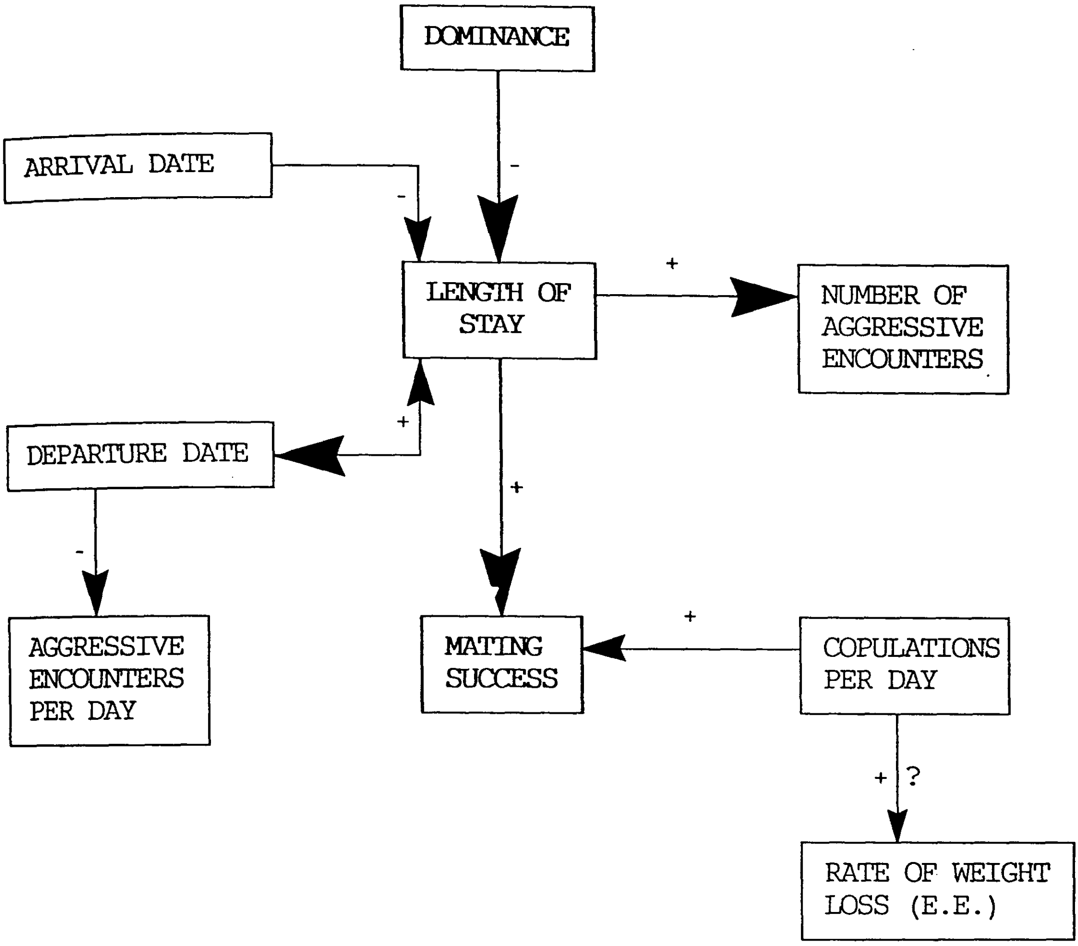
In this study, the main correlate of individual male mating success at North Rona is the length of stay on the breeding grounds. Males that are able to maintain their position on the colony for longer have access to more oestrus females. Length of stay has similarly been found to be the main predictor of mating success in previous studies of grey seals at North Rona (Anderson *et al.* 1975, Anderson and Fedak, 1985) and on Sable Island, Nova Scotia (Boness and James 1979).

Males that depart later in the season attain both greater daily copulation rates and greater overall mating success. There are two potential reasons for this. The first is that a majority of successful copulations occur in the latter half of the season, thus late departing males gain relatively greater mating success. Alternatively, mating success is mediated via some other variable, which is strongly correlated with both departure date and mating success, the prime candidate being length of stay. This was tested in the multiple regression procedure and found to be the case. Also, males that depart later in the season tend to have lower daily rates of aggression.

Obviously length of stay is affected by both arrival and departure date, as few males once established on the breeding grounds depart and return later. However, from the analyses presented in this chapter, departure date has a greater influence on length of stay than arrival date. Similarly, males that remain ashore for longer are involved in more aggressive interactions in total.

The main correlate of length of stay is dominance status. Dominant individuals, whilst not necessarily arriving earlier than subordinates, do maintain their position on the colony for significantly longer and tend to depart later in the season. This gives the immediate benefit of allowing dominant males access to more oestrus females. Dominance status has been shown to be related to mating success in many species (Hausfater 1975, Howard 1978, Lott 1979, McCann 1981, Clutton-Brock *et al.* 1979, Appleby 1982, Cowlisham and Dunbar 1991).

Figure 7.4: Final flow diagram showing determinants of male mating success and inter-relationships of measured variables - North Rona 1987 to 1989.



Notes :

1. Dominance score shows a negative relationship with length of stay as the more dominant individuals have lower dominance scores.

2. Similarly, arrival date shows a negative relationship with length of stay as males arriving earlier have a lower arrival date value.

3. E.E. = Rate of energy expenditure.

These findings are summarised in Figure 7.4 which presents a flow diagram based upon all the analyses conducted in this chapter.

The relationship between weight loss (energy expenditure) and copulations per day is questionable. There is no firm evidence to support this but rate of weight loss does correlate with percentage of time spent in copulation as assessed by the activity budgets.

Mating system:

The mating system of grey seals has long been established as polygynous (Anderson *et al.* 1975, Boness and James 1979, Anderson and Fedak 1985) but the actual form of polygyny is far from clear in the previous literature. Early authors described the system as territorial (Fraser-Darling 1939, Cameron, 1967, Hewer, 1957 and 1974) and even as monogamous (Mansfield, 1967, Hook and Johnels, 1972). This was based primarily upon anecdotal observations and has since been refuted by more quantitative studies (Anderson *et al.* 1975, Anderson and Fedak 1985, Boness and James 1979). Male grey seals do not conform to the strict definition of territorial males (a territorial individual is here defined as an one who maintains exclusive access to a geographically fixed area by means of some combination of advertisement, threat and aggression). Boness and James (1979) divided males into tenured and transient (see Chapter 4). They provide evidence that in general transient males lose to tenured males in aggressive encounters, but suggested that tenured males were of equal status. However, this was an arbitrary classification of males based upon the number of consecutive days a male remained ashore. As length of stay is the main determinant of mating success, this classification sheds little light on the factors affecting length of stay. Anderson and Fedak (1985) were able to assess the outcome of aggressive interactions between males during part of the breeding season. They concluded that more dominant individuals gained greater mating success but males did not form a true linear hierarchy (defined strictly as a dominance system in which one member of a dyad consistently gives way to the other, and there are no reversals of dominance, Manning 1981) as reversals of success in encounters did occur. However, some males were "conspicuously unsuccessful, and some seemed invincible".

Their study was based on 250 inter-male encounters gathered over a period of 2 weeks and a major problem was the lack of interactions between most males. The present study has collected data on inter-male aggressive encounters throughout the entire breeding season in three consecutive years, a total of over 3000 inter-male aggressive interactions. As such we have established a more complete interaction matrix with more interactions in total. The relative dominance of these males does in fact approximate to a linear hierarchy. There are reversals of dominance, hence, they do not conform fully to a linear hierarchy in the strict definition of the term, however, in a natural system this is to be expected (Lott 1979, found a similar degree of reversals in male American bison). There is still the problem that some males never encountered each other, though this has been minimised by the extensive observations. Reversals are expected in certain circumstances, for example, dominant males approaching the end of their tenure, with few remaining females, may defer to more subordinate males as the potential benefits decline. Males that are about to depart will often do so after an aggressive encounter. Similarly, a dominant male who has just been involved in a strenuous fight may subsequently be defeated by a fresh subordinate male. Also, location will affect not only the number of encounters but also the outcomes of interactions as prior residency appears to play an important role. A majority of the reversals occur in the mid-range of dominance scores. This agrees with predictions made from the distribution of dominance scores; there are few highly dominant males, few very subordinate males, with a majority of mid-ranking males. Thus, these mid-range males have more near-equals, hence the greater degree of reversal here. McCann (1981) found that in Southern elephant seals a strictly linear hierarchy existed amongst the top males, but this tended to break down with the lower ranking males finding several reversals. McCann however, had only 20 males, with many more lying offshore. Thus, the more subordinate of McCann's 20 males may be equivalent to my mid-range males.

Grey seal bulls are clearly not territorial, at least not in the strictest sense as discussed above (see Chapter 10 for a discussion of the compatibility of other definitions of territoriality). In comparison to many otariids, grey seals have a much looser arrangement. Males do not defend discrete areas but endeavour to maintain their position within the groups of females. However, from the observations made in this study it is clear that the division of males into simply dominants and subordinates or even tenured and transients is a gross oversimplification, as suggested by Anderson and Fedak (1985). The results also show that these "tenured" bulls are not all of equal status. As the size and density of female groups on the breeding colony varies spatially and temporally (see Anderson *et al.* 1975) certain positions on the colony are clearly preferable to others from a male's point of view. Obviously not all the males can gain the preferred site(s), and whichever male successfully holds this position will be rewarded by potentially high mating success.

Thus I have established that some form of dominance hierarchy exists amongst grey seal bulls and that the more dominant males (defined solely on the basis of inter-male aggressive encounters) do indeed gain significantly higher overall mating success than more subordinate males. These dominant bulls are able to maintain their positions on the colony for significantly longer than subordinates, as shown by the clear correlation between dominance and stay. Thus, the more dominant males are those individuals previously described as "tenured" in Boness and James (1979). However, rather than arbitrarily assigning males to either "tenured" or "transient" status, it would be more accurate to consider length of stay as a function of dominance, ranging from a few hours for the most subordinate males to almost the entire season for the most dominant. Thus, the mating system observed on North Rona approximates to a dominance hierarchy.

Dominance, age and size

There was no relationship between dominance and age. From examination of individuals through all three seasons it appears that each male attains a peak success of differing magnitude and at varying ages. Thus, it appears that within each age cohort, once sexually mature, there are certain "fit" individuals which are more dominant and more successful than some older males and some younger males. Lott (1979) also found no relationship between dominance and age in male bison.

The range of ages of males active on the colony (i.e. those we caught) extended from 7 to 21 years. Harwood and Prime (1978), Boness and James (1979) and Boyd (1982 a) suggested that only males of greater than about 10 years of age were seen on the colony, though, Anderson *et al.* (1975) sighted one known 7 year old male on the breeding colony of North Rona in 1972, but this was regarded as clearly a subordinate male. The data collected here suggest that younger males can indeed gain positions on the colony. In Northern elephant seals the earliest marked males have been observed to mate is at 6 years of age (Le Boeuf and Reiter, 1988), though it must be noted that their life span also differs.

The results presented here show no relationship between age and length of stay. This appears to contradict Boness and James' (1979) suggestion that acquisition of "tenure" is related to age.

There was no relationship between age and weight. Although the range of ages obtained extend from 6 years to 21 years, these are all sexually mature males. Examining the plots of weight against age presented by Hewer (1964), Mansfield (1977) and Anderson and Fedak (1985), it is apparent that at approximately 6 years of age the graph begins to plateau with considerable scatter in weight (though some of this scatter can be attributed to the fact that the data are a composite of weights taken throughout the year, pers. comm. S. Anderson). As we are in effect dealing only with this portion of the graph, it is not entirely surprising we have found no clear relationship between age and weight. Thus, once males are sexually mature, age appears to have little effect upon weight attained. Also, our measure of weight is affected to some extent by the arrival date of the individual. Even using an estimated weight on a hypothetical day one may not be particularly accurate as each individual male may cease foraging prior to the breeding season at different times and then experience differing rates of weight loss. There may in fact be no particular date at which weights of individual males are directly comparable.

Male dominance is clearly established by male competitive ability. In much of the literature on intra-sexual competition, relative dominance has been attributed to size (eg McCann 1981). One often sees phrases such as "size appears to be a major factor in deciding the outcome of intrasexual competition through its effect on fighting ability" referring to male Southern elephant seals (McCann 1981). However, McCann fails to explain precisely what advantage size provides. Similarly Alcock (1983) provides the sweeping statement of "body size is so important in determining who will win an actual fight". Indeed, it may be true that size is important, but this rather general and seemingly hasty statement in fact has little empirical evidence to support it. Though it is naturally intuitively logical and attractive to assume that bigger males are better fighters there are few studies which have demonstrated a clear causal relationship, rather than merely showing a link between size and success. In these examples size may indeed be an important determinant of male competitive ability. However, males of different species compete in different ways, in different contexts, for different rewards, employ different techniques perhaps dependent largely upon morphology, and compete in different mediums. All these factors must be examined in order to determine which features give a male a competitive edge. Size may not be the only factor, indeed, in some species it may be a disadvantage to be particularly big. Speed, agility, awareness, strength, experience and knowledge of surroundings are just a few of the many potential factors that may be important depending upon how, where and when males compete.

The results presented in this chapter demonstrate that dominant male grey seals are not necessarily heavier or bigger than subordinates. At first this may seem particularly surprising. This appears to contradict traditional theory of sexual selection, with the particularly intense inter-male competition in polygynous systems leading to sexual size-dimorphism (Darwin 1871, Trivers 1972, Halliday 1976) . Precedents do exist however. Huntingford *et al.* (1990) suggest that in Atlantic salmon parr (*Salmo salar* L.) dominance status in early social interactions depends upon behavioural properties rather than size. Even in Northern elephant seals, Haley (1989) found that neither length nor estimated mass determined the outcome of short inter-male fights, and the winners of long fights actually weighed less than the losers. Amongst other mammalian groups, Lott (1979) found no relationship between weight and dominance in male bison. Lott used the weight at the end of the rut as his weight measure. Anderson and Fedak (1985) therefore attributed Lott's lack of relationship to this fact, however, Lott did state that weight loss during the rut was similar in all males. Here though, I present incontrovertible evidence of no relationship between measures of weight, either at the start or end of the breeding season, and dominance status for male grey seals.

A classic example of the theory of inter-sexual competition has always been the relationship between polygyny potential and degree of dimorphism in a cross-species comparison of pinnipeds (Alexander *et al.* 1979). Indeed, several studies show clear relationships between male size and dominance and therefore mating success (see Huntingford and Turner 1987). In bees for example (Alcock *et al.* 1977), spiders (Suter and Keiley 1984), crayfish (Stein 1976) and in pinnipeds in particular (Le Boeuf and Peterson 1969, Le Boeuf 1974, McCann 1981). However, is this necessarily the case in all species? Few of these examples are phocid species, and all of these are land breeding species, the remainder being otariids in which females adopt rather different strategies for reproduction. Similarly, the data on which Alexander *et al.* (1979) base their interpretation may have been superseded by more recent information. Data for land breeding pinnipeds are rather extensive, as it is relatively easy to gather. However, data on pagophillic species are rather limited. A majority of the work on ice breeding pinnipeds is based on observations of animals on the ice. Relative distributions of males and females and the few observed copulations have lead to the assumption that some pagophillic species are either monogamous or have very low degrees of polygyny due to a low polygyny potential (i.e. little opportunity to monopolise females). However, recent evidence has suggested that this may not be the case. For example, Crabeater seals (Siniff *et al.* 1979) and hooded seals (Boness, Bowen and Oftedal 1988 and Kovacs 1989) have been shown to be truly polygynous, though the extent of the variation in male mating success remains to be resolved. In such species a majority of the inter-male competition and mating occurs in the water (Le Boeuf, 1991). Males may hold "territories" or "maritories" in the water at sites where females congregate to forage or pass frequently, as observed in Weddell seals (Kaufman *et al.* 1975, Bryden *et al.* 1984). Females may even be selecting males on the basis of aquatic displays. Recent telemetry work on harbour seals provides new insights into male and female movements during the breeding season, and may indicate a greater degree of polygyny than previously assumed (pers. comm. D. Thompson, Sea Mammal Research Unit). Thus, if these species are rather more polygynous than has been supposed in the past, the graph presented in Alexander *et al.* is inaccurate.

Size dimorphism may indeed be related to polygyny potential, but perhaps only in land breeding species. Size dimorphic species of pinnipeds are land breeding species, and fighting ability is likely to be related to size. Pagophillic species are rather less dimorphic or monomorphic. Similarly, phocid species in which females pup at the waters edge and mate in the water are less dimorphic (eg. common seals, monk seals). In these species mating and in particular inter-male competition occurs in the water, thus, agility may be more important than size. Thus, the selection pressures producing dominant males which can obtain high mating success may differ between species where males compete in an aquatic medium and those that compete on land. In the former, qualities such as agility may be favoured, whilst in the latter "bulk on the ground" may be more important.

So, why, given that the grey seals of North Rona are terrestrial breeders, is there no relationship between size and dominance in male greys seals at Rona?

Grey seals mate both on land and in water, though a majority of copulations at North Rona occur on land. However, throughout the breeding season there is remarkably little inter-male aggression, the vast majority of which (over 95%) is composed of low level threats involving no physical contact. The peak of aggressive activity occurs at the start of the season. Anderson and Fedak (1985) state that "aggression is not important once males have established their positions on the breeding grounds". Dominant males spend much of their time resting, seemingly secure in their position. In fact, dominant males are rarely challenged; subordinate males tend to avoid conflict with dominants (pers. obs., Cox 1983) which could potentially be very damaging. The role of individual recognition may be important in this, especially odour. Males emit a powerful musky odour which can be detected from tens of meters downwind. I therefore propose that at least the basis of male dominance relationships is established prior to the breeding season, in the water.

Aggression on the colony is merely maintenance of status and a few ambitious males. Therefore, agility is more important than size in attaining high status, and thus, there is no apparent relationship between size and dominance on the breeding grounds.

Several pieces of evidence support this explanation. (1) In Southern elephant seals a similar process occurs (McCann 1981). Males arrive at the breeding grounds "up to one month before the arrival of the first cows". During this period the males establish "the framework of a dominance hierarchy". Similarly, in Northern elephant seals, Le Boeuf and Reiter (1988) state that the "important shifts in (male) rank usually occur before the females come into oestrus". As both Northern and Southern elephant seal males are competing on land, size is related to status. However, grey seal males, though sighted at colonies well before the onset of breeding, do not come ashore until the first pups are born (see data presented in Chapter 4, also; Boness and James 1979, Anderson and Fedak 1985). In fact Boness and James (1979) state that "this degree of synchrony in the arrival of adults of both sexes at the breeding site is not known to occur in any other land breeding pinniped". Thus, any prior establishment of status will occur in the water. (2) When southern elephant seals compete, they fight face to face, with much pushing and shoving, a process in which size is most likely very important ("Sumo wrestlers!). Grey seal males however, fight in a different manner. Males initially approach each other face to face, they then lunge at each others necks, but the ultimate aim is always to get around the opponents guard to his back or his rear end. Once this is achieved the male bites his opponents' hind flippers and tail and the fight then promptly ends with the opponent fleeing. This method of combat (mud wrestling!) may require more agility and strength than that employed by elephant seals, and is also remarkably reminiscent of mammals that combat almost entirely in water, such as common seals and otters (pers. obs., per. comm. W. N. Bonner). (3) When two male grey seals approach each other on land, they adopt a peculiar stance. One male holds his head low to the ground, the other holds his head relatively high. It is always this latter male that loses the encounter, an encounter that is usually resolved easily. On the few occasions where this signal is not so clear, a long and protracted fight often ensues. This, together with the low aggression levels on the breeding grounds may indicate some prior "knowledge" of relative status. (4) There is no correlation between energy expenditure and rates of aggression during the breeding season. If dominance is established solely on the breeding grounds, and is an important determinant of mating success, one might expect a relationship here. There is, however, a correlation between rate of weight loss and time spent in sexual activity. (5) Boyd (1982 a) presents data on seasonal changes in male testes size and testosterone levels in grey seals. The testes tubule diameter increases significantly approximately 2.5 months prior to the onset of breeding. Also, the prostate gland, an organ particularly sensitive to testosterone levels increases in size prior to the breeding season (Boyd, pers. comm.). Thus, it appears that male androgen levels increase at least a month prior to seals coming ashore at the colony, suggesting that male aggression is also increased during this period. Similarly, Griffiths (1984) presents data on prostate gland size in male Southern elephant seals, again showing an increase prior to the breeding season. (6) Davies (1957), McClaren (1960) and Boness and James (1979) suggest that grey seals were an ice breeding species in recent evolutionary history. If this is so, males would perhaps have competed and mated predominantly in the water. Thus, the present mating system on North Rona may have been influenced by this history.

This may then be why there is no clear relationship between size and dominance in male grey seals, however, there is one wee problem with this explanation; why, then, are grey seals sexually size dimorphic?

I have already established that males which remain ashore for longer gain greater mating success, this is the main predictor of mating success and highly correlated in all three seasons. Therefore, all males which intend to breed in any one season will attempt to remain ashore for as long as possible. Evolution will select those males with the capacity to remain ashore for long periods. As male grey seals fast during the breeding season the length of stay will depend upon having sufficient energy reserves to stay ashore for as long as necessary. We will assume for the time being that a seals energy reserves are the fat deposits in the blubber (this in fact accounts for approximately 80% of the energy utilised - Fedak and Anderson, 1985). Any individual can accommodate only a certain proportion of fat, in grey seals total fat content has been estimated as a maximum of approximately 50% of body weight (Fedak and Anderson, 1985), and blubber reserves approximately 40% (Anderson and Fedak 1985). Larger individuals, though not necessarily able to carry proportionately more fat can carry greater absolute amounts. Although there is a trade off between size and the extra energy requirements required to maintain greater body mass, the data gathered during this study indicates that heavier males do not have significantly greater proportional rates of weight loss, but do have greater absolute rates of weight loss, a relationship also found by Anderson and Fedak (1985). Thus, we shall assume that the extra metabolic costs of being bigger do not outweigh the advantages of being bigger, at least within the range of sizes of male grey seals. In order for a male to gain high mating success he must remain ashore for almost the entire season, the maximum recorded stay in this study was 54 days. All males that intend to partake in breeding are "optimists" - as energy reserves are accrued prior to the breeding period, males will gain sufficient condition in order to stay ashore for the maximum period in the "hope" that they will get an opportunity to use it. It would be pointless to arrive at the colony with insufficient reserves (this point is discussed in more detail below). The average rate of weight loss in male grey seals is 2.2 kg per day. Thus, males must be large enough to carry 118.8kg (54 x 2.2 kg) of fat. In contrast, females have a much higher rate of weight loss, 3.8 kg per day, but only remain ashore for a maximum of 21 days. Thus, females must accommodate only 79.8 kg (21 x 3.8 kg) of fat. If these computed weights of fat are expressed as a percentage of the mean male and female observed starting weights (257kg and 170 kg respectively) the results are 46% fat for males upon arrival, and 47% for females. This is very close to the maximum estimate of fat content. As blubber in fact accounts for only 80% of energy reserves, these figures can be adjusted giving respective values of 37% and 37.6%. These are remarkably close to Anderson and Fedak's (1985) maximum blubber content. Similarly the ratio of male to female computed fat content is the same as the ratio of their mean starting weights, i.e. 1.5 : 1.

Therefore, it is possible that male grey seals are larger than females as they need to stay ashore for considerably longer in order to attain high mating success which would be selected for in a polygynous system. Thus, there is a range of weights for males, the mean of which is greater than for females, but the scatter in male weights does not relate directly to an individuals dominance or success. Fedak and Anderson (1985, 1987 b) state that "males can stay ashore for longer than females because they are larger and, since they are not lactating, experience a lower rate of weight loss" however, they then go on to say that "greater size confers an advantage to males in competition", which has been refuted by the data presented here.

Energy expenditure and colony attendance:

Other interesting aspects of the results concern the lack of relationship between measures of energy expenditure and duration of stay.

The most striking feature of the male grey seal activity budget is the large proportion of time devoted to resting (see also data presented by Harwood 1976, Anderson and Harwood 1985, Boness 1984 and in Chapter 5). Similarly high proportions of time spent resting have been found in other pinniped species; in breeding walruses (Miller, 1976, Salter, 1979), New Zealand fur seals (Crawley *et al.* 1977), common seals (Sullivan 1982), Northern elephant seals (Sandegren 1976) and Southern elephant seals (McCann 1983). Several of these authors have attributed this to the need to conserve energy during a period of finite energy reserves. Harwood (1976) states that both males and female grey seals spend so long resting as they "have a strictly limited amount of energy available for utilization on the breeding grounds". Similarly, Anderson and Harwood (1985) confirm that the "time allocation patterns are consistent with the fact that grey seal energy reserves are limited during the breeding season". However, Boness (1983) disputes this idea. Boness found that the most active males in fact had the greatest copulatory success, and suggested that fasting did not place severe limitations on male activity levels. Anderson and Harwood (1985) attributed this to the fact that Boness did not allow for variation in male size, as Anderson and Fedak (1985) demonstrated that bigger males were more sexually active as they could "afford" to be so, though both large and small males would "ultimately be limited by their finite resources in the time that they can spend ashore".

As male grey seals do spend such an inordinate amount of time resting, it is immediately attractive to assume they are constrained to do so by their finite and therefore supposedly limiting energy reserves. However, there may be other reasons for this high degree of inactivity. Male grey seals do not defend strict territories, thus, there is no requirement to patrol a perimeter. There are generally low levels of aggressive activity on the breeding grounds, a vast majority of inter-male interactions being resolved by low level threats or even a simple glance. Only receptive females can be mated and generally females move very little during lactation. Thus, males may not need to be continually active in order to maintain a position in the colony. A further possible explanation, is that many land breeding phocids may be under considerable thermal stress during the breeding season (Pierotti and Pierotti 1980, 1983), though this has been disputed by Lavigne (1982).

The results presented in this chapter tend to agree with Boness (1984), that male grey seals do not spend so much time resting for energy conservation considerations. Whilst the correlation between weight and time spent in copulation agrees with Anderson and Fedak (1985), no evidence of an energetic constraint could be found. There was no relationship between percentage of time spent resting or active with either absolute or proportional rates of weight loss. This latter rate of weight loss adjusts for differences in male arrival weights as suggested by Anderson and Harwood (1985). The only activity category showing a significant correlation with rate of weight loss was the proportion of time spent in copulation, though even this did not correlate with proportional rate of weight loss. Thus, there is at least some indication that males gaining greater mating success incur greater absolute rates of weight loss. However, as males devoting a greater proportion of time to sexual activity and/or those that remained ashore for longer did not necessarily spend more time resting, this tends to refute the concept that male grey seals are energetically constrained. Unlike Boness' (1984) subjects, the males gaining greater mating success were not necessarily more active, but neither were they less active.

There was no consistent relationship between either absolute rate of weight loss or proportional rate of weight loss and length of stay. It would appear that their are two possible explanations for this lack of correlation between either absolute or proportional rates of weight loss and length of stay. The idea that males able to remain ashore for long periods are those that are able to minimise energy expenditure and perhaps divert more into sexual activity is negated by the results of the activity budgets; males that remain ashore for longer do not necessarily spend a lower percentage of time in high energy activities. It would appear both from the activity budgets and the weight loss data that male grey seals are not severely limited by energy reserves. Whilst this may not seem logical at first, there is a plausible explanation. Indeed this explanation appears to me to be more plausible than the concept that energy reserves are severely limiting. Body condition is attained prior to the breeding season. Once the season has commenced there is little scope for a male to further enhance his condition. Thus, all males that intend attempting to breed in a particular season will attempt to attain maximal body condition prior to the onset of the breeding season. They will do this with the intention of gaining a position on the breeding grounds. If they fail to gain a position they have merely wasted foraging effort. In contrast, assume a male did not attempt to gain full condition prior to the breeding season and yet gained a position on the colony, his lack of condition would then restrict his period of tenure and therefore, limit his mating success. As each male may only be sexually active for a few years, this would constitute a major loss in lifetime reproductive success. Thus, each male will attempt to maximise condition on the hope that they will gain a position. Thus, energy reserves are not severely limiting in terms of length of stay and hence mating success, but the opportunities to gain positions on the colony are, by more dominant individuals restricting access. Fedak and Anderson (1985) computed a predicted length of stay from weight data and concluded likewise that there was "little difference between males in their ability to stay ashore".

It is possible that length of stay may be determined by a combination of factors, for example initial condition and subsequent rate of energy expenditure. These possibilities were tested in multiple regression procedures using measures of initial weight and rates of weight loss. There was no indication that either initial weight, subsequent rate of weight loss or some combination of both influence length of stay. Any potential limiting effect of energy reserves and expenditure upon length of stay is masked by the effect of dominance. So few males get the opportunity to remain ashore for the total time allowed by their energy reserves that it is impossible to discern any influence of energetics upon length of stay.

Also, as in Anderson and Fedak (1985), a positive correlation between absolute rate of weight loss and my measures of initial weight (arrival weight and weight on day one) was found. However, in both of these last comparisons it must be noted that the measure of starting/initial weight used is slightly different. Anderson and Fedak used simply the weight of the animal on the first day it was weighed. Here, the weight has been extrapolated back to the first day on which the male was sighted on the study site using the rate of weight loss. However, Fedak and Anderson (1985) present a mean initial weight for males from the same data of 257 kg which agrees closely with the mean values of arrival weight in this study (1987; 256.14 kg, 1988; 260.82 kg, 1989; 256.34 kg).

The relationship between weight loss and both arrival weight and weight on day one was examined further, by calculating a specific rate of weight loss. This gives the percentage decrease in weight per day for each male, thus accounting for differences in males' starting weights. It was found that there was no significant relationship between a male's starting weight and his specific rate of weight loss. Thus, both males that were initially "heavy" and those that were initially "light" lose a similar percentage of their body weight each day.

It must be noted that this may be a somewhat biased sample, as the males caught are those that stay. Males on the periphery of the colony or those remaining ashore for very short periods are not caught. Therefore, the sample effectively represents those males termed by Boness and James as "tenured" males. From the observations it is clear that "transient" males do come ashore throughout the season, but usually only stay for short periods and are unable to establish "tenure". The few that achieve "tenure" then become possible candidates for capture. Thus, at present weight change data can only be used with regards to males adopting the "tenured" mating strategy.

Earlier arriving males are subject to greater levels of overall inter-male aggression. This is most probably due to the higher levels of inter-male aggression in the early part of the season (see Chapter 3).

The "costs" of being successful:

Dominant males, which remain ashore for longer, whilst being involved in more inter-male aggressive encounters in total, do in fact, have lower daily rates of aggression. There are several potential explanations for this. First, males that maintain a position for long periods are the more dominant individuals. By the nature of the topography of Rona (i.e. limited access, clumped female distribution influenced by topography) these central males are buffered from incursions from the many itinerant males around the periphery by the presence of surrounding males with secured positions. Thus, few peripheral males will encounter these top males. When encounters do occur between central and peripheral, itinerant males they are often brief and resolved by low level threats. More often than not, the itinerant will move away as soon as he is sighted by a central male. Central males have low levels of aggression with neighbouring males after an initial period of high aggressive activity. Once their relative status and position has been firmly established upon first arrival, they appear to accept one another's presence (see also Hewer 1957, Anderson and Fedak 1985). Any interactions are predominantly low level threats. However, if a fight does break out between two neighbouring males, it is generally intense, long and with no clear victor, as these males are very closely matched. Whilst such fights are extremely costly, they are quite rare. In comparison, subordinate males around the periphery of the colony are in greater concentrations (particularly with the limited access to the breeding site) and are constantly jockeying to establish some kind of position on the edge of the colony. Anderson *et al.* (1975) also suggest that there are relatively few aggressive interactions between central males compared to amongst more peripheral males and McCann (1981) states that there are more fights amongst the subordinate southern elephant seals which have more near equals to interact with than the dominant bulls. Thus, in terms of aggressive activity at least, it appears that dominant males are indeed able to minimise daily energy expenditure.

It is also possible that males that remain ashore are actively restricting aggression rates in order to conserve energy expenditure. However, from activity budgets and weight loss data this does not appear to be the case. Also, if aggressive activity is necessary to maintain a position, males will not defer from this activity at any one point in an attempt of saving a few KJ of energy. Whilst the saved energy may allow them to remain ashore for a few hours more at the end of the season, opting not to defend ones position would result in the male being ousted there and then. Conservation of energy is more likely to play a role in the general reluctance of all males to escalate aggression from threats to physical contact. It is more likely a combination of the former factors, providing these dominant males with a further advantage in that they can devote a greater proportion of time to sexual activity.

Dominant bulls tend to suffer greater absolute daily energy expenditure than subordinates as demonstrated by their higher rate of weight loss (though significant only at $p < 0.05$). This greater rate of weight loss together with their longer periods of tenure result in dominant males incurring considerably higher losses in body weight during the breeding season than the more subordinate bulls. Thus, the acquisition of greater mating success by these dominant males does require greater energy expenditure, but as stated above this does not appear to be a severely limiting factor.

Conclusion:

In summary, by the collection of detailed and extensive behavioural records we have been able to calculate a "dominance score" for individual males. This score has allowed us to compare relative dominance with various other behavioural and energetic parameters. The results have demonstrated that in grey seal males the length of stay on the breeding colony varies in relation to dominance and that not all males are of equal status. The length of stay is the primary determinant of mating success, thus, more dominant individuals secure a majority of the breeding opportunities.

Dominant males are not necessarily older nor bigger individuals. The proposed explanation for this is that male grey seals establish the basis for dominance relationships prior to the breeding season in the water. Thus, size is not particularly important in inter-male competition. Grey seals are sexually size dimorphic primarily due to the differing energy storage requirements of the two sexes determined by the different strategies adopted by males and females in order to maximise individual reproductive success.

CHAPTER 8 - INTER-SEASONAL CHANGES

INTRODUCTION

In the previous chapter we have determined from the data available that the primary correlate of individual male mating success is the length of stay on the breeding grounds. The more dominant individuals are able to maintain a position on the colony for significantly longer and thus attain greater mating success. As shown in Chapter 6, there is considerable variation in male mating success within each season, with only a few individuals gaining high success.

However, the grey seal is a long lived species, and males may be active for a number of years (see Chapter 4). Thus, in examining the extent of polygyny within the Rona population it is necessary to look at relative success of individuals over as many seasons as possible. If the same individuals are successful in successive years, the degree of polygyny on a time scale greater than one season will be greatly enhanced. Similarly, if this is so, the major determinant of individual lifetime mating success and presumably reproductive success may be the number of seasons a male is able to return to the breeding site, rather than success in any single season.

In this chapter, data collected during this study are examined in order to discern any inter-seasonal trends, and to elucidate which factors determine whether males return in successive seasons or not.

METHODS

All males that were positively identified using the methods detailed in Chapter 2 were divided into various sub-groups based upon their yearly attendance patterns. Firstly, males were simply classified upon the basis of the number of years they were present, whether one, two or three seasons. Secondly, a more complex division was made; (1) males present in 1987 only, (2) males present in 1988 only, (3) males present in 1989 only, (4) males present in 1987 and 1988, (5) males present in 1988 and 1989, (6) males present in 1987 and 1989 but not 1988 and (7) males present in all three seasons. Summary statistics were obtained for each of these groups and for each year where males were present for more than one season.

To examine more closely the nature of changes in mating success between years, the change in mating success was calculated for all males present for at least two seasons. These were divided into males present in 1987 and 1988, 1988 and 1989, 1987 and 1989. A further sub-division was made, examining the nature of changes between these years for males present only in the two stated seasons and for males present in all three seasons. Finally, the nature of changes in mating success over all three seasons was examined in detail for males present in all three years.

In an attempt to assess the number of seasons for which individual male grey seals are present on the breeding colony, past brand sighting records were examined. These records of sightings of branded males on North Rona extend from 1980 to 1989. Brand sightings prior to the onset of this study were provided by the Sea Mammal Research Unit. All records of marked (branded) individuals were collated giving the number of breeding seasons in which each male was sighted on North Rona.

Statistical analyses involved the use of oneway analysis of variance with Scheffe's Multiple Range tests, Wilcoxon matched-pairs signed-ranks tests, Mann-Whitney U tests and Chi square tests (with Yates correction where necessary). Each statistical technique was applied where appropriate, and if necessary upon transformed data (see Chapter 3 and 7).

RESULTS

8.1. Changes in individuals' mating success between seasons

Of the 275 individually identified males 80.4 % (221) were present in the study area for only one season of the study. Thirty five males (41.2 %) of the identified 85 males present in 1987 were present only in that season. During 1988, a total of 117 males were present, of which 67 (57.3 %) were present in 1988 only. In 1989, a total of 145 males were present, of which 96 (66.2 %) were present in 1989 only. Those males first observed in 1989, and therefore recorded as being present only in 1989, did not have the opportunity to be present in more than one season, thus, 179 males (275-96) had the opportunity to be recorded in more than one season. Only 36 males (20.1 % of the 179 males) were present in any two seasons, 11 being present in 1987 and 1988, 21 present in 1988 and 1989 and only four males were present in 1987, absent in 1988 and returned for 1989. Thus, excluding these males, only 18 males were present in all three seasons. However, it must be noted that only those 85 males present in 1987, had the opportunity to remain for all three seasons, thus 21.2 % of these males were present in all three seasons. Whilst these figures may not be biologically realistic, as males may have been present in seasons before and after the period of this study, these figures do explain the sample sizes used in subsequent analyses. In fact, data from branded males show that some individuals are present for considerably longer periods than the three seasons of this study (see below - section 8.6).

Even fewer males were able to maintain relatively high mating success in successive seasons. Four males were in the top ten males in terms of mating success in 2 seasons (males 023, 035, 063 and 011) and only one male was in the top ten in all three seasons (male 001). All these males apart from male 035 were present in all three seasons of the study. Table 8.1.1 illustrates their observed mating success in each year and their ranked position in terms of mating success.

Table 8.1.1

Table showing details of observed mating success and ranked mating success (in parentheses) of males in the top ten in terms of mating success in either two or three seasons.

MALE IDENTITY CODE	OBSERVED MATING SUCCESS (RANK) 1987	1988	1989
023	8 (2)	8 (3.5)	0 (94.5)
035	5 (8)	5 (9)	ABSENT
063	0 (54.5)	8 (3.5)	9 (3.5)
011	1 (34.5)	7 (7)	6 (8)
001	11 (1)	8 (3.5)	6 (8)

Table 8.1.2

Table of summary statistics of observed total mating success for males present in one, two or three breeding seasons.

NUMBER OF YEARS PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1	198	0.00	0.45	1.34	0.10	0	12
2	36	2.00	3.11	3.50	0.58	0	16
3	18	12.00	10.44	6.46	1.52	0	25

Figure 8.1 depicts the summated values for total number of observed copulations over all seasons present for each male. The mean total mating success is 1.38 (median = 0.00, SE = 0.21, n = 275). The variance of this skewed distribution is 11.86. This compares with values of 4.97 for 1987 alone, 4.49 for 1988 alone and 5.90 for 1989 alone. Similarly, in Figure 8.1.1, 71.28 % of males gained no observed copulations. The top 5 males in terms of mating success accounted for 22.88 % of observed total copulations, whilst the top male accounted for 6.43 percent. The standardised variance ($I = s^2/x^2$ - see Chapter 6) for the distribution of summated mating success is 6.18. This compares with I values of 2.15, 5.31 and 5.26 respectively for the 1987, 1988 and 1989 seasons separately (see Chapter 6). Green's coefficient for this distribution is 0.020, which compares with values of 0.018, 0.037 and 0.030 respectively for 1987, 1988 and 1989 separately (see Chapter 6). Finally, the cumulative percentage of copulations accounted for by each successive 10 % of males (ranked in order of decreasing mating success) was plotted (Figure 8.2) together with those for each season separately (see Chapter 6). These curves were compared by means of Kolmogorov Smirnov 2 sample tests. No significant differences were found between the summated mating success and any of the three study seasons taken separately.

Figure 8.1 also shows whether males were present for one, two or all three seasons. It is evident, and not surprising, that males attending for more years tend to gain greater mating success overall. However, it is interesting that one of the males (028) present in all three seasons, failed to gain any observed copulations. Conversely, one male (225), present in 1989 only, gained 12 copulations, greater success than 8 of the males present in all three seasons, and all but one of those present in 2 seasons. Table 8.1.2 gives the mean total mating success and summary statistics for males present in one, two and three seasons.

In order to assess the "degree of polygyny" (see Chapter 6) expressed in the three groups of males presented in Table 8.1.2, measures of relative variation were calculated. The standardised variances (I) for the three groups in Table 8.1.2 were 8.87 for males present in one year only, 1.27 for males present in any two seasons and 0.38 for males

Figure 8.1 : Distribution of summated mating success for all identified males

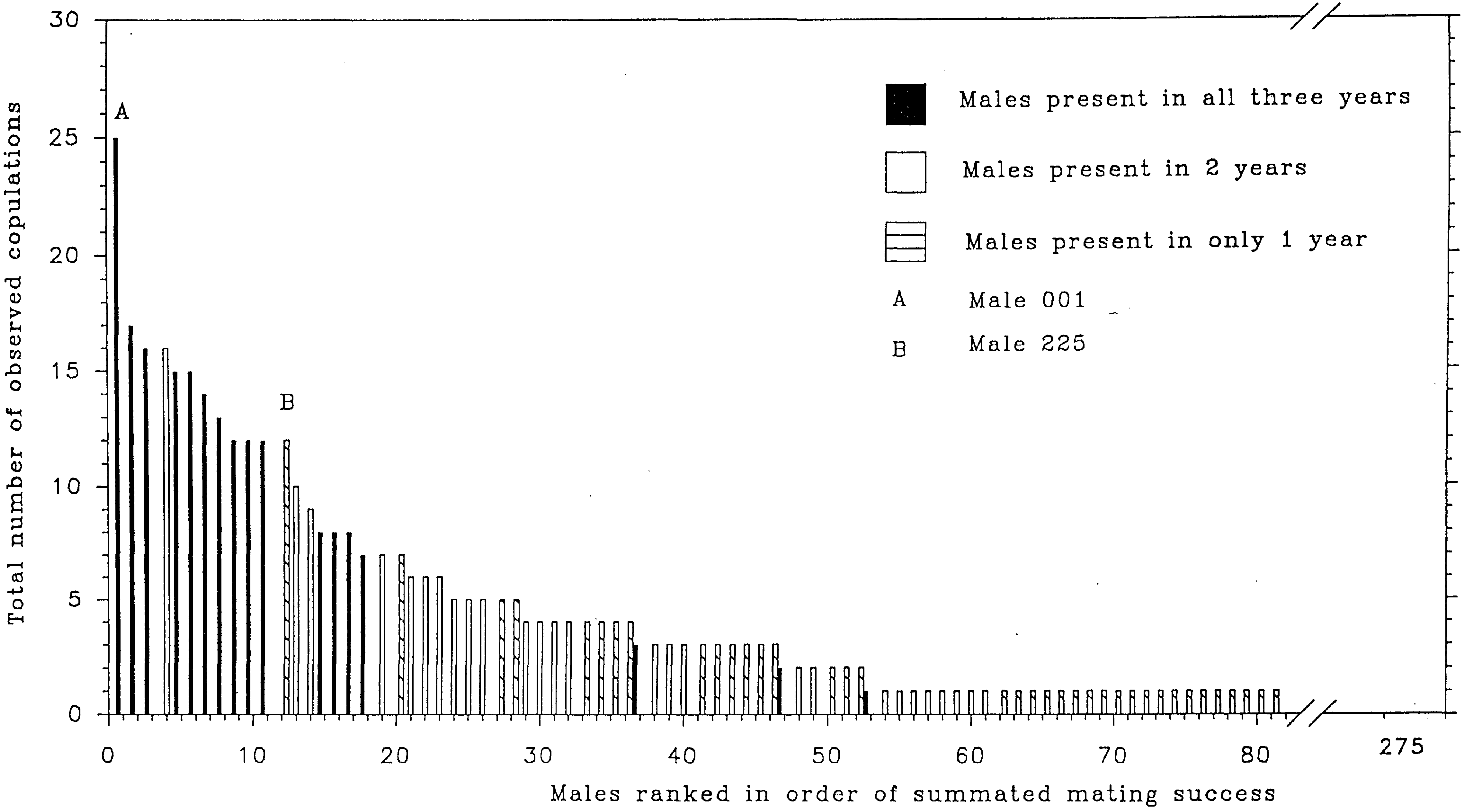


Figure 8.2 : Comaprison of relative degrees of polygyny for Rona including all three seasons data taken together

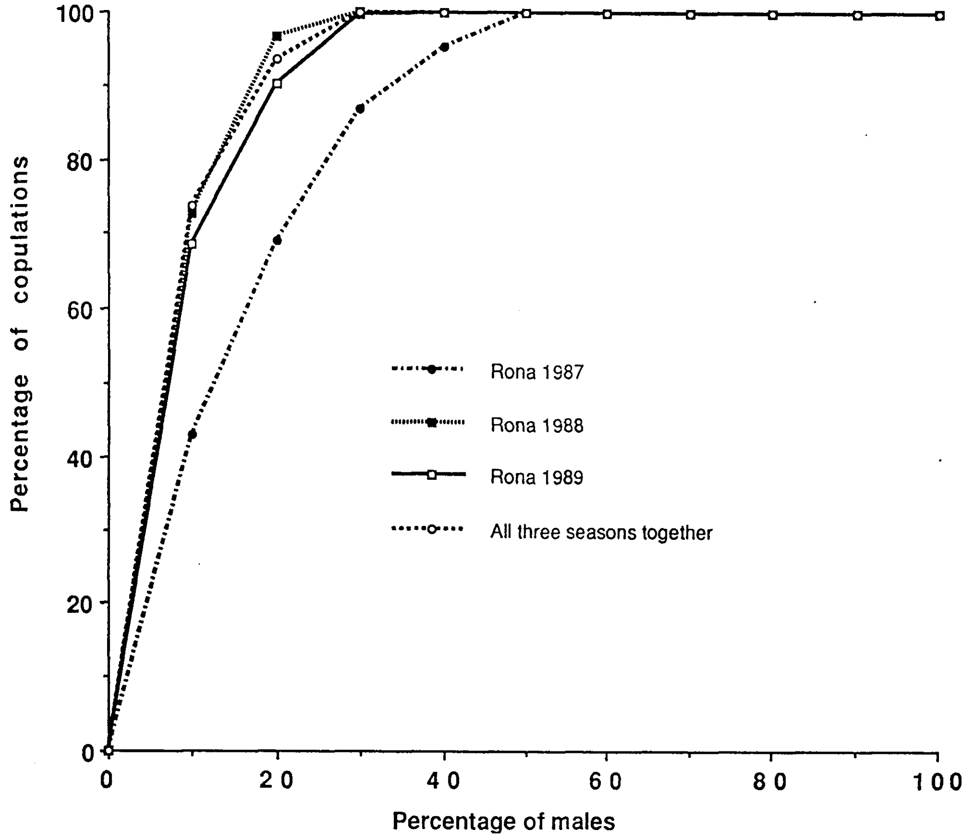
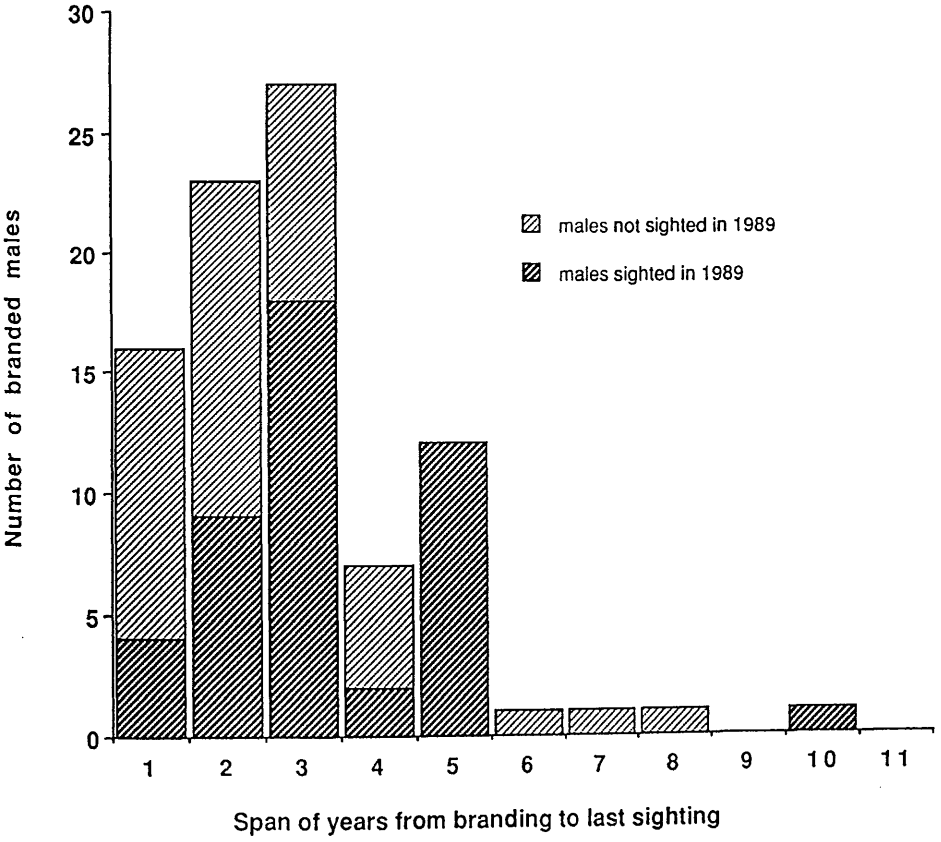


Figure 8.3 : Distribution of span of years from branding to last sighting



present in all three years. The corresponding Green's coefficient's were 0.034, 0.027 and 0.016 respectively.

In order to examine potential differences in mean mating success of males present for differing numbers of years, oneway analysis of variance (with Scheffe's Multiple Range test) was conducted upon the data presented in Table 8.1.2 (all data were transformed where appropriate, as described in Chapter 7). This analysis revealed highly significant differences between all three groups ($F_{2,272} = 147.20$, $p < 0.001$). Males present for only one year had a significantly lower mean total mating success than males present for either two or all three seasons. Males present for two seasons had a significantly lower total mating success than those that were present in all three years of the study.

Thus, the ability to return to the colony in successive seasons clearly confers an advantage in terms of total mating success gained. Further analyses in this chapter firstly examine more closely the nature of changes in mating success between seasons and then assess which factors are related to whether a male returns in the following season or not.

Tables 8.1.3 a and b depict the changes in the mating success of known individual males between seasons. An increase refers to males gaining more observed copulations in year B than year A, and a decrease refers to the opposite. Table 8.1.3 a shows the numbers of males that either increased or decreased in observed mating success between years and those that remained the same. These are also divided depending upon which years the males were present. Thus, in order to examine changes between 1987 and 1988, for example, the table shows changes, firstly, in males present only for these two years (absent in 1989) and secondly, the changes experienced from 1987 to 1988 amongst males that were present for all three seasons. Finally a total figure is given.

Table 8.1.3 b details the nature of changes only for those males present in all three seasons. This divides these males into every possible succession of changes in mating success over the three seasons.

Table 8.1.3 a

Table of details of changes between seasons in individual male mating success for males present in different combinations of only 2 breeding seasons and those present in all three years but showing only the changes between those years listed.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES IN EACH CATEGORY (%)		
	present for only 2 seasons	present for all 3 seasons	total
1.1987 AND 1988;			
INCREASE FROM '87 TO '88	1 (9.09)	8 (44.44)	9 (31.03)
DECREASE FROM '87 TO '88	9 (81.82)	3 (16.67)	12 (41.38)
SAME IN '87 AND '88	1 (9.09)	7 (38.89)	8 (27.59)
2.1988 AND 1989;			
INCREASE FROM '88 TO '89	7 (33.33)	8 (44.44)	15 (38.46)
DECREASE FROM '88 TO '89	2 (9.52)	9 (50.00)	11 (28.21)
SAME IN '88 AND '89	12 (57.14)	1 (5.56)	13 (33.33)
3.1987 AND 1989;			
INCREASE FROM '87 TO '89	2 (50.00)	10 (55.56)	12 (54.55)
DECREASE FROM '87 TO '89	2 (50.00)	4 (22.22)	6 (27.27)
SAME IN '87 AND '89	0	4 (22.22)	4 (18.18)

Table 8.1.3b

Table of details of changes between successive seasons in individual male mating success for males present in all three breeding seasons.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES (%)
DECREASE FROM '87 TO '88 & FROM '88 TO '89	1 (5.56)
INCREASE FROM '87 TO '88 & FROM '88 TO '89	2 (11.11)
INCREASE FROM '87 TO '88 BUT DECREASE FROM '88 TO '89	6 (33.33)
DECREASE FROM '87 TO '88 BUT INCREASE FROM '88 TO '89	2 (11.11)
SAME IN '87 & '88 BUT INCREASE FROM '88 TO '89	4 (22.22)
SAME IN '87 & '88 BUT DECREASE FROM '88 TO '89	2 (11.11)
SAME IN ALL THREE YEARS	1 (5.56)
INCREASE FROM '87 TO '88 BUT SAME IN '88 & '89	0
DECREASE FROM '87 TO '88 BUT SAME IN '88 & '89	0

Table 8.1.3 c shows the numbers of males present for differing combinations of years, whether present, for example, in only 1987, or both 1987 and 1988 etc. For each of these sub-groups the table shows their median, mean, standard error and range of observed copulations.

Tables 8.1.3 d and e depict information in the same format as Table 8.1.3 a and b respectively; however, these tables refer to changes between seasons in males' **rank order** of observed mating success. This is such that a male with a low rank value e.g. rank 1, has higher mating success than males with higher rank values for the year in question (in this example, rank 1 is the male with the most copulations). Thus, when discussing changes between seasons, an improvement in a male's relative mating success causes him to move up in the hierarchy, gaining a rank closer to one.

Table 8.1.3 f shows these ranks expressed in the same format as Table 8.1.3c, giving number of males, median and mean ranks for the subgroups of males present for differing combinations of years.

Table 8.1.3c

Table of summary statistics of observed individual male mating success for males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	35	0.00	1.17	1.60	0.27	0	5
1988 ONLY	67	0.00	0.22	1.00	0.12	0	7
1989 ONLY	96	0.00	0.35	1.37	0.14	0	12
1987 & '88;							
1987	11	4.00	3.55	2.29	0.69	0	7
1988	11	0.00	0.60	1.66	0.50	0	5
1988 & '89;							
1988	21	0.00	0.82	1.42	0.31	0	4
1989	21	1.00	1.52	2.15	0.47	0	9
1987 & '89							
1987	4	0.50	0.75	0.96	0.48	0	2
1989	4	1.00	4.50	7.68	3.84	0	16
ALL 3 YEARS;							
1987	18	1.50	2.56	3.10	0.73	0	11
1988	18	3.50	4.06	3.39	0.80	0	9
1989	18	5.00	3.83	3.01	0.71	0	9

Table 8.1.3d

Table of details of changes between seasons in individual males' **ranked** mating success for males present in different combinations of only 2 breeding seasons and those present in all three years but showing only the changes between those years listed.

NB: Decreased rank is defined as a decrease in rank status, i.e. individuals that decline in relative mating success. Increased rank refers to the opposite, i.e. males that improve their relative mating success.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES IN EACH CATEGORY (%) present for only 2 seasons	present for all 3 seasons	total
1.1987 AND 1988;			
INCREASE FROM '87 TO '88	2 (18.18)	12 (66.67)	14 (48.28)
DECREASE FROM '87 TO '88	9 (81.82)	6 (33.33)	15 (51.72)
SAME IN '87 AND '88	0	0	0
2.1988 AND 1989;			
INCREASE FROM '88 TO '89	7 (33.33)	6 (33.33)	13 (33.33)
DECREASE FROM '88 TO '89	14 (66.67)	11 (61.11)	25 (64.10)
SAME IN '88 AND '89	0	1 (5.56)	1 (2.56)
3.1987 AND 1989;			
INCREASE FROM '87 TO '89	2 (50.00)	7 (38.89)	9 (40.91)
DECREASE FROM '87 TO '89	2 (50.00)	11 (61.11)	13 (59.09)
SAME IN '87 AND '89	0	0	0

Table 8.1.3e

Table of details of changes between successive seasons in individual males' **ranked** mating success for males present in all three breeding seasons.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES (%)
DECREASE FROM '87 TO '88 & FROM '88 TO '89	3 (16.67)
INCREASE FROM '87 TO '88 & FROM '88 TO '89	3 (16.67)
INCREASE FROM '87 TO '88 BUT DECREASE FROM '88 TO '89	8 (44.44)
DECREASE FROM '87 TO '88 BUT INCREASE FROM '88 TO '89	3 (16.67)
SAME IN '87 & '88 BUT INCREASE FROM '88 TO '89	0
SAME IN '87 & '88 BUT DECREASE FROM '88 TO '89	0
SAME IN ALL THREE YEARS	0
INCREASE FROM '87 TO '88 BUT SAME IN '88 & '89	1 (5.56)
DECREASE FROM '87 TO '88 BUT SAME IN '88 & '89	0

Table 8.1.3f

Table of summary statistics of individual males' ranked mating success for males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	35	54.50	40.23	17.16	2.90	8.00	54.50
1988 ONLY	67	68.50	65.29	12.74	1.57	7.00	68.50
1989 ONLY	96	94.50	83.16	24.98	2.55	2.00	94.50
1987 & '88;							
1987	11	10.50	19.41	16.28	4.91	3.00	54.50
1988	11	68.50	59.09	21.23	6.40	9.00	68.50
1988 & '89;							
1988	21	68.50	56.76	21.58	4.71	14.50	68.50
1989	21	35.50	54.17	36.57	7.98	3.50	94.50
1987 & '89							
1987	4	44.50	42.38	14.42	7.21	26.00	54.50
1989	4	35.50	41.63	38.82	19.41	1.00	94.50
ALL 3 YEARS;							
1987	18	30.25	30.83	19.94	4.70	1.00	54.50
1988	18	12.75	23.44	25.71	6.06	1.00	68.50
1989	18	11.50	34.53	38.65	9.11	3.50	94.50

Tables 8.1.3 a and d show clearly that, of those males present in only 1987 and 1988, a vast majority (81.82 %) declined in both number of observed copulations and their rank status from 1987 to 1988, with very few enhancing their success or even remaining the same. Conversely, of those males present in all three years a majority gained either more or the same number of copulations in 1988 compared to 1987, and similarly, considerably more improved their rank (i.e. obtained relatively more matings) than declining in rank status.

In order to test the null hypothesis that there was no significant difference between males present in 1987 and 1988 only and males present in all three seasons in the tendency to either increase or decrease in relative mating success between 1987 and 1988, the data in Table 8.1.3a were tested with a chi squared analysis. To produce expected frequencies greater than 5 those males showing either an increase in mating success from 1987 to 1988 or remaining the same were combined. This resulted in only one degree of freedom thus, Yates' correction was applied. The results showed a significant difference from the expected values ($\text{chi}^2 = 10.83$, degrees of freedom = 1, $p = 0.001$). Therefore, of those males present in only in 1987 and 1988 more than expected declined in mating success whilst less than expected either increased in mating success or remained constant. Of those males present in all three seasons, more than expected showed either an increase or maintained the same mating success in 1988 as in 1987 and fewer than expected declined in success over this period.

Combining males present in 1987 and 1988 only with those present in all three seasons, the overall pattern of changes in mating success between 1987 and 1988, showed that most males experienced a reduction in observed mating success, the remainder being fairly evenly divided between increased success and attaining the same number of copulations. In terms of ranked mating success, approximately half the males improved their rank, whilst the remainder declined.

Examining the changes in mating success between the 1988 and 1989 seasons (Table 8.1.3 a), the vast majority those males present only in 1988 and 1989 either gained the same number of copulations in both years or increased. However, most of these declined in relative rank over the same period (Table 8.1.3 d). The changes in observed mating success (Table 8.1.3 a) over this period for males present in all three years was fairly evenly divided between those decreasing and those either increasing or remaining the same, though, again a majority of these were worse off in terms of rank in 1989 compared to 1988. Again, the null hypothesis, of no significant difference in the nature of changes in relative mating success from 1988 to 1989 between males present in 1988 and 1989 only and males present in all three seasons was tested using a chi-squared analysis, though in this instance there was no need to aggregate groups and hence apply Yates' correction. The results ($chi^2 = 13.67$, degrees of freedom = 2, $p < 0.001$) showed a significant departure from the expected values. In both males present for only 2 seasons and those present for all three seasons the numbers showing an increase from 1988 to 1989 were approximately as expected. However, of those present only in 1988 and 1989, fewer than expected showed a decline and more than expected remained the same from 1988 to 1989. The opposite was true of those males present in all three years, more than expected declining in mating success and less than expected remaining the same.

The total scores for this period, combining males present in 1988 and 1989 only with those present in all three seasons, reflect the patterns described above. Most males either gained the same success in 1988 and 1989 or increased their number of copulations, whilst a majority of the ranks declined from 1988 to 1989.

Only four males were present in 1987 and 1989 and absent in 1988. Of these two gained more copulations and an enhanced rank in 1989 compared to 1987 whilst the other two declined both in mating success and rank (Tables 8.1.3a and d). Of those males present in all three years most either increased in actual mating success or gained the same success in 1987 and 1989. However, a majority declined in rank status. There were too few cases to conduct statistical analyses on this group of males. The total scores showed a majority of males gaining either more or the same number of copulations in 1989 than 1987, though again a majority declined in rank.

Tables 8.1.3b and e examine the nature of changes in both number of observed copulations and rank for males present in all three years in more detail. These tables show a wide range in the nature of changes in success over the three seasons. However, both show that a majority of males tended to increase in mating success and improve their rank between 1987 and 1988 and then decline in both in 1989.

Tables 8.1.3c and f show that males present in only one year tended to have low median scores (and mean) for mating success and similarly low positions in the rank order of mating success (in fact, the lowest possible rank in each year). Those males present in only 1987 and 1988 had a very high median success in the first of these years, but this dropped to zero in 1988. Similarly, they had good median ranks in 1987 which declined markedly in 1988. Males present in only 1988 and 1989 showed the opposite pattern, having low median mating success in 1988 with a correspondingly poor rank position, but improve somewhat in both in 1989. For the few males present in only 1987 and 1989, there was a slight improvement overall in 1989, but with such a small sample size and very high variance in 1989 this is difficult to interpret. The males present in all three years showed high median values in all years for observed copulations and yet improved in median mating success in all consecutive years. A similar pattern was shown in the ranks of these males.

The data in Table 8.1.3c were entered into a oneway analysis of variance with Scheffe's Multiple Range tests to examine these potential differences in mean mating success between various groups of males. All sub-sets of data were transformed to approximate to normal distributions (see Chapter 7) prior to statistical analysis. Comparing the mating success of males present only in 1987 with those present only in 1988 and those present only in 1989 revealed that the 1987 only group had a significantly higher mean mating success than 1988 or 1989 ($F_{2,193} = 6.87$, $p = 0.013$). There was no significant difference between 1988 and 1989.

A comparison of the mating success of males present only in 1987 with the 1987 results for those males present in 1987 and 1988, those present in 1987 and 1989 and those present in all three years was made. This revealed that the observed mating success for 1987 of those males present in both 1987 and 1988 was slightly greater than the 1987 results for those present only in 1987 ($F_{3,64} = 4.24$, $p = 0.009$). No other significant differences between groups were found. On excluding those males present in 1987 and 1989 (where the sample size was only four individuals) from this analysis the same result was produced ($F_{2,61} = 5.56$, $p = 0.006$).

Comparing the results for 1988 between groups (those males present only in 1988, those present in 1987 and 1988, those present in 1988 and 1989 and those present in all three years), revealed that the 1988 mean mating success of males present in all three years was significantly greater than that of all the remaining groups ($F_{3,111} = 26.19$, $p < 0.0001$).

The same process was repeated to compare the 1989 mating success of those males present only in 1989, those present in 1988 and 1989, those present in 1987 and 1989 and those males present in all three years. Both these latter two groups were found to have a significantly higher mean mating success in 1989 than those males present in 1989 only but not those present in 1988 and 1989 ($F_{3,135} = 17.70$, $p < 0.0001$). Again, removing those males present in 1987 and 1989 from the analysis showed that the mean mating success in 1989 of those males present in all three years was significantly greater than the two remaining groups ($F_{2,132} = 29.37$, $p < 0.0001$). Also, those males present in 1988 and 1989 had a significantly greater mean 1989 mating success than those males present only in 1989.

A Wilcoxon matched-pairs signed-ranks test (2 tailed) was used to test the mean mating success in 1987 and 1988 for males present in only these two years. The mean success in 1987 was found to be significantly greater than in 1988 ($z = -2.60$, $n = 11$, $p = 0.0093$). The same process was applied to those males present only in 1988 and 1989. Here, there was no significant difference between the mean mating success in 1988 and 1989 for this group ($z = -1.72$, $n = 21$, $p = 0.086$). Similarly, no significant difference was found between the 1987 and 1989 mating success of males present in only these two years ($z = -0.37$, $n = 4$, $p = 0.715$), however, it must be noted that the sample size is particularly small.

To test between the mean mating success in each of the three years for males present in all three years, Wilcoxon matched-pairs tests were performed comparing all three combinations of the three seasons. No significant difference in mating success was found between any of the three seasons (1987-1988: $z = -1.51$, $p = 0.13$, 1988-1989: $z = -0.24$, $p = 0.81$, 1987-1989: $z = -1.29$, $p = 0.20$, $n = 18$ in all three tests).

8.2 Changes in colony attendance between seasons

Tables 8.2.1 a, b and c depict summary statistics for length of stay, arrival date and departure date respectively for males present in different combinations of years.

Statistical comparisons were made between various groups in Table 8.2.1 a utilising either oneway analysis of variance or Mann-Whitney U tests where appropriate. Again, all sub-sets of data were transformed to approximate to normal distributions, where appropriate, prior to statistical analyses. When comparing the lengths of stay in 1987 for males present only in 1987, males present in 1987 and 1988, males present in 1987 and 1989 and those present in all three years, it was found that the mean stay for males present in 1987 and 1988 was significantly longer than those present in 1987 only ($F_{3,64} = 4.65$, $p = 0.006$). This difference was maintained if those males present in 1987 and 1989 only (where $n = 4$) are excluded from the analysis ($F_{2,61} = 6.77$, $p = 0.002$).

The lengths of stay in 1988 for males present in all three years was significantly longer than all other groups present in 1988. Also, the 1988 stay for males present in 1988 and 1989 was significantly longer than those males present in 1988 only ($F_{3,113} = 24.62$, $p < 0.000$), but not significantly different to the 1988 stay for males present in 1987 and 1988.

In 1989, the lengths of stay for males present in all three years and those present in 1988 and 1989 were significantly longer than that for males present in 1989 only ($F_{3,135} = 27.78$, $p < 0.0001$). Again this difference was maintained if those males present in 1987 and 1989 ($n = 4$) were excluded ($F_{2,132} = 41.87$, $p < 0.0001$).

Comparison of the lengths of stay of males present in only one year revealed that the mean stay of the 1987 only group was significantly longer than for 1988 only or 1989 only ($F_{2,195} = 9.24$, $p < 0.001$).

The length of stay in 1987 for males present also in the following year (1988) was

Table 8.2.1a

Table of summary statistics of length of stay in days for males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	35	5.00	9.92	11.57	1.97	0.33	42.50
1988 ONLY	67	1.50	3.57	7.04	0.86	0.25	36.00
1989 ONLY	96	1.00	3.25	7.42	0.78	0.17	40.25
1987 & '88;							
1987	11	24.75	22.77	11.34	3.42	0.50	36.50
1988	11	1.33	5.86	7.54	2.27	0.34	22.00
1988 & '89;							
1988	21	5.50	14.72	15.92	3.48	0.25	54.00
1989	21	12.00	17.17	16.59	3.62	0.25	48.50
1987 & '89							
1987	4	16.00	13.25	8.01	4.00	1.50	19.50
1989	4	11.63	16.00	16.19	8.09	2.25	38.50
ALL 3 YEARS;							
1987	18	17.42	19.14	12.35	2.91	1.00	37.00
1988	18	31.50	27.30	16.30	3.84	3.00	54.00
1989	18	29.50	26.24	16.90	3.98	1.00	53.75

Table 8.2.1b

Table of summary statistics for arrival dates of males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	35	27.00	29.51	16.05	2.71	9.00	55.00
1988 ONLY	67	13.00	19.21	12.42	1.52	4.00	54.00
1989 ONLY	96	25.00	28.05	18.75	1.91	4.00	63.00
1987 & '88;							
1987	11	18.00	21.46	11.80	3.56	10.00	44.00
1988	11	15.00	21.82	14.79	4.46	4.00	41.00
1988 & '89;							
1988	21	17.00	19.91	12.99	2.83	4.00	49.00
1989	21	13.00	20.24	16.33	3.56	4.00	52.00
1987 & '89							
1987	4	23.00	23.25	2.99	1.49	20.00	27.00
1989	4	8.00	8.50	3.42	1.71	5.00	13.00
ALL 3 YEARS;							
1987	18	15.00	20.06	10.99	2.59	10.00	48.00
1988	18	10.50	17.11	14.94	3.52	1.02	53.00
1989	18	9.00	14.00	12.21	2.88	4.00	53.00

significantly longer than their length of stay in 1988 (Wilcoxon matched-pairs: z = -2.58, n = 11, p = 0.009). However, there was no significant difference in lengths of stay in 1988 and 1989 for males present in these two years only (Wilcoxon matched-pairs: z = -0.99, n = 21, p = 0.32) or between 1987 and 1989 for males present in these two years (Wilcoxon matched-pairs: z = -0.37, n = 4, p = 0.72). Also, as with mating success, no significant difference was found in the lengths of stay in any of the three years for males present in all three years (Wilcoxon matched-pairs tests: 1987-1988: z = -1.94, p = 0.053, 1988-1989: z = -0.11, p = 0.91, 1987-1989: z = -1.85, p = 0.064, n = 18 in all three tests).

The same statistical analyses were conducted for arrival date (Table 8.2.1b) as for length of stay. When comparing the arrival dates in 1987 for males present only in 1987, males present in 1987 and 1988, males present in 1987 and 1989 and those present in all three years it was found that there was no significant difference ($F_{3,64} = 2.26$, p = 0.090). Similarly, no difference was found if those males present in 1987 and 1989 (where n = 4) are excluded from the analysis ($F_{2,61} = 3.19$, p = 0.050).

The arrival dates in 1988 showed no significant difference between any groups of males present in 1988 ($F_{3,113} = 0.32$, p = 0.814).

In 1989, the arrival date for males present in 1989 only was significantly later than that for males present in all three years ($F_{3,135} = 5.01$, p = 0.003). Again this difference was maintained if those males present in 1987 and 1989 (n = 4) were excluded ($F_{2,132} = 5.67$, p = 0.004).

Comparison of the arrival dates of males present in only one year revealed that the mean arrival date of the 1989 only group was significantly later than for the 1988 only group ($F_{2,195} = 6.47$, p = 0.002).

The arrival dates in 1987 and 1988 for males present in these two years only showed no significant difference (Wilcoxon matched-pairs: z = -0.09, n = 11, p = 0.93). Similarly, there was no significant difference in arrival dates in 1988 and 1989 for males present in these two years only (Wilcoxon matched-pairs: z = -0.56, n = 21, p = 0.58) or between 1987 and 1989 for males present in these two years (Wilcoxon matched-pairs: z = -1.83, n = 4, p = 0.068). For males present in all three seasons, no significant difference was found between their arrival dates in 1987 and 1988 (Wilcoxon matched-pairs: $z = -1.37$, $n = 18$, $p = 0.17$), nor between 1988 and 1989 (Wilcoxon matched-pairs: $z = -0.97$, $n = 18$, $p = 0.33$). However, there was a significant difference between their 1987 and 1989 arrival dates (Wilcoxon matched-pairs: $z = -3.10$, $n = 18$, $p = 0.0019$). Thus, these males tended to arrive relatively later in 1987 than in 1989. This may be due to the later onset of observations in 1987 (see Chapter 2).

Again, statistical comparisons of data subsets for departure date (Table 8.2.1c) were conducted, utilising the same procedures as for arrival date. Upon comparing the departure dates in 1987 for males present only in 1987, males present in 1987 and 1988, males present in 1987 and 1989 and those present in all three years it was found that there was no significant difference ($F_{3,64} = 1.23$, $p = 0.031$) between groups. Similarly, no difference was found if those males present in 1987 and 1989 (where $n = 4$) are excluded from the analysis ($F_{2,61} = 1.82$, $p = 0.173$).

In 1988, departure date for males present in 1988 only was significantly earlier than either males present in 1988 and 1989 or those present in all three years ($F_{3,110} = 19.76$, $p < 0.0001$).

Similarly, during 1989, the departure date for males present in 1989 only was significantly earlier than that for males present in either 1988 and 1989 only or those present in all three years ($F_{3,135} = 5.66$, $p = 0.001$). However, this difference was not maintained if those males present in 1987 and 1989 ($n = 4$) were excluded ($F_{2,132} = 7.80$, $p = 0.010$).

When comparing the departure dates of males present in only one year, it was revealed that the mean departure date of the 1988 only group was significantly earlier than either the 1987 only or 1989 only groups ($F_{2,187} = 13.89$, $p = 0.000$).

There was no significant difference at $p < 0.01$ in mean departure dates in 1987 and 1988 for males present in these two years only (Wilcoxon matched-pairs: $z = -2.19$, $n = 10$, $p = 0.03$). Similarly, comparing departure dates in 1988 and 1989 for males present in these two years only, no significant difference was found (Wilcoxon matched-pairs: $z = -1.53$, $n = 20$, $p = 0.13$). Also, there was no significant difference in departure dates in

Table 8.2.1c

Table of summary statistics for departure date of males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	28	46.50	42.11	10.90	2.06	13.00	55.00
1988 ONLY	66	19.00	23.47	13.72	1.69	8.00	55.00
1989 ONLY	96	35.50	32.30	18.91	1.93	5.00	68.00
1987 & '88;							
1987	11	50.00	49.09	4.74	1.43	40.00	55.00
1988	10	36.00	33.80	16.22	5.13	11.00	57.00
1988 & '89;							
1988	20	45.50	39.30	15.60	3.49	5.00	60.00
1989	21	51.00	45.57	15.68	3.42	14.00	65.00
1987 & '89							
1987	4	43.50	42.75	10.72	5.36	29.00	55.00
1989	4	24.00	26.00	14.45	7.22	11.00	45.00
ALL 3 YEARS;							
1987	18	48.50	44.61	11.76	2.77	16.00	55.00
1988	18	53.50	49.56	10.56	2.49	24.00	60.00
1989	18	48.00	46.44	17.18	4.05	7.00	68.00

1987 and 1989 for males present in these two years (Wilcoxon matched-pairs: z = -1.83, n = 4, p = 0.068). Likewise, no significant difference was found in the departure dates between any of the three years for males present in all three years (Wilcoxon matched-pairs tests: 1987-1988: z = -1.52, p = 0.127, 1988-1989: z = -0.66, p = 0.508, 1987-1989: z = -0.76, p = 0.449, n = 18 in all three tests).

Tables 8.2.1d depicts the nature of changes in length of stay between successive years for different combinations of seasons. Males are divided into those present in only 2 seasons and those present in all three years. Tables 8.2.1e and f utilise the same format to show changes between years in arrival date and departure date respectively.

As with changes in mating success (section 8.1), null hypotheses were constructed, stating that there was no significant differences between males present for two seasons only and males present in all three seasons in their tendency either increase, decrease or maintain their length of stay/arrival date/departure date over the two seasons in question. These hypotheses were tested by chi square analyses.

When examining the data presented in Table 8.2 d (length of stay), it was found that analyses could not be conducted on data for group 3 (1987 and 1989) as there were too few cases to produce expected values of 5 or greater. In each of the remaining groups (1987 and 1988, 1988 and 1989) males showing the same length of stay were aggregated with those showing an increase in stay in order to gain sufficient expected values of at least 5. Thus, in each analysis Yates' correction was applied to the chi square test.

In group 1 (1987 and 1988) a significant deviation from expected was found (chi^2 = 9.9, degrees of freedom = 1, $p < 0.01$). Of the males present in only 2 seasons fewer than expected increased or maintained their length of stay from 1987 to 1988 whilst more than expected declined. The opposite pattern was true of those males present in all three years.

In group 2 (1988 and 1989) no significant difference was found between observed and expected values (chi^2 = 1.22, degrees of freedom = 1, $p > 0.01$).

Table 8.2.1d

Table of details of changes between seasons in length of stay in days for males present in different combinations of only 2 breeding seasons and those present in all three years but showing only the changes between those years listed.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES IN EACH CATEGORY (%) present for only 2 seasons	present for all 3 seasons	total
1.1987 AND 1988;			
INCREASE FROM '87 TO '88	1 (9.09)	12 (66.67)	13 (44.83)
DECREASE FROM '87 TO '88	9 (81.82)	4 (22.22)	13 (44.83)
SAME IN '87 AND '88	1 (9.09)	2 (11.11)	3 (10.35)
2.1988 AND 1989;			
INCREASE FROM '88 TO '89	11 (52.38)	7 (38.89)	18 (46.15)
DECREASE FROM '88 TO '89	7 (33.33)	9 (50.00)	16 (41.03)
SAME IN '88 AND '89	3 (14.29)	2 (11.11)	5 (12.82)
3.1987 AND 1989;			
INCREASE FROM '87 TO '89	2 (50.00)	12 (66.67)	14 (66.67)
DECREASE FROM '87 TO '89	2 (50.00)	5 (27.78)	7 (31.82)
SAME IN '87 AND '89	0	1 (5.56)	1 (4.55)

Table 8.2.1e

Table of details of changes between seasons in arrival date for males present in different combinations of only 2 breeding seasons and those present in all three years but showing only the changes between those years listed.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES IN EACH CATEGORY (%) present for only 2 seasons	present for all 3 seasons	total
1.1987 AND 1988;			
INCREASE FROM '87 TO '88	5 (45.45)	6 (33.33)	11 (37.93)
DECREASE FROM '87 TO '88	6 (54.55)	12 (66.67)	18 (62.07)
SAME IN '87 AND '88	0	0	0
2.1988 AND 1989;			
INCREASE FROM '88 TO '89	7 (33.33)	5 (27.78)	12 (30.77)
DECREASE FROM '88 TO '89	13 (61.91)	12 (66.67)	25 (64.10)
SAME IN '88 AND '89	1 (4.76)	1 (5.56)	2 (5.13)
3.1987 AND 1989;			
INCREASE FROM '87 TO '89	0	2 (11.11)	2 (9.09)
DECREASE FROM '87 TO '89	4 (100.00)	15 (83.33)	19 (86.36)
SAME IN '87 AND '89	0	1 (5.56)	1 (4.55)

Table 8.2.1f
Table of details of changes between seasons in departure date for males present in different combinations of only 2 breeding seasons and those present in all three years but showing only the changes between those years listed.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES IN EACH CATEGORY (%)		
	present for only 2 seasons	present for all 3 seasons	total
1.1987 AND 1988;			
INCREASE FROM '87 TO '88	3 (30.00)	12 (66.67)	15 (53.57)
DECREASE FROM '87 TO '88	7 (70.00)	6 (33.33)	13 (46.43)
SAME IN '87 AND '88	0	0	0
2.1988 AND 1989;			
INCREASE FROM '88 TO '89	13 (65.00)	7 (38.89)	20 (52.63)
DECREASE FROM '88 TO '89	6 (30.00)	10 (55.56)	16 (42.11)
SAME IN '88 AND '89	1 (5.00)	1 (5.56)	2 (5.26)
3.1987 AND 1989;			
INCREASE FROM '87 TO '89	0	11 (61.11)	11 (50.00)
DECREASE FROM '87 TO '89	4 (100.00)	6 (33.33)	10 (45.45)
SAME IN '87 AND '89	0	1 (5.56)	1 (4.55)

In order to tests the null hypothesis developed for arrival date (see above), chi square analyses were conducted on the data presented in Table 8.2.1 e. As for length of stay, analyses could not be conducted on data for group 3 (1987 and 1989) as there were too few cases to produce expected values of 5 or greater. Similarly, in each of the remaining groups (1987 and 1988, 1988 and 1989) males showing the same arrival date in the two seasons were aggregated with those showing an increased (later) arrival date in order to gain sufficient expected values of at least 5. Thus, in each analysis Yates' correction was applied.

No significant difference between observed and expected values were found for either group 1, 1987 and 1989 ($chi^2 = 0.56$, degrees of freedom = 1, $p > 0.01$) or group 2, 1988 and 1989 ($chi^2 = 0.21$, degrees of freedom = 1, $p > 0.01$).

Again, chi square analyses were conducted on the data presented in Table 8.2.1 f to test the null hypothesis for departure date (see above). As in the case of arrival date, and for the same reason, analyses could not be conducted on data for group 3 (1987 and 1989). Again, for the remaining groups (1987 and 1988, 1988 and 1989), males showing the same departure date in both seasons were aggregated with those showing an increased (later) departure date in order to gain sufficient expected values of at least 5. Again, Yates' correction was applied in each analysis.

As with arrival date, no significant difference between observed and expected values were found for either group 1, 1987 and 1989 ($chi^2 = 3.62$, degrees of freedom = 1, $p > 0.01$) or group 2, 1988 and 1989 ($chi^2 = 2.64$, degrees of freedom = 1, $p > 0.01$).

Tables 8.2.1 g, h and i give further details of the nature of changes in length of stay, arrival and departure date respectively for males present in all three seasons.

Table 8.2.1g

Table of details of changes between successive seasons in length of stay in days for males present in all three breeding seasons.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES
DECREASE FROM '87 TO '88 & FROM '88 TO '89	0
INCREASE FROM '87 TO '88 & FROM '88 TO '89	3 (16.67)
INCREASE FROM '87 TO '88 BUT DECREASE FROM '88 TO '89	8 (44.44)
DECREASE FROM '87 TO '88 BUT INCREASE FROM '88 TO '89	3 (16.67)
SAME IN '87 & '88 BUT INCREASE FROM '88 TO '89	1 (5.56)
SAME IN '87 & '88 BUT DECREASE FROM '88 TO '89	1 (5.56)
SAME IN ALL THREE YEARS	0
INCREASE FROM '87 TO '88 BUT SAME IN '88 & '89	1 (5.56)
DECREASE FROM '87 TO '88 BUT SAME IN '88 & '89	1 (5.56)

Table 8.2.1h

Table of details of changes between successive seasons in arrival date for males present in all three breeding seasons.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES
DECREASE FROM '87 TO '88 & FROM '88 TO '89	6 (33.33)
INCREASE FROM '87 TO '88 & FROM '88 TO '89	0
INCREASE FROM '87 TO '88 BUT DECREASE FROM '88 TO '89	6 (33.33)
DECREASE FROM '87 TO '88 BUT INCREASE FROM '88 TO '89	5 (27.78)
SAME IN '87 & '88 BUT INCREASE FROM '88 TO '89	0
SAME IN '87 & '88 BUT DECREASE FROM '88 TO '89	0
SAME IN ALL THREE YEARS	0
INCREASE FROM '87 TO '88 BUT SAME IN '88 & '89	0
DECREASE FROM '87 TO '88 BUT SAME IN '88 & '89	1 (5.56)

Table 8.2.1i

Table of details of changes between successive seasons in departure date for males present in all three breeding seasons.

NATURE OF CHANGE IN VARIABLE BETWEEN YEARS	NUMBER OF MALES
DECREASE FROM '87 TO '88 & FROM '88 TO '89	3 (16.67)
INCREASE FROM '87 TO '88 & FROM '88 TO '89	4 (22.22)
INCREASE FROM '87 TO '88 BUT DECREASE FROM '88 TO '89	7 (38.89)
DECREASE FROM '87 TO '88 BUT INCREASE FROM '88 TO '89	3 (16.67)
SAME IN '87 & '88 BUT INCREASE FROM '88 TO '89	0
SAME IN '87 & '88 BUT DECREASE FROM '88 TO '89	0
SAME IN ALL THREE YEARS	0
INCREASE FROM '87 TO '88 BUT SAME IN '88 & '89	1 (5.56)
DECREASE FROM '87 TO '88 BUT SAME IN '88 & '89	0

8.3. Changes in weight parameters and age

Table 8.3.1a presents summary statistics for estimated arrival weight (see Chapter 5 and 7) of males present in differing combinations of years. As can be seen from Table 8.3.1a the sample sizes in all groups of males are rather small. A similar table was constructed for all other weight parameters i.e. weight on day one, departure weight, total percentage weight loss, absolute and proportional rate of weight loss and also age. These tables are not presented here, but for all weight parameters the sample sizes were the same as those in Table 8.3.1 a.

As with the behavioural parameters already examined in sections 8.1 and 8.2, the weight parameters were examined for differences in mean values between the sub-groups of males presented in Table 8.1.3 a. Statistical analyses were conducted on these data using oneway analyses of variance (with Scheffe's Multiple Range tests), Wilcoxon matched-pairs tests and Mann-Whitney U tests where appropriate. All sub-sets of data were examined for conformity to normal distribution prior to statistical analyses, those failing to do so were transformed as detailed in Chapter 7. Some groups could not be used in these analyses due to particularly low sample sizes, and all of these analyses must be viewed with caution because of the sample sizes. Upon comparison of the mean values for 1987 of males present only in 1987, males present in 1987 and 1988, males present in 1987 and 1989 and those present in all three years, it was found that there was no significant difference between the values for any of the weight parameters (using oneway analyses of variance).

Similarly, each weight parameter showed no significant difference in their mean values when comparing the 1988 values for males present in 1988 only, males present in 1988 and 1989 and those present in all three years (oneway analyses of variance).

Again, when comparing the mean values for 1989 of those males present in 1989 only, those present in 1988 and 1989 and those present in all three seasons, there was no significant differences between the mean values for any of the weight parameters (oneway analyses of variance).

Table 8.3.1 a

Table of summary statistics for arrival weight of males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	6	243.14	253.29	24.45	9.98	234.52	297.67
1988 ONLY	2	275.37	275.37	73.47	51.95	223.42	327.32
1989 ONLY	4	248.57	248.01	50.35	25.17	200.20	294.70
1987 & '88;							
1987	4	258.71	258.82	24.20	12.10	232.34	285.50
1988	0						
1988 & '89;							
1988	6	248.58	247.15	38.61	15.76	191.00	295.60
1989	6	232.47	233.60	18.68	7.63	208.84	260.98
1987 & '89							
1987	1		275.12				
1989	1		282.00				
ALL 3 YEARS;							
1987	8	252.84	254.87	18.29	6.47	228.43	278.50
1988	13	259.66	264.89	45.69	12.67	161.80	317.09
1989	7	256.90	258.03	31.54	11.92	198.36	293.81

A comparison of the mean values of those males present in 1987 only, those present in 1988 only and those present in 1989 only again revealed no significant difference in the mean values of any of the weight parameters (oneway analyses of variance).

For comparisons of the weight parameters between years of males present in 2 of the three seasons, Mann-Whitney U tests were performed. This was due to the fact that very few, or none, of the males weighed in the first season were also weighed in the second season. Thus, pairwise tests (Wilcoxon matched-pairs) could not be used. No comparison of the 1987 and 1988 weights of males present in these two seasons only could be made, as none of the 4 males weighed in 1987 were weighed in 1988. Using Mann-Whitney U tests, the mean values for 1988 and 1989 of those males present only in these two seasons were compared. Again, no significant difference was found in any of the weight parameters.

When comparing the mean values for each of the three seasons for males present in all three years, both oneway analysis of variance and Wilcoxon matched-pairs tests were performed. As the identities of those males weighed in each of the three seasons varied, the sample sizes in the pairwise tests were reduced (1987-1988: $n = 7$, 1988-1989: $n = 7$, 1987-1989: $n = 4$). Thus, a oneway analysis of variance was also conducted as this included all males weighed in each of the three seasons. In none of these tests were any significant differences found between the three seasons in any of the weight parameters.

All these tests showed no significant differences even at $p < 0.05$ level. Comparisons between other groups shown in Table 8.3a were not possible due to small or zero sample sizes.

Thus, with the limited data, it was not possible to discern any significant differences in any of the weight parameters between groups of males present for differing combinations of seasons. Whether this is merely due to the limited sample sizes cannot be said.

8.4. Changes in dominance score

Table 8.4.1 presents summary statistics for dominance score of males classified by their yearly attendance patterns.

In order to examine potential differences in the mean dominance scores (Table 8.4.1 a) for males present in different combinations of years the same statistical analyses were conducted as the previous data sets, again utilising either oneway analyses of variance with Scheffe's Multiple Range tests or Mann-Whitney U tests. As stated in Chapter 3 and 7, it must be noted that a lower dominance score indicates a more dominant individual.

When comparing the dominance scores in 1987 for males present only in 1987, males present in 1987 and 1988, males present in 1987 and 1989 and those present in all three years it was found that there was no significant difference ($F_{3,64} = 2.34$, $p = 0.083$). Similarly, no difference was found if those males present in 1987 and 1989 (where n is particularly small i.e 4) are excluded from the analysis ($F_{2,61} = 3.39$, $p = 0.04$).

The mean dominance score in 1988 of males present in all three seasons showed a significantly lower value for than those present in 1988 only, but was not significantly different to the mean values for males present in 1987 and 1988 nor those present in 1988 and 1989 ($F_{3,78} = 5.90$, $p = 0.001$).

In 1989, the dominance score showed no significant difference between males present in 1989 only, males present in either 1988 and 1989 or those present in all three years ($F_{3,85} = 2.75$, $p = 0.048$). However, if those males present in 1987 and 1989 ($n = 4$) were excluded, the analysis shows that at $p < 0.05$ but not $p < 0.01$, the mean 1989 dominance score for males present in all three years was significantly lower than that of males present in 1989 only ($F_{2,82} = 3.94$, $p = 0.023$).

Comparison of the dominance scores of males present in only one year (i.e. males present in 1987 only, 1988 only and 1989 only) revealed no significant differences in the mean dominance score of these three groups ($F_{2,124} = 0.09$, $p = 0.917$).

When comparing the mean dominance scores in 1987 and 1988 for males present in these two years only, there was no significant difference in their dominance scores (Wilcoxon matched-pairs: $z = -1.54$, $n = 8$, $p = 0.124$). Similarly, there was no significant

Table 8.4.1

Table of summary statistics for dominance score of males present in different combinations of breeding seasons.

YEAR(S) PRESENT	n	median	mean	standard deviation	standard error	min.	max.
1987 ONLY	35	4.91	4.56	1.27	0.22	2.33	6.64
1988 ONLY	40	4.97	4.77	1.16	0.18	2.50	7.00
1989 ONLY	48	4.63	4.60	1.00	0.14	2.34	6.25
1987 & '88;							
1987	11	3.71	3.75	0.85	0.26	1.75	4.50
1988	8	4.99	4.87	1.10	0.39	2.55	6.38
1988 & '89;							
1988	17	5.00	4.67	1.16	0.28	2.70	6.67
1989	19	4.00	4.06	1.02	0.23	2.00	5.50
1987 & '89							
1987	4	4.39	4.42	1.03	0.52	3.24	5.65
1989	4	3.60	3.99	1.14	0.57	3.13	5.65
ALL 3 YEARS;							
1987	18	3.83	3.82	1.14	0.27	2.17	5.94
1988	17	3.25	3.51	0.96	0.23	2.49	6.00
1989	18	3.48	3.89	1.14	0.27	2.72	7.00

difference in mean dominance scores in 1988 and 1989 for males present in these two years only (Wilcoxon matched-pairs: z = -2.17, n = 16, p = 0.030) nor between 1987 and 1989 for males present only in these seasons (Wilcoxon matched-pairs: z = -1.10, n = 4, p = 0.273).

Finally, comparison of the mean dominance scores in each of the three years for males present in all three seasons revealed no significant difference between any of the years (Wilcoxon matched-pairs tests: 1987-1988: z = -0.69, n = 17, p = 0.493, 1988-1989: z = -1.59, n = 17, p = 0.113, 1987-1989: z = -0.07, n = 18, p = 0.948).

8.5. Differences between males that return and those that do not

The analyses presented so far merely describe in detail the nature of changes in the various parameters examined between seasons. It is evident that the changes in length of stay most accurately mirror the changes in mating success. However, as length of stay is the main correlate of mating success, this is not entirely unexpected.

Relatively few males return in successive seasons, and even fewer were present for the entire three years of the study. Thus it appears that the number of years a male gains on the colony can exert a strong influence upon his lifetime mating success. The variables collected will now be examined in order to examine potential factors which may determine whether a male returns in the following seasons or does not return.

The males were divided into two groups, those males which returned in the following breeding season (group 1) and those that did not return in the following season (group 2). Comparative analyses were then conducted upon data for the year prior to returning (group 1) or not returning (group 2). Thus, data for group one males included the 1987 data of males present in 1987 and 1988 but absent in 1989, the 1988 data of males present in 1988 and 1989 but absent in 1987, and both the 1987 and 1988 data of males present in all three seasons. Data for group 2 males consisted of the 1987 data from males present only in 1987, the 1988 data from males present only in 1988, the 1988 data of males present in 1987 and 1988 but absent in 1989 and the 1987 data for males present in 1987 and 1989, but absent in 1988. Obviously, 1989 data could not be included as we have no knowledge as to whether these males returned the following season or not.

The summary statistics for group 1 males are presented in Table 8.5.1 a and those for group 2 males in Table 8.5.1 b. For all behavioural parameters only males involved in at least 10 inter-male aggressive encounters were selected as in previous statistical analyses (see Chapter 3 and Chapter 7). This is in fact a more conservative comparison of the two groups, as a vast majority of males involved in less than 10 inter-male aggressive encounters belonged to group 2, by excluding these males the mean values for group 2 are brought closer to those of group 1.

These two data sets (shown in Tables 8.5.1 a and b) were then compared by means of Mann-Whitney U tests, the results are given in Table 8.5.2.

Those males which returned in the following year (group 1) were males which in the previous year stayed ashore for significantly longer. However, these males did not necessarily arrive at the study site earlier than group 2 males (at $p < 0.01$), but did depart significantly later. Group 1 males attained significantly higher total mating success, most probably due to the longer stay (see Chapter 7). However, there was no significant difference in the daily copulation rates of the two groups.

Examining the weight parameters, it is revealed that there is no significant difference in the initial weights (either weight on day one or arrival weight) of males that returned in the next season (group 1) and those that failed to return (group 2). However, group 1 males did have significantly lower departure weights. Again, this is most likely a function of the longer stays of these males. Accordingly, the total percentage weight loss of group one males was significantly greater than that of group 2 males, though only at $p < 0.05$ and not at $p < 0.01$.

Perhaps the most interesting feature of the weight parameters is the lack of significant difference in daily rate of weight loss between the two groups. Thus, males failing to return in the following season are not necessarily those with higher rates of energy expenditure in the previous season. In fact, the results for proportional rate of weight loss indicates a trend in the opposite direction. Group 1 males tend to have a greater proportional rate of weight loss than group 2 males (significant at $p < 0.05$, but

Table 8.5.1 a
Table showing summary statistics for all variables for **group 1 males.**

VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
LENGTH OF STAY (DAYS)	51	26.00	24.63	12.81	1.79	2.25	54.00
ARRIVAL DATE	51	14.00	17.39	10.48	1.47	1.00	40.00
DEPARTURE DATE	51	50.00	47.31	10.34	1.45	16.00	60.00
MATING SUCCESS	51	3.00	3.31	2.96	0.41	0	11
COPULATIONS/DAY	51	0.10	0.12	0.09	0.01	0.00	0.33
Wt. ON DAY ONE	31	295.66	285.91	35.35	6.35	187.54	336.76
ARRIVAL Wt (a)	31	254.40	258.01	35.60	6.39	161.80	317.09
DEPARTURE Wt (b)	31	172.87	173.30	22.36	4.02	111.70	208.90
(b/a) x 100	31	68.52	67.98	9.97	1.79	44.96	91.91
RATE OF Wt LOSS	31	-2.06	-2.07	0.62	0.11	-0.56	-3.08
SPECIFIC Wt LOSS	31	1.03	1.02	0.29	0.05	0.26	1.55
TOTAL No. A.I.s	51	38.00	46.55	28.96	4.06	10	118
A.I.s PER DAY	51	1.89	2.37	2.33	0.33	0.60	13.09
DOMINANCE SCORE	51	3.61	3.77	0.98	0.14	2.17	5.94
AGE	38	11.00	11.32	2.62	0.43	7	17

Table 8.5.1 b

Table showing summary statistics for all variables for **group 2 males.**

VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
LENGTH OF STAY (DAYS)	35	7.67	12.46	11.51	1.95	0.50	42.50
ARRIVAL DATE	35	20.00	22.66	11.12	1.88	8.00	47.00
DEPARTURE DATE	35	43.00	40.06	13.04	2.20	12.00	57.00
MATING SUCCESS	35	1.00	1.51	1.90	0.32	0	7
COPULATIONS/DAY	35	0.06	0.11	0.14	0.02	0.00	0.50
Wt. ON DAY ONE	10	287.19	302.17	42.99	13.59	259.33	399.75
ARRIVAL Wt (a)	10	255.75	273.42	51.73	16.36	223.42	388.55
DEPARTURE Wt (b)	10	191.62	206.36	37.84	11.97	173.50	288.46
(b/a) x 100	10	75.76	75.83	6.90	2.18	66.09	88.13
RATE OF Wt LOSS	10	-1.81	-1.93	0.41	0.12	-1.11	-2.80
SPECIFIC Wt LOSS	10	0.88	0.83	0.19	0.06	0.36	1.03
TOTAL No. A.I.s	35	22.00	28.57	21.07	3.56	10	92
A.I.s PER DAY	35	2.69	4.46	4.83	0.82	0.61	24.09
DOMINANCE SCORE	35	4.45	4.27	1.10	0.19	2.49	6.14
AGE	6	16.50	16.33	4.18	1.71	11.0	21.0

not at $p < 0.01$). Thus, it appears that males incurring relatively higher energetic costs are those that are more likely to return.

Group 1 males experience significantly more aggressive interactions in total, again due to the longer stays of these males. However, these males in fact have significantly lower daily rates of aggression than group 2 males.

Group 1 males have a significantly different mean dominance score to group 2 males (at $p < 0.05$), with group 1 males having lower (i.e. more dominant) scores on average. Thus, more dominant males tend to be those males that return in the following season.

Finally, the average age of group 1 males is significantly lower than that of group 2 males. Thus, it appears that older males tend not to return in the following year.

Table 8.5.2

Table showing results of Mann-Whitney U tests comparing mean values for group 1 and group 2 males.

VARIABLE	U	W	z	p
LENGTH OF STAY (DAYS)	418.5	1048.5	-4.17	0.0001
ARRIVAL DATE	650.5	1764.5	-2.13	0.0331
DEPARTURE DATE	577.5	1207.5	-2.77	0.0056
MATING SUCCESS	561.0	1191.0	-2.97	0.0030
COPULATIONS/DAY	734.5	1364.5	-1.41	0.1583
Wt. ON DAY ONE	132.0	233.0	-0.70	0.4850
ARRIVAL Wt (a)	144.0	221.0	-0.33	0.7384
DEPARTURE Wt (b)	66.5	298.5	-2.69	0.0072
(b/a) x 100	82.0	283.0	-2.22	0.0267
RATE OF Wt LOSS	148.5	301.5	-1.02	0.3099
SPECIFIC Wt LOSS	88.5	143.5	-2.02	0.0434
TOTAL No. A.I.s	530.5	1160.5	-3.18	0.0015
A.I.s PER DAY	556.0	1859.0	-2.96	0.0031
DOMINANCE SCORE	653.0	1762.0	-2.10	0.0353
AGE	37.0	212.0	-2.65	0.0080

8.6. Estimation of the number of breeding seasons for which individual males were present

Using all available brand sighting information in conjunction with data gathered during the course of this study, estimates of the number of years for which individual males were present on North Rona during the breeding season were made.

These estimates can be taken only as minimum values and must be viewed with considerable caution for various reasons. Both the numbers of males branded in each season (see Chapter 2) and the observation regimes varied considerably from year to year. Brand sightings were made throughout much of the breeding seasons of 1980 and 1981 (Anderson and Fedak 1985), and observers were present on the island for only a brief period in 1982. No observations were made in 1983 and 1984, though observers were present for much of the 1985 and 1986 seasons (pers. comm. S. Anderson and P. Pomeroy). Extensive observations were conducted during 1987, 1988 and 1989, the years of this study. Even in seasons where extensive observations were made, it was still possible that individuals were present and yet not sighted.

A further problem is that it is impossible to say whether males were present on the colony prior to being branded (with the exception of unbranded males identified in the study area during the course of this study), and whether any returned in seasons after 1989. Thus, it is impossible to accurately assess the number of seasons for which each branded male was present.

Also, those males that are caught and branded tend to be the more centrally located males and those that tolerate disturbance. These are often males that hold positions within groups of females, and are therefore, reluctant to depart. Itinerant males tend to flee more readily, and are rarely caught and branded. Thus, the sample of branded males may be somewhat biased towards the more successful males. These males are those that are more likely to return in successive seasons (see section 8.5 above).

Despite these problems, it is possible to derive a rough estimate of the minimum number of seasons for which individual males were present in the breeding colony. This estimate is based on the assumption that males generally do not "opt" out of a year (i.e.

present in year 1, are absent in year 2 but return in year 3 - see Chapter 4 and this chapter), but are active from the year of their first arrival at the colony to their last appearance. The data presented in this thesis suggest that this is the case, with only 4 individuals being present in 1987 and 1989, but absent in 1988 (see Chapter 4). Thus, the estimate is in fact the number of years from the first sighting of the male (when he was branded) to the last sighting. Figure 8.2 depicts the distribution of the span of years between which individual males were sighted on North Rona, and shows those individuals which were sighted in 1989 (i.e. males that have the potential to return in the following season, 1990, based on the assumption that males do not "opt" out as described above).

Bearing in mind the considerations alluded to above, Figure 8.3 shows that the estimate of years present ranges from 1 to at least 10 seasons. The mean estimate is 2.94 (SE = 0.17, n = 89), effectively 3 seasons. The vast majority of the males (74.2 %) have estimates of 3 seasons or less. However, of these males, approximately half (47.0 %) were still present in 1989. Of the remaining 23 (25.8 %) of all 89 males with estimates greater than 3 seasons, 15 (65.2 %) were present in 1989. Of the 4 males with the longest estimates (6 or more seasons), only one was present in 1989. This male was branded in 1980, he has been one of the study area males throughout this study (male identity code 001, brand X0) and has the longest estimate - 10 seasons. Male 001 was the only male in this study to have been in the top 10 males in terms of mating success in all three study seasons (Table 8.1.1) and has the highest summated value for total number of observed copulations (see Figure 8.1).

DISCUSSION

From the data on sightings of branded males, the range of estimated minimum number of years for which males are present on the breeding colony extends from only one season to at least 10 consecutive years. Despite this large range, few males had estimates of over 5 seasons, with the majority of individuals having estimates of only 1, 2 or 3 seasons. Although these estimates must be viewed with extreme caution (for reasons detailed above), it appears that there is not only considerable variation in the ability of individuals to gain matings within each season and in successive seasons, but also in the number of breeding seasons each male attends.

Clearly, and not unexpectedly, males which return to the study site in more seasons tend to gain more copulations. Males present for two seasons gain more copulations than those present for only one, and males present in all three years do even better on average. Thus, in addition to the fact that only a few males are able to monopolise a disproportionate amount of the observed copulations in any given year, the differing abilities of individuals to either enhance or maintain their success, or lack of, in successive years, may contribute further to the variation in male mating success. Whether this is so seems unclear from the measures of variation used. Both the variance and standardised variance for the summated total mating success distribution (Figure 8.1) do indicate greater variation in individual mating success when all three season's data are combined compared to examining each year separately. However, the Green's coefficient (which accounts for sample size) indicates that the summated mating success distribution is less aggregated than those for 1988 and 1989 separately, though not 1987 (the relatively low coefficient for 1987 is most probabaly due to the late onset of observations in this season - see Chapter 6). When plotted as the cumulative percentage of copulations accounted for by each successive 10 % of males (see Chapter 6), there is no significant difference between the summated mating success curve and those for each season separately. Thus, whether the effect of individual ability to maintain high mating success in successive years increases the variation in male mating success in the long term remains unclear. However, it is interesting that both the standardised variances and Green's coefficients for the distributions of summated mating success for males present in only 1 season, males present in 2 seasons and males present in all three seasons (see Table 8.1.2) show a marked decline from the former to the latter group. Thus, it appears that the relative variation in male mating success declines as the number of seasons that a group of males is present for, increases. A longer time series (i.e. several consecutive seasons) of similar observations are required in order to make predictions about individual variation in male lifetime mating, and perhaps reproductive, success.

Male 001 was undoubtedly the most successful of the identified individuals during the course of this study. Not only was he present in all three seasons of this study, but was branded in 1980 and has been sighted whenever observers have been present on North Rona during the breeding season. He was the only male in this study to have been in the top 10 males in terms of mating success in all three study seasons of this study and has the highest summated value for total number of observed copulations (25 observed copulations).

It must be noted that, although males that return in successive seasons generally gain greater overall (summated) mating success, there are exceptions to this rule. For example, male 028 was present in all three seasons of this study and yet failed to gain any observed copulations. Conversely, one of the more successful males was present in the study area only in 1989 (male 225). However, this male was identified solely by his pelage pattern. Therefore, whilst 1989 was his first appearance in the study site during the course of this study, it is possible that he was present elsewhere in the North Rona breeding colony in previous seasons.

Examining the changes in mating success between 1987 and 1988 reveals that this declined between years in the majority of those males only present for these two years. The changes in relative rank order of mating success also reflect this pattern. These males are then absent in 1989. It may be that due to their declining performance they "opt" out of the 1989 season, deferring efforts for some future year or move elsewhere. This latter case seems improbable as movements of branded males within the colony on Rona is very limited (see Chapter 4) and no sightings of these individuals have been recorded at other breeding colonies. Alternatively, and more probably, the decline in success from 1987 to 1988 may reflect some decline in, for example, dominance status, or other potential determinant of success, a decline which continues such that in 1989 they are unable to even gain a position on the colony. In fact, the changes in length of stay do mirror the changes in mating success, as would be expected from the results presented in Chapter 7. Conversely, of those males present in all three years a majority enhance their success or at least maintain their success from 1987 to 1988. These males, similarly may either "opt" to compete again in 1989, or simply be able to do so. From 1988 to 1989, of those males present only in these two years most enhance or maintain success. Again, this is reflected in the mean and median values in the changes in rank. In the case of these males it would appear that in 1988 they attained a high enough "standard" in whatever determinant is important, to establish a position on the colony and make further improvements in 1989. Of those males present for all three years, half continue to improve or maintain success, whilst the remainder decline. However, for these males the average values continue to increase from year to year.

Thus, in general, the pattern of changes in individual male mating success generally indicate an increase in success for males present in 1988 and 1989. It appears that males absent in 1987 achieve a certain degree of success in their first year ashore, but generally continue to enhance this success in the following season. Conversely, males present in 1987 and 1988, but absent in 1989, generally show declining fortunes over the two years. The predominant form of changes in mating success for males present in all three seasons show an increase followed by a decrease in success. The fact that very few males were present in 1987 and 1989 and absent in 1988 suggests that the idea that males may "opt" out of a year is improbable or at least rare. It would appear that most males gain positions on the colony for a period of successive years, if any at all, ranging from just one season to at least 10 seasons. Thus, it appears that most males may be active for a severely limited number of years, during this period each male increases to a peak success, of varying magnitude, then declines until he fails to gain a position on the colony.

As stated above, the patterns of changes in length of stay reflected closely those of mating success. However, those of arrival date bore little resemblance, with very few significant differences between the various categories of males. The nature of inter-seasonal changes in departure date showed some similarities to those of mating success, though they still displayed some incongruities. Likewise, the dominance score exhibited some parallel changes to those of mating success, though again disparities were evident. However, it must be noted that inter-seasonal comparisons of the dominance score may not be appropriate. As the dominance is calculated from the outcome of inter-male aggressive interactions, an individual's actual score may be comparable with those of other males within a season, but not between successive seasons. The relative ranked position of an individual's dominance score would perhaps be a better means of comparing inter-seasonal changes in relative dominance. The weight parameters and age showed no significant differences between the various categories of males in any of the analyses presented in this chapter.

These patterns of inter-seasonal changes are as would be predicted from the flow diagram presented in Chapter 7. With length of stay being the main correlate of mating success, it is not surprising that the inter-seasonal changes in length of stay follows those of mating success most closely.

A fundamental problem with interpretation of these data is that the study period was limited to only three seasons. Thus, for males present in 1987 we have no information concerning their success in previous season(s). Likewise, there is no information for subsequent years for males present in 1989. Only 1988 is in effect "buffered" by a year either side of it. Whilst, it appears that few males opt out of a single year to return the following year, we cannot determine whether males opt out of more than one season in succession. Thus, these interpretations must be viewed with considerable caution.

Although the data presented cannot confirm a causal link between the variables measured and the probability of returning the following year, it is possible to describe the attributes of those males that return and those that do not. Males that returned, were generally the more dominant individuals in the previous season, therefore remained ashore for longer and consequently gained greater mating success. Thus, more successful males tend to return in the following year. This is most probably mediated via dominance though I have no direct evidence to support this. These returning males are also younger than those that fail to return. This is again as would be expected, young males failing to gain a position will have several more opportunities to do so, whereas older males, once ousted from the colony, probably do not return.

Also, returning males were not necessarily the heavier males in the previous season, and more importantly did not necessarily incur lower rates of energy expenditure. In fact, the results indicate the opposite, that returning males suffered greater proportional rates of weight loss in the previous season.

It must be noted that here we examine aspects of a males performance in the previous breeding season and attempt to relate these to whether an individual returns or not in the following season. It may be the case that factors operating outside the breeding season are more important in determining whether a male returns or not.

CHAPTER 9 - SABLE ISLAND

INTRODUCTION

Important insights into the functional significance of mammalian mating systems are not only obtained by comparing the various species of a group, such as the pinnipeds. It is often the case that valuable information concerning the determinants of mating systems can be gathered by examining differences seen in various populations of the same species. The grey seal is a prime example, having populations that breed on land (eg Scotland), on sand (Sable Island), on ice (Gulf of St. Lawrence), and on both land and ice (Baltic). Stirling (1975) stated that the grey seal "offers the greatest opportunity for study of the effects of different breeding habitats on social behaviour".

Here the behavioural components of male activity during the breeding season are compared at two very different colonies, that of North Rona, and that of Sable Island.

The topography of the breeding environment strongly influences the distribution of females during the breeding season (Bartholomew 1970, Stirling 1975, Le Boeuf 1978, Boness 1991, Le Boeuf 1991). The habitats of North Rona and Sable Island are markedly different. Rona is a small, largely cliff bound island, with restricted access to the colony and a wide range of topography from open grass "lawns" to broken irregular rock strewn gullies. This causes females to exhibit a more contagious distribution. Females gather around pools of water, in gullies and in less exposed sites. In contrast, Sable provides vast expanses of suitable breeding ground, with few limits to access. The topography ranges from large expanses of uniform flat sand to intricate patterns of dunes. It is primarily the former areas that are colonised by the breeding females which tend to be more uniformly dispersed. The relative distribution of females will clearly influence the behaviour of males.

Topography can also exert a direct effect upon males, particularly in terms of access to the breeding site. Access to the breeding grounds of Rona are largely restricted to narrow gullies, usually with several males present. Thus, any male coming ashore must run a gauntlet of opponents. On Sable, the long uniform beaches allow access at any point, thus males can come ashore unopposed.

Much work on the social behaviour and breeding biology of grey seals has been conducted at both North Rona (Anderson *et al.* 1975, Anderson 1978, Anderson and Harwood 1985, Anderson and Fedak 1985, 1987a, 1987b and the present study) and at Sable Island, Nova Scotia (Boness 1979, Boness and James 1979, Boness 1984). Striking differences between the two seal colonies have already been noticed. The seals of the Canadian population, both males and females, grow more rapidly, live longer and are larger and heavier than those of the eastern Atlantic population (Mansfield, 1977, also pers. obs. in terms of size). These morphological data are too sparse to accurately assess whether Canadian grey seals are more or less sexually dimorphic in size than those of British waters. However, using Mansfield's mean adult body lengths and those provided by Platt, Prime and Whitthames (1975) the ratio of male to female body length is remarkably similar, 1 : 0.89 for Canadian seals and 1 : 0.88 for British seals.

The breeding season at Sable is much shorter than on Rona, being approximately 4-5 weeks as opposed to 9-10 weeks. The Sable breeding season extends from the early January to early February, whilst that of Rona is autumnal.

The most striking difference of the social organisation is the apparent operational sex ratio of seals on the breeding colonies. Boness and James (1979) show a significant difference in sex ratios at the time of peak adult numbers, 1 : 1.3 on Sable (Boness and James 1979) and 1 : 9 on Rona (Anderson *et al.* 1975). Similarly, Boness and James (1979) showed that males on Sable were generally in closer proximity to each other than on Rona. This difference in relative numbers and spacing is clearly evident when observing the two colonies (pers. obs.). On discussing this point, both Boness and James (1979) and Anderson and Fedak (1985) suggested that levels of inter-male competition were more intense on Rona.

Indeed, using the apparent operational sex ratio at the two colonies as the traditional yardstick for degree of polygyny, one would suggest that polygyny is more extreme on Rona. Similarly, extrapolating from the relative degree of clumping of females caused by topography, one would be drawn to the same conclusion, as groups of females are more easily monopolised by individual males than widely dispersed females.

However, these assumptions may not be correct. The greater numbers of males able to gain positions on the colony at Sable may in fact lead to more intense inter-male competition. Although more males gain positions on the colony on Sable, how many of these are actually involved in reproduction in a single season?

From the data presented in previous chapters, in particular the analyses of chapter 7, it is possible to make certain predictions about the determinants of mating success on Sable Island.

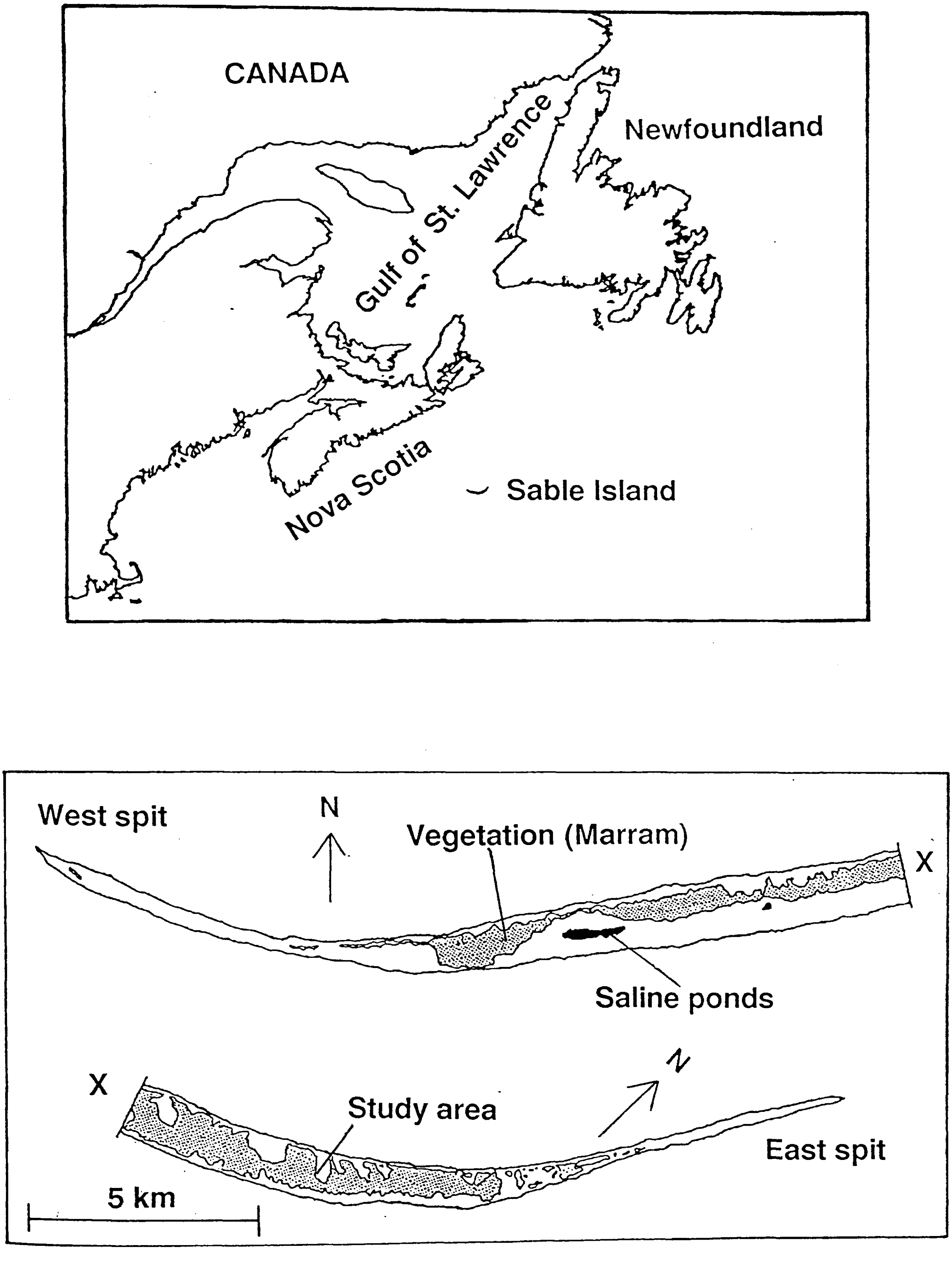
If access to the breeding grounds is relatively unrestricted, most males will be able to come ashore. If the mating system on Sable is one of a lower degree of polygyny than Rona, and copulations are more evenly distributed amongst the males, then an individual's length of stay will still be the prime predictor of mating success. Also, with less variation in male mating success, levels of inter-male competition will be lower than seen on Rona. However, if polygyny is more extreme than is indicated by the apparent sex ratio and female distribution, then length of stay may not be the primary predictor. Due to the unrestricted access of Sable, many males may be ashore for much of the season, but fail to attain high levels of mating success. Some other factor such as dominance may be more important in determining final access to oestrus females. If variation in mating success is more extreme, accordingly there will be higher levels of inter-male competition.

METHODS

Study site

Sable Island (43° 55' N, 60° 00' W) is a sand bar some 35 km long and 1.5 km wide located 288km ESE of Halifax, Nova Scotia, Canada. It lies approximately 160 km from the nearest point of Nova Scotia (Figure 9.1a). The island consists of shifting sand dunes and large areas of flat sand. The only vegetation consists of marram grass, growing on the more stable dunes. Details of this remarkable island can be found in Boulva (1971),

Figure 9.1 a : Map showing location of Sable Island, and the location of the study site on Sable Island.



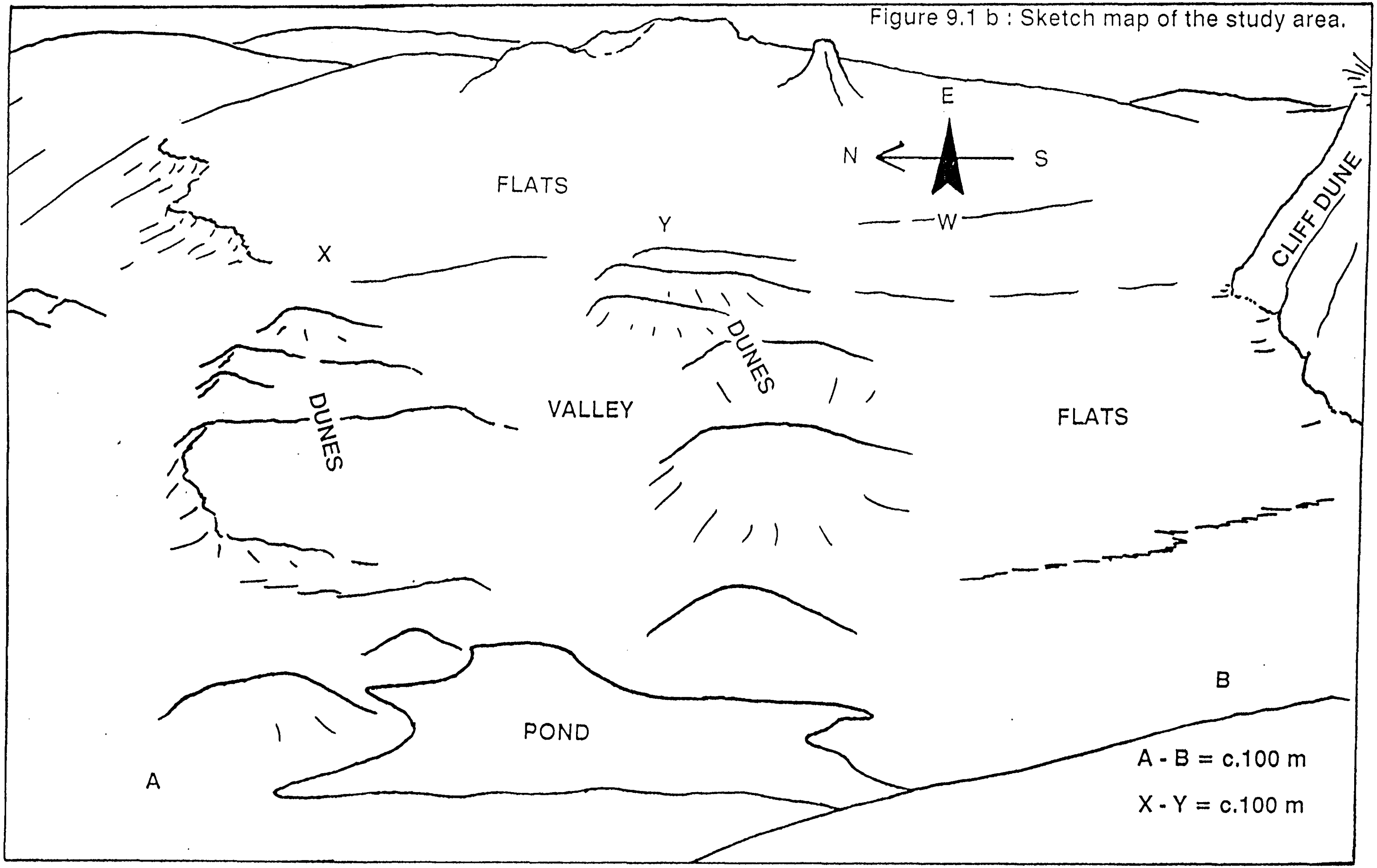


Figure 9.1 b : Sketch map of the study area.

McLaren (1972), Boness (1979) and Boness and James (1979).

Figure 9.1 a shows the location of the study area within Sable island. The study area was located at the periphery of a large flat grey seal breeding area known as West 4. This site was selected primarily for logistical purposes, in that other researchers were working in adjacent areas. A hide was constructed from two plywood boards and driftwood on the edge of a high dune overlooking the study site. Figure 9.1 b is a sketch map of the study area as seen from the hide. To the south and west the study area was delimited by the arc of the high dune. The northern boundary was delimited by a line of small dunes running east-west. To the east, no clear boundary existed, but no seals were resident in the open flat expanse east of the small dunes shown on the map. The pool fluctuated markedly in size, at some points drying up completely, although it was usually frozen, or slush after snowfalls.

The study site lay approximately 15 km east of the accommodation, and travel to and from the study site was by Honda trike.

Observations

Behavioural observations were made from the hide using the same format as applied on North Rona (see Chapter 2). All males in the study area were individually identified using scars, pelage patterns and/or brands. Brands have been applied to many weaned pups on Sable intermittently since 1963 (Stobo, Kees and Zwanenburg, 1990, Zwanenburg and Bowen, 1990). A total of 80 males were individually identified.

Records of all sexual and aggressive behaviour were taken as on Rona, noting the identity of participants, the duration and the outcome. Concurrently, scan samples were taken at 5 minute intervals noting the behaviour category of each male present.

As with the North Rona data, all instances where attempted copulations or actual copulations were directed more than once at the same female were recorded as such, where possible (see Chapter 3). For the calculation of daily frequencies of sexual activity, and individual activity budgets, all attempted copulations and actual copulations were used, whether the female in question had previously been mated or not. However, for the assessment of individual male mating success a system of first male paternity was assumed as with the North Rona data. Thus, mating success for an individual male is in fact the observed number of occasions in which he copulated with different females not previously mated (or not observed in a copulation before). The reasons for assuming first male paternity were given in Chapter 3.

Figure 9.2 depicts the observation regime. This was primarily limited by the work periods that other researchers on Sable kept as it was necessary to traverse the 15 km from the study site to the base together. Behavioural observations commenced on the 11th of January and ceased on the 2nd of February. Only three days were lost to adverse weather conditions, making either the journey to the study site impossible, or observations impossible. However, daily censuses of the study site were made from the 6th of January, whilst I constructed the hide, and continued to the 3rd of February, the date on which the hide was dismantled.

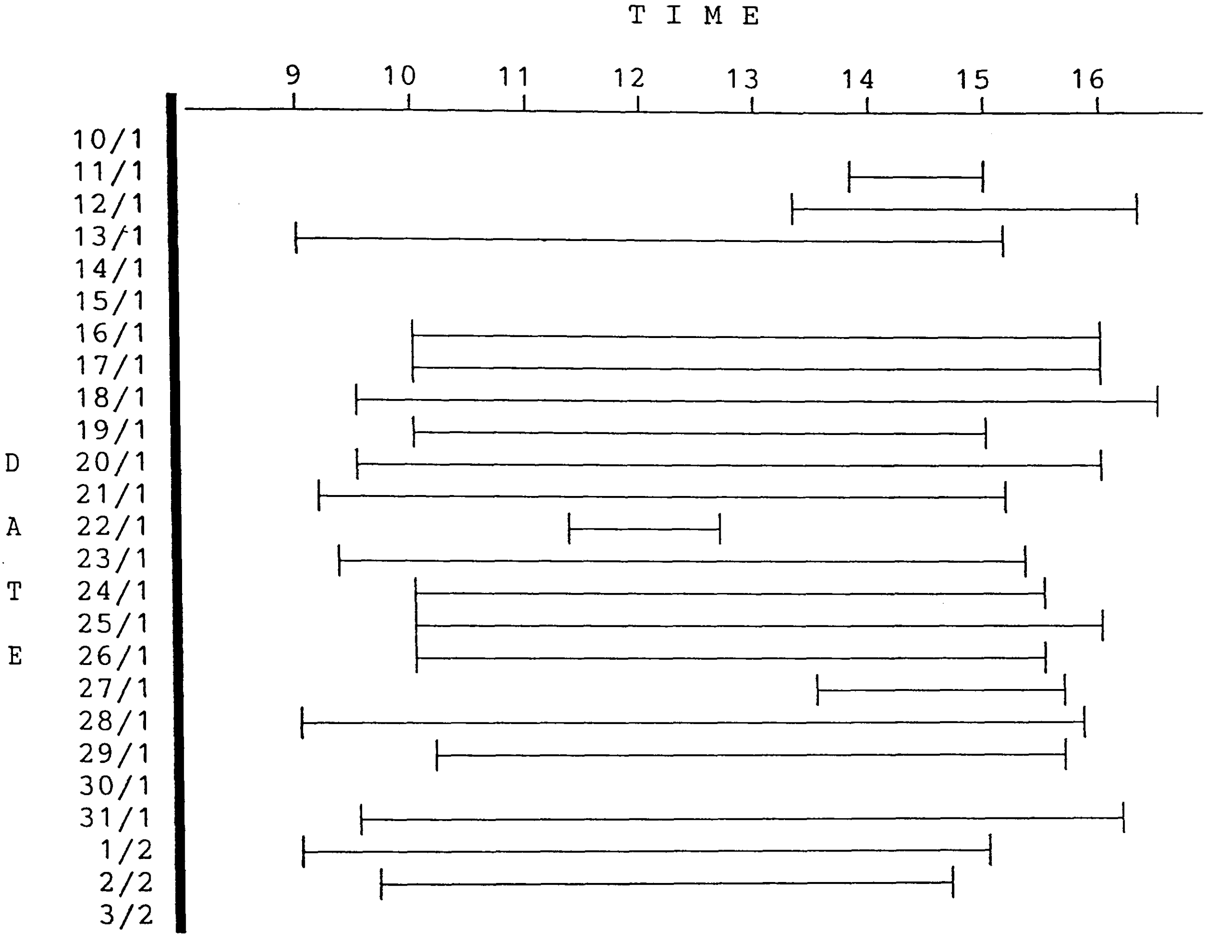
The daily censuses of the study area involved noting the number, identity and position of all males, females and pups. These were recorded on sketch maps. On days where no observations could be made, males present prior to and immediately after the break in observations were assumed to have been present throughout. During the breeding season a total of 80 males were individually identified.

No data on male weights were obtained, as I was working alone and had no equipment for this purpose.

Statistical analyses utilised the same tests as for North Rona data, where appropriate, including oneway analyses of variance with Scheffe's Multiple Range tests, Mann-Whitney U tests and Chi square tests. Where appropriate all data sets were transformed to approximate to normality prior to applying statistical procedures (see Chapter 3 and 7).

As for the North Rona data, summary statistics for parameters other than activity budgets, are presented in two formats. The first includes all identified males for which data are available. The second includes only cases where the individual males were involved in at least 10 inter-male aggressive interactions. Again, this was necessary to

Figure 9.2 : Observation regime - Sable 1990



ensure that individuals included in the analyses of inter-relationships between parameters were involved in sufficient inter-male aggressive interactions to allow accurate calculation of the dominance score (see Chapter 3).

RESULTS

9.1. Behaviours

9.1.1. *Description of behaviours*:

The same behavioural categories were used as defined in Chapter 3. Two additional behaviours were observed on Sable Island;

(1) Eating snow - Standing pools of fresh water are rare on the sand substrate of Sable, and are often frozen. Males, and females, were observed eating snow (see Plate 9.1). Often after a sand storm had covered lying snow, individuals were observed scraping at the sand with their fore-flippers to reveal the snow below.

(2) Yodelling - this behaviour is fully described in Boness and James (1979). Only males were observed making this loud call, described as a "falsetto part of a yodel" being "essentially a pure tone with a gradual onset". This call is audible from considerable distance (several kilometres) and is difficult to localise. Many males were observed making the call, though the frequency of calling varied considerably amongst the males. The call is somewhat individually recognisable, and different males adopt slightly different postures when producing the call. Some males hold their necks outstretched, others crane their necks with the head pointing towards the ground. In all cases the male's neck can be seen vibrating. Yodels were produced in a variety of situations, often after an aggressive encounter, but also males would often rouse momentarily from a long period of rest to yodel, then return to resting. Responses of surrounding males varied considerably,from no apparent response, to approaching and attacking the yodeller. No author has yet been able to discern the function of this call. No similar call has been observed in male grey seals of the eastern Atlantic population.

Plate 9.1 : Male grey seal eating snow (Sable Island, 1990).

9.1.2. *Activity Budgets*:

Table 9.1 presents the summary statistics for the activity budgets. The percentage of time spent in each activity category was computed for each individual male, and then the mean, and accompanying statistics, were calculated. The data presented in Table 9.1 were subjected to arc-sine transformation prior to computing these statistics (as used in Chapter 5). As for the North Rona activity budgets, a cut off of 180 scans was found to yield an accurate representation of proportion of time spent in each activity category (i.e. where percentage of time in each activity becomes independent of number of scans made - see Chapter 5). This is responsible for the reduction of the sample size from 80 individuals to twenty. The abbreviations used are the same as in Chapter 5. The categories of observant, sexual activity, aggression, non-active and active behaviours are composites constructed from the same individuals activity categories as defined in Chapter 5, with the exception that the additional categories for Sable (drinking, eating snow and yodelling) are also included in the composite category non-active.

Each activity category was compared with the relevant categories of the activity budget presented for North Rona 1988. Since the arc-sine transformation did not normalise the data (Table 9.1), the two data sets were compared by Mann Whitney-U tests. Again, only cases with at least 180 scans were selected. The sample sizes (number of males) were 26 for Rona, and 20 for Sable. The following categories showed no significant difference between the values obtained at Sable and North Rona; resting, drinking, alert, locomotion, approach to female, non-aggressive flippering, open mouth threats, lunge/bite/flippering, fighting, observant, non-active and active.

Significant differences were found in several categories, some of which were inevitable. Males at Sable island obviously spent more time eating snow as there was no snow on Rona. Similarly, Sable males spent more time yodelling as North Rona males do not yodel! In both these activities, however, the time involved was small (Table 9.1).

The more important differences are to be found in the relative proportion of time devoted to sexual and aggressive behaviour. Although there is no difference in the amounts of time spent resting (which is in fact remarkably similar in the two study groups) or inactive and active, the relative division of active time between aggressive and sexual behaviour differs. Sable males spent significantly more time than the Rona males observing other males ($U = 91$, $z = -4.72$, $p < 0.0001$), approaching other males ($U = 117$, $z = - 4.24$, $p < 0.0001$) and chasing other males ($U = 159.5$, $z = -2.26$, $p = 0.024$). Sable bulls also spent more time rolling ($U = 67.5$, z -5.02, $p < 0.0001$). Conversely, Sable males spent relatively less time in sexual activities, in particular, attempted copulations ($U = 164.5$, $z = -2.13$, $p = 0.033$) and copulation ($U = 172$, $z = -1.99$, $p = 0.046$) although the durations of particular sexual activities did not differ significantly in the two study groups (see below).

In summary, using the broader amalgamated categories from Table 10.1, Sable males spent more time in aggressive activity ($U = 138$, $z = -2.71$, $p = 0.007$) and less time in sexual activity ($U = 156$, $z = -2.31$, $p = 0.021$).

Table 9.1 Summary statistics for activity budgets for Sable Island males. Mean and median values are shown for the proportion of time spent in each type of activity and various groups of activities. Only males recorded in at least 180 scans are used in the calculation of these statistics.

ACTIVITY	n	median	mean	standard deviation	min.	max.
RESTING	20	81.45	79.76	9.05	52.10	93.90
DRINKING	20	0.00	0.01	0.02	0.00	0.10
EATING SNOW	20	0.00	0.13	0.35	0.00	1.50
ALERT	20	10.60	11.77	5.67	4.40	28.10
LOCOMOTION	20	1.55	1.83	1.16	0.20	4.20
YODEL	20	0.00	0.72	1.48	0.00	5.20
SEXUAL ACTIVITIES						
APPROACH TO FEMALE	20	0.05	0.26	0.34	0.00	1.00
ATTEMPTED COPULATION	20	0.35	0.51	0.64	0.00	2.20
COPULATION	20	0.00	0.90	1.38	0.00	4.80
NON-AGGRESSIVE FLIPPERING	20	0.00	0.01	0.02	0.00	0.10
AGGRESSIVE ACTIVITIES						
ALERT - LOOKING AT MALE	20	0.25	0.44	0.51	0.00	1.40
APPROACH TO MALE	20	0.10	0.25	0.29	0.00	1.00
OPEN MOUTH THREAT	20	1.35	1.61	1.16	0.00	4.00
LUNGE/BITE/FLIPPERING	20	0.00	0.00	0.00	0.00	0.00
FIGHTING	20	0.00	0.24	0.46	0.00	2.00
CHASING	20	0.60	0.70	0.64	0.00	2.50
ROLLING	20	0.60	0.76	0.68	0.00	2.00
COMBINED CATEGORIES						
OBSERVANT	20	10.75	12.21	5.89	4.40	29.40
SEXUAL	20	1.10	1.68	2.02	0.00	7.40
AGGRESSIVE	20	3.50	3.24	1.70	0.00	5.90
NON-ACTIVE	20	93.20	92.81	3.37	85.60	99.00
ACTIVE	20	7.20	7.49	3.55	0.90	15.50
NUMBER OF SCANS/MALE	20	409.50	445.90	220.75	180.00	893.00

Diurnal variation in activities

Figures 9.3 a to j illustrate diurnal variation in the various activities recorded. As on North Rona, there is clearly no significant diurnal change in mean proportion of time spent in any activity. Although, individuals may vary their activity patterns during the course of a day, and there is some suggestion of a morning and afternoon increase in activity, the overall patterns show no significant change.

Seasonal variation in sexual and aggressive activity is presented below.

9.1.3. *Aggressive behaviour:*

Male - female aggression

As on North Rona inter-sexual aggression usually resulted in either no clear outcome or the female being the victor. Of 102 encounters, 20 (19.61%) were draws, 81 (79.41%) resulted in the male withdrawing, and only 1 (0.98%) lead to a male victory. These interactions were primarily low level, 82.35% consisting of threats, the remainder being isolated lunges, bites or aggressive flippering.

Male - male aggression

Of the 1337 observed inter-male aggressive encounters only 47 (3.5%) involved physical contact (i.e. fights). This is very similar to the low level of escalated aggression already shown for North Rona.

Table 9.2 a and b summarises the statistics for mean values of total number of aggressive interactions, aggressive interactions per day and dominance score. Utilising the same procedure as for the North Rona data, Table 9.2 a presents these statistics for all males identified, whilst 9.2 b gives values for only those males involved in 10 or more aggressive interactions.

Figures 9.3a to j: Diurnal variation in activity categories. Mean values (± standard errors) for estimated percentage of time in various activity categories on an hourly basis. Only males recorded on at least 180 scans within each hour were included in the analyses. Sample sizes (number of males) are given in Figure 9.3a.

Figure 9.3 a : Diurnal variation in resting

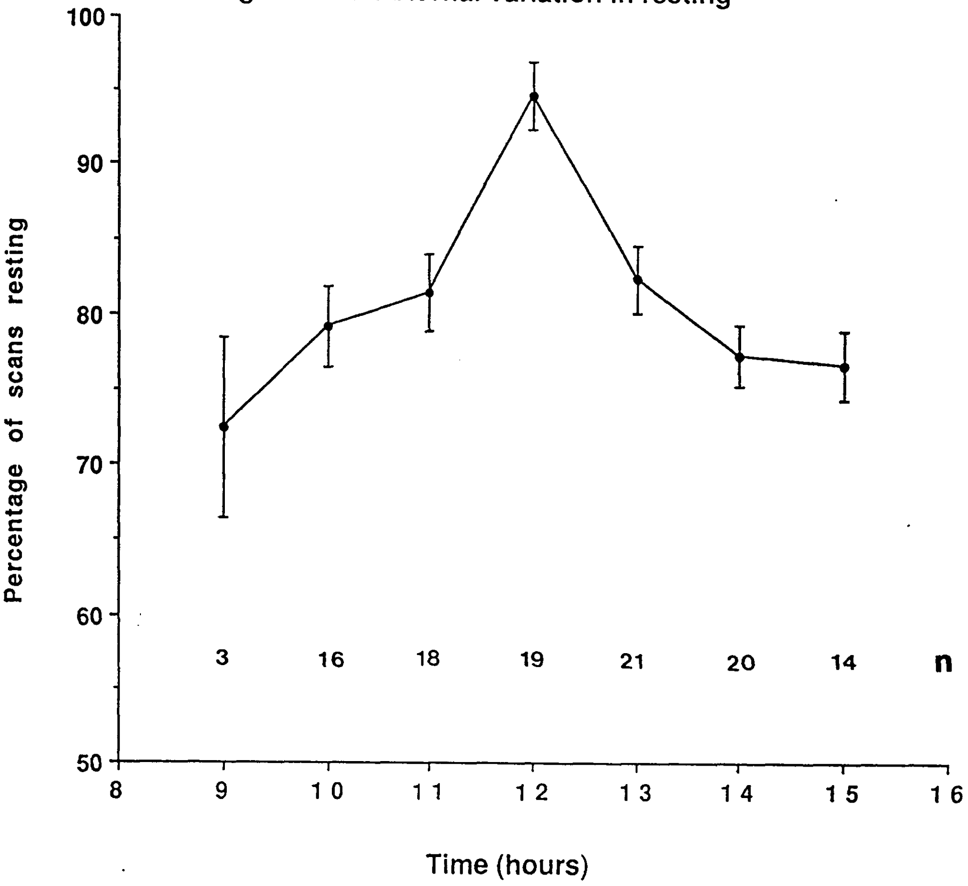


Figure 9.3 b : Diurnal variation in alert

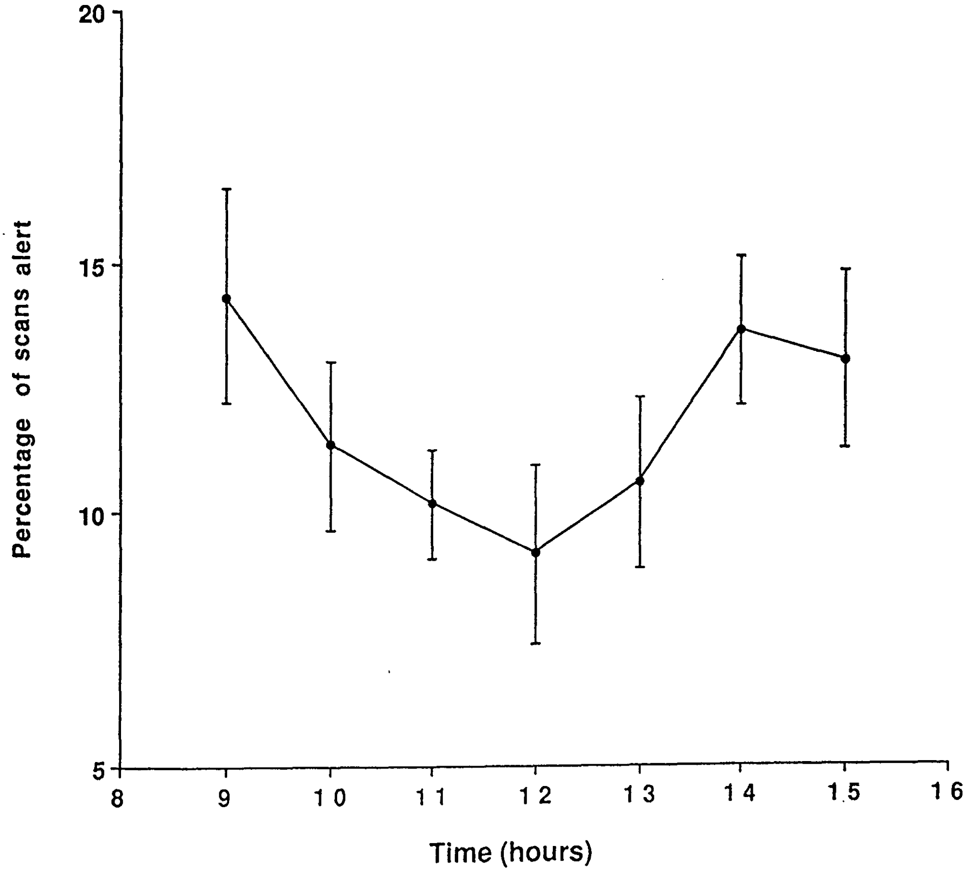


Figure 9.3 c : Diurnal variation in locomotion

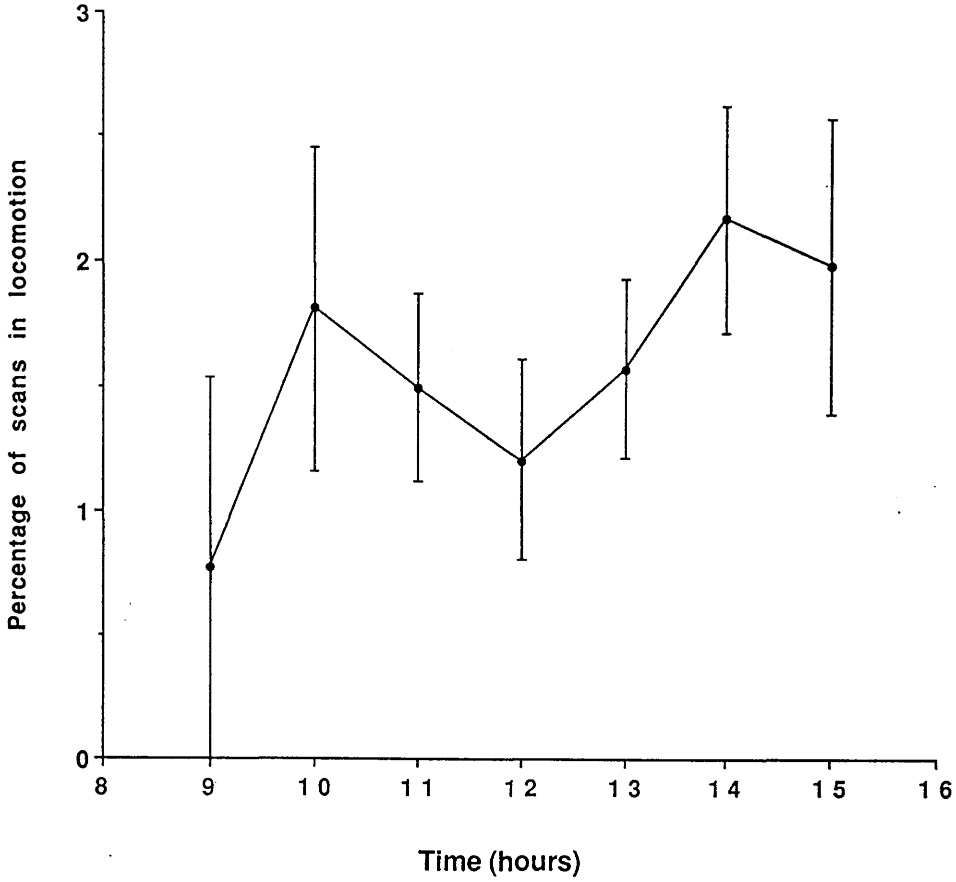


Figure 9.3 d : Diurnal variation in approaches to females

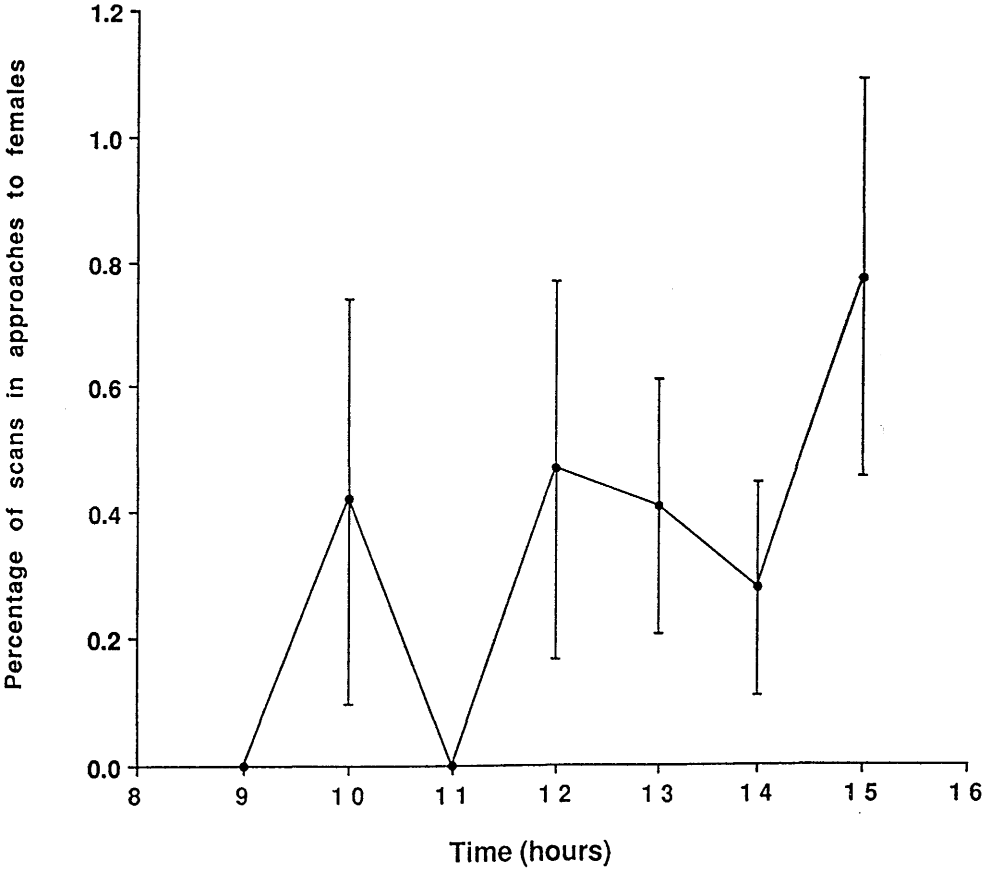


Figure 9.3 e : Diurnal variation in attempted copulations

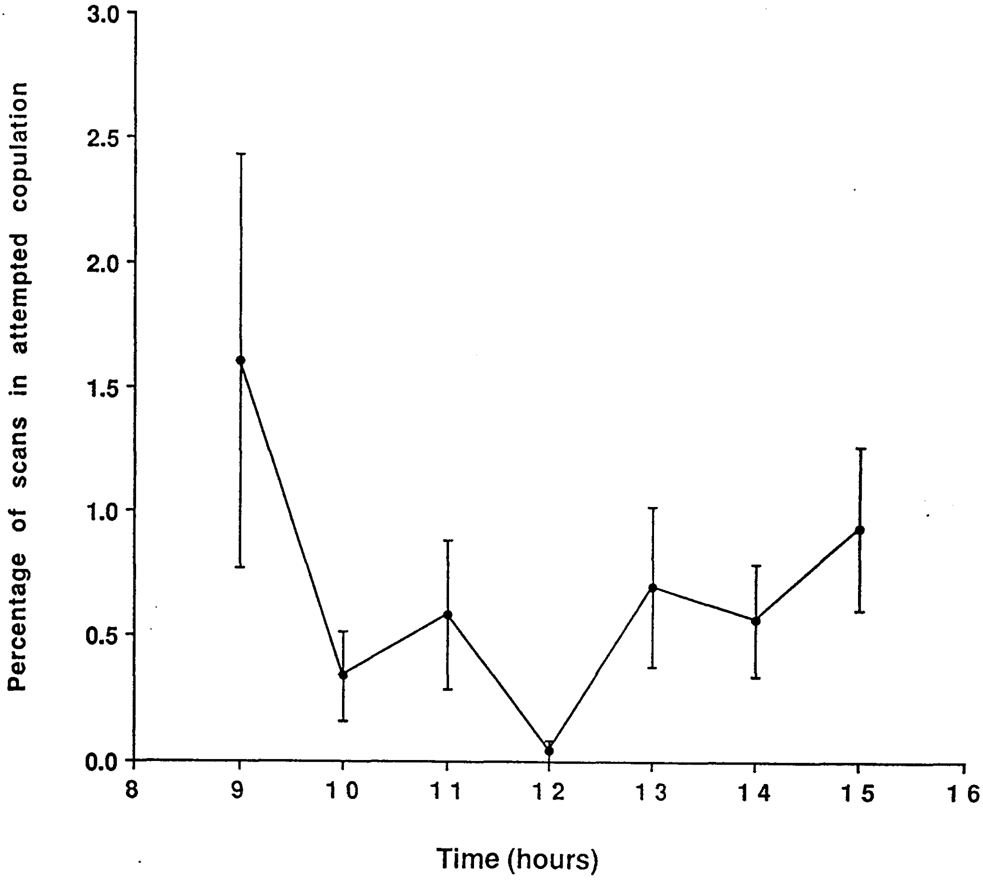


Figure 9.3 f : Diurnal variation in copulation

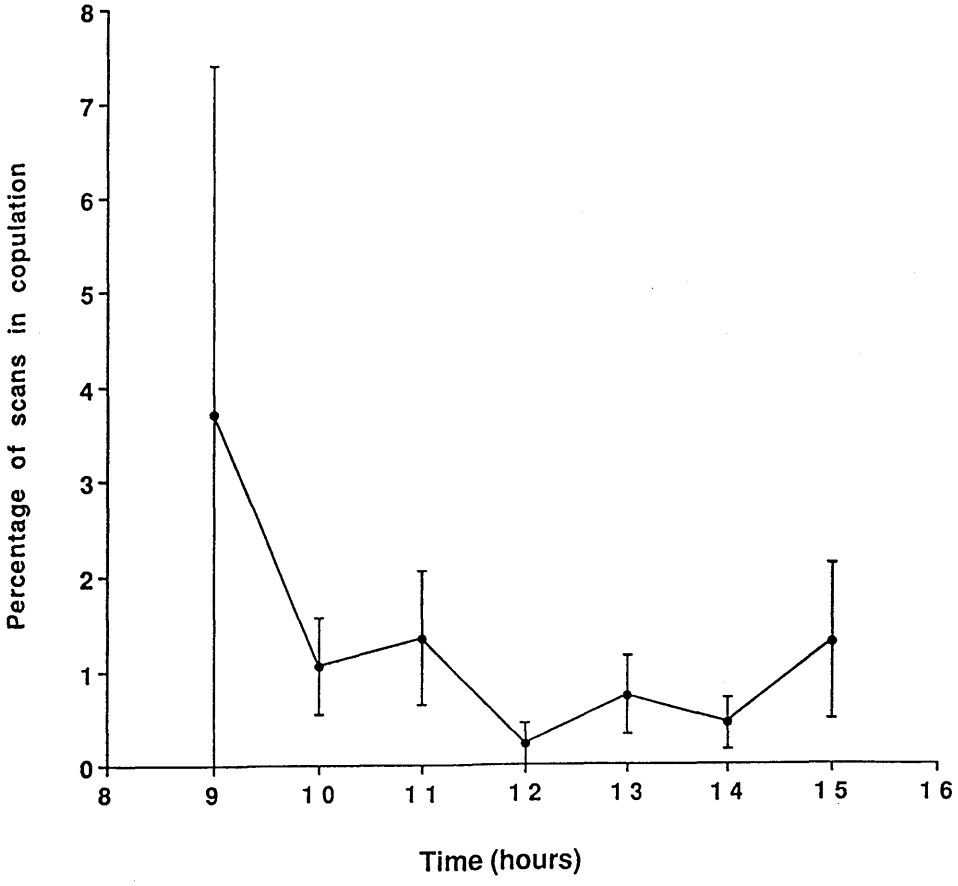


Figure 9.3 g : Diurnal variation in open mouth threat

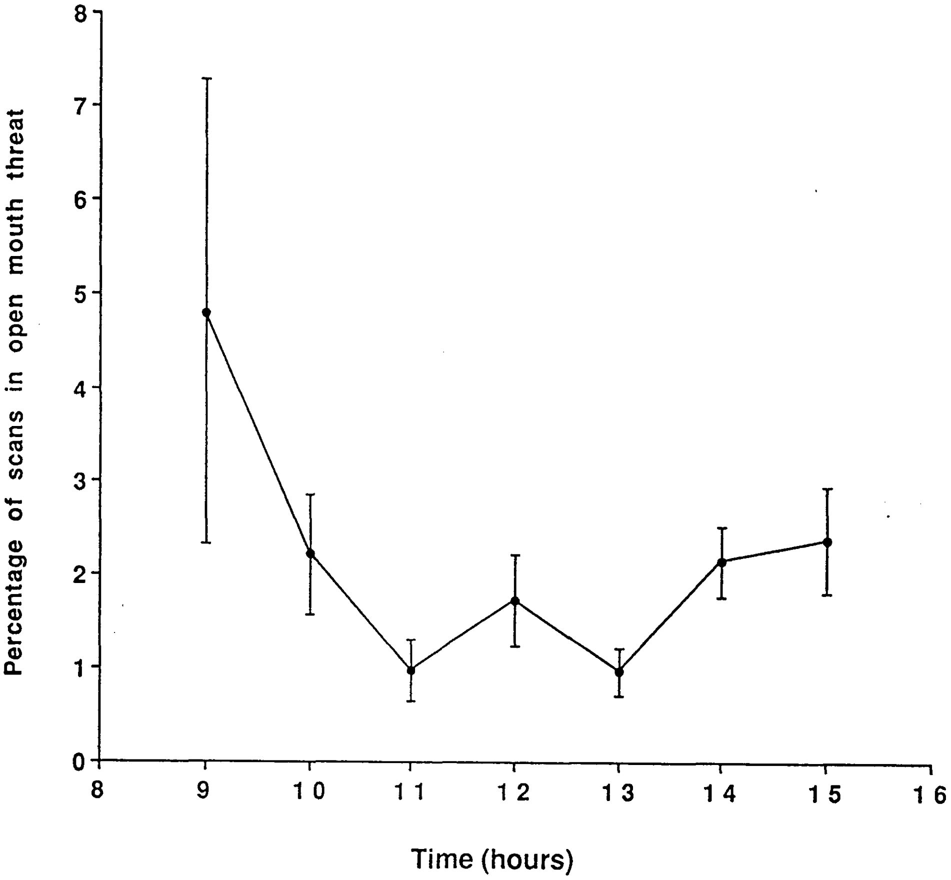


Figure 9.3 h : Diurnal variation in fighting

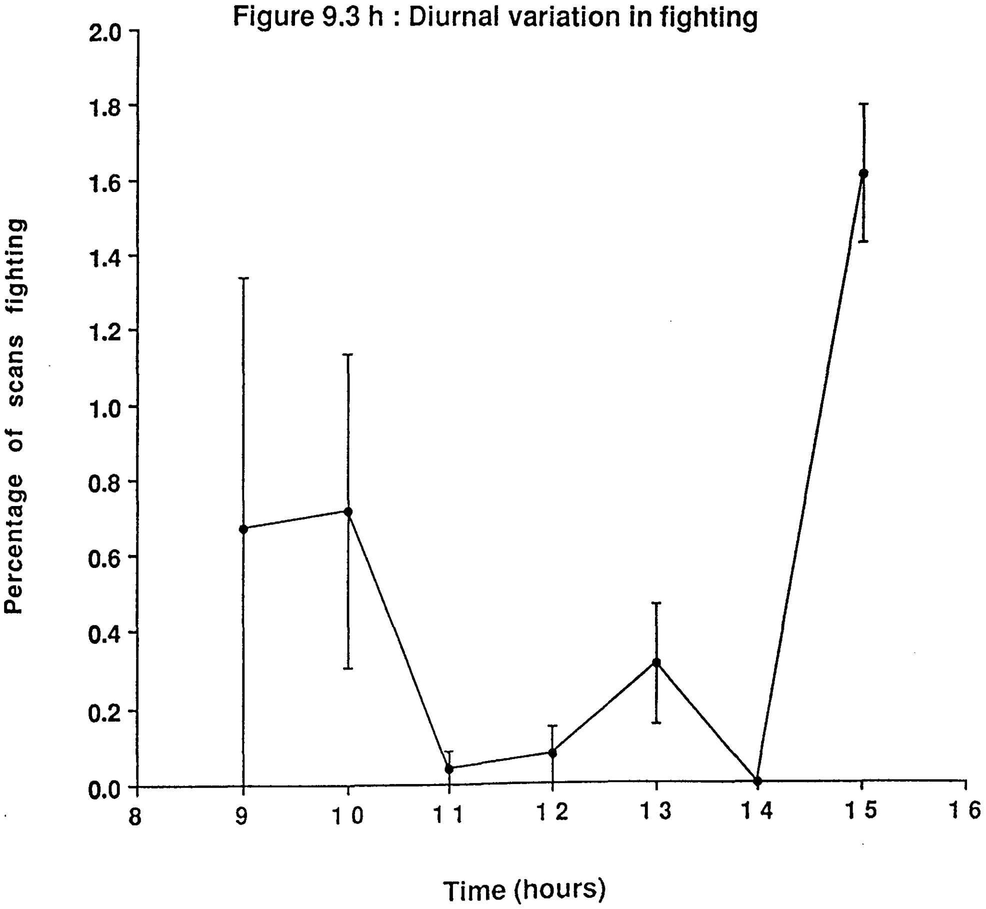


Figure 9.3 i : Diurnal variation in chasing

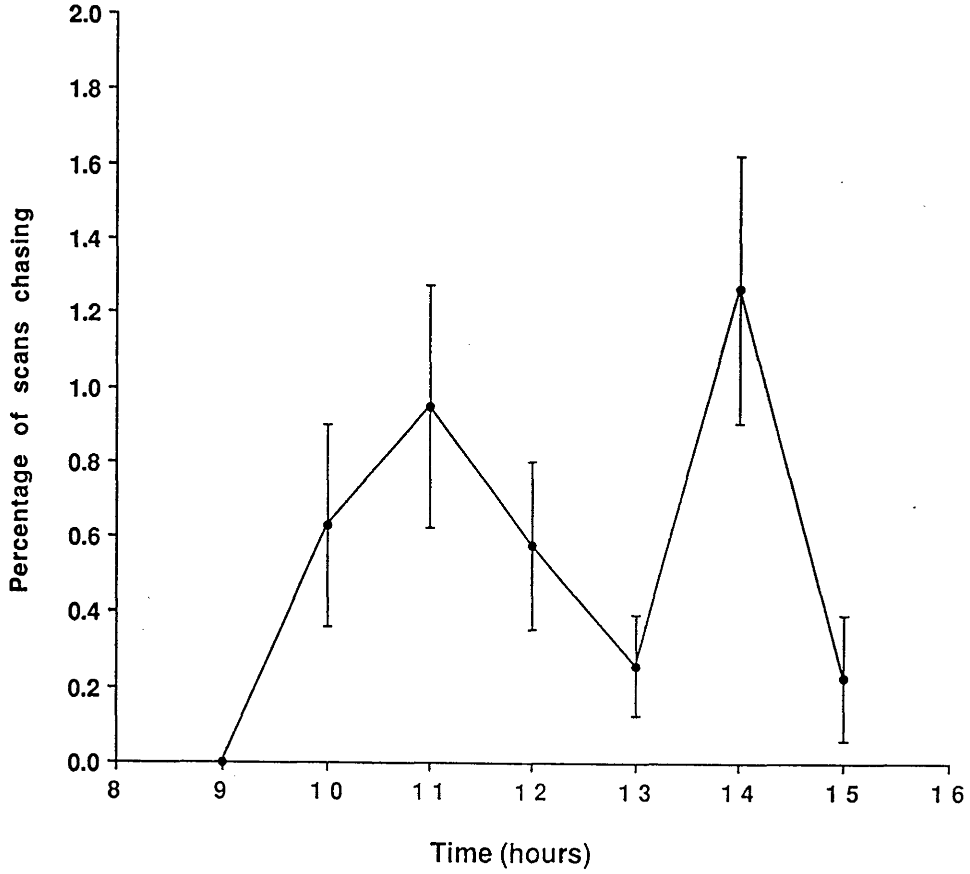


Figure 9.3 j : Diurnal variation in yodelling

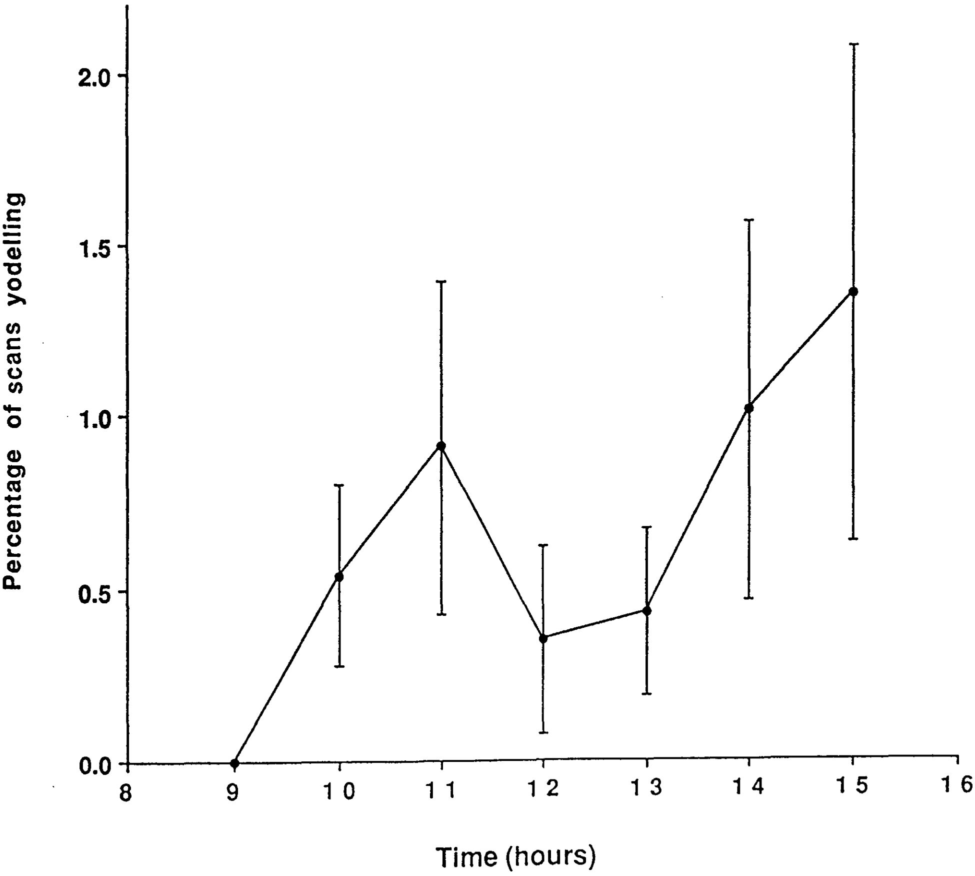


Table 9.2a

Summary statistics for observed inter-male aggressive activity and dominance score for all identified males on the study area (A.I.s = Aggressive interactions).

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1990	TOTAL No. A.I.s	68	14.50	43.09	59.40	7.20	1	273
	A.I.s/DAY	66	11.55	15.06	12.30	1.51	1	55
	DOMINANCE SCORE	66	4.35	4.37	0.88	0.11	2.95	6.00

Table 9.2b

Summary statistics for observed inter-male aggressive activity and dominance score for all identified males on the study area which were involved in 10 or more inter-male aggressive encounters (A.I.s = Aggressive interactions).

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1990	TOTAL No. A.I.s	42	42.00	66.95	65.09	10.04	10	273
	A.I.s/DAY	40	14.60	17.18	10.93	1.73	1.25	55
	DOMINANCE SCORE	41	3.92	4.01	0.77	0.12	2.95	5.83

The data presented in Table 9.2 b were compared with the equivalent data sets for each of the three seasons on North Rona by means of oneway analysis of variance with Scheffe's Range tests. All data sets were transformed to approximate to normality as outlined in Chapter 7. The Sable Island males had the highest mean values for total number of aggressive interactions but this was not significantly different to any of the three seasons at North Rona ($F_{3,\ 179} = 1.79$, $p = 0.15$). However, considering that the span of the breeding season on Sable is much shorter than that of Rona, the daily rates of aggression for Sable males were much higher than any of the three Rona seasons ($F_{3,178} = 48.56$, $p < 0.0001$). As expected, there was no significant difference in the mean dominance scores ($F_{3,\ 178} = 0.54$, $p = 0.65$).

Duration of inter-male fights

The mean duration of fights was 3.42 minutes (n = 47, S.E. = 0.79, median = 3.00) with durations ranging from 0.5 to 9.0 minutes. The durations of fights were compared with those gained for North Rona (Chapter 3) using a oneway analysis of variance with Scheffe's Range tests. There was no significant difference in the duration of male-male fights between Sable data and the three seasons at North Rona ($F_{3,\ 98} = 0.17$, $p = 0.92$).

Outcome of aggressive interactions with respect to initiator

As found on North Rona, there was a strong correlation between dominance and the percentage of inter-male aggressive interactions initiated ($R = -0.82$, $n = 42$, $p < 0.001$). Thus, dominant individuals initiate relatively more aggressive encounters than subordinate males. Table 9.3 depicts the relative frequencies of victories, draws and losses for initiators of aggressive encounters in various categories of aggression.

It is clear that the initiator of an interaction was seldom the loser, as would be expected from the correlation with dominance. However, in low level aggression (all encounters other than fights and chases) a greater proportion of interactions are unresolved (draws). If an interaction escalated to a fight, these were usually resolved, mostly in the favour of the initiator. Chases were exclusively won by the initiator. This pattern was also found in the North Rona data.

Table 9.3

Table of details of outcomes of inter-male aggression, showing number and percentage of encounters won and lost by initiator or drawn.

TYPE OF AGGRESSIVE INTERACTION	N	PERCENTAGE OF ENCOUNTERS		
		won by initiator	drawn	lost by initiator
ALL ENCOUNTERS	1337	48.9	48.8	2.3
FIGHTS	47	72.3	17.0	10.6
CHASES	308	100.0	0.0	0.0
OPEN MOUTH THREATS	460	59.6	36.3	4.1
ALL REMAINING A.I.s	552	27.8	70.9	1.4

Table 9.4: Summary statistics for durations of sexual activities recorded at Sable island.

				DURATION (minutes)				
YEAR	ACTIVITY	OUTCOME	n	median	mean	standard error	min.	max.
1990	ATTEMPTED COPULATION	SUCCESSFUL	24	4.00	4.77	0.65	2.00	15.00
	ATTEMPTED COPULATION	UNSUCCESSFUL	31	2.00	2.99	0.62	0.50	18.00
	COPULATION	SUCCESSFUL	23	17.00	17.39	1.27	9.00	28.00
	COPULATION	UNSUCCESSFUL	2	5.00	5.00	3.00	2.00	8.00

Seasonal variation in male-male aggression

Figure 9.4 a illustrates the seasonal variation in rates of inter-male fights and open mouth threats. As for North Rona there is considerable fluctuation in the mean values and large standard errors, but a general trend can be discerned showing relatively low levels of aggression at the onset of the season with increased levels in the mid and late portions of the breeding season.

Dominance hierarchy

The males were arranged in order of dominance and the outcomes of interactions examined for all observed dyads. The resulting matrix is presented in Figure 9.4 b. As with the Rona data, a close approximation to a linear hierarchy was established, with 88.33 % of cases above the diagonal. This compares with values of 89.5 %, 93.5 % and 90.0 % for Rona 1987, 1988 and 1989 respectively.

9.1.4. *Sexual activity*:

Duration of sexual activities

Table 9.4 summarises the statistics for durations of sexual activities observed at the study site on Sable Island.

A total of 32 successful copulations and 90 attempted copulations were observed, for which accurate durations were recorded for 23 and 55 respectively. Of the 90 attempted copulations 32 (35.6 %) were successful.

The mean durations for both attempted and actual copulations were compared with those established for North Rona (see Chapter 6) using oneway analysis of variance with Scheffe's Range tests. There was no significant difference in durations of either successful or unsuccessful attempted copulations between Sable and any of the three seasons' data for Rona (successful; $F_{3, 368} = 0.62$, $p = 0.60$, unsuccessful; $F_{3, 491} = 1.32$, $p = 0.27$). Similarly, there was no difference in the durations of successful copulations between Sable and Rona ($F_{3, 346} = 1.18$, $p = 0.32$).

Using Mann-Whitney U tests the durations of successful and unsuccessful attempted

Figure 9.4: Seasonal variation in the frequency of inter-male aggression (open mouth threats and fights) in 1990. Values plotted are daily mean values (rate per male per 24 hours) ± standard error.

Figure 9.5: Seasonal variation in the frequency of sexual activities (attempted copulations and successful copulations) in 1990. Values plotted are daily mean values (rate per male per 24 hours) ± standard error.

Figure 9.4 : Seasonal variation in inter-male aggression - Sable 1990

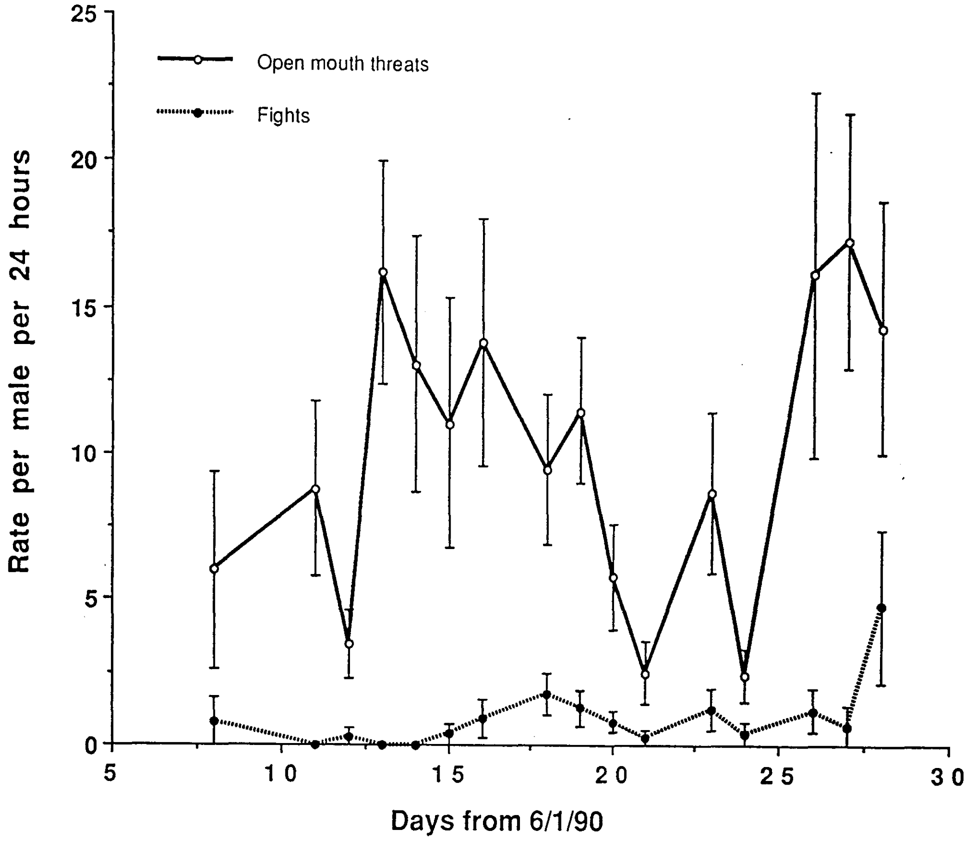


Figure 9.5 : Seasonal variation in frequency of sexual activities - Sable 1990

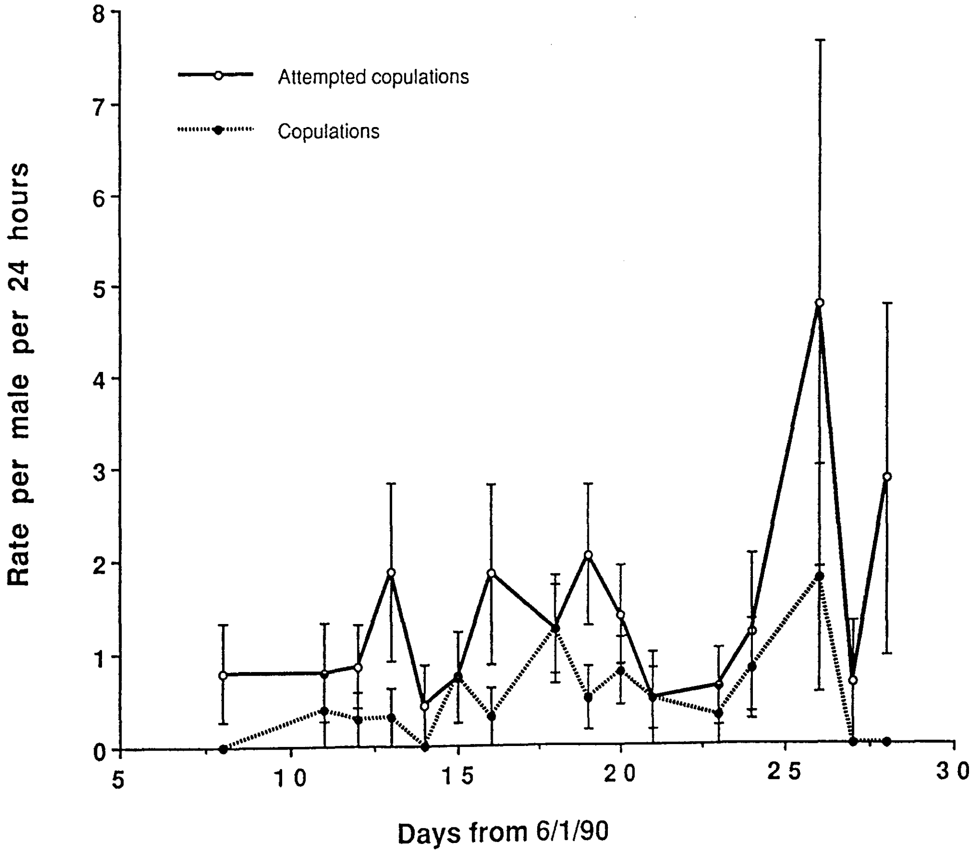
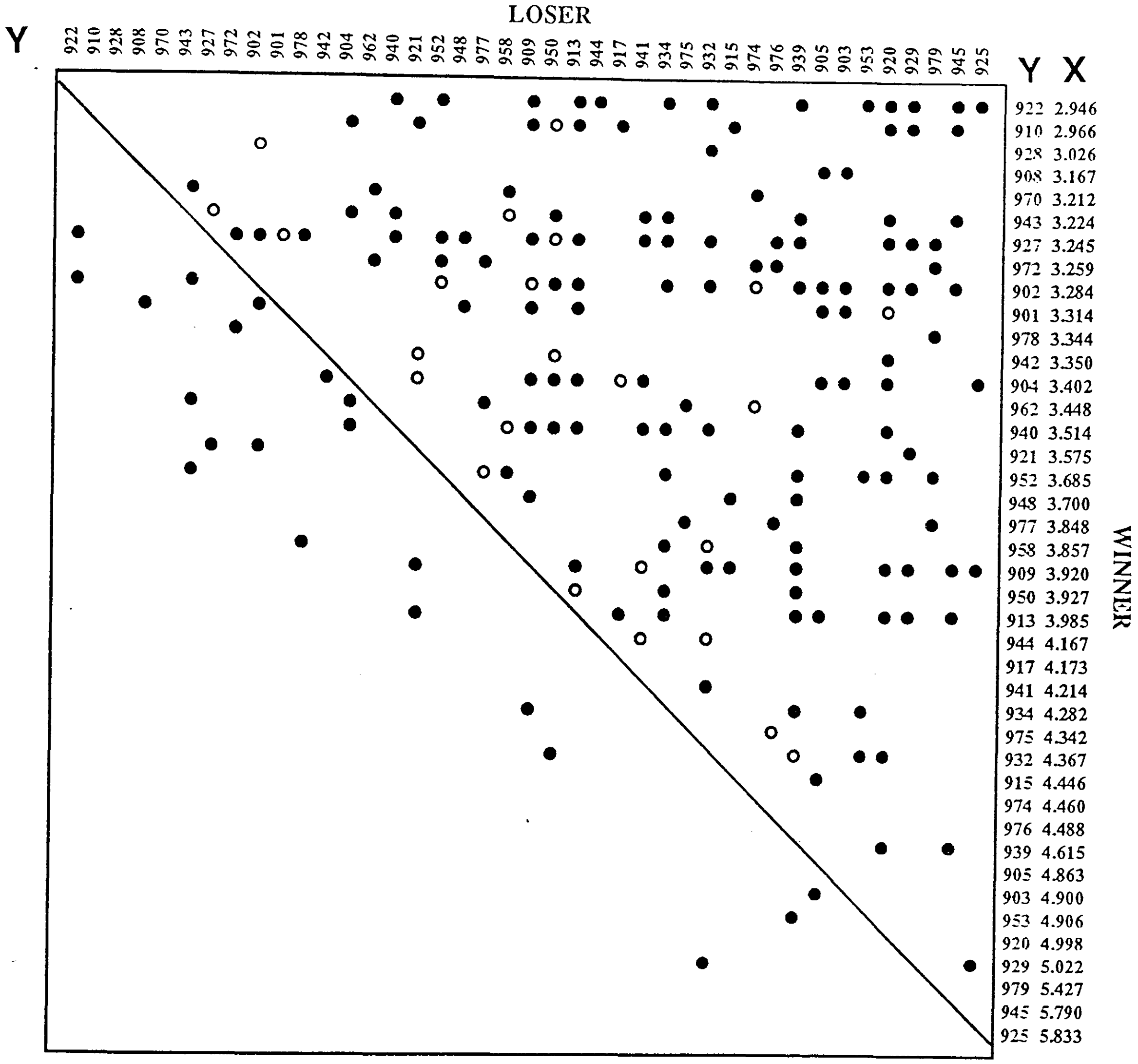


Figure 9.4 b : Mean outcome of inter-male aggressive encounters between all observed dyads. Males are arranged in order of decreasing dominance. Full circles indicate victory, open circles indicate draws. Sable 1990.



X = Dominance score

Y = Male identity code

copulations were examined for differences within the Sable data. There was a significant difference between the durations of successful and unsuccessful attempted copulations ($U = 176.5$, $z = -3.36$, $p = 0.001$, $n = 55$) with successful attempts being significantly longer.

Seasonal variation in sexual activity

Figure 9.5 illustrates the changes in the levels of sexual activities (attempted copulations, both successful and unsuccessful, and successful copulations) throughout the breeding season. The values are expressed as average rates per male per 24 hours with standard errors. The difference between the line for attempted copulations and that for successful copulations represents the number of unsuccessful attempted copulations.

As in the case of North Rona the standard error about the mean remains relatively high throughout each season and there is considerable fluctuation from day to day. However, a general trend, of low levels of sexual activity at the start of the season, but increasing in the mid season period with a decline in the latter half of the season and a final peak of activity at the close of the season, can be discerned.

Unlike North Rona, the pattern of sexual activity follows that of aggressive activity closely.

Individual variation in mating success

Figure 9.6 shows the frequency distribution of observed copulations amongst the males in the study area at Sable. It must be noted that the graph represents only observed copulations and not estimates of individuals total mating success for the entire season. However, the observation regime was sufficiently uniform throughout the entire season to prevent biases occurring due to more intensive observations at any particular point of the season, and thus the relative rankings are probably accurate.

A total of 80 males were individually identified throughout the season, being present at different times and for varying lengths of time in the study area. Slightly less than one fifth (18.75 %) gained at least one observed copulation. The top ranking bull (in terms of mating success) accounted for 18.75 % of all observed copulations and the top 5 males accounted for 59.38 percent.

Figure 9.6 : Distribution of observed copulations - Sable 1990

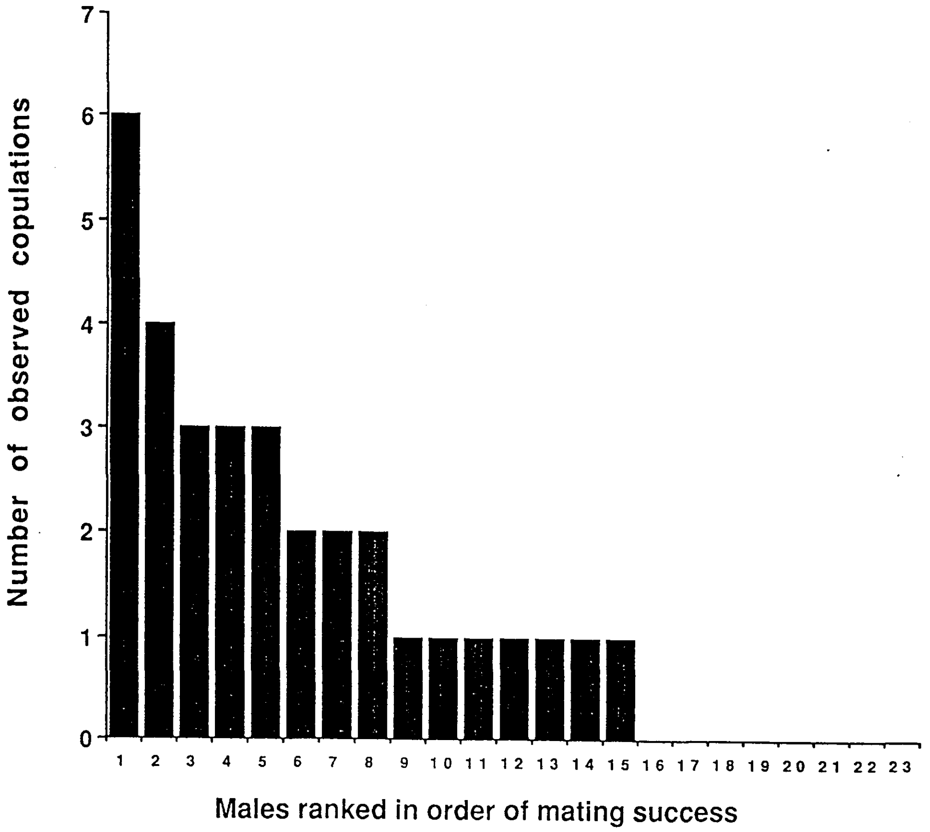
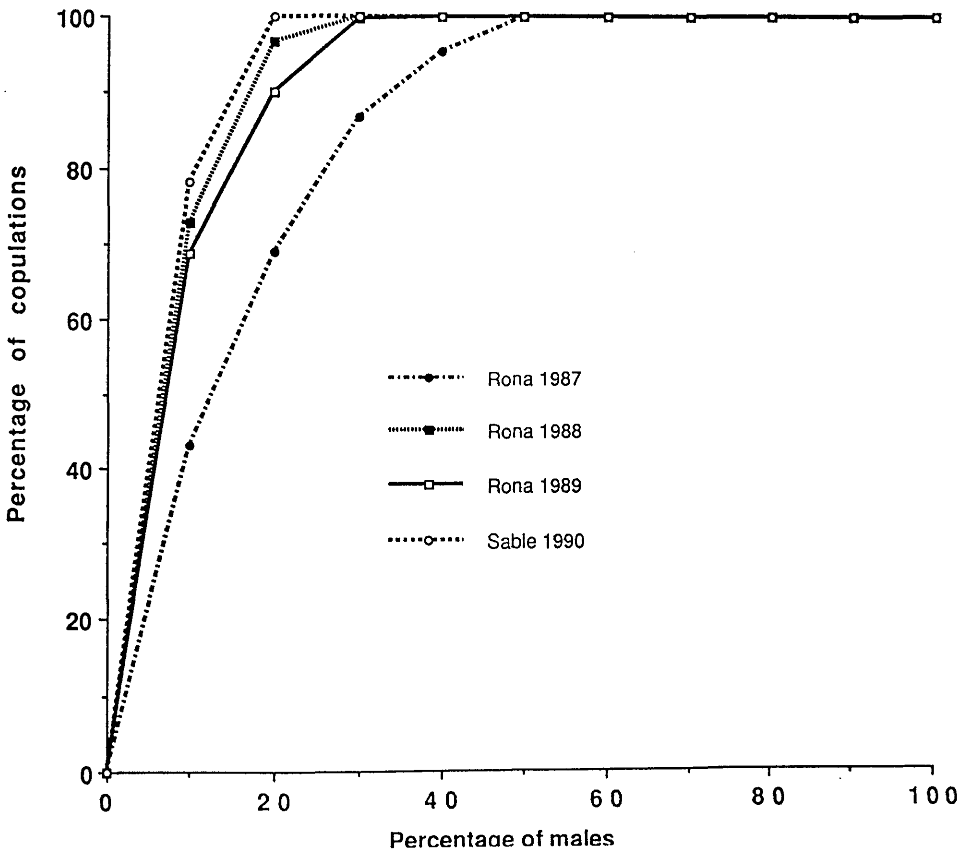


Figure 9.7 : Comparison of the relative degrees of polygyny at Sable and Rona



Tables 9.5 a and b provide summary statistics for observed mating success and the daily copulation rate for males present in the study area. Table 9.5 a includes all identified males in the study area, whilst Table 9.5 b gives statistics for only those males involved in ten or more inter-male aggressive encounters. As for the North Rona data, this excludes males for which there is insufficient data to allow calculation of dominance scores, generally males present for very short periods.

Oneway analyses of variance with Scheffe's Range tests were conducted on the data presented in Table 9.5 b to compare these means with those for North Rona. All data sets were transformed to approximate to normality as outlined in Chapter 7. The Sable island males had a significantly lower mean number of copulations than any of the three seasons at North Rona ($F_{3,\ 178} = 6.18$, $p = 0.0005$). However, there was no significant difference in the mean rate of copulations ($F_{3,178} = 1.15$, $p = 0.33$) although Sable had the lowest mean value.

Table 9.5a

Summary statistics for observed mating success and copulations per day (copulation rate) for all identified males on the study area.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1990	MATING SUCCESS	80	0.00	0.40	1.04	0.12	0	6
	COPULATION RATE	80	0.00	0.06	0.16	0.02	0.00	1.0

Table 9.5b

Summary statistics for observed mating success and copulations per day (copulation rate) for all identified males on the study area which were involved in 10 or more inter-male aggressive encounters.

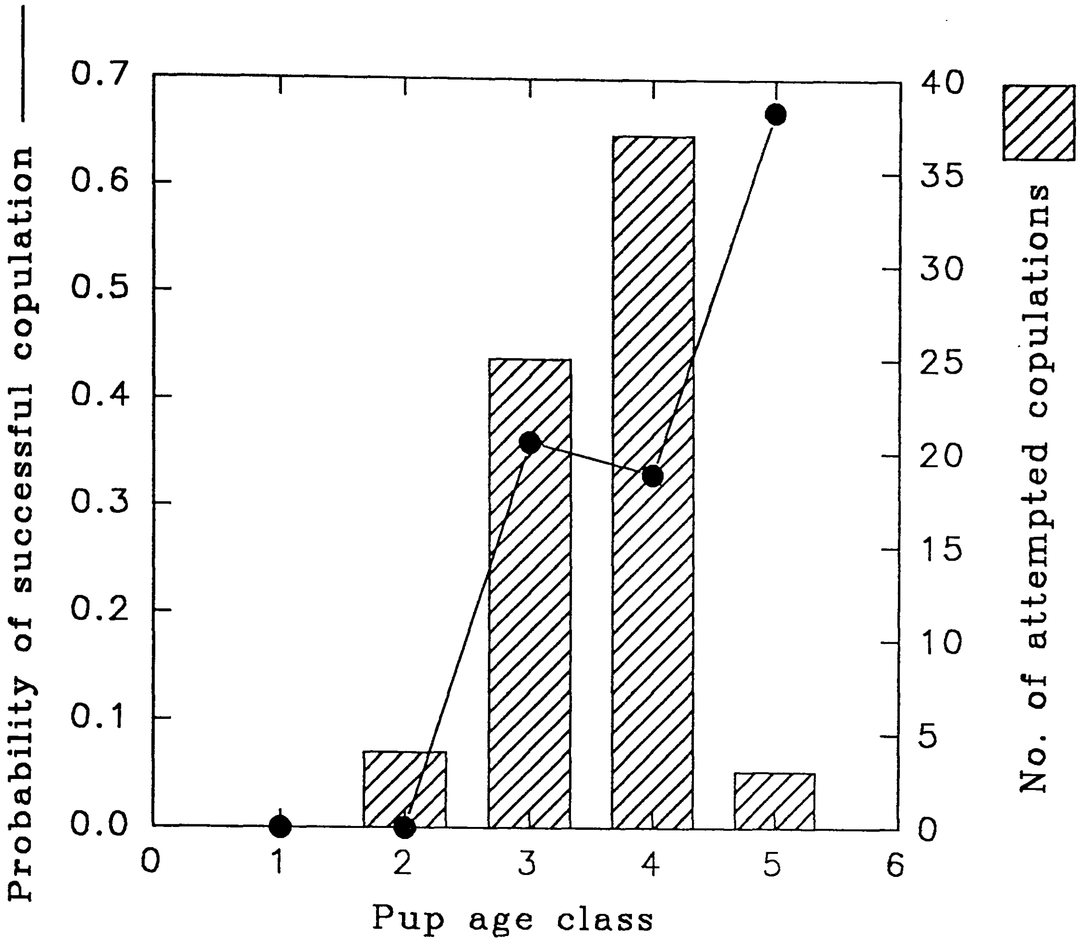
YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1990	MATING SUCCESS	42	0.00	0.76	1.34	0.21	0	6
	COPULATION RATE	42	0.00	0.11	0.21	0.03	0.00	1.00

Assessing the degree of polygyny

In an attempt to assess the degree of polygyny observed on Sable Island and to compare this with data from North Rona, the same measures of variability in male mating success were computed as for the North Rona data (see Chapter 6). The standardised variance (I) for the distribution of mating success at the Sable Island study site was 6.76. This value is in fact greater than any of those observed on North Rona (2.15, 5.31 and 5.26 for 1987, 1988 and 1989 respectively - see Chapter 6), indicating greater variance in male mating success at Sable Island. Similarly, Green's coefficient (see Chapter 6) was calculated in order to quantify the dispersion pattern of the distribution of mating success (Krebs 1989). Using mating success data for all identified males in the study area a coefficient of 0.055 was produced. Again, this is in fact greater than the comparable coefficients computed for North Rona, which were 0.018, 0.037 and 0.030 for 1987, 1988 and 1989 respectively. These values indicate that the distribution of mating success for Sable Island is the most aggregated when considering the sample size, thus, suggesting a greater degree of polygyny on Sable. However, there is no sampling distribution available for Green's coefficient, so confidence limits could not be assigned.

In order to assess whether there were in fact, any significant differences in the "degree of polygyny" between the Sable and North Rona data a further analysis was conducted. As with the Rona data, the cumulative percentage of copulations accounted for by each successive 10 % of identified males (ranked in order of decreasing mating success) present in the study area was plotted (see Figure 9.7). This figure also provides the equivalent data sets for each of the three seasons on North Rona for comparison. The curve obtained for Sable Island was statistically compared with each of the curves for North Rona by Kolmogorov Smirnov 2 sample tests. There were no significant differences between the Sable data and any of the Rona data sets. The greatest difference was found in the comparison with the 1987 season on Rona ($z = 0.64$, $n = 161$, $p = 0.808$) as would be expected from Figure 9.7. The comparison with Rona 1989 yielded values of $z = 0.43$, $n = 185$, $p = 0.993$, whilst with Rona 1988 showed little difference ($z = 0.21$, $n = 139$, $p = 1.00$). Thus, there was no significant difference in the "degree of polygyny"

Figure 9.8 : Distribution of attempted copulations and probability of success against pup age – Sable 1990



between Sable and Rona. In fact, examining Figure 9.7, the steepest curve and the one which attains 100 % first, is that for Sable Island.

Detection of female reproductive state by males

Figure 9.8 shows the distribution of attempted copulations, whether successful (leading to intromission) or not, directed by males towards females with pups of each age class. As was the case at North Rona there was a significant difference between the female groups with more attempted copulations were directed towards females with older pups (Chi square test; $chi^2 = 77.30$ at 4 degrees of freedom, $p < 0.001$).

This figure also gives the probability of these attempted copulations being successful (the proportion of successful attempts). The probability of success is greater with females of older pups as also seen in the Rona data (Chapter 6).

Interrupted sexual acts

Table 9.6 shows the number of approaches to females, attempted copulations and copulations, that were interrupted by other males. A successful interruption was deemed to have occurred when the interrupting male succeeded in preventing the male involved in the sexual encounter from completing that particular behaviour. This basically took two forms. The first is where the interrupter succeeded in displacing the initial male by some aggressive encounter, effectively "chasing" the initial male off. The second occurred where the interrupter approached the initial male who was engaged in sexual behaviour, and upon being noticed was then "chased off" by the initial male who in doing so ended his sexual interaction. An unsuccessful interruption occurred when the intruding male failed to end the sexual interaction by either of the means outlined above.

As can be seen from Table 9.6, very few interruptions occurred at all (47 out of 258 observed sexual interactions). Of these the vast majority were successful interruptions. Only one case was an unsuccessful interruption, where the male continued the sexual act despite the interruption. Unfortunately, there were too few cases to allow statistical analysis of this data. However, the general pattern agrees closely with that of the North

Rona data (see Chapter 6).

Comparison of the successful interruptions where the male involved in the sexual act chased off the intruder with those cases where the intruder chased off the male involved with the female, similarly agrees with the data presented for North Rona 1989. For approaches relatively few interruptions involved the initial male chasing off the intruder whilst a majority involved the intruder chasing off the initial male. In the case of attempted copulations, most cases involved the initial male chasing away the intruder whilst only a small proportion involved the intruder chasing off the initial male. In the case of actual copulations, the two categories of successful interruption have approximately equal numbers of cases.

Table 9.6
Table showing occurrence of forms of interrupted sexual acts.

SEXUAL ACTIVITY	OUTCOME OF INTERACTION		
	SUCCESSFUL INTERRUPTION		UNSUCCESSFUL
	♂ involved in sexual act leaves to chase off the interrupter	interrupter chases off ♂ involved in sexual act	
APPROACH TO FEMALE	5	12	0
ATTEMPTED COPULATION	16	4	1
COPULATION	5	4	0

9.1.5. *Colony attendance*:

Seal Numbers

Figures 9.9 summarises the records of numbers of bulls, cows and pups throughout the breeding season.

Females:

Pregnant females were present in the study area prior to the onset of observations on the 6th of January, but only in low numbers (7 females and 3 pups). The number of females continued to increase from this point reaching a maximum on the 18th of this month. As in British colonies the period of lactation is stated as being between 16 and 21 days (see Chapter 1). Therefore, it is not until 2 to 3 weeks into the season that the numbers begin to decline as the earliest arriving cows are mated and leave the colony. After the 18th the number of departing females exceeds the number of new arrivals and a steep decline in ensues. Although the occasional arrival still occurs even into February, the vast majority of females are departing, and by the end of observations (3rd of February) the number of cows was reduced to only three.

It is noticeable that the period over which females were present is much shorter than at North Rona, the breeding season only lasting for approximately 4 weeks (see also Boness 1979, Boness and James 1979). The absolute numbers of females present is much lower than the Rona study site; however, this was inevitable due to the sex ratio on the Sable colony (see below). Nonetheless, despite the condensed breeding season, the general pattern of female numbers is very similar to that seen on North Rona.

Pups:

The number of pups is obviously less than the number of cows early in the season. The increase in numbers follows closely that of the females as effectively each female produces one pup. Unlike Rona, the decline in pup numbers follows that of the females closely. This can be explained by an apparent difference in pup behaviour. Upon departure of the females at the end of lactation, pups were often seen following their mothers who lead them out of the study area. However, it is still noticeable that the number of pups is always slightly greater than the number of females during this latter half of the season.

Males:

The pattern of male numbers through the season is the main difference in colony attendance between Sable and Rona (Boness and James 1979). At Sable, males can be seen on the study site from the start of the observations. Previous authors have described their behaviour at the start of the season. The males remain ashore only when the first pups are born (Boness and James 1979).

The number of males increases gradually throughout the first half of the season, but then increases markedly around the 21st of January to reach a peak on the 25th, some 7 days after the peak number of females. A decline then ensues at a similar rate and level to that of the females, with only 3 males remaining on the 3rd of February.

Sex ratios

The main difference between Sable and Rona is the relative sex ratio on the colony. As can be seen from Figure 9.9, relatively more males gain access to the breeding colony compared to the number of females present at any one time than on North Rona (see Chapter 4). Figure 9.10 shows the ratio of females to males present during the seasons at Sable. It must be noted that these figures represent the sex ratio of only those animals on land in the study area.

The general pattern is very similar to that seen on North Rona, though at a lower ratio throughout the season. The highest ratio occurs at the start of the season (1 male : 3.5 females); this declines rapidly and remains reasonably stable for the first half of the season at approximately 1 male : 2 females. Most importantly, the lowest sex ratios occur in the latter half of the season, with a decline in the ratio occurring after the peak number of females. The declining female numbers and increasing male numbers decreases the sex ratio to below 1 : 1 on the 24th of January. The ratio continues to decline to a minimum of one male : 0.45 females on the 29th. The ratio remains at this low level until the close of the season when it returns to parity.

Figure 9.9 : Numbers of seals - Sable 1990

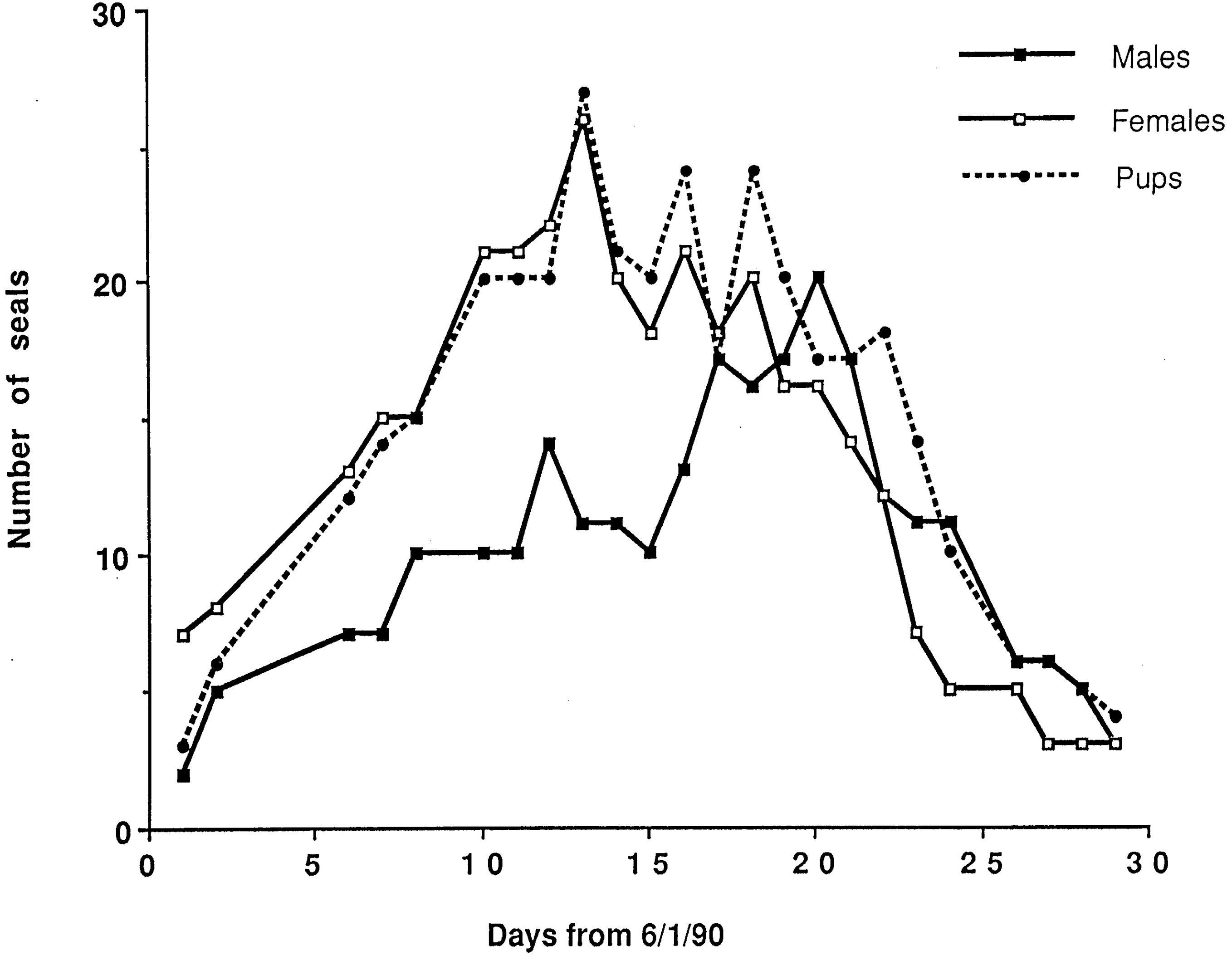


Figure 9.10 : Variation in sex ratio - Sable 1990

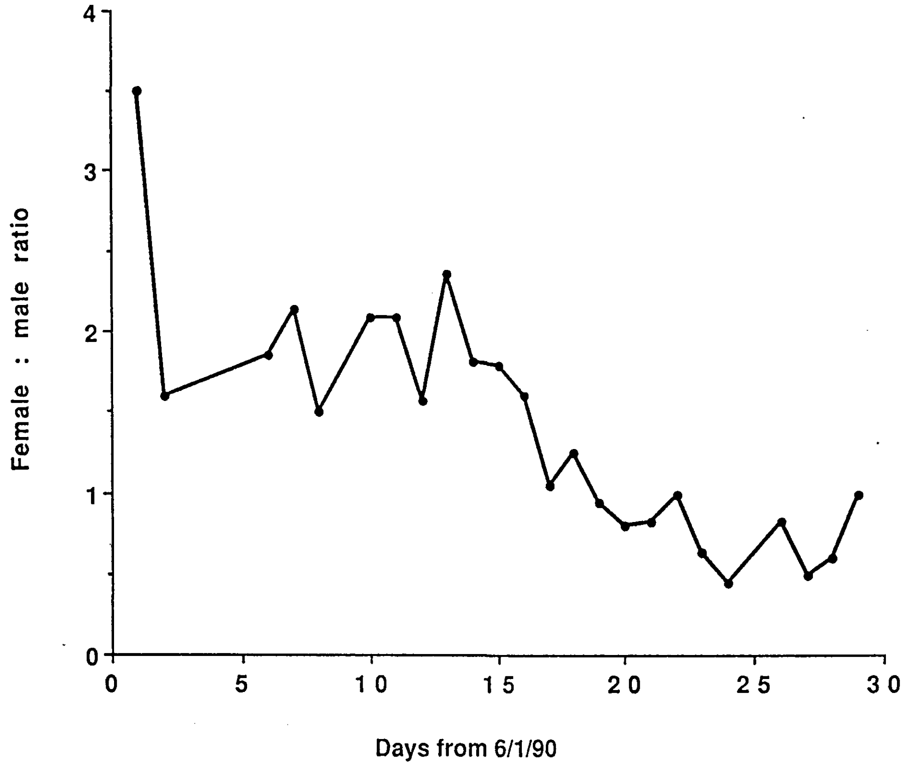
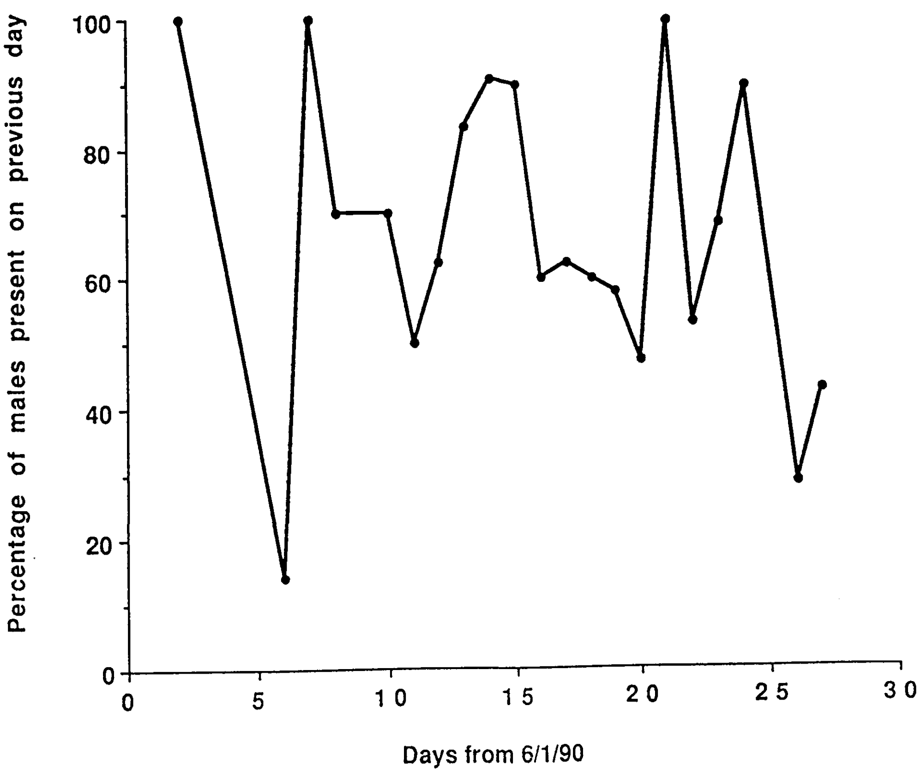


Figure 9.11 : Male turnover rates - Sable 1990



The mean sex ratio for the entire season in each year was 1 male to 1.41 females with a median of 1 : 1.38. Taking only values from the date of the first observed copulation (16th of January) the mean was 1 male : 1.18 females and a median of 1 : 1.0.

Male turnover rates

Figure 9.11 illustrates the relative turnover rates of males during the season. As with the North Rona data (see Chapter 4), this turnover rate is expressed as the proportion of males present in the study area on any given day that were also present on the previous day. Thus, a low proportion indicates a relatively high turnover of males, whilst a high percentage indicates little change in the identities of males present from one day to the next.

There is considerable fluctuation from day to day and, unlike the Rona data, no general trend can be discerned. However, it appears that the greatest male turnover occurs primarily in the mid-season period. The high turnover on the 6th of January was due to a sudden influx of males whereas prior to this date only one male had been present, and consistently so.

Distribution of seals

The series of maps shown in Figure 9.12 a to d illustrate key points in the colonisation of the study area throughout the breeding season. These maps depict the relative distributions of breeding females and the positions of males. All males have an individual 3 digit identification code. Any male brands are shown in parentheses.

It is clear that, despite the lower numbers, the females tend to be more widely dispersed and less clumped than on Rona (see Chapter 4). At the start of the season the females appear to gather around the pool (map a) but then become more widely and evenly dispersed. This is most probably due to the topography of the site. The dunes are small and present no barrier to seal movement, nor do they provide much shelter. As seen from the activity budgets, many seals eat snow, thus, negating the need to gather around the one pool in the study area, which was more often than not frozen.

Length of stay on the breeding colony

Tables 9.7 a and b show summary statistics for length of stay, date of arrival in the study area and date of departure from the study area. Table 9.7a includes all identified males in the study area, whilst Table 9.7b gives statistics for only those males involved in ten or more inter-male aggressive encounters. As for the North Rona data, this excludes males for which there are insufficient data to allow calculation of dominance scores, which are generally males present for very short periods.

Figure 9.12: Maps showing changes seal distribution in the study area during the 1990 season on Sable.

Notes: see Figure 9.1 b for details of study area.
Males are denoted by blue dots, each with the relevant male identity code (and brand where appropriate).
Females are denoted by red dots.

Figure 9.12 : Maps showing seal distribution - Sable 1990

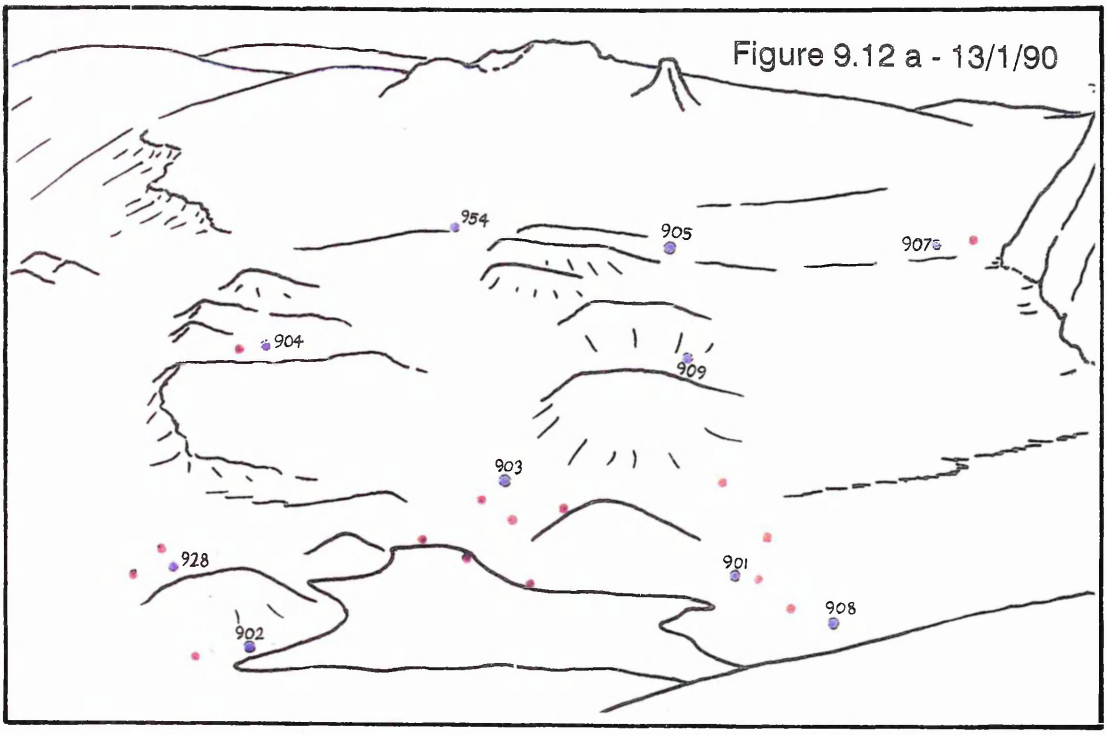


Figure 9.12 a - 13/1/90

● **Males**

● **Females**

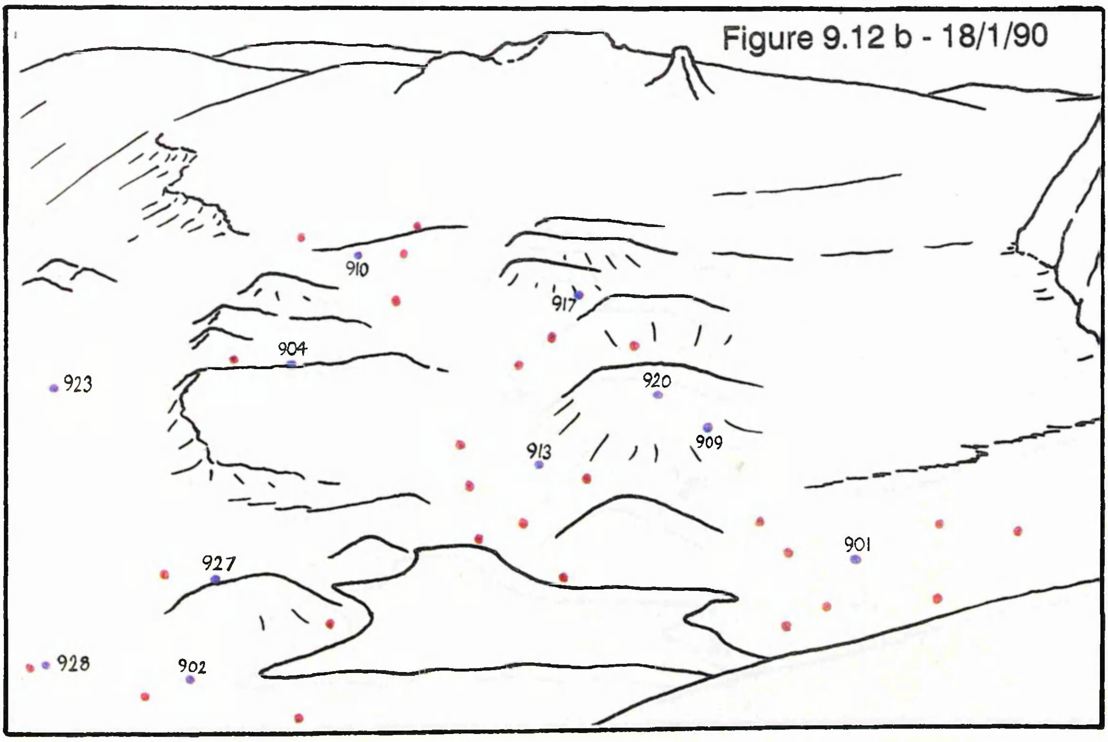


Figure 9.12 b - 18/1/90

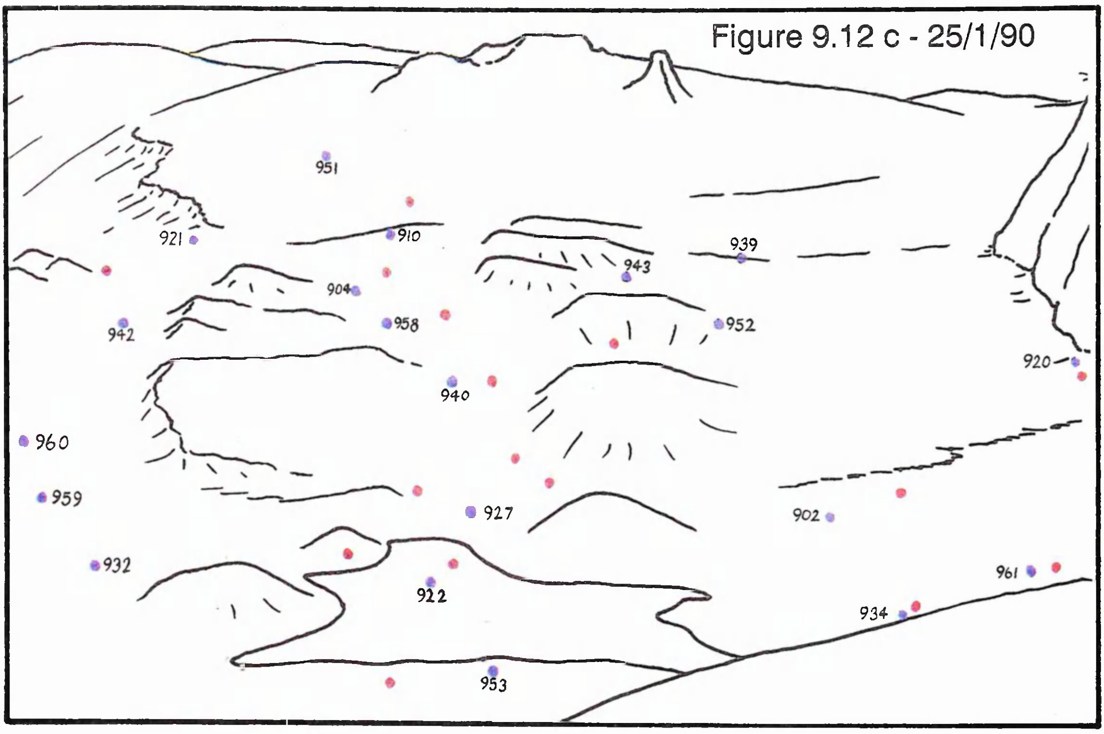


Figure 9.12 c - 25/1/90

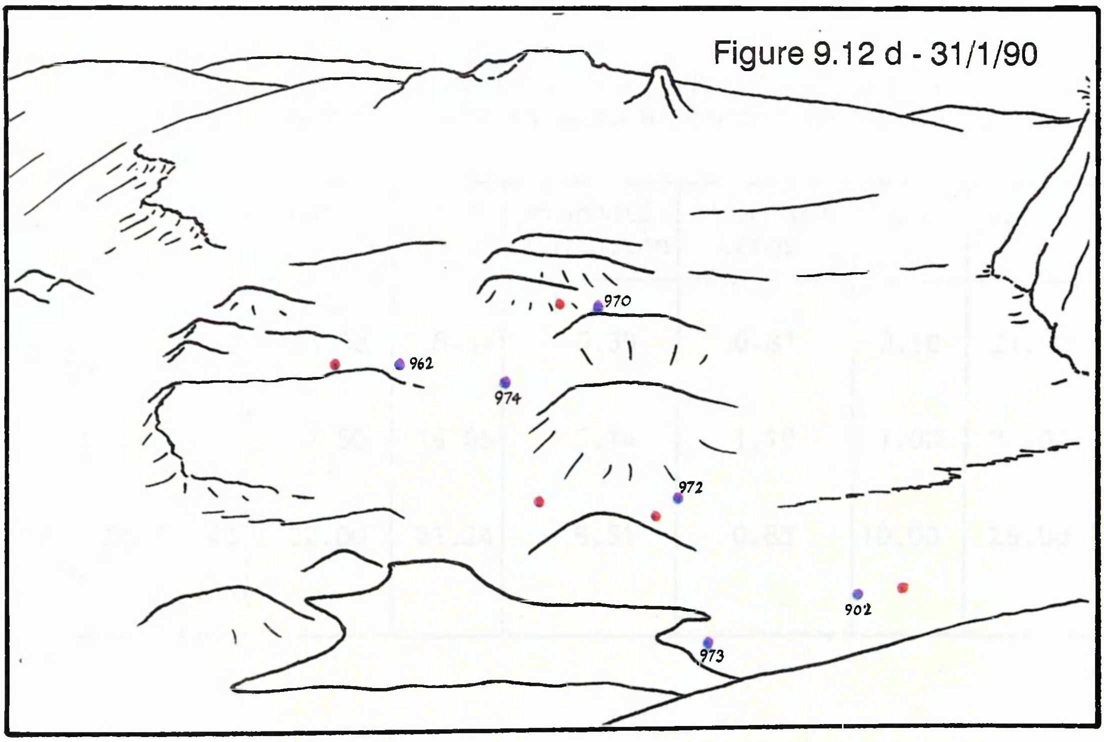


Figure 9.12 d - 31/1/90

Table 9.7a

Statistics illustrating length of stay, arrival date and departure date of all identified males on the study area.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1990	No. DAYS ASHORE	80	1.00	3.16	4.51	0.50	0.10	21.00
	ARRIVAL DATE	80	17.00	16.56	6.33	0.71	1.00	28.00
	DEPARTURE DATE	80	20.00	19.34	5.74	0.64	7.00	28.00

Notes: (these apply to both Table 9.7a and b)

No. DAYS ASHORE - this represents a measure of the length of stay in terms of entire days spent in the study area.

ARRIVAL DATE - for each male present a value was given denoting the day upon which he arrived, a value of 1 representing the 6th of January (the first date on which observations were made), 2 representing the 7th etc, etc.

DEPARTURE DATE - each male received a number recording the day on which he was last sighted on the study area using the same numbering system as for arrival date.

Table 9.7b

Statistics illustrating length of stay of all identified males on the study area which were involved in 10 or more separate inter-male aggressive encounters.

YEAR	VARIABLE	n	median	mean	standard deviation	standard error	min.	max.
1990	No. DAYS ASHORE	42	3.25	5.31	5.39	0.83	0.10	21.00
	ARRIVAL DATE	42	17.50	16.05	7.14	1.10	1.00	28.00
	DEPARTURE DATE	42	22.00	21.24	5.51	0.85	10.00	28.00

The actual amount of time spent on land by each male during the entire breeding period can vary from a matter of hours to almost the entire season. There is considerable variation in lengths of stay, with a standard deviation of 4 to 5 days.

A vast majority of the males have relatively short stays, 70.0% of the males were ashore in the study area for less than a tenth of the breeding season, 93.8% of bulls remaining in the study area for less than half the season. In contrast, none of the males stayed for greater than 90% of the season, the longest stay being 21 days.

The data presented in Table 9.7 b were transformed to approximate to normality as in Chapter 7. A comparison by oneway analysis of variance (with Scheffe's Range tests) of the mean values of each variable in Table 10.6 b was then made with the respective counterparts for each of the three seasons at Rona. This revealed that Sable males stayed in the study area for significantly shorter periods than the North Rona males remained ashore on Rona in any of the three years ($F_{3, 178} = 17.49$, $p < 0.0001$). This is not entirely surprising, as the breeding season on Sable is much shorter. There was however, no significant difference in mean arrival date at Sable and the three seasons' data for Rona, although the Rona 1987 data was significantly different to Rona 1989 ($F_{3, 178} = 5.06$, $p = 0.002$, see Chapter 4). Comparison of arrival dates between Sable and Rona must be viewed with caution, as both utilise arbitrary dates as the onset of the season which may not be strictly comparable. The mean departure date at Sable was significantly earlier than all three seasons on Rona ($F_{3, 178} = 22.90$, $p < 0.0001$). This is not surprising since,as mentioned previously, the season at Sable is much shorter than at Rona.

9.2. *Factors affecting individual male mating success*

The variables described above were examined for inter-relationships. The method of analysis used was the same as applied to the Rona data in Chapter 7. Only cases with at least 10 inter-male aggressive encounters were selected. All data sets were examined for normality, those failing the criteria were transformed as follows;

Length of stay - Log$_{10}$(stay)
No. aggressive encounters - Log$_{10}$(No. A.I.s)
Mating success - Log10(mating success)
Copulations/day - Square root(copulations/day)
Aggression/day - Log$_{10}$(aggression/day)

The remaining variables did not require transformation. These variables were then examined for Pearson correlations at $p < 0.01$. The correlation matrix is provided in Appendix C. Obviously with only one years' data, the analysis of covariance technique used in Chapter 7 could not be used. Multiple regression models were then developed for each dependent variable as in Chapter 7. Utilising the results of these analyses a final flow diagram was constructed.

9.2.1. *Colony attendance parameters:*

Arrival date

As might be expected arrival date shows a strong negative correlation at $p < 0.01$ with length of stay ($r = -0.53$, $n = 42$, $p < 0.001$). Males arriving earlier have the opportunity to remain in the study area for longer. There is also a strong, but positive correlation with departure date ($r = +0.58$, $n = 42$, $p < 0.001$). Thus, males that arrive early tend to depart relatively earlier in the season. This appears to contradict somewhat the first correlation. However, males that arrive early and stay for long periods, may still depart relatively earlier. This will be examined further in the multiple regression models.

One particularly interesting point is the lack of correlation at $p < 0.01$ with total number of inter-male aggressive interactions ($r = -0.33$, $n = 42$, $p = 0.032$). Conversely, there is a highly significant and positive correlation with daily rates of aggression ($r = 0.42$,

$n = 42$, $p = 0.005$). Thus, early arrivals show a slight tendency for greater overall aggression, but have significantly lower daily rates of aggression. Since this may be acting via length of stay, it is tested in subsequent multiple regressions.

No multiple regression analysis was conducted with arrival date as the dependent as the only plausible independent variable for which data are available is dominance score, with which there is no significant correlation ($r = +0.14$, $n = 41$, $p = 0.38$).

Departure date

Unlike arrival date, departure date shows no significant correlation with length of stay ($r = +0.21$, $n = 42$, $p = 0.19$). However, as mentioned above departure date does correlate with arrival date.

Departure date exhibits no other correlations significant at $p < 0.01$, though there are correlations at $p < 0.05$ with dominance score ($r = -0.31$, $n = 41$, $p = 0.05$) and total aggression ($r = +0.34$, $n = 42$, $p = 0.028$). Thus, there is a suggestion that dominant males may depart later, and that males departing later were involved in more aggressive interactions. Again this may be mediated via length of stay.

The multiple regression model (Table 9.8.1) revealed arrival date to be the primary predictor of departure date. Length of stay was entered on the second step, thereby making a significant contribution independently of arrival date. The reverse regression confirmed this, by entering departure date on the first step, and again, length of stay on the second step.

Table 9.8.1

Table summarising results of multiple stepwise regression model developed for departure date. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1990	DEPENDENT VARIABLE - DEPARTURE DATE n = 41			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	2	0.37725	< 0.0001	0.69791
TOTAL No. A.I.s				
MATING SUCCESS				
DOMINANCE SCORE				
ARRIVAL DATE	1	0.33577	0.0001	0.31874
REVERSE REGRESSION - DEPENDENT = ARRIVAL DATE				
DEPARTURE DATE	1	0.33577	0.0001	0.31874
LENGTH OF STAY	2	0.45215	< 0.0001	0.77676
MATING SUCCESS				
TOTAL No. A.I.s				
DOMINANCE SCORE				

Notes;

Independents not used;

Copulations and aggressive interactions per day are not included as these are mean daily rates, sexual and aggressive behaviour are represented by total mating success and aggressive interactions and length of stay. Also, when included in the regression, the outcome remains the same.

Length of stay in the study area (days)

There is a significant positive correlation between length of stay and total mating success ($r = +0.56$, $n = 42$, $p < 0.001$). Males able to maintain a position on the colony for long periods gain greater mating success.

Similarly, length of stay is highly correlated with total number of aggressive encounters ($r = +0.73$, $n = 42$, $p < 0.001$). Males that remain ashore for longer are, not surprisingly, involved in significantly more aggressive interactions.

There is no significant correlation at $p < 0.01$ between length of stay and daily copulation rate ($r = +0.38$, $n = 42$, $p = 0.014$), although there is a significant negative correlation at $p < 0.01$ between stay and aggression rates ($r = -0.67$, $n = 42$, $p < 0.001$). Males that are ashore for longer, although being involved in more aggressive encounters in total are in fact involved in less aggression per day.

Length of stay is highly significantly correlated at $p < 0.01$ with dominance score ($r = -0.67$, $n = 41$, $p < 0.001$). Thus, more dominant individuals are able to maintain a position on the colony for significantly longer than more subordinate individuals.

Correlations between length of stay and both arrival and departure date are discussed above.

Multiple regression models developed for length of stay (Table 9.8.2) revealed that the main behavioural determinant of stay was dominance. Arrival date and departure date were then entered, making a comparatively small, but significant contribution. The reverse regression confirmed this result as length of stay was entered on the first step when dominance score was used as the dependent variable.

Table 9.8.2

Table summarising results of multiple stepwise regression model developed for length of stay. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1990	DEPENDENT VARIABLE - LENGTH OF STAY n = 41			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE	1	0.45323	< 0.0001	0.43921
ARRIVAL DATE	2	0.20306	< 0.0001	0.63819
DEPARTURE DATE	3	0.15336	< 0.0001	0.79421
REVERSE REGRESSION - DEPENDENT = DOMINANCE SCORE				
LENGTH OF STAY	1	0.45323	< 0.0001	0.43921
ARRIVAL DATE				
DEPARTURE DATE				

Notes;
Independents not used;
Total aggressive interactions and mating success are assumed not to be determinants of length of stay, but are themselves determined by length of stay.
Aggressive encounters and copulations per day are not determinants of stay (both are daily rates).

9.2.2. *Dominance and aggression levels*:

Dominance

The dominance score calculated shows the most significant correlation with mating success ($r = -0.57, n = 41, p < 0.001$). More dominant individuals clearly gain greater mating success than more subordinate males. Dominant individuals also have greater daily rates of copulation ($r = -0.43, n = 41, p = 0.005$).

Similarly, there is a strong correlation between length of stay and dominance, again significant at $p < 0.01$ (see above). Thus, more dominant individuals remain ashore for significantly longer than more subordinate males. Relationships with arrival and departure date are detailed above.

There was no significant correlation with total number of aggressive encounters at $p < 0.01$ ($r = -0.33, n = 41, p = 0.034$), however, dominant males did have significantly less aggression per day ($r = +0.64, n = 41, p < 0.001$).

No multiple regression model was constructed for dominance as no variables for which data were collected were deemed possible determinants of dominance.

Total number of aggressive inter-male encounters

Total number of inter-male aggressive encounters is highly correlated with total mating success ($r = +0.53, n = 42, p < 0.001$). However, as total aggression is also highly correlated with length of stay, as is mating success, this relationship may be mediated via the length of stay. This is tested by use of multiple regression procedures.

Total aggressive encounters is correlated with daily rate of copulation at $p < 0.05$, but not at $p < 0.01$ ($r = +0.36, n = 42, p = 0.017$). There was no significant relationship with daily aggression levels.

Correlations with arrival date, departure date and dominance are detailed above.

Table 9.8.3 presents the results of the multiple regression procedure applied to the number of inter-male aggressive encounters. The primary determinant was length of stay. Again, the reverse regression confirmed the result, as the number of aggressive interactions was entered on the first step.

Table 9.8.3

Table summarising results of multiple stepwise regression model developed for total number of inter-,ale aggressive interactions. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1990	DEPENDENT VARIABLE - TOTAL NUMBER OF A.I.s n = 41			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY	1	0.54408	< 0.0001	0.53239
MATING SUCCESS				
ARRIVAL DATE				
DEPARTURE DATE				
DOMINANCE SCORE				
REVERSE REGRESSION - DEPENDENT = LENGTH OF STAY				
TOTAL No. A.I.s	1	0.54408	< 0.0001	0.53239
MATING SUCCESS				
ARRIVAL DATE	3	0.08106	0.0002	0.81784
DEPARTURE DATE				
DOMINANCE SCORE	2	0.20635	< 0.0001	0.73730

Daily rate of inter-male aggressive activity

Daily rate of aggression exhibits significant correlations with arrival date, length of stay and dominance. Details of these are provided above.

Multiple regression analyses revealed that arrival date was the main predictor of rates of aggression. Dominance score was entered on the second step (Table 9.8.4). However, in the reverse regression, with arrival date as the dependent variable, departure date was entered first with the number of aggressive interactions per day being entered on the second step.

9.2.3. *Age*:

Only seven of the 80 identified males were branded and therefore of known age. The ages ranged from 12 to 19 years, a mean of 15.57 (S.E. = 1) and a median of 16 years. The sample size was to small to enable any firm conclusions to be drawn from the correlations of age with the other variables, though some interesting trends were seen. The correlation results are presented in Appendix C. None of the correlations were significant, even at $p < 0.05$; however, relatively high r values were found in some cases. There was a positive trend with length of stay ($r = 0.70$, $n = 7$, $p = 0.078$) indicating that older males may remain in the study area for longer. A high negative r value was found with dominance score ($r = -0.67$, $n = 7$, $p = 0.096$), indicating that older males may be the more dominant individuals. Although there was little sign of a trend with overall mating success ($r = 0.46$, $n = 7$, $p = 0.30$) there was an indication that older males gain greater copulations per day ($r = 0.65$, $n = 7$, $p = 0.115$). A larger sample size is required to examine whether these potential relationships are in fact real.

Table 9.8.4

Table summarising results of multiple stepwise regression model developed for daily rate of inter-male aggressive interactions. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.
X = order in which independent variables were entered

1990	DEPENDENT VARIABLE - No. AGGRESSIVE INTERACTIONS/DAY n = 41			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE	2	0.16016	0.0032	0.39220
ARRIVAL DATE	1	0.26403	0.0008	0.24414
DEPARTURE DATE				
COPULATIONS/DAY				
REVERSE REGRESSION - DEPENDENT = ARRIVAL DATE				
AGGRESSION/DAY	2	0.16094	0.0015	0.48211
DOMINANCE SCORE				
DEPARTURE DATE	1	0.34843	0.0001	0.33082
COPULATIONS/DAY				

Notes;

Independents not used;

Length of stay and total number of aggressive interactions are not included as they are not truly independent of aggression per day.
Total mating success - this is replaced by copulations per day as a measure of sexual activity, this being a daily rate like aggression per day.

9.2.4. *Mating success*:

Table 9.8.5 details all correlations with mating success. These are described in detail in the relevant previous sections of this chapter.

Table 9.8.6 shows the multiple regression models produced for mating success. Dominance score was entered as the primary predictor, with total number of aggressive encounters being entered on the second step. However, the reverse regression fails to confirm this, as length of stay was entered on the first step when dominance score was used as the dependent variable.

Table 9.8.7 provides the model for the daily rate of copulations. Again, dominance score was entered as the main determinant of copulation rate. The reverse regression fails to confirm this, with the number of inter-male aggressive interactions per day being entered on the first step when dominance score was used as the dependent variable.

Figure 9.13 shows the final flow diagram developed from all the analyses conducted above. Although both length of stay and dominance were highly correlated with mating success, dominance was entered in preference to length of stay in the multiple regression procedure. Thus, at the Sable Island study site the main determinant of male mating success was relative dominance. The more dominant males gain greater mating success. This is not only because dominant males remain in the study area for significantly longer, but they also gain greater daily rates of copulation.

Obviously, males that arrive earlier, and those that depart later tend to have longer stays. However, in contrast to the model developed for North Rona, arrival date appears to have a greater influence on length of stay than departure date.

Males that remain ashore for longer are involved in more aggressive interactions in total but are subject to lower daily rates of aggression.

Table 9.8.5

Table showing relationships of mating success with other variables from data collected at Sable Island, 1990. Analyses are Pearson correlations, only cases with at least 10 inter-male aggressive encounters have been used. Bold type denotes significance at 0.05 > p > 0.01, bold type with * denotes significance at p < 0.01.

VARIABLE	r	n	p
COPULATIONS/DAY	**+0.86**	**42**	**< 0.001***
TOTAL No. A.I.s	**+0.53**	**42**	**< 0.001***
A.I.s / DAY	-0.24	42	0.134
DOMINANCE SCORE	**-0.57**	**41**	**< 0.001***
COLONY ATTENDANCE PARAMETERS			
ARRIVAL DATE	-0.26	42	0.095
DEPARTURE DATE	+0.27	42	0.089
STAY (DAYS)	**+0.56**	**42**	**< 0.001***

Table 9.8.6

Table summarising results of multiple stepwise regression model developed for mating success. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

1990	DEPENDENT VARIABLE - MATING SUCCESS n = 41			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
LENGTH OF STAY				
TOTAL No. A.I.s	2	0.12604	0.0054	0.42169
DOMINANCE SCORE	1	0.32457	0.0001	0.30725
ARRIVAL DATE				
DEPARTURE DATE				
REVERSE REGRESSION - DEPENDENT = DOMINANCE SCORE				
MATING SUCCESS				
TOTAL No. A.I.s				
LENGTH OF STAY	1	0.45323	< 0.0001	0.43921
ARRIVAL DATE				
DEPARTURE DATE				

Notes;

Independents not used;

Copulations per day - not truly independent of mating success.
Aggression per day like copulations per day, is a daily rate, not an overall measure for the entire season as is mating success.

Table 9.8.7

Table summarising results of multiple stepwise regression model developed for copulations per day. Results of the reverse regression are displayed in the latter portion of the table, where the dependent variable is that independent variable which was entered first in the forward regression procedure.

X = order in which independent variables were entered

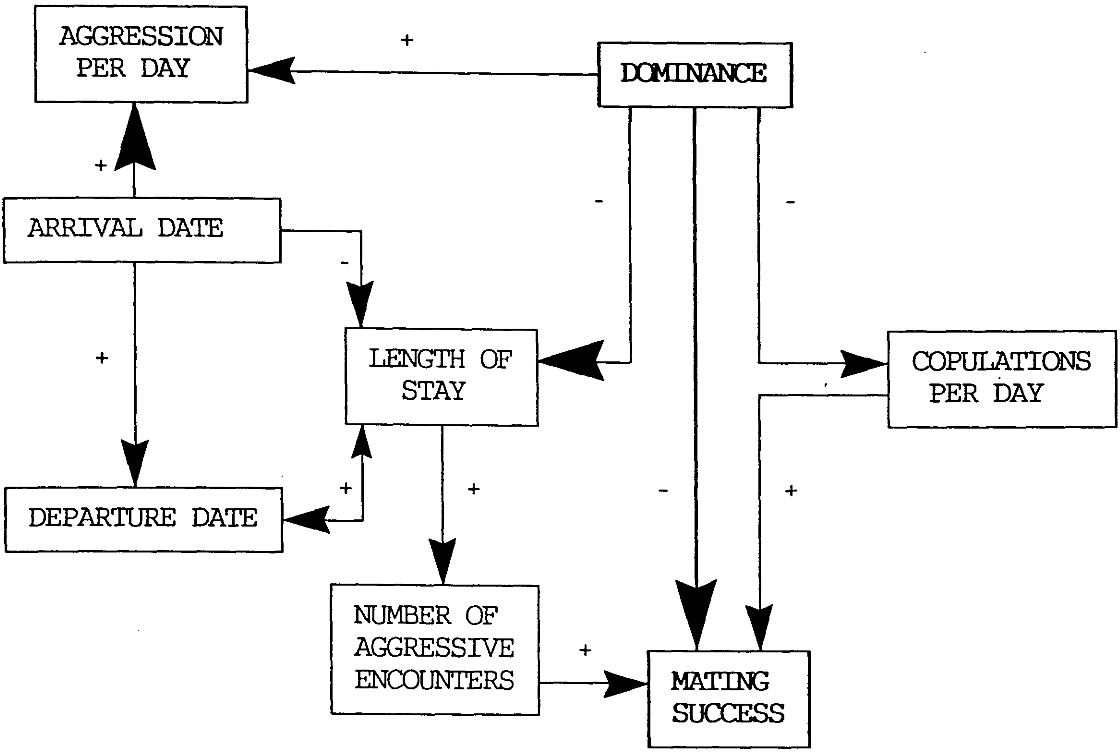
1990	DEPENDENT VARIABLE - COPULATIONS PER DAY n = 41			
INDEPENDENT VARIABLES	X	R^2 CHANGE	SIGNIFICANCE OF F CHANGE	ADJUSTED R^2
DOMINANCE SCORE	1	0.16874	0.0094	0.14627
ARRIVAL DATE				
DEPARTURE DATE				
AGGRESSION/DAY				
REVERSE REGRESSION - DEPENDENT = DOMINANCE SCORE				
COPULATIONS/DAY				
DEPARTURE DATE				
ARRIVAL DATE				
AGGRESSION/DAY	1	0.23605	0.0017	0.21540

Notes;

Independents not used;

Length of stay - this is not truly independent of copulations per day.
Total aggressive interactions - aggressive behaviour is represented by aggression per day, which expresses this parameter as a mean daily rate, as is copulations per day.

Figure 9.13 Final flow diagram constructed from the regression analyses for Sable Island (1990) study area males.



Notes :

1. Dominance score is calculated such that the more dominant individuals have a lower score than more subordinate males. Thus the relationships between dominance and mating success, copulations per day and length of stay are all negative.

2. Similarly, arrival date is recorded such that early arrivals have a lower value than late arrivals, hence the negative relationship with length of stay.

DISCUSSION

Interpretation of the data presented in this chapter must be viewed with caution. Unlike the Rona data, conclusions have, of necessity, been drawn from only a single season's data. Examining the correlation matrices for Rona reveals how a few inconsistent, spurious correlations can provide differing interpretations when viewing a single seasons data in isolation. Also, unfortunately, due to the constraints on selection of study site, and no prior knowledge of this site, only a maximum of 26 females were observed on the study site. However, with the sex ratio averaging close to 1 : 1 on Sable, this was perhaps inevitable. As the maximum number of males present at any one time was 20 individuals, which is comparable with the maximum numbers on Rona and close to the limit at which observations of individuals would become impossible, it was not possible to find a site with more females without also increasing the number of males.

However, despite these problems, the remarkable similarity of certain behavioural parameters from the Sable data set with those of Rona provide some confidence in examining the potential differences between the two colonies.

The topography of a breeding site has important influences on male behaviour. This acts indirectly through its effect on female distribution and directly by available access to the breeding grounds. Boness and James (1979) dismissed any differences in female distribution when comparing Sable and Rona, stating that "any differences between the Rona and Sable colonies in the way in which the cows distribute themselves over the breeding grounds are likely to be small in relation to the differences in the spacing of males". However, as in most mating systems, the grey seal breeding organisation is essentially female driven. Females disperse according to individual requirements for suitable pupping sites (Anderson, Baker, Prime and Baird, 1979). The topography largely influences the availability of sites and hence female distribution. Males are then forced to compete for the prime sites in terms of availability of females. Although the relative distribution of males is more strikingly different between Sable and Rona, the small but apparent differences in female distribution may be more important in explaining male behaviour. Unfortunately, it was not possible to obtain detailed quantitative data on female dispersion at Rona or at Sable, primarily due to reluctance to enter the study areas more than necessary and the perspective of the daily census maps. As these maps were made from the hides, it has proved difficult to accurately assess distances between individuals due to the compression of space with distance from the hide. This is particularly so, on the more uneven terrain of the Rona study site. However, data from aerial photography could be valuable in resolving this dilemma. Detailed analysis of female dispersion is essential for a complete picture of these mating systems.

However, from the maps presented in this chapter and Chapter 4, it is apparent that females are more evenly dispersed than on Rona. It is also clear that access to the breeding grounds of Sable is relatively unrestricted. Thus, relatively more males gain positions on the colony. As the females are more evenly dispersed, individual males are unable to monopolise groups of females, hence more males gain positions amongst the females. Thus we have a relatively even apparent operational sex ratio on Sable Island.

Traditionally, this would be taken to represent a lower degree of polygyny as outlined in the introduction to this chapter. However, it is now possible to answer the question; how many males are actively involved in reproduction? From the data presented on mating success a lower proportion of the identified males gained at least one copulation than on North Rona, approximately one fifth as opposed to one quarter (1988) to a half (1987). Accordingly, the mean percentage of time spent in sexual activity on Sable as assessed by the activity budgets is significantly lower than on Rona. Similarly, the top male and top five males in terms of mating success at Sable accounted for a greater proportion of the observed copulations than did the corresponding males on Rona in any of the three seasons. Thus, it appears that the degree of polygyny on Sable is perhaps more extreme than on Rona, at least within the study sites chosen. The analyses of the distribution of mating success and the comparison with equivalent data from the three seasons on Rona (Figure 9.7) demonstrated that the degree of polygyny amongst the male grey seals of Sable Island was certainly not less than observed on Rona. Why then is this so, and what determines individual mating success on Sable Island?

As shown in the analyses presented in this chapter, of the measured variables, dominance is the main predictor of mating success. Although most males gain positions on the colony, subordinate bulls are prevented access to oestrus females by more dominant individuals. Thus, dominance is a more important determinant of mating success than time spent on the colony. However, obviously,successful males need to remain ashore for long periods.

This process requires that males can assess the reproductive state of females. This has been suggested by Boness and James (1979) and data are provided here to support this, in that a vast majority of attempted copulations are directed towards females with older pups.

If the system on Sable is highly polygynous, with access to receptive females determined by dominance status, then one would expect higher levels of inter-male competition. The data presented in this chapter supports this. The total levels of inter-male aggression on Sable were not significantly greater than those for Rona, however, it must be taken into account that the breeding season is much shorter at Sable. Thus, examining mean daily rates of aggression we see a highly significant difference, with much greater levels of aggression amongst Sable males. Similarly, the activity budgets reveal a greater proportion of time spent in aggressive activity for Sable males. Thus, it would appear that the greater number of males present does not indicate lower levels of inter-male aggression as suggested by Boness and James (1979) and Anderson and Fedak (1985), but quite the opposite.

The seasonal variation in aggression also supports this explanation. On Rona, the highest levels of inter-male aggression occur at the onset of the season, whereas on Sable the levels of aggression reflect more closely the levels of sexual activity. Thus, during the period of peak availability of oestrus females there is relatively higher level of male-male competition.

Thus, access to the colony for males is not restricted by topography or more dominant individuals. However, access to oestrus females is restricted by the presence of the dominant males, which are therefore able to monopolise a disproportionate amount of mating opportunities.

There is still a strong relationship between length of stay on the study site and mating success in the study site. However, unlike on Rona, I was unable to observe marked males in other parts of the colony. Males on Rona seldom moved from one site to another, thus, the length of stay in the study site could be taken as a reasonable measure of their length of stay on the breeding grounds as a whole. However on Sable this may not be the case. Godsell (1991) shows that on Sable Island a majority of the inter-male aggression is directed from older males to younger individuals. Hence, older males appear to be the more dominant individuals. This aggression was responsible for the relatively short stays of younger males in a single area. The older males therefore tended to remain in a single area for much of the breeding season, whilst younger males moved around the island, attempting to gain copulations at various breeding sites. This is in broad agreement with the trends indicated by the age relationships shown in this chapter. Godsell also found no correlation between body weight and length of stay or copulation rate.

Most males, therefore, appear to remain ashore for much of the season, whether in a single area or moving around the island. Thus, initial energy reserves and subsequent energy expenditure may be an important determinant of total time spent ashore on Sable. On Rona, any effect of energetics on length of stay is masked by the effect of dominance determining length of stay, so that few males get the opportunity to remain ashore for long periods. It would be particularly interesting to conduct an energetics study on branded Sable males. A contributory factor to Sable males remaining ashore may be the presence of Great White sharks offshore. These predators feed mainly on pups of the year, but many males were observed with scars most probably from shark attacks. The presence of such marine predators is not a problem at Rona.

As we were unable to gain weights and measurements on the Sable males we cannot make any comment on the relative sizes of males and females. From the limited data presented by Mansfield (1977) it appears there is little difference in the proportional size dimorphism of eastern and western atlantic populations. This does not agree with traditional sexual selection theory if Sable seals were less polygynous. However, there are insufficient data to address this problem as yet, hopefully, in the course of ongoing studies at Sable more data on relative male and female sizes will be obtained.

Predictions on the relative size dimorphism can be made based on the theories presented in the discussion to Chapter 7. If inter-male competition actually on the colony is important in determining access to females, one might expect a greater disparity in sizes at Sable, assuming that male size is related to competitive ability on land. Conversely, if size is not important in fighting and/or dominance relationships are established prior to the breeding season, one might expect a lower degree of dimorphism. As the breeding season is shorter than on Rona, the maximum stay necessary for Sable males is only 7 days longer than the maximum stay for females, hence a lower degree of size dimorphism. As yet, there are insufficient data to decide between these two possibilities.

The work presented in this chapter can only be viewed as a preliminary study of male reproductive behaviour on Sable Island. There is much scope for research on Sable Island, in particular, a similar study to that made on North Rona, combining both behavioural observations and energetics studies over several seasons. Perhaps, with more males remaining ashore for much of the season, the role of energetics will be more readily elucidated.

CHAPTER 10 - DISCUSSION

The preceding chapters have discussed the important points raised by the data presented therein. In this general discussion, a few points of particular interest are discussed in more detail.

Mating system

As stated in Chapter 7, there is ample evidence to demonstrate that the breeding system of the grey seal is one of polygyny (Anderson *et al.*, Boness 1979, Boness and James 1979, Anderson and Fedak 1985) and the data presented here confirm this. However, there has been considerable disagreement about the precise form of polygyny adopted, and whether this varies between colonies with apparently differing social organisations (see Chapter 9). The form of polygyny has been variously described as territorial (Darling 1947, Davies 1949, Hewer 1957, 1960, 1974 Cameron 1967) and as a dominance hierarchy (Mansfield 1966, Anderson *et al.* 1975, Anderson and Fedak 1985) or neither (Boness 1979, Boness and James 1979) who reduced the males to 2 classes, "tenured" and "transient".

Various forms of polygyny have been described, including resource defence polygyny, female defence polygyny and male dominance polygyny (Emlen and Oring 1977, Bradbury and Vehrencamp 1977). As Boness (1979) states, resource defence is effectively synonymous with territoriality (although the definition of territoriality is rather flexible - see below), whilst female defence is synonymous with dominance hierarchies. Some authors have suggested that the various forms of polygyny are simply parts of a continuum, ranging from territoriality to dominance hierarchies (Wilson 1975, Owen-Smith 1977). Whether a continuum or not, it is clear that territoriality and dominance hierarchies are at opposite ends of the spectrum of forms of polygyny. Therefore, are male greys seals territorial or do they exhibit dominance hierarchies?

Pinnipeds are predominantly, if not exclusively polygynous (see below). Most fur seals and sea lion (otariids) species' so far studied, exhibit territorial or resource defence mating systems. For example, *Arctocephalus forsteri* (Stirling 1971, Miller 1974, 1975, Gentry 1975), *Arctocephalus gazella* (Doidge *et al.* 1984, McCann 1980), *Callorhinus ursinus* (Bartholomew and Hoel 1953, Peterson 1968), *Eumetopias jubatus* (Gentry 1975, Higgins *et al.* 1988) and *Otaria byronia* (Campagna and Le Boeuf 1988a). However, other forms of polygyny have been reported. One colony of *Otaria byronia* (at Punta Norte, Argentina) exhibits female defence polygyny (Campagna and Le Boeuf 1988a and b, Campagna *et al.* 1988) where female herding occurs. Also, a form of lekking has been described in both *Phocarctos hookeri* (Marlow 1975) and *Zalophus californianus* (Peterson and Bartholomew 1967, Heath and Francis 1983, 1987). Amongst territorial otariid species, males generally arrive at the breeding colonies prior to the females, and males that attain the bulk of the matings are territory holders (holding geographically fixed areas, showing clear boundaries about which much inter-male aggression and displaying is seen, and excluding other males). These comply with the strict definition of territoriality.

The situation amongst phocids is rather less clear. As discussed in Chapter 7, much information is available for land breeding phocids, but species in which females give birth on ice and matings generally occur in the water are rather more poorly studied. The Weddell seal is perhaps the best studied of these (Cline *et al.* 1971, Kaufman *et al.* 1975, Siniff *et al* 1977, Wartzok *et al.* 1989), where males hold aquatic territories (maritories). As data collection is particularly difficult for ice breeding species, it is not entirely surprising that there is some confusion over, not only the type of polygyny exhibited by these species, but also the actual degree of polygyny (see below). More substantial data have been gathered for land breeding phocids, in particular elephant seals. Both Northern and Southern elephant seals exhibit dominance hierarchies (Le Boeuf and Peterson 1969, Le Boeuf 1972, 1974, Cox and Le Boeuf 1977, Le Boeuf and Reiter 1988, McCann 1981, 1983). In these species, there is little or no evidence of boundaries. Males gather at the breeding sites prior to the arrival of females and establish the basis of the dominance hierarchy (McCann 1981). An individual's movements are only restricted by higher ranking males.

So, just what form of polygyny do grey seals exhibit? Various authors have provided substantial evidence that grey seals are not territorial in the strictest definition of the term

(Boness 1979, Boness and James 1979, Anderson *et al.* 1975, Anderson and Fedak 1985). These observations are supported by the data presented here. There are no overt boundary displays, no clear fixed boundaries, with the number of males within and around groups of females changing daily (Chapter 4). Also, dominant males will often "allow" more subordinate individuals to lie close by (within 10 m) and even approach females, though these females are almost invariably unreceptive. Thus, grey seals do not conform to the strict definition of territoriality (i.e. an individual maintains exclusive access to a geographically fixed area by means of some combination of advertisement, threat and aggression). However, amongst the literature, the definition of territoriality is extremely flexible (Kaufmann 1983). Definitions range from the strict version of complete exclusion from a fixed area to looser definitions incorporating non-exclusive areas which may alter spatially and/or temporally. All definitions however, maintain that territory owners have priority of access to resources within the territory. The looser, more inclusive definitions of territory could perhaps be applied to grey seals. However, defining the grey seal mating system as such would shed little light on the matter, considering the flexibility of the term territoriality. Kaufmann (1983) selected for his definition of territoriality "a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others who have priority elsewhere or at another time" and that "priority of access must be achieved through social interaction". Again, this could, perhaps, be applied to grey seals. Indeed, one cause of some of the few reversals in dominance occurred when one male departed from his own position on the colony and ventured elsewhere. However, these cases were rare and usually occurred towards the end of the season and the departing male appeared to be leaving the colony, and would therefore be reluctant to exert himself in a fight. Occasionally, temporary boundaries between two males do appear (Anderson *et al.* 1975, pers. obs.), generally where some physical boundary exists (e.g. a line of rocks). Again, these cases are rare, and inconstant. For example, consider 2 males (A and B) with secure and adjacent positions on the colony. Male A may be reluctant to cross this boundary when exchanging threats with male B. However, if a third, itinerant male (C) approached male A's position, male A would chase male C, and if male C fled across this temporary boundary, male A would follow and do likewise, at least for a short distance. Thus, the case for defining the mating system of grey seals as territorial is weak.

Boness (1979) and Boness and James (1979) also discarded the notion that grey seals were territorial. They suggested that their "transient" males were subordinate to the "tenured" males, but that "tenured" individuals were effectively of equal status. This is not supported by my work on both North Rona and Sable island. The extensive data presented in this thesis demonstrate a clear dominance hierarchy. Whilst not strictly linear, there are relatively few reversals, and indeed these would be expected in a natural system with multifarious extraneous factors impinging upon interactions between males (as discussed in Chapter 7). Hence, the data gathered during this study support the contention of Anderson *et al.* (1975) and Anderson and Fedak (1985) that males are organised in some form dominance hierarchy. However, with the more extensive observations, this suggestion has been refined. Anderson and Fedak (1985) stated that some males were "conspicuously unsuccessful" whilst others "seemed invincible". Here, I have demonstrated that males are arranged in a close approximation to a linear hierarchy, not only on North Rona, but also on Sable Island, and that dominance is the main behavioural correlate of individual mating success.

Finally, the possibility that the grey seal exhibit a lekking system must be considered. From the available data, it appears that this is not so. Females generally, arrive at the colony prior to the males. Although many males are present when the first females come into oestrus, the females do not appear to move far from their original pupping site (Anderson *et al.* 1975, Boness 1979, Boness *et al.* 1982, pers. obs.). Females show no overt signs of active mate choice, and rarely solicit the attentions of males (see Chapter 3). Again, dominant males will often allow more subordinate males to lie close by for long periods.

The degree of polygyny

As stated above, pinnipeds are exclusively polygynous. However, the relative degrees of polygyny appear to vary between species. The mating systems of pinnipeds appear to range from very low degrees of polygyny to incredibly extreme forms of polygyny (see Introduction to Chapter 6).

In the presentation of the results for this study, several measures of the degree of polygyny have been calculated. One of these, the standardised variance of male mating success (I) has been used in several other studies. Table 10 presents I values from studies of various species and those obtained for male grey seals in this study.

Whilst these measures of the degree of polygyny (Table 10) may not be strictly comparable due to differences in methodology, the measure of I does provide a useful indication of the degree of polygyny. The values of I obtained from North Rona during this study (excluding that for 1987 - see notes to Table 10) are approximately 5.3. These values are higher than all the non pinniped examples and 3 of the pinniped examples provided in Table 10. Two of the remaining pinniped examples show slightly greater values of I, whilst the remaining three show more extreme degrees of polygyny. The value for Sable Island is slightly greater than that for Rona, with only the three extreme cases exhibiting greater degrees of polygyny. It is clear that the degree of polygyny amongst grey seals is by no means as great as that found in Northern elephant seals, *Mirounga angustirostris* (Le Boeuf and Reiter 1988), or the Alaska fur seal, *Callorhinus ursinus* (Bartholomew and Hoel 1953). However, grey seals do still exhibit a relatively high degree of polygyny. It must be noted that some of the values given in Table 10 pertain to variation in estimates of lifetime reproductive success. Similarly, differences in methodology may cause problems in interpreting these values. This is particularly so in the case of pinnipeds, where it is often the case that many males fail to even come ashore onto the breeding site. As such it is difficult to determine the proportion of males gaining copulations. If these males are not included, potentially erroneous estimates of standardised variance of mating success may result. Ideally, results would be obtained from long term studies, following cohorts of males, individually marked at weaning,

Table 10: Standardised variance of measures of male mating success (I) for various species.

SPECIES	I	REFERENCES
Amphibians:		
Rana sylvatica[1]	2.02	Howard, 1988
Rana catesbeiana[1];		
1976	1.38	Howard, 1988
1977	1.50	Howard, 1988
1978	1.83	Howard, 1988
Birds:		
Delichon urbica[2]	0.084	Bryant, 1988
Tetrao tetrix L.[1]	3.63	Kruijt and de Vos, 1988
Tetrao tetrix L.[3]	3.19	Kruijt and de Vos, 1988
Pinnipeds:		
Arctocephalus forsteri	6.5	Miller, 1975 *
Arctocephalus galapogoensis	3.3	Trillmich, 1987 *
Callorhinus ursinus	45.9	Bartholomew and Hoel, 1953 *
Eumetopias jubatus	9.7	Gentry, 1970 *
Otaria byronia	2.3	Campagna, 1987 *
Phocarctos hookeri	3.3	Gentry and Roberts, in prep *
Zalophus californianus	5.9	Heath, unpubl. data *
Mirounga angustirostris	21.19	Le Boeuf and Reiter, 1988
Halichoerus grypus;[1]		
North Rona 1987[4]	2.15	
North Rona 1988	5.31	
North Rona 1989	5.26	
Sable Island 1990	6.76	

Notes:

* Data taken from Boness (1991).

1 - This is standardised variance of seasonal measures of the number of matings obtained by males
2 - This is the standardised variance of the lifetime estimate of the number of eggs fertilised by individual males.
3 - These are measures of variance in estimated life time reproductive success, not the variance observed in a single season.
4 - The relatively low value of I for Rona 1987 is considered to be due to the late onset of observations (see Chapter 6).

throughout their life span. Not only would this yield valuable information concerning life history parameters (mortality rates, age at first breeding etc.) but would allow reasonably accurate assessment of the variance in lifetime reproductive success of individuals. Such studies would truly be comparable. Perhaps the best example of this, to date, is the long term studies of Northern elephant seals (Le Boeuf and Reiter 1988).

Boness (1991) examines other potential measures of the degree of polygyny. These include the operational sex ratio, and he demonstrates a relatively high correlation between this and I ($r = 0.857$, $n = 6$, $p = 0.029$). This appears to support the traditional theory that species with highly skewed operational sex ratios are generally more polygynous. This may be true for cross species comparisons such as this; however, can the same be said when comparing different colonies of the same species? Boness (1991) states that not enough information is available to evaluate the level of intraspecific variation in degrees of polygyny, and implies that this may be considerable for otariid species, citing the example of the South African fur seal (*Arctocephalus pusillus pusillus*) for which a 6 fold difference in operational sex ratios has been reported. In Chapter 9, I provided evidence that the relative degrees of polygyny on North Rona and Sable Island were not significantly different. This contradicts predictions made from comparisons of the apparent operational sex ratios at the two sites. I use the term apparent, as the sex ratio observed on Sable may not in truth be the operational sex ratio. As access to the Sable colony is effectively unlimited, relatively more males gain positions on the colony. This yields a low apparent sex ratio, from which past authors have predicted a low degree of polygyny. However, the data presented in Chapter 9 demonstrate that mating remains the prerogative of a restricted number of males, the more dominant individuals. Thus, although most males may be ashore, only a few are actively involved in reproduction. Therefore, to gain a measure of the true operational sex ratio, one would have to exclude individuals not observed copulating. This is in effect the same as observing mating success directly. The data presented in Chapter 9 demonstrate the potential hazards in extrapolating from perceived operational sex ratios to actual degrees of polygyny.

The fact that there was no significant difference in the relative degrees of polygyny on Sable and Rona have implications for the plasticity of forms of mating systems. Emlen and Oring (1977) stated that "variability in social organisation, including mating systems, is widespread". They suggest that plasticity in the form of mating systems should arise when the spatial and/or temporal distribution of a critical resource (oestrus females in the case of pinnipeds) alters from year to year, or if the energetic costs of monopolising resources/mates change due to fluctuations in population density, sex ratios or length of the breeding period.

The grey seal provides ample opportunity to examine the plasticity of mating systems, particularly in terms of variation in sex ratios and relative densities of oestrus females (see Chapter 9). Data presented in Chapter 9 compare the determinants of male mating success at North Rona and at Sable Island. On Sable Island, females are more uniformly dispersed, the sex ratio is much lower and the breeding season is shorter compared to Rona. Thus, the spatial distribution of oestrus females on Sable is less clumped, whilst they are more temporally aggregated. In the terms of Emlen and Oring (1977) this should produce a lower "environmental polygamy potential" than that predicted for Rona. Despite this, no differences were found in the relative degrees of polygyny, and at both sites the primary behavioural correlate of male mating success was dominance. Contrary to predictions made by Boness (1979), Boness and James (1979) and Anderson and Fedak (1985), inter-male competition was more intense on Sable Island than on Rona, however, at both sites dominance hierarchies existed. Thus, it appears that the form of mating systems may not exhibit such plasticity as previously believed. Boness (1979) discusses this subject well, similarly concluding that the extent of plasticity may be less than has been thought.

Why is there no apparent difference in the degrees of polygyny observed at Rona and at Sable? Perhaps the relative spatial and temporal dispersions of oestrus females at the two sites are not sufficiently different to induce a marked change in male mating behaviour. This however, is a rather uninformative postulation, as the difference in the distributions of females at these sites are probably as great as one can observe amongst grey seal populations. It appears that, despite the differences in social organisation at the two colonies, dominant males are able to employ effectively the same strategy to gain copulations. However, access to the Sable colony is not restricted by topography (unlike Rona), hence more subordinates are able to gain positions on the breeding grounds. This may explain why Sable males spend proportionately more time observing each other, approaching opponents and in actual inter-male aggression (see Chapter 9). Conversely, on Rona, the limited access causes back logs of males in the gulleys leading up to the breeding grounds. Less males gain positions on the colony, thus there are lower levels of aggression. The major differences in male strategies will be amongst the subordinates. On Rona, subordinate males lie around the periphery of the colony waiting for an opportunity to enter the breeding grounds proper. Once achieved, they appear to approach as many females as possible, generally being chased of by nearby dominant males. On Sable however, subordinates lie amongst the dispersed females and dominant males, waiting for the opportunity to copulate a receptive female. Dominants appear to tolerate these males, at least until they make advances on females. Godsell (1991) provides some evidence which implies that subordinate males tend to move around the Sable colony more than dominant individuals. Despite these differences, subordinates are still generally excluded from mating.

A third, and yet not mutually exclusive, putative explanation is that Rona does in fact provide a greater environmental polygamy potential, but dominant males are unable to realise this full potential. This requires some limiting factor on the rate of copulations. On Rona, the only activity found to correlate with measures of energy expenditure (rates of weight loss) was time spent in and frequency of copulation (unfortunately weight measurements could not be made for the Sable males). Even other sexual activities (approaches to females, attempted copulations) were not correlated with weight loss, nor were any of the aggressive activities. Similarly, Anderson and Fedak (1985) found a correlation between copulation rate and the rate of weight loss. Does this suggest then that the cost of ejaculation (Dewsbury 1982) is an important consideration in grey seal energetics?

It is not inconceivable that sperm competition occurs in grey seals as females may be mated by more than one male (Anderson *et al.* 1975). Indeed, sperm competition appears to be rather more prevalent amongst mammals than previously suspected (Harcourt *et al.* 1981, Moller and Birkhead 1989). Moller and Birkhead (1989) provide lists of mammalian species in which multi-male copulations of the same female in a single oestrus period have been observed. These include several otariids, *Otaria byronia*, *Zalophus californianus*, *Arctocepalus galapogoensis* and *Phocarctos hookeri*. Although ejaculate volume has not been quantified for male grey seals, it is certainly rather large (pers. obs.!), and it is likely that sperm competition would primarily be by the production of copious sperm. Thus, the rates of replenishment of sperm may limit the rates of copulation of an individual male and hence the maximum number of matings attainable during his stay ashore. This may then limit the degree of polygyny to below the environmental potential. Those males able to replenish depleted sperm reserves most rapidly and/or divert greater energy reserves to sperm production, therefore have greater potential for matings.

Returning to the comparison of Sable and Rona, it is noticeable that on Sable, dominant males have a higher copulation rate than subordinates, whilst on Rona, there was no such relationship (though there was a correlation in 1987 and it must be noted that only one season's data is available for Sable). This may simply be due to the fact that more males gain positions ashore on Sable, thus there is a greater range of dominance status. However, a contributory factor may be the limitation of ejaculate costs. If the polygamy potential on Sable is lower, perhaps dominant males are able to realise the potential fully, whilst subordinates are obviously restrained from doing so by the dominants. Conversely, on Rona, the dominant males are restrained from realising the full polygamy potential due to limitations on copulation rates, whilst the few subordinates coming into the breeding grounds copulate at a similar rate, but remain ashore for considerably less time.

Dewsbury (1982) suggests that due to the costs of ejaculates, males "can and do discriminate among females as potential mating partners". If dominant males on Rona are limited by the costs of ejaculation, it is possible to further speculate that these same males may show some choice of mates. It is clear that the variation in grey seal male reproductive success is considerable, though it is generally believed that females show less variation. However, recent analysis of long term data on North Rona females indicates that there may be rather more variation in female reproductive success (pers. comm., P. Pomeroy, Sea Mammal Research Unit). Data for 143 adult females over a 9 year period (1978 to 1989) showed a high variation in the number of pups raised to weaning by individual females. Only 57 % of these females pupped 3 or more times over a period of five consecutive years, accounting for 74 % of the pups born to this sample. Also, pup mortality was found to be lower in females which pupped more frequently (data in prep., P. Pomeroy). There is also a potential difference in post weaning survival of pups which must be considered. Thus, it appears that there is greater variation in female reproductive success than previously believed. This raises the possibility that dominant (and successful) males may "prefer" to mate with these more successful females. Indeed, there is evidence that females often mate with the same male in different seasons, from both observations of site fidelity (pers. obs., pers. comm. S. Anderson) and DNA fingerprinting analyses (pers. comm. B. Amos, Department of Genetics, University of Cambridge). Thus, if successful males mate with the more successful females, this provides a potential positive feedback in a polygynous system, assuming the traits conferring success are heritable.

The degree of polygyny, sexual size dimorphism and dominance

As discussed in Chapter 7, it is generally believed that larger males are more successful in intra-sexual aggressive encounters, and are therefore more dominant (Darwin 1871, Trivers 1972, Halliday 1976, McCann 1981, Alcock 1983). This dominance gives them priority of access to oestrus females (Hausfater 1975, Howard 1978, Lott 1979, McCann 1981, Clutton-Brock *et al.* 1979, Appleby 1982, Cowlisham and Dunbar 1991). However, the data presented in this thesis shows no relationship between measures of size or weight and dominance. It must be noted that the data presented here are based only on information collated from males that gain a position on the colony, those males failing to come ashore are excluded. This, unfortunately, is a common problem in studying pinnipeds. Despite this, the analyses presented in Chapter 7 show that the dominant, and more successful, male grey seals are not necessarily larger or heavier than those males which come ashore and realise low or zero mating success. The postulated explanation for this, is that male grey seals establish at least the basis of relative dominance status prior to the onset of the breeding season. This process occurs in the water, and therefore, size is not necessarily a vital component of competitive ability. A comparable situation is found amongst Weddell seals, where males establish three dimensional maritories in the water below access and breathing holes to and from the ice where the females pup (Cline *et al.* 1971, Kaufman *et al.* 1975, Siniff *et al* 1977, Wartzok et al. *1989*). In this species males are in fact slightly smaller than females (Kaufmann *et al.* 1975, Bryden *et al.* 1984). Although relatively little is known about inter-male competition in this species, it is apparent that much of this occurs in the water. In contrast, many otariid species and much studied phocid species, such as the elephant seals, generally exhibit considerable size dimorphism, with males being larger than females. Amongst otariids in general, there are high levels of inter-male aggression and display during the breeding season. As mentioned in Chapter 7, Southern elephant seals establish the basis of dominance prior to the breeding season, but do so on land, hence size may well be an important factor in inter-male aggression (though Haley, 1989, provides evidence to the contrary for Northern elephant seals).

Both otariids and elephant seals also show considerable dimorphism in other morphological features; in many otariid species dominant adult males have large "manes" (e.g Southern sea lion, *Otaria byronia*) and strikingly different facial features. Similarly, male elephant seals possess the characteristic exaggerated proboscis. Such morphological differentiation of the sexes is less marked in grey seals. Adult male grey seals possess rugose necks and a more exaggerated Roman nose compared to females. Also, as stated by Boness (1979) and Boness and James (1979), male grey seals exhibit no clear (or at least, readily observable) vocal or behavioural signals of status during the breeding season.

As discussed in Chapter 7, Alexander *et al.* (1979) demonstrated a relationship between the degree of polygyny and the degree of sexual size dimorphism. However, this was based on the earlier studies of pinniped behaviour. Subsequent research has provided more details of pinniped mating systems. For example, Boness (1991) summarised measures of the degree of polygyny found amongst several otariid species (see above), and found up to 6 fold differences in measures of the degree of polygyny within a single species. It is noticeable from the data presented by Alexander *et al.* (1979) that the phocid species denoted as having relatively low levels of polygyny (and exhibiting little sexual size dimorphism) are generally ice breeding species, where much inter-male competition may occur in the water. It is perhaps no coincidence that these species are also the least studied, both in terms of assessing the degree of polygyny and obtaining observations of inter-male relationships during the breeding season. It must be said, that there is ample reason for this lack of knowledge, in particular the logistic challenges of studying species in inhospitable arctic and antarctic environments. One species which may provide some clues as to mating systems and male behaviour during the breeding season in such species is the common seal. Common seals breed in rather more amenable climes and yet much of the male behaviour appears to transpire in the water. Previous descriptions of the breeding organisation of the common seal have been rather indeterminate; King (1983) states that "there is no obvious social organisation at the breeding season, and the seals appear to be promiscuous". However, recent studies, including the use of telemetry, indicate a more structured organisation, with males displaying offshore (pers. comm. D. Thompson). Female common seals give birth on sandy beaches or low lying rocks close to the shore. Pups shed their lanugo in utero, or shortly after parturition (unlike grey seal pups) and are able to swim well shortly after birth. These characteristics resemble somewhat, aspects of the biology of ice breeding species. It may be that the shore line pupping sites of the common seal are analogous to the expanses of ice utilised by other phocid species.

Much remains to be learnt about phocid mating systems, especially in species where much of the proceedings occur in the water and where the environment makes behavioural studies logistically untenable. It would be particularly instructive to examine the contexts of inter-male aggression in phocid species in more detail. Even amongst the relatively little studied ice breeding phocids there are considerable differences in the degrees of sexual dimorphism. Dimorphism ranges from the reversed size dimorphism of

Weddell seals to the situation found in Hooded seals, where males are approximately one third heavier than females and possess the remarkable inflatable hood (nasal septum). It is also important to consider the strategies employed by males of different species during the breeding season. Do males fast, and if so for how long relative to the female and what is the level of energy expenditure during the fast? These aspects may also have important consequences for the relative degrees of size dimorphism, as suggested in Chapter 7 for the grey seal, a may be more important than intra-sexual competition in determining size dimorphism.

Recent advances in techniques applicable to the study of pinniped behaviour may provide a key to unlocking these hidden systems (Harwood *et al.* 1989). Telemetry and photo identification methods may provide some insight into seal movements in the water. Paternity assessment may also generate some indication of the relative degrees of polygyny in such species.

Whether dominance relationships amongst male grey seals are maintained throughout the year, rather than merely the breeding season, is unknown. It is unlikely that outside the breeding season any manifestation of dominance would occur by overt aggression. Relative dominance may be exhibited by very subtle behaviours, for example, shifts in positions on haul out sites.

SUMMARY

(1) Potential behavioural and energetic determinants of male grey seal mating success were examined over three successive breeding seasons (1987 to 1989) on North Rona (Scotland). A total of 275 males were individually identified. Records of individual male mating success, inter-male aggression (to yield dominance indices), colony attendance patterns and detailed activity budgets were obtained. Selected individuals were caught and weighed and rates of weight loss (both absolute and proportional) and weights on date of arrival to and departure from the colony were calculated. Standard measurements were taken and a single incisor tooth extracted for age determination.

(2) Length of stay on the breeding colony was the primary correlate of mating success.

(3) Using records of inter-male aggressive encounters a clear dominance hierarchy was found amongst the males. Dominant males were not necessarily heavier or bigger, nor were dominant males older than subordinates on average. There were low levels of inter-male aggression on the colony, and evidence of prior knowledge of relative status amongst males. It is proposed that male dominance relationships are predominantly established in the water prior to arrival on the colony. Thus, size may not be an important determinant of male competitive ability in grey seals.

(4) Mating success was also highly correlated with dominance in all three seasons. Dominant individuals were able to establish positions amongst the groups of females and maintain these for significantly longer than more subordinate males, thus giving access to more oestrus females.

(5) Dominant males experienced lower daily rates of aggression and did not incur greater rates of weight loss (either absolute or proportional).

(6) No evidence of energetic constraints on male mating success could be found. Due to the topography of North Rona, dominant males were able to exclude subordinates from the breeding grounds (the average sex ratio on the colony during the breeding season was approximately 1 male : 7 females). Relatively few males were therefore, able to remain on the colony for the length of time that their energy reserves permitted, thus masking any

potential energetic limits on length of stay.

(7) It is suggested that grey seals are sexually size dimorphic primarily due to the differing energy storage requirements of the two sexes determined by the different strategies adopted by males and females in order to maximise individual reproductive success.

(8) Males that returned in successive seasons were the more dominant individuals of the previous season, therefore remained ashore for longer and gained greater mating success in the previous year. Also, returning males were younger on average than those that failed to return, were not necessarily the heavier males but were those that incurred greater proportional rates of weight loss in the previous season.

(9) One male, present in all three seasons, was conspicuously successful in all three years and had by far the greatest mating success of all males observed during the course of the study. This male had been present on North Rona since at least 1980.

(10) A comparative study was conducted with one field season on Sable Island (Nova Scotia, Canada). Unlike North Rona, dominance was the primary correlate of mating success. Considerable differences in the apparent sex ratios were observed between Sable (1 male : 2 females) and Rona (1:7). Also, oestrus females on Sable were spatially more evenly distributed and temporally more aggregated than on Rona. Thus, one would predict a lower environmental polygamy potential on Sable Island. However, there were no significant differences in measures of the "degree of polygyny" at the two sites. Thus, although relatively more males gained positions ashore on Sable (access was not restricted by topography), dominant individuals still monopolised mating opportunities. These results suggest that plasticity of the form of mating system shown amongst grey seal populations is limited.

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John Reilly
2nd half of the season - Bernie McConnell
Bruce Herod

1988: 1st half of the season -	Peter Witty John Baker Rosa Baker
2nd half of the season -	Gordon Liddle Andrew Reed
and with me for the entire 1988 season -	Jack Lawson
1989: 1st half of the season -	Sheila Anderson Paddy Pomeroy Colin Pomeroy Roy Armstrong!!
2nd half of the season -	Rob Harcourt Andrea Brock Adrian Jones

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APPENDIX A - NOTES ON THE RESPONSES OF SEALS TO IMMOBILISATION

The response to the darting was evidently extremely variable both with Ketamine-valium (KV) and Zoletil, though more so with the former sedative. Some seals responded very rapidly and became deeply sedated. In a few seals the response was so profound that they became unconscious and stopped breathing, that is, apnoeic (hence the necessity to monitor the seals condition continually) as detailed in Chapter 2. In stark contrast to this, some seals responded very poorly to the drug, indeed, in some cases there seemed to be no effect whatsoever. These seals were given "top ups", though these additional doses rarely had any significant effect unless they could be administered intra-venously, due to the time to take effect if injected intra-muscularly. These seals were, therefore, often rather "lively" when it came to ensnaring them in the pole net, causing delays and greater disturbance in the colony.

Although the recommended mean dose rate for KV was 6mg per kg of seal, effective doses ranged from 8.1mg/kg to elicit a degree of immobilisation of only 1, to a mere 4.4mg/kg for a level of 4 (see Baker *et al.* 1988).

The response to Zoletil was less variable, although, as with KV, males seemed to become more heavily sedated for the given dose rate than females. Darted seals appeared to become sedated more rapidly with Zoletil (approximately 10 minutes as opposed to 15 with KV), recover sooner and more quickly, so reducing stress to the seal. Effective doses of Zoletil ranged from 1.43 mg/kg to elicit a degree of immobilisation of 2, to 0.98 mg/kg for a level of 5. In general Zoletil was deemed far more favourable, both in terms of ease of use in the field and, more importantly, in the predictability and consistency of the responses of the seals.

In no year and for neither drug was there any correlation between dose rate administered and the degree of immobilisation attained. However, in general, each individual appeared to show a reasonably consistent response to repeated immobilisations (see below).

There are numerous possible reasons or contributory factors to this enormous variability in response. Firstly, the position of the dart may be important, although all possible efforts were made to target the same area, high on the flanks of the seal in the muscular region just anterior to the pelvis. The depth to which the dart penetrates (dependent upon the needle length and the force with which the dart is fired) in comparison to the blubber depth, and whether the dart hits a relatively large blood vessel or not are important in how rapidly the drug takes effect. Also, the response appears to depend on how active the seal is both prior to and after darting. For example, bulls fresh from a fight tend to respond poorly, whilst having just copulated a bull will be rather placid. Darted males are particularly prone to attacks from surrounding bulls whilst they are in this vulnerable state. Such "excitement" reduces the drug's effectiveness, therefore, drugged males must be defended. Much of the variability may be due to individual temperaments, certain seals were always relatively placid and handled easily, whilst others were well known as "difficult" seals.

In 1987 only 3 of the 91 catches of males utilised Zoletil and nine of the 78 females were sedated with Zoletil. During this season a total of 8 catches (4.8% of all catches made) resulted in the seal becoming apnoeic, 6 whilst using KV (3.9% of all KV catches) and 2 using Zoletil (16.7% of all Zoletil catches). Only two of these incidences involved females, one under KV and one under Zoletil. Of the 5 cases of apnea in males involving KV only 4 individuals were involved, one male (branded T1) succumbed to apnea on successive captures, despite a relatively low dosage on the second catch.

In contrast, during the 1988 season only 5 of the 61 male catches and none of the 36 female catches utilised KV. A total of 4 cases of apnea occurred (4.1% of all catches) all involving different males, though two (T1 and X2) had succumbed in 1987. T1 was again darted with KV whilst X2 was sedated with Zoletil, as in 1987. Male T1 was the only case of apnea under KV. As in 1987, the occurrence of apnea under each drug largely reflects the extent to which each drug was used, though the overall number of cases was reduced by using mainly Zoletil. Again, males appeared more susceptible than females.

In 1989 KV was not used at all and a total of 5 cases of apnea occurred (4.1% of all catches), all involving different males. Again X2 became apnoeic, though T1 was not captured. Three of these 5 males became apnoeic during the first catch of a double-immobilisation for the H_3O technique. None of these males succumbed during the recapture some 3 to 6 hours later.

In order to examine individual responses to Zoletil, the degree of immobilisation (DI) attained was divided by the dose rate (DR) to give a measure of an individual's response (DI/DR), thus controlling for variation in the dose rates given.

On the whole individuals were remarkably consistent in their response to repeated use of Zoletil. The response (DI/DR) of 24 of the 29 males darted on more than one occasion with Zoletil during 1988 and 1989 varied by less than one standard deviation from the mean overall response. There was no consistent correlation between DI/DR and the age of the animal, its weight at time of darting or any of the other body size parameters taken. Those males at greatest risk (those which became apnoeic) from the drug tended to be those with the most variable response. Of the seven individuals requiring resuscitation and caught more than once, five had a DI/DR which varied by greater than one standard deviation from their mean response.

For the double-immobilisations, the response of each individual on the 3 to 6 hour recapture was compared with the mean and standard deviation of all previous catches of the individual under normal darting procedures. Five out of the six individuals showed responses for the recapture which were approximately normal. However, all these males were under-dosed on the recapture. The only males which received the usual 1.0 mg/kg dose rate on the recapture deviated markedly from his mean response. This individual had the lowest standard deviation of all the males under normal darting conditions.

The relative consistency of response to Zoletil shown by the majority of the males was somewhat surprising, considering the numerous extraneous variables which may affect the degree of immobilisation (as discussed above). However, these variables may merely influence the rate at which the drug takes effect, rather than the intensity of the animal'al's response. There appears to be no residual effect when Zoletil is used for repeated immobilisation of individual grey seals at intervals of at least three days (normal darting procedure). A majority of the males darted under these conditions showed relatively predictable responses to Zoletil at the recommended dose rate of 1.0 mg/kg. Those males with highly variable and thus unpredictable responses were at greater risk of apnea. However, rapid, immediate resuscitation ensured recovery in all cases.

The double-immobilisation of individuals within a three to six hour period proved to be effective with a dose rate of 1.0 mg/kg for the first catch and 0.8 to 0.9 mg/kg for the recapture. The majority of males showed normal responses under this regime indicating that Zoletil has no or little residual effect even after these short periods. This is clearly preferable to sedatives such as KV which can leave individuals somewhat disorientated for several hours after darting. Therefore, a slight under-dosing for the recapture may be advisable when conducting such double-immobilisations.

APPENDIX B - NOTES ON CATCHING FEMALES AND PUPS

When darting females it was particularly important to minimise disturbance both to the target animal and surrounding females, of which there can be many in close proximity. A team of two people approached the female, one advanced towards the pup which attracted the female's attention whilst the second darted the adult.

The sampling regime on the female was effectively the same as with the males, though samples of milk were taken. The mother was sampled first, the pup being sampled when the female had been weighed and two members of the field party were free. It was not necessary to drug the pup, indeed, sedating a young pup would be very hazardous. The pups were placed in a "pup bag" (a canvas bag with two rope handles) and weighed using either 0-50kg or 0-100 kg Salter scales, whichever was appropriate. The pup was then sexed and aged (using pup age classes as defined in Anderson, Burton and Summers, 1975) and blood samples taken. The pup was then tagged.

Finally, it is important to ensure that the seals recover from the drug peacefully. In the case of females it is vital to ensure that they are close to and aware of the presence of their pups otherwise the mother may wander off while still drowsy and become separated from the pup.

APPENDIX C - CORRELATION MATRICES

The following pages present correlation matrices for each of the three seasons on North Rona and that of Sable Island. Detailed descriptions of each variable are provided in Chapters 3 to 7 for the North Rona data and in Chapter 9 for the Sable data. Only cases where males were involved in 10 or more inter-male aggressive interactions were included in the correlations (see Chapter 3).

Notes:

(1) Each of the variables listed in the vertical axis are accompanied by a number. This number is used to represent the variable in the horizontal axis.

(2) A.I.s = Inter male aggressive interactions.

(3) COPS. = copulations

(4) The results of the correlations are presented in the following format; the top number (e.g. +.56) denotes the r value, the bottom number (e.g. .095) denotes the p value (p values of .000 denote p values < 0.001).

(4) Sample sizes (N) - For each pair of variables the lowest sample size dictates the number of cases used in the correlation. **N.B:** Correlations involving age and weight parameters had samples sizes of 7, 15 and 16 in 1987, 1988 and 1989 respectively. Correlations involving prior experience and age had sample sizes of 6, 11, 23 respectively, whilst correlations between prior experience and weight parameters had sample sizes of 8, 12, 13 for 1987, 1988 and 1989 respectively.

RONA 1987 - CORRELATION MATRIX

	N	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.
N	X	47	47	47	14	14	14	14	14	14	47	47	47	13	10	47
MATING SUCCESS	47	+.69 .000	-.30 .038	+.43 .002	+.10 .738	+.30 .291	+.28 .336	-.06 .834	+.05 .872	-.44 .112	-.51 .000	+.46 .001	-.45 .001	+.37 .216	-.36 .299	+.88 .000
1. LENGTH OF STAY	47	X X	-.57 .000	+.57 .000	+.23 .425	+.69 .006	+.46 .100	-.35 .217	-.24 .404	+.01 .981	-.71 .000	+.57 .000	-.64 .000	+.22 .465	-.22 .538	+.37 .011
2. ARRIVAL DATE	47		X X	+.10 .514	+.06 .828	-.55 .040	-.42 .132	+.22 .457	+.35 .223	-.30 .301	+.24 .108	-.48 .001	+.19 .195	-.08 .790	-.17 .643	-.11 .450
3. DEPARTURE DATE	47			X X	-.10 .742	-.17 .551	-.09 .752	+.13 .655	+.59 .026	-.47 .087	-.47 .001	+.18 .230	-.61 .000	+.22 .475	-.33 .345	+.30 .044
4. WEIGHT ON DAY ONE	14				X X	+.77 .001	+.45 .104	-.45 .102	-.66 .011	+.33 .256	-.46 .096	+.06 .846	-.12 .691	+.42 .346	-.32 .439	+.07 .817
5. ARRIVAL WEIGHT (a)	14					X X	+.72 .004	-.43 .127	-.62 .018	+.32 .269	-.66 .010	+.43 .126	-.13 .648	+.13 .783	-.57 .138	+.11 .705
6. DEPARTURE WEIGHT (b)	14						X X	+.32 .266	-.20 .497	-.18 .539	-.17 .570	+.31 .286	-.11 .700	+.02 .972	-.67 .067	+.08 .781
7. a/b x 100	14							X X	+.59 .026	-.67 .008	+.70 .006	-.19 .520	+.04 .885	-.12 .800	-.24 .572	-.05 .863
8. RATE OF WEIGHT LOSS	14								X X	-.73 .003	+.55 .044	-.22 .443	-.08 .788	-.16 .739	+.19 .650	+.10 .725
9. SPECIFIC Wt LOSS RATE	14									X X	-.55 .042	+.27 .343	+.31 .277	-.23 .620	+.22 .593	-.46 .101
10.DOMINANCE SCORE	47										X X	-.36 .012	+.48 .001	-.25 .401	+.18 .624	-.33 .022
11. TOTAL No. A.I.s	47											X X	+.12 .429	+.02 .951	+.07 .839	+.36 .014
12. A.I.s PER DAY	47												X X	-.28 .349	+.40 .256	-.27 .067
13. AGE	13													X X	-.76 .082	+.39 .187
14. PRIOR EXPERIENCE	10														X X	-.34 .342
15. COPS. PER DAY	47															X X

RONA 1988 - CORRELATION MATRIX

	N	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.
N	X	39	39	39	16	16	16	16	16	16	39	39	39	20	19	39
MATING SUCCESS	39	+.84 .000	-.51 .001	+.54 .000	+.50 .051	+.49 .052	-.19 .476	-.66 .005	-.77 .001	+.59 .017	-.48 .002	+.75 .000	-.34 .032	+.52 .020	+.18 .456	+.85 .000
1. LENGTH OF STAY	39	X X	-.51 .001	+.62 .000	+.38 .150	+.55 .028	-.40 .124	-.78 .000	-.55 .029	+.61 .012	-.44 .006	+.80 .000	-.47 .003	+.40 .079	+.36 .128	+.53 .000
2. ARRIVAL DATE	39		X X	+.19 .235	-.16 .560	-.60 .014	+.02 .951	+.54 .032	+.46 .072	-.41 .117	+.09 .589	-.64 .000	-.09 .580	-.49 .028	-.49 .032	-.26 .113
3. DEPARTURE DATE	39			X X	+.19 .493	-.09 .742	-.17 .529	+.03 .902	+.16 .557	-.10 .714	-.33 .042	+.38 .017	-.59 .000	+.03 .908	+.14 .556	+.49 .002
4. WEIGHT ON DAY ONE	16				X X	+.82 .000	+.18 .506	-.52 .041	-.71 .002	+.35 .179	-.40 .127	+.17 .522	-.01 .984	-.27 .338	-.07 .838	+.45 .083
5. ARRIVAL WEIGHT (a)	16					X X	+.29 .279	-.54 .031	-.60 .015	+.28 .179	-.42 .104	+.50 .047	+.33 .213	-.10 .733	+.16 .626	+.33 .208
6. DEPARTURE WEIGHT (b)	16						X X	+.62 .011	+.31 .237	-.76 .001	-.14 .617	-.18 .504	+.11 .697	-.34 .217	-.23 .468	-.05 .850
7. a/b x 100	16							X X	+.82 .000	-.92 .000	+.18 .501	-.63 .009	-.26 .329	-.26 .352	-.16 .629	-.45 .082
8. RATE OF WEIGHT LOSS	16								X X	-.81 .000	+.52 .039	-.34 .192	-.03 .905	-.30 .905	-.03 .938	-.66 .005
9. SPECIFIC Wt LOSS RATE	16									X X	-.20 .454	+.47 .066	+.14 .593	+.41 .132	+.15 .643	+.44 .092
10. DOMINANCE SCORE	39										X X	-.20 .215	+.45 .004	-.55 .013	+.04 .862	-.48 .002
11. TOTAL No. A.I.s	39											X X	0.00 .998	+.21 .376	+.32 .185	+.54 .000
12. A.I.s PER DAY	39												X X	-.19 .422	+.01 .972	-.20 .032
13. AGE	20													X X	+.29 .393	+.45 .047
14. PRIOR EXPERIENCE	19														X X	-.04 .856
15. COPS. PER DAY	39															X X

RONA 1989 - CORRELATION MATRIX

	N	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.
N	X	54	54	54	16	16	16	16	16	16	54	54	54	26	36	54
MATING SUCCESS	54	+.78 .000	-.08 .554	+.60 .000	+.64 .008	+.78 .000	+.55 .028	-.58 .019	-.43 .099	+.10 .699	-.56 .000	+.60 .000	-.51 .000	+.19 .361	+.55 .001	+.66 .000
1. LENGTH OF STAY	54	X X	-.31 .024	+.65 .000	+.13 .625	+.46 .072	+.18 .498	-.54 .030	+.06 .818	-.34 .192	-.60 .000	+.76 .000	-.63 .000	+.02 .904	+.61 .000	+.26 .055
2. ARRIVAL DATE	54		X X	+.25 .070	+.59 .017	0.00 .999	-.06 .814	-.11 .699	-.41 .110	+.47 .067	+.13 .331	-.45 .001	-.07 .606	+.05 .815	-.26 .133	+.23 .092
3. DEPARTURE DATE	54			X X	+.15 .582	-.05 .862	-.02 .930	-.07 .791	+.49 .057	-.49 .056	-.33 .014	+.49 .000	-.59 .000	-.09 .662	+.35 .037	+.40 .003
4. WEIGHT ON DAY ONE	16				X X	+.79 .000	+.60 .014	-.52 .040	-.69 .003	+.42 .110	-.05 .846	+.02 .929	-.02 .934	+.53 .035	+.62 .023	+.67 .005
5. ARRIVAL WEIGHT (a)	16					X X	+.81 .000	-.59 .017	-.43 .094	+.02 .951	+.01 .984	+.13 .634	-.07 .795	+.48 .059	+.57 .044	+.73 .001
6. DEPARTURE WEIGHT (b)	16						X X	0.00 .998	-.22 .422	-.15 .583	+.28 .300	+.18 .493	+.11 .691	+.35 .181	+.12 .708	+.57 .021
7. a/b x 100	16							X X	+.46 .071	-.24 .369	+.43 .095	+.10 .718	+.34 .199	-.38 .144	-.66 .013	-.47 .064
8. RATE OF WEIGHT LOSS	16								X X	-.86 .000	+.53 .035	+.04 .878	+.02 .941	-.46 .070	-.49 .089	-.48 .057
9. SPECIFIC Wt LOSS RATE	16									X X	-.57 .021	-.05 .865	+.10 .710	+.21 .440	+.33 .277	+.20 .450
10.DOMINANCE SCORE	54										X X	-.41 .002	+.59 .000	-.21 .295	-.43 .008	-.15 .273
11. TOTAL No. A.I.s	54											X X	-.18 .190	+.06 .776	+.52 .001	+.24 .078
12. A.I.s PER DAY	54												X X	+.15 .478	-.28 .102	-.10 .484
13. AGE	26													X X	+.18 .408	+.13 .542
14. PRIOR EXPERIENCE	36														X X	+.26 .124
15. COPS. PER DAY	54															X X

SABLE 1990 - CORRELATION MATRIX

	N	1.	2.	3.	4.	5.	6.	7.	8.
N	X	42	42	42	41	42	42	7	42
MATING SUCCESS	42	+.56 .000	-.26 .095	+.27 .089	-.57 .000	+.53 .000	-.24 .134	+.46 .300	+.86 .000
1. LENGTH OF STAY	42	X X	-.53 .000	+.21 .187	-.67 .000	+.73 .000	-.67 .000	+.70 .078	+.38 .014
2. ARRIVAL DATE	42		X X	+.58 .000	+.14 .384	-.33 .032	+.42 .005	+.06 .914	-.07 .680
3. DEPARTURE DATE	42			X X	-.31 .050	+.34 .028	+.06 .686	+.52 .295	+.22 .169
4. DOMINANCE SCORE	41				X X	-.33 .034	+.64 .000	-.67 .096	-.43 .005
5. TOTAL No. A.I.s	42					X X	+.02 .909	+.37 .471	+.36 .017
6. A.I.s PER DAY	42						X X	-.39 .477	-.16 .322
7. AGE								X X	+.65 .115
8. COPS. PER DAY	42								X X

APPENDIX D - EQUATIONS USED IN THE LABELLED WATER ANALYSES

The calculations of individual total body fat in kg (TBFkg), total body protein in kg (TBPkg) and total body energy in MJ (TBGE) were computed utilising the following relationships derived by Reilly (1990):

$\%TBF = 105.1 - 1.47(\%TBW)$

$\%TBP = 0.42(\%TBW) - 4.75$

$TBGE\ (MJ) = 40.8(\text{mass in kg}) - 48.5(\text{TBW in kg}) - 0.4$

where: %TBW = percentage total body water as assessed by H_3O dilution.

%TBF = percentage total body fat.

%TBP = percentage total body protein.

From the known weights of the individuals at the time of the body composition assessment the parameters TBFkg and TBPkg were calculated using the values of %TBF and %TBP respectively.

APPENDIX E - DETAILS OF THE CALCULATION OF THE DOMINANCE SCORE

The outcomes of all observed inter-male aggressive encounters were graded with a value ranging from 1 to 7. The classification of the outcome of a particular dyadic encounter into one of these seven grades depended upon the degree of response of the loser of the encounter. For example, consider an encounter between male A and male B. First, the encounter outcome was coded with respect to male A. An outcome of grade 1 indicates that male A was the outright victor of the encounter, a grade of 4 would indicate a draw and a grade of 7 would indicate that male A was the outright loser. A victory for male A is defined as an encounter where male B withdraws, by either backing away, turning and moving away, or being chased away, with the encounter ceasing after male B has withdrawn. A draw occurs where neither male withdraws, both ceasing the encounter, but remaining in their original positions, or where both males withdraw simultaneously. A loss is defined as the opposite to a victory. The response of the loser to the encounter varies in its intensity (degree of response). Grey seals on land have three distinct modes of locomotion. The first is a slow movement, largely involving the use of the fore flippers with relatively little lifting of the torso (I have termed this "walking"). Secondly, a more rapid pace is produced, with greater movement of the torso (termed "running"). Finally, the males can move very rapidly, using both the fore flippers and large undulations of the torso, with the body often lifting clear of the ground. In the context of withdrawing from an encounter I have termed this "fleeing". In the example encounter between males A and B, the assignment of outcome grades for male A would be as follows, depending upon which male was the victor and the degree of response of the loser;

Grade 1 = male B loses and flees from the encounter
Grade 2 = male B loses and runs from the encounter
Grade 3 = male B loses and walks from the encounter
Grade 4 = draw
Grade 5 = male A loses and walks from the encounter
Grade 6 = male A loses and runs from the encounter
Grade 7 = male A loses and flees from the encounter

In order to compute dominance scores for both male A and male B, the outcome of this single encounter was coded twice, once with respect to male A (as shown above), and once with respect to male B. The grade applied for male B will be the antithesis of that for male A. Thus, if an encounter outcome is graded 1 with respect to male A (i.e. male A was the outright victor and male B fled from the encounter) then the respective grade from male B's perspective is grade 7 (i.e. male B was the outright loser, fleeing from the encounter). Similarly, grades 2 and 6 and grades 3 and 5 are opposites. Obviously grade 4 (draw) would be the same for both males involved in the encounter.

In order to compute the final dominance score for male A, the following calculations were made. For each opponent that male A encountered a mean outcome was computed utilising the outcomes graded with respect to male A. Secondly, the average of these mean grades was computed to yield the dominance score for male A. For male B, the mean outcome for each dyad in which he was involved was computed utilising outcomes graded with respect to male B. Again, an average of these means yielded the dominance score for male B. This process was repeated for each identified male.

Sean/'90