THE INFLUENCE OF FOOD SUPPLY ON THE PARENTAL INVESTMENT OF ARCTIC TERNS *STERNA PARADISAEA*

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Uttley, J., Monaghan, P. & White, S. 1989b. Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. Ornis scand. 20: 273-277.

SUMMARY

The aims of this project were to examine the effects of food shortage on the breeding biology of the Arctic tern *Sterna paradisaea*, a small, surface-feeding seabird with a short foraging range in the breeding season. A comparative approach was adopted, and various aspects of Arctic tern breeding biology were studied both on Shetland, where the main prey of Arctic terns, lesser sandeels *Ammodytes marinus* are less available than they have been previously, and other suitable prey are absent, and on Orkney, where food supply for Arctic terns appears to be better. Further data from Coquet Island, Northumberland, collected during a broader study, of which this study is a part, were also utilised.

Investment in egg production was investigated through measurements of courtship feeding rates and clutch size, egg size and quality. This was followed by analyses of the time budgets of male and female Arctic terns during laying, incubation, hatching, early chick life and later chick life. The results showed that egg production was little affected, if at all, by food shortage, and evidence was presented to show that adjustments in male and female investment patterns enabled the maintenance of clutch quality. This is discussed in relation to Arctic terns' breeding strategy.

The performance of adult Arctic terns feeding chicks was assessed in detail, in relation to food supply, brood age and weather conditions. Differences in the diet of chicks and the rate at which they were provisioned were discussed and the profitability of feeding sandeels to chicks was shown to be lower on Shetland than on Orkney. Potential reasons why Arctic terns did not exploit alternative prey to a greater extent were discussed. The behaviour of Arctic terns in a situation of food shortage was also shown to influence the rate at which young were provisioned. Conspecific kleptoparasitism had a very large impact on chicks' food intake rates at the poor food supply site, and the occurrence of kleptoparasitism and its frequency for different prey categories was shown to concur with predictions from the literature. A model showed that the risk of kleptoparasitism could not explain the lack of large prey items in the diet of chicks in terms of energetics, and other explanations were discussed. Diversion of food from chicks to females was also more frequent where food supply was poor, and the implications of this were also discussed.

Finally the results of a pilot study into the free-ranging energetics of Arctic terns, as measured by the doubly-labelled water method, were presented. Although inconclusive, the results suggested that Arctic terns raising young in conditions of food shortage may incur high levels of energy expenditure. The usefulness of the doubly-labelled water technique is discussed in the light of its potential behavioural consequences.

1. INTRODUCTION

1.1. What is parental investment?

Parental investment (Low 1978) is defined as the cost of an individual's contribution to the production and survival of current offspring. The currency of investment must be fitness costs and benefits (Wittenberger 1982, Burger 1987) but, because these parameters are difficult to quantify in the field, investment is often measured in terms of the levels of energy expenditure or risks of predation or injury incurred over the course of the breeding cycle, or the frequency and intensity of the activities necessary for reproduction. The fitness cost of increased investment is the consequent decrease in residual reproductive value (Williams 1966). Although there is great debate about how such costs can and should be measured (see Stearns 1989 for review) it seems likely that they are real and have played a major role in the evolution of life-history strategies. Life-history theory predicts that such costs of reproduction will be traded off against the benefits of increased current reproductive success such that lifetime reproductive success is maximised (Williams 1966, Winkler & Wilkinson 1988). A consequence of this trade-off is a cost ceiling on parental investment (Goodman 1974).

We can envisage a breeding organism as having a limited amount of time and energy which it can expend on a reproductive attempt, after it has allocated sufficient to ensure its own maintenance and survival. The time and energy available, and hence the height of the cost-ceiling, will be determined by an individual's quality (as defined by its ability to harvest and efficiently use resources) and the social and physical environment (Hirschfield & Tinkle 1975, Drent & Daan 1980, Martin 1987).

Within this limitation, organisms have to allocate their investment to the various activities necessary for the production, development and survival of their young. Both the proximate (time and energy) and ultimate (fitness) costs of different activities such as foraging, brooding and defence will change according to environmental conditions such as weather, food supply and predation risk.

This formulation of life-history theory leads to two predictions about the parental effort of long-lived birds in variable environments. Firstly, in extreme conditions the trade-off between current and future reproduction may be such that breeding will not be attempted at all, or abandoned after initiation. Secondly, when breeding is attempted the level and allocation of parental effort will be variable, and contribute to variation in the age of onset of breeding, time of breeding, clutch size, hatching success, chick growth and survival and breeding success.

1.2. Why study seabirds?

Several lines of evidence suggest that seabirds, where they breed in large colonies, may have a considerable impact on their prey populations as suggested by Ashmole (1963), *e.g.* bioenergetics modelling: Furness (1978, 1990); effects of colony size on the size of neighbouring colonies and on breeding performance: Furness & Birkhead (1984), Hunt *et al.* (1986); direct measurements of prey populations: Birt *et al.* (1987). They are often dependent on a small range of prey *e.g.* Furness (1978), Anderson *et al.* (1982), Schaffner (1986), which makes them very susceptible to changes in their prey populations, especially when the same populations are subject to human exploitation *e.g.* Furness (1982), Furness & Ainley (1984), Hislop & Harris (1985), Barrett *et al.* (1987), Montevecchi *et al.* (1988). Populations able to exploit alternative food sources may be able to continue to breed successfully when their major prey are depleted *e.g.* Anderson (1989), Barrett & Furness (1990).

Seabirds are generally long-lived birds and thus have ample opportunity to adjust their annual breeding effort according to environmental conditions which may vary naturally *e.g.* as a result of climatic events such as the El Nino Southern Oscillation events in the Pacific ocean (Schreiber & Schreiber 1984, Anderson 1989) as well as under human influence. Amongst them there are many examples of non-breeding, curtailed breeding and reduced breeding success in poor conditions *e.g.* Anderson *et al.* (1982), Schreiber & Schreiber (1984), Monaghan & Zonfrillo (1986), Schaffner (1986), Barrett *et al.* (1987), Anderson (1989), Boekelheide & Ainley (1989).

Thus seabirds are an interesting group in which to study life-history strategies. Furthermore, because of their potential responsiveness to environmental variation their study is of value from the points of view both of their own conservation (Furness & Ainley 1984) and as monitors of their environment *e.g.* Monaghan & Zonfrillo (1986), Cairns (1987a), Monaghan *et al.* (1989b), Barrett *et al.* (1990), which may often be much more difficult to study directly than the birds themselves.

1.3. The arctic tern

The arctic tern *Sterna paradisaea* is the most northern tern species, breeding from temperate latitudes to the high arctic. They are migratory, performing the most extensive known movements of any bird; the main wintering zone is thought to lie in the area of Antarctic pack-ice (Cramp & Simmons 1985). They return to the breeding grounds between early May and late June, depending upon the latitude, and breeding commences very shortly afterwards. They often form very large breeding colonies, especially in the south of their range, but may also breed singly or in small groups. Within colonies breeding activities are highly synchronised. They lay between one and three eggs, which are incubated for approximately 21 days. On hatching the chicks are covered in down and have well developed tarsi which reach adult proportions a week after hatching (Ewins 1985). They are capable of thermoregulation after approximately ten days (Klaassen *et al.* 1989) before which they are brooded by their parents. Initially the young remain at the nest, but after a few days they may move away in order to seek cover from sun, rain and predators. Parents feed their young on fish, crustacea and insects, which they deliver whole, directly from the bill.

The following review of their foods is summarised from Cramp & Simmons (1985). Marine fish often predominate in the diet, especially oil-rich species such as sandeels (*Ammodytes marinus*, *A. tobianus*, *A. americanus*, *A. lanceolatus*) and Clupeidae (*Clupea harengus*, *Sprattus sprattus*). Many other species are also found *e.g.* Capelin *Mallotus villosus*, sticklebacks *Gasterosteus aculeatus*, lumpsuckers *Cyclopterus lumpus*, saithe or coalfish *Pollachius virens* and butterfish *Pholis gunnellus*. Crustaceans include isopods, amphipods, euphausiids and mysids, and may form an important component of the diet, especially in the arctic. Insects, including Hymenoptera, Diptera, Lepidoptera, Ephemeroptera, Odonata and Coleoptera are sometimes taken, and there are even records of birds eating earthworms *Lumbricus* sp. and scavenging from rabbit *Oryctolagus cuniculus* corpses (perhaps for insects) (G. Scanlon pers. comm.). Plant material has also been recorded in the diet. Prey may be caught by plunge diving or surface dipping, the maximum depth reached probably being no greater than 0.5 metres. Insects are taken by hawking over land, often in the evening in Shetland, where Ghost moths *Hepialus humuli thulensis* were eaten (pers. obs., moths identified by M. Young, University of Aberdeen).

Arctic terns are amongst the smallest of the Laridae, weighing only approximately 110g, although gravid females may weigh up to 140g and the weight of birds at the end of a breeding attempt may fall below 90g (P. Monaghan & J. Uttley, own data). Young birds may attempt to breed at only 3 years old but most recruit to the breeding population at 4 years (Coulson & Horobin 1976). Subsequent annual mortality has been estimated to be in region of 12.5% resulting in an average breeding lifespan of 7.2 years (Coulson & Horobin 1976); the oldest recorded ringed bird was 34 years old (Cramp & Simmons 1985).

1.4. Seabirds in Shetland

Arctic terns

A survey carried out in 1980, under the auspices of the Royal Society for the Protection of Birds showed that Shetland held almost 32,000 breeding pairs of arctic terns, with a similar number in Orkney (Bullock & Gomersall 1981). Thus the Northern Isles at that time held over 80% of the UK population (Thomas 1982). Breeding success was high in the early 1980's as shown by data provided by the Shetland Ringing Group (Monaghan *et al.* 1989b) and Ewins (1985). However, since 1984, production of young has been virtually nil throughout Shetland (Monaghan *et al.* 1989b) with birds either failing to breed at all, deserting their eggs or failing at the chick-rearing stage. Of those chicks which do hatch, very few survive beyond the first week of life (Monaghan *et al.* 1989a, Uttley *et al.* 1989a). The cause of death is either starvation or exposure or both, and it has been shown that breeding adults on Shetland are lighter and may lose weight faster than those at successful colonies (Monaghan *et al.* 1989a, 1990). As a result the numbers breeding in Shetland more than halved between 1980 and 1989 (Avery & Green 1989) with a further fall of approximately 50% to 1990 (P. Ellis & D. Suddaby pers. comm.). This is likely to be due to a combination of low recruitment, non-breeding and possibly emigration. Thus in the late 1980's, Shetland's arctic terns were exhibiting all of the responses expected of a long-lived seabird experiencing environmental stress.

Other seabirds

Shetland holds a high proportion of the UK breeding population of many seabirds (Furness 1990). These range from species which may forage far offshore *e.g.* Fulmars *Fulmarus glacialis* and Gannets *Sula bassana*, to inshore feeders such as arctic terns, shags *Phalacrocorax aristotelis*, and arctic skuas *Stercorarius parasiticus*. They also include both surface feeding birds such as arctic terns and kittiwakes *Rissa tridactyla*, and diving species *e.g.* guillemots *Uria aalge*, shags and red-throated divers *Gavia stellata*.

Although initially unaffected, many of these species have subsequently suffered the same problems as arctic terns have experienced since 1984. In particular, kittiwakes, which although they may feed far offshore are also surface feeders, have shown poor breeding success and have declined in breeding numbers (Heubeck 1989). In general, it has been surface feeding species which have been worst affected, and within these, inshore feeders were affected earlier and more severely (Heubeck 1989).

The problem

Seabirds in UK waters depend to a large extent upon three energy rich species of fish: lesser sandeels *Ammodytes marinus*, sprats *Sprattus sprattus* and young herring *Clupea harengus*. In the Shetland area, the latter two species are uncommon (Kunzlik 1989) and lesser sandeels are the predominant prey in the diet of nearly all of Shetland's seabirds *e.g.* Furness (1978), Ewins (1985), Martin (1989), Uttley *et al.* (1989b). The lesser sandeel has been exploited by a local fishery since 1974 and is monitored by the Department of Agriculture and Fisheries for Scotland (DAFS). Fisheries data show that the production of young sandeels fell considerably after reaching a peak in the early 1980's and more recently a fall in spawning stock has also been detected (Bailey *et al.* in press). The initial manifestation of this phenomenon in the arctic tern, a small, surface and inshore feeding species (*sensu* Furness & Ainley 1984) was highly suggestive of poor food supply being its cause and there is a consensus of opinion that reduced availability of sandeels has been responsible for events over the past decade (Heubeck 1989). Controversy rages over the cause of this reduction (Avery & Green 1989, Heubeck 1989) and over the geographical extent of the reduction in seabird breeding success (Harris & Wanless 1990), but such debates are beyond the scope of this study.

1.5. Aims

The work carried out for this thesis was undertaken within a much larger project with the aim of examining the responses of breeding arctic terns to food shortage. The comparison between terns breeding in Shetland and elsewhere has been framed as a natural experiment in which food availability has been reduced for birds breeding in Shetland. The assumption is therefore made that differences which occur between Shetland and elsewhere are due to differences in food availability. Most comparisons have been drawn with terns breeding on Papa Westray, Orkney, which is only approximately 140km south of my study sites on Shetland, and where seabirds are also highly dependent on sandeels as food. Other comparisons have been made with terns breeding in Northumberland, where alternative or even preferable prey are available.

In this thesis I have investigated the effects of food shortage on some components of parental effort of arctic terns, specifically courtship feeding and clutch quality, allocation of effort to incubation, brooding and chick provisioning and energy expenditure.

2. GENERAL STUDY METHODS

The majority of the data which are to be examined in the following four chapters cannot be treated separately as far as their collection is concerned without much repetition or clumsy cross-referencing, so I intend to treat the collection of this common data-base as a whole and describe and justify the methods used in a single chapter. Specialised methodologies and statistical techniques which apply only to a single chapter are dealt with in the chapter concerned.

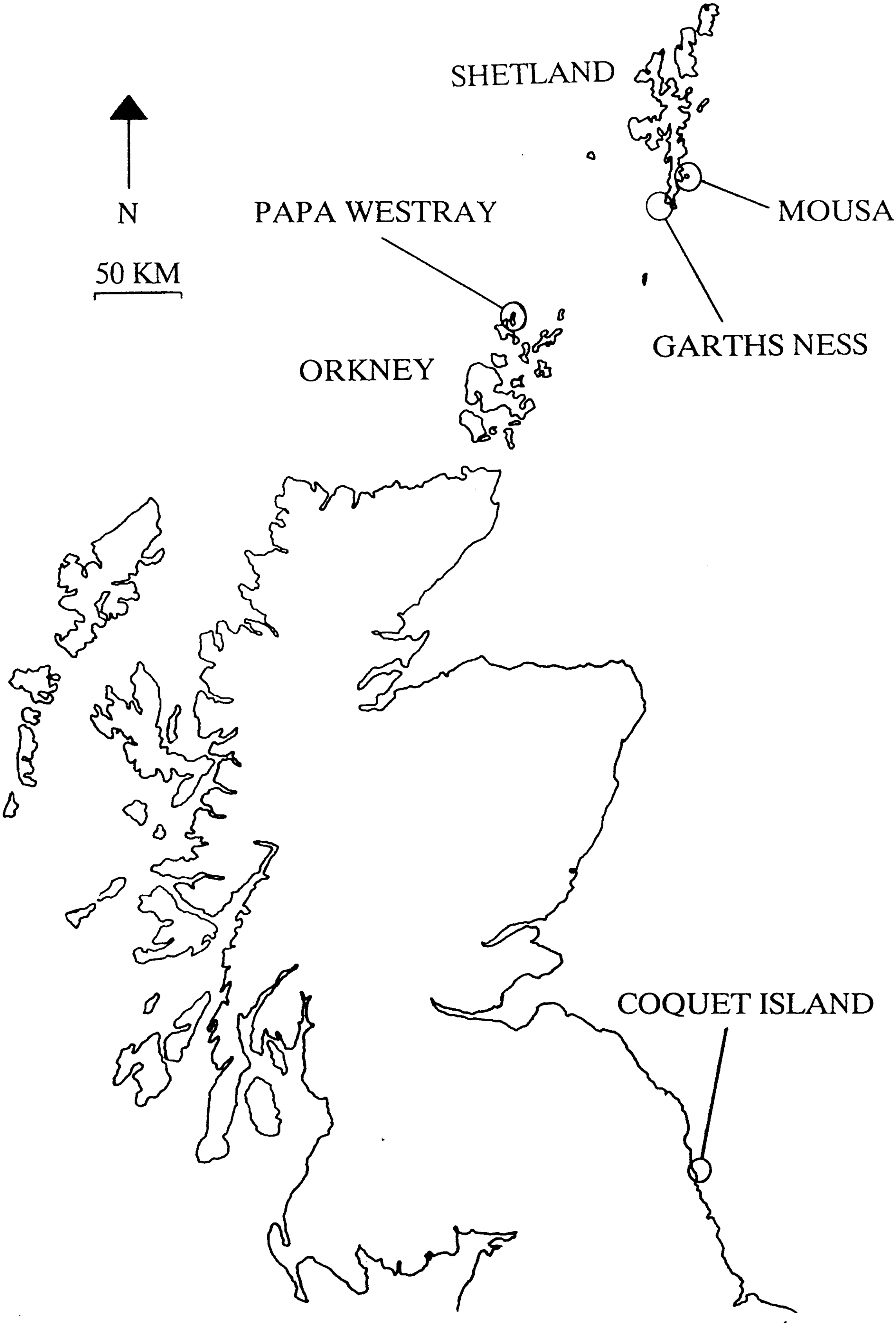
The colonial breeding habit of Arctic terns in Britain facilitates the collection of data on large numbers of breeding pairs during one breeding season. From a hide one can observe as many pairs simultaneously as it is possible to record observations for, and the breeding chronology and egg and chick measurements may be simultaneously recorded for a large number of nests.

The distribution of the study sites is shown in figure 2.1. One study site was used in each of the three years 1987, 1988 and 1989. In 1987, after beginning work at a colony at Dalsetter (59^{O} 56' N, 1^{O} 16' W) on the south mainland of Shetland, I had to move to another colony at Garths Ness (59^{O} 53' N, 1^{O} 23' W), also on the south mainland. This was due to the effects of hedgehogs at the former colony (Uttley *et al.* 1989a). In 1988, the Garths Ness colony was unoccupied, as were most other known colonies on south mainland, and the study site was located on the uninhabited island of Mousa (60^{O} 00' N, 1^{O} 10' W), *ca.* 1km east of south mainland. In 1989, I moved to Orkney, where I studied terns breeding on the North Hill of Papa Westray (59^{O} 22' N, 2^{O} 25' W). All of the colonies were immediately adjacent to the sea, and terns were nesting in short vegetation. Sheep grazed the area where terns bred on Garths Ness and Mousa, as did cattle on Papa Westray, but they had very little effect on the birds, normally being kept away from nesting areas by mobbing terns.

2.1. Study Site selection and establishment

At the beginning of each breeding season, a study plot was established within which the majority of data on breeding chronology and performance, time budgets and foraging

Figure 2.1. Map of northern Britain, showing the location of the study colonies on Shetland and Orkney, and the supplementary site on Coquet Island.


SHETLAND
N
50 KM
PAPA WESTRAY
MOUSA
GARTHS NESS
ORKNEY
COQUET ISLAND

performance were collected. Several factors needed to be considered during the selection of a study plot. These included physical features, such as topography, drainage, vegetation and exposure, and biotic factors such as the abundance and density of nesting terns, the likely age and breeding experience of those terns (see below) and the exposure of the nests to predators.

The location of breeding colonies within an area was unpredictable and selection of a study plot entailed monitoring the establishment of several colonies or sub-colonies over the pre-laying period. During the early part of the breeding season on Shetland, Arctic terns were very mobile and colonies appeared and disappeared overnight. On Papa Westray, Orkney, the distribution of displaying birds amongst sub-colonies differed radically from day to day, until birds settled down to lay eggs.

The primary requirements of a study plot were that it contained sufficient nests on which to make the observations described in 2.4 that were visible and close enough together for an observer to make detailed observations from a hide on up to ten nests at a time. I tried to aim for at least 50 nests in the plot, with about half visible for the purpose of making observations. To be observable a nest had to be within approximately 25 metres of the hide, beyond which it became difficult to observe events in sufficient detail. Since the study plots were established in the early part of the season, before all of the birds had laid, it was necessary to select the area to be used on the basis of the number and density of courting birds within it rather than the absolute number of nests which were eventually present. Two other factors had a bearing on the number of active nests in the plot remaining visible later in the season. Firstly, at the time of study plot establishment the short northern growing season had barely begun and the vegetation was very short. Some components of the vegetation, notably grasses, sedges and rushes grew rapidly after egg-laying and during chick-rearing, especially in damp areas; such areas were avoided since nests in this kind of vegetation were difficult to observe later in the season. Furthermore nests in damp areas were liable to be flooded after heavy precipitation.

The final criterion for study plot selection concerned the age and breeding experience of the terns breeding within it. Age and breeding experience have a significant influence on the breeding performance of terns and other seabirds (*e.g.* Coulson 1966, Coulson & Horobin 1976, Pugesek 1983, Nisbet *et al.* 1984, Boekelheide & Ainley 1989) and different age groups may show differences in laying date and in distribution within the colony - younger or less experienced pairs may lay later and in more peripheral or less densely colonised areas, lay smaller clutches and have a lower hatching and fledging success. If comparisons are to be made between colonies it is important to standardise as far as possible the age and experience of the birds from which the data are collected. To achieve this I tried to ensure that the peak laying date in the study plot was similar to that in the colony as a whole and that the area chosen was not peripheral to the main colony. Differences between sites and years were more difficult to avoid, but selecting birds laying about the modal laying date ought to have ensured that an unbiased cross-section of breeders was studied. Peripheral areas were also more vulnerable to attack by ground and aerial predators since terns and other larids rely on a colonial umbrella for the defence of their nests (Cullen 1960, Kruuk 1964, Uttley *et al.* 1989a). I avoided areas of the colony which I could not approach without causing a large amount of disturbance.

2.2. Breeding chronology and success

The study plot was established during the courtship phase of breeding, before egg-laying commenced. As soon as the hide was in place I began observations on courting birds. Since Arctic terns initiate incubation as soon as the first egg is laid, pairs with eggs were immediately apparent amongst those still courting. As birds laid I marked their nests with either canes coded with coloured flags made of plastic tape (1987) or with numbered stakes (1988,89). From the time of laying of the first egg, nests were checked each morning for fresh eggs. Each egg was marked 'a', 'b' or 'c' according to laying sequence, with a permanent marker pen, weighed by a 50g capacity 'Salter' spring balance to the nearest 0.5g, and measured on its length and maximum breadth with a pair of dial calipers to the nearest 0.1mm. Following clutch completion (three eggs in the nest, or no further eggs for three mornings) I ceased to check the nest daily. Each nest was checked at least twice during the incubation period to monitor egg-loss. The length of incursions into the colony for the purpose of checking for and measuring eggs, and later on to measure chicks, was limited in order to keep disturbance as low as possible. Nests were not checked during rain, and I tried to restrict the length of incursions into the colony to less than 15 minutes at a time and to no more than once per day.

Observations on the nests were continued during incubation, each nest being watched at least every other day. Deserted nests were identified during watches, by the continuous absence of a sitting bird. Normally, this was a certain indication of nest failure, but occasionally, especially early on in incubation, a nest would remain unattended for several hours, before one of the pair resumed incubation. Thus a nest appearing to have failed on one day might be attended as normal subsequently.

The semi-precocial chicks of Arctic terns become highly mobile within days of hatching. Their tarsi are highly developed at hatching, and are fully grown at about ten days old (Ewins 1985, Klaassen *et al.* 1989). This poses a major problem for the biologist wishing to investigate their growth and development in the field. Left undisturbed, the chicks will find suitable hiding places within the territory from aerial predators, where they spend most of the time that the parents are away and to which they retreat when in danger. However, heavy and persistent disturbance, such as caused by an making daily checks of nest contents can cause chicks to disperse widely or encourage their parents to lead them away to a less disturbed area. This causes two main problems. Firstly, chicks which stray into other territories may become lost and unable to relocate their parents or their natal territory. Even if this is only temporary it may be lethal if accompanied by wet and cold conditions under which young chicks require brooding if they are to avoid chilling and hypothermia. Choosing appropriate weather conditions in which to make incursions into the colony obviously helps to reduce such dangers, but weather conditions may change rapidly. In addition, chicks straying into foreign territories run a high risk of attack from the resident adults and such attacks may, in the extreme, be fatal. Secondly, the tendency of disturbed chicks to disperse widely makes them very hard to find. This results in fewer measurements being made, more time being taken to make them and a large degree of uncertainty about the fate of those chicks which are never re-located.

To counter this problem I followed several previous workers on terns (*e.g.* Nisbet & Drury 1972) and used wire-mesh fences to limit the movement of chicks within the colony. I used a mesh size of 13mm which prevented the passage of even the smallest chicks, and was also too small to allow larger chicks to get their heads or wings caught in the mesh. The earliest fences which I erected were around groups of nests covering *ca.* 25m^2, but I found that small (ca. 4m^2) enclosures around single nests were more efficient in terms of both the use of wire and locating young. I always ensured that there was some shelter from rain and sunlight within the enclosure, either natural, in the form of rocks or vegetation, or artificial, constructed from wood or rocks. To habituate the adults to the enclosures I erected them during the second half of incubation. All of the birds became used to the fences very quickly and all incubating birds returned to their clutches within two hours of installation of the fences.

Nest checks for newly hatched chicks were resumed at 18 days after the laying date of the first egg in each nest, the average incubation period being 21 days. Eggs which were 'starred' (small cracks in eggshell, but still intact) or 'pipping' (eggshell pierced by egg-tooth) were noted as these eggs would certainly hatch in the following two or three days. Newly hatched chicks were weighed to the nearest 0.5g using a spring balance and their maximum chord wing-length measured to the nearest 1mm using a stopped metal rule. Chicks were individually marked using British Trust for Ornithology numbered metal rings; they were sometimes temporarily marked with leg flags made from plastic insulating tape before being metal ringed. Subsequent to hatching I measured chicks on every third day. The wing length on growing chicks was measured to the tip of the growing feather i.e. not including the downy tip. Chicks which were not measured on any one day were recorded as either 'found', 'not found', 'dead' or 'not checked'. Records of the status of chicks taken during rounds of the study plot were supported by observations of broods from the hide during observation periods. Thus chick survival could be monitored on a day to day basis.

2.3. Marking and sexing individuals

Several aspects of this study required recognisable individuals. This was necessary in order to study the roles of males and females and to measure the foraging rates of known individuals. Non-breeding birds and failed breeders from other territories did intrude into the territory of a pair, but seldom attended the eggs and chicks as a parent would do for any length of time and these intruders were often chased away from the territory by the owners. This meant that, even when unmarked, a breeding bird in its own territory could be distinguished from intruders. Since all incubation, brooding and chick feeding took place inside the territory, all that was necessary was to devise a method of distinguishing between the members of a pair. There is little or no sexual dimorphism in the external morphology of Arctic terns. Therefore it is generally not possible to discriminate between the members of a pair without some artificial means of telling them apart. In a small minority of pairs I could discriminate between the male and female on the basis of some physical characteristic such as bill-shape or colouration or the absence of one or more tail-streamers on one of the birds. In most cases however I had to resort to marking birds temporarily with picric acid, a yellow dye which bonds to protein molecules and dyes the feathers yellow until they are lost in moult. This dye does not fade on exposure to sunlight or salt-water and thus has distinct advantages over other dyes available such as Rhodamine-B (red) or Sevron Blue. The method of dying was as follows. A small square (2 x 2 cm) of domestic cleaning sponge was cut, soaked in a solution of picric acid in absolute alcohol, and placed at the edge of the nest scrape, taking care not to allow dye to adhere to the eggs. I found no evidence that eggs which came into contact with the dye suffered from any reduction in hatching or fledging success, but the eggshell is a porous membrane and application of toxic chemicals such as picric acid was avoided if possible. After placing the sponge in the nest I retired to the hide to watch the birds return to their nests and note which were successfully marked. Most birds showed one of two responses to the sponge. The most frequent was to be alarmed for a short period, usually less than five minutes, before eventually settling on the eggs once more and sitting on the sponge, thus becoming marked. Some individuals were more wary and took longer, up to an hour, to resume incubation. Alternatively, some birds removed the sponge from their nest with the bill and dropped it some distance from the nest site before returning to the nest to incubate the eggs. When birds were nesting on green vegetation the use of blue sponges, which appeared green when soaked in dye, improved the success rate markedly. The disadvantage of this method is that if a changeover occurs whilst the sponge is still damp both members of a pair can become marked. Because the orientation of sitting birds is determined by the wind direction (Skipnes 1983) the new incubator normally sits in the same orientation as the bird which is being relieved, resulting in a similar mark. Therefore if both members of a pair were dyed it was often impossible to differentiate between them and a second attempt to mark one of the birds had to be made. I tried to prevent such dual marking by emerging from the hide to remove the sponge if the second bird came to relieve the first within about fifteen minutes of placing the sponge in the nest. With persistence over 75% of pairs could be marked in this way.

Terns may begin to incubate their eggs as soon as the first has been laid (Cramp & Simmons 1985, pers. obs.). By marking birds as soon as they began to lay it was possible to ascertain the sex of marked and unmarked birds by their behaviour in copulation or in courtship feeding. Mutual feeding was a reliable method of sexing birds because females never fed males; no bird identified as male by observation of copulation behaviour was subsequently seen to receive food from its mate at any time during the breeding attempt.

2.4. Time budgets and foraging performance

To obtain data on the time budgets and foraging performance of breeding birds I made observations on marked nests from a hide. Between 5 and 15 nests were observed synchronously, depending upon the stage of the breeding season and hence the level of activity at individual nests (events occurred more frequently at nests with chicks than at nests with eggs). The maximum number of nests which could be observed without missing events at some nests was determined by preliminary observations in 1987. These observations were not included in the set of data analysed. All observed nests were within 25 metres of the hide. The length of hide watches varied from two to six hours, most being approximately four hours long, totalling up to 12 hours per day when more than one observer was available. The timing of observations was randomised through the daylight hours to avoid bias towards any particular time of day. All observations were made with the aid of 10x40 binoculars.

Foraging performance was measured in terms of three components: 1) quality, 2) frequency of feeds, and 3) time spent foraging. The quality of feeds itself is made up of two components: prey type and prey size, which were measured as follows. Male terns feeding females, and adults feeding chicks, always bring food to the territory carried crossways in their bills, usually a single item at a time but occasionally more (Hays 1970, pers. obs.). This habit contrasts with the food delivery behaviour of many species of seabird which regurgitate their prey or derivatives of it to their young, and makes it relatively easy to assess the size and type of each prey item delivered. Where possible, prey were identified to species level e.g. saithe, sprat, lumpfish. Some prey species could be separated from others only by detailed examination in the hand e.g. *Ammodytes marinus* and *A. tobianus*. However, it was easy to separate sandeels from non-sandeels. In addition, the speed with which terns transfer food from male to female or adult to chick sometimes made accurate identification impossible. Prey were classified into broad categories e.g. sandeel, non-sandeel, gadoid spp., shrimp, insect (predominantly moth) or unknown. The length of prey items was estimated relative to bill-length (ca. 32 mm from Cramp & Simmons 1985), and each item was assigned to one of four broad categories, each of which approximated to a multiple of bill-length: 0-4cm, >4-8cm, >8-12cm, >12cm (in practice this largest size class was 12-16cm). The four centimetre width of size classes was chosen because this neatly divides 0-group from older fish. In addition, there were qualitative differences in the appearance of sandeels from the two smallest size categories. Fish in the 0-4cm class were barely metamorphosed from the larval stage, and appeared watery and translucent, whereas fish from the >4-8cm size class were silvery and much more substantial. The size classes identified by different observers were validated through side-by-side observations to avoid observer bias. The abilities of myself and one other observer to correctly assign prey to length categories were tested by one person holding up, one at a time, thirty sandeels in a pair of forceps, marked to imitate the length of an Arctic tern's bill, for five seconds. Both observers correctly assigned all of the fish. On the infrequent occasions when more than one item of prey was brought in at a time, they were invariably of the same type category, but sometimes of different sizes, so I recorded the number of items of each size class. The frequency of feeds could be assessed simply by recording the number of feeds during a known time interval i.e. the length of the observation period. In addition to these data I recorded the following information for each prey item: the time of arrival of each bird carrying prey; the fate of each prey item (eaten by self, mate or chick, kleptoparasitised, dropped or unknown); the time at which each prey item met its fate, and time of departure of birds from the territory. The time spent foraging can only be measured accurately with knowledge of the activity of birds absent from the breeding territory, since birds may perform activities other than foraging when they are away e.g. preening, washing and roosting. In a species such as the Arctic tern, which breeds in large colonies and feeds at sea, individuals cannot be followed without the use of radio telemetry. This technique is very time consuming and could not have been employed without detracting from other aspects of the study, so the information necessary to accurately measure time spent foraging was unavailable. Instead I had to use the length of periods away from the colony in between feeding events as an estimate of this parameter.

Other time-budget information was collected to assess the amount of time that birds spent at and away from the territory, and the amount of time on territory devoted to incubation, brooding and loafing. In 1987, I attempted to collect these data by recording complete time budgets for each pair under observation. I recorded the presence or absence of each bird at the beginning of the observation period together with the activity of the birds which were present (incubating, brooding or loafing). All subsequent changes in activity, and arrivals and departures were recorded, and from this information complete time-budgets could be constructed. This method had two major disadvantages. Firstly, it was impossible to follow more than about five nests during a hide watch with any degree of accuracy, which resulted in small sample sizes and detracted from the measurement of foraging performance which could often be measured for a larger number of nests. Secondly, the data collected in this way were time consuming to analyse and were more detailed than was necessary for the purpose for which they were collected, i.e. to compare territory attendance and the care of eggs and chicks between males and females and between different sites. Therefore, in 1988 and 1989 I used instantaneous scan sampling as recommended by (Altmann 1974) for the measurement of percentage time spent in different states. This was simpler and less prone to error, could be carried out quickly on a large number of nests without detracting from continuous recording of foraging performance, and generated simple, easily analysable data which could readily be compared between different groups of birds or nests. A sample of about fifteen nests was used in each watch and the presence and behaviour of the birds at each nest recorded at fifteen minute intervals; the state of each nest was regarded as representative of the following fifteen minutes until the next scan. The fifteen minute interval between scans was a compromise between maximising the number of scans and hence the accuracy of the attendance estimates and minimising the frequency of scans and hence the time spent not concentrating on feeding events. A single scan took less than thirty seconds to complete. Status was classified as present (not incubating or brooding), absent, incubating or brooding. The data for each observation period for each nest were summarised and the proportion of scans when two birds, one bird and no birds were on territory were totalled; the number of scans for which eggs/chicks were incubated/brooded was also calculated. For pairs which were individually marked I also recorded the proportion of scans for which each individual was on territory and the proportion of scans in which each was brooding or incubating.

2.5. Statistical analyses

Data analyses were performed with procedures described in Sokal & Rohlf (1981) and Siegel & Castellan (1988).

In chapters 3 and 5, where foraging performance is examined, means of diet composition and foraging rates have been taken for each day across all nests watched on that day; these means have subsequently been used in the analyses of intersite differences. Where possible, the occurrence of inter-nest differences in foraging parameters was tested for prior to analysis. No significant variation between nests was found, partly because in all years breeding success was low, with little variation in brood size between nests. The same nests were not always watched on each day. Since all nests were subjected, more or less, to the same food availability on any given day, pair means, calculated across days may not be independent.

Where data were normally distributed parametric tests were used to explore differences and relationships between samples and variables. T-tests, including paired tests and analysis of variance were performed using procedures T-TEST, ONEWAY and ANOVA on SPSSX v.2.1 and v.3.0 (SPSS Inc.), with multiple comparisons after 1-way Anova being made using the Scheffe multiple comparison procedure (Day & Quinn 1989). Pearson product-moment correlations were performed using procedures PEARSON CORR and PARTIAL CORR of SPSSX. Analyses of co-variance were made with procedure MANOVA. Where proportional data were analysed using parametric procedures they were first transformed with the arcsine transformation.

Where parametric tests were inappropriate, the best non-parametric alternatives were employed. Mann-Whitney U-tests, Kruskal-Wallis analysis of variance, Wilcoxon matched pairs - signed ranks tests and Spearman's rank correlations were performed on SPSSX using procedures NPAR TESTS and NONPAR CORR. Multiple comparisons after Kruskal-Wallis Anovas were carried out with the procedure described in Siegel & Castellan (1988).

Contingency table analyses were made with the chi-squared test. Tables were partitioned with the aid of a programme in Siegel & Castellan (1988). Goodness of fit tests were made by the G-test (Sokal & Rohlf 1981).

All tests of significance were made using two-tailed test statistics. Where levels of significance are displayed in tables or figures the following convention has been used: ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

3. AN INVESTIGATION OF THE RESPONSE OF COURTSHIP FEEDING AND CLUTCH QUALITY TO VARIATION IN FOOD SUPPLY

3.1. Introduction

Clutch quality may be defined by those characteristics of a clutch of eggs which bear upon breeding success, namely the number, size and composition of eggs, and the time at which they are laid.

The primary constraint on the clutch size of birds which provision their young is considered to be the ability of parents to raise them (Lack 1968). Implicit in this view is the assumption that clutch size is not limited by the capacity for egg production. However, in precocial species, which do not feed their offspring, clutch size may be limited by nutritional factors such as reserves or dietary intake (Lack 1968, Winkler & Walters 1983). The nutrition hypothesis may also apply to non-precocial species with high energetic or nutritional costs of egg production (Drent & Daan 1980, Winkler & Walters 1983). These two hypotheses are not exclusive since a clutch size which has evolved within the ultimate constraint of parental capacity during the chick-rearing period may be limited proximately by nutritional factors. Neither are they independent since the consequent reduction in energy and nutrient reserves resulting from increased investment in egg production may reduce the capacity of parents for investment at later stages of the breeding attempt (Martin 1987).

The Laridae, which include the terns, are classified as semi-precocial (Nice 1962); their young are fed by the parents, but hatch covered in down and are capable of locomotion within a short time. The cost of egg production in larids is high, requiring an estimated 1.7 x basal metabolism per day (Ricklefs 1974) and 2.32 x daily protein requirement (Robbins 1981). Both of these estimates place larid eggs amongst the most expensive of avian eggs to produce and the daily cost of egg production in Arctic terns may be even higher than the larid average due to the comparatively greater proportion of adult body weight which their eggs represent (Ricklefs 1974).

The importance of egg quality, as defined by size and composition varies between species in relation to the precocity of the offspring (Martin 1987) or the demands of embryonic and hatchling metabolism (Ricklefs 1977, Williams *et al.* 1982). Many studies have shown various parameters of egg quality to increase with precocity *e.g.* egg size relative to female body size (Rahn *et al.* 1975) and yolk and lipid content (Romanov & Romanov 1949, Nice 1962, Ricklefs 1977, Carey *et al.* 1980, Pettit *et al.* 1984). Increased investment by precocial species in eggs may be seen as an adaptation to increase offspring survival during the post-hatching period when they may have to survive a period of learning to self-feed and/or suffer exposure before they are capable of thermoregulation (Galbraith 1988a). Similar advantages may accrue to semi-precocial species such as terns where high chick mobility and early ability to thermoregulate are important mechanisms whereby the need for brooding and guarding of the young may be reduced. Amongst seabirds, larids have the highest of embryonic growth rates, with associated high levels of embryonic oxygen consumption and water loss (Rahn *et al.* 1984). Consequently, high egg quality is an important contributor to their breeding success and the lipid and water contents of their eggs are only slightly below those characteristic of fully precocial species (Collins & Lecroy 1972, Carey *et al.* 1980).

The advantages of laying high quality eggs are complex, manifold and well documented. Large eggs generally contain absolutely more lipid (Romanov & Romanov 1949, Parsons 1970, Ricklefs *et al.* 1978) and relatively (but also absolutely) more albumen (Parsons 1976, Nisbet 1978, Ricklefs *et al.* 1978, Ricklefs & Montevecchi 1979, Meathrel & Ryder 1987). Large eggs have greater hatching success (Thomas 1983) and give rise to large hatchlings (Schifferli 1973, Galbraith 1988a) which may be large in terms of absolute body size (Nisbet 1973, Ricklefs *et al.* 1978, Lundberg & Vaisanen 1979) or possess large lipid reserves (Romanov & Romanov 1949, Parsons 1970, Ricklefs *et al.* 1978, Williams 1980, Birkhead & Nettleship 1982, Birkhead & Nettleship 1984). This may confer advantages on the newly hatched chick in terms of competitive ability (Ricklefs *et al.* 1978) and mobility (Veen 1977, Quinn & Morris 1986) (via large body size), capacity to endure periods of fasting or exposure (via increased lipid reserves) (e.g. Parsons 1970), or cope with diets containing low water or high salt content such as those of marine birds (via high water content) (Ricklefs *et al.* 1978). Chicks from large eggs may go on to grow faster

(Nisbet 1973, Schifferli 1973, Birkhead & Nettleship 1982, Galbraith 1988b, Amundsen & Stokland 1990) and survive better than those from smaller eggs (Parsons 1970, Nisbet 1973, Schifferli 1973, Murton *et al.* 1974, Davis 1975, Nisbet 1978, Lundberg & Vaisanen 1979, Thomas 1983, Quinn & Morris 1986, Galbraith 1988a). Larger nestlings may have higher post-fledging survival than small nestlings (Dhondt 1979, Garnett 1981, Newton *et al.* 1983, Nur 1984b), but in several studies the advantage conferred upon the chicks from large eggs only lasted for an initial portion of its life (Parsons 1970, Schifferli 1973, Nisbet 1978, Galbraith 1988a&b, Amundsen & Stokland 1990). The only disadvantage of laying large eggs, apart from the nutritional cost of producing them, appears to be the longer incubation interval of larger eggs than small eggs (Parsons 1972), which may be an important factor where time constraints impose a cost on late hatching young.

Clutch quality is dependent upon the amount of nutrients and energy invested in them directly by the female, and, in some species, indirectly by the male via courtship feeding *e.g.* Royama (1966a), Nisbet (1973), Nisbet (1977), Tasker & Mills (1981), Morris (1986), Salzer & Larkin (1990). Consequently, food supply and female body condition have both been invoked as proximate factors controlling egg production. Most evidence is circumstantial, food supply normally being inferred from other data, but convincing evidence does exist from some species that investment in egg production may be food limited (Red-billed Quelea *Quelea quelea* Jones & Ward 1976, Sparrowhawk *Accipiter nisus* Newton & Marquiss 1981, Kestrels *Falco tinnunculus* Dijkstra *et al.* 1982, California gull *Larus californicus* Winkler 1985, Ural owl *Strix uralensis* Pietainen *et al.* 1986, Glaucous-winged gull *Larus glaucescens* Reid 1987, Lapwing *Vanellus vanellus* Galbraith 1988a, Common Guillemot Hatchwell & Pellatt 1990, Lesser black-backed Gull *Larus fuscus* Hiom *et al.* in press).

Courtship feeding is thought to play an important role in the provision of nutrition for egg-laying in many bird species including several gulls and terns. Nisbet (1973, 1977, 1978) and Morris (1986) have shown that clutch-size, egg-size, egg composition and early chick survival in common terns *Sterna hirundo* are all related to the performance of males in courtship feeding. During the courtship period, female larids spend a large amount of their time on territory (Mills 1979, Pierotti 1981, Wiggins & Morris 1987, Salzer & Larkin 1990), and are fed by the male (Nisbet 1973, Mills 1979, Salzer & Larkin 1990). Thus females are able to conserve energy and nutrients for investment in egg production. Salzer & Larkin (1990) examined the pattern of investment of protein and energy in eggs and the changes in courtship feeding through egg-laying in glaucous-winged gulls. They concluded that the females were food-limited during egg-laying and that courtship feeding contributed substantially to the protein costs of albumen production.

Martin (1987) outlined the possible responses that birds may make to reduced food supplies, which were as follows.

1/ reduce clutch size, and maintain egg quality. This option has a stepwise effect on potential breeding success, but maintains the survival potential of chicks.

2/ reduce egg size/quality, and maintain clutch size. This option reduces potential breeding success, through its effect on potential hatching success and chick survival. This may be considered to be a fine tuning of breeding success, in contrast to the relatively coarse tuning of option 1, above.

3/ maintain egg quality and clutch size, by increasing foraging effort and/or more extensive use of reserves. This option increases the cost of laying which could result in a decrease in residual reproductive value.

4/ delay breeding to allow further reserve formation. This option may lead to decreased offspring survival in species where breeding attempts later in the season are less successful.

5/ don't breed. This option is only available to long-lived birds which have a high probability of breeding in the future.

The studies presented here were intended to assess the effects of reduced food supplies on the courtship feeding performance, clutch size and egg quality of Arctic terns.

3.2. Methods

3.2.1. Courtship feeding rates

The frequency with which males fed their mates and the type and size of food items were recorded according to the methods described in 2.4. Data were collected on Shetland in 1987 and 1988. Comparative measurements of courtship feeding performance were obtained by identical methods on Orkney in 1988 by C. Thain, as part of the wider study.

In the closely related common tern, courtship feeding takes place in three distinct phases (Nisbet 1973). Initially males at the colony present fish to many different females until a pair-bond is established. At this point the second phase begins, during which the pair spend a great deal of time away from the colony, when the male feeds the female frequently. Finally, the female remains in the pair's territory for the majority of the time and is fed there by the male until the clutch is complete. In this study, courtship feeding rates were measured during the latter part of this third phase, beginning not more than two days before clutch initiation and ending with clutch completion. This period is similar to that used in Nisbet's common tern studies (Nisbet 1973, 1977, 1978).

Wet weights of sandeels, sprats and saithe were calculated from the length/weight relationships given in Harris & Hislop (1978). Energy contents of sandeels were estimated using the relationship for the month of May between length and energy content in Hislop *et al.* (in press). Energy content of saithe was calculated from the length/weight relationship and energy density (kJ per gram) in Harris & Hislop (1978). The mass of sandeels and saithe were calculated from the length/weight relationships in Harris & Hislop (1978). Since fish were classified into four length categories in the field as described in 2.4. the lengths used in these calculations were the midpoints of the categories *i.e.* 2cm, 6cm, 10cm and 14cm (taking the largest size class as 12-16cm). The mass and energy content of fish are related length by power relationships *e.g.* $E = 0.0024 L^{3.806}$ for June sandeels (Hislop *et al.* in press). Therefore the accuracy of estimations of calorific and mass intake are constrained by the accuracy of size estimation and the validity of the assumption, implicit in the use of size classifications, that fish are normally distributed within each size class. This validity of this assumption could only be tested by collecting large numbers of fish from incoming terns with prey, a procedure which could not be justified, as it would be extremely disturbing to the birds. Since it was not possible to estimate size any more accurately in this study it is worth noting that the differences in calorific content of small and large fish within a single size class are of similar magnitude to those between the midpoints of neighbouring size classes.

3.2.2. Clutch size, egg size and egg composition

Information on clutch and egg size was collected on Shetland in 1987 and 1988 in the course of procedures described in 2.4. Egg volume (ml) was estimated as length x breadth^2 x 0.48 (Coulson 1963, Dunn 1972). Since the composition of eggs was determined for eggs laid in 1988 on Shetland, Orkney and Coquet Island (see below) I have included comparable data on clutch and egg size from the latter two sites in this year. These data were collected using identical methods to my own by C. Thain and N. Gartshore on Orkney and Coquet respectively as part of the wider study.

Egg quality was assessed in 1988 from colonies of Arctic terns on Coquet Island (Northumberland), Papa Westray (Orkney) and Mousa (Shetland). A small, central area of each colony was chosen, from which 10 two-egg clutches were collected under licence from the Nature Conservancy Council within 24 hours of completion. All nests within the chosen areas were marked upon laying of the first egg and all eggs were marked with laying order and measured as described in 2.2.

After collection all eggs were hard-boiled, wrapped in paraffin coated film, placed in labelled, sealed bags and frozen until analysis. This procedure has previously been described by Ricklefs (1982) who found that it had a small but significant effect upon the composition of sampled eggs as opposed to fresh eggs. The main effect was a reduction in water content, although he also suggested possible effects upon the volatilisation and extractability of ether-extractable material *i.e.* lipids. However, this method of processing eggs did allow cleaner separation of shell, albumen and yolk, and moreover, this was the only practicable method to store eggs collected in a remote field situation without means for immediate analysis.

Separation of shell, albumen and yolk was made easier by partially defrosting the eggs for approximately one hour, in order to defrost the film of water which seeps between shell and albumen during boiling, and for the albumen to become flexible. The separated components were then placed in individual, labelled petri-dishes and dried in an oven at constant 60^{0}c for five days. The contents of the dishes were then weighed and placed in individual filter paper envelopes fastened by staples. Batches of these envelopes were subjected to exhaustive lipid extraction by chloroform in a soxhlet apparatus. Albumen samples were extracted for 12 hours and yolk for 24 hours, to ensure complete extraction. The materials were then dried and reweighed.

Since accurate fresh weights were not available for all eggs, analyses of the results were carried out on a dry weight basis due to the effects described by Ricklefs (1982) on water content. Initial dry weights of unextracted materials are referred to as DRY (SHELL (DS), ALBUMEN (DA), YOLK (DY) and TOTAL (DT = DS + DA + DY)). Fat extracted yolk is referred to as YOLK NON-LIPID (YNL) and fat content (DY - YNL) is referred to as YOLK LIPID (YL). The total non-lipid content of the eggs (DS + DA + YNL) is TOTAL NON-LIPID (TNL) (albumen samples contained negligible lipid). Lipid indices of the whole egg (TOTAL LIPID INDEX) and yolk (YOLK LIPID INDEX) were calculated from dry lipid mass (YL) divided by dry weight (DT or DY respectively). The proportion of the whole egg dry weight consisting of yolk is PERCENT YOLK.

3.2.3. Experimental manipulation of hatching location

In 1988 in a further test of the hypothesis that Arctic terns in Shetland were producing viable eggs *i.e.* eggs which did not possess any inherent defects, such as small size, poor quality, high pollutant burden or genetic abnormality, which may have hindered normal development, nine clutches of two eggs were transported from Mousa, Shetland, to Papa Westray, Orkney, where they replaced clutches taken for composition analysis. Clutches collected from Papa Westray were temporarily replaced with dummy eggs made from modelling clay. These dummies ensured that adults continued to incubate until donor clutches arrived from Shetland. The collected donor clutches were packed in cotton-wool in a large cut-out polystyrene block. They were then sent by boat, car and plane to Papa Westray, where they were exchanged for the dummy clutches approximately 12 hours after collection on Mousa. Donor and recipient nests were selected and matched in order that there was no more than one day's difference between clutch initiation dates. Incubation spans were therefore as normal as possible, preventing effects on adult behaviour from extended or shortened incubation periods.

The nine clutches were taken from the same area of the Mousa colony as were the eggs for analysis, and the order of laying and measurements of each egg were recorded as described in 2.2.

The hatching success of the eggs and the growth and survival of the chicks were subsequently monitored by C. Thain as described for the observational study plots in 2.2.

3.3. Results

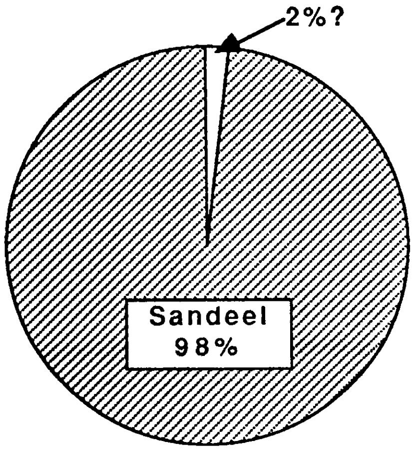
3.3.1. Courtship feeding

The species of fish fed to females at the nest site by males during courtship are shown in figure 3.1 and the size of sandeels in table 3.1. The size of saithe did not vary from approximately 6cm.

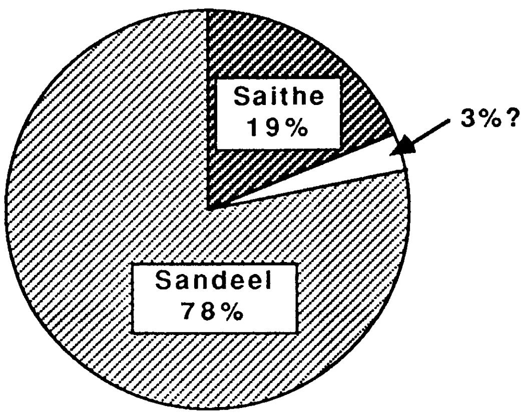
The proportion of courtship items which were sandeels varied significantly between the three sets of data in fig. 3.1 ($X^2 = 43.4$, d.f. = 2, $p < 0.001$). Partitioning of the contingency table (Siegel & Castellan 1988) confirmed that non-sandeels were more frequent on Shetland in 1988 than in 1987 ($X^2 = 32.4$, d.f. = 1, $p < 0.001$). Overall, non-sandeels were more frequent on Shetland (1987 and 1988 combined) than on Orkney (partitioned contingency table. $X^2 = 10.9$, d.f. = 1, $p < 0.01$); this effect was due to the

Figure 3.1. The proportion of items fed to females by male arctic terns during courtship which were sandeels and saithe in Shetland in 1987 (no. items = 122), Shetland in 1988 (n = 378) and Orkney in 1988 (n = 63).

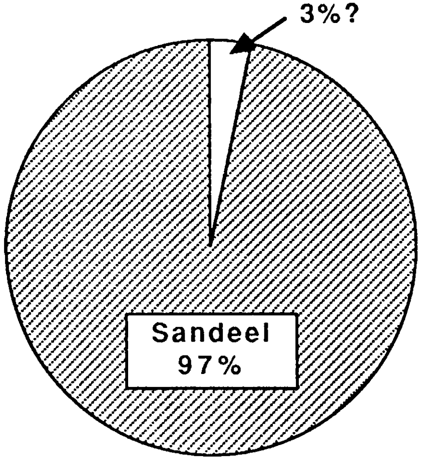
Shetland 1987



Shetland 1988



Orkney 1988



increased frequency of non-sandeels amongst courtship items on Shetland in 1988.

Table 3.1. The percentage of sandeels of different sizes fed to females by males during courtship

LOCATION	YEAR	n	SIZE CLASS (CM)			
			0-4	>4-8	>8-12	>12
SHETLAND	1987	120	4	1	26	69
SHETLAND	1988	291	40	18	24	18
ORKNEY	1988	61	11	69	20	0

The size of sandeels fed to females by males varied between the three situations (Tab. 3.1. $X^2 = 238.8$, d.f. = 6, $p < 0.001$). Partitioning of the contingency table showed that sandeels were larger on Shetland in 1987 than in 1988 and that sandeels of 4-8cm were more common on Orkney than Shetland (1987 and 1988 combined), whilst smaller and larger fish were less common.

The average number of items fed to females per hour is presented in table 3.2. Using the data on feeding frequency and prey size and type, the average mass and energy gathered per foraging trip were estimated , as were energy and mass delivered to the female per hour.

The frequency with which females were fed by males was highest on Shetland in 1988, intermediate on Orkney and lowest on Shetland in 1987. A Kruskal-Wallis ANOVA followed by a multiple comparison procedure (Siegel & Castellan 1988) showed these differences to be significant (Tab. 3.2. H = 37.4, d.f. = 2, $p < 0.001$).

As a result of the differences in diet composition and size of sandeels fed to females by males in the three situations, the mass of food and energy per feeding event also varied between them. These two quantities were smallest on Orkney, intermediate in 1988 on Shetland, and greatest on Shetland in 1987 (Tab. 3.2. Kruskal-Wallis ANOVA. mass / feed: H = 19.4, d.f. = 2, $p < 0.001$; kJ / feed: H = 20.6 , d.f. = 2, $p < 0.001$). A multiple comparison procedure failed to find any difference between Orkney and Shetland in 1988, whilst each quantity was greater on Shetland in 1987 than in either of the other two situations.

Table 3.2. The daily mean (s.e.) rate of courtship feeding on Shetland in 1987 (based on 12 nests observed for 49 hours) and 1988 (based on 20 nests observed for 64 hours), and on Orkney in 1988 (based on 14 nests observed for 33 hours)

LOCATION	YEAR	N (DAYS)	TRIPS /HR	MASS /TRIP	kJ /TRIP	MASS /HR	kJ /HR
SHETLAND	1987	20	0.04 (.01)	2.93 (.33)	13.71 (1.68)	0.14 (.04)	0.68 (.23)
SHETLAND	1988	22	1.03 (.17)	1.29 (.23)	5.97 (1.06)	1.11 (.23)	5.25 (1.16)
ORKNEY	1988	15	0.46 (.06)	0.84 (.10)	3.49 (1.86)	0.39 (.06)	1.62 (1.02)

The rank orders of the rates at which females were provisioned with energy and mass of food per hour were the same as was found for feeding frequency. Both energy and mass of food supplied to females per hour was greatest on Shetland in 1988, intermediate on Orkney and least on Shetland in 1987 (Tab. 3.2. Kruskal-Wallis ANOVA. mass / hour: $H = 24.6$, d.f. = 2, $p < 0.001$; kJ / hour: $H = 26.3$, d.f. = 2, $p > 0.001$). The multiple comparison procedure failed to find any significant differences between Shetland in 1987 and Orkney, but provisioning rate on Shetland in 1988 was greater than at either of the other two sites.

3.3.2. Clutch size

The distribution of clutch sizes laid by Arctic terns on Shetland in 1987 and 1988 and Orkney and Coquet in 1988 is shown in table 3.3. The mean clutch size was approximately 2 in all situations (tab. 3.4) as was the modal clutch size (tab. 3.3).

Table 3.3. Distribution of clutch sizes of arctic terns on Shetland, Orkney and Coquet Island in 1987, 1988 and 1989

LOCATION	YEAR	CLUTCH SIZE		
		1	2	3
SHETLAND	1987	56	194	28
SHETLAND	1988	30	82	3
ORKNEY	1988	11	46	7
COQUET	1988	16	69	6

Table 3.4. Mean (s.e.; n) clutch sizes of arctic terns on Shetland in 1987 and 1988, and Orkney and Coquet Island in 1988

LOCATION	YEAR	CLUTCH SIZE
SHETLAND	1987	1.90 (.03;278)
SHETLAND	1988	1.77 (.05;115)
ORKNEY	1988	1.94 (.07;63)
COQUET	1988	1.89 (.05;91)

Arctic terns laid smaller clutches on Shetland in 1988 than in 1987 (tab. 3.4.). This was due to a decline in the number of 3-egg clutches laid in the second year, as shown by partitioning of the contingency table of the frequencies of clutch size (tab. 3.3. (Shetland) comparison of '87/'88 and clutch-size $<=2$ / clutch-size $= 3$. $X^2 = 6.2$, d.f. $= 1$, $p < 0.05$).

Mean clutch size varied between the three sites in 1988. Chi-squared analysis of the contingency table yielded an insignificant result ($X^2 = 7.4$, d.f. $= 4$, $p > 0.1$). Partitioning the contingency table suggested that 3-egg clutches were less common on Shetland than on Coquet or Orkney (comparison of Coquet + Orkney / Shetland, clutch-size $<= 2$ / clutch-size $= 3$. $X^2 = 4.0$, d.f. $= 1$, $p < 0.05$), but this procedure cannot be reliably interpreted when the overall contingency table analysis is not statistically significant.

3.3.3. Egg volume

The mean size of eggs laid by Arctic terns on Shetland in 1987 and 1988, on Coquet and Orkney 1988 is shown in table 3.5.

Within site variation

The volume of a- and b-eggs laid on Shetland did not differ between 1987 and 1988 (tab. 3.5a. 2-way ANOVA by year and clutch size. year effect: ns); the sample size of c-eggs on Shetland in 1988 was very small and no comparison was performed. On Shetland a-eggs from clutches of one were smaller than those from clutches of two (tab. 3.5. clutch size effect: $F_{1,289} = 6.73$, $p < 0.01$), and this effect was the same in both years (year x clutch size interaction: ns). For subsequent analyses the two years of data were combined.

Clutch size had a significant effect on the volume of a-eggs (tab. 3.5b. 2-way ANOVA by location and clutch size. Clutch size effect: $F_{2,468} = 3.06$, $p < 0.05$), but the effect was not consistent between the three locations (location x clutch size interaction: $F_{4,468} = 3.20$, $p < 0.05$). A-egg volume decreased with increasing clutch size on Coquet and Orkney, but was highest in 2-egg clutches on Shetland

Between site variation

The volume of a- and b-eggs varied significantly between Shetland, Orkney and Coquet (tab. 3.5. 2-way ANOVA by location and clutch size. Location effect: a-eggs - $F_{2,468} = 3.20$, $p < .05$; b-eggs - $F_{2,360} = 4.03$, $p < 0.05$). A series of 1-way ANOVAs showed that the volume of a-eggs varied with location in single-egg clutches only ($F_{2,95} = 5.75$, $p < 0.01$), whilst the volume of b-eggs varied with location in two-egg clutches only ($F_{2,325} = 4.25$, $p < 0.05$). In both cases, eggs from Coquet were larger than those from Shetland (Scheffe's MCP). Total clutch volume did not vary between the sites.

Table 3.5. The estimated volume of eggs laid by arctic terns on Shetland, Orkney and Coquet Island

	Volume (ml)							
Site/Year	a-egg			b-egg		c-egg	total clutch	
	1-egg	2-egg	3-egg	2-egg	3-egg	3-egg	2-egg	3-egg
a) SHETLAND								
1987	16.22(.17) (n=51)	16.67(.11) (n=193)	16.18(.27) (n=25)	16.02(.10) (n=192)	16.30(.23) (n=26)	15.69(.26) (n=27)	32.70(.18) (n=191)	48.24(.73) (n=73)
1988	16.23(.28) (n=20)	16.78(.12) (n=49)	17.54(.20) (n=2)	16.24(.18) (n=38)	16.51(.64) (n=2)	16.41(.46) (n=2)	33.09(.29) (n=31)	50.47(-) (n=1)
b) ALL DATA								
SHETLAND	16.22(.14) (n=71)	16.69(.09) (n=242)	16.28(.26) (n=27)	16.06(.09) (n=230)	16.32(.22) (n=28)	15.74(.25) (n=28)	32.74(.16) (n=222)	48.32(.70) (n=26)
COQUET	17.74(.82) (n=16)	16.92(.16) (n=69)	15.43(.85) (n=6)	16.58(.17) (n=68)	16.42(.68) (n=6)	15.16(.59) (n=6)	33.50(.31) (n=68)	47.02(1.60) (n=6)
ORKNEY	17.14(.42) (n=11)	16.87(.24) (n=31)	16.21(.21) (n=4)	16.39(.20) (n=30)	16.25(.32) (n=4)	14.94(.42) (n=4)	33.30(.41) (n=30)	47.39(.85) (n=4)

Variation with laying sequence

Within clutches of two eggs paired t-tests showed that a-eggs were consistently of greater volume than b-eggs (Shetland: $t_{221} = 7.04$, $p < 0.001$; Orkney: $t_{29} = 3.07$, $p < 0.01$; Coquet: $t_{67} = 2.90$, $p < 0.01$). Insufficient 3-egg clutches were measured on Coquet and Orkney but on Shetland no differences were observed between first- and second-laid eggs in clutches of three. Both were of greater volume than c-eggs (Shetland: (a vs. c) $t_{25} = 2.59$, $p < 0.05$, (b vs. c) $t_{25} = 3.01$, $p < 0.01$)

The volumes of a-eggs were significantly correlated with the volumes of b- and c-eggs from the same clutch; the volume of the a-egg explaining 26% (Shetland: $r = 0.510$, $n = 230$, $p < 0.001$), 44% (Coquet: $r = 0.663$, $n = 68$, $p < 0.001$) and 77% (Orkney: $r = 0.877$, $n = 30$, $p < 0.01$) of variation in the volume of b-eggs, and 59% of variation in the volume of c-eggs on Shetland ($r = 0.77$, $n = 27$, $p < 0.01$).

Table 3.6. The volume (s.e.) of eggs from two-egg clutches collected for analysis of composition on Shetland, Orkney and Coquet Island in 1988

	VOLUME (ML)		
	SHETLAND	ORKNEY	COQUET
n	10	8	8
(a)	16.9 (0.2)	16.6 (0.5)	17.5 (0.3)
(b)	16.3 (0.2)	16.0 (0.3)	17.0 (0.2)

3.3.4. Egg composition

The mean volume of the eggs collected for analysis of composition from Shetland, Orkney and Coquet in 1988 is shown in table 3.6. These eggs were not significantly different in size from eggs of clutches of two from the larger sample of measured eggs from each site analysed in 3.3.2. This small sample of eggs was also similar to the latter in that the volume of a-eggs tended to be greater than that of b-eggs, but this was only significant in Shetland (Paired t-test. Shetland: $t_9 = 3.01$).

Within-clutch variation

Paired t-tests showed that there were no differences between first- and second laid eggs in the total weight, weight of shell, albumen, yolk lipid, total lipid index or percentage yolk (tabs 3.7 & 3.8). Considering the yolk, there was a consistent trend for the dry weight of a-yolks to be greater than that of b-yolks (tab. 3.7) though this was significant only for eggs from Shetland (Paired t-test. Shetland: $t_9 = 3.48$, $p < 0.01$). This was due to the non-lipid component of the a-yolk being greater than that of the b-yolk (tab. 3.7) (Paired t-tests. Shetland: $t_9 = 3.29$, $p < 0.01$; Coquet: $t_7 = 2.61$, $p < 0.05$; Orkney: $t_7 = 2.21$, $p = 0.06$). B-yolks tended to have a higher lipid index than a-yolks (tab. 3.8) but this was significant only for eggs from Coquet (Paired t-test. Coquet: $t_7 = -2.58$, $p < 0.05$). Although albumen content did not vary with laying sequence, total non-lipid content was generally higher in first- than second-laid eggs (tab. 3.7) (Paired t-tests. Shetland: $t_9 = 2.35$, $p < 0.05$; Coquet: $t_7 = 2.01$, $p = 0.08$; Orkney: $t_7 = 2.01$, $p = 0.08$) presumably as a result of the difference in non-lipid yolk content already noted.

Between site variation

Differences between sites were examined by 1-way ANOVA. Average egg dry weight (a & b combined) differed significantly between eggs from different sites (tab. 3.7) ($F_{2,49}$ = 4. was due to eggs from Orkney having less albumen (tab. 3.7) ($F_{2,49} = 22.35$, $p < 0.001$) than those from Shetland or Coquet (Scheffe's MCP, $p < 0.05$). Dry yolk lipid mass varied between sites (tab. 3.7) ($F_{2,49} = 3.54$, $p < 0.05$) eggs from Orkney containing less than those from Coquet or Shetland, but insignificantly so (Scheffe's MCP). As a result, the yolk lipid index was lower for Orkney eggs (Scheffe's MCP, $p < 0.05$) in both first- ($F_{2,23}$

Table 3.7. The mean (s.e.) dry composition by weight (g) of eggs from two egg clutches on Shetland, Orkney and Coquet Island in 1987 and 1988

		SITE		
		SHETLAND	ORKNEY	COQUET
n		10	8	8
PARAMETER	EGG			
WHOLE EGG				
TOTAL	a	5.02 (.07)	4.84 (.14)	5.15 (.12)
	b	4.89 (.07)	4.67 (.13)	4.99 (.11)
NON-LIPID	a	3.38 (.06)	3.26 (.10)	3.47 (.08)
	b	3.27 (.05)	3.15 (.10)	3.34 (.06)
LIPID	a	1.67 (.04)	1.58 (.05)	1.68 (.05)
	b	1.63 (.04)	1.53 (.05)	1.65 (.06)
SHELL				
TOTAL	a	1.02 (.02)	1.08 (.05)	1.05 (.04)
	b	1.02 (.02)	1.04 (.03)	1.02 (.03)
ALBUMEN				
TOTAL	a	1.42 (.02)	1.24 (.04)	1.48 (.03)
	b	1.39 (.03)	1.21 (.07)	1.47 (.03)
YOLK				
TOTAL	a	2.58 (.05)	2.51 (.09)	2.61 (.09)
	b	2.48 (.05)	2.42 (.07)	2.50 (.08)
NON-LIPID	a	0.91 (.02)	0.94 (.04)	0.93 (.04)
	b	0.85 (.82)	0.89 (.03)	0.85 (.03)
LIPID	a	1.67 (.04)	1.58 (.05)	1.68 (.05)
	b	1.63 (.04)	1.53 (.05)	1.65 (.06)

= 6.70, $p < 0.05$) and second-laid eggs ($F_{2,23}$ = 7.72, $p < 0.05$) (tab. 3.8). The volume of eggs in the sample from Orkney was smaller than those from Shetland or Coquet (tab. 3.6) ($F_{2,49}$ = 4.53, $p < 0.05$; Scheffe's MCP).

Table 3.8. The mean (s.e.) lipid indices and percentage composition by yolk of eggs from two-egg clutches on Shetland, Orkney and Coquet Island in 1988

PARAMETER	EGG	SHETLAND	ORKNEY	COQUET
n		10	8	8
PERCENT YOLK	(a)	51.36 (.49)	51.86 (.80)	50.66 (.80)
	(b)	50.66 (.60)	51.76 (.90)	50.06 (.90)
YOLK LIPID INDEX	(a)	.648 (.004)	.628 (.004)	.645 (.005)
	(b)	.656 (.007)	.632 (.005)	.660 (.003)
TOTAL LIPID INDEX	(a)	.333 (.004)	.325 (.005)	.326 (.005)
	(b)	.333 (.005)	.326 (.006)	.330 (.007)

The mass of each egg component was significantly correlated with egg volume, suggesting that the lower albumen and yolk lipid content of eggs in the sample from Orkney may have been a consequence of the smaller volume of those eggs. Analysis of co-variance revealed that the elevations of the relationship between egg volume and albumen dry weight varied between the three sites (site effect: $F_{2,48}$ = 17.5, $p < 0.001$; site x volume interaction effect: ns). Examination of the regression lines shows that the Orkney relationship was indeed at a lower elevation than those for the Shetland or Coquet eggs (regressions of albumen (A) versus egg volume (V): Shetland: $A = 0.06V + 0.445$, n = 20, r = 0.59, $p < 0.01$; Coquet: $A = 0.03V + 1.009$, n = 16, r = 0.24, n.s.; Orkney: $A = 0.08v - 0.044$, n = 16, r = 0.63, $p < 0.01$). Analysis of co-variance of the yolk lipid / egg volume relationships yielded no significant differences.

3.3.5. Manipulation of hatching location

Transported eggs were not different in size to two-egg clutches from the measured sample of eggs on Shetland (3.3.3) and there is therefore no reason to suspect that the former possessed any intrinsic advantage over untransported eggs.

Hatching success

Of the clutches of eggs transferred from Shetland to Orkney, mean hatching success (0.889, s.d. = 0.22, n = 9) not significantly different from the observed mean hatching success of native Orkney clutches (0.692, s.d. = 0.44, n = 13).

Fledging success

The donor nests were outside the main study plot on Papa Westray and the fate of the young was hard to determine, since regular visits were not possible and some broods disappeared without known cause and may simply have wandered away from the 'natal' area. However, of those 12 chicks whose progress it was possible to monitor, three fledged (25%), which was not significantly different from the overall fledging success of 33% in the main study plot, and much higher than the fledging success of chicks from eggs which were laid and hatched on Shetland.

Growth rate

Table 3.9. The linear growth rates of chicks from eggs transported from Shetland and chicks from native Orkney eggs in 1988

GROUP	n[1]	mean slope	s.d.
A. WING WITH AGE			
ORKNEY	10	7.09	2.42
TRANSPORTED	10	6.07	2.40
B. WEIGHT WITH AGE			
ORKNEY	10	4.67	1.77
TRANSPORTED	9	4.99	2.01

1 - number of chicks

The linear rate of wing growth and weight gain with age of the chicks which hatched from transported eggs is shown in table 3.9, along with data from untransported chicks from Orkney. Transported Shetland chicks gained weight ($t_{17} = 0.426$, $p > 0.05$) and grew their wings ($t_{28} = 0.790$, $p > 0.05$) at similar rates to those of native Orkney chicks..

3.4. Discussion

3.4.1. Food supply and courtship feeding effort

Data from the Department for Agriculture and Fisheries for Scotland show that 1988 was an especially poor year in Shetland for one-year old sandeels (1-group), which are particularly important for Arctic terns in the courtship period (*e.g.* Ewins 1985). The poorness of the 1987 cohort of sandeels is supported by their scarcity as young fish (0-group) in the diet of chicks in 1987 (see chapter 5). Further evidence is provided by the shift in courtship prey of males on Shetland between 1987 and 1988 (3.3.1) whereby sandeels occurred at reduced frequency in the diet in 1988 and those sandeels which were fed to females tended to be small, probably of the 0-group.

Despite the apparent shortage of 1-group and older sandeels, males on Shetland in 1988 were observed to provision their females with more mass of prey and energy than in either 1987 or on Orkney in the same year. This was brought about by a combination of a shift to young saithe, which contained more energy than the 0-group sandeels, and an apparent increase in the work-rate of males - they made trips twice as frequently as did males on Orkney and 25 times as frequently as on Shetland in 1987. Sandeels remained the dominant item in the diet, and were much smaller than in the previous year. Morris (1986) also found courtship feeding frequency to be inversely related to prey quality in common terns. How can the apparent contradiction of higher provisioning rate in poorer conditions of food supply be reconciled?

Firstly, it is of course possible that food availability is not measured accurately by fisheries statistics, and that food was readily available to Arctic terns during egg formation in Shetland in 1988. However, other evidence supports the contention that food was in short supply. In addition to that noted above, data on adult body weight show that Arctic terns in Shetland were very light early in the season in 1988, and the nest desertion rate was very high during incubation (Monaghan *et al.* 1990).

Nisbet (1977) showed that female common terns probably had all of the reserves which they need for egg laying by the end of the second phase of courtship feeding or 'honeymoon' period. Thus the final phase of courtship feeding may have little importance for egg production when food supply is good. Instead it may have greater bearing upon mate selection and retention (Nisbet 1978, Wiggins & Morris 1986) although no evidence has ever been provided to support this claim. In periods of poor food supply however, the third phase of courtship feeding may assume greater importance for egg production and this may explain the increased provisioning of females by males in Shetland in 1988. This idea is explored in more detail in the next chapter.

3.4.2. Food supply and clutch quality

Mean clutch size on Shetland declined from 1987 to 1988 so that it was less than the mean clutch laid on Orkney and Coquet in 1988, although insignificantly so. Thus there is some evidence that Arctic terns experiencing food shortage in the pre-laying period reduced their clutch size according to option 1 (3.1). There is also evidence that they responded according to option 2 (3.1) by reducing the size of their eggs. However, this was not supported by data on egg composition, which suggest, albeit inconclusively, that egg quality was poorer on Orkney than on Shetland in 1988.

Thus Arctic terns facing poor feeding conditions early in the breeding season may adopt a hybrid strategy of reducing both clutch size and egg quality. Two other studies have examined the clutch size of terns in fluctuating conditions of food supply. Ewins (1985) found no change in the clutch size of Arctic terns in Shetland between 1982/1983 when feeding conditions appeared to be good, and 1984, when signs of the current food shortage were first manifested. However, Safina *et al.* (1988) found an increase in the clutch size of common terns in a year when food was abundant. Becker *et al.* (1985), showed that the clutch size of common terns was sensitive to the amount of rainfall in the five days preceding clutch initiation, a factor which they thought influenced foraging success.

The decision as to whether to reduce egg quality or lay fewer eggs depends upon the shape of the trade-off function between egg quality and chick survival. Martin (1987), following the work of Nur (1984b) on chick weight and survival, postulated a logistic form to this relationship. In this model, the steeper the slope the greater the cost of reducing egg quality, or conversely, the greater the benefit of maintaining egg quality at the plateau level. The cost of reducing egg quality may be so severe as to render clutch size reduction a better strategy to adopt. The shape of the function may vary between individuals of different quality since better quality parents may be able to compensate for poor quality eggs by giving higher quality parental care. Coulson & Horobin (1976) showed that old (> 8 years old) Arctic terns had a higher breeding success than younger birds, despite laying smaller clutches and eggs. This suggests that their quality of parental care was better, indeed Coulson & Horobin (1976) also showed that chicks of older birds grew faster than did those of younger birds. Similar trends have been reported by Nisbet *et al.* (1984) for common terns. Furthermore, individuals of different quality may vary in their ability to invest in egg production (Drent & Daan 1980). Thus the best strategy may not be the same for different birds, and some may reduce egg-size whilst others lay fewer eggs. High quality or more experienced breeders may maintain clutch quality (option 3 (3.1)) since they may have more time and energy to devote to reproduction.

Eggs transported from Shetland to be hatched by Orkney birds did not appear to give rise to chicks any less viable than those laid by native Orkney birds which shows that any reduction in the size of Shetland eggs in 1988 did not reduce their viability in the apparently good feeding conditions found on Orkney (Chapter 5). This does not rule out the possibility that reduced egg-size contributed to chick mortality in the poorer feeding conditions found on Shetland since the increased reserves of young hatching from large eggs may assume greater importance in marginal conditions (Nisbet 1978). However, the conditions on Shetland appear to be rather worse than 'marginal' for breeding Arctic terns and such considerations are unlikely to apply in this case.

One factor which may obscure the response of Arctic terns to this situation is the extent to which birds adopt option 5 (3.1) by failing to breed at all. This is clearly a potential response for Arctic terns, since they are long-lived and may have the opportunity to breed again in better conditions. However, because of the nature of the changes with age of clutch and egg size described by Coulson & Horobin (1976) its impact on the aspects of Arctic tern breeding biology studied in this chapter are hard to predict.

3.4.3. Intraclutch variation in egg quality

It is a well established fact that the last laid eggs of larids are often smaller than the preceding eggs in the clutch *e.g.* Coulson (1963), Parsons (1970), Nisbet (1978), Quinn & Morris (1986), Meathrel & Ryder (1987). Clutches of both two and three eggs in this study conform to that pattern (3.3.3), b-eggs being smaller than a-eggs in clutches of two, c-eggs smaller than a- and b-eggs in clutches of three. This pattern of egg size has been explained variously as an adaptation for brood reduction *e.g.* Parsons (1976), a method to reduce hatching asynchrony (Parsons 1972) or as a consequence of the onset of incubation and decrease in nutrient intake (Reid 1987, Salzer & Larkin 1990). In two-egg clutches of Arctic terns, the difference between a- and b-eggs appears to be a consequence of less non-lipid material in the dry yolk portion of the egg (3.3.4). This may lead b-chicks to be smaller than a-chicks on hatching. However, there was no difference in the lipid content of a- and b-eggs, so newly hatched b-chicks may be smaller than their earlier hatched siblings, but possess relatively greater energy reserves. The protein content of yolk material has been linked with use of protein reserves, whilst lipid content has not been associated with depletion of lipid reserves (Houston *et al.* 1983). Hence it seems that protein reserves may be depleted during yolk formation in Arctic terns.

4. FOOD SUPPLY AND THE ALLOCATION OF PARENTAL EFFORT IN ARCTIC TERNS.

4.1. INTRODUCTION

Despite the prevalence of monogamy and bi-parental care amongst birds (Lack 1968) little research has been conducted into the allocation of male and female parental investment within this framework, nor into the variation in allocation caused by environmental factors (Wittenberger & Tilson 1980). This contrasts strongly with the large number of studies dealing with these aspects of breeding biology in rarer polygamous mating systems. This may reflect an apparent desire to explain the existence of the unusual, rather than to understand the maintenance of the ordinary. Perhaps it also stems from a desire on the part of sociobiologists and behavioural ecologists to extrapolate their results to human behaviour!

Male and female reproductive success are potentially limited by different factors (Alexander and Borgia 1979), resulting in different strategies to maximise fitness (Trivers 1972). Therefore the cost-benefit functions of parental effort and hence the time and energy budgets of the two sexes should differ (Brunton 1988a, 1988b). The responses of these functions to environmental variation should also differ between the sexes leading to differences in the effects of changes in environmental conditions on male and female time budgets.

According to the definition of Wittenberger & Tilson (1980) Arctic terns are a monogamous species: that is they 'maintain a prolonged and essentially exclusive relationship with one partner during the breeding season'. Busse (1983) has shown that they exceed this criterion by maintaining pair-bonds from year to year. However, such definitions do not preclude promiscuous behaviour entirely. Numerous studies have revealed extensive promiscuous activity by apparently monogamous birds (reviewed by Gladstone 1979, Ford 1983). Arctic terns are sexually monomorphic (Cramp & Simmons 1985) though the possibility of slight differences, such as that shown by Coulter (1986) in common terns cannot be ruled out.

The aim of this chapter is to examine the roles of male and female Arctic terns in detail, as has been done for the common tern (Wiggins & Morris 1987, Wagner & Safina 1989, Wiggins 1989). I then go on to use the comparison between birds breeding on Shetland in 1988 and on Orkney in 1989 to investigate the effects of changes in food supply on male and female time-budgets through the breeding attempt. Such an analysis may help to identify some of the factors maintaining monogamy in this species and also reveal the existence of bottlenecks in the breeding cycle.

4.2. Methods

Data were collected on chick provisioning, territory attendance and activity on the territory according to the methods in chapter 2. Marked birds were sexed from observations of copulations and courtship feeding on Shetland in 1988 (n = 8 sexed pairs), and on Orkney in 1989 (n = 22).

For analyses the breeding season has been divided into five phases: laying (from start to end of laying inclusive; 0-5 days), incubation (from day after end of laying to day before start of hatching inclusive; 15-21 days), hatching (from start to end of hatching inclusive; 0-5 days), first week of chick life (from end of hatching to end of eldest chick's first week of life; 2-7 days) and remainder of chick life (everything subsequent to this; up to 18 days).

4.3. Results

4.3.1 Total parental care

Total parental care refers to the overall level of care provided by the parents, regardless of the proportion supplied by each member of the pair. Figure 4.1 shows the proportion of the time in each study area for which eggs and chicks were incubated and brooded on each day relative to the hatching of the first chick. The data plotted include all of the nests which were active on each day, regardless of their ultimate success or failure.

Inactive nests i.e. nests which had already failed by the day in question are not included. There is no significant difference in the consistency of incubation between Shetland (99.3%, s.e. = 0.22, n = 167 nest-days) and Orkney (99.9%, s.e. = 0.02, n = 298) (Mann-Whitney U-test).

The mean proportion of time for which chicks were brooded declined with chick age at both sites (fig. 4.1) although this was only significant on Orkney (Pooled data for all nests over first ten days, sexed and unsexed. Shetland: $r_s = -0.46$, $p > 0.1$, $n = 10$; Orkney: $r_s = -1.00$, $p < 0.001$, $n = 10$) but chicks on Shetland were, on average, brooded consistently less than chicks on Orkney from the day of hatching to day 9 inclusive (Wilcoxon matched-pairs signed ranks test: $T_s = -2.0$, $p < 0.01$, d.f. = 8).

4.3.2 Allocation of male and female parental effort

Table 4.1 shows the allocation of male and female time to incubation and brooding recorded on Shetland in 1988 and on Orkney in 1989.

'Good food supply' site

On Orkney, males and females contributed equally to daytime incubation both during and after laying (t-test for each phase: ns) (tab. 4.1), but females (n = 37 observations) tended to be incubating more often than males (n = 15) at the end of the day (after 2200) but this was significant on only one evening out of five (each night tested separately for deviation from 50:50 ratio with binomial test). Females spent significantly more time brooding than males during the whole of the post-hatching period (hatching:$t_{32} = 3.89$, $p < 0.001$; less than 1 week old: $t_{36} = 2.42$, $p < 0.05$; more than 1 week old: $t_{34} = 2.26$, $p < 0.05$) (tab. 4.1).

During the first week of the oldest chicks' life (hatching and first week of life phases combined) adult males spent more time away from the territory than females (fig. 4.2) (Wilcoxon's matched pairs signed ranks test: $T_s = 0.0$, $p < 0.02$), and the amount of time

Figure 4.1. The mean proportion of time per day for which eggs were incubated and chicks up to 9 days old were brooded on Shetland in 1988 (○) and on Papa Westray in 1989 (●).

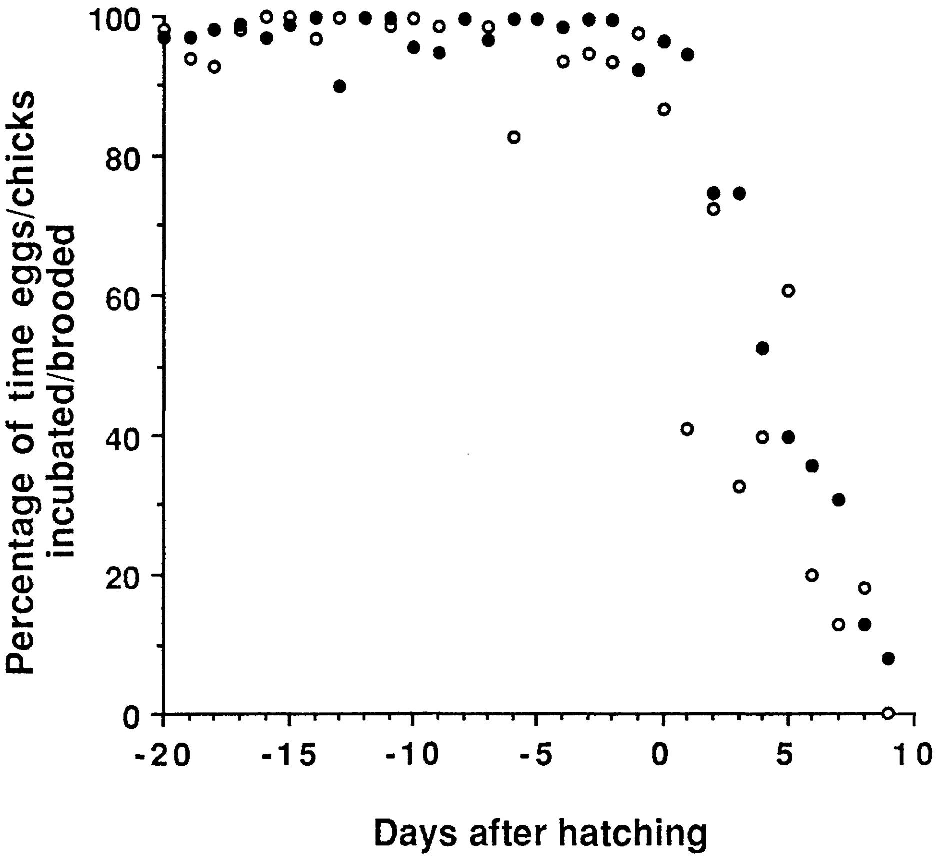

100
80
60
40
20
0
Percentage of time eggs/chicks incubated/brooded
-20
-15
-10
-5
0
5
10
Days after hatching

Table 4.1. Mean (s.e.) proportion of time spent incubating eggs and brooding chicks by male and female Arctic Terns (n refers to number of pairs observed)

Stage of breeding	Orkney		Shetland	
	Males	Females	Males	Females
Laying	0.48(0.005) n=11	0.50(0.004) n=11	0.05(0.025) n=5	0.75(0.039) n=5
Incubation	0.50(0.001) n=21	0.48(0.001) n=21	0.35(0.017) n=8	0.57(0.006) n=8
Hatching	0.24(0.001) n=17	0.62(0.001) n=17	0.25(0.152) n=2	0.11(0.111) n=2
Chicks < 1 week	0.14(0.001) n=19	0.27(0.001) n=19	0.10(0.052) n=5	0.12(0.005) n=5
Chicks > 1 week	0.01(0.000) n=18	0.02(0.000) n=18	-	-

which both sexes spent away from the territory increased with chick age (males: r_s = 0.976, d.f. = 6, $p < 0.01$; females: r_s = 0.925, d.f. = 6, $p < 0.01$). In addition males contributed more than 50% of the feeds which the chick received during the first week of life (G-test (goodness of fit) G = 47.94, d.f. = 1, $p < 0.001$) (fig. 4.3). The proportion of total feeds delivered by the male did not decrease significantly during this period (r_s = -0.762, d.f. = 6, $p > 0.05$). The size of fish which males and females fed to the chicks over this first week was different; males fed chicks a significantly larger proportion of large sandeels (>12cm) than did females (fig 4.4b) ($X^2 = 9.56$, d.f. = 3, $p < 0.05$).

'Poor food supply' site.

Unlike on Orkney, during the laying period males on Shetland incubated for significantly less time than did females ($t_8 = 3.29$, $p < 0.05$), but this difference did not

Figure 4.2. The mean proportion (± 1 s.e.) of time spent away from the territory during the first week of chick life by males (○) and females (●) on Shetland, 1988 and on Orkney, 1989 shown on an arcsine transformed axis.

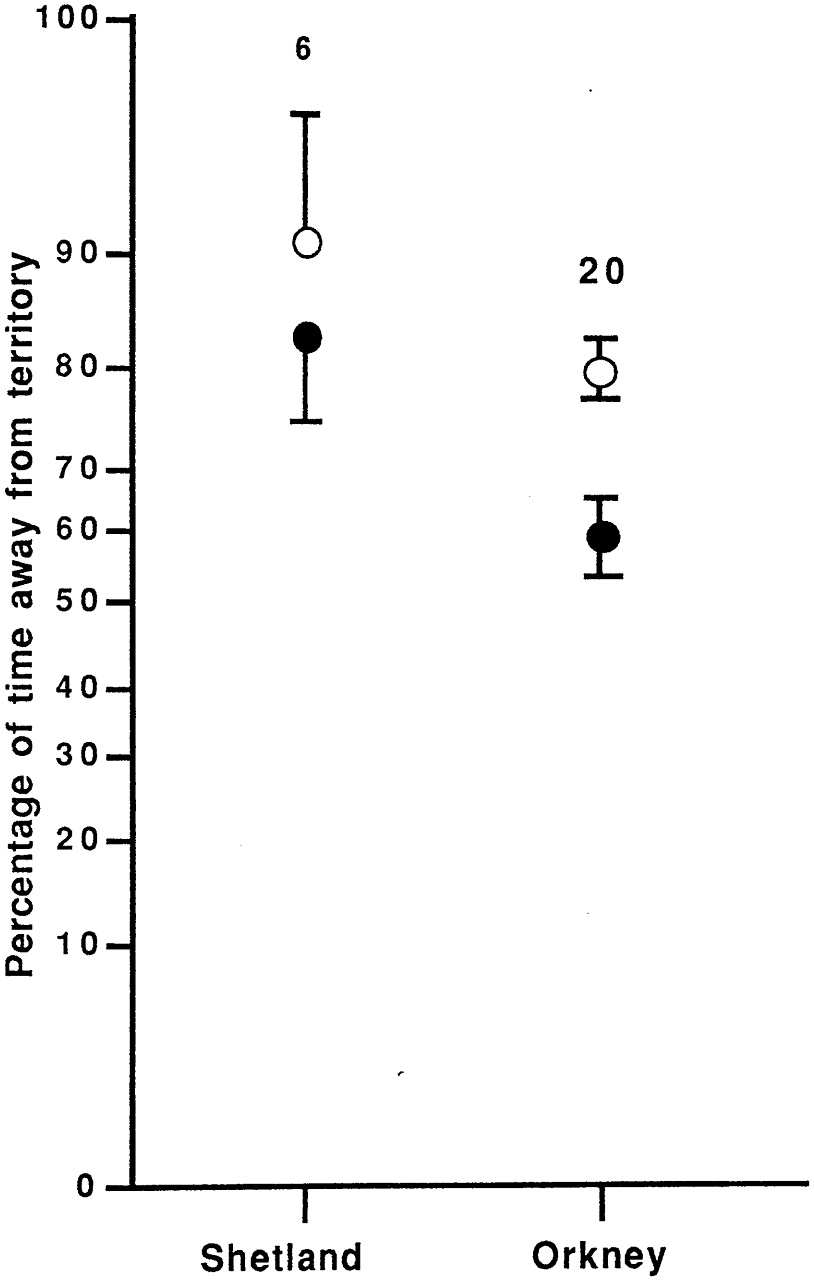

Percentage of time away from territory
100
90
80
70
60
50
40
30
20
10
0
6
20
Shetland
Orkney

Figure 4.3. The mean proportion (± 1 s.e.) of all the feeds received by the chick during the first week of life which were supplied by the male (○) and the female (●) shown on an arcsine transformed axis.

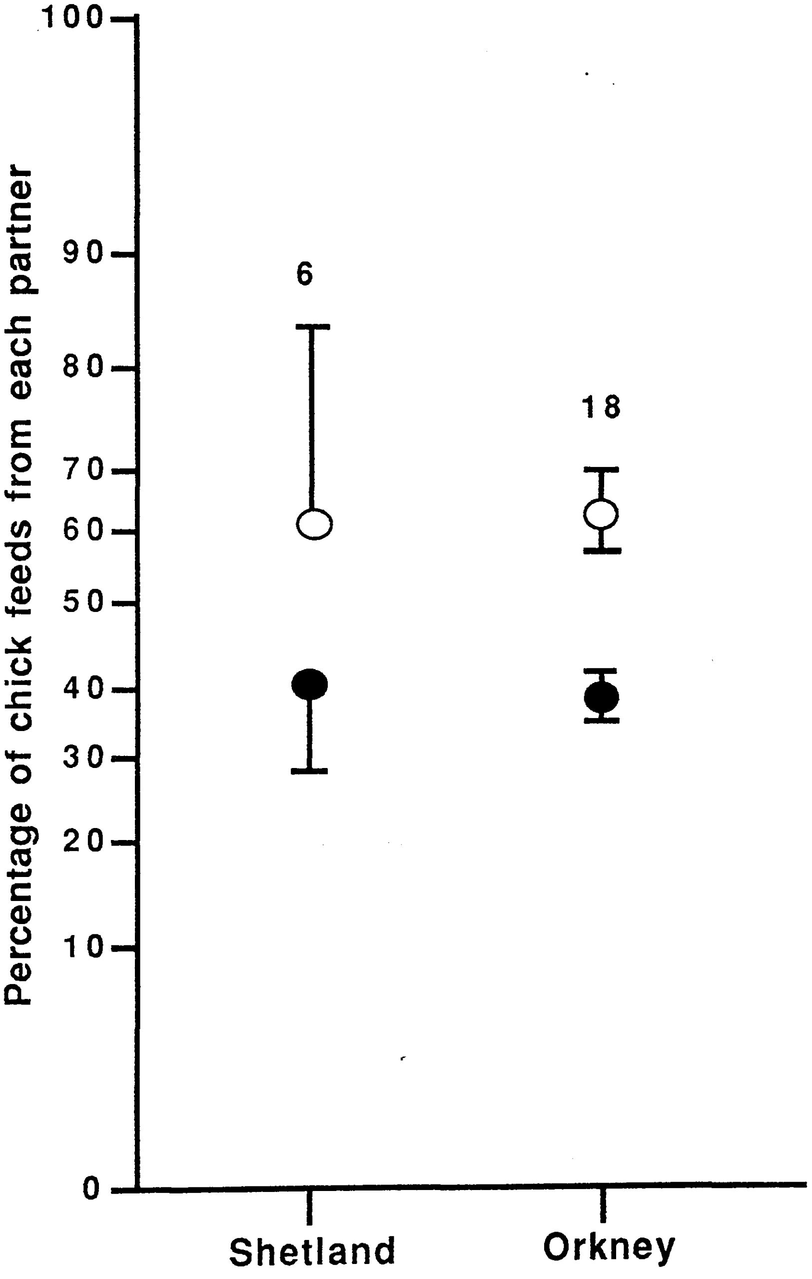
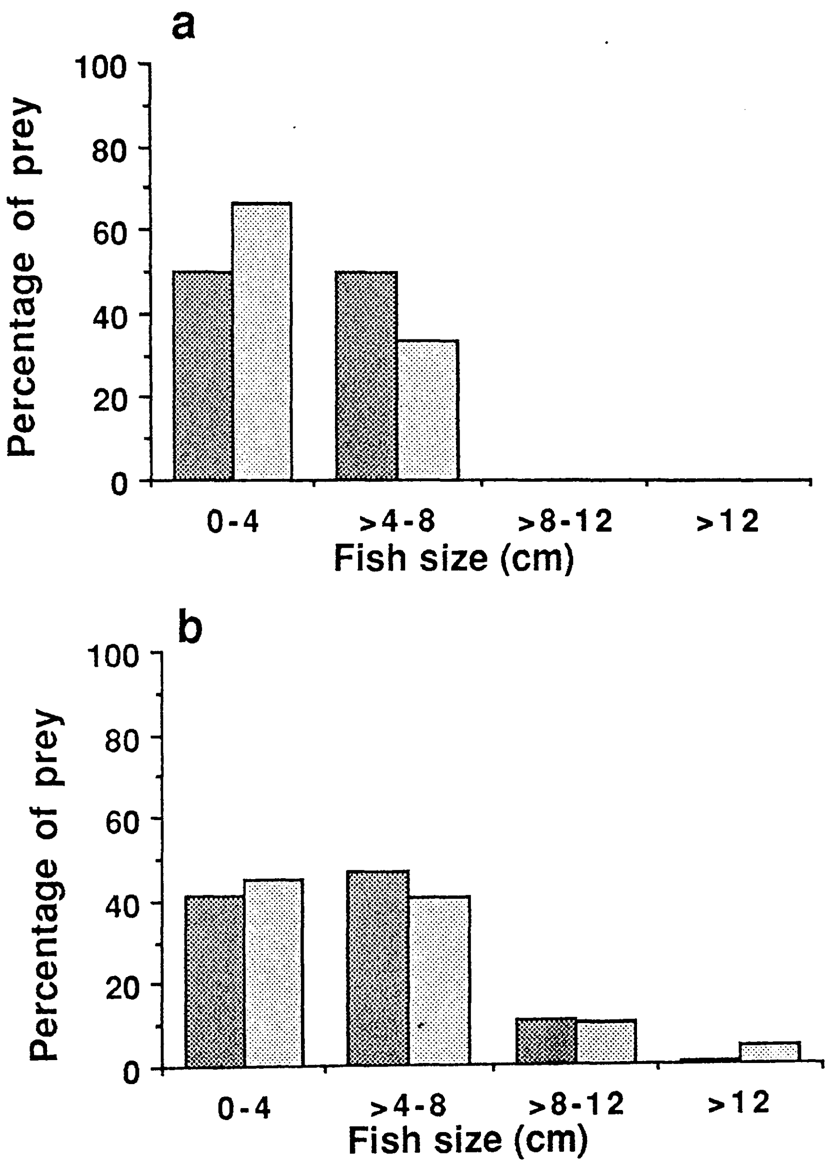

Percentage of chick feeds from each partner
100
90
80
70
60
50
40
30
20
10
0
6
18
Shetland
Orkney

Figure 4.4. The size distribution of fish brought to chicks in their first week of life by males (light stippling) and females (dark stippling), on a) Shetland, 1988 and b) Orkney, 1989.


a
Percentage of prey
100
80
60
40
20
0
0-4
>4-8
>8-12
>12
Fish size (cm)
b
Percentage of prey
100
80
60
40
20
0
0-4
>4-8
>8-12
>12
Fish size (cm)

persist for the remainder of the incubation period (tab. 4.1). As on Orkney, females (n = 27 observations) tended to incubate at the close of daylight more frequently than males (n = 13) but this was significant with a binomial test on only one night out of four. Later in the breeding attempt further differences between Orkney and Shetland were apparent; there was no post-hatch specialisation of males and females on Shetland where they brood the young for equal amounts of time (tab. 4.1).

Males and females on Shetland spent the same amount of time away from the territory during the first week of the chicks' lives ($t_{10} = 0.56$, $p > 0.1$) (fig. 4.2), and they contributed equally to the number of feeds received by the chicks (G-test (goodness of fit) $G = 2.99$, d.f. = 1, $p > 0.1$) (fig. 4.3). Furthermore, there was no significant difference in the size of fish which they delivered to the young ($X^2 = 0.45$, d.f. = 1, $p > 0.1$) (fig. 4.4a).

Intersite comparison: males

Shetland males incubated for significantly less time than Orkney males during laying ($t_{14} = 2.99$, $p < 0.01$) (tab. 4.1), but the amount of time which they allocated to incubating and brooding was similar at the two sites for the rest of the breeding attempt. During the first week of chick life there was no difference between the two sites in the proportion of time which males spent away from the colony (fig. 4.2) ($t_{24} = 0.56$, $p > 0.1$) or in the proportion of the total number of feeds received by chicks which were delivered by males ($t_{22} = 0.10$, $p > 0.1$) (fig. 4.3).

Intersite comparison: females

Shetland females incubated for a significantly greater proportion of their time during laying than did Orkney females ($t_{14} = 2.14$, $p < 0.05$) (tab. 4.1). During the hatching phase they brooded the chicks for significantly less time than did Orkney females ($t_{17} = 2.23$, $p < 0.05$) (tab. 4.1), and while there was a difference in the same direction during the rest of the first week of the chicks' lives this was not statistically significant (t_{22}

$= 1.73$, $p < 0.10$) (tab. 4.1). If the two early phases of the chicks' lives are combined then the overall difference is significant ($t_{39} = 2.64$, $p < 0.01$). Shetland females spent significantly more of their time away from the colony during the first week after hatching than did Orkney females ($t_{20} = 3.12$, $p < 0.001$) (fig. 4.2).

4.4. Discussion

Although the reproductive investments of male and female Arctic terns appear to be approximately equal it is clear that the precise allocation of parental effort to the various tasks involved in reproduction differs. Most notably, and in common with all anisogamous organisms, the female must make a greater direct investment in the zygote than males. However, as described in the previous chapter, male larids and those of other groups may make a substantial indirect contribution to egg formation via courtship feeding. Such differences in the form of investment create great, and perhaps insurmountable difficulties, when comparisons are made (Knapton 1984, but see Todd & Cowie 1990). Although in this case, at least in theory, a common currency such as energy expenditure may be used to contrast the investments of males and females, there remain differences in other aspects, such as the risk of predation, injury or cuckoldry, between different forms of investment. Similar problems arise later in the breeding cycle when partners may specialise in different forms of parental care. In some species females may undertake all, or a majority of incubation, whilst the male feeds her, or as in Arctic terns on Orkney, females may take on the majority of brooding duties, leaving the male responsible for the greater part of feeding the brood. In this particular study, only time-budget data were available, and although these may be interpreted energetically, the potential influence of other costs should be borne in mind.

This study reveals differences in the pattern of male and female investment between two sites with different levels of food availability. The two study sites are close together, both absolutely and relative to the Arctic tern's circumpolar distribution, and the breeding birds probably form a part of the same population. It is therefore unlikely that the two colonies are sufficiently far apart that the two colonies have evolved different strategies of investment allocation, and the differences in patterns of parental investment are likely to be the result of low sandeel availability in Shetland.

4.4.1 Changes in the pattern of parental investment during laying

On Orkney, where food supply was good, there was no detectable difference between the time spent incubating by males and females. This was unexpected during the laying period, when *a priori* reasons exist for us to suspect that intersexual differences may occur *i.e.* the two sexes have different roles to perform, but not unexpected during the subsequent portion of incubation, when parental duties consist only of incubation plus defence of the territory from conspecifics and predators.

In the previous chapter I showed that male Arctic terns on Shetland in 1988 increased the rate at which they fed their mates at this time; females were fed more often and provided with more energy and mass of food on Shetland than on Orkney. The data presented here show that Arctic terns experiencing food shortage during the early part of the season on Shetland changed their allocation of investment, resulting in females remaining on territory and incubating the eggs for longer than they did on Orkney. A corollary of this is that males incubated less and spent less time on territory when food was short. Most studies of the energetics of incubation have found it to be a cheap activity relative to foraging in terms of absolute energy expenditure (Walsberg 1983, Grant 1984, Drent *et al.* 1985). The low relative cost of incubation will tend to be exacerbated during laying by the fact that gravid females, being heavy and with an abnormal weight distribution, may find foraging more difficult and energetically more expensive than at other times (Nisbet 1977). Therefore by spending more time on territory and in incubation, and less in foraging, females may be able to reduce their energy expenditure and devote more resources to egg production. These results are further evidence of the nutritional function of courtship feeding. Avery *et al.* (1988) highlighted the difference in value of increasing food intake for females and males when resources for egg production are being acquired: 'during egg-laying ... for the female, the number and quality of eggs are determined by the excess food intake over maintenance, so that the fitness value of food increases with increasing intake', in comparison to males, for whom excess food intake over maintenance requirements is of little value, or possibly even deleterious, through increasing flight costs (Freed 1981, Norberg 1981). They also showed that male European bee-eaters *Merops apiaster* foraged more intensely and efficiently when courtship feeding than when feeding themselves and that they preferentially fed females large prey. In short, the male maximises female gain subject to meeting his own requirements. The courtship feeding behaviour of terns is somewhat similar to that of bee-eaters in that they act as central place foragers (Orians & Pearson 1979), the female remaining at a fixed site. Taylor (1979) showed that male common terns preferentially provide large prey for their mates. In a situation of food shortage, where it is adaptive to maintain clutch quality, the fitness value of increasing the female's intake rate, at the cost of reducing male intake and/or reserves, will be amplified.

Thus the shift in the allocation of investment by males and females may benefit both sexes by allowing females to lay a clutch of normal size and quality even though food is scarce. Such a strategy may be adaptive if adults cannot predict conditions for chick rearing at the time of laying. This is probably the case for adult Arctic terns, which feed on 1-group sandeels early in the season during courtship, but feed smaller 0-group fish to their young chicks (Ewins 1985, chapter 5). 1-group sandeels are not a part of the spawning stock (Reay 1970), and their abundance could not be used by terns to predict the abundance of the 0-group, unless 0-group production in the previous year is a good predictor of production in the current year.

4.4.2 Changes in the pattern of parental investment during chick rearing.

Males and females in Orkney, where the food supply is good, showed a degree of specialisation during the early chick-rearing phase with males taking the dominant role in chick feeding and females undertaking the majority of the brooding. In addition to provisioning the chicks at a faster rate than females, males also brought more large fish, which have a higher energy density than small fish (Harris & Hislop 1978). If feeding rate and prey size are combined, it is apparent that males would contribute significantly more to the energetic intake of the chicks than females. Such patterns of investment have been found in many other studies of monogamous seabirds (Pierotti 1981, Burger 1987, Wiggins & Morris 1987, Wagner & Safina 1989, Wiggins 1989, Quinn 1990) but not in all (*e.g.* J. Burger 1981). Such specialisation may allow more efficient use of time during a period when chicks need brooding and feeding. The fact that males forage more than females early in the season when they are courtship feeding could provide a means by which males become more familiar with foraging grounds and more skillful and efficient foragers. Nisbet *et al.* (1978), found that male common terns could successfully raise young after the death of their mates.

In contrast to Orkney, in the poor feeding conditions found in Shetland, females, but not males, altered their time allocation so that they spent less time brooding their chicks and more time away from the territory; this time could be used for either self-maintenance or provision for the chicks. Unlike the changes that occurred during laying, this resulted in total parental care, *i.e.* brooding, being reduced in comparison to the level in good foraging conditions. Thus chicks on Shetland had a greater exposure to adverse weather conditions and predators.

The implications of this shift in the balance between brooding and foraging are complex but can be considered within the framework of time and energetic constraints. Klaassen *et al.* (1989) showed that brooding by adult Arctic terns may save chicks up to 26% of energy requirements during the first ten days of life, after which they acquire full locomotory and thermoregulatory abilities. Thus any reduction in the amount of time for which chicks are brooded in this period will have implications for the chicks' energy budgets, and for the rate at which adults have to supply food in order to provide for their chicks' growth and maintenance. From this point of view it may be advantageous for chicks to be brooded for longer, so that their energy requirements are reduced. Wittenburger (1982) found that female bobolinks (*Dolichonyx oryzivorus*) gave a higher priority to brooding their young in poor weather, even when food was scarce, but in good weather they also brooded less and foraged more. Two other factors may be responsible for inducing the observed reduction in brooding. Firstly, Arctic tern chicks have a higher BMR than the closely related common tern, which is probably an adaptation to allow a greater thermoregulatory capacity and deposition of fat reserves as a buffer against periods of food shortage (Klaassen *et al.* 1989). Although there may be some scope for reducing chick BMR during periods of food stress, such a high energy requirement may reduce the scope for increasing foraging rate. Terns are known to have little leeway in their time and energy budgets during the breeding season (Pearson 1968), particularly when they have young chicks, and one adult may be unable to provide enough food to sustain growth in the young, even when they are being brooded and have a relatively low energy requirement. Under these circumstances any decrease in food availability should be met with a decrease in the amount of time for which the chicks are brooded. Secondly, adult terns in Shetland are in poor condition at the start of the breeding season and continue to decline in weight as it proceeds (Monaghan *et al.* 1989a). Breeding birds may adjust their breeding effort by monitoring their own body condition (Drent & Daan 1980, Monaghan *et al.* 1990) and the shift in female behaviour from brooding to foraging may be the result of a decision to reduce breeding effort and devote more resources to self-maintenance.

5.FACTORS AFFECTING CHICK PROVISIONING

5.1. Introduction

In species of birds which feed their young, the demands on energy and time during the period between hatching and fledging may be considerable. In fact, clutch and brood size are often held to be ultimately constrained by the ability of parents to provide food for their young during this time (Lack 1968, Drent & Daan 1980, Martin 1987), although in some cases clutch size may be constrained by proximate and ultimate factors acting earlier in reproduction (see Chapter 3). The same all pervading influence of food supply and the ability of birds to utilise it is thought to have influenced the timing of breeding seasons, including that of colonial seabirds, so that they enter the demanding phase of chick-rearing at a time when food supply is maximal (Lack 1968, Pearson 1968, Perrins 1970, Veen 1977, Gochfeld 1980, Safina & Burger 1985).

The aim of the work presented in this chapter is to examine the effects of food shortage on the brood provisioning performance of Arctic terns breeding on Shetland. This is achieved by examining differences in various parameters of Arctic tern foraging performance between two years of varying, but poor, food supply on Shetland and one year of apparently good food supply on Orkney. The data are explored further to examine the effects of brood age and weather on foraging performance. The influence of poor food supply on conspecific kleptoparasitism is also investigated.

5.2. Methods

The data on the type and size of prey offered to young, feeding frequency and fate of food items were collected according to the methods described in 2.4. on Shetland in 1987 and 1988 and on Orkney in 1989.

The energetic content and wet weight of sandeels and saithe were estimated from equations in the literature according to the procedures described in 3.2.1, but no figures were available for rockling *Ciliata mustela*, which were common prey on Orkney and were all of approximately 4cm in length. Their weight and energy content were derived from data in table II in Harris & Hislop (1978) who recorded rockling as a common food of young Puffins *Fratercula arctica*. I used all of their data sets to which rockling contributed at least 10% of recorded items and calculated the mean energy content and wet weight of single rockling from the number of rockling recorded and the total amount of energy and wet matter contributed by rockling. I calculated an overall mean figure from the eleven occasions when the 10% criterion was attained. The mean figures were - energy content: kJ/fish = 2.051, s.e. = 0.374; wet weight: Grams/fish = 0.290, s.e. = 0.054).

In addition to the parameters of foraging performance used in chapter 3 *i.e.* feeding frequency, energy gathered per trip, energy provisioning rate, mass gathered per trip and rate of provisioning with mass of food (see 3.2.1), I also calculated the length of foraging trips from the data collected on times of arrival and departure of adults from the territory (2.4.). Data permitting this to be calculated were collected only on Shetland in 1988 and Orkney in 1989. For the remainder of this chapter, feeding frequency refers to the frequency at which broods were provided with food items (trips per hour), whilst provisioning rates refer to the rate of supply of energy or mass of food (kJ or g per hour). Finally, I estimated a measure of the profitability of each trip by calculating the energy gathered per minute of absence. This is not profitability in its strict sense which must incorporate the energy costs of searching for, handling and transporting prey, but it is nevertheless an estimate of an important component of profitability *i.e.* energy gain per unit time foraging.

The age and size of broods was measured by the methods described in 2.4.. The main comparisons are made using data only on broods up to one week old since few broods survived beyond this age on Shetland (Uttley *et al.* 1989a). Brood age, which is used in several analyses in this chapter, refers to the days elapsed since the hatching of the first chick.

The data on mean daily windspeed (knots) (the average of four daily spot samples) and total daily rainfall were obtained via the UK Meteorological Office, Bracknell, Berkshire, and are from the local meteorological stations at Lerwick (Shetland) and

Kirkwall (Orkney). Each of the three study sites was between 30 and 60km from the nearest weather station.

5.3. Results

5.3.1. Diet of chicks

Analysis of the food with which chicks were provided by their parents consisted of two components. Firstly, I considered the species of prey which adults provide for their young, and secondly, the size of food items.

Table 5.1. The average proportion (s.e.) of young (up to one week old) chicks' diets consisting of different food types calculated from the mean daily figures for each food type

	a) broods up to one week old			b) broods over one week old
	Shetland 1987^5	Shetland 1988	Orkney 1989	Orkney 1989
n fish	1481	148	859	2396
n days	17	7	17	20
n nests	43	13	26	19
n hours obs.	82	94	47	73
Sandeel^1	0.67 (.06)	0.68 (.04)	0.59 (.05)	0.85 (.02)
Saithe^1	-	0.26 (.02)	0.00 (.00)	0.00 (.00)
Rockling^1	-	0.00 (.00)	0.37 (.04)	0.15 (.02)
Other^{1,3}	0.33 (.05)	0.06 (.01)	0.04 (.01)	0.00 (.00)
Unknown^{2,4}	0.15 (.03)	0.15 (.02)	0.22 (.03)	0.28 (.03)

1 - as a proportion of prey of known type (including other)
2 - as a proportion of all food items fed to chicks
3 - includes prawns, moths, earthworms and lumpfish
4 - not seen clearly enough to assign to other categories
5 - food items categorised only as sandeels/non-sandeels in 1987

In each year, and at both sites, sandeels were the dominant item in the diet of Arctic tern chicks (tab. 5.1). There was no significant variation in chick diet, as assessed by the proportion of observed prey per day which were sandeels, between different nests sampled in the same year (Kruskal-Wallis Anova. Shetland 1987: H = 91.8, d.f. = 84, p > 0.05; Shetland 1988: H = 11.9, d.f. = 11, p > 0.05; Orkney 1989: H = 33.7, d.f. = 24, p >

0.1), so data from different nests were lumped to produce daily mean figures for the proportion of each food type. The following analyses are based on these daily means which are summarised in table 5.1.

Table 5.2. The correlations[1] and partial correlations (significance) of the relationships between the proportion of sandeels in the diet of chicks, the date of observation and age of brood.

		Zero-order correlations			Partial correlations	
		% sandeels with		date with	% sandeels with	
Location/Year	n [2]	date	age	age	date	age
a) chicks up to one week old						
Shetland '87	72	-.202 ns	-.018 ns	.280 *	.205 ns	.041 ns
Shetland '88	18	.522 *	.586 **	.635 **	.240 ns	.386 ns
Orkney '89	47	.437 **	.380 **	.503 ***	.308 *	.205 ns
b) chicks of all ages						
Orkney '89	147	.731 ***	.713 ***	.902 ***	.290 ***	.183 *

1 - correlations performed on arc-sine transformed data
2 - n = number of date/age combinations

In broods up to one week old there was no difference in the proportions of chicks' diets consisting of sandeels between Shetland in 1987 and 1988 and Orkney in 1989 (Kruskal Wallis Anova. H = 1.4, d.f. = 2, p > 0.05). Although the identity of non-sandeels was not recorded in 1987, it was apparent that saithe were relatively uncommon compared with 1988, and moths and prawns were far more common (pers. obs.). An example of the moths fed to young Arctic tern chicks on Shetland in 1987 was identified as a swift moth *Hepialus* sp., probably *H. humuli thulensis* or *H. fusconebulosa* (M. Young pers. comm.). However, there was a marked difference in the non-sandeel component of chick diet between Shetland in 1988 and Orkney in 1989, the former consisting almost entirely of saithe whilst the latter was dominated by rockling (tab. 5.1a).

In two out of the three years the importance of sandeels in the diet varied significantly between days (Kruskal-Wallis Anova. Shetland 1987: $H = 30.8$, d.f. = 16, $p < 0.05$; Shetland 1988: $H = 6.0$, d.f. = 6, $p > 0.40$; Orkney 1989: $H = 29.0$, d.f. = 15, $p < 0.05$). Since Arctic terns breed highly synchronously, observation date is highly correlated with the age of broods being observed (tab. 5.2). I therefore examined the importance of sandeels in the diet of young chicks by partial correlation analyses (tab 5.2a) to see whether day to day variation was the result of a) changes in diet with chick age, b) changes in diet with seasonal progression *per se* or c) daily fluctuations in prey availability/choice unrelated to the previous two hypotheses.

The results of the zero-order correlations of % sandeels with date and age show that the proportion of sandeels tends to rise with both the increasing age of the brood and the advance of date except on Shetland in 1987 (tab. 5.2a). The partial correlation coefficients do not support the hypothesis that the increase of importance in sandeels during the first week of the chicks' life is due to their increasing age, but do lend some support to the hypothesis that the trend is associated with advance in calendar date, but the partial correlation coefficient for date, controlling for age was only significant for Orkney in 1989. However, it is possible that in natural circumstances such as these there is insufficient variation in age within days for such effects to be detectable. Therefore the correlation between date and age means that these two variables explain more or less the same component of total variation in chick diet. To examine the effect of age and date upon diet further I included all of the data from Orkney from chicks of all ages, *i.e.* including those beyond the first week of life, (tabs 5.1a, 5.1b, 5.2b,). All of the trends were much stronger in this case, and the results of the 1st-order correlations show that the percentage of sandeels in the diet rises with both advancing date and age, independently of each other (tab. 5.2b).

Secondly, I examined the size of food items fed to their young by adult Arctic terns. The size of prey fed to young chicks, summed over all days and nests are displayed in tables 5.3a and 5.4a. The size of sandeels fed to young chicks in Shetland in 1988 differed from than those fed in 1987 (tab. 5.3a) ($X^2 = 295.3$, d.f. = 3, $p < 0.001$). Partitioning of the contingency table showed that in 1987 the proportion of sandeels less than 4cm was

Table 5.3. The size of sandeels fed to young chicks, summed over all days and nests.

		Fish size (cm)			
Location/Year	n	0-4	>4-8	>8-12	>12
a) broods up to one week old					
Shetland '87	1008	87%	3%	5%	5%
Shetland '88	103	49%	51%	0%	0%
Orkney '89	409	11%	66%	17%	6%
b) broods over one week old					
Orkney '89	1583	3%	91%	5%	5%

Table 5.4. The size of non-sandeels fed to young chicks, summed over all days and nests.

		Fish size (cm)			
Location/Year	n	0-4	>4-8	>8-12	>12
a) broods up to one week old					
Shetland '87	412	94%	6%	0%	0%
Shetland '88	34	65%	35%	0%	0%
Orkney '89	261	85%	14%	1%	0%
b) broods over one week old					
Orkney '89	142	69%	30%	1%	0%

greater than in 1988 ($X^2 = 290.1$, d.f. = 1, $p < 0.001$), whilst in 1988 there were more sandeels of >4-8cm ($X^2 = 5.9$, d.f. = 1, $p < 0.05$). Furthermore, non-sandeels fed to chicks in 1988 also differed in size from those fed in 1987 (tab. 5.4a) ($X^2 = 35.3$, d.f. = 2, $p < 0.001$). This latter difference was probably due to the aforementioned observed difference in the composition of the non-sandeel component of the diet between the two years *i.e.* fewer saithe and more moths and prawns in 1987, rather than a difference in the size of saithe. Sandeels fed to young chicks on Orkney in 1989 tended to be of a different size from those fed on Shetland in 1988 ($X^2 = 49.0$, d.f. = 3, $p < 0.001$). Specifically, sandeels less than 4cm were more frequent than expected in 1988 (partitioned contingency table. $X^2 = 57.9$, d.f. = 1, $p < 0.001$) whilst sandeels greater than 12cm long were more abundant in 1989 on Orkney ($X^2 = 6.6$, d.f. = 1, $p < 0.05$)

The effect of chick age on the size of prey fed to chicks was assessed by comparing the diet of chicks up to one week old on Orkney in 1989 (tabs 5.3a, 5.4a) with that of older chicks (tab. 5.3b, 5.4b). The size of both sandeels and non-sandeels (primarily rockling) fed to chicks changed with brood age (sandeels: $X^2 = 181.7$, d.f. = 3, $p < 0.001$; non-sandeels: $X^2 = 15.3$, d.f. = 2, $p < 0.001$). Partitioning of the contingency tables showed that sandeels under 4cm in length were more frequently fed to young chicks ($X^2 = 58.7$, d.f. = 1, $p < 0.001$), as were sandeels greater than 8cm ($X^2 = 71.2$, d.f. = 1, $p < 0.001$). In other words, as chicks grew they were fed a greater proportion of >4-8cm sandeels, at the expense of both smaller and larger fish. More large rockling were fed to old broods than to young broods.

5.3.2. Feeding and provisioning rates

In this section, data on feeding frequency and rates of provisioning with energy and mass of food are presented and analysed. Each was considered on a brood-wise basis and also on a chick-wise basis whereby provisioning rates were adjusted for brood size, so that rates could be compared on a per chick basis. Considering young chicks up to one week old, there was no variation between nests in any of these parameters. Data from different nests are therefore lumped to give daily mean rates which are presented in figures 5.1, 5.2 and 5.3.

The feeding frequency of Arctic terns feeding young broods of chicks on Shetland in 1988 was lower than in 1987 (fig. 5.1a) (Mann-Whitney U Test. $z = 2.54$, $p < 0.05$), and this difference remained when feeding frequency was adjusted for brood size (fig 5.1b) ($z = 2.19$, $p < 0.05$). However, there was no significant difference between the two years in the rate at which broods or chicks on Shetland were provisioned with either energy or mass of food (figs 5.2 and 5.3).

Differences in chick provisioning rates between Orkney and Shetland were

Figure 5.1. The feeding frequency of adults feeding broods up to one week old on Shetland in 1987 (43 nests, total observation time 82 hours) and 1988 (13 nests, total observation time 94 hours) and Orkney in 1989 (26 nests, total observation time 47 hours), showing mean (■), s.e. (wide vertical bar), median (long horizontal bar) and upper and lower quartiles (short horizontal bars). Asterisks show significant differences from Mann-Whitney U-tests. a) Brood feeding frequency; b) Chick feeding frequency.

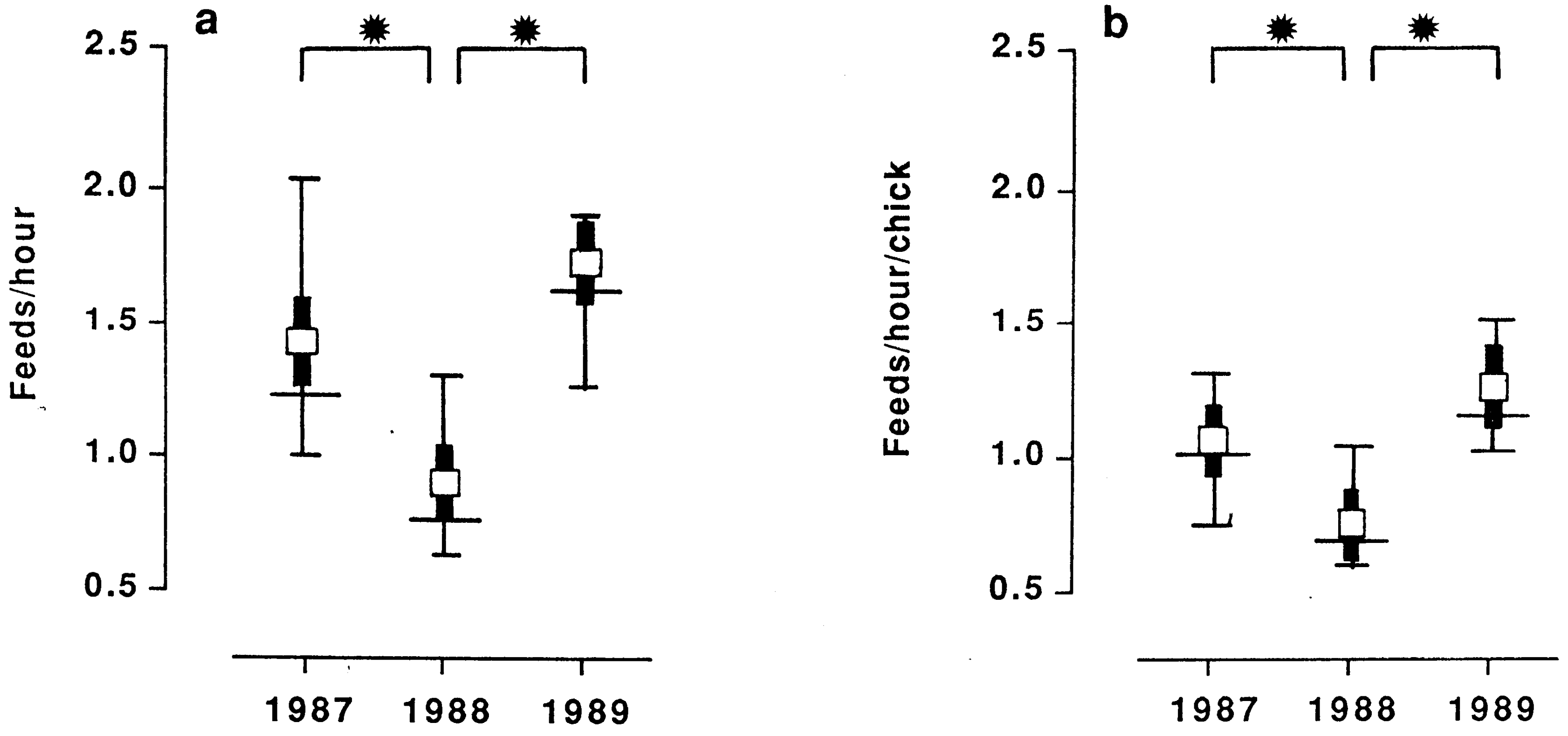

a
b
Feeds/hour
Feeds/hour/chick
2.5
2.0
1.5
1.0
0.5
1987
1988
1989

Figure 5.2. The rate at which a) broods and b) chicks were provisioned with energy by adults feeding broods up to one week old on Shetland in 1987 (43 nests, total observation time 82 hours) and 1988 (13 nests, total observation time 94 hours) and Orkney in 1989 (26 nests, total observation time 47 hours), showing mean (■), s.e. (wide vertical bar), median (long horizontal bar) and upper and lower quartiles (short horizontal bars). Asterisks show significant differences from Mann-Whitney U-tests.

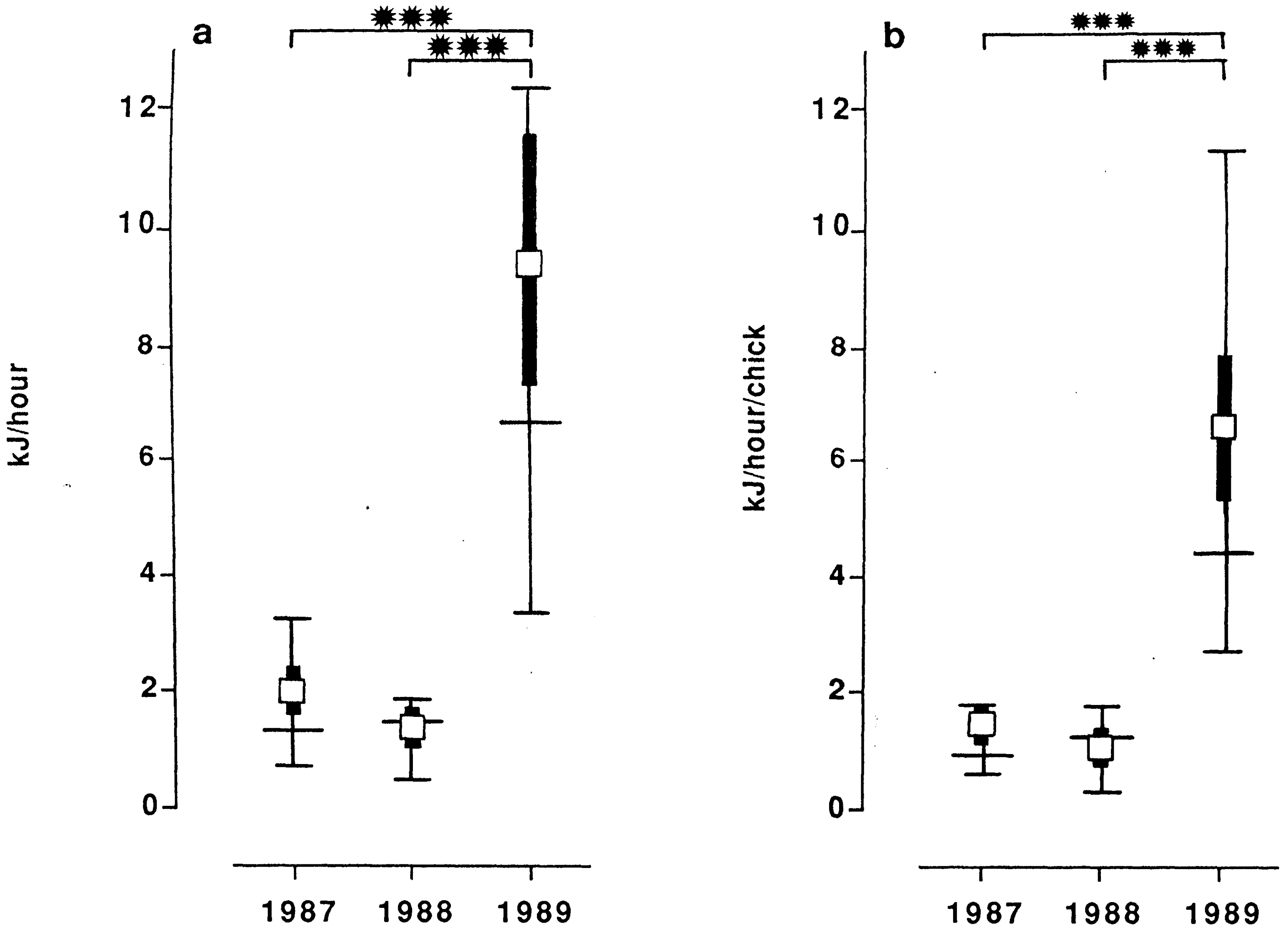
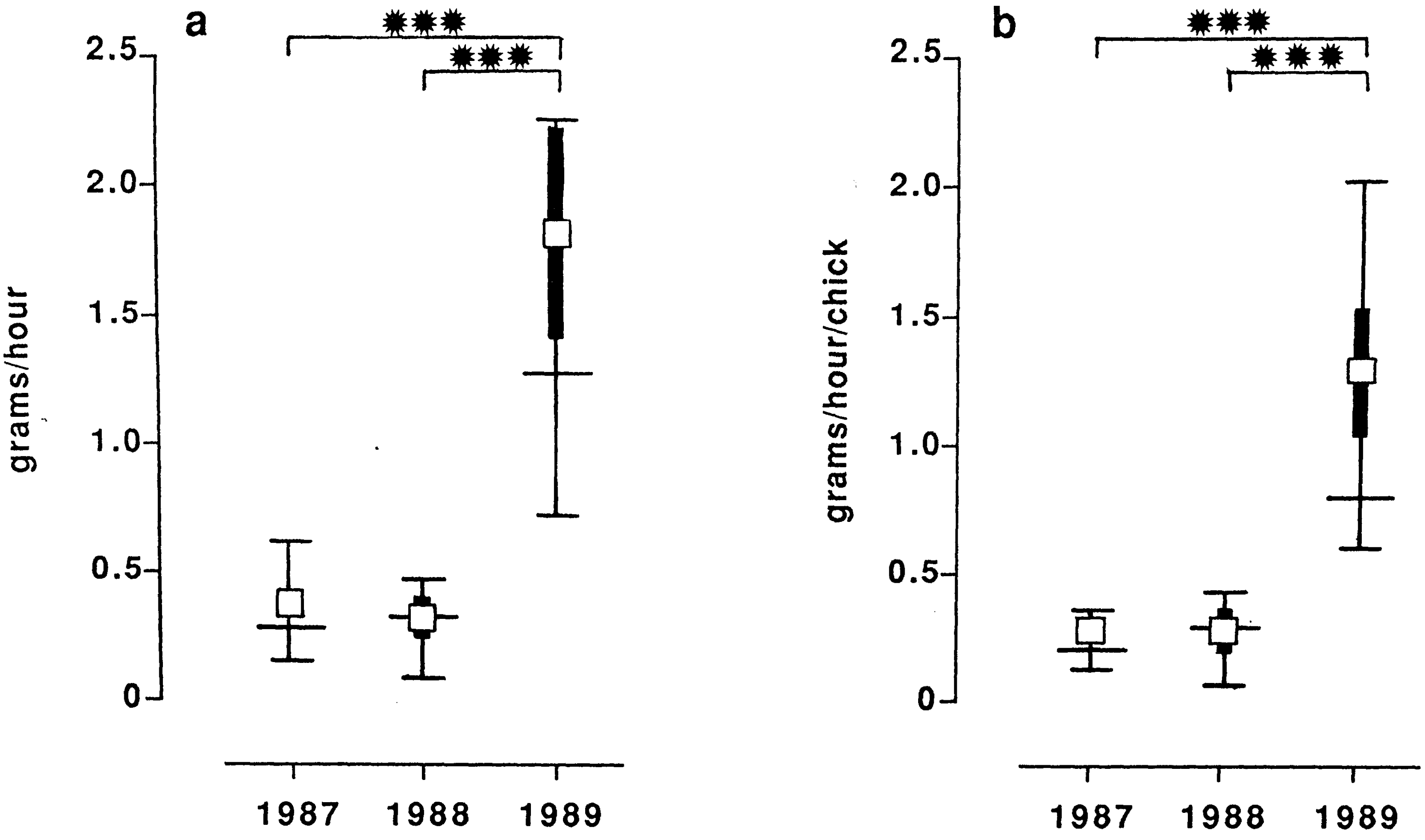

a
***
***
kJ/hour
12
10
8
6
4
2
0
1987
1988
1989
b
***
***
kJ/hour/chick
12
10
8
6
4
2
0
1987
1988
1989

Figure 5.3. The rate at which a) broods and b) chicks were provisioned with mass of food by adults feeding broods up to one week old on Shetland in 1987 (43 nests, total observation time 82 hours) and 1988 (13 nests, total observation time 94 hours) and Orkney in 1989 (26 nests, total observation time 47 hours), showing mean (■), s.e. (wide vertical bar), median (long horizontal bar) and upper and lower quartiles (short horizontal bars). Asterisks show significant differences from Mann-Whitney U-tests.


a
grams/hour
2.5
2.0
1.5
1.0
0.5
0
***
***
1987
1988
1989
b
grams/hour/chick
2.5
2.0
1.5
1.0
0.5
0
***
***
1987
1988
1989

examined by a Kruskal-Wallis Anova (d.f. = 2) followed by a multiple comparison procedure (Siegel & Castellan 1988). The frequency with which broods and chicks were fed was significantly higher in Orkney than in Shetland in 1988, but not in Shetland in 1987 (fig. 5.1) (brood feeding frequency: $H = 8.84$, $p < 0.05$); chick feeding frequency: $H = 6.90$, $p < 0.05$). The rate at which broods and chicks were provisioned with energy (fig. 5.2) and mass of food (fig. 5.3) was greater on Orkney than on Shetland in either year (brood energy provisioning rate: $H = 20.2$, $p < 0.001$; chick energy provisioning rate: $H = 20.5$, $p < 0.001$; brood mass provisioning rate $H = 20.6$, $p < 0.001$; chick mass provisioning rate: $H = 21.0$, $p < 0.001$).

Table 5.5. Rank correlation coefficients (significance) between provisioning and brood age

Provisioning rate	Shetland 1987	Shetland 1988	Orkney 1989
a) Chicks up to one week old (n = 7)			
Trips/Hr	-.821 *	.750 *	-.383 ns
Trips/Hr/Chick	-.679 ns	.607 ns	.214 ns
kJ/Hr	-.107 ns	.857 *	.821 *
kJ/Hr/Chick	-.321 ns	.607 ns	.929 **
Grams/Hr	-.107 ns	.929 **	.750 *
Grams/Hr/Chick	-.321 ns	.643 ns	.929 **
b) Chicks of all ages (n = 26)			
Trips/Hr	-	-	.679 ***
Trips/Hr/Chick	-	-	.714 ***
kJ/Hr	-	-	.293 ns
kJ/Hr/Chick	-	-	.507 **
Grams/Hr	-	-	.549 **
Grams/Hr/Chick	-	-	.645 ***

The relationship between feeding and provisioning rates and brood age was examined in two ways. Firstly, rank correlations were performed between rates and age, the results of which are shown in table 5.5. Adults feeding young broods on Shetland did not increase their rate of food delivery with brood age in terms of either feeding frequency, energy or mass provisioning rates, at least when changes in brood size are allowed for (tab. 5.5a). On Orkney however, although feeding frequency did not change significantly with brood age, the rate of delivery of energy and food mass increased. The effects of age were even stronger when the whole of the chick-rearing period was examined (tab. 5.5b) when an increase in feeding frequency was also found.

Secondly, the rates at which broods up to one week old and broods older than one week on Orkney in 1989 were compared using daily means for each age class. In every respect, older broods were fed at a faster rate than younger broods (figs 5.4, 5.5 and 5.6).

5.3.3. Foraging economics

Data on the length of foraging trips were not collected on Shetland in 1987, so this measure of foraging performance, together with profitability which is derived from it, are only examined for Shetland in 1988 and Orkney in 1989.

Neither the energy nor mass gathered per trip differed between nests, on either Shetland in 1987 or in 1988 or on Orkney in 1989. Similarly, there were no inter-nest differences in either profitability or length of foraging trips on Shetland in 1988 or Orkney in 1989. The following analyses are based on daily mean figures derived from all nests observed each day. The distributions of these means are presented in figures 5.7, 5.8, 5.9 and 5.10.

On Shetland in 1988, the length of trips was not related to the energy or mass gathered and returned to the young. On Orkney however there was a tendency for longer trips to result in heavier ($r_S = 0.302$, $n = 345$ trips, $p < 0.001$) and more energy rich ($r_S = 0.281$, $n = 345$, $p < 0.001$) loads being returned to the young although there was considerable variation caused by other unknown factors.

The quantity of energy (fig. 5.7) or mass (fig. 5.8) gathered per foraging trip did not differ between the two years on Shetland. However, both of these were significantly lower on Shetland in either year than on Orkney in 1989 (figs 5.3, 5.4) (Kruskal-Wallis Anova, followed by multiple comparison procedure. kJ / trip: $H = 12.1$, d.f. $= 2$, $p < 0.01$; grams /

Figure 5.4. The feeding frequency of adults feeding broods aged up to one week old (26 nests observed, total observation time 47 hours) and over one week old (19 nests observed, total observation time 73 hours) on Orkney in 1989, showing mean (■), s.e. (wide vertical bar), median (long horizontal bar) and upper and lower quartiles (short horizontal bars). a) Brood feeding frequency; b) Chick feeding frequency. Asterisks show significant differences from Wilcoxon matched pairs tests.

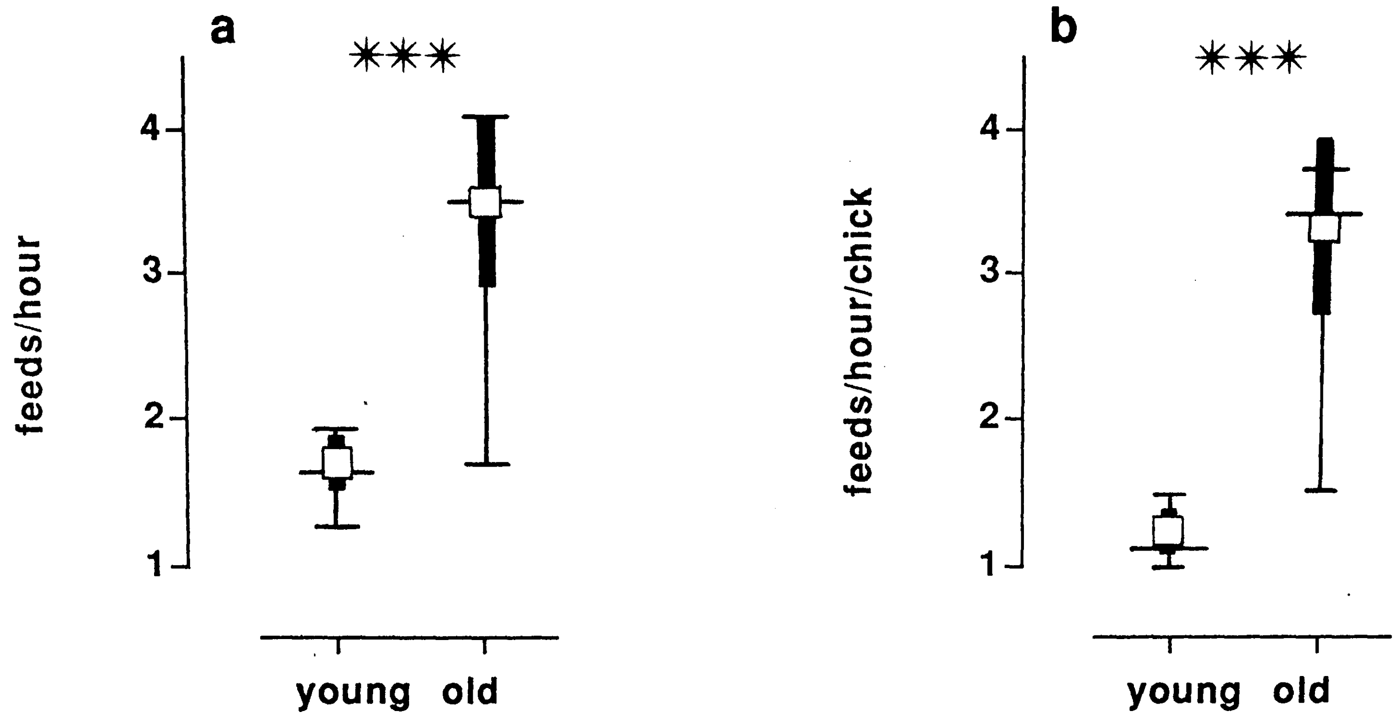

a
feeds/hour
1
2
3
4
***
young
old
b
feeds/hour/chick
1
2
3
4
***
young
old

Figure 5.5. The rate at which a) broods and b) chicks were provisioned with energy by adults feeding broods aged up to one week old (26 nests observed, total observation time 47 hours) and over one week old (19 nests observed, total observation time 73 hours) on Orkney in 1989, showing mean (■), s.e. (wide vertical bar), median (long horizontal bar) and upper and lower quartiles (short horizontal bars). Asterisks show significant differences from Wilcoxon matched pairs tests.

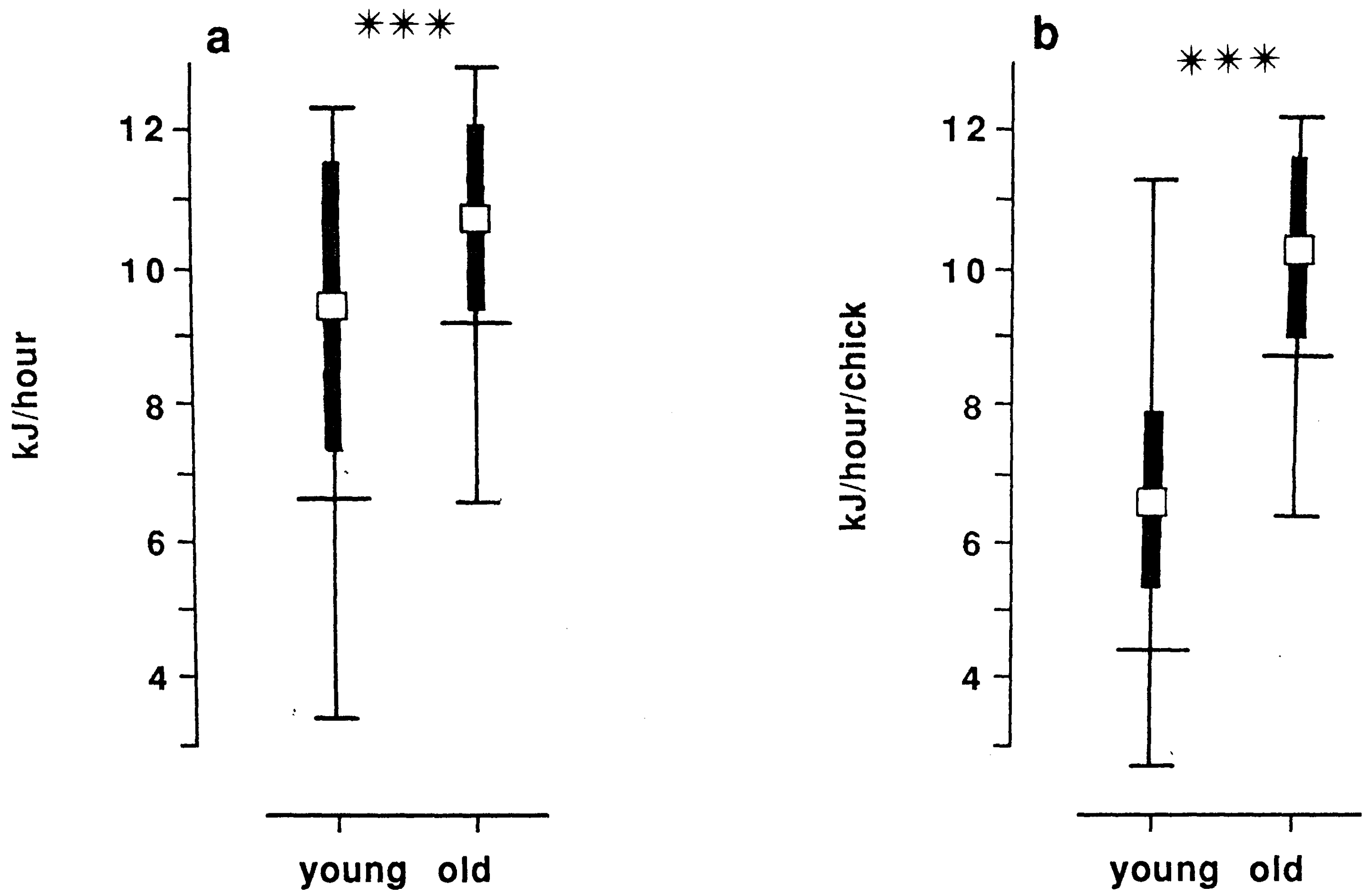
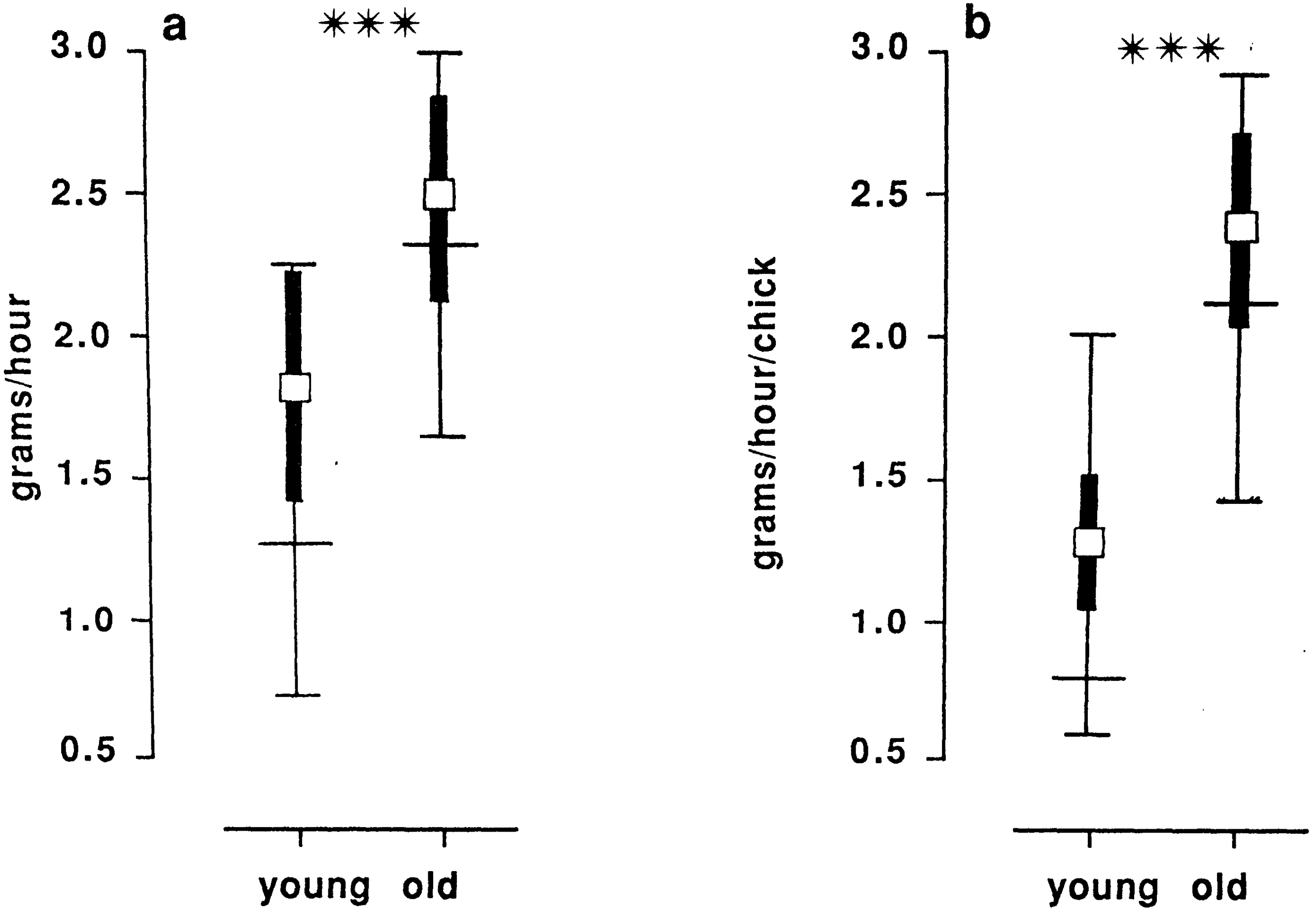

a
***
kJ/hour
12
10
8
6
4
young
old
b
***
kJ/hour/chick
12
10
8
6
4
young
old

Figure 5.6. The rate at which a) broods and b) chicks were provisioned with mass of food by adults feeding broods aged up to one week old (26 nests observed, total observation time 47 hours) and over one week old (19 nests observed, total observation time 73 hours) on Orkney in 1989, showing mean (■), s.e. (wide vertical bar), median (long horizontal bar) and upper and lower quartiles (short horizontal bars). Asterisks show significant differences from Wilcoxon matched pairs tests.


a
***
grams/hour
3.0
2.5
2.0
1.5
1.0
0.5
young
old
b
***
grams/hour/chick
3.0
2.5
2.0
1.5
1.0
0.5
young
old

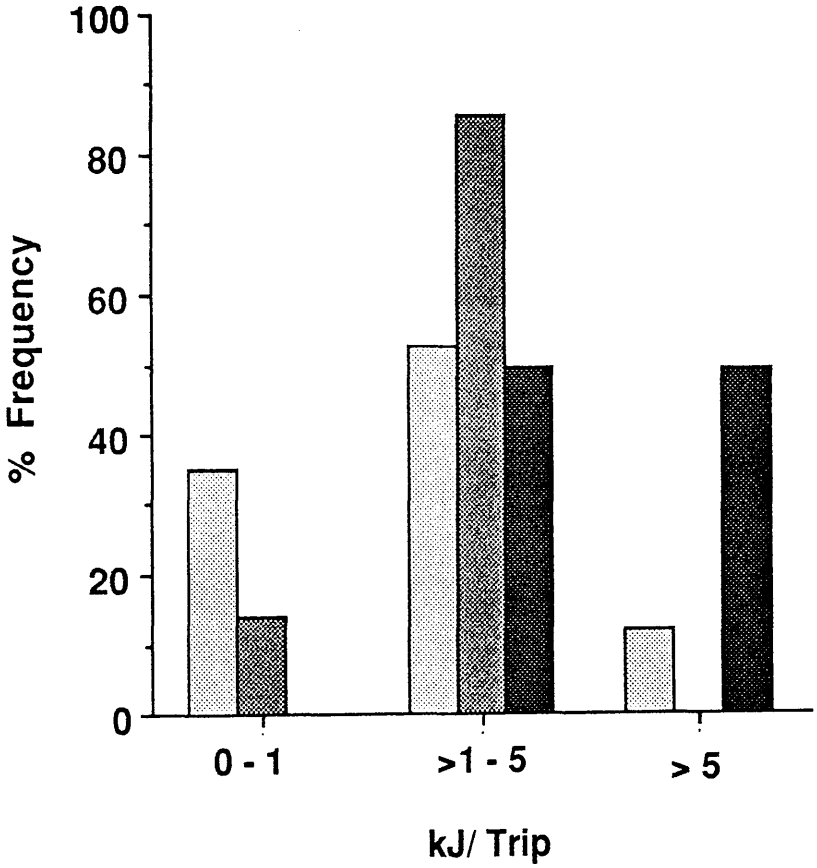
trip: $H = 13.6$, d.f. $= 2$, $p < 0.001$).

Neither the profitability of trips (fig. 5.9) nor the length of foraging trips (fig. 5.10) differed between Shetland in 1988 and Orkney in 1989 (Mann-Whitney U-test). However, when sandeels and non-sandeels are considered separately, some differences do emerge (figs 5.11 and 5.12). On Shetland, saithe were a more profitable prey than sandeels (fig. 5.11a) (Mann-Whitney U-test. $z = 2.52$, $p < 0.05$) although there was no difference in the length of foraging trips between the two prey species (fig. 5.12a). On Orkney, there was no difference in the profitability of trips between rockling and sandeels (fig. 5.11b), since foraging trips were longer when sandeels were returned than when rockling were returned (fig. 5.12b) (Mann-Whitney U-test. $z = 3.30$, $p < 0.001$). Sandeels had a higher profitability on Orkney than on Shetland (Mann-Whitney U-test. $z = 3.09$, $p < 0.01$), whereas saithe were more profitable for Arctic terns on Shetland than were rockling on Orkney (Mann-Whitney U-test. $z = 1.976$, $p = .048$).

The effects of age on foraging economics were again investigated by two methods. Firstly, the relationships of energy/mass gathered per trip, trip profitability and trip length with brood age were examined using Spearman's rank correlation. The energy and mass gathered per trip by adults feeding young broods showed no response to increasing chick age. The results for trip profitability and trip length are shown in table 5.6. Trip length on Shetland in 1988 declined with brood age over the first week, whilst profitability remained similar. However, these correlations were significant only at the 5% level; given the number of individual tests performed on these data, the high probability of a type-I error occurring means that they should be treated with caution. On Orkney in 1989 no changes in foraging economics occurred with advancing chick age. When the whole nestling period is considered on Orkney trip-length declines highly significantly ($p < 0.001$) with increasing brood age, and the probability of type-I errors occurring with these correlations is small.

Changes in foraging economics with brood age were also considered for the different prey types separately (tab. 5.6). On Shetland in 1988 the length of trips where a sandeel was obtained decreased with chick age (once again, only at the 5% level). The

Figure 5.7. The frequency distribution of energy gathered per foraging trip by adults feeding broods up to one week old on Shetland in 1987 (43 nests and 1302 trips observed) (light stippling), 1988 (13 nests and 137 trips observed) (medium stippling) and on Orkney in 1989 (26 nests and 670 trips observed) (dark stippling).



100
80
60
40
20
0
% Frequency
0 - 1
>1 - 5
> 5
kJ/ Trip

Figure 5.8. The frequency distribution of the mass of food gathered per foraging trip by adults feeding broods up to one week old on Shetland in 1987 (43 nests and 1302 trips observed) (light stippling), 1988 (13 nests and 137 trips observed) (medium stippling) and on Orkney in 1989 (26 nests and 670 trips observed) (dark stippling).

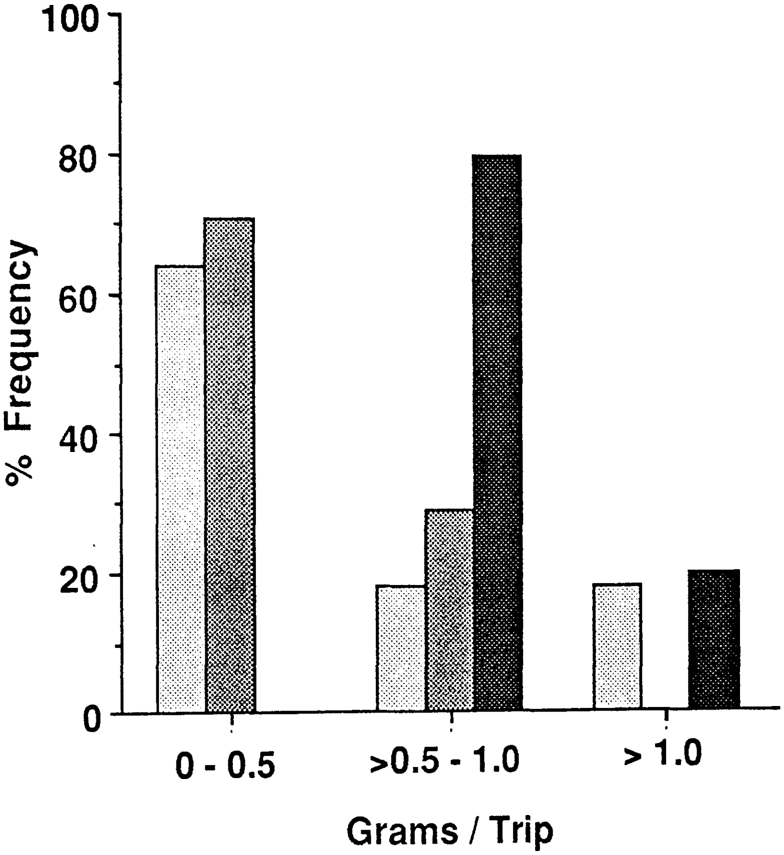

100
80
60
40
20
0
% Frequency
0 - 0.5
>0.5 - 1.0
> 1.0
Grams / Trip

Figure 5.9. The frequency distribution of the profitability (energy gathered / trip-length) of foraging trips by adults feeding broods up to one week old on Shetland in 1988 (13 nests and 114 trips observed) (light stippling) and on Orkney in 1989 (26 nests and 624 trips observed) (dark stippling).

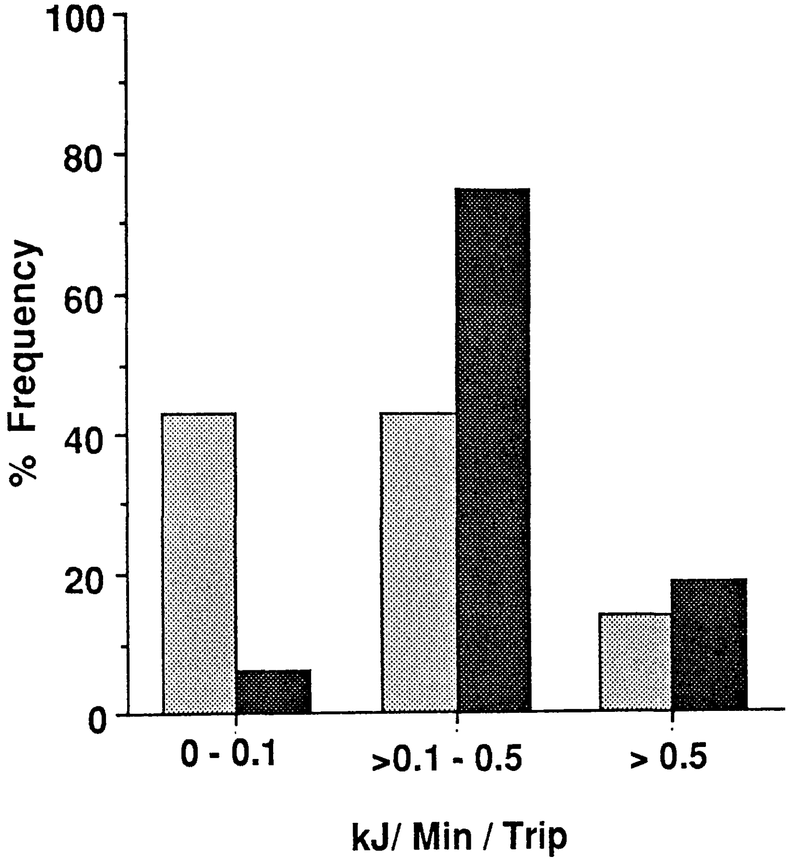

100
80
60
40
20
0
% Frequency
0 - 0.1
>0.1 - 0.5
> 0.5
kJ/ Min / Trip

Figure 5.10. The frequency distribution of the length of foraging trips by adults feeding broods up to one week old on Shetland in 1988 (13 nests and 117 trips observed) (light stippling) and on Orkney in 1989 (26 nests and 634 trips observed) (dark stippling).

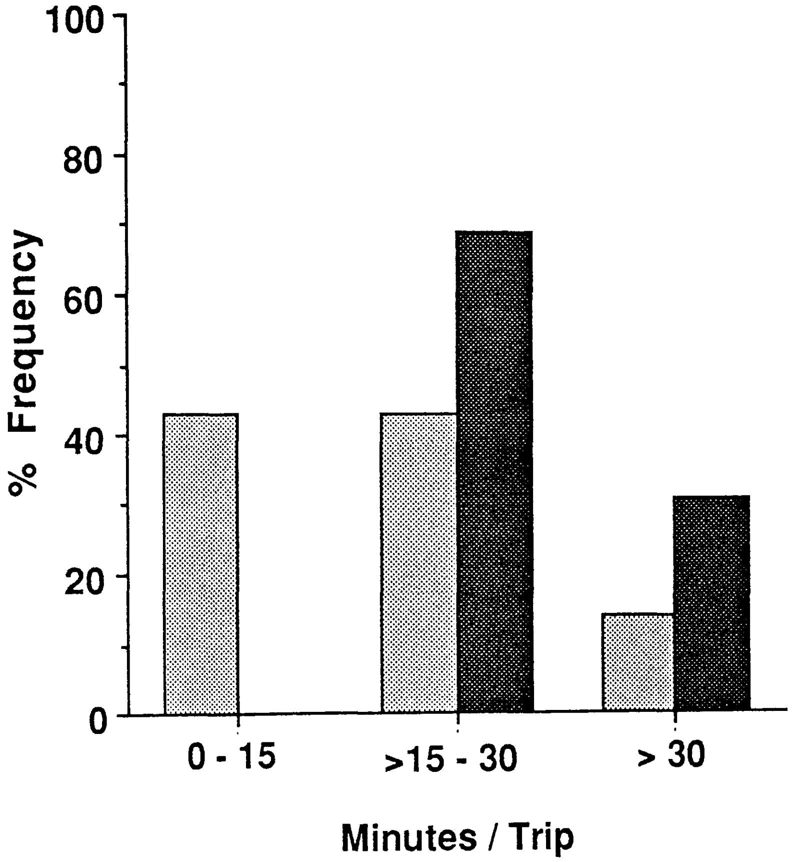
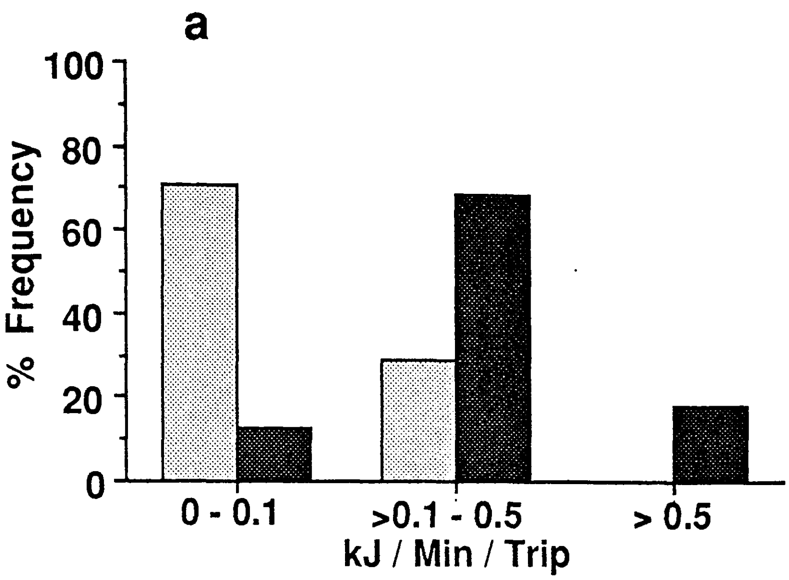

100
80
60
40
20
0
% Frequency
0 - 15
>15 - 30
> 30
Minutes / Trip

Figure 5.11. The frequency distributions of the profitability (energy gathered / trip-length) of foraging trips for sandeels (light stippling) and non-sandeels (dark stippling) by adults feeding broods up to one week old on a) Shetland in 1988 (13 nests and 96 sandeels and 18 non-sandeels observed) and b) Orkney in 1989 (26 nests and 382 sandeels and 252 non-sandeels observed).


a
100
80
60
40
20
0
% Frequency
0 - 0.1
>0.1 - 0.5
> 0.5
kJ / Min / Trip

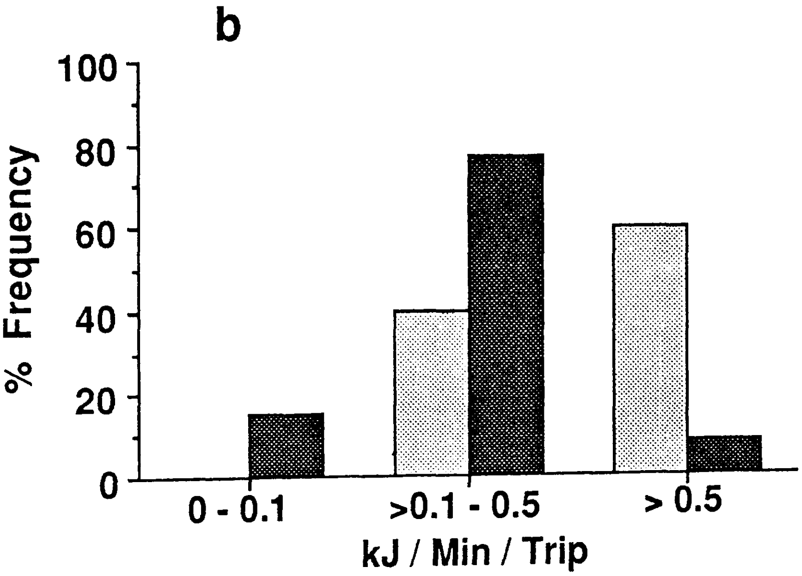
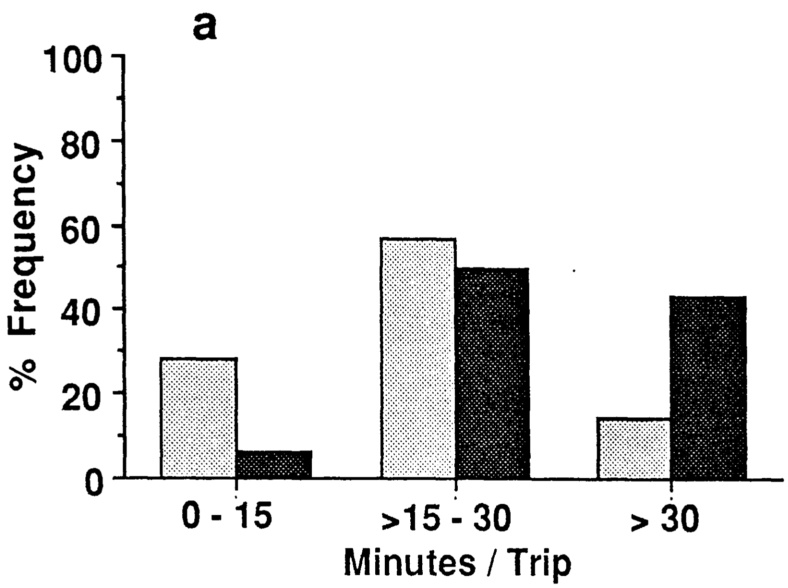
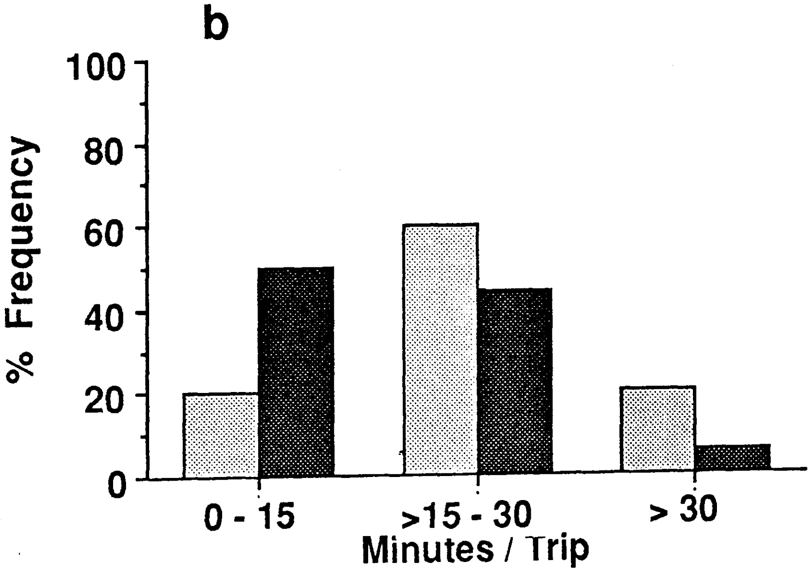

b
100
80
60
40
20
0
% Frequency
0 - 0.1
>0.1 - 0.5
> 0.5
kJ / Min / Trip

Figure 5.12. The frequency distributions of the length of foraging trips for sandeels (light stippling) and non-sandeels (dark stippling) by adults feeding broods up to one week old on a) Shetland in 1988 (13 nests and 97 sandeels and 20 non-sandeels observed) and b) Orkney in 1989 (26 nests and 378 sandeels and 246 non-sandeels observed).


a
% Frequency
100
80
60
40
20
0
0 - 15
>15 - 30
> 30
Minutes / Trip


b
% Frequency
100
80
60
40
20
0
0 - 15
>15 - 30
> 30
Minutes / Trip

economics of foraging for saithe did not change. On Orkney in 1989 none of the parameters of foraging economics changed significantly with chick age during the first week after hatching. When all ages of chicks on Orkney are considered, the length of sandeel trips decreased highly significantly with advancing chick age, but not sufficiently strongly to effect an increase in profitability. The length of rockling trips also decreased with advancing age and profitability increased.

Table 5.6. Rank correlations (significance) of profitability and length of foraging trips with brood age

	Shetland 1988	Orkney 1989 (young broods)	Orkney 1989 (old broods)
n	7	7	26
Age vs. Profitability			
Sandeels	0.536 ns	0.679 ns	0.048 ns
Non-sandeels	0.400 ns	-0.036 ns	0.471 *
Overall	-0.036 ns	0.714 ns	0.039 ns
Age vs. Trip-length			
Sandeels	-0.893 *	0.214 ns	-0.757 ***
Non-sandeels	-0.400 ns	-0.179 ns	-0.725 ***
Overall	-0.893 *	0.357 ns	-0.743 ***

I also assessed the influence of age on foraging economics by comparing the performance of adults on Orkney rearing chicks up to one week old with those rearing older chicks. The results were similar to the results of the correlational analysis. Neither the energy (fig. 5.13) nor mass gathered per trip (fig. 5.14) differed between the two groups (Mann-Whitney U-test). Trip length showed a strong negative response to increasing chick age (fig. 5.15) (Mann-Whitney U-test. $z = 3.53$, $p < 0.001$), but this did not result in a corresponding increase in trip profitability (fig. 5.16). Considering sandeels and rockling separately, the length of sandeel trips was shorter in the group raising older chicks (fig. 5.17a) (Mann-Whitney U-test. $z = 3.12$, $p < 0.01$), but profitability was similar (fig. 5.18a). The economics of foraging for rockling did not differ between the two groups

Figure 5.13. The frequency distribution of the energy gathered per foraging trip by adults feeding young broods (26 nests and 670 trips observed) (light stippling) and adults feeding older broods (19 nests and 1725 trips observed) (dark stippling) on Orkney in 1989.

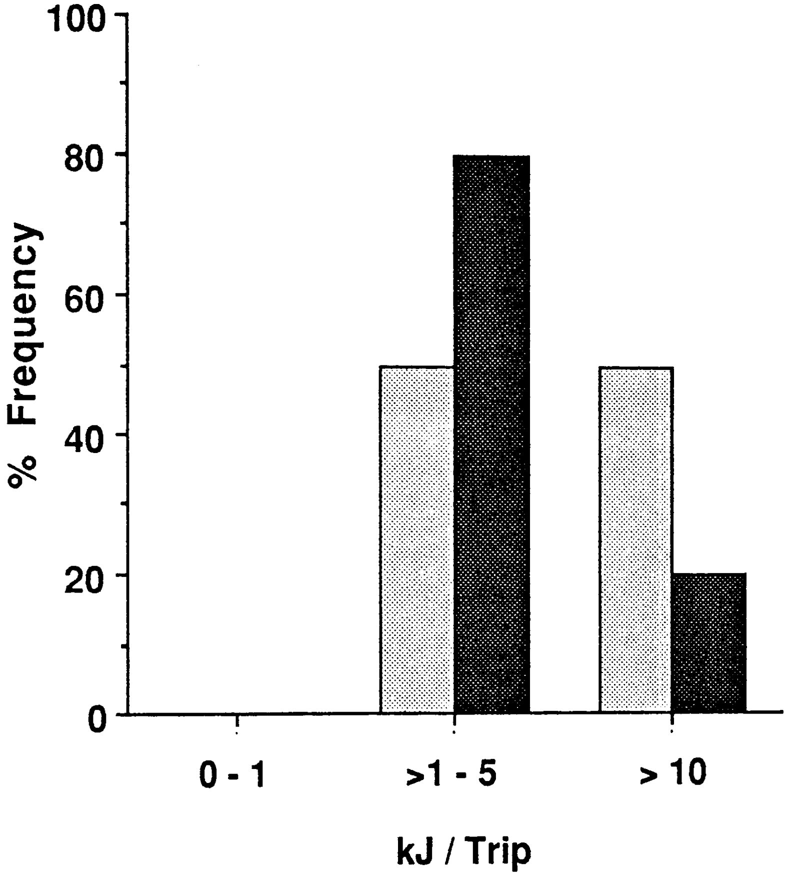

100
80
60
40
20
0
% Frequency
0 - 1
>1 - 5
> 10
kJ / Trip

Figure 5.14. The frequency distribution of the mass gathered per foraging trip by adults feeding young broods (26 nests and 670 trips observed) (light stippling) and adults feeding older broods (19 nests and 1725 trips observed) (dark stippling) on Orkney in 1989.

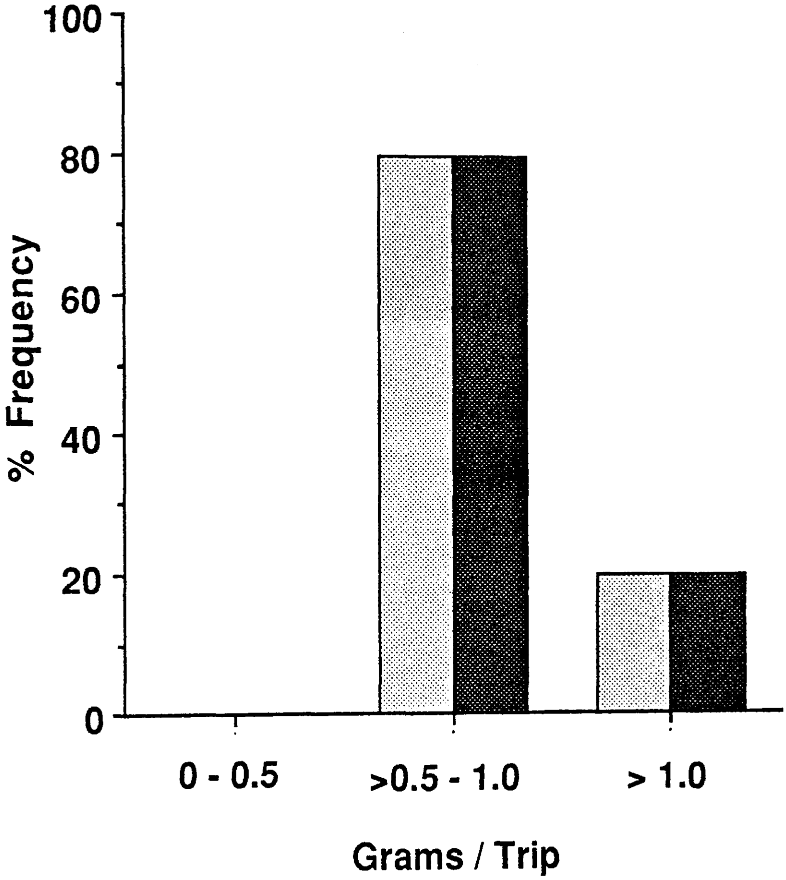

100
80
60
40
20
0
% Frequency
0 - 0.5
>0.5 - 1.0
> 1.0
Grams / Trip

Figure 5.15. The frequency distribution of the profitability (energy gathered / trip-length) of foraging trips by adults feeding young broods (26 nests and 634 trips observed) (light stippling) and adults feeding older broods (19 nests and 1543 trips observed) (dark stippling) on Orkney in 1989.

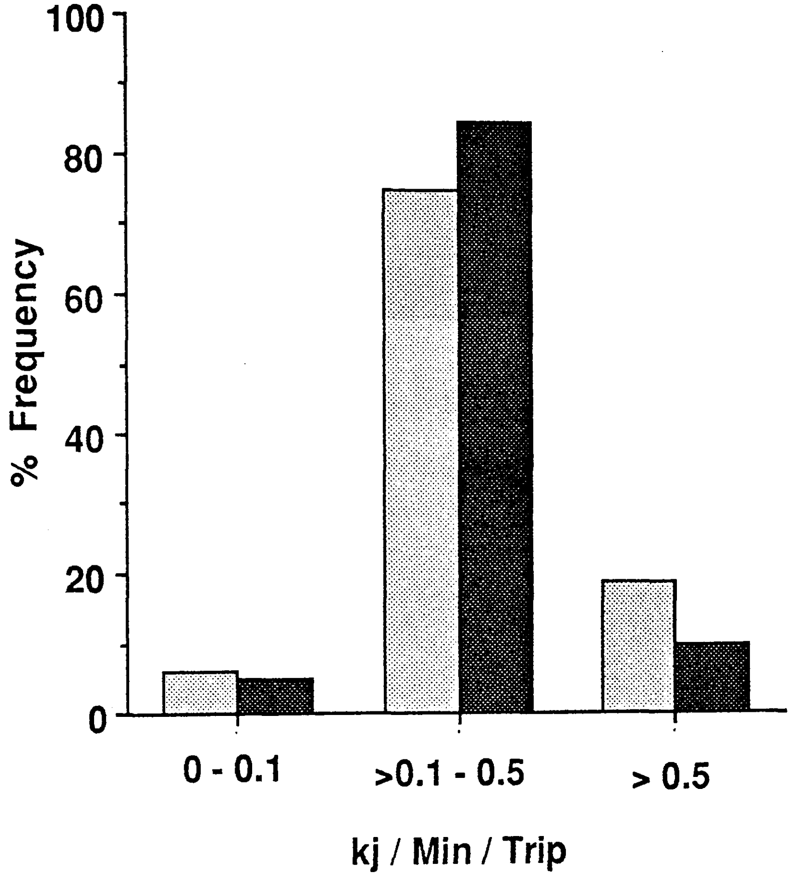

100
80
60
40
20
0
% Frequency
0 - 0.1
>0.1 - 0.5
> 0.5
kj / Min / Trip

Figure 5.16. The frequency distribution of the length of foraging trips by adults feeding young broods (26 nests and 634 trips observed) (light stippling) and adults feeding older broods (19 nests and 1597 trips observed) (dark stippling) on Orkney in 1989.

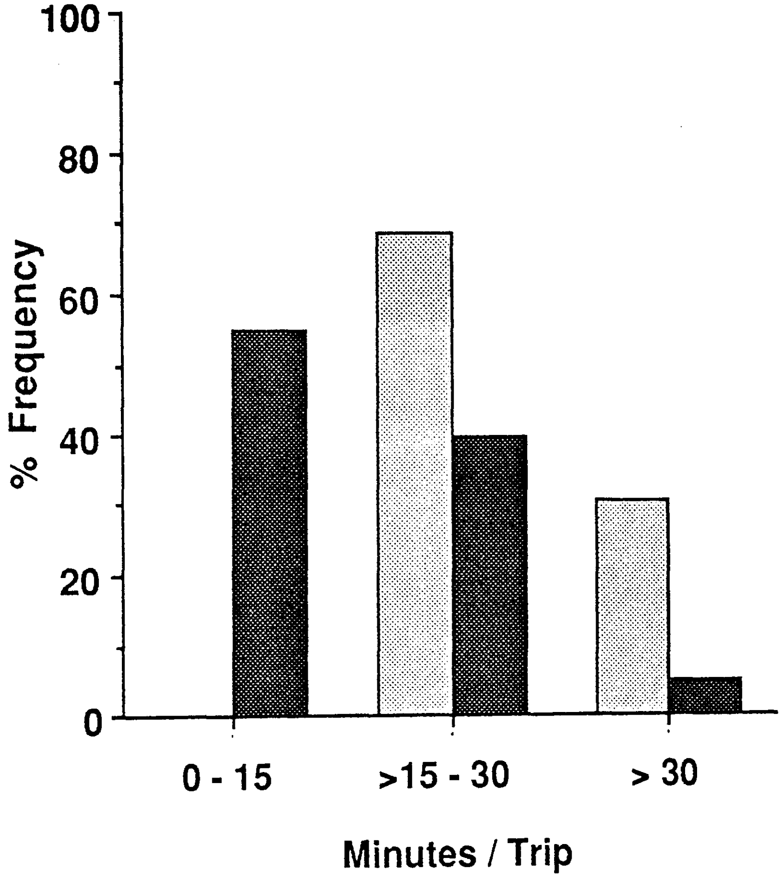
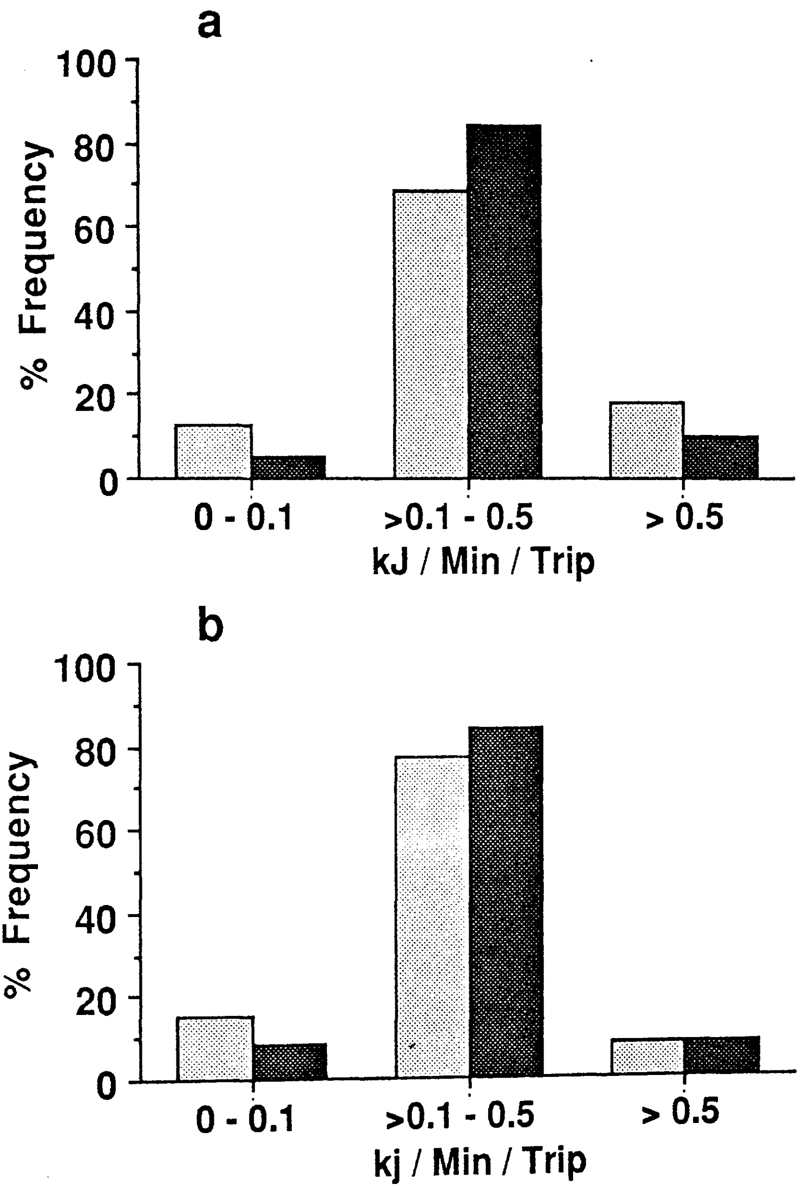

100
80
60
40
20
0
% Frequency
0 - 15
>15 - 30
> 30
Minutes / Trip

Figure 5.17. The frequency distributions of the profitability (energy gathered / trip-length) of foraging trips on Orkney in 1989 for a) sandeels and b) rockling by adults feeding young broods (26 nests and 382 sandeels and 252 non-sandeels observed) (light stippling) and adults feeding older broods (19 nests and 1415 sandeels and 128 non-sandeels observed) (dark stippling).


a
% Frequency
100
80
60
40
20
0
0 - 0.1
>0.1 - 0.5
> 0.5
kJ / Min / Trip
b
% Frequency
100
80
60
40
20
0
0 - 0.1
>0.1 - 0.5
> 0.5
kj / Min / Trip

(fig 5.17b, 5.18b).

5.3.4. The influence of weather on diet, provisioning rate and foraging economics.

Windspeed and rainfall were not correlated at either of the sites in any year during the chick-rearing period (Spearman Rank Correlation). Mean daily windspeed was lower on Orkney in 1989 than on Shetland in either 1987 or 1988 (ANOVA: $F_{2,50} = 12.3$, $p < 0.001$, followed by Scheffe's multiple comparison procedure), but there was no difference in rainfall between Shetland in 1987 and 1988 and Orkney in 1989 (Kruskal-Wallis Anova. $H = 4.2$, d.f. = 2, $p > 0.1$).

Neither daily mean windspeed nor rainfall were correlated with the mean daily proportion of sandeels in the diet of young chicks (Spearman Rank Correlation). The effects of weather on the size of prey was assessed by classifying days according to the strength of the wind or amount of precipitation and testing the difference between the size of the prey in the different groups with chi-squared tests. Days were classified into three groups in each year on the basis of the relative amount of rainfall (rainfall = 0, rainfall <= median (median of days when rainfall > 0), rainfall > median) and into two groups on the basis of relative windspeed (windspeed <= mean, windspeed > mean). The size of sandeels fed to chicks on days in each group are shown in figures 5.19 and 5.20, together with the levels of windspeed and rainfall used to classify days. The size of non-sandeels fed to chicks of any age was unaffected by wind or rain. A relative increase in windspeed was associated with an increase in the size of sandeels fed to young chicks in Shetland in 1987 (fig. 5.19a) and in Orkney in 1989 (fig. 5.19c) but not in Shetland in 1988 (fig. 5.19b). Considering chicks of all ages on Orkney in 1989 the effect of increasing windspeed was maintained (fig. 5.19d). Increasing rainfall was associated with an increase in the size of sandeels fed to chicks on Shetland in 1987 and Orkney in 1989, but with a decrease in sandeel size on Shetland in 1988 (fig 5.20).

The effects of rainfall and windspeed on chick provisioning rates were assessed by examining the relationship between mean daily weather and daily provisioning rate.

Figure 5.19. The size of sandeels offered to chicks on days of windspeed less than (light stippling), and greater than (dark stippling) mean windspeed. a) young broods on Shetland in 1987 (mean windspeed = 9.9 knots, n fish = 1481, $X^2 = 12.6$, d.f. = 3, $p < 0.05$); b) young broods on Shetland in 1988 (mean windspeed = 10.6 knots, n fish = 148, $X^2 = 3.4$, d.f. = 1, n.s.); c) young broods on Orkney in 1989 (mean windspeed = 4.9 knots, n fish = 859, $X^2 = 25.5$, d.f. = 3, $p < 0.05$); d) all age broods on Orkney in 1989 (mean windspeed = 4.6 knots, n fish = 3255, $X^2 = 40.4$, $p < 0.001$).

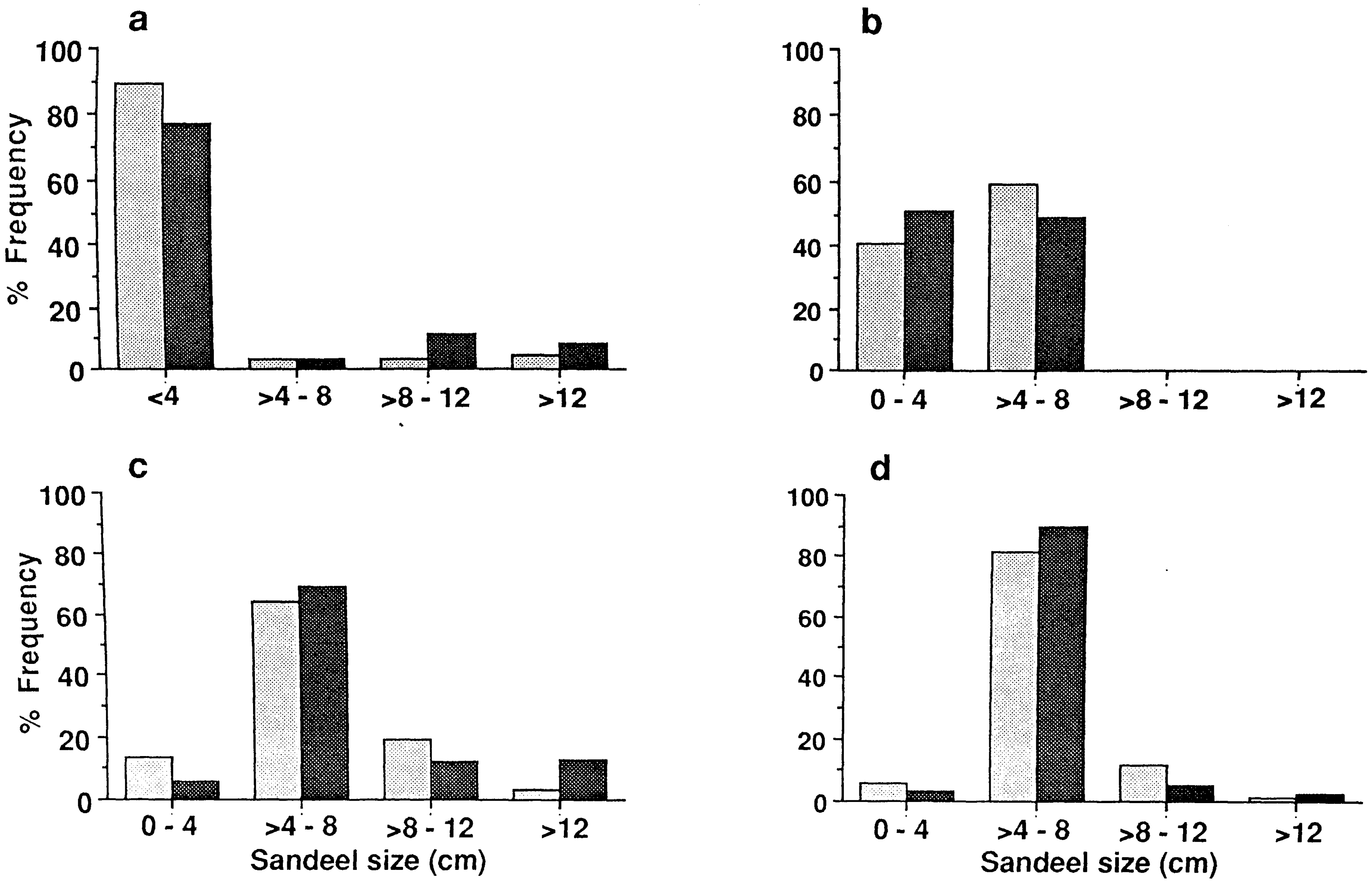
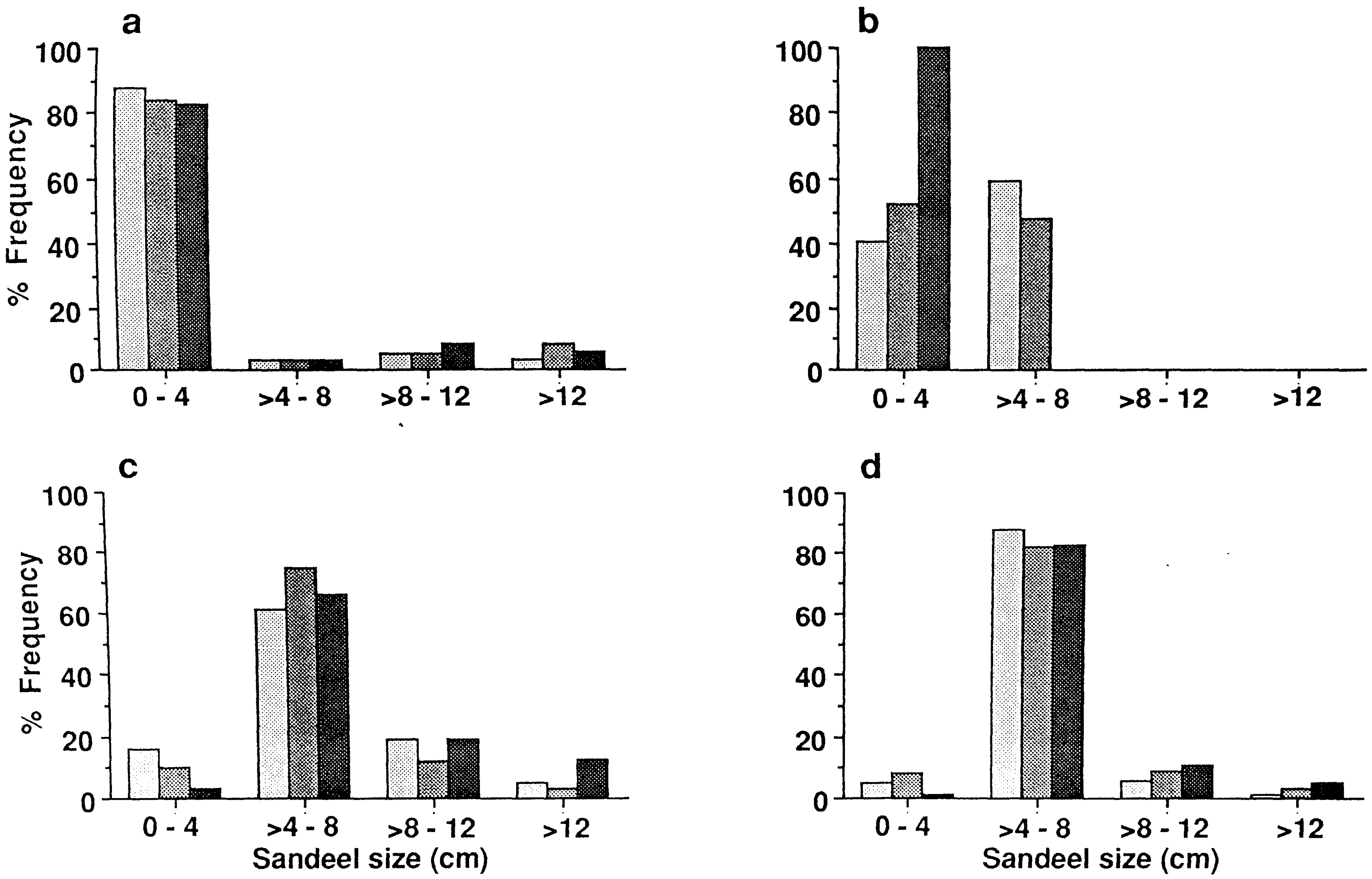

a
b
c
d
% Frequency
100
80
60
40
20
0
<4
0 - 4
>4 - 8
>8 - 12
>12
Sandeel size (cm)

Figure 5.20. The size of sandeels offered to chicks on days of rainfall of zero (light stippling), less than (medium stippling), and greater than (dark stippling) median rainfall. a) young broods on Shetland in 1987 (median rainfall = 2.5mm, n fish = 1481, $X^2 = 18.4$, d.f. = 6, $p < 0.01$); b) young broods on Shetland in 1988 (median rainfall = 1mm, n fish = 148, $X^2 = 7.2$, d.f. = 4, $p < 0.05$); c) young broods on Orkney in 1989 (median rainfall = 2mm, n fish = 859, $X^2 = 22.5$, d.f. = 6, $p < 0.001$); d) all age broods on Orkney in 1989 (median rainfall = 2mm, n fish = 3255, $X^2 = 25.2$, d.f. = 6, $p < 0.001$).


a
b
c
d
% Frequency
% Frequency
100
80
60
40
20
0
0 - 4
>4 - 8
>8 - 12
>12
Sandeel size (cm)
Sandeel size (cm)

Windspeed had a non-significant depressive effect on feeding frequency in Shetland in 1987 (r_s = -0.44, p = .08, n = 17), but had no other effects. Increasing rainfall had a marginally non-significant negative influence on feeding frequency on Shetland in 1988 (r_s = -0.7, p = .07, n = 7) and a significantly depressive effect on the feeding frequency of adults feeding chicks older than one week on Orkney in 1989 (r_s = -0.49, $p < 0.05$, n = 20) Neither windspeed nor rainfall had significant effects on rate of provisioning with energy or mass of food in any year.

There were no significant effects of weather on the economics of foraging trips, but increasing windspeed tended to be associated with shorter foraging trips by adults feeding old (> one week old) broods on Orkney in 1989 (r_s = -0.434, p = .056, n = 20). This effect appeared to be due to an effect of windspeed on the duration of sandeel trips (r_s = -0.437, p = .054, n = 20) rather than rockling.

All of the effects of windspeed and rainfall noted above are clearly very marginal and are by no means considered definitive evidence of any influence which they may have upon foraging terns.

5.3.5. Conspecific kleptoparasitism

Conspecific kleptoparasitism of food items was very common on Shetland in 1987. Adults returning to their territory with food for young were frequently harassed extremely intensely, often by large groups of other Arctic terns. Very often, one of these birds successfully stole the food item from the parent bird. All stolen fish were observed to be eaten more or less immediately after the theft, and none were seen to be fed to young. No marked adults, *i.e.* known breeders, were observed to take part in these kleptoparasitic events. The proportion of sandeels of each size-class which were stolen by conspecifics is shown for Shetland in 1987 and Orkney in 1989 in fig. 5.21. No prey items were observed to be stolen in 1988 on Shetland, and very few non-sandeels were stolen in either 1987 or 1989.

On both Shetland, in 1987, and Orkney, large sandeels were stolen in preference to

Figure 5.21. The proportion of sandeels of different sizes stolen from parents attempting to feed young by conspecifics, on Shetland in 1987 (n fish = 1481) (light stippling) and Orkney in 1989 (n fish = 859) (dark stippling).

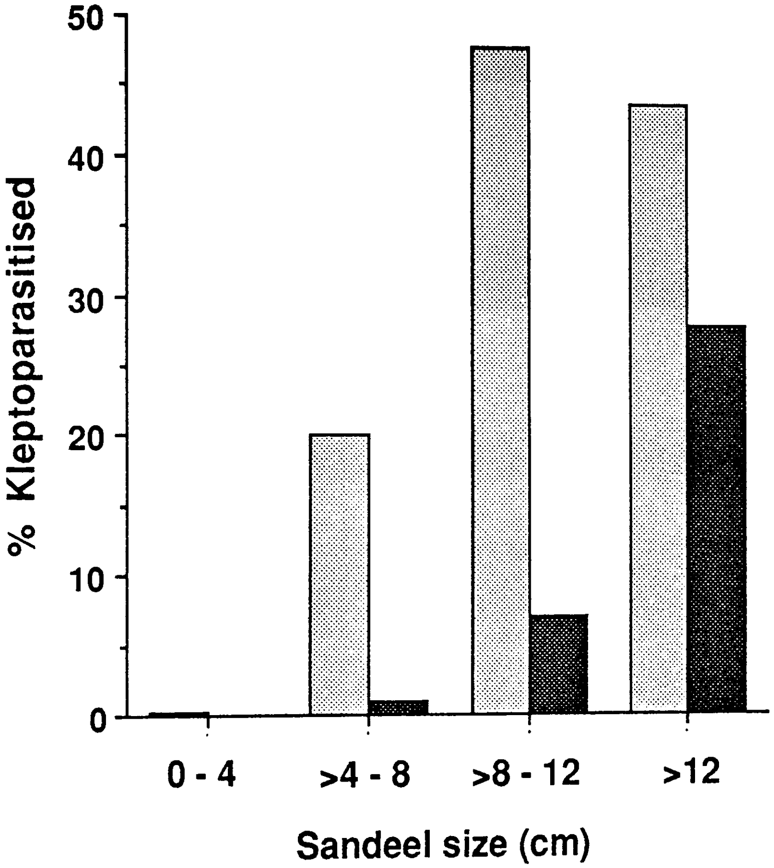
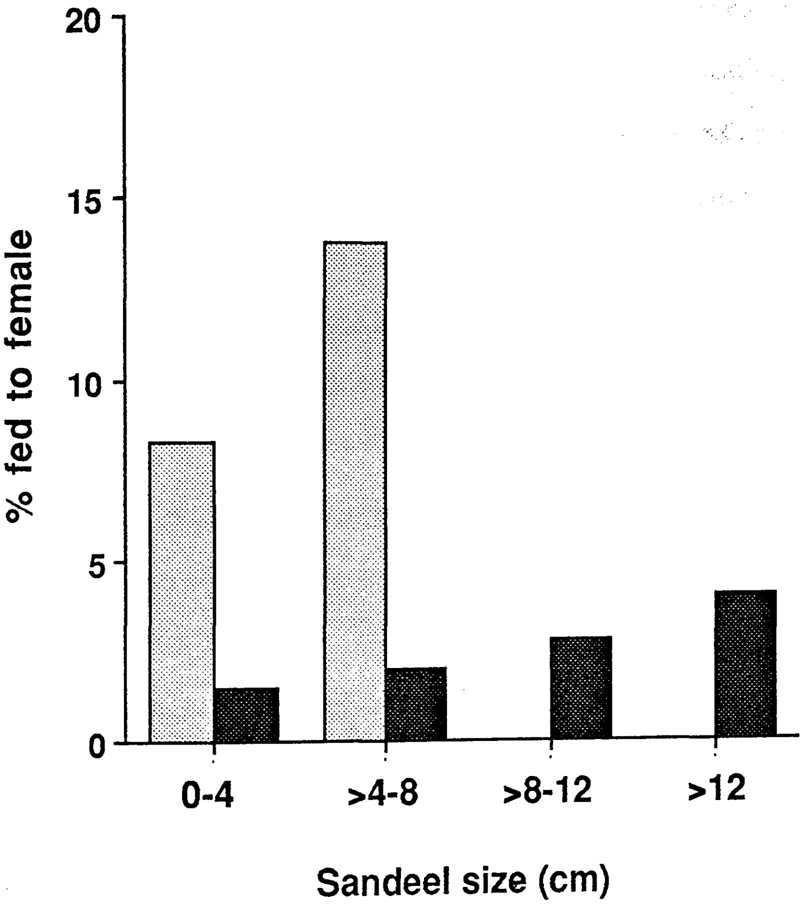

50
40
30
20
10
0
% Kleptoparasitised
0 - 4
>4 - 8
>8 - 12
>12
Sandeel size (cm)

Figure 5.22. The proportion of prey of different sizes fed to females by birds returning with food for young broods, on Shetland in 1988 (n fish = 148) (light stippling) and Orkney in 1989 (n fish = 859) (dark stippling).


20
15
10
5
0
% fed to female
0-4
>4-8
>8-12
>12
Sandeel size (cm)

small sandeels (Shetland: $X^2 = 357.3$, d.f.= 3, $p < 0.001$; Orkney: $X^2 = 52.8$, d.f. = 2 (fish < 8cm treated as one size to avoid expected values = 0), $p < 0.001$. Considering large (>8cm) sandeels, fish on Shetland were more likely to be stolen than fish on Orkney ($X^2 = 26.1$, d.f. = 1, $p < 0.001$).

5.3.6. Consumption of 'chick food' by females.

Food items which were brought to the colony by adults were not always fed to chicks. If prey were not kleptoparasitised they were sometimes eaten by the female rather than fed to the young. This behaviour was recorded at each location in all three years, but the outcome of such begging bouts was only recorded in 1988 and 1989. The frequency with which different sized fish were fed to females, instead of to the chicks, is shown in fig 5.22. There was no difference on either Orkney or Shetland in the likelihood of sandeels and non-sandeels being diverted to the female from the chicks (Shetland 1988: $X^2 = 0.04$, d.f. = 1, $p > 0.1$; Orkney: $X^2 = 0.03$, d.f. = 1, $p > 0.1$), nor was there any evidence of female preference for particular sizes of fish (Shetland 1988: $X^2 = 0.5$, d.f. = 3, $p > 0.1$; Orkney: $X^2 = 1.9$, d.f. = 3, $p > 0.1$). Overall, 10.9% of fish brought to young chicks on Shetland in 1988 were fed to females, whereas on Orkney in 1989 the corresponding figure was only 1.8%. This difference is significant ($X^2 = 29.3$, d.f. = 1, $p < 0.001$). These figures include all fish brought to the territory by both males and females. On Orkney (but not on Shetland) males brought significantly more fish to young broods than did females (see Chapter 4). Therefore the difference between Orkney and Shetland in the proportion of male-delivered items which females are fed must be even greater than that shown here.

5.4. Discussion

5.4.1. Effects of food shortage on chick provisioning

Figures compiled for the Department of Agriculture and Fisheries for Scotland for

ICES show that 1987 was an extremely poor year for the production of young sandeels in waters around Shetland. Production in 1988 was better, but still low in comparison with that recorded in the late 1970's and early 1980's when Shetland's Arctic terns and other seabirds fared very well (Bailey *et al.* in press).

Diet and Foraging performance

Despite the low number of 0-group sandeels (*i.e.* sandeels which spawned in the previous December/January) , upon which Arctic terns rely extensively when feeding chicks (Cramp & Simmons 1985, Ewins 1985) sandeels remained the most important component of the diet in both years. Indeed they comprised as important a part of the chicks' diet as they did on Orkney in 1989. This continued reliance upon sandeels probably reflects the lack of suitable alternative prey in Shetland waters where other energy rich, oily fish such as sprats and herring are absent in the appropriate size-classes at time of year when terns are breeding. On Coquet Island, Northumberland, Arctic terns can prosper on other high value foods when sandeels are absent from the diet (Langham 1968). In the Wadden Sea, common terns can utilise poorer quality *i.e.* less energy rich fresh-water prey, but these only act as a supplement during times of poor foraging and cannot sustain healthy chicks on their own (Massias & Becker 1990). Further north in their range, in the Baltic Sea, Arctic terns may rely extensively on poor quality prey such as sticklebacks (Lemmetyinen 1973), but it is hard to compare two such different ecosystems, when so little is known of the abundance, distribution and availability of prey. It is likely that Arctic terns feeding exclusively on sticklebacks must increase their feeding rate considerably, as do common terns supplementing their chicks' diet in the Wadden Sea (Frank 1990). Possible reasons why other fish, in particular saithe, may not be suitable prey for Arctic terns to feed to young chicks are discussed later. The difference between 1987 and 1988 in the abundances of saithe, moths and prawns in tern chicks' diet on Shetland is interesting. Saithe are noted as being common in Shetland's inshore waters by Berry & Johnston (1980), but more precise data on distribution are absent. Studies in the two years were located at different colonies. In 1987 the study colony was located on Garths Ness at the south end of Shetland Mainland. In 1988 the Garths Ness colony was unoccupied and a colony on the small island of Mousa, off the east coast of Shetland Mainland was studied instead. Perhaps the availability of saithe differed between the two sites.

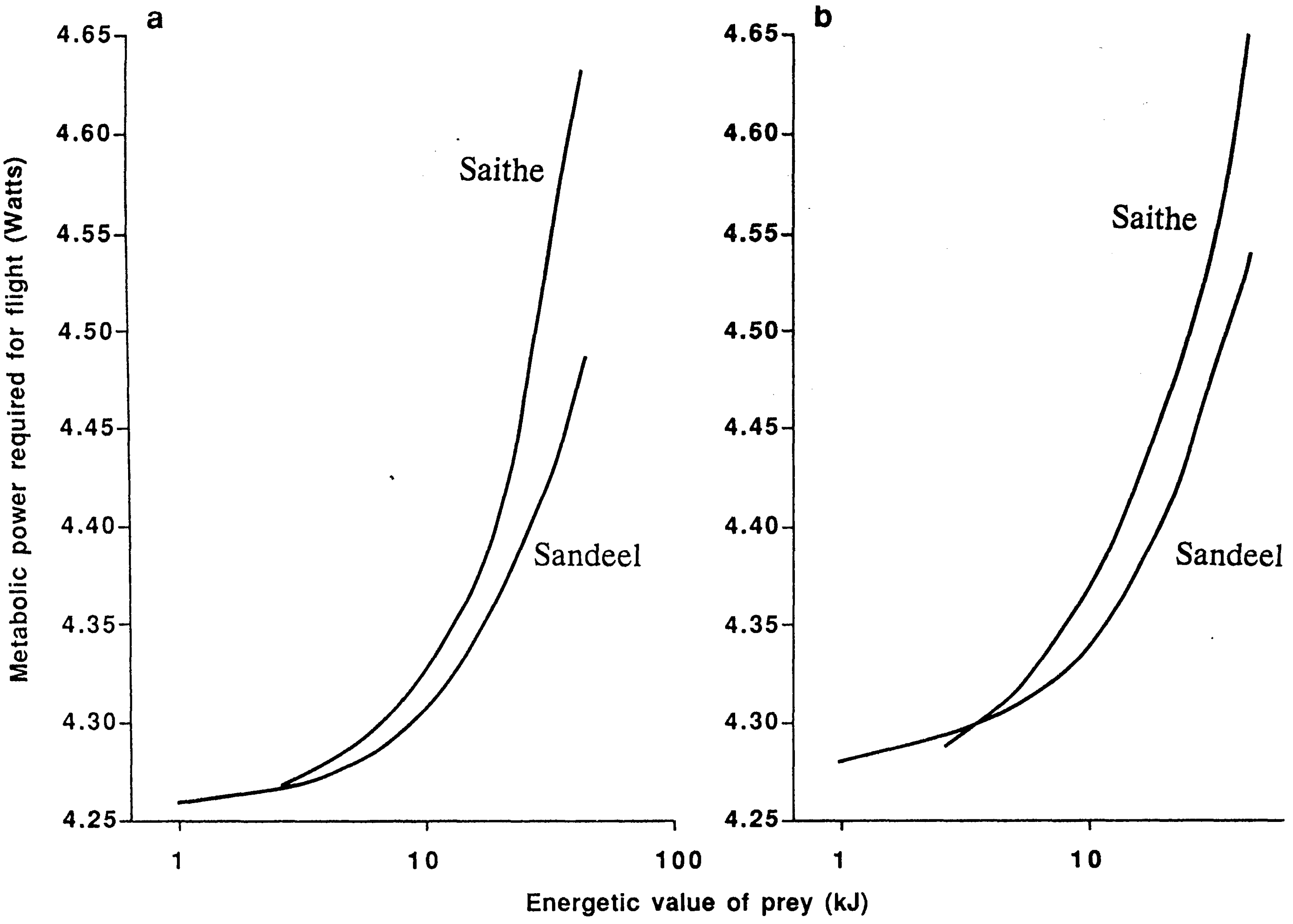
Although sandeels were still the dominant component of the diet on Shetland in 1987 and 1988, the size of sandeels offered to chicks differed between the two years, and from sandeels fed to chicks on Orkney. Chicks on Orkney were fed primarily with sandeels of the 4-8cm size-class, which agrees with the findings of studies at other thriving tern colonies (examples in Cramp & Simmons 1985, Ewins 1985). In June and July this size-class consists of the 0-group fish spawned during the previous winter. Sandeels of the 4-8cm class were conspicuously absent from the chicks' diet in 1987 reflecting the poor sandeel production shown by the DAFS. The 0-group sandeels which were fed to chicks in 1987 were much smaller and of a size which suggests that they had barely metamorphosed from the larval stage (Reay 1970). This in itself suggests possible reasons why measured sandeel production was poor in 1987; it may have been due to the lateness of the arrival of young fish or their slow growth. Adult Arctic terns appeared to attempt to compensate by increasing the frequency with which they fed their chicks in comparison to 1988, when sandeels fed to chicks, although still somewhat smaller than on Orkney and other colonies without food shortage, were larger than in 1987. This effort was sufficient to ensure that chicks received energy and mass of food at similar rates in the two years on Shetland, although in both years the rate at which chicks were provisioned was far lower than on Orkney, even though feeding frequencies on Shetland in 1987 and Orkney in 1989 were similar.

The larger sandeels fed to their chicks by Arctic terns on Orkney resulted in the average return per foraging trip of energy or mass of food being greater than on Shetland. This led to the difference in chick provisioning rates already shown. However, the average profitability of trips, in terms of energy value of food gathered per minute's absence was similar, probably because trip-length tended, albeit insignificantly, to be greater on

Orkney. On Orkney, the length of foraging trips was correlated with the energetic value of food brought to the brood. This may have been due to trips for rockling being shorter than trips for sandeels, which were of greater energy value due to their larger size, which more than compensates for their lower energy density (7.1 kJ / g wet weight for rockling versus 6.5 kJ / g w/w for sandeels, Harris 1984). On Shetland there was no such relationship and trips for saithe and sandeels were of similar duration. However, trips for saithe were more profitable. The shortage of sandeels in Shetland is reflected in their lower profitability there than on Orkney.

The fact that on Shetland in 1988 foraging trips when saithe were brought to broods yielded more energy (and certainly more mass) per minute's absence than trips for sandeels begs the question as to why this species did not contribute more to the diet of the chicks in Shetland when sandeels were in short supply. The difference in profitability arises from the fact that, because of their deeper keel, saithe, on a length for length basis, are of greater weight than sandeels (see equations in appendix of Harris & Hislop 1978). This results in the energetic content of the average sized saithe fed to chicks being greater than that of the average sized sandeel, since their greater weight more than makes up for their lower energy density (5.1 kJ / g w/w for saithe versus 6.5 kJ / g w/w for sandeels). In fact, a 6cm sandeel is predicted to weigh 0.59g, whereas a saithe of the same size would weigh 1.72g and their respective energy contents are estimated as 3.68kJ and 8.77kJ (derived from Harris & Hislop 1978). This difference in energy density means that in order to provide their chicks with a given amount of energy Arctic terns would need to provision them with 25 % more mass of saithe than of sandeel. It is possible that the net profitability of saithe *i.e.* including foraging, handling and transport costs may be lower than that of sandeels. A further difference between saithe and sandeels lies in the chemical form of energy within them. Sandeels have a much greater fat content than white fish such as saithe, and chicks fed on fish with low fat contents may have to utilise protein as an energy source which may reduce the amount of protein available for growth (Harris 1984). The generation of energy from protein is a less efficient metabolic process than using fat (Brody 1945) and this may increase still further the discrepancy in the mass of

Figure 5.23. The power requirements for flight (Watts) of a) arctic terns and b) common terns carrying energetically equivalent loads of sandeels and saithe, calculated from Progamme 1 (Pennycuick 1989) using parameters in table 5.7.


a
b
Metabolic power required for flight (Watts)
4.65
4.60
4.55
4.50
4.45
4.40
4.35
4.30
4.25
Saithe
Sandeel
1
10
100
Energetic value of prey (kJ)

saithe and sandeels needed to satisfy the needs of a growing brood of young. Common terns on Shetland frequently feed their chicks on saithe and appear to be able to breed successfully on such a diet (Ewins 1985, Uttley *et al.* 1989a). However, common terns have chicks with lower energy requirements than Arctic terns (Klaassen *et al.* 1989) and may thus be less constrained by the differences in energy density between the two species of fish. Alternatively, by virtue of their larger size (breeding adult body mass of Arctic tern = 110g, of common tern = 125g, Cramp & Simmons 1985) common terns may be better adapted to feed on larger prey such as saithe through differences in foraging and transport costs. Studies of the two species in sympatry have shown that common terns take larger food items than Arctic terns (Boecker 1967, Langham 1968, Lemmetyinen 1973, Uttley *et al.* 1989a) although Pearson (1968) found no difference. Such an effect could come about either because their larger size reduces the incremental flight costs associated with handling larger prey or their chicks may be better able to cope with large and deep keeled prey. However, I saw no evidence that saithe were difficult for young tern chicks to handle and consume. The flight costs incurred by Arctic and common terns feeding their young on sandeels or saithe of various sizes were modelled using the power requirements for flight generated by Programme 1 in Pennycuick (1989) for the power requirements of horizontal flight. The parameters fed into the model are shown in table 5.7. Over the size range of fish normally fed to chicks (4-10cm long) saithe were always more expensive to carry than sandeels of similar energy content due to the former's lower energy density (fig. 5.23a). However, the difference was small, ranging from 0.005 Watts (W) to 0.16 W (0.1% to 3.6% of the cost of carrying an energetically equivalent sandeel) depending on the energy value of the prey. In terms of energy requirements over a whole day, to feed a chick entirely with saithe would cost only between 0.1kJ and 0.2kJ more in flight costs than it would feeding it with sandeels only. For common terns there is even less difference between the two fish species. Over the same size range of fish, saithe are between 0.005 W cheaper, and 0.11 W more expensive to carry than sandeels of similar energy content (fig. 5.23b). Daily differences in transport costs for birds specialising in saithe versus sandeels ranged from a saving of 0.1kJ to extra expenditure of 0.1kJ. It is clear, despite the crude nature of the model, that feeding chicks on saithe ought not to be excessively demanding of Arctic terns in terms of transport costs, and that common terns do not hold any appreciative advantage over them in this regard. However it is possible that there may be differences between Arctic terns and common terns in the costs of capturing saithe.

Differences in preferred foraging sites may also be involved in such dietary differences. Several studies have shown that common terns tend to breed and/or forage in more inshore waters than Arctic terns (Boecker 1967, Langham 1968, Dunn 1972, Lemmetyinen 1973, Uttley pers. obs.), and saithe are extremely common in Shetland's inshore waters (Berry & Johnston 1980).

Table 5.7. Parameters used in estimating the power requirements of flight and daily transport costs of arctic and common terns feeding their young on saithe and sandeel of various sizes.

Parameter	Arctic tern	Common tern
Body Mass (kg)	0.11[1]	0.125[2]
Wing Span (m)	0.78[1]	0.80[2]
Daily energy requirement of 5 day old chick (kJ)[3]	87.0	67.0
Assimilation efficiency (%)[4]	80.0	80.0
Time to fly from feeding grounds (min)	10.0	10.0

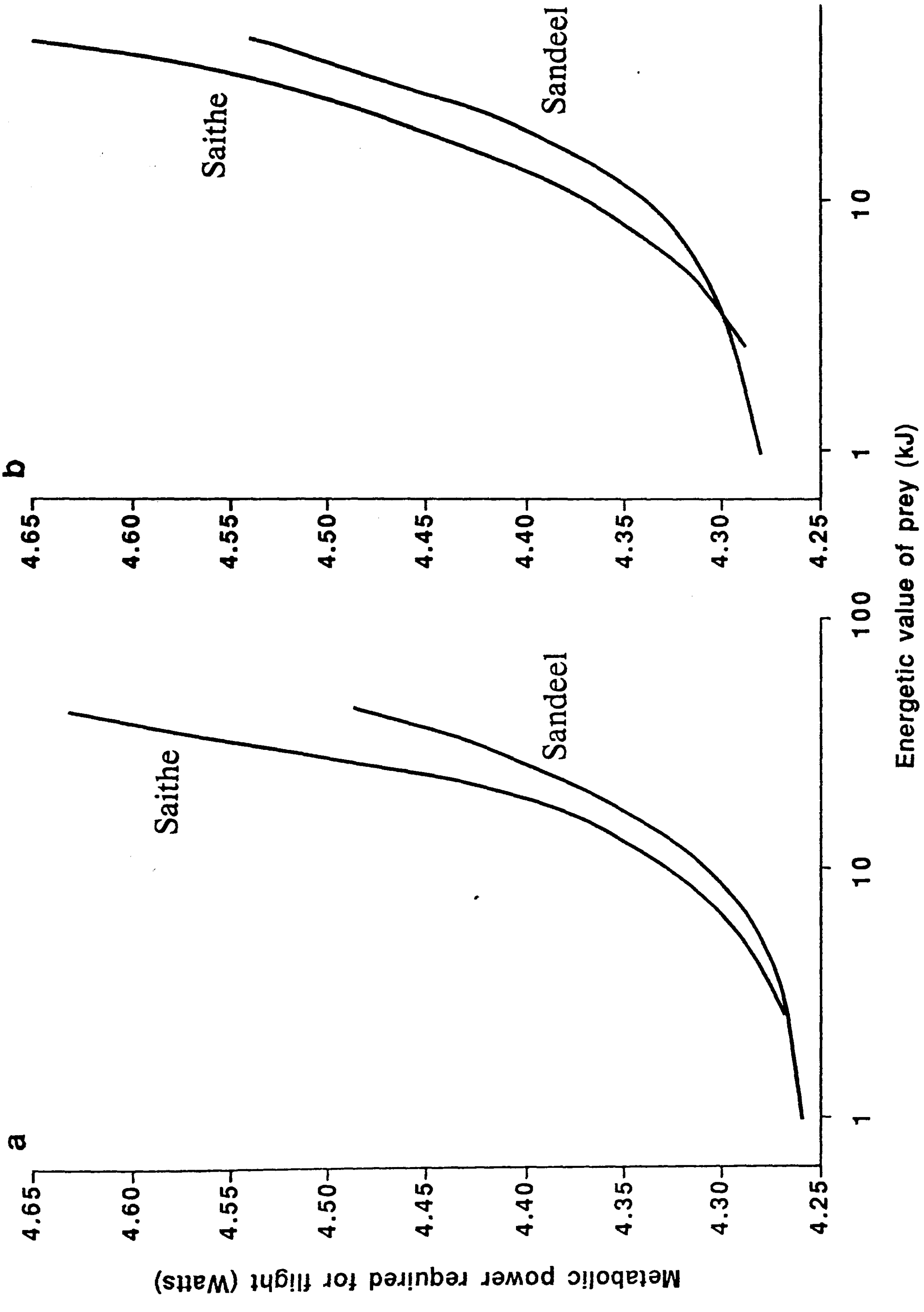
Sources - 1: own data
2: Cramp & Simmons (1985)
3: Klaassen et al. (1989)
4: Ricklefs (1974)

Conspecific kleptoparasitism

Kleptoparasitism is a very common foraging strategy amongst birds, but within the order Aves it is concentrated in the Charadriiformes and Falconiiformes which hold 60% of kleptoparasitic species, but only 7% of all bird species (Brockmann & Barnard 1979). Arctic terns have been recorded as interspecific kleptoparasites (Norrevang 1960 on Puffins, Bengston 1966 on Slavonian Grebes *Podiceps auritus* and Bardarson 1975 on Black Guillemots *Cepphus grylle* - all quoted in Cramp & Simmons (1985), but not previously as intraspecific kleptoparasites, although its close relatives the common and roseate (*Sterna dougallii*) terns are well known for kleptoparasitising conspecifics (Hays 1970, Dunn 1972, 1973a).

In terms of the frequency with which stealing occurred, fish were stolen twice as often on Shetland in 1987 (3.6% of all items) as on Orkney in 1989 (1.8%). However, because kleptoparasites preferred large to small fish in both years, the impact on the energy intake of chicks was more severe than is suggested by an examination of its impact on the number of items stolen alone. On Shetland this was exaggerated by the lack of intermediate sized food items, and the total energy value of food fed to chicks was reduced by 46% below what it would have been had no kleptoparasitism occurred. On Orkney, because intermediate sized sandeels were common and only infrequently stolen, and the non-sandeel prey were energy rich rockling, the energetic impact was less, kleptoparasitism resulting in a reduction of chick energy intake by only 15%. Do terns avoid large sandeels because of the attendant high risks of kleptoparasitism? A model can be used to examine the potential effects of kleptoparasitism on the provisioning of the young with energy (fig. 5.24, see legend for full explanation). It is clear that, at observed intensities of kleptoparasitism, large sandeels still result in higher net energy gains by broods per fish caught, despite being kleptoparasitised to a much higher degree. The model shows that the increases in the probability of kleptoparasitism which would be necessary for the net energy gain from a given size-class to drop below that of the next smallest size-class are considerable. Assuming other factors being equal, large sandeels should be preferred to small ones. The data on the size of sandeels fed to chicks show that large sandeels are always rare in the diet of broods. It is possible that large sandeels are less available and/or more difficult to capture than small ones, thus reducing their profitability by increasing capture costs or search time. However, even if neither of these suggestions were true, there are other risks from kleptoparasitism in addition to the loss of food for the young. The parent bird may run some risk of personal injury during the frenzied attacks by groups of kleptoparasites. Furthermore the risks to the chick are also great. Large sandeels take longer to handle than small sandeels (*c.f.* Hulsman 1981); I

Figure 5.24. A model of the impact of kleptoparasitism on the amount of energy provided to the young per sandeel caught after kleptoparasitism, where P_i = observed probability (P) of size-class i being kleptoparasitised and e_i = net amount of energy provided to the young (e) per sandeel of size-class i at P_i. Note that e_i is always greater than e_{i-1}. Thus at observed levels of P_i, larger sandeels still result in higher net energy levels being provided for the young, despite being kleptoparasitised to a greater extent. P'_i = the level of kleptoparasitism necessary for e_i to be reduced to equal e_{i-1}, assuming P_{i-1} remains constant.


a
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Metabolic power required for flight (Watts)
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4.55
4.50
4.45
4.40
4.35
4.30
4.25
Energetic value of prey (kJ)
1
10
100
Saithe
Sandeel

have seen a large (> 12cm) sandeel take longer than one minute to be completely swallowed by a chick. The sandeel is susceptible to kleptoparasitism for as long as it protrudes from the gape and the chick may be accidentally carried off by a kleptoparasite, or be attacked itself (pers. obs.). The moment of food delivery may also be a time of great predation risk, as in Black Skimmers *Rynchops niger* (Quinn 1989). These risks may be more important than that of prey loss *per se* . Yet another disadvantage of feeding chicks on large prey is the delay in delivery of food to the brood that is brought about by parents being constantly disturbed during the feeding process. Adults with large sandeels often made several approaches to their chick before finally passing the food to them, and delays of up to 20 minutes often elapsed between the arrival of adults with prey and consumption by the chick.

The lack of kleptoparasitism on Shetland in 1988 was not surprising given the preference of thieves for large fish, and the complete absence of large fish from the diet of Arctic terns in that year.

The pattern of kleptoparasitism observed amongst Arctic terns during the three years of this study conforms with the preconditions set by Brockmann & Barnard (1979) for the occurrence of food stealing. They proposed six conditions which would facilitate the evolution of kleptoparasitism. 1) The presence of large concentrations of hosts. This condition is obviously met by colonially breeding seabirds including the Arctic tern. 2) Large quantities of food. Once again, seabird colonies during the breeding season are characterised by high concentrations of food being brought from feeding areas to chicks. 3) Large high quality food items. Kleptoparasitism occurred in 1987 on Shetland but not in 1988, when large prey were not brought back to the colony by foraging adults. 4) Food supply predictable. As long as breeding attempts are in progress then food will be brought to the chicks by adults. 5) Food visible. Arctic terns carry food for the chicks held in their bills which is conspicuous to both conspecifics and human observers. 6) Food shortage. Kleptoparasitism was more frequent on Shetland, when food was in short supply than on Orkney where it was not. Hays (1970) similarly found that kleptoparasitism amongst common terns was more frequent in years of food shortage.

From conditions 1 and 2 (above) it is apparent that colony size and density may affect the prevalence of kleptoparasitism. The size of the three study colonies did indeed vary; Garths Ness, Shetland, 1987: *ca.* 400 pairs; Mousa, Shetland, 1988: *ca.* 50 pairs; Papa Westray, Orkney, 1989: *ca.* 5500 pairs. The Mousa colony was also less dense than the other two. It is therefore possible that the small size and low density of the Arctic tern colony there was a factor in making kleptoparasitism unprofitable.

Thompson (1986), in his work on the interactions between black-headed gulls *Larus ridibundus*, golden plovers *Pluvialis apricarius* and lapwings, showed that the probability of attack depended on the cost of attack, the success rate and the value of the prey. I could not measure the cost of attack in this study because attacks were highly chaotic incidents involving many individuals at once, and consisted of long chases which could not be followed for their whole duration from a hide, making it almost impossible to follow individuals for complete attacks. Moreover, it seemed likely that an important component of the cost of attack might be the physical risk involved in participation. The success rate of attacks was not measured either. However, on a qualitative basis it seems safe to assume that attacks on birds carrying large fish might be more successful than those on birds carrying small fish, since the time taken for chicks to handle large prey is very much longer than for small fish. However, it is conceivable that this factor may be countered by the greater number of attackers when large fish are encountered, thus reducing the chances of success per individual. Thompson's third factor affecting probability of attempted theft was the value of the prey. It is clear that Arctic terns preferentially attempted to steal large food items, which contain considerably more energy than the average food item encountered. Ens *et al.* (1990) found that Curlews *Numenius arquata* also steal high value prey, and they also showed that this preference was not an artefact of more attacks being made on items requiring longer handling time which were therefore easier to steal.

Dunn (1972, 1973a) found that certain roseate terns specialised in food stealing, and thought that most of the items which they stole were fed to their chicks. In contrast, nearly all fish stolen by Arctic terns were eaten by the robber immediately. This may have been because the thief would have risked being kleptoparasitised itself had it attempted to feed its chick. However, it is also possible that most thieves were non-breeders. In support of this, I never saw any marked (*i.e.* breeding) adults robbing despite approximately 25% of adults in the vicinity of the hide being marked. Non-breeding adults are common in all tern colonies during the chick-rearing phase, and especially so in Shetland where young birds which do not attempt to breed are supplemented by failed breeders. The lack of robbing by marked birds, despite the fact that they remained in the vicinity of their nests for several days after failing, suggests that most robbing was done by young birds. Inexperienced birds are probably less skillful feeders than older birds (Dunn 1972). Furthermore they arrive at the breeding areas later than breeders (Coulson & Horobin 1976) and will be less acquainted with the foraging areas. Their relative inefficiency at hunting may make kleptoparasitism a more profitable feeding strategy for them, especially when hunting is made less profitable by food shortage. It may also have additional benefits in that it allows them to remain in the colony where they may gather more information to help them in future breeding attempts.

Consumption of 'chick food' by females

Female Arctic terns often begged for food items which their mates brought in to feed to chicks. Such behaviour often elicited no response from the male who proceeded to feed the food to the young. Sometimes the begging of the female appeared to confuse the male, who would take some time before either feeding a chick or giving the food item to his mate.

The greater proportion of fish brought to the brood by the male which was eaten by the female on Shetland in 1988 compared with Orkney in 1989 seems a clear manifestation of reduced commitment to the breeding attempt or increased food requirement, at least on the part of females. One consequence of the poor food availability on Shetland is that the adult terns are lighter and may lose weight faster than at colonies where food is in good supply (Monaghan *et al.* 1989a, 1990). Body weight may be an important cue for birds making decisions on whether or not to continue with a breeding attempt (Monaghan *et al.* 1990). Courtship feeding occurs throughout the breeding period, even on Orkney (pers obs.), and its increased frequency on Shetland may simply be a consequence of the females' increased hunger. Increased begging for food by females in times of food shortage has also been noticed in common terns (Safina *et al.* 1988).

Diversion of food from the chicks to the female may represent either a total breakdown in the breeding attempt as the 'decision' to desert is being made, or it may be a deliberate strategy to prolong the breeding attempt by maintaining the females' body condition. Failed breeders often return to their territory after the death of their brood and re-enact the courtship period, although re-nesting seems rare in both Orkney and Shetland (pers. obs.). However, Smith *et al.* (1989), studying pied flycatchers *Fidecula hypoleuca*, showed that males regulated the amount of food with which they supplied their incubating mates according to their female's nutritional state. They also showed that female nest attentiveness was increased by giving her extra food. Given that female terns on Shetland brood their young less than they do on Orkney (Chapter 4), some parallels can be drawn between the two studies, although there are obviously major differences, namely that the pied flycatchers were not depriving their offspring of valuable food, as the terns on Shetland appeared to be doing. It may be that such behaviour could be adaptive in enabling terns to withstand short periods of food shortage during the post-hatching period when time is severely limited by the need to self-forage and feed and brood chicks. Tinbergen (1981) in his studies of the starling *Sturnus vulgaris* took the opposite view, stating that females respond to increased demand by foraging more and directing the most profitable food items to the young. However, he was studying a much shorter lived species in which considerations of survival and future reproduction would be far less important in determining current reproductive investment.

5.4.2. Effects of brood age on chick provisioning

As chicks increased in age over their first week of life several changes took place in the way in which they were provisioned by their parents. These changes may be considered with respect to changes in the demands of chicks as they develop, and to differences in conditions of food supply between the three years.

On Shetland in 1988 and Orkney in 1989 sandeels became progressively more important in their diet. However, the origins of this trend are not so clear due to the confounding influences of age and date which were strongly correlated. On Orkney in 1989 the change was accounted for by a progressive increase in the proportion of sandeels occurring in chick diet with the advance of date, but this was not so on Shetland in 1987. When broods of all ages on Orkney are considered, clearer trends emerge, with sandeels increasing in importance as a function of both age and date independently of each other. Lemmetyinen (1973) also found a dietary shift as Arctic tern chicks in the Baltic developed. He found that small prey such as crustacea were replaced by sticklebacks. Tinbergen (1981) found that starling chicks were fed a wider range of items when they were young and speculated that nutrients other than energy may be maximised in the diet at this stage. However, as he also pointed out, this could be a consequence of the need of young chicks for smaller items which are easier to handle and digest. It is perhaps unsurprising that changes in diet with age are absent in the first week of life since there are, by definition, only 7 days over which changes can occur, as against more than 20 for the whole nestling period. Furthermore, broods may contain nestlings differing in age by up to 3 days. This age differential is relatively greater in young than old broods, and may restrain parents from making dietary adjustments for the older chick. Young chicks may require food which is small, easy to handle or digestible (*e.g.* Pierotti & Annett 1987) and this may constrain the foraging strategy adopted by parents with asynchronously hatching broods (Armstrong in prep.). The independent increase in the importance of sandeels in chicks' diets with age and date when all chicks are considered is interesting, and lends support to the contention that the timing of breeding is evolved to coincide peak demand with peak food availability. The lack of any increase in the importance of sandeels with date on Shetland in 1988 may be another consequence of poor sandeel recruitment there.

Increases in the size of food (Dunnet 1955, Royama 1966b, Lemmetyinen 1973, Tinbergen 1981, Biermann & Sealy 1982, Carlson & Moreno 1982, Cairns 1987, Grundel 1987, Jones 1987a) and its rate of delivery (Courtney & Blokpoel 1980, Tinbergen 1981, Biermann & Sealy 1982, Jones 1987a) with the age of the brood have been found in many species of birds.

The available data permitted the size of food fed to chicks to be considered between young (up to one week old) and old (over one week old) broods on Orkney in 1989. The size of sandeels differed between these two groups, but rather than a simple increase or decrease in size, sandeels of 4-8cm *i.e.* the typical 0-group size, became more common at the expense of smaller and larger fish. I can think of two possible explanations of this change. Firstly, parents may simply become more experienced at feeding their young as the brood grows older and choose fewer very small fish, which are of little value, and fewer large fish which are more likely to be kleptoparasitised. Secondly, the change in diet may reflect changes in the fish population as the 0-group fish grow, and increasing numbers metamorphose. In addition, adult sandeels may change their behaviour and distribution at this time of year by occurring deeper in more offshore waters (P. Wright pers. comm.). In contrast, rockling showed a straightforward increase in size with brood age, which could also be explained by either of the above hypotheses.

If differences in brood size are not accounted for, then birds on Shetland in 1987 decreased their feeding frequency, and in 1988 increased their feeding frequency as a function of chick age. Both of these trends became insignificant when corrected for brood size. In other words, in 1987 Arctic terns reduced their feeding frequency in response to decreasing brood size, whilst in 1988 they increased their feeding frequency in response to increasing brood size. Such differences may be accounted for by changes in the patterns of hatching and mortality between the two years. On Orkney in 1989, neither brood nor chick feeding frequencies changed in response to chick age. However, the rate at which chicks there were provisioned with energy and mass of food did increase as broods grew older, probably as a result of the switch from rockling to sandeels during that first week noted above. Brood provisioning rates on Shetland in 1988 increased with brood age, but this was a result of the change in feeding frequency in response to brood size noted above, and chick provisioning rates did not show a significant response to age. It may be worth noting that all relationships between brood age and feeding and provisioning rates were negative on Shetland in 1987, but positive in 1988, and could be indicative of the relative conditions of food supply in the two years. When broods of all ages are considered on Orkney in 1989 feeding frequency is seen to increase with age. However, the return of energy and mass of food per foraging trip actually decreased as the brood grew older. Despite this all parameters of chick provisioning rate were higher for old than for young chicks. There are two methods of increasing the rate at which chicks are provisioned with energy. One is to increase the quality of food, and the other is to increase the rate at which it is supplied. Arctic terns appear to be able to use both mechanisms.

Associated with the decline in energetic return per trip noted above, foraging trip length declined through the chick-rearing period. Thus the profitability of foraging trips remained constant. No trends in trip length or profitability were apparent during the first week of chick life on Orkney, but on Shetland in 1988 trip length declined with brood age, although this change did not apply to trips from which saithe were brought. Once again, profitability did not change. The constancy of return of energy or mass of food per unit time away, combined with the increased demand of the growing brood for food suggests that adult Arctic terns must spend an increasing proportion of their time foraging for food for their chicks as they grow. This must result in a decrease in the amount of time available for self-provisioning and for non-foraging activities, such as brooding, defence against predators, resting, washing, preening and self-maintenance. The potential conflict between provisioning of the chicks and activities necessary for self-maintenance, notably self-feeding were highlighted by Jones (1987b) who showed that daily mass changes of adult swallows *Hirundo rustica* were negatively correlated with energy delivery rates to their brood.

Swennen *et al.* (1989) found that Oystercatchers *Haematopus ostralegus* faced with decreasing lengths of low tide periods for feeding could increase their feeding rate both by increasing the amount of time which they spent feeding and by increasing their intake rate during feeding periods. The latter was accomplished by reducing search time and handling time. Only part of this was due to an increase in the breadth of the diet to include more common and easily handled, but less profitable prey. Whether or not Arctic terns have this option is doubtful. Further south in their range, on the Farne Islands, where daylength in summer is approximately 18 hours, they already spend a very large proportion of their day foraging (54 - 100% of daylight hours. Pearson 1968) and appear to have little leeway in which to increase their foraging efficiency. On Shetland and Orkney, where daylength in June is longer (approximately 21 hours) they may be less constrained by the time available for foraging.

5.4.3. Effects of weather on chick provisioning

The perceived effects of rainfall and windspeed on chick provisioning were few, perhaps because weather variables were either daily means (windspeed) or summed over a whole day (rainfall) and thus do not allow for variation within each day. Terns probably respond to weather (if at all) on a finer scale than this, adjusting their behaviour or experiencing effects on their foraging performance according to actual conditions at the time. Three studies of foraging terns which have measured weather variables concurrently with foraging performance have shown windspeed to have effects (Dunn 1973b, Taylor 1983, Safina & Burger 1988). However, other studies, which have utilised daily weather statistics have also shown effects of windspeed (Dunn 1975) and rainfall (Becker *et al.* 1985) albeit indirectly.

Neither rainfall nor windspeed had any apparent effect on the proportion of non-sandeels in the diet of young chicks, but there was a significant effect of windspeed on the size of sandeels caught in 1987 and 1989, and of rainfall in each year. The size of sandeels caught increased with both increasing rainfall and windspeed, but the magnitude of the effects was small and perhaps insignificant biologically, since the significance of each trend lay in the numbers of very small and very large sandeels caught, each of which were rare in the diet in all conditions. The only other effects were shown by terns feeding broods of over one week old on Orkney in 1989, when increasing rainfall led to a decrease in feeding frequency, perhaps associated with the increase in sandeel size noted above, since the rate of provisioning with energy or mass of food remained unchanged. Also in this group of birds, increasing windspeed was associated with a decrease in mean trip length.

The small amount of evidence which there is from these data suggests that the effects of increasing windspeed and rainfall (if any) are positive as far as foraging performance is concerned, although they obviously will have other, negative, effects on chicks through increased chilling and thermoregulatory costs.

The direct effects of windspeed on foraging Arctic terns have not been investigated, but Anon. (1968) reported that the growth rate of Arctic tern chicks was not retarded by strong winds whereas growth was greatly reduced in roseate terns. Dunn (1975) examined the effects of windspeed and other environmental factors on the growth of common, roseate and sandwich (*Sterna sandvicensis*) terns and found that windspeed had a depressive effect on the growth of common tern chicks in some years, notably when the range of windspeeds experienced by foraging birds was large. The effect on roseate terns was greater, a 10 knot increase in wind strength depressing growth by 67%, but he found no effect on growth of sandwich terns. The indirect effects of weather, in this case rainfall, were also studied by Becker *et al.* (1985), who showed that clutch-size in common terns nesting on islands in the Wadden Sea was inversely related to rainfall over the 5 days prior to laying. Furthermore, they found that this was not the case for birds nesting on the coast, which are able to exploit alternative food sources less affected by weather and available for longer periods than the marine prey upon which island birds depend. LeCroy & LeCroy (1974) and Feare (1976) also found rainfall deleterious to the rate at which tern chicks were fed. Dunn (1973b) examined the direct effects of windspeed and sea surface conditions on foraging common and sandwich terns. He found that prey capture rate was positively correlated with both windspeed and surface conditions, and that each of these affected capture rates independently. He went on to suggest that optimal windspeeds may exist for foraging terns, due to the beneficial effects of low windspeeds on steady hovering and thus their ability to remain unperceived by their prey. Since Arctic terns are the most pelagic and offshore of the palearctic terns they are likely to exhibit a higher optimum windspeed than other species (Uttley *et al.* 1989a).

As Safina & Burger (1988) pointed out, 'variability in the physical aspects of the ocean can affect fish abundance and location'. They showed that fish went deeper as water clarity increased, a change interpreted by them as a predator avoidance strategy. However, it could equally be a response to changes in the distribution of plankton, and terns foraged more successfully in less clear waters. Such an effect could explain the positive relationship which Dunn (1973b) found between sea surface conditions and capture rate. However, in their study Safina & Burger (1988) found that prey fish (primarily sandeels *Ammodytes* sp. and anchovies *Anchoa* sp. (Safina *et al.* 1988)) went deeper as windspeed and surface choppiness increased, and this was associated with a decrease in the success rate of plunge dives. These studies show that the inter-relationships between predators, their prey and physical environment are both extremely important and complex. Variations in windspeed and rainfall may influence foraging patterns through direct effects on the behaviour of foraging birds (*e.g.* Taylor 1983) and through changes in the behaviour of their prey (Safina & Burger 1988).

The effects of physical variables on predator-prey relationships are difficult to generalise, even within a relatively small group, such as piscivorous seabirds. Different prey species may behave in radically different ways, partly because their behaviour is more likely to have evolved in response to their fish predators than to seabirds (Dunn 1972).

6. THE ENERGY EXPENDITURE OF FREE-LIVING ARCTIC TERNS

6.1 Why Study Energetics?

The elucidation of the factors shaping avian reproductive strategies has been a major preoccupation of ornithological researchers. Lack's (1968) contention that food availability is of prime importance has been particularly influential, and has stimulated an enormous amount of research over the past twenty years, most of which has concluded that his hypothesis is correct (Martin 1987). Having accepted the role of food supply in determining such features of avian reproduction as laying dates, clutch sizes and growth rates, we must explore how food availability is translated into reproductive strategy. As Drent & Daan (1980) framed the question, what is 'the substrate of decision' upon which individuals rely?

The concept of parental effort has become central to the study of the limits to reproductive output (Winkler and Wilkinson 1989), and in particular to how variation in effort can result in different costs to the parents in terms of their lifetime fitness (Williams 1966, Charnov & Krebs 1974, Drent & Daan 1980, Nur 1984a, 1988, Winkler & Wilkinson 1989). Energy expenditure has come to be seen as one of the most promising measures of reproductive effort and costs (Hails & Bryant 1979, Drent & Daan 1980) because it is a direct, tangible and meaningful measure of many aspects of parental effort and may conceivably be linked directly to fitness through its interplay with parental body condition and food requirements.

Drent & Daan (1980), following the reasoning of Haartmann (1954) and Royama (1966b) postulated that birds were limited by physiological constraints to a 'maximum sustainable work load' beyond which they lost condition and incurred consequent costs. Having explored the available evidence they concluded that there exists a maximum sustainable work load for all parent birds of approximately 4 x basal metabolic rate (BMR). Although it is doubtful whether energy expenditure alone will adequately describe parental effort and its consequent costs (Bryant 1988, Winkler & Wilkinson 1989), the estimation of energy expenditure of breeding birds remains a powerful means of measuring parental effort.

The utility of energy expenditure is not limited to its use in investigating the adaptiveness of various reproductive traits. It is also of importance to those who wish to explore the demands of birds upon their environments, their role within communities and the impact of environmental changes on population dynamics (Kendeigh *et al.* 1977, Wiens 1984). Seabirds have been the subject of many such studies (reviewed in Wiens 1984) since their marine environment has frequently been seriously perturbed by human activities such as fishing, and because they often occur in large discrete breeding colonies which facilitates the study of population energy flows.

The aim in this aspect of the study was to carry out a pilot project to examine the feasibility of measuring and comparing the daily energy expenditure of Arctic terns breeding on Shetland, where breeding success was low and foraging conditions poor, with Arctic terns breeding on Coquet Island and Orkney, where breeding success was good and no food shortage was evident. The results were to be examined in the context of differences in foraging rate, adult weight loss and breeding success.

6.2. Estimation of energy expenditure.

The energy expenditure of free-living birds may be estimated either indirectly, using time-activity budgets converted to energy expenditure using activity costs, or directly, using the doubly-labelled water (DLW) technique. At this point it may be useful to introduce some commonly used terminology which will be followed in this chapter. Basal metabolic rate (BMR) refers to the level of energy expenditure required for maintenance when the subject is in the thermoneutral zone *i.e.* incurring no costs of thermoregulation, inactive, and in a post-absorptive state *i.e.* incurring no costs of digestion. Field metabolic rate (FMR) is the daily rate of energy expenditure (kJ / day) of a free-living animal involved in normal daily activities, and comprises BMR plus the energy costs of thermoregulation, activity and digestion. Kendeigh *et al.* (1977) produced equations for predicting 'existence metabolism' (EM) of non-passerines, which encompasses BMR, thermoregulatory costs, specific dynamic action and costs of locomotion within a cage, for birds maintaining constant mass. Their equations also provided for different temperature and photoperiod regimes.

6.2.1. Time-activity budget method.

The conversion of time-activity budgets into estimated energy expenditure requires that the energetic cost of each activity be measured or predicted. Predictions of energy cost may be made either by allometric equations based on body mass, or as multiples of BMR, which may itself be either measured or predicted. Actual measurement of energetic cost may be made either by respirometry or by the DLW technique and such measurements have been performed on free-living and captive birds.

Predictive equations have been developed for a variety of the components of total energy expenditure and these can be divided into four main areas: basal metabolic rate; existence metabolism; locomotion; and other activities *e.g.* egg production, incubation and moult.

Various models exist for the prediction of BMR. Lasiewski & Dawson (1967) provided an allometric equation (based on body mass) to predict BMR in all non-passerines, including seabirds. Aschoff & Pohl (1970) refined this to allow for the circadian rhythm in measured BMR, it being higher during the active phase than the resting phase. Ellis (1984) showed that the BMR of seabirds was generally elevated with respect to the levels predicted by these equations and provided an equation based solely on data from seabirds. Weathers (1979) suggested that BMR was a function of breeding latitude, birds breeding at higher latitudes having higher BMR, and this pattern is indeed found in seabirds (Ellis 1984, Gabrielsen & Mehlum 1989), many of which breed in the Arctic and Antarctic regions. Since the equations of Lasiewski & Dawson (1967) and Aschoff & Pohl (1970) are based mainly on birds of temperate and tropical latitudes they would not therefore be expected to apply to seabirds as a group. A further influence on BMR appears to be peak power requirements as indicated by flight mode, foraging method and, indeed, ambient temperature through its effect on thermoregulatory costs

(Ellis 1984, Gabrielsen & Mehlum 1989). Ellis (1984) proposed that elevated BMR allows a greater peak power output, such that birds with an energetic flight mode *e.g.* flapping versus gliding or energetic foraging method *e.g.* plunge diving versus surface dipping (Ashmole 1971) require a higher BMR.

Although BMR is an important component of energy requirements it is seldom the case that free-living birds do not incur further metabolic costs in addition. It is therefore of little use in the estimation of energy consumption of free-living birds, unless the costs of other activities are being estimated relative to BMR (*e.g.* A.E. Burger 1981). EM may be a useful measure of the energy expenditure of seabirds at the nest, but it still suffers from the limitation that it cannot be adjusted for the affects of latitude and lifestyle on BMR. Birt-Friesen *et al.* (1989) provided a predictive allometric equation for the metabolic rate of seabirds at the nest which may be more useful for researchers of seabird energy expenditure. While they did not find the expected difference between the equations for seabirds from cold- and warm-water regions, their sample size was small (five species in each group).

The prime mode of locomotion in birds is flight, but amongst seabirds two others demand attention: swimming *e.g.* Kooyman *et al.* (1982), Davis *et al.* (1983) and Nagy *et al.* (1984); and walking *e.g.* Le Maho & Dewasmes (1984). However, at present no allometric equations have been developed for predicting the cost of these activities and any predictions must be made relative to BMR on the basis of previous studies.

The cost of flight has been approached both theoretically and empirically on free-ranging and captive birds. Theoretical studies of the cost of flight rely on aerodynamic theory to predict power requirements in various flight modes and for birds of different design *e.g.* Tucker (1973), Greenewalt (1975), Pennycuick (1975, 1989). Oxygen consumption during flight may be measured in captivity using birds in wind-tunnels wearing masks *e.g.* Berger *et al.* (1970), Tucker (1972) and Baudinette & Schmidt-Nielsen (1974). However, this technique does not allow for ways in which free-ranging birds might reduce the cost of flight as suggested by Greenewalt (1975) *e.g.* aerodynamic adaptations (Flint & Nagy 1984) or modifications of flight technique e.g. soaring (Pennycuick (1983), ground effect (Withers & Timko 1977) and hovering (Withers 1979). The only study of the cost of flight in a free-ranging seabird, on the sooty tern *Sterna fuscata* (Flint & Nagy 1984), did indeed show that the cost of flight, as measured by the DLW technique, was substantially less than predicted from wind-tunnel or aerodynamic studies, and this has also been found in studies of highly aerial passerine species (LeFebre 1964, Utter & LeFebre 1970, Hails 1979). A further complicating factor in predicting the cost of flight is the interspecific variation in the speed of flight (Flint & Nagy 1984), although various possibilities exist for predicting optimal flight speed (Schnell & Hellack 1979). Birt-Friesen *et al.* (1989) produced a tentative equation for the cost of flight based on studies of free-living seabirds but their sample size was too small to examine differences between species using primarily flapping and primarily gliding flight.

The direct daily energetic cost of egg production is relatively easy to model, using information on the number of eggs produced, their caloric value and the phenology and efficiency of their production (Ricklefs 1974, Wiens 1984). However, such models do not take into account behavioural changes which may be associated with egg formation, such as the possible need to utilise different foraging strategies to collect foods rich in specific nutrients *e.g.* sulphur-rich amino acids, or reduced activity levels in species where the female is fed by the male during the pre-laying period.

The energy cost of incubation varies widely according to factors such as the speed of egg development, the length of incubation bouts and the microclimate experienced by the incubating bird (Walsberg 1983), but it has been measured in a variety of species by the DLW technique *e.g.* Ricklefs *et al.* (1986); by mass loss in fasting seabirds *e.g.* Croxall (1982), Croxall & Ricketts (1983), Weimerskirch (1990); by volumetric techniques e.g. Grant & Whittow (1983), Brown & Adams (1984); and by heat exchange methods *e.g.* Kendeigh 1963, Mertens (1980).

6.2.2. The doubly-labelled water method.

The doubly-labelled water method for estimating carbon di-oxide production, and hence energy expenditure, rests upon the observation that the oxygen of body water is in isotopic equilibrium with the oxygen of respiratory carbon dioxide (Lifson *et al.* 1949). It is a direct measure of energy expenditure and integrates energy expended on all activities. Because of these two attributes the method has been seized upon as a much better tool with which to investigate energy expenditure than the traditional methods based on extrapolations from either laboratory or theoretically derived estimates of energy consumption. Body water is labelled by injection of deuterium (D) and oxygen-18 (^{18}O) in heavy water. As a result of the equilibrium noted above, ^{18}O is lost from the body as either respiratory carbon dioxide or water. Loss of ^{18}O as water can be independently estimated by the loss of D, which is lost by this route only. Thus the differential turnover of ^{18}O and D may be used to measure carbon dioxide production directly (Lifson & McClintock 1966). This can be converted into energy expenditure by using a constant for the heat value of $1cm^3$ CO_2 which is a function of the respiratory quotient (Brody 1945) of the food consumed.

The field and laboratory protocols have recently been described by Tatner & Bryant (1989), and the validity of the six major assumptions associated with the theory (Lifson & McClintock 1966) have been discussed by Nagy (1980). Tatner & Bryant (1989) also reviewed the validation studies to date and found that the discrepancy between DLW measured carbon dioxide production and that measured by volumetric or energy input/output measurements was generally less than 10% for vertebrates. These reviews of the method have shown that the DLW technique is a reliable and robust measure of the energy expenditure of free living animals. To give a meaningful measure of typical metabolic costs it is essential that the animal does not respond to the technique in such a way that its energy expenditure is abnormal. Such a situation could arise through the direct effects of stress on metabolic rate, or indirectly through its effect on behaviour.

Briefly, the DLW technique requires that the animal be captured and injected with labelled water which is allowed to equilibrate with body water. A blood sample is then taken, to establish the initial levels of ^{18}O and D, after which the animal is released. After a set time-period the animal is recaptured and a repeat blood sample is taken to establish the isotope levels at the end of the period of measurement. The figure for carbon dioxide production which is calculated represents the average metabolic rate for the period (Lifson & McClintock 1966) and is dependent on the behaviour of the animal between the initial and final blood samples. Since BMR exhibits a diurnal cycle (Aschoff & Pohl 1970) the measuring period is set at a multiple of 24 hours so that the value of energy expenditure obtained is not biased by the inclusion of a disproportionate amount of either the resting or active phases *i.e.* it is a measure of daily energy expenditure (Tatner & Bryant 1989). Two other pieces of information are necessary to calculate carbon dioxide production: body water content and natural isotopic abundance. The former may be calculated by either carcass analysis or by the isotopic dilution method (Pace *et al.* 1947, Nagy & Costa 1980) which utilises the isotopic concentration at equilibrium to measure dilution space. *i.e.* the total volume of body water into which the injectate dilutes. Natural isotopic abundance is measured from blood samples of uninjected animals.

6.3. Methods.

The field metabolic rate (FMR) of Arctic terns was measured in 1988 at three sites and at two stages of the breeding season. Measurements were made on adults feeding chicks in the first week of life at Shetland (Mousa) (27-29 June) and at Northumberland (Coquet Island) (20-21 June) where previous studies (Monaghan *et al.* 1989a) had already shown food supply to be adequate for young to be reared successfully. Later in the season, measurements were made on adults feeding chicks close to fledging at Orkney (Papa Westray) (9-12 July), another site where food appeared sufficient for successful breeding by terns (see chapter 5).

6.3.1. Trapping Arctic terns.

Arctic terns were trapped whilst feeding chicks using box-traps fitted with a drop-lid. The traps were constructed out of 13mm wire mesh and placed around the nests during incubation, without the lids on, to accustom the adult birds to them. The traps caused very little disturbance, being essentially similar to the enclosures put up around nests to prevent chicks from wandering (2.2). When the time came to catch the birds, the lids were fitted, such that half of the opening at the top was covered whilst the other half could be shut rapidly by the observer in the hide pulling on a length of cord attached to the hinged lid. The birds were captured when they entered the traps to feed their chicks.

All of the birds were fitted with a numbered metal BTO ring and their wing-lengths, head and bill lengths and weights were measured and recorded. After processing for DLW (6.3.2) each bird was individually marked on the head with typewriter correction fluid and permanent coloured marker pen and released. Where no initial blood sample was taken (6.3.2) birds were released in less than five minutes after capture.

6.3.2. Doubly labelled water administration and initial blood sampling.

Once the birds had been captured and processed each was injected intra-peritoneally (under licence from the Home Office) with a previously calculated dose of DLW from a 1ml sterile syringe. The dose rate was based on predicted fractional turnover rates of $K_O=0.04995$ and $K_D=0.03815$, which were calculated from the relationships between fractional turnover rates and body mass in breeding birds (Tatner & Bryant 1989, equations 8 and 9); it was calculated to be 0.9ml of DLW (14.5 atom% ^{18}O and 5.04 atom% D) using equations 12 and 13 from Tatner & Bryant (1989). Extreme care was taken not to damage any internal organs with the syringe needle and not to lose any injectate via the puncture when withdrawing the needle. As a precaution against infection the area of skin around the puncture was swabbed with sterile cotton wool soaked in absolute alcohol before and after the injection. The time of injection was noted together with details of capture time, biometrics, individual colour mark (6.3.1) and sex (if known from nest-sponging, see 2.3) on specially prepared data sheets. The first five birds caught on Coquet Island were held for one hour in a cloth bag to allow the injectate to equilibrate with body water (6.2.2). At the end of this time an initial blood sample was obtained from the femoral vein. After swabbing the leg with absolute alcohol the vein was punctured with a sterile hypodermic syringe needle and the oozing blood was collected in graduated 10 microlitre heparinised pipettes (Vitrex) which were then sealed by drawing off the ends under a flame from a butane gas torch. Up to ten of these tubes were collected from each bird. However, it appeared that holding the birds captive for this length of time severely affected their subsequent behaviour, indeed two of the five, which were members of the same pair, deserted their young. Since it is a prerequisite for the successful use of the DLW method that the birds' behaviour is not affected, the remaining birds were released immediately after injection, without an initial blood sample being taken. A mean initial concentration was calculated from those birds which were held, and applied to the rest of the subjects. This latter method was also used in Shetland and Orkney and has previously been used by Ricklefs & Williams (1984).

In addition to the experimental birds which were injected and then released, with or without an initial blood sample, 5 birds (one on Coquet, two on Shetland and two on Orkney) were captured and blood sampled at the same time as the experimental birds, but without injection, in order that natural abundance levels of ^{18}O and D could be determined. These birds were released immediately after blood sampling.

6.3.3. Behavioural observations and final blood sampling.

The nests of injected adults were kept under continuous observation for all of the daylight hours from hides, and full time-budget information was collected for each experimental bird and its mate, except for one nest on Coquet Island (AT5) which could not be seen sufficiently clearly. The data recorded were the number of feeds brought to the chicks by each bird, and the total amount of time spent by each bird in its territory. In addition, comparable data were collected from non-experimental birds from within the colony as part of other aspects of this study.

After approximately 24 or 48 hours had elapsed since the time of the initial injection (6.3.2) the experimental birds were recaptured and a second blood sample was taken in a similar manner to the first. In the case of one individual on Shetland (AT10) a second sample was obtained after 24 hours and a third after 48 hours. Multiple samples from one bird can be used to calculate several estimates of FMR.

6.3.4. Analysis of blood samples.

Analyses of the blood samples to determine $^{18}O/^{16}O$ and D/H ratios were carried out in the winter and autumn of 1989 at the Scottish Universities Research Reactor Centre, East Kilbride. The technique, which has been fully described by Tatner & Bryant (1989), involved cryogenic isolation of pure carbon dioxide and hydrogen gases from the blood samples, performed under a complete vacuum to prevent contamination from the atmosphere. The concentration of the minor isotope *i.e.* ^{18}O or D was then determined by isotope ratio mass spectrometry (IRMS) on a VG-ISOGAS SIRA-10 (^{18}O) or a VG-ISOGAS SIRA-9 (D).

6.3.5. Calculation of field metabolic rates.

The initial output from the IRMS consisted of a 'delta value' proportional to the ratio of the minor isotope to the major isotope. To convert these 'delta values' to concentrations of minor isotope, standard samples of known dilution were run at the same time as the blood samples so that calibration equations could be produced (equations [1] and [2]).

$$\text{ppm } ^{18}O = (\text{delta} + 918.75) / 0.44 \qquad [1]$$

$$\text{ppm D} = (\text{delta} + 401.39) / 7.49 \qquad [2]$$

These equations were appropriate for calculating the isotope ratios of enriched samples, but for natural abundance samples, and for final samples from which the 'delta values' were close to natural abundance, more accurate equations appropriate to unenriched samples were obtained from geologists using the same equipment (equations [3] & [4]; T. Donnelly pers. comm.).

$$\textbf{ppm }^{18}\textbf{O} = [(1.012\ \text{delta} + 12.292)\ 2.0052] + 2005.2 \qquad [3]$$

$$\textbf{ppm D} = [(0.952\ \text{delta} - 51.98)\ 0.1559] + 155.9 \qquad [4]$$

Where time and the number of samples allowed, replicates were carried out and a mean 'delta value' was carried forward to calculate ppm.

From the isotope concentrations of the initial and final samples, and the estimates of natural abundance, the excess concentrations of ^{18}O and D above natural abundance were calculated. These excess concentrations, together with body water content and the duration of the experiment were all that was necessary to calculate the FMR of birds from which both initial and final blood samples had been taken [equations 5 to 9].

$$rCO_2 = [(N/2.08)(K_O - K_D)] - 0.015.K_D.N \qquad [5]$$

where rCO_2 = rate of production of CO_2 in mMol h^{-1}.

N = body water content.

K_O = fractional turnover rate of oxygen.

K_D = fractional turnover rate of hydrogen.

$$K_O = (\ln O^*_i - \ln O^*_f) / t \qquad [6]$$

$$K_D = (\ln D^*_i - \ln D^*_f) / t \qquad [7]$$

where O^*_i = initial excess ^{18}O concentration

O^*_f = final excess ^{18}O concentration

D^*_i = initial excess D concentration

D^*_f = final excess D concentration

$$ADMR = rCO_2 . 22.4/M \qquad [8]$$

where ADMR = average daily metabolic rate $cm^3\ CO_2\ g^{-1}\ h^{-1}$

M = average body mass of bird

$$FMR = ADMR \times M \times 24 \times 24.7 \qquad [9]$$

where FMR = field metabolic rate kJ day^{-1}

n.b. 24.7 = energy equivalent (J ml^{-1})of CO_2 for fish eating birds determined by Flint & Nagy (1984).

In practice however, equations 5 to 8 could not be used for all birds because of the lack of initial blood samples for some. The equation of Ricklefs & Williams (1984; equation 4) was used instead (equation [10]) since this allowed the use of those initial samples which were collected, in the calculation of ADMR for all birds.

$$\mathbf{ADMR = [(622.23\, WF) / t]\ [\ \ln(O^*_i/D^*_i) - \ln(O^*_f/D^*_f)]} \qquad \mathbf{[10]}$$

where WF = water fraction

The water fraction (WF) i.e the proportion of body mass consisting of water was calculated by solving equation [11] for each bird with an initial blood sample.

mix in bird =

$$\frac{(\text{body water vol. x nat. abund.}) + (\text{inj. vol.} + \text{inj. conc.})}{\text{water vol.} + \text{inj. vol.}}$$

injected volume = 0.9 ml

injected concentration = 145500 ppm ^{18}O

natural abundance = 1996.2 ppm ^{18}O (see 6.4.1)

This simplifies to:

$$\text{body water vol.} = \frac{130950 - (0.9 \times O_i)}{(O_i - O_{NA})}$$

$$\text{thus } \mathbf{WF = \frac{130950 - (0.9 \times O_i)}{(O_i - O_{NA}) \times M}} \qquad \mathbf{[11]}$$

where O_i = initial ^{18}O concentration

O_{NA} = natural abundance of ^{18}O

6.3.6. Estimation of FMR from allometric equations.

The time-budget data collected from the experimental birds were used in conjunction with allometric equations and measured BMR of Arctic terns (from M. Klaassen, Univ. of Groningen) to predict FMR on the basis of current knowledge of seabird energetics to see how closely these estimates fitted the actual FMR as measured by DLW. The equations used were for field metabolic rate for cold water seabirds using flapping flight (equation [12]), nest metabolism (equation [13]), metabolism at sea (*i.e.* not at nest) of seabirds not using gliding flight (equation [14], metabolism in flight in seabirds (equation [15]), (Birt-Friesen *et al.* 1989), and the cost of flight in the sooty tern (equation [16]) (Flint & Nagy 1984).

Field metabolic rate (kJ h^{-1})

$$\log y = 3.24 + 0.727.\log M \qquad [12]$$

Nest metabolism (kJ h^{-1})

$$\log y = 1.45 + 0.737.\log M \qquad [13]$$

Metabolism at sea (kJ h^{-1})

$$\log y = 1.89 + 0.662.\log M \qquad [14]$$

Metabolism in flight (kj h^{-1})

$$\log y = 1.86 + 0.748.\log M \qquad [15]$$

Metabolism in flight (sooty tern) (kJ h^{-1})

$$y = 4.77.BMR \qquad [16]$$

where y = metabolic cost

M = mass in kg

BMR = 77 kJ day^{-1} = 3.21 kJ h^{-1}

Four separate methods were used to calculate FMR, as follows.

a) FMR was estimated from equation [12] using only the mass of the bird.

Using equation [13] to calculate energy expenditure at the nest, three different predictions of FMR were made from the time-budget information, with energy expenditure at sea being estimated by:

b) equation [14]

c) equation [15]

d) equation [16]

In the case of methods c and d it had to be assumed that all of the time away from the colony was spent in flight. This may be a reasonable assumption about the terns' use of their time away from the colony, since terns forage in flight and seldom land on the water surface (pers. obs.); however, they may form large roosts on land at certain times.

6.4. Results

The traps proved very effective, with 18 birds being caught in all (tab. 6.1); 11 of 14 available (see below) being recaptured approximately 24 or 48 hours later. Four birds were unavailable for recapture (tab. 6.1). Two out of nine adults captured on Coquet Island were members of the same pair and these deserted their young. Only one bird from each nest was captured after this, and no further desertions occurred. Of five birds captured initially on Orkney, the chick of one bird fledged and left the trap, whilst another died and its parents ceased to attend the nest after this.

Of the eleven birds for which final blood samples were available, only eight yielded energy expenditures; the analyses of three birds (AT10, AT14 and AT15) failed at the laboratory stage (tab. 6.1).

Table 6.1. Details of capture, biometrics and energy expenditure of arctic terns subjected to doubly-labelled water technique.

	1st Capture date	Wing (mm)	Head & bill (mm)	Mean* mass (g)	Initial sample ?	Retrapped ?	Time period (h)	ADMR (cm$_3$g$_{-1}$h$_{-1}$ CO^2)	FMR (kJ day^{-1})	Behavioural observations?	Notes
COQUET											
AT1	19.6.88	274	69	96.5	Y	Y	47.7	3.62	207.08	Y	
AT2	19.6.88	292	75	111.0	Y	Y	47.4	4.18	275.05	Y	
AT3	19.6.88	267		(92.0)	Y	N					DESERTED
AT4	19.6.88	276		(120.0)	Y	N					DESERTED
AT5	20.6.88	265	69	94.5	Y	Y	25.7	4.91	275.06	N	
AT6	20.6.88	285	73	97.0	N	Y	22.1	4.04	232.31	Y	
AT7	20.6.88	274	74	(106.0)	N	N					
AT8	20.6.88	266	72	105.0	N	Y	23.2	6.18	384.67	Y	
AT9	20.6.88	274	71	107.5	N	Y	24.4	4.75	302.70	Y	
SHETLAND											
AT10	27.6.88	285	74	98.5	N	Y	24.4			Y	NO RESULTS
AT11	27.6.88	295	74	98.0	Y	Y	24.3	7.43	431.64	Y	
AT12	27.6.88	277		(94.0)	N	N					CHICK DIED
AT13	28.6.88	276	71	(93.0)	N	N					
ORKNEY											
AT14	9.7.88	274	71	104.0	N	Y	47.8				NO RESULTS
AT15	9.7.88	288	68	101.5	N	Y	46.8				NO RESULTS
AT16	10.7.88	269	73	99.5	N	Y	48.3	9.64	568.45	Y	
AT17	10.7.88	281	76	(105.0)	N	N					CHICK DIED
AT18	10.7.88	279	76	(100.0)	N	N					FLEDGED

* Measurements of mean mass in brackets represent single mass measurements where birds were not recaptured and hence only weighed once.

6.4.1. FMR from the DLW method.

The natural abundances of ^{18}O and D were calculated using equations [3] and [4] respectively, with data from two birds for ^{18}O and three birds for D. The mean determined levels were 1996.2 ppm ^{18}O (from individual measurements of 1989.3, 2003.2) and 151.2 ppm D (s=1.3) (from individual measurements of 150.5, 150.4 and 152.7), both of which fall well within the range of natural abundances found in a variety of temperate bird species (Tatner & Bryant 1989).

The water fraction of four terns (AT1, AT2, AT4, AT11) from which an initial blood sample had been taken and successfully analysed for ^{18}O enrichment were estimated using equation [11] (oxygen analysis of the initial sample from AT5 failed and one of the six terns from which an initial sample had been taken (table 6.1) (AT3) was excluded from this calculation since some injectate oozed from the puncture after injection). The mean water fraction of these four birds was 0.632 (s=0.083) which is very similar to the mean of 0.63 reported by Tatner & Bryant (1989) for seven species investigated by carcass analysis and similar to the figure of 0.599 determined by Ricklefs & White (1981) for the closely related common tern *Sterna hirundo*, again using carcass analysis.

The initial ratio of excess ^{18}O to excess D required to calculate ADMR from equation [10] was determined using data from three birds (AT1, AT2, AT4) for which initial enrichments of both isotopes were determined (D analysis of the initial sample from AT11 failed, so it was excluded from this calculation along with AT5 and AT3). The calculated value of $\ln(O^*_i/D^*_i)$ was 1.12808 (s=0.01516). Despite the small sample of birds available the method appeared satisfactory since the coefficient of variation was small (1.3%).

The fractional turnover rate of oxygen (K_O) could be calculated for three birds (AT1, AT2, AT5) and averaged K_O = 0.08062 (s=0.01167) and K_D, the fractional turnover rate of hydrogen was estimated from three birds also (AT1, AT2, AT11), averaging K_D = 0.06375 (s=0.00231). These values were 61% and 60% respectively higher than those predicted and on which dosage rates were calculated (6.3.2). As a result of this higher than expected turnover rate, the final levels of ^{18}O and D came too close to background abundance in three terns (AT10, AT14, AT15) for their energy expenditure to be reliably estimated. Analytical errors have a greater effect upon calculated rCO_2 as final isotope levels approach natural abundance (Nagy 1980).

Energy expenditure was calculated using values of $\ln(O^*_f/D^*_f)$ in equation [10] along with the figures for water fraction and initial excess isotope ratio derived above, average body mass as estimated by the mean of measurements at the beginning and end of the experimental period, and the length of the experimental period. The latter was the period from the time of the last initial blood sample to the time of the last recapture blood sample for birds sampled initially, and was estimated as the period from the time of injection to the time of the last recapture blood sample minus one hour for equilibration for birds released without an initial sample being taken. The results of the analyses are shown in table 6.1.

Treating the Coquet Island birds as a discrete sub-sample, they had a mean FMR of 279.5 kJ day^{-1} (s=61.8, n=6). The Shetland bird, at the same stage of breeding, had a higher FMR of 431.64 kJ day^{-1}, whilst that of the Orkney bird feeding a 17 day old chick was still higher, at 568.45 kJ day^{-1}. Using an estimate of BMR of 77 kJ day^{-1} (M. Klaassen pers. comm.) the Coquet birds were working at 3.63BMR (s=0.80, n=6), with the Shetland and Orkney birds working at 5.61BMR and 7.38BMR respectively.

6.4.2. Time budgets.

Table 6.2 shows the proportion of time that each experimental bird and its mate spent attending their chicks, together with the feeds provided by each for the chick and the average rate of mass change of the experimental birds between capture and recapture. Figures 6.1 to 6.4 compare the behaviour of the experimental birds with that of control (uncaptured) birds at a similar stage of the breeding season in each colony. The small sample sizes did not allow the behaviour of experimental birds to be statistically compared with that of untrapped birds, but the data did allow tentative examination of the effect of the technique on the birds' behaviour. Except in Shetland, where the DLW birds spent considerably less time at the colony than untrapped birds, there was no suggestion that the procedure reduced or increased the amount of time which birds attended their chicks (fig. 6.1).

Table 6.2. Summary of time-budget data for doubly-labelled water birds and their mates.

Bird	Time between captures (h)	% time at colony *	no. of feeds *	rate of weight change (g day^{-1})
COQUET				
AT1	47.7	19.8 / 8.1	0 / 13	+ 1.5
AT2	47.4	29.2 / 8.5	6 / 2	+ 1.0
AT3	n/r	1.2 / AT4	0 / AT4	-
AT4	n/r	1.7 / AT3	1 / AT3	-
AT5	25.7			- 1.0
AT6	22.1	39.7 / 16.5	1 / 6	+ 6.0
AT7	n/r	0.1 / 0.6	0 / 2	-
AT8	23.2	8.9 / 17.0	2 / 7	- 2.0
AT9	24.4	56.5 / 24.2	0 / 7	+13.0
SHETLAND				
AT10	24.4	3.1 / 0.6	6 / 2	+ 3.0
AT11	24.3	2.6 / 43.9	0 / 2	- 6.0
AT12	lost chicks within 12 hours of capture			
AT13	n/r	0.3 / 21.4	0 / 20	-
ORKNEY				
AT14	47.8	2.9 / 0.3	33 / 20	- 1.0
AT15	46.8	3.8 / 0.0	22 / 43	+ 1.5
AT16	48.3	0.0 / 0.3	46 / 55	- 0.5
AT17	chick killed within 12 hours of capture			
AT18	chick fledged within 12 hours of capture			

* Figures to the left refer to the labelled birds, and figures to the right to their mates.

n/r - $D_2{}^{18}O$ bird not recaptured; all behavioural data gathered over 48 hour period after initial capture.

However, when the total amount of time for which chicks were attended was considered (fig. 6.2) *i.e.* by both the DLW bird and its mate, the chicks of experimental pairs were attended less than chicks of control pairs. When the number of feeds received by the chicks was examined it appeared that DLW birds with young chicks, *i.e.* on Shetland and

Figure 6.1. The proportion of time the injected birds spent at the colony in the period between release and recaptapture. The sex of each bird, male (M), female (F), or unknown (U) is given at the top of each histogram bar. An asterisk denotes birds subjected to both initial and final sampling. Also shown are the colony averages based on untrapped birds of known sex (horizontal lines) ± one standard error (vertical lines at right-hand side). Time budget data could not be collected for AT5, AT12, AT17 and AT18.

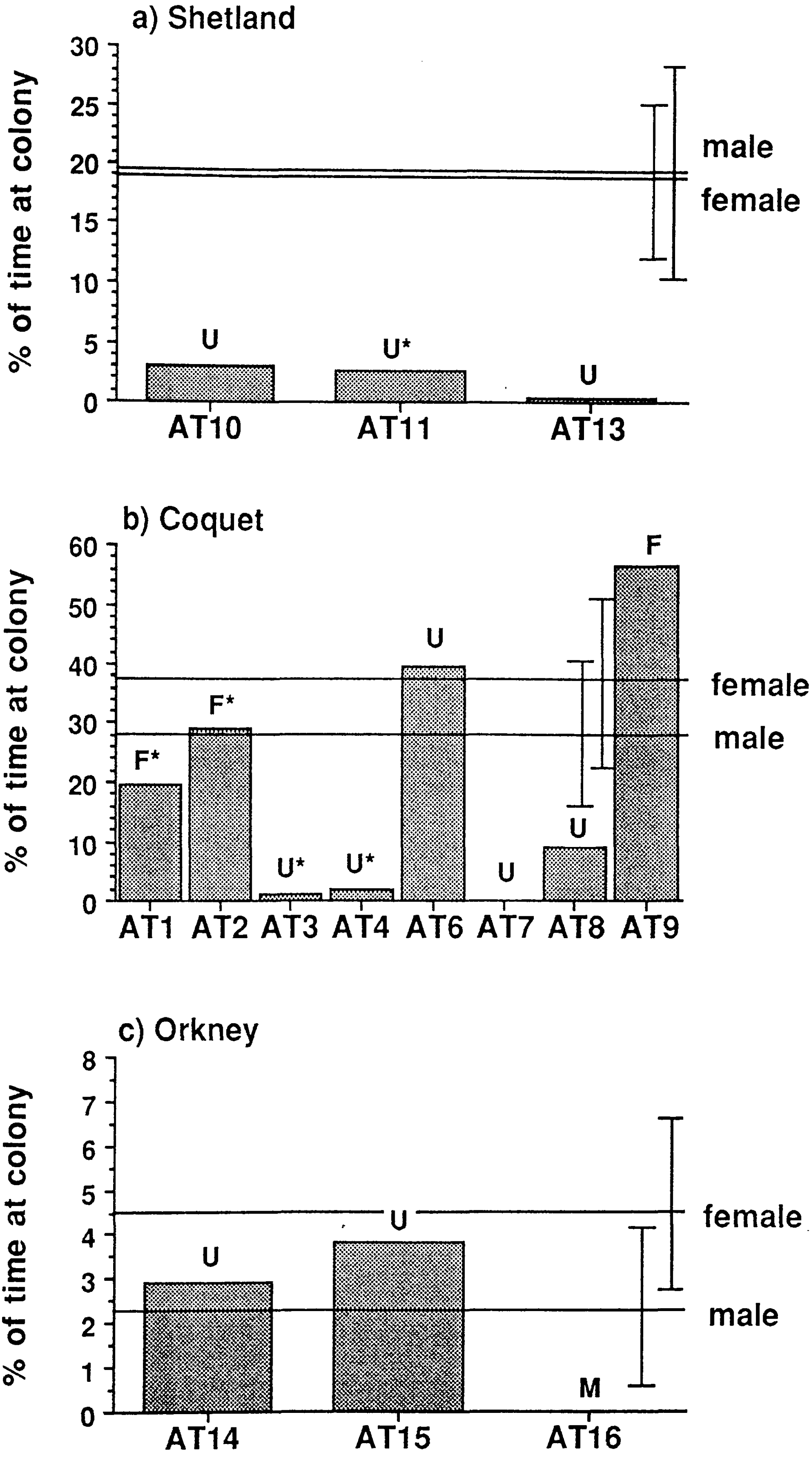
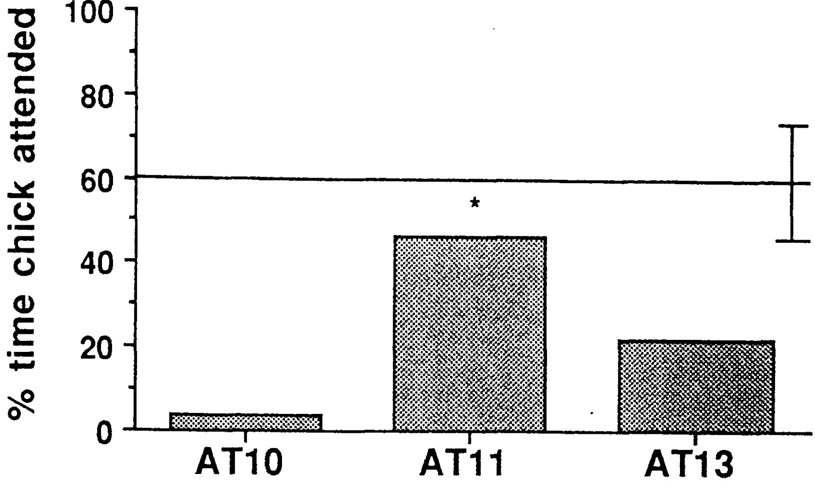
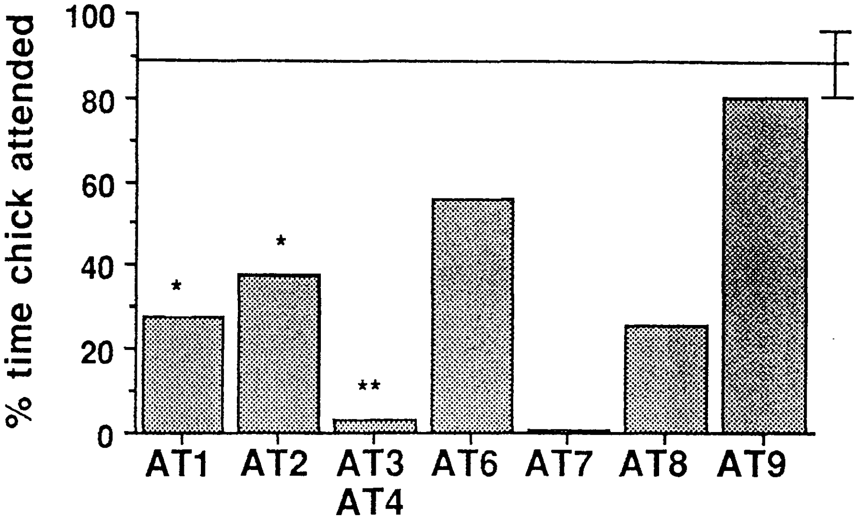

a) Shetland
% of time at colony
0
5
10
15
20
25
30
male
female
U
U*
U
AT10
AT11
AT13
b) Coquet
% of time at colony
0
10
20
30
40
50
60
female
male
F*
F*
U*
U*
U
U
U
F
AT1
AT2
AT3
AT4
AT6
AT7
AT8
AT9
c) Orkney
% of time at colony
0
1
2
3
4
5
6
7
8
female
male
U
U
M
AT14
AT15
AT16

Figure 6.2. The total time the chicks of the injected birds were attended by either parent during the period between release of the injected bird and its recapture. An asterisk denotes pairs where birds were subjected to both initial and final sampling. Also shown are the colony averages based on nests with untrapped birds (horizontal lines) ± one standard error (vertical lines at right-hand side). AT3 and AT4 on Coquet were mates, and both were sampled initially and finally. Time budget data could not be collected for AT5, AT12, AT17 and AT18.

a) Shetland



b) Coquet



c) Orkney

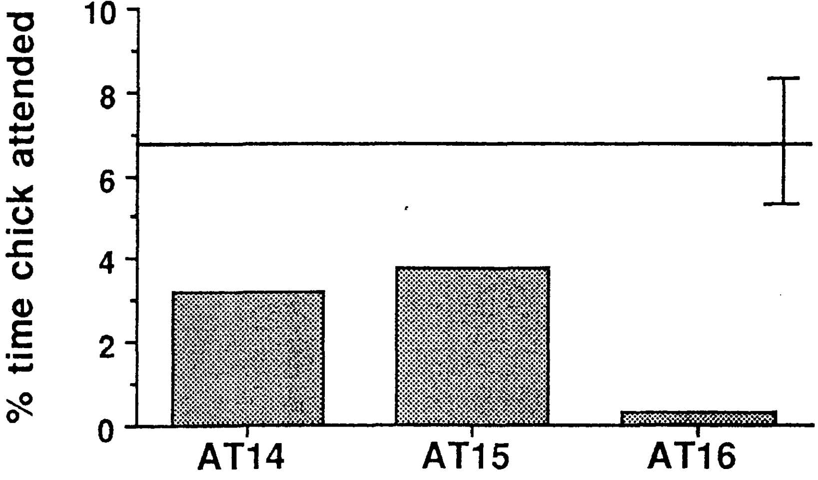


Figure 6.3. The number of feeds per hour given to the chicks by the injected birds during the period between release and capture. The sex of each bird, male (M), female (F), or unknown (U) is given at the top of each histogram bar. An asterisk denotes birds subjected to both initial and final sampling. Also shown are the colony averages based on untrapped birds of known sex (horizontal lines) ± one standard error (vertical lines at right-hand side). Time budget data could not be collected for AT5, AT12, AT17 and AT18.

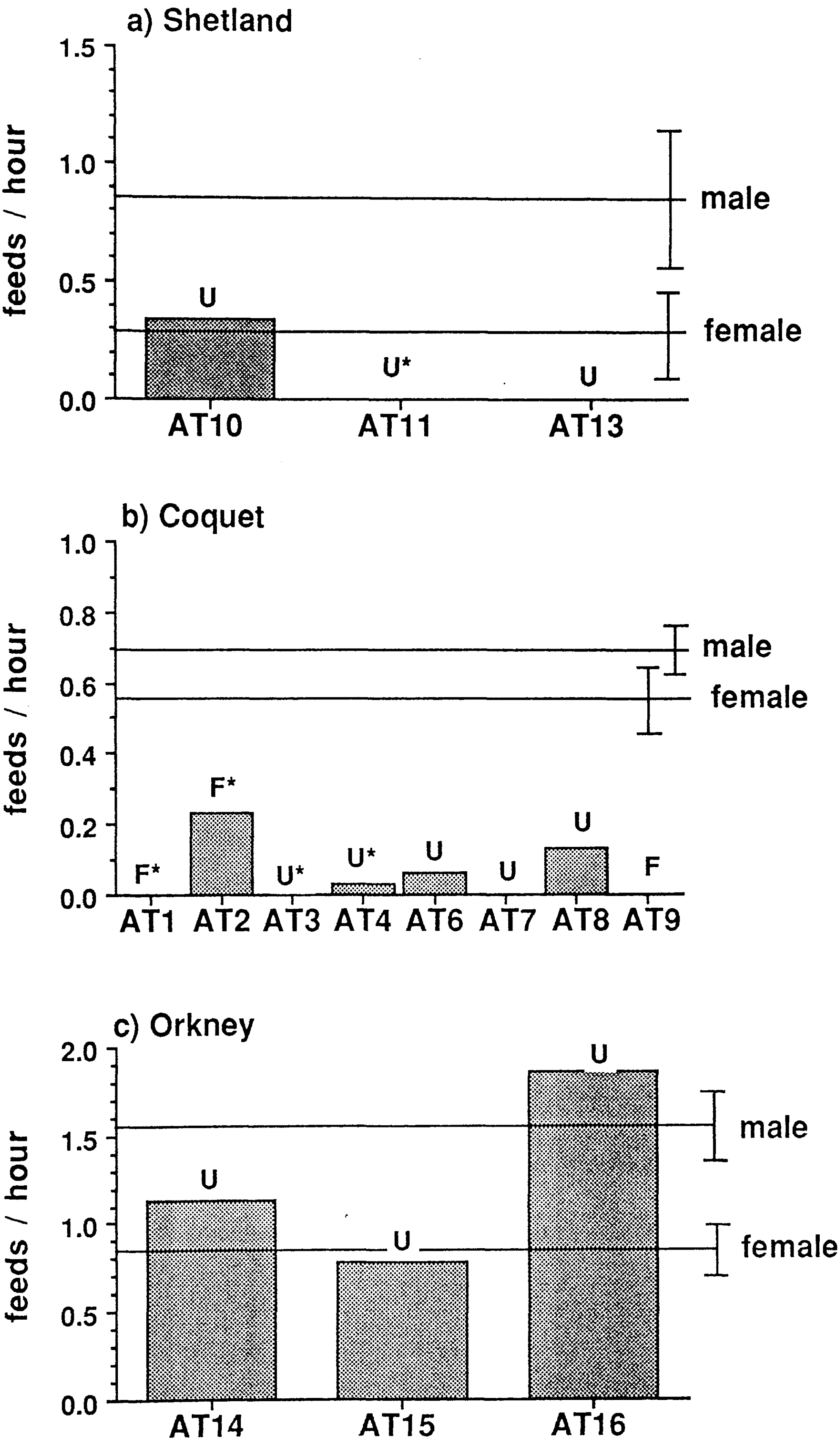
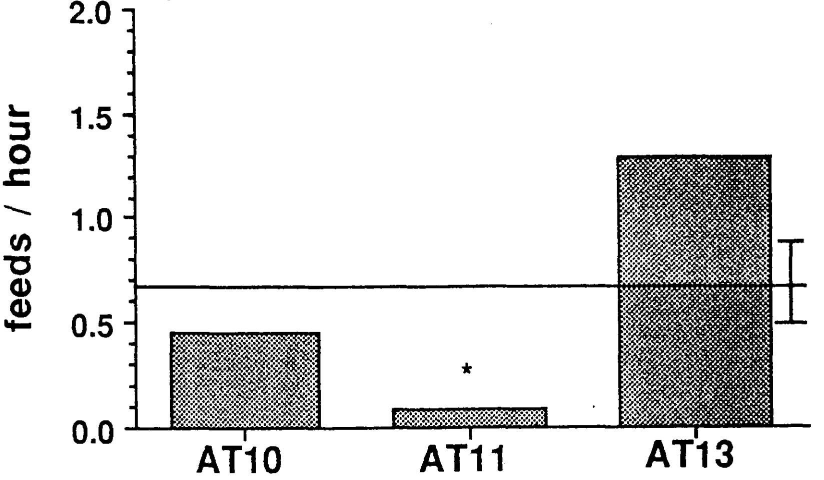
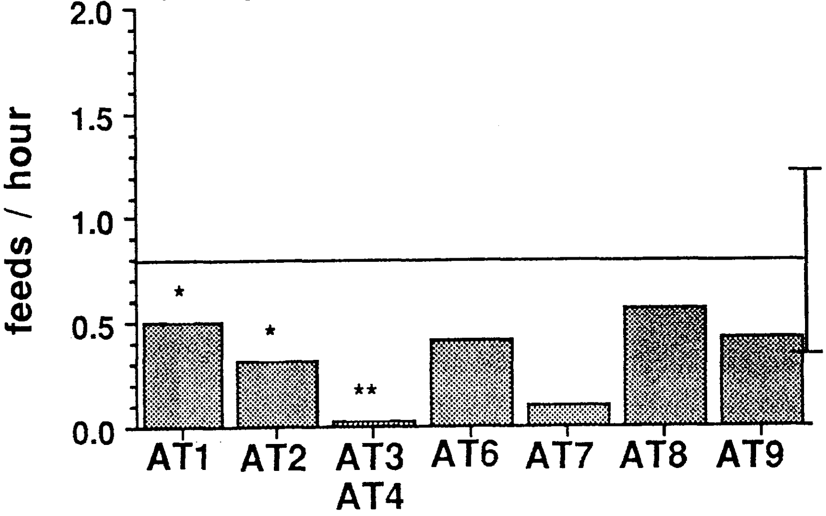

a) Shetland
feeds / hour
1.5
1.0
0.5
0.0
U
U*
U
AT10
AT11
AT13
male
female
b) Coquet
feeds / hour
1.0
0.8
0.6
0.4
0.2
0.0
F*
F*
U*
U*
U
U
U
F
AT1
AT2
AT3
AT4
AT6
AT7
AT8
AT9
male
female
c) Orkney
feeds / hour
2.0
1.5
1.0
0.5
0.0
U
U
U
AT14
AT15
AT16
male
female

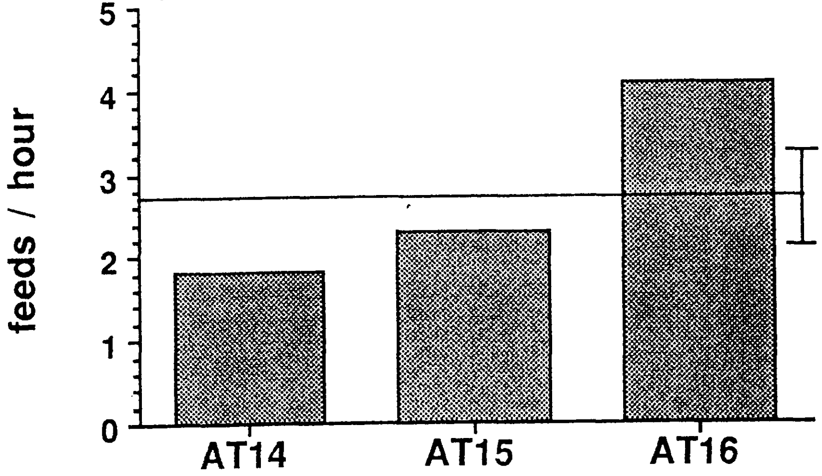
Figure 6.4. The total number of feeds per hour which the chicks of injected birds received from either parent during the period between the release and recapture of the injected bird. An asterisk denotes pairs where birds were subjected to both initial and final sampling. Also shown are the colony averages based on nests with untrapped birds (horizontal lines) ± one standard error (vertical lines at right-hand side). AT3 and AT4 on Coquet were mates, and both were sampled initially and finally. Time budget data could not be collected for AT5, AT12, AT17 and AT18.



a) Shetland



b) Coquet



c) Orkney

Coquet Island, fed their young less than control birds, whilst the provisioning rate of DLW birds with older chicks *i.e.* on Orkney was unaffected (figs. 6.3 and 6.4). In retrospect it appears that the disturbing effect of initial blood sampling was a negligible addition to the general disturbance of capture and injection.

6.4.3 Energy expenditure and behaviour.

The relationships between the birds' behaviour an their energy expenditure was examined within the sample of birds from Coquet. There was no relationship between either the percentage of time spent away from the colony, or the number of feeds given to the chick per day and energy expenditure (figs. 6.5a, b). This was not surprising given the small sample of birds available, but neither were there any suggestions of trends. Therefore it was not possible to estimate either metabolism at the nest or away from it on the basis of incremental energy expenditure with time or the metabolic cost of feeding young through incremental energy expenditure with feeding events. The lack of any relationship between time away and ADMR suggests that much of the time away from the colony by birds which were absent for a high proportion of the time was spent in low-cost activities *i.e.* not in flight or foraging, and birds did not incur energetic costs above those which they would have incurred at the nest. Neither was there any significant relationship between ADMR and weight change (fig. 6.5c). However, there was a very good relationship between the time birds spent away from the colony and weight change between release and recapture (fig. 6.6).

6.4.4.Estimating FMR from predictive equations and time budgets.

In addition to the measure of energy expenditure obtained from the DLW technique, it was also estimated by methods a to d using predictive equations [12] to [16] and the mass and time budget of each individual.

The estimates of FMR from time-budget data and allometric equations are

Table 6.3. Summary of time-budget data, DLW measured energy expenditure, and predicted energy expenditure using allometric equations.

Bird	Mean mass (g)	Time at colony (h)	Time at sea (h)	FMR (kJ day^{-1})	Predicted FMR (kJ day^{-1}) (% of FMR by DLW)			
					a	b	c	d
COQUET								
AT1	96.5	4.75	19.25	207.08	317.5 (153)	342.3 (165)	266.1 (129)	319.3 (154)
AT2	111	7.00	17.00	275.05	351.5 (128)	347.8 (126)	277.8 (101)	300.2 (109)
AT6	97	9.50	14.50	232.31	318.7 (137)	289.3 (125)	232.5 (100)	271.1 (117)
AT8	105	2.10	21.90	384.67	337.6 (88)	393.9 (102)	305.5 (79)	346.8 (90)
AT9	107.5	13.60	10.40	302.70	343.4 (113)	260.1 (86)	217.8 (72)	234.9 (78)
SHETLAND								
AT11	98	0.60	23.40	431.64	321.1 (74)	393.4 (91)	301.4 (70)	361.4 (84)
ORKNEY								
AT16	99.5	0.00	24.00	568.45	324.7 (57)	404.4 (71)	309.4 (54)	367.3 (65)

a - FMR calculated using equation 12 for field metabolic rate.

b - FMR calculated using equation 13 for metabolism at nest plus equation 14 for metabolism at sea.

c - FMR calculated using equation 13 for metabolism at nest plus equation 15 for metabolism at sea.

d - FMR calculated using equation 13 for metabolism at nest plus equation 16 for metabolism at sea.

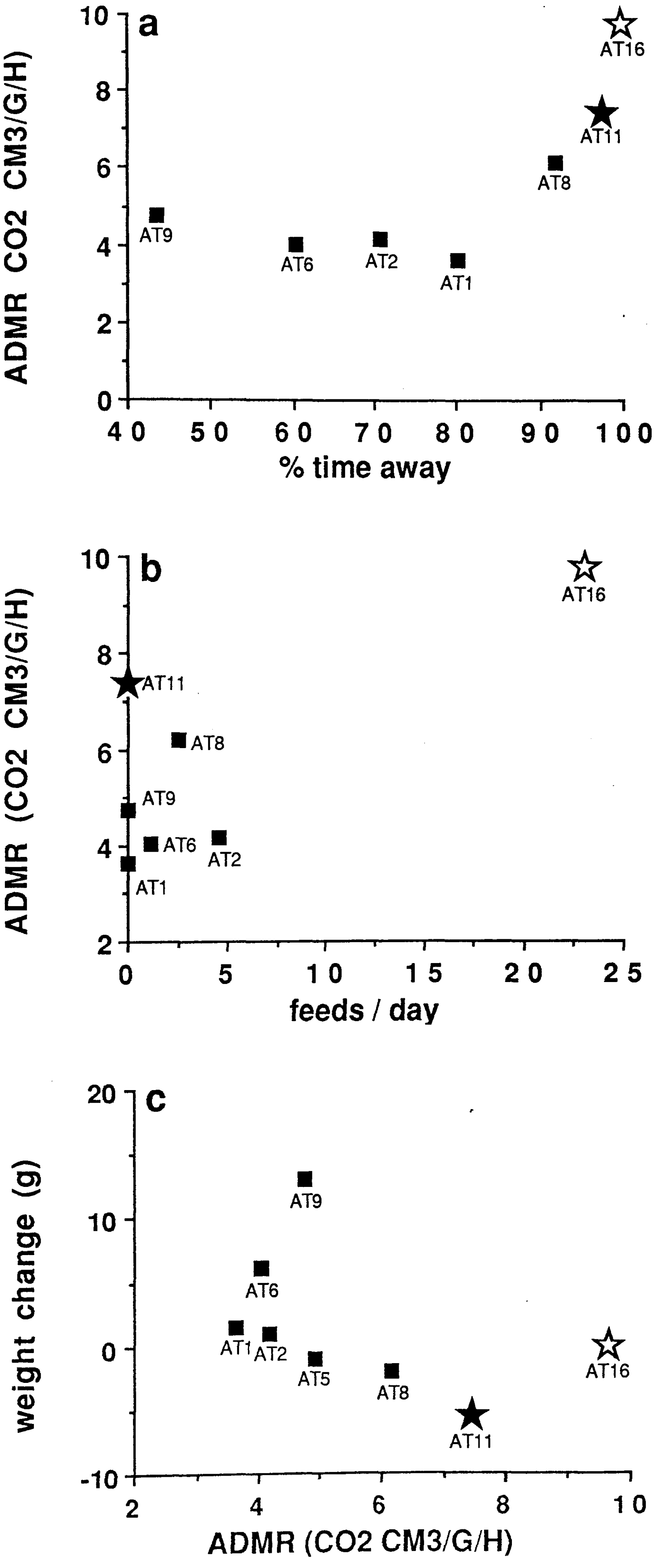
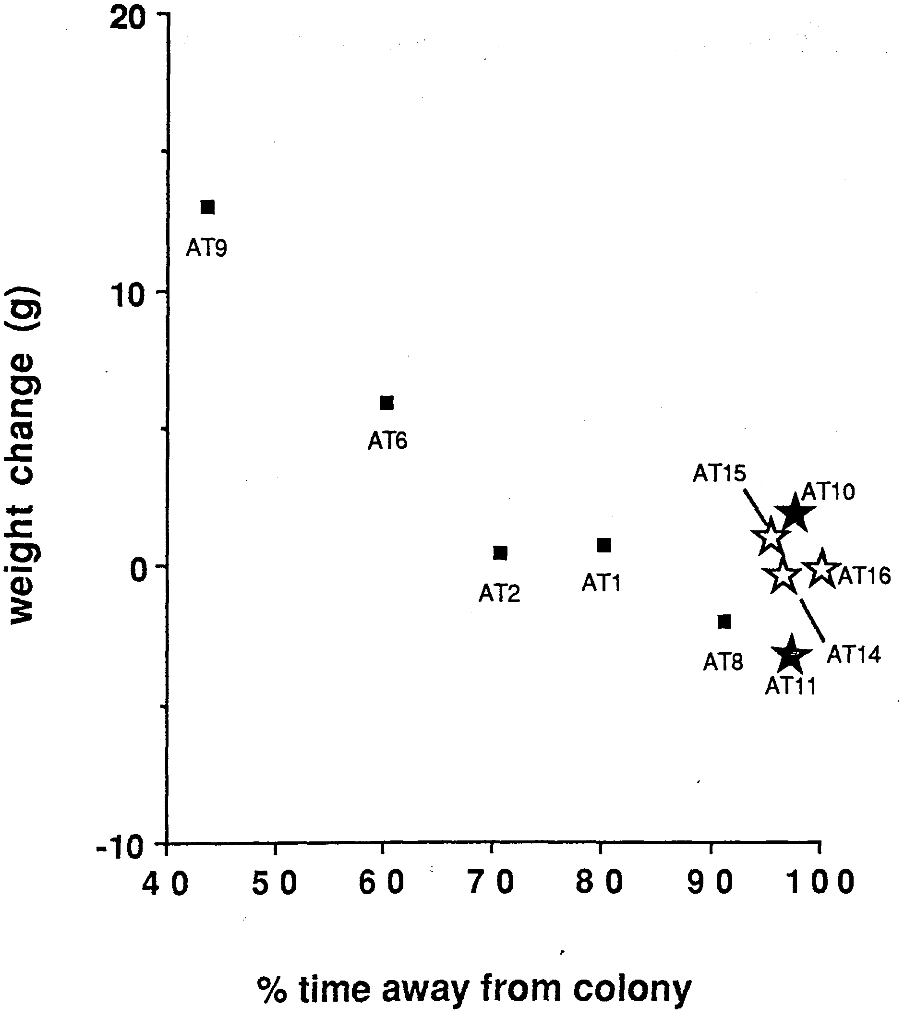

a
ADMR CO2 CM3/G/H)
10
8
6
4
2
0
40
50
60
70
80
90
100
% time away
AT16
AT11
AT8
AT9
AT6
AT2
AT1
b
ADMR (CO2 CM3/G/H)
10
8
6
4
2
0
5
10
15
20
25
feeds / day
AT16
AT11
AT8
AT9
AT6
AT2
AT1
c
weight change (g)
20
10
0
-10
2
4
6
8
10
ADMR (CO2 CM3/G/H)
AT9
AT6
AT1
AT2
AT5
AT8
AT16
AT11

Figure 6.6. The relationship between the time spent away from the colony by the injected bird and its weight loss over the period between its release and recapture. Squares = Coquet, solid stars = Shetland, open stars = Orkney.



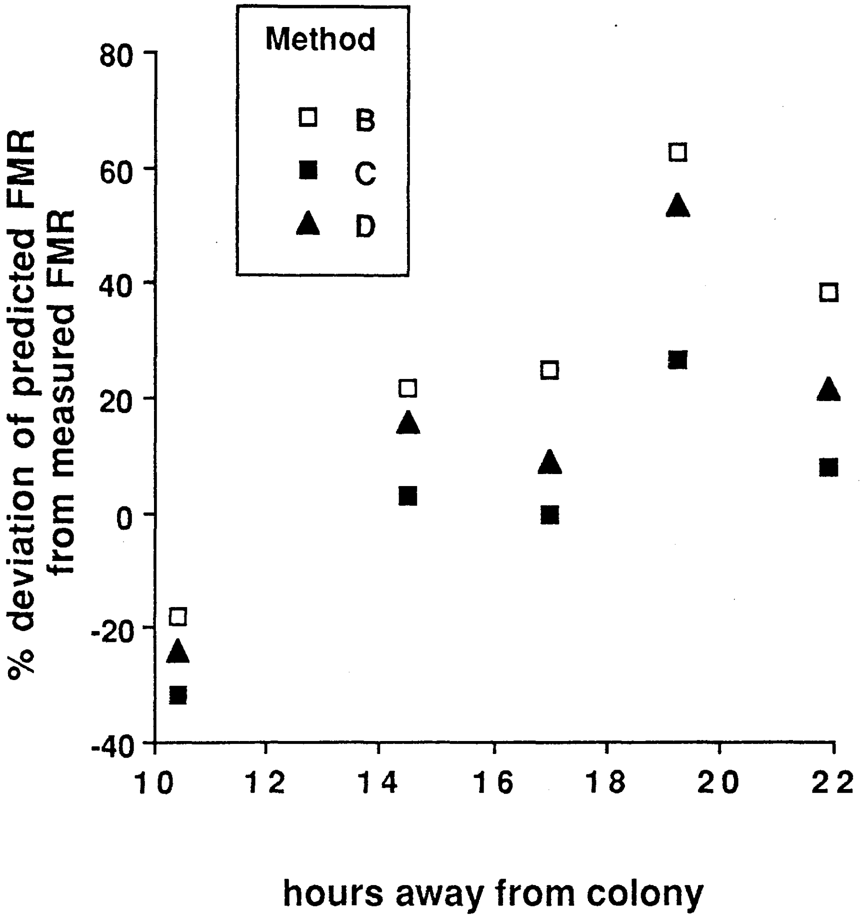
20
10
0
-10
weight change (g)
40
50
60
70
80
90
100
% time away from colony
AT9
AT6
AT2
AT1
AT8
AT15
AT10
AT16
AT14
AT11

shown for individual birds in table 6.3. DLW measured FMR is also shown for comparison.

FMR was estimated using equation [12] which was derived from data for non-gliding seabirds in high latitudes and which does not require information on the time-budgets of birds (method a) (tab. 6.3). For Coquet Island birds it gave a mean predicted FMR of 333.7 kJ day^{-1} (s = 15.1) of which the DLW measured value (279.5, 6.4.1) was only 83.7%. However, the DLW measured FMR's of the Shetland and Orkney birds were 34% and 75% respectively higher than the predicted levels.

FMR, as predicted from time budgets and equations [12] to [15] differed widely from FMR measured by DLW. Method (b) produced individual estimates of FMR ranging from 71% to 165% of measured FMR whilst estimates from (c) and (d) ranged from 54% to 129% and 65% to 154% respectively (table 6.3). Taking the Coquet data set alone the deviation of predicted FMR from DLW measured FMR was significantly correlated with the amount of time spent at sea for each of the three methods of prediction (fig. 6.7). Thus, using the equations, FMR was overestimated when most of the time was spent at sea and underestimated when less than half of the time was spent at sea. This suggests that metabolism away from the nest was over estimated whilst metabolism at the nest was under estimated. If the greater amount of time spent away from the nest by DLW birds relative to control birds (6.4.2) was a result of disturbance then it is very likely that the birds were not engaging in their normal activities, *i.e.* foraging and may have been spending more time loafing, which would result in a reduced level of energy expenditure when away from the nest. The FMR's produced by each method did not differ significantly (paired t-tests) from FMR measured by DLW, whether the comparisons were made on the Coquet sample alone or on all of the birds. However they clearly did for individuals.

Figure 6.7. The relationship between the deviation of FMR as predicted by time budgets and allometric equations from DLW measured FMR and the amount of time which the birds from Coquet Island spent at sea during the measurement period on Coquet Island.


Method
B
C
D
% deviation of predicted FMR from measured FMR
80
60
40
20
0
-20
-40
10
12
14
16
18
20
22
hours away from colony

6.5 Discussion

6.5.1. Daily energy expenditure of breeding Arctic terns

Arctic terns feeding young appear to have very little leeway in their time budgets when feeding young and this is especially so when they are having to brood chicks (Pearson 1968). They might be expected to be working extremely hard and expending large amounts of energy at this time. Evidence from studies of adult weight which show that weight loss is rapid at this time (Monaghan *et al.* 1990) supports this. The level of energy expenditure of birds on Coquet Island feeding young chicks (3.63BMR) is indeed close to that proposed by Drent & Daan (1980) as the 'maximum sustainable work level' in birds, but it is by no means exceptionally high. Amongst seabirds with higher DLW measured daily energy expenditures are brown noddies *Anous stolidus* (5.2BMR, stage of life-cycle not stated) and wedge-tailed shearwaters *Puffinus pacificus* (4.8BMR, stage of life cycle not stated) (Ellis 1984) and northern gannets (6.6BMR, breeding, but stage of breeding season not stated) (Birt-Friesen *et al.* 1989). Furthermore, two birds from this study whose FMR's were measured under different conditions had considerably higher rates of energy expenditure. AT11, feeding young chicks in Shetland, where food was in short supply had an FMR 54.4% higher than the mean FMR on Coquet at the same stage of breeding and 42.6% higher than the highest recorded FMR on Coquet Island, where food is adequate (Monaghan *et al.* 1989a). For AT16, feeding a nearly fledged chick on Orkney, where food is also apparently adequate for breeding terns, the equivalent figures were 103% and 87.8%.

It is clear that terns can work at rates greater than 4 x BMR, but this does not necessarily preclude the notion of a 'maximum sustainable work level'. Drent & Daan (1980) acknowledged that the limit which they proposed (4 x BMR) was open to question, raising the possibility that it may be at some greater level. In addition they suggested that circumstances could arise in which such a limit might be exceeded in the short term, though the time-scale on which physiological constraints on metabolic rate operate are not known. Drent & Daan (1980) argued that above the limiting work level parents incurred the penalty of lost condition, perhaps because food could not be assimilated rapidly enough to meet demand, which therefore had to be met from reserves. The value of nutrient and energy reserves to an individual may vary according to, amongst other factors, the likelihood of poor foraging conditions (Pienkowski *et al.* 1979, Davidson *et al.* 1986), proximity to time of migration (Metcalfe 1984) or stage of the breeding season (Monaghan *et al.* 1990). The latter proposed a model whereby breeding Arctic terns monitored their body mass relative to a threshold, below which breeding was terminated. This threshold declined through the breeding season, such that birds could tolerate a lower weight later in the breeding attempt than earlier. This threshold weight may decline because birds nearing completion of a breeding attempt are closer to the time when they will be free of parental duties and their reserves consequently need to last for less time than those of birds at earlier stages. Therefore a parent with old chicks can be more certain of their survival than a parent with young chicks or eggs *i.e.* the balance in the trade-off between current and future reproductive value shifts in favour of current output and therefore current effort. Both of these models are consistent with the view of optimal strategy as a dynamic concept, with a continual shifting of the different behavioural options (McCleery 1978). Since birds nearing the end of the reproductive season are able to maintain a lower body mass they may also be able, in the short term, to work harder and incur greater loss in condition.

6.5.2. The use of the DLW technique on Arctic terns and other seabirds.

Six major assumptions about turnover of oxygen and hydrogen/deuterium are made when DLW is employed to estimate CO_2 production by means of equation [5] and its derivatives (Lifson & McClintock 1966). These are 1) body water volume is constant; 2) rates of water flux and carbon dioxide are constant; 3) isotopes label only water and carbon dioxide in the body; 4) isotopes leave the body only as water and carbon dioxide; 5) the isotopic enrichments in water and carbon dioxide leaving the body are the same as in body water; 6) water or carbon dioxide do not enter the body via the skin or lung surfaces. The accuracy of these assumptions and the implications of deviations from them have been carefully considered (Lifson & McClintock 1966, Nagy 1980), and although some are obviously unjustified *e.g.* assumptions 1 and 2 (Aschoff & Pohl 1970), the DLW technique has been shown to be valid under a wide range of conditions, including those encountered in seabirds.

However, a further very important assumption which is made when using the DLW technique to measure the energy consumption of free-living birds is that the energy consumption and behaviour of the birds is unchanged relative to those which they would have exhibited had they not been subjected to the technique, i.e they are representative of normal energy consumption and behaviour. Validation studies which have been undertaken for a wide range of animals show that the technique is accurate, but most of these studies were performed on captive animals in the resting phase when ADMR is several times lower than during the active phase (Tatner & Bryant 1989). Thus these studies do not assess the possibility of changes induced in behaviour by the technique and only show that captive animals do not incur any energetic stress due to the technique above those resulting from captivity.

The data set from this study, although small, suggests that the behaviour of Arctic terns is affected by the technique. DLW birds feeding young chicks attended and fed them less than control birds and their energy expenditure showed no relationship with the amount of time which they spent away from the nest, suggesting that birds did not behave consistently. The disruptive effect appears to be less marked with birds feeding older chicks on Orkney. The effect of such an intrusive technique may vary with many factors such as age and experience of the breeding birds, environmental conditions and stage of the breeding season. It is therefore essential that if DLW measured estimates of FMR are to be used as measures of daily energy expenditure (rather than as measures of the cost of certain activities) that the behaviour of experimental birds be compared to control individuals, not subjected to capture, injection, blood-sampling, re-capture and re-sampling. Of the 13 doubly-labelled water studies used by Birt-Friesen *et al.* (1989) to generate predictive equations for seabird metabolism only their own compared the behaviour of DLW and control birds, whilst 12 made no mention of any such comparisons, apart from two studies of storm-petrels, which suggested some adverse affects on the birds. It is admittedly very difficult to monitor the behaviour of many seabirds *e.g.* procellariformes, which spend long periods at sea, and many of these studies measured FMR whilst at sea. However, the increasing availability of ever smaller telemetry devices for monitoring behaviour of seabirds *e.g.* Cairns *et al.* (1987) should enable such measurements to be incorporated into future DLW studies as has already been undertaken with common terns (P. Becker pers. comm.). In the meantime more effort should be made to assess the effect of the DLW technique on behaviour.

7. DISCUSSION

7.1. The reproductive strategies of Arctic terns

Fitness, in an evolutionary sense, is measured by the relative genetic contribution of individuals to subsequent generations. Life-history theory attempts to explain reproductive patterns within an evolutionary framework. From an explicit assumption of a trade-off between the costs and benefits of current reproduction it predicts that individuals should allocate their resources of time and energy to breeding and maintenance such that lifetime reproductive success is maximised. Organisms such as Arctic terns, which are long-lived and may breed more than once may exploit this trade-off and adjust breeding effort in any one year or season such that: 1) breeding effort is not wasted in years when the chance of raising offspring which will themselves go on to breed is low; and 2) risk of adult mortality is kept low in order to ensure a high probability of survival to a 'good year' in which the chances of success are high.

Arctic terns in Shetland are undoubtedly experiencing difficulty in finding sufficient food for successful breeding. Fisheries derived data show that production of young lesser sandeels, which in good years comprise the major component of the diet fed to chicks, has fallen drastically in the seven years since 1983. In addition, sandeel stock size has also fallen recently. Corroborative, though not in itself conclusive, evidence of these changes is found in this and other studies of seabird breeding biology in Shetland. Sandeels are less important in the diet of Arctic tern chicks than they were found to be in a study in the early 1980's (this study and Ewins 1985); breeding adults are in poorer condition than those at successful colonies (Monaghan *et al.* 1989a, 1990). Further evidence of changes in the Shetland sandeel population comes from studies of other sandeel dependent seabird species (Heubeck 1989).

The most dramatic effects of the food shortage have been the very low (almost nil) breeding success of Arctic terns and the rapid decline in size of the Shetland breeding population. Recent population trends show a reduction in breeding numbers of 70% between 1980 and 1989 (Avery & Green 1989) with a further fall of 50% to 1990 (P. Ellis pers. comm.). Arctic terns in Northumberland usually begin to breed at the age of four years, after which they suffer an annual mortality of approximately 12.5% (Coulson & Horobin 1976). Thus, a simple model, assuming a population in equilibrium *i.e.* recruitment equal to adult mortality, and continued recruitment of young from all successful years (1983 cohort would recruit, on average, in 1987), would predict no population decline until 1988, and a total decline of only 24% by 1989. If no recruitment had occurred from 1984 onwards, when the food shortage began, the same model would predict a population fall of some 57% by 1989. Thus it would appear that one or a combination of extensive non-breeding, low recruitment, emigration or excessive adult mortality has been occurring. The very low body weights of breeding Arctic terns on Shetland (Monaghan *et al.* 1989a, Avery *et al.* in prep.) raises the possibility that adult survival may have been below the level recorded by Coulson & Horobin (1976) at a very successful colony on the Farne Islands in Northumberland, although Arctic terns may be able to modify their breeding effort according to their body condition (Monaghan *et al.* 1990). Some evidence of young birds recruiting elsewhere or of emigration comes from the discovery of dead adults ringed as young on Shetland at colonies in Orkney in 1988 and 1989 (E. Meek pers. comm., pers. obs.). All of these could increase the age and/or quality of birds attempting to breed on Shetland, since more extensive non-breeding and emigration, and higher mortality, might be expected amongst younger or poorer quality birds. Several studies have shown increasing reproductive performance in older or more experienced birds *e.g.* Coulson (1966), Coulson & Horobin (1976), Coulson & Porter (1985). In other words, the study may not be comparing like with like; the sample of breeding birds on Shetland may perhaps contain more high quality birds than the samples from Coquet and Orkney. Although such a response is beyond the scope of this study to measure it remains a possibility.

In addition to such potential major changes in behaviour, such as non-breeding, emigration and delayed recruitment, Arctic terns breeding on Shetland also display more subtle responses to food shortage. Evidence is presented in this study to show that a change in the pre-laying behaviour of male and female Arctic terns may have facilitated the maintenance of clutch quality despite poor food availability. The adaptiveness of this shift in behaviour was discussed in chapter 4. However, its adaptiveness is clearly extremely limited in this particular case since it did not result in successful breeding. It would be interesting to examine the responses of breeding terns to less dramatic fluctuations in food availability.

Such behavioural shifts may have altered the relative cumulative investments of males and females at the time of laying. Trivers (1972) suggested that, early in the season, females would have invested more in the breeding attempt than males. This view was based entirely on the anisogamous nature of sexual reproduction. However, as Gladstone (1979) pointed out, Trivers ignored the large amount of investment which males may make in territory and mate acquisition, territory defence, mate guarding and courtship feeding. It would appear that males in Shetland increase their investment prior to egg laying by maintaining courtship feeding for longer than they would in good food supply conditions. Whether this means that females do not need to draw more heavily on their reserves than they would otherwise have to is not clear. This may have a double-edged effect; not only do males increase their investment, and therefore the cost of reproduction, they may also decrease their certainty of paternity. Although Extra Pair Copulations (EPC's) and mate guarding have not been studied in terns, it seems likely that this switch in behaviour will result in a higher frequency of EPC's and Forced EPC's (FEPC's). However, since the existence of a food shortage increases the amount of male investment required for successful breeding, males should be less prone to attempt EPC's since these reduce the time available for investment in their primary female. On the other hand, if non-breeding is widespread in such conditions, there may be a large pool of unattached males which could profit through EPC's with already mated females, thus usurping the cuckolded partner's parental investment. It has already been suggested that courtship feeding in terns may play a role in mate choice and retention (Wiggins & Morris 1986), and therefore female terns may have a high degree of certainty as regards the quality of their mates. In addition, and especially in poor conditions when non-breeding is common, non-breeding males may be likely to be 'poor quality' birds, with whom already mated females might be unwilling to mate. Gladstone (1979) has proposed that females should resist FEPC's since males are more likely to desert their mates if cuckoldry occurs.

Food shortage appeared to have little effect on the consistency of incubation or its allocation between partners. However, in the post-hatching phase, Shetland females brooded their young less than they may have done under conditions of good food supply. Although the food requirements of young broods are less than those of older broods, the time constraints imposed by the need to brood the young may be severe. Brooding may be a significant factor in the determination of foraging strategies (Fagerstrom *et al.* 1983), affecting both the frequency of nest visits and the size and type of prey fed to young. Evidence for the existence of a bottleneck in the breeding cycle of Arctic terns at this point comes from a small amount of information on the performance of Arctic terns widowed at various stages of the breeding season, through natural causes. Four birds were widowed on Orkney in 1989. Of two which were widowed in the second half of incubation, both continued the nesting attempt up to hatching, but neither kept any chicks alive for more than one day. Both clutches hatched at a time when the weather was good and other broods hatched at this time survived beyond the brooding phase. The other two birds were widowed three and five days after the first chick hatched respectively. Both of these birds were able to continue raising their young until predation terminated all breeding attempts in the study plot. Indeed, one of these widowed birds was at one of only two nests which maintained a brood of two chicks beyond the first week after hatching. This is strongly suggestive of brooding being a major bottleneck in the breeding cycle and is similar to the result obtained experimentally by Sasvari (1986) who showed that widowing tits after their young had reached half of their maximum weight had no effect on chick survival whereas widowing before this point massively reduced fledging success. Bart & Tornes (1989) in a review of male removal studies on passerines concluded that male help was most important when males helped with brooding, either by sharing the duties, or feeding the female while she brooded the young. Dunn & Hannon's (1989) study of mate removal in the magpie also suggests that male help during the brooding period is crucial to breeding success.

The Arctic tern population of Shetland has been affected by the reduction in sandeel availability to a greater extent than any other of Shetland's seabirds. One reason for this may be that they are more flexible than other seabird species in their choice of breeding site and emigrate more readily. They are less site tenacious than some other species, such as guillemot and kittiwake, which enables them to move more easily to new breeding locations. Factors such as position within the colony and physical characteristics of the nest site may be more important for other species, especially cliff-nesters, which effectively limits the availability of nesting sites for them. Moving breeding site for established adults of such species may be so costly in terms of reduced breeding success that it is not even available within their behavioural repertoire, whilst such moves may be less costly for Arctic terns. However, there have not been the dramatic increases in nearby Arctic tern populations which we might have expected had movements of breeding birds been large-scale. This suggests that emigration has been relatively unimportant as a contributory factor to the population decline. Therefore it seems that Arctic terns have indeed been more adversely affected by the food shortage than have other species. Certainly, their breeding success has been reduced to a far greater extent. Such a response is in line with general predictions made by Furness & Ainley (1984) who suggested that small surface-feeding seabirds with specialised and energetically expensive foraging habits would be most vulnerable to reductions in their food supply. Such species have very limited amounts of spare time and energy gathering ability with which to buffer themselves against food shortage and other environmental fluctuations. Pearson (1968) showed that larger seabirds such as shags and guillemots spend a much smaller amount of their time foraging for their young than did small species such as terns. In addition to simply increasing the time which they spend foraging, better buffered species may be capable of changing their foraging behaviour, by flying further and exploiting a wider area, or by diving deeper or more frequently. Clearly, such changes in behaviour will not be without potential impacts on breeding success and adult survival, since poorer quality or less experienced individuals may be less capable of increasing the amount of time and energy spent foraging or may increase their prey capture rates to a lesser extent than better or older individuals for the same increment in effort. However, the capacity to increase foraging effort will offset to some extent any reductions in breeding success produced by food shortage. Continued study of a range of species over the period of food shortage and any future reversal of the current trends would enable us to assess the extent to which different species can buffer themselves and the mechanisms which they employ to do so.

7.2. Relevance to conservation

The protection, conservation and sustainable use of our environment is increasingly accepted as a desirable and necessary aim of society. Perhaps, in an ideal world, all policy would be framed with the best interests of our environment as a central requirement, but with current population levels and lifestyle aspirations, policy and practice will always be compromised by economic and social considerations.

In order to make rational decisions on what measures should be introduced, and when, legislators and policy makers require knowledge of when problems are occurring, or are likely to occur, their causes, and options for preventative or remedial action. Thus we require two levels of knowledge about the ecosystems on which human activities impinge. Firstly, we need to understand the processes which maintain and degrade individuals, populations and communities. Secondly, we require to know when things are wrong; to be able to measure the 'health' of what we wish to conserve. Each of these may demand biological research at all levels, from biochemical to community, in addition to research in the physical sciences such as hydrology, climatology, geology and oceanography. Though high quality research is necessary for the fulfilment of both of these needs, the practical achievement of the second is normally treated separately as a monitoring exercise. Basic biological research is necessary for the design of appropriate monitoring programmes. The rational and execution of monitoring studies has been concisely reviewed by Dunnet (1981) especially as applied to seabirds.

Seabirds are integral to marine ecosystems, being top predators which may consume a large proportion of the sea's production *e.g.* Furness (1978, 1990). There are perhaps three reasons why seabirds may be of interest to those concerned with the conservation of the marine environment. Firstly, although not necessarily most importantly, they are a relatively large, obvious, attractive and often spectacular component of coastal and marine areas. From the point of view of human appreciation of the environment this renders them highly desirable, and whilst by no means being the only criterion by which judgements are made, this must remain an important consideration in the formulation of conservation goals. Secondly, as top predators they may be useful indicators of other events in the ecosystem which are difficult to monitor directly (Furness & Monaghan 1987). The effects of pollutants may often be detected in such animals *e.g.* Ratcliffe (1970), and changes in fish and plankton populations may be difficult or very expensive to detect directly; using top predators as sampling tools is often a more efficient method of monitoring events lower down the food chain. Thirdly, they may, as top predators, compete directly with humans for the limited resources which may be harvested from the sea. As a result, their food requirements have important consequences for fisheries scientists modelling stock sizes and setting catch limits (Furness 1990).

How do Arctic terns rate as monitoring subjects for each of these purposes? Certainly, on a cultural level seabirds are important to the residents of Shetland, playing a similar role to that of the swallow in England as a messenger of spring and summer to come. Indeed, given the importance of tourism to Shetland's economy, their potential economic importance should not be overlooked. As competitors with humans for the same resource they are probably of little importance. Although they take sandeels of the same size-class as the fishery (Monaghan *et al.* 1989b) the actual amount they take is trivial compared with the fishery and other seabirds in the Shetland area (less than 1% of total seabird consumption of sandeels in the Shetland sea area during the breeding season, Furness 1990). However, as potential monitors of the state of sandeel stocks around Shetland, Arctic terns may be of great value as a monitoring species. They were the first species to be visibly affected by the current sandeel shortage, and will presumably be the last to recover, in terms of breeding performance, when, and if, stocks ever recover. In the past, data from the fishery has been the only means of monitoring the stocks apart from a small amount of effort put into fisheries independent sampling by the DAFS. Now that the fishery is closed as of 1991 fishery data are unavailable. Furthermore, since the fishery may well be controlled by the use of closed seasons and licensing restrictions if it is ever re-opened the data from it are likely to be unreliable in the future. Seabirds may present a viable alternative means of monitoring stocks, at least at a qualitative level. As a monitoring species, Arctic terns are attractive because of their apparent sensitivity to food shortage, and the strength of their response to it. This is a direct result of their conservative life-history strategy and the high level of investment necessary for successful reproduction. This study has shown that Arctic terns in Shetland responded to changes in the sandeel population with dietary shifts, changes in feeding frequency and reductions in colony attendance at certain times and possibly increases in their energy expenditure during breeding. Other studies have revealed reductions in body mass, poor chick growth and breeding success and population declines (Avery & Green 1989, Monaghan *et al.* 1989a, Uttley *et al.* 1989a). Although counts of seabirds have long been used to monitor their populations *e.g.* Harris (1987), behavioural changes promise to provide far more subtle indicators of the ease with which seabirds can find food during the breeding season, since they may be able to compensate behaviourally for food shortage and thus reduce or nullify its effects on breeding success or population numbers. However, Arctic terns possess some serious disadvantages for monitoring such changes. Unlike the cliff-dwelling species, observation of terns normally requires the observer to be so close as to disturb the birds, even if a hide is used. They are very susceptible to disturbance during breeding, which may raise predation levels. In Shetland at least, their colonies may be very ephemeral, with great fluctuations from year to year (Thomas 1982, Furness 1983, pers. obs.). For these reasons, population counts and attendance monitoring are difficult to carry out on Arctic terns on a regular basis. Monitoring of behavioural changes and diet may be more easily carried out on cliff-nesting species such as kittiwakes, which also have been severely affected by the sandeel problem, or on larger more sedentary birds such as great skuas. A great advantage of using cliff-nesting species is that it is relatively easy to set up permanent study plots, which may be monitored easily from year to year. However, given the arguments presented above for monitoring Arctic terns, it is important that some means be found of doing so. The approach taken by Monaghan *et al.* (1989b) whereby constant effort ringing of chicks is carried out would be an effective means of monitoring the production of young, and perhaps the stocks of sandeels also. This method is simple, cheap and can easily be performed by enthusiastic amateurs and professionals alike.

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