Within Brood Trade-Offs in Reproductive Effort: An Experimental Study on the Common Tern *Sterna hirundo*

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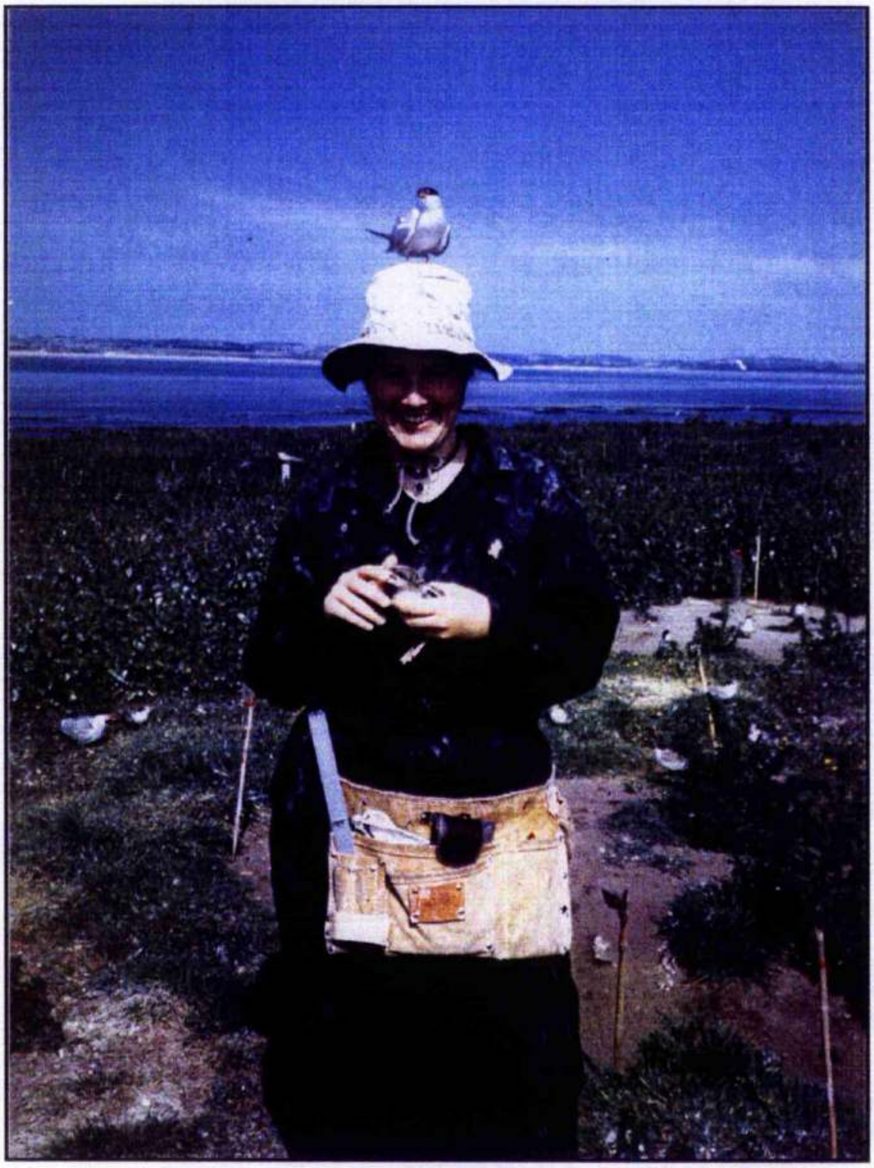

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Summary

The optimal allocation of effort during reproduction is a key component of life history theory, with trade-offs predicted to operate both within and between reproductive attempts. Experimental work in this field has largely concentrated on the latter. The need to partition investment between the different phases of the current reproductive event, and how this varies between individuals, has received little empirical investigation. The primary aims of this project were to investigate the capacity of birds to adjust their reproductive effort in response to increasing demand, and to investigate within brood trade-offs between the different phases of the reproductive attempt. To do this the project involved experimental manipulation of effort (within the natural range) at the stages of egg production, incubation and chick rearing.

Only those pairs that were given a free chick (incurring chick rearing costs only) were able to rear a significantly larger brood than unmanipulated controls. When parents incurred the full costs (egg production, incubation and chick rearing) of producing additional young to their intended clutch size, their capacity to rear an enlarged brood was negated. A within clutch trade-off was identified between producing and rearing extra young, with experimental parents subsequently showing reduced chick provisioning, growth and survival. In an experiment to increase the costs of incubation alone, which have often been considered relatively trivial, study birds showed a significantly depressed performance in the later stage of chick rearing. Again a within clutch trade-off in reproductive effort was identified with second hatched chicks in experimental nests growing at a significantly lower rate and fledging at a significantly lighter mass than those in control broods. The effects of experimental manipulation on aspects of the dynamics of parental foraging suggested that an increase in reproductive demand may affect strategy, but the relationship was not clear. An increase in the costs of egg production alone was not found to decrease parental performance or the quality of the additional egg or chick. These results cast doubt on the interpretation of previous brood enlargement experiments as providing empirical evidence that observed clutch sizes are often less than the Lack value, as such experiments have failed to include the costs of egg production and much of the incubation costs also. They lend support to the Individual Optimisation Hypothesis, in that the parents appear to be raising the clutch size that maximises their number of recruits.

The effect of increased cost in relation to individual quality was also examined. The capacity of individuals to compensate for deviations from their allocation of effort to different reproductive phases was found to differ. The negative fitness effects of an increase in incubation demand were most marked in lower quality pairs. Also, the capacity to lay additional eggs in response to experimental egg removal differed between individuals and between years. Only birds in a good enough condition prior to, and during, egg laying appeared able to increase their allocation of effort to the egg production phase and replace the removed egg. A significant proportion of (presumably poorer quality) birds simply deserted the nest site. The adaptive significance of a conditional response to egg loss is discussed, particularly in relation to the finding that egg production alone did not result in any significant within clutch trade-offs.

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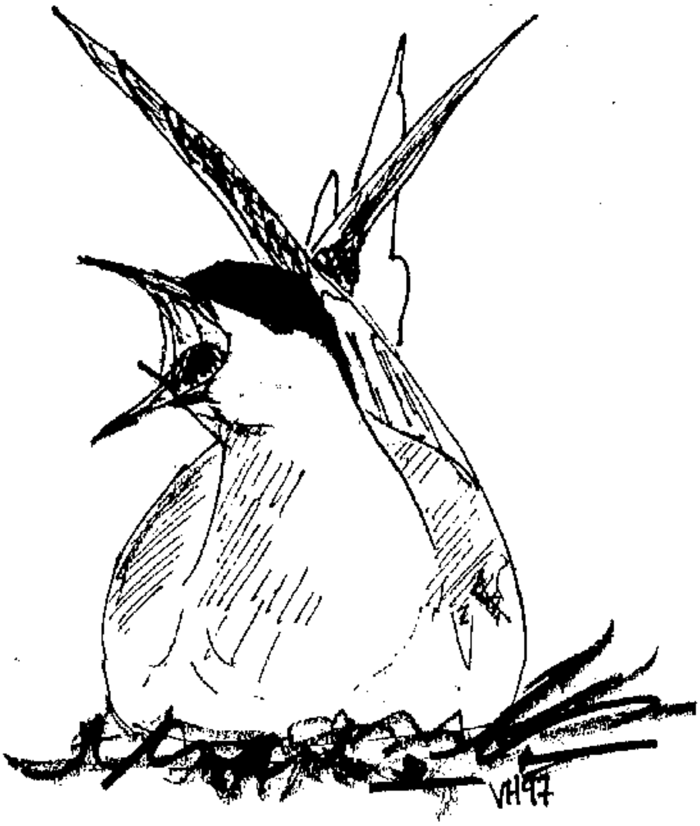
Chapter 1 : General Introduction



Natural Selection and Life History Theory

In Darwinian terms the ultimate goal of any organism is to reproduce. Life History Theory attempts to explain the scheduling of this reproduction throughout an organism's lifespan and to account for the diversity of patterns of reproductive behaviour and investment (Roff 1992, Stearns 1992, McNamara & Houston 1996). The life history of a species is the combination of age-specific survival rates and fertilities seen in a typical individual. Thus it describes the broad demographic features or traits of an organism's life cycle; how fast it grows, it's age and size at maturity, the number, size and sex ratio of the offspring it produces, the level of parental care it provides, and it's life expectancy. Optimal life histories are those that maximise the Malthusian parameter *r*, or intrinsic rate of population increase of the genotype specifying the trait under the prevailing ecological conditions (Lindén & Møller 1989, Partridge 1990).

Trade-Offs in Life History Strategy

To be well adapted requires compromise (Reznick 1985). The basic hypothesis underlying most analyses of the evolution of life history traits is that variation is constrained in large measure by compromise or trade-offs between traits (Stearns 1992). A trade-off exists when a benefit realised through a change in one trait is linked to a cost paid out through a detrimental change in another (Stearns 1989). If there were no trade-offs, then selection would drive all traits correlated with fitness to limits imposed by history and design (Stearns 1989). The optimal life-history balances the costs and benefits of such trade-offs against environmental sources of mortality in a way that maximises individual fitness (Reznick 1985).

The most prominent life history trade-off involves the cost of reproduction. To maximise the intrinsic rate of increase, *r*, an evolutionarily ideal organism would commence breeding at birth at the maximum possible rate and would continue to do so throughout its infinite lifespan. The great diversity seen in age at first breeding, reproductive rate and lifespan would make no evolutionary sense if this were possible. Most theoretical models of life history evolution therefore assume that reproduction incurs a cost in terms of survival and future fertility, so that only certain constrained combinations are possible in practice (Partridge 1990). Each organism has a total amount of energy available for reproduction and survival. This is the sum of the energy and nutrient reserves stored prior to the reproductive event, plus those acquired by feeding during the reproductive event (Martin 1987). Birds can be split into capital and income breeders according to the differences in their reliance on stored reserves and current foraging for reproductive cues (see Drent & Daan 1980). A trade-off between the allocation of resources to current versus future reproduction is a fundamental assumption of Life History Theory; this trade-off is the 'cost of reproduction' (Reid 1987). It has two major components, costs paid in survival and costs paid in future reproductive output (Stearns 1989).

Reproductive Effort

Reproductive Effort describes the energetic demands of breeding. It is usually measured in terms of the number, weight, or calorific values of the eggs or neonates. It may also be assessed in terms of the levels of energy expenditure and the frequency and intensity of the activities necessary for reproduction (e.g. Uttley 1991). This is different from parental investment (Trivers 1972, Low 1978), which is defined as the cost of an individual's contribution to the production and survival of current offspring. The currency of this investment must be measured as ultimate fitness costs (in terms of reduced survival and future reproduction, Pianka 1976, Bell 1980, Wittenberger 1982, Burger 1987).

Brood Manipulation Experiments

Avian brood manipulation experiments have strongly influenced the development of life history theories, particularly in relation to the evolution of clutch size (a large component of reproductive effort, see Partridge 1989, Godfray *et al.* 1991, Lessells 1991, Stearns 1992, Roff 1992, Monaghan & Nager 1997). In iteroparus species, life history theory predicts that the 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). In long-lived species, where increases in fecundity may occur with increasing age and maturity, the optimal amount of reproductive effort will depend on the organisms Residual Reproductive Value, that is its future potential for reproductive success (Williams 1966). If a bird were to allocate more energy to, say, egg production, it must either reduce the energy for itself or the proportion of energy for the young in the stages after egg production. Both of these responses have associated costs. If increased investment in the current reproductive event results in a decrease in the energy available for somatic effort, adult survival and maintenance, condition is reduced and thus a cost may be paid in terms of future reproductive potential; a between brood trade-off. If sufficient energy and nutrients are allocated to ensure adult maintenance and survival, there will be a ceiling on the parental effort available (Goodman 1974), and an increase in one stage of the attempt will effect a decrease in the energy available at a later stage in the reproductive event resulting in reduced survival of the young; a within brood trade-off. To understand the extent to which individuals should sustain reproductive mortality (the ultimate fitness cost, through the death of young or adults associated with reproductive effort) in their reproductive strategy requires an understanding of the trade-offs in adult and juvenile survival resulting from differential energy allocation by parents (Martin 1987).

Experimental studies on clutch size in birds, manipulating the allocation of energy to the current reproductive attempt (through brood augmentation), have demonstrated fitness costs according to both of the types of trade-off in reproductive effort described above:

i). *Between brood trade-offs*: Following experimental brood augmentation several studies have shown a reduction in parental survival (e.g. pied flycatcher Askenmo 1979, song sparrow Smith 1981, blue tit Nur 1984 (but see Pettifor 1993b), great tit Tinbergen *et al.* 1985, glaucous-winged gull Reid 1987, kestrel Daan *et al.* 1996), and of those birds that do survive to breed again, subsequent attempts may be delayed (e.g. great tit Slagsvold 1984, Lindén 1988, Canada geese Lessells 1986) and brood size and success reduced (e.g. great tit Slagsvold 1984, rook Roskaft 1985, collared flycatcher Gustafsson & Sutherland 1988, Gustafsson & Part 1990). They may also show other indications of increased cost with increased clutch sizes causing subsequent delay in moult (e.g. Canada geese Lessells 1986), and a reduction in resistance to parasites (e.g. barn swallow nest mites Møller 1990).

ii). *Within brood trade-off:* Some studies have shown that an experimental increase in brood size reduces the number of offspring surviving from the nest when compared with control nests (e.g. great tit Pettifor *et al.* 1988, blue tit Pettifor 1993a). However, experimentally enlarged broods are often shown to fledge more young than control clutches (e.g. collared flycatcher Gustafsson & Sutherland 1988, great tit Pettifor *et al.* 1988, Lessells 1991, Roff 1992, Stearns 1992). These broods may show a trade-off between the number and size of offspring fledged; often fledging more young at the expense of the quality of these young. For example young fledging from experimentally enlarged broods maybe less likely to be recruited into the breeding population (e.g. Gustafsson & Sutherland 1988, Pettifor *et al.* 1988, Smith *et al.* 1989) and show a lower subsequent reproductive performance (e.g. Gustafsson & Sutherland 1988, Lindén 1990, Dijkstra *et al.* 1990).

Differences Between Individuals

Individuals vary in the overall amount of energy they acquire and in the fraction of this energy that they allocate to reproduction (Drent & Daan 1980, Pettifor *et al.* 1988, Stearns 1989, Daan *et al.* 1990, McNamara & Houston 1996). These differences are important in determining their level of reproductive effort and thus their reproductive success or fitness. The 'quality' of an individual may be described as its ability or general proficiency and will be an index of the intrinsic fitness of that individual. This will be determined by an interaction between genotype and phenotype, and be influenced primarily by age, size and experience (and thus ability to harvest and efficiently use resources, care for young, obtain a good territory etc.).

The 'condition' or 'state' of an individual will be determined by an interplay between the intrinsic quality of the parent and local environmental conditions, both social and physical (e.g. food availability, temperature, mate quality, population density, predation, competition, parasites). Thus condition will primarily describe the nutritional status of an individual and may include, among other things, fat reserves (Witter & Cuthill 1993), protein reserves (Houston *et al.* 1995a), territory quality (Daan *et al.* 1990, Perrins 1965), parasite load (Møller 1993), and the state of the immune system (Gustafsson *et al.* 1994).

Why Experiment?

The time and energy available to an individual for survival and reproduction, will be determined by the condition or state of that individual (Hirschfield & Tinkle 1975, Drent & Daan 1980, Martin 1987). Reproductive effort will depend on the total energy available, and thus parameters such as clutch size, in species where clutch size varies, are likely to reflect differences in state among individuals (Pettifor *et al.* 1988). Parents with greater total energy due to environmental and/or individual quality, can allocate more reproductive effort allowing larger brood sizes yet still retaining greater somatic effort.

Individuals in a superior state or condition will perform better at all stages of the life-cycle (Coulson & Horobin 1976, Nisbet *et al.* 1984, Clutton-Brock 1984). Therefore, we cannot use non-manipulative studies to investigate trade-offs, since in a high quality individual or in a good year, we are likely to find a positive relationship between traits (van Noordwijk & de Jong 1986). This correlation between traits does not indicate that reproduction has no cost, only that the traits are all correlated with a state variable (such as territory quality or breeding experience) (Clutton-Brock 1984, Partridge & Harvey 1985, Reznick 1985, Stearns 1992, Roff 1992, Pettifor *et al.* 1988).

The role of experiment is to control for such confounding variables and to manipulate those variables of interest, so that their effects can be deduced (Partridge 1990). Thus, to control for the effects of differences in total energy among individuals it is essential to manipulate reproductive effort away from the intended level (e.g. manipulate brood size) in order to investigate the exact nature of the trade-offs that have produced this level (Pettifor *et al.* 1988, Parker & Maynard Smith 1990). The experimental approach can also provide more information about the exact mechanisms involved in the mediation of reproductive costs (Partridge 1990).

If the costs of reproduction are to be estimated realistically, it is important that manipulations only change the brood size slightly and are within the natural range of clutch size for the species (Pettifor *et al.* 1988, Lindén & Møller 1989). Parent birds are more likely to face a strategic choice of whether or not to lay one extra egg, rather than the more extreme problem of whether or not to lay, say, five extra eggs (Lindén & Møller 1989). Population density, parasites and nest predation may interact and significantly affect reproductive success, survival prospects and the costs of reproduction. Thus, trade-offs should also be studied in natural settings where the experimental manipulation does not cause extensive alterations in the selective regime (Lindén & Møller 1989). As well as ecological constraints, the importance of phylogeny and allometric and physiological constraints needs also to be considered (Lindén & Møller 1989).

The cost of experimental manipulations is likely to vary according to the state or quality of the individual. Individuals will have varied, but limited, capacities to compensate for deviations from their individual allocation of effort. The effect of an increase in reproductive demand may have a greater significance and be relatively more costly to an individual in poorer condition (Drent & Daan 1980, Clutton-Brock 1984, Wright & Cuthill 1989, Pettifor *et al.* 1988, Partridge 1990, McNamara & Houston 1996). Thus, trade-offs may only be expressed under conditions of food stress or in poorer quality individuals (Tuomi *et al.* 1983, Partridge & Harvey 1985, Reznick 1985, Bell & Koufapanou 1986, Stearns 1989, Linden & Møller 1989, Pettifor 1993a). In order to control for these confounding effects of individual condition, manipulations should be carried out on birds that are roughly equivalent, and perhaps from the lower end of the quality spectrum (Pettifor *et al.* 1988, Lindén & Møller 1989).

The number of eggs laid by an individual can be used as a measure of quality (Nisbet *et al.* 1984, Coulson & Porter 1985, Pettifor 1993a), and so experimental comparisons should only be carried out on individuals intending the same original clutch size. However, changes in clutch size act as a primary adjustment in reproductive effort and represent major stepwise changes in reproductive potential especially if the species' range of clutch size is relatively small. They are only part of a whole 'bag of tricks' available to birds for tailoring their reproductive effort to their environment (see figure 1, Winkler & Walters 1983). Thus, within the subset of birds intending a particular clutch size we might expect a to find a further range of condition, expressed by more subtle measures such as variation in egg size (Nisbet *et al.* 1984, for reviews see Martin 1987, Williams 1994, Carey 1996), and laying date (Nisbet *et al.* 1984, for review see Daan *et al.* 1990).

Possible Problems with Brood Manipulation Experiments

Brood size manipulations may not always have the effect of manipulating the parental work rate. If a bird has in some sense 'decided' on its work rate for the brood before the manipulation is done, or is already working at maximum capacity (Drent & Daan 1980), then the manipulation will be informative about the effect of parental work rate on the offspring, but not about the effects on the parent. Thus, detailed study of the behavioural effects on the experimental birds are needed to assess the effects of the manipulation (Partridge 1990). The ability to manipulate effort experimentally is dependent on the plasticity of the life-history. An absence of a response to the manipulation of 'effort' may be because of either an absence of cost or an absence of plasticity in the pattern of resource allocation, e.g. a tendency for foraging time to plateau in enlarged broods so that allocation of resources per chick is reduced (Reid 1987). To equate such plasticity with the concept of 'costs' in Life History Theory is to assume that this plasticity reflects underlying genetic correlations (Reznick 1985).

This leads to the second problem; the measurement of reproductive cost through experimental manipulation of reproductive effort is a measure of phenotypic rather than genotypic response (Reznick 1985, Reid 1987). In order to assess the evolutionary importance of phenotypic responses we must measure the ultimate fitness and survival costs and benefits of the manipulations - the raw materials of natural selection (Pianka 1976, Clutton-Brock 1984, Daan *et al.* 1990). However, the effect of selection for different levels of reproductive effort may be different from the effect of the experimental manipulation because the evolutionary response will depend on genetic correlations. Thus, the phenotypic responses measured with experimental manipulations may not reflect how the organism will respond to selection (Reznick 1985). For example, a selection pressure may exist where a strong negative phenotypic correlation exists between two traits, however, if they have no genetic basis whatsoever no evolutionary response is possible.

Genetic variation has been found in the few cases where it has been looked for, thus providing the raw material for the evolution of reproductive trade-offs (Partridge & Harvey 1985). For example selection experiments in *Drosophila* have revealed antagonistic pleiotrophy as a genetic basis for the costs of reproduction. Pleiotrophy is a measure of the degree to which a single gene affects the expression of two or more traits. In these experiments females selected for high fertility early in life have low longevity, and those selected for fertility late in life show increased longevity and lowered early fertility (Rose & Charlesworth 1981, Luckinbill *et al.* 1984). Thus, a gene with age specific effects that causes high fertility when young will be selected despite deleterious (side-)effects which are persistent and increase in impact with age (Williams 1957, Partridge 1990). Other cases of antagonistic pleiotrophy have also been identified (e.g. in human reproduction female sex hormones that promote fertility early in life are also involved in disturbances in calcium metabolism later in life, Stearns 1989). However, these genetic selection experiments have their own set of problems (see Reznick 1985).

Ultimately, it is not a question of either genetic, phenotypic or physiological correlations or trade-offs but of how such measurements combine to deliver information about potential evolutionary responses (Stearns 1989). The main task for phenotypic experiments is to identify the nature of any reproductive costs and hence design the appropriate experiments to measure their magnitude. They provide a qualitative index for costs and correlated responses to selection, demonstrating how the costs might be manifested in real organisms and what their magnitude might be (Reid 1987). The observed trade-off between reproductive effort and survival provides a qualitative picture of the actual trade-off. The reliability of this picture is enhanced by knowledge of the mechanism of the cost (Reznick 1985, Reid 1987).

Aims

This thesis aims to investigate the capacity of birds to adjust their reproductive effort in response to increasing demand, and how different adjustments influence behaviour and breeding success. While survival changes can often be documented from survey data, more subtle effects of increased breeding demand and cost can only be identified from detailed study. It has previously been shown in several larids (arctic terns, kittiwakes and lesser black-backed gulls) that high breeding demands, as results from changes in food availability either environmentally or evolutionarily determined, are manifested in changes in egg production, incubation and foraging behaviour, and in adult body condition during the breeding season (Monaghan *et al.* 1989, Hiom *et al.* 1991, Monaghan *et al.* 1992, Bolton *et al.* 1992, Bolton *et al.* 1993, Hamer *et al.* 1993).

This project aims to extend this research particularly in relation to the evolution of clutch size and within brood trade-offs in the partitioning of effort during reproduction. Birds are especially useful for this sort of study because they have three easily recognisable and distinct phases within a breeding attempt; egg production, incubation, and chick-rearing (in some species the post-fledging stage may also be an important part of parental effort Martin 1987). Previous studies, which have been highly influential in the study of life history theory, have generally effected brood size manipulation only by the addition or removal of a newly hatched chick (Monaghan & Nager 1997, Stearns 1992). This approach fails to consider the cost of egg production and incubation of this young, which may be considerable (Lessells 1991, Partridge 1989, Stearns 1992, Monaghan & Nager 1997). In this thesis I intend to emphasise the importance of these earlier stages in producing young.

To elucidate the exact nature of within brood trade-offs and the optimal allocation of effort between the three stages described above, the different components of reproductive effort have been manipulated and their effect on reproductive cost examined. The project involved independent manipulations (increasing demand at each stage, both in combination and in isolation) of;

i). Egg production: by removal of first egg to make birds lay an additional egg.

ii). Incubation: by manipulations of clutch size.

iii). Chick rearing: by altering brood sizes.

The effect (behavioural adjustments and ultimately fitness costs) of these manipulations on adults (and their broods) was examined by studying attendance, foraging rate and efficiency, chick growth and survival.

Study Species

The study was conducted on the common tern, *Sterna hirundo* (Linnaeus 1758). Generally the commonest and most widespread tern in Britain and Europe, the common tern is a relatively small seabird, about 33-35 cm from bill tip to tail tip, weighing 100-140g. As the Latin name suggests, it is the epitome of a sea swallow; an elegant sea tern with an evenly curved line to the upper head, long wings, a slim, rather oval body, and an obviously forked tail. In summer the adult shows a neat black crown, with a pointed black-tipped orange-red bill, a grey upper wing and mostly white under-parts (see **Figure 1**). In winter the forehead is white.

As a species, the common tern has a wide distribution and rather loosely defined ecological requirements. It breeds both along coasts and on inland fresh waters, anywhere from the fringe of the Arctic to the tropics, taking in temperate and Mediterranean beaches and vast areas of continental Asia and North America on the way. In the main part it is a bird of low coasts with accumulating sand and shingle. The terns winter along the west coast of Africa, and here the juveniles will remain for the first year or two of their lives. In Western Europe the arrival of the common tern in April is considered a signal of the advent of spring and summer.

Common terns nest in highly synchronous colonies which rarely reach more than 1500 - 2000 pairs. The pair defend a small territory, usually little more than a sharp beak's length from the next, and scrape a simple shallow nest in loose sand. They lay between one and three eggs (sub-elliptical, smooth, cream to buff, and very variably marked with streaks and blotches of dark brown to black), which are incubated for approximately 21 days. On hatching, the chicks are covered in down with well developed tarsi, and are capable of thermoregulation after approximately 10 days (Klaassen 1994). The main diet of both adults and chicks is marine fish, caught by aerial plunge dives often preceded by hovering. Within that basic role, however, the common tern is an opportunistic feeder, where changing circumstances dictate changes in the type of prey taken and the way in which it is caught.

Seabirds are ideal for studies of life history theory, because in comparison with many other types of bird, they are long-lived, lay small clutches and show deferred maturity, delaying breeding until at least the second year of life and often considerably longer (see Furness & Monaghan 1987 for references). The demands of breeding on the adult bird can be considerable, and the time of maximum adult mortality coincides with the end of the breeding season in some species (Coulson *et al.* 1983, Monaghan & Metcalfe 1986).

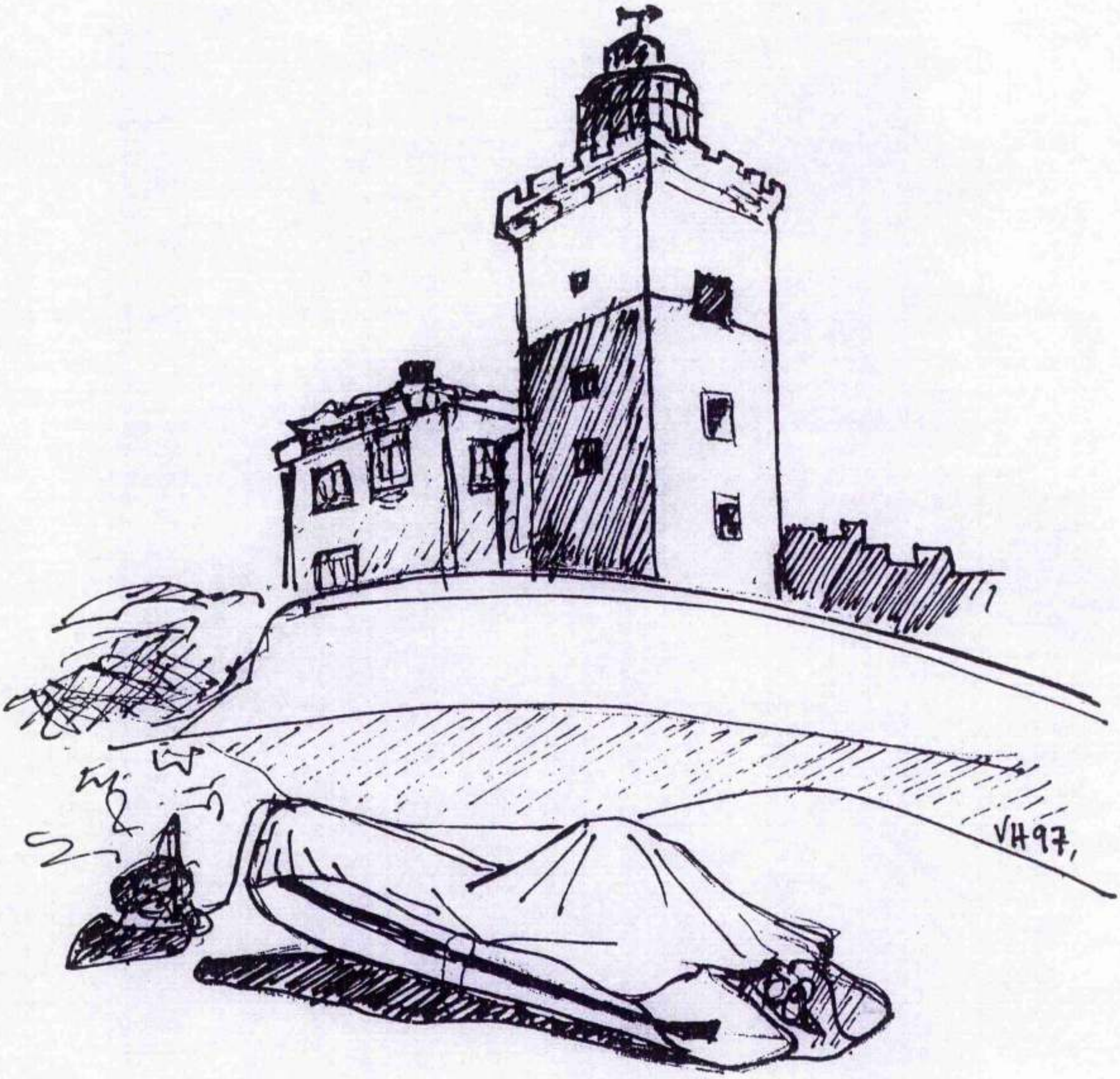
Common terns do not breed until 3 or 4 years of age, and may have over 7 years as breeding adults, with some individuals surviving in excess of 18 years (Nisbet *et al.* 1984). They are amongst the smallest of the laridae, and have less leeway in their annual energy budgets than do larger species. They spend a very high proportion of the available time foraging when they have young (Pearson 1968), and only have a limited period in which to breed before deteriorating weather and changes in food availability necessitate departure for their wintering quarters (Cramp & Simmons 1985). This, coupled with their small foraging ranges (Pearson 1968) and specialised surface feeding techniques, makes them ideal for studying of trade-offs in reproductive effort, since any increase in demand is likely to have measurable costs (Furness & Ainley 1984, Hamer *et al.* 1993). Where breeding is attempted at all, parental effort will be variable and contribute to the onset of breeding, time of breeding, clutch size, hatching success, chick growth and survival and breeding success (Uttley 1991). Their breeding in reasonably large, highly synchronous colonies also facilitates data collection and experimental design.

The highly constrained nature of common tern breeding, however, also causes problems for its use as a study species. The expected trade-off of current against future reproductive potential in this species and seabirds in general means that in poor years (perceived as a result of low food availability, experimental increase in reproductive demand, or some other reason), they are more likely to abandon a breeding attempt after initiation if the perceived risks to their survival are too great (e.g. Drent & Daan 1980, Reznick 1985, Pugesek 1987). This is especially so at the start of the breeding attempt when the investment is not so great (Williams 1966), so that disturbance, especially egg removal or trapping at this time may make the birds particularly prone to nest desertion (Nisbet 1981, Nisbet pers. comm.). This complication with trapping makes assessment of parental body weight and condition difficult. Another problem with common terns for the study of life history trade-offs is that they are not especially site faithful and with predictions of no breeding in poor years (Drent & Daan 1980, Uttley 1991), they are less suitable for longitudinal survival studies and analysis.

Mark Bolton

Figure 1. The common tern (breeding adult).

Chapter 2 : General Methods



In order to avoid much repetition and cross-referencing, the general data collection methods employed in the two years of the study are described in detail in this second chapter. Where a chapter uses specialised methodologies or statistical techniques, they are dealt with in that chapter.

Study site

The study was conducted on Coquet Island, Northumberland (grid reference: NU 293045, 55° 20'N, 1° 32'W). The island lies about 1.25 miles from the mouth of the River Coquet (from which it gets its name) and about 20 miles S.S.E. of the Farne Islands (see **Figure 1**). Coquet is a low flat island, not rising more than about 10m above sea level, and has an area of nearly 70 000m^2. It is composed of sandstone and its erodable nature has left it with extensive shelves of rock, which when exposed at low tide, represent an area about twice that of the vegetated plateau (see **Figure 2**). There is a pebble beach at the south-east end, a sandy beach at the south-west and a concrete jetty on the landward side, the later two being suitable for landing small inflatables. To the north and south there are large sandy bays, Alnmouth and Druridge, respectively, which in combination with other neighbouring areas rich in fish provide suitable fishing grounds for seabirds.

Despite its small size, Coquet Island has been a place of sanctuary since the time of St. Cuthbert, who landed there in AD 684. The island served as a monastic retreat and was home to St. Henry (also known as Henry the Hermit) who established a coenobitic cell there in the 12th century. In the 17th century sandstone was cut on the island and low cliffs have resulted from this activity. Coal was also mined around this period in the island's history, and shipped to Newcastle. Angora rabbits were bred on the island during the 1800s and 1900s, and local fishermen exploited the nesting seabirds, selling eggs to supplement their income. The quarrymen and the monks have long since gone.

The present lighthouse was built in 1841 on the vault of an older tower at the south end of the island, and incorporates the ruins of an ancient chapel into some of the out-buildings (see **Figure 3**). The oldest surviving part, the hermit's cell, serves as an oil store. The light itself, with a square tower and ramparts, was designed to complement Warkworth Castle, visible on the mainland. The lighthouse and associated buildings and gardens (occupying about 3 000m^2), housed the families of two lighthouse keepers, and the family of the buoy-keeper. In the past these residents cultivated land outside the gardens and kept livestock ranging the length of the island. Such intrusions evidently disturbed the breeding birds, and it is likely that only Eider continued to breed, with terns disappearing altogether by about 1882 (Marples 1934), and only starting to return in the late 1950's when farming activities ceased (Coulson cited in Langham 1968).

Today, with the lighthouse automated since 1990, the keepers have gone also. Coquet is owned by the Duke of Northumberland, and is currently leased to the Royal Society for the Protection of Birds. The RSPB works with other nature conservation bodies on the Coquet Management Committee to conserve the island as a nature reserve. Other member bodies of the management committee include the Natural History Society of Northumbria, Trinity House, Northumberland Estates and the Northumberland Wildlife Trust. The island is wardened from April to October, and through careful management and a no landing policy, the birds have returned to Coquet, so that today a particularly diverse community of more than 20 000 pairs of seabirds breed on the island. In 1993, 19 species of birds were recorded nesting on Coquet. This included approximately 16 000 pairs of puffins, over 3 000 pairs of black-headed gulls, and 340 pairs of eider ducks, as well as fulmars, oystercatchers, ringed plover, shelduck and a small but growing colony of Kittiwakes on the east 'cliffs'. In addition, four species of tern nest on the island, of which the sandwich tern is the most numerous, with approximately 1 700 breeding pairs. The colonies of common and arctic tern both number about 800 pair, and there are about 35 nesting pairs of the endangered roseate tern. Breeding numbers of most species on the island (including common, arctic and roseate terns) continue to rise, although control measures for the large gull population (about 40 pairs of herring and lesser black-backed) are currently under review (RSPB unpublished reports). The island is also an important winter roost for waders.

Most of the island is covered in low-lying vegetation, mainly grass kept in check by the ubiquitous rabbit population (*Oryctolagus cuniculus*). However, probably as a result of human use in the past, large areas are occupied by bugloss (*Lycopsis arvensis*) and extensive stinging nettle-beds (*Urtica dioica* L.). As part of the Coquet Island reserve management plan, the nettle-beds are sprayed with herbicide at the beginning of each season to aid the breeding terns, reducing the density of vegetative growth. The clear spraying is done in discrete plots within the nettle-beds roughly 10m x 10m. (see **Figures 4 & 5**), and the majority of the breeding common terns settle in these sprayed plots, since they allow easy access, but afford the growing chicks shelter at the edges.

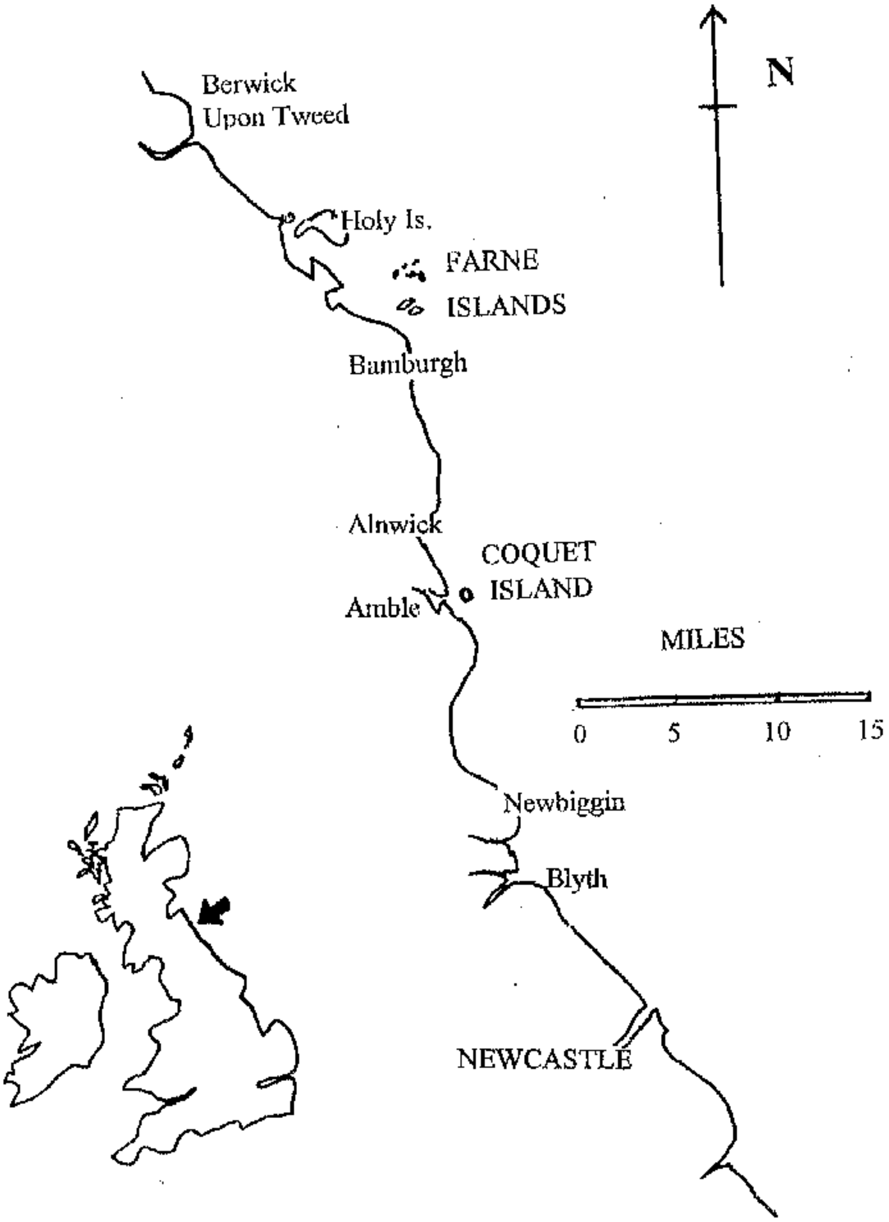
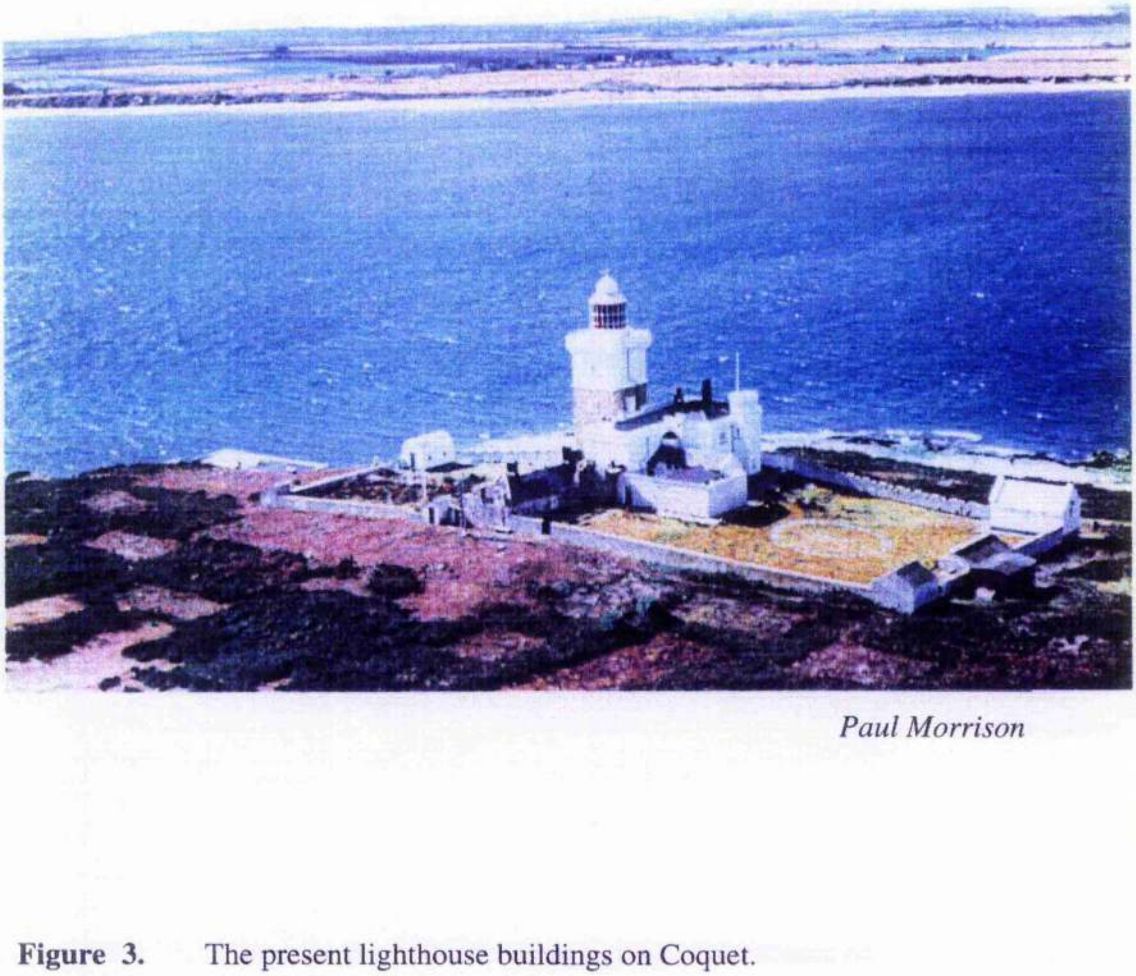


Figure 1. The location of the study site, Coquet Island, Northumberland.

Paul Morrison

Figure 2. Coquet island from the air.



Paul Morrison

Figure 3. The present lighthouse buildings on Coquet.

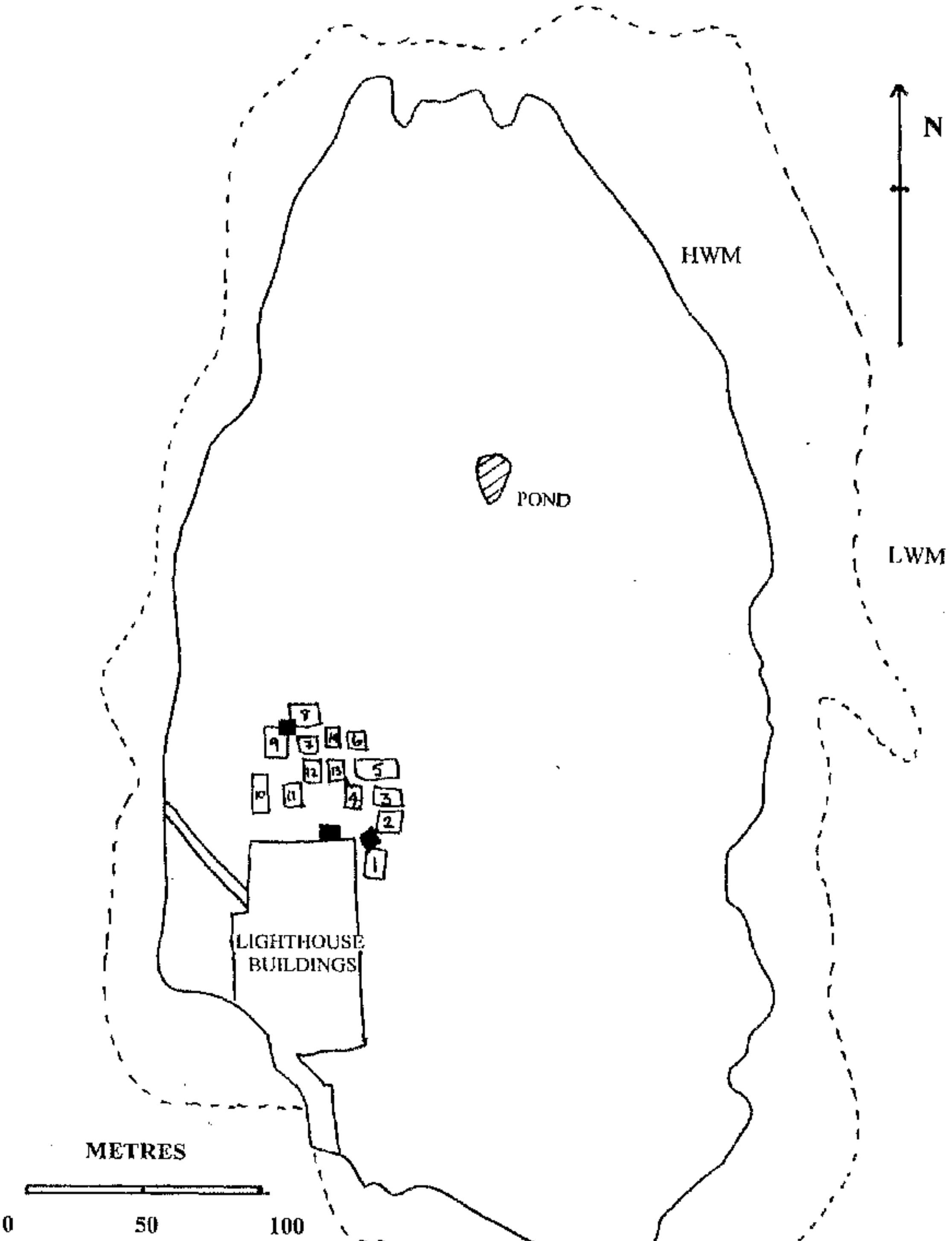


Figure 4. Coquet Island, detailing the location of the spray/ study plots (open rectangles) and observation hides (closed squares). The study plots labelled 1-10 were used in 1994. The same plots were used in 1995 along with the four additional areas labelled 11-14.

Figure 5. View from the lighthouse tower of the study plots and hides.

Nest History Records

In this study birds were observed during the pre-laying courtship period (from the beginning of May), and study areas chosen in the centre of the colony, according to maximum nest density (study area: 1994 $1020m^2$; 1995 $1205m^2$). Once egg-laying had begun, the study site was visited at approximately the same times, twice daily, and new nests staked with a bamboo cane and numbered flag to the N. E. of the scrape. Each egg was marked with indelible ink on the day of laying, according to laying sequence (*a*, *b*, *c* egg etc.), nest number and date. Eggs were weighed (to the nearest 0.5g) using a 50g capacity Salter spring balance, and maximum length and breadth measured (to the nearest 0.1 mm) using plastic dial callipers. Egg volume was calculated from the equation;

Volume (cc) = length x breadth^2 x 0.000478 (after Dunn 1972).

Tern chicks are very mobile, and tend to wander considerable distances (Morris *et al.* 1991, Saino *et al.* 1994), and this can affect estimates of survival. In order to prevent this, towards the end of incubation, nests were fenced in individual 13 mm mesh chicken wire surrounds (*c.* 25 cm high). Each enclosure was pegged to the ground and provided with a wooden shelter for the growing chicks, since the fencing denied them access to thick vegetation or burrows in which to hide. This procedure has been used successfully in a number of other studies on terns (Langham 1968, Nisbet & Drury 1972, Monaghan *et al.* 1989). In this study over 200 nest surrounds were erected, and in some of these adverse effects were recorded; two chicks showed leg and wing damage respectively, possibly due to entanglement in the wire mesh, and two surrounds were removed early to avoid excessive beak damage of chicks trying to escape. Other studies have reported similar problems with fencing (Langham 1968, Nisbet & Drury 1972, Horn pers. comm.).

During incubation egg loss was monitored and late laying recorded. Near to expected hatching (*c.* 18 days) nests were checked twice daily. Hatching success was recorded as the proportion of incubated eggs which hatched, that is where chicks were able to break free from the egg completely. Eggs that had not hatched after four weeks were examined for damage and any signs of embryonic development. On hatching all chicks were individually marked with colour coded insulation tape around the tarsus (*a* blue, *b* white, *c* green), the nest number recorded on the leg flag. The chicks were then weighed (to the nearest 0.5g) using a 50g capacity Salter spring balance, and the maximum chord wing length was measured (to the nearest 0.1 mm) using a stopped metal rule. This measurement did not include the fluffy

Figure 6. Collecting tern chick measurements.

down on young chicks, but did include the primaries as they grew through. Subsequent chick measurements (using a 200g capacity spring balance as necessary) were taken approximately every two days through the first 10, and thereafter every four days, with fledging measurements taken on day 20 (see **Figure 6**).

Nests were visited regularly throughout the chick rearing phase, and all chick losses were recorded. No measurements were taken during a period of rain to avoid unattended chicks becoming wet. Once all the surviving chicks in a brood had reached 14 days the leg flags were removed and replaced with BTO metal rings. Chicks surviving to 20 days were considered fledged (even if found dead subsequently), since some were capable of flight a few days later and were able to escape from their enclosures. In order not to separate broods, when the oldest chick in the brood reached 20 days the enclosure was removed and all the remaining chicks were considered fledged, unless discovered dead before 20 days of age. At the end of the breeding season, the exact size of the study area was measured and the position of the study nests recorded, for calculating nest density (see chapter 5).

Establishment of experimental groups

To obtain an equal spread of laying dates between experimental and control groups, and to minimise any effects due to differences between groups in parental age or other qualities (Nisbet *et al.* 1984), study pairs were selected from the centre of the colony during the peak of laying and one pair commencing laying at the same time (measured to the nearest half day) was randomly assigned to each of the different treatment groups.

Egg Removal and Storage

Eggs removed from nests on the day of laying as part of brood manipulation experiments (see chapters 3 & 5-9), were laid in cotton wool in a polystyrene box. On return to the accommodation buildings they were immediately removed from the cotton wool and individually placed in labelled re-sealable plastic bags, and in egg trays in a cool box. The eggs were turned daily and the ambient temperature inside and out of the box recorded with a digital thermometer accurate to ± 1 °C, every 6 hours. As closely as possible the eggs were maintained at a temperature of 11 °C, by storage in either the living accommodation or out-buildings according to the daily weather conditions and temperature. In 1995 no eggs were kept in storage longer than 3 days, although duration of storage for some eggs in 1994 was longer (see appendices 1 & 2).

Fourth laid *d* eggs collected for composition analysis in 1995 (see chapter 6) were hard-boiled on return to the accommodation buildings and, after cooling, sealed in labelled parafilm and frozen until subsequent laboratory analysis in Glasgow. In 1995 some experiments involved the swapping of entire clutches between nests (see chapter 7). In order that no nests were left empty during this process, plaster model eggs were temporarily substituted. All egg collection and egg and chick movements between nests were done under licence from English Nature (licence numbers: 1994 **SB:21:94**; 1995 **SB:36:95**).

Observational data

Once the study areas had been chosen, two green canvas hides were set up in order to observe activities at the study nests. A permanent shed on the island also afforded a reasonable view of some of the study plots and so was used as a hide in both years. Observational data were collected on a subset of the study nests located within 25 m of an observation hide. This was close enough to allow clear views of the nest and of the incoming adults and food delivered with or without the use of binoculars. Later in the chick rearing phase as the vegetation grew up (especially perennial nettles and bugloss) some growth was cleared to allow continued uninterrupted views of the nests.

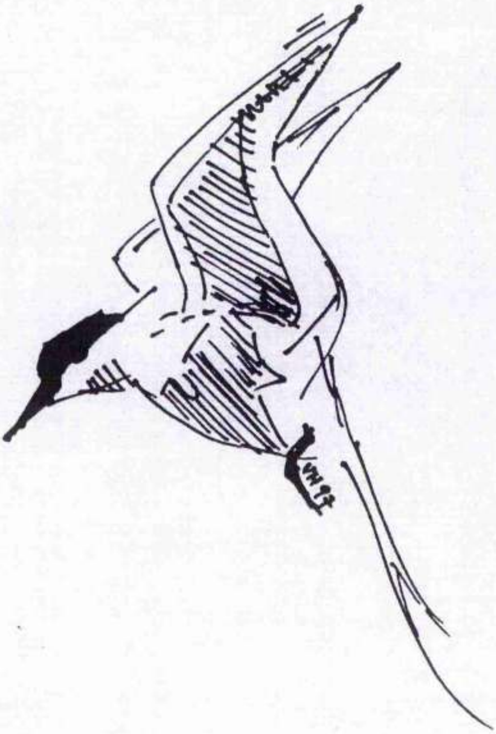
During incubation and chick rearing adult attendance at the nest was recorded using Instantaneous Scan Sampling (Altmann 1974). Every 15 minutes, for as many nests as possible, the nest status was noted, recording the two adults of each nest as either present (standing/preening), incubating/brooding or absent. For detailed monitoring, visible nests were grouped according to proximity, with all the treatment groups represented in each set. No more than 12 nests were observed during one watch to avoid missing any feeding events. Hide watches were generally 3 hours in length (never less than 2). To avoid bias towards any particular time of day, the timing of an average of three watches per day was randomised over the daylight hours. Each set of observation nests was rotated on a timetable for equal representation throughout the day and chick rearing period, and data on each individual observation nest collected consistently, being watched at least once every 2 or 3 days.

When adults approached the nest with food, the prey species and size class were recorded. This is possible because common terns carry food cross-wise in their bills and the rate of provisioning can be monitored by direct observation. Fish were assigned to either Ammodytidae (long slender fish), or to Clupeoideae (broad fish with bifid tail). It is possible therefore that a number of gadoids (whiting etc.), previously recorded as food items of terns on the Farne islands (Pearson 1968, Langham 1968, Horn 1994), were included in the Clupeoid category, being broad fish sometimes caught in the area. However, closer examination of 'Clupeoids' found on the colony site (lost during feedings) revealed that they were almost exclusively sprat, suggesting that this was not a large source of error. Prey items falling into neither of these fish categories, were recorded as 'other' (either unknown, sticklebacks or invertebrates) but this category only made up a very small proportion of the diet in either year. The size of the fish was estimated with reference to the adults bill and head (bill & head *c.* 8 cm length), and the prey items grouped into four size classes (size class 1 0-4 cm; 2 >4-8 cm; 3 >8-12 cm; 4 >12 cm).

The energy content of the prey items was estimated using the conversion factors for the appropriate species and size class published by Harris & Hislop (1978). An error check was completed by presenting series of fish (that had been accidentally dropped by adults at the colony) to observers, briefly and at a distance, in pliers decorated with reference to the size and markings of the head of an adult common tern. We found no significant error, or bias in categorisation of fish by different observers (1994 Philippa Bond & V. H., 1995 Moira Malcolm & V. H.).

The fate of prey items delivered to the nest was also recorded; if it was eaten by the adult itself or begged by its mate, lost or dropped as a result of a kleptoparasitic attack, or most commonly successfully consumed by the chick. If the same item was repeatedly presented to the chick, usually through difficulty in feeding the chicks because of harassment by kleptoparasites, the number of presentations was recorded but the item itself only recorded once. Other occurrences of interest during hide watches, such as any predation events or disturbance, were also recorded and the weather conditions noted.

Chapter 3 : A Within-Clutch Trade-Off Between Egg Production and Rearing



The data presented in this chapter were published in

V. Heaney, P. Monaghan, *Proc. R. Soc. Lond* B (1995) 261, 361-365

Introduction

Avian brood-manipulation experiments have strongly influenced the development of life-history theories, particularly in relation to the evolution of clutch size (Lessells 1991, Roff 1992, Stearns 1992). David Lack initially suggested that clutch size is set by the number of young parents can adequately provision (Lack 1947); this has become known as the Lack value. Subsequently, brood-enlargement experiments have shown (in many bird species) that parents can apparently rear more young than the number of eggs they lay: this is taken as important empirical evidence that observed clutches are less than the Lack value (Lindén & Møller 1989, Partridge 1989, Dijkstra *et al.* 1990, Godfray *et al.* 1991, Lessells 1991, Roff 1992, Stearns 1992).

Such brood enlargement experiments involve giving parents extra eggs or chicks taken from another pair. This protocol is presumed to mimic realistically the cost of producing additional young because it is assumed that the major reproductive constraints operate after the young hatch. However, the fact that these experiments fail to include the full cost of an increased brood - because they omit the process of egg production and generally most of the incubation demand - is potentially very important. It is possible that the inclusion of these costs could influence the outcome of such experiments, so rendering many previous interpretations invalid (Partridge 1989, Dijkstra *et al.* 1990, Godfray *et al.* 1991, Lessells 1991, Monaghan *et al.* 1995). The aim of this study was therefore to examine this possibility by comparing the reproductive performance of parents given an extra egg or chick with those having to lay the additional egg themselves.

Methods

The study was conducted on common terns *Sterna hirundo* breeding on Coquet Island, Northumberland in 1994. Common terns lay between 1-3 eggs and, in common with most larids, are indeterminate layers: removal of the first laid egg shortly after laying results in the production of an extra egg (Haywood 1993a). It is therefore possible to manipulate parents into producing an additional egg, and thereby to make them incur the full cost of an increased brood size (i.e. they lay and incubate the egg as well as rear the additional chick). By giving parents an egg from another pair as soon as their own clutch is complete, it is also possible to make pairs incur incubation and rearing, but not laying, costs. The aim of this study was to compare the chick rearing capacity of such full-cost and free-egg pairs with pairs obtaining the additional young by the methods used in other studies, i.e. being given a free chick, thus incurring rearing costs only.

To ensure that the brood enlargement was within the normal range, an important consideration in such studies (Lindén & Møller 1989), the clutch/brood size of birds laying two eggs was increased by one. In the full-cost group, the first-laid egg was removed within 12h of laying and returned to the nest approximately two days after the laying of the last egg, thus maintaining the normal hatching interval between chicks. To set up this group, eggs were removed from 30 pairs in total: 9 laid a further two eggs; 11 laid a further three eggs; and 2 one more egg. This was not significantly different from the ratio of two-, three and one-egg clutches laid over the same period in the colony as a whole ($X^2_2 = 0.53$, n.s.). The remaining eight pairs moved nests site and were not studied further. Only those with an intended clutch size of two, laying three eggs in total, were used in this experiment. (The 11 pairs laying four eggs in total, and the small sample of two pairs with an apparent intended clutch of one, are not considered further here).

The free-egg group was given an additional third-laid egg (produced by another female laying on the same day) on completion of their own clutch of two. The free-chick group was given a newly hatched, third-hatched chick the day after their own two chicks hatched. The three treatment groups used are summarised in **Table 1**. To obtain an equal spread of laying dates between treatment groups and to minimise any effects due to differences in parental age (Nisbet *et al.* 1984), study pairs were selected from the centre of the colony during the peak of laying and one pair commencing laying at the same time was assigned to each treatment group. A control group of unmanipulated pairs with clutches of two was also monitored. The overall spread of laying in the study birds was nine days.

Table 1. *The brood manipulation treatments used.*

Treatment	Intended clutch	Eggs laid	Eggs incubated	No. pairs	No. hatching all eggs	Initial brood
Free Chick	2	2	2	14	14	3
Free Egg	2	2	3	18	11	3
Full Cost	2	3	3	9	7	3
Unmanipulated	2	2	2	17	12	2

All eggs were measured (volume and fresh mass) on the day of laying and the chicks within 36h of hatching: nests and chicks were marked and breeding success, chick growth and provisioning were recorded using standard methods (see chapter 2). Instantaneous growth rates over the period of linear growth were calculated using the formula:

$$R = (\ln W_2 - \ln W_1)/ (t_2 - t_1),$$

where R = instantaneous growth rate, W = mass and t = time. Fish brought to chicks are carried in the adult's bill, and thus prey species could be identified, their size estimated with reference to the adult bill and their energy content calculated from the conversion factors given in Harris & Hislop (1978). Observations were made on those nests within 25m of hides during an average of three 3h watches per day randomised over the daylight hours (free-chick, free-egg and full-cost groups: 20, 22 11 and 15, 18, 8 nest watches on 7, 8 and 3 nests in weeks 1 and 2 respectively). Non-parametric statistical tests have been used in comparisons where variances between groups were non-homogeneous, or distributions non-normal (Sokal & Rohlf 1981, Siegel & Castellan 1988).

Results

There was no significant difference between the full-cost, free-egg and unmanipulated birds in hatching success, which was high in all groups (76-89%, Kruskal Wallis ANOVA, X^2_2 = 0.50, n.s.). To standardise the initial brood size at three, and take into account the fact that in the free-chick group the third young was not exposed to losses during the incubation stage (and this group could thus have a higher success for this reason), only pairs who hatched all of their eggs are included in the analyses of chick rearing capacity.

As expected from previous brood manipulation studies, birds given a free chick reared significantly more young than unmanipulated birds that laid and hatched two eggs (unmanipulated birds mean 1.58 ± 0.15 s.e. chicks fledged, n = 17; free-chick 1.93 ± 0.07 s.e., n = 14, Mann Whitney U_{29} = 55, p = 0.041), but this was the only treatment group that did so. There was a highly significant difference among the experimental groups in the number of young fledged (see **Figure 1*a***, one-way ANOVA $F_{2,29}$ = 5.8, p = 0.007), and a comparison of the values in each group showed that chick-rearing success followed the order predicted by the degree of cost incurred, with the full-cost birds tending to have the lowest success, and the free-chick birds the highest (Jonckheere Test for Ordered Alternatives, Siegel & Castellan 1988, p = 0.003). Thus both incubation and egg-laying costs reduced young production in an apparently additive manner. In all three treatment groups, the majority of last-hatched chicks died within a few days, and most of the first-hatched chicks fledged (see **Figure 1*b***). However, a large difference between groups occurred in the survival of the second-hatched chick, which was very low in the full-cost group (see **Figure 1*b***).

In the full-cost group, the first-laid egg was returned to the nest after laying was complete; this means that the second-hatched chick is from the additional (third-laid) egg. It is therefore important to consider the possibility of reduced egg quality and small hatchling size influencing its survival (Monaghan *et al.* 1995). There was no significant difference among the groups in volume or fresh mass of the second-hatched egg (Kruskal-Wallis ANOVA X^2_2 = 0.23, n.s. and $F_{2,29}$ = 0.50, n.s. respectively), or in the size of the resulting chick, a good indication of egg quality (Williams 1994; one-way ANOVA wing length $F_{2,27}$ = 0.08, n.s.; mass $F_{2,28}$ = 0.36, n.s.). Nor was there any difference among groups in its hatching date (one-way ANOVA $F_{2,29}$ = 2.20, n.s.). These data are shown in **Table 2**.

Table 2. *Egg and hatchling parameters for second-hatched chicks in the three experimental groups. (Probability values are based on* ANOVAS*, see text for details).*

Treatment group	mean	s.e.	min.	max.	*n*	*p*
Egg mass (g)						
Free Chick	19.70	0.28	18.50	22.50	14	
Free Egg	19.23	0.47	16.50	21.00	11	0.77
Full Cost	19.21	0.55	16.50	21.00	7	
Egg volume (cc)						
Free Chick	17.56	0.48	15.63	20.96	14	
Free Egg	17.97	0.49	15.81	19.83	11	0.64
Full Cost	18.12	0.30	16.72	20.87	7	
Hatching date (days after 1 May)						
Free Chick	38.14	0.78	34.00	44.00	14	
Free Egg	39.09	0.78	35.00	44.00	11	0.11
Full Cost	40.71	0.42	39.00	42.00	7	
Hatchling wing length (mm)						
Free Chick	17.5	0.03	16.0	19.0	13	
Free Egg	17.3	0.06	15.0	21.0	10	0.92
Full Cost	17.4	0.04	16.0	19.0	7	
Hatchling mass (g)						
Free Chick	16.38	0.64	10.50	19.00	13	
Free Egg	15.91	0.85	11.50	20.50	11	0.52
Full Cost	15.43	0.72	13.00	17.50	7	

However, the pattern of mortality of this chick differed; although there was no significant difference among the groups in the proportion of second-hatched chicks dying in the first week post-hatching (see **Figure 2**, $X^2_2 = 5.48$, n.s.), mortality of these chicks was negligible in the second week of life in the free-egg and free-chick groups (with only one of 22 chicks dying), but was high in the full-cost group (three of 5 chicks dying, Fisher Exact Test, $p = 0.007$, see **Figure 2**). This reflected differences between groups in feeding rates of the broods: the rate of energy delivered per chick per hour did not differ among the groups during the first week after hatching, but in the second week the rate of provisioning of the brood in the full-cost group was less than a third of that in the other experimental groups (see **Figure 2**). Moreover, there were differences in the growth of the surviving chicks. Initially brood growth rates were similar, but, by near fledging, growth in broods in the full-cost group was significantly less than that in the other two groups, with the chicks in these broods losing mass at a time when chicks in the free-chick group continued to gain mass (see **Figure 3**).

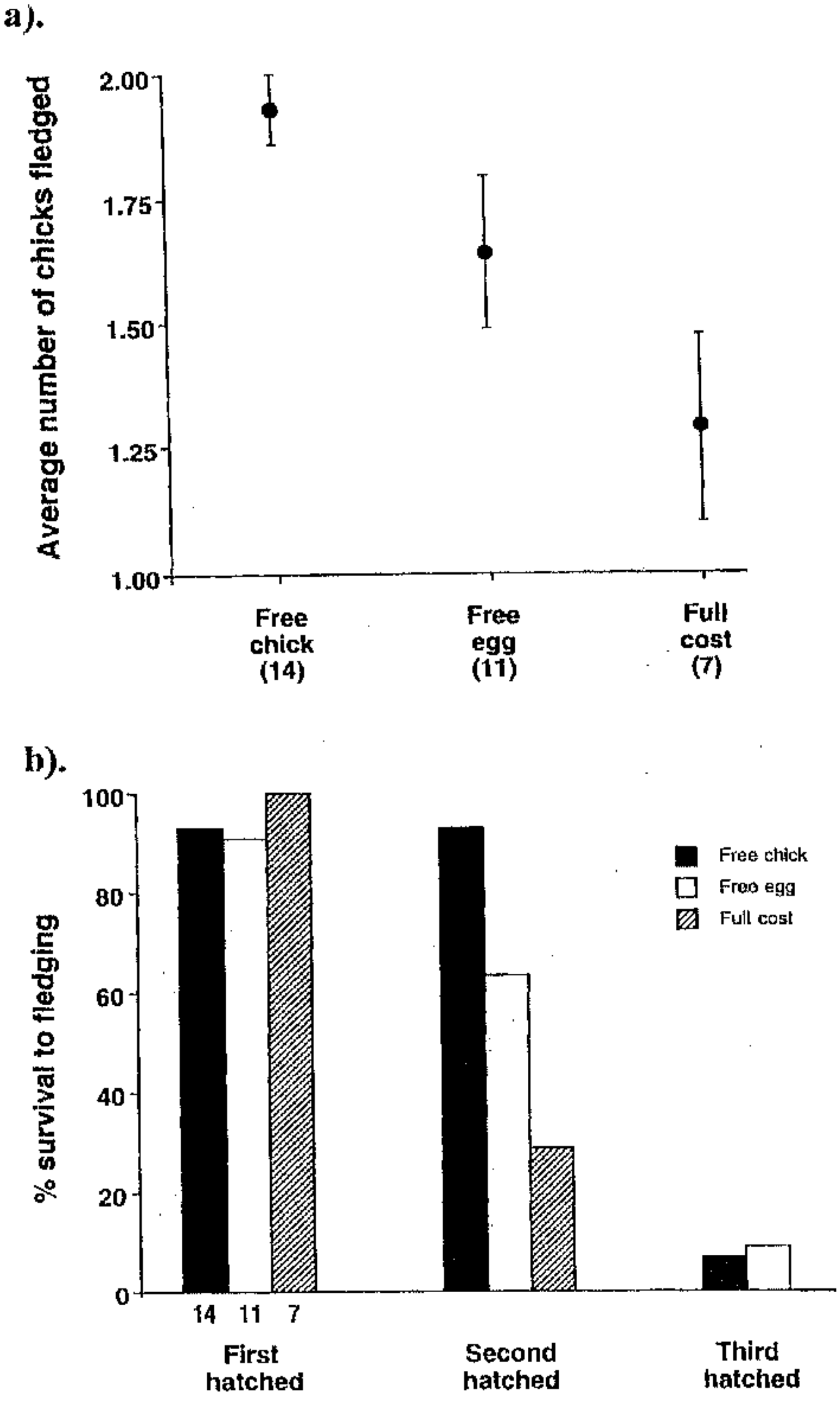


Figure 1. (*a*) The mean ± s.e. number of chicks successfully fledged according to treatment group. (*b*) The percentage of chicks surviving to fledging in each group in relation to hatching order. There was no significant difference between the experimental groups in the survival of first- or of third-hatched chicks, but the survival of second-hatched chicks was much poorer in the full-cost birds ($X^2_2 = 11.04, p < 0.004$).

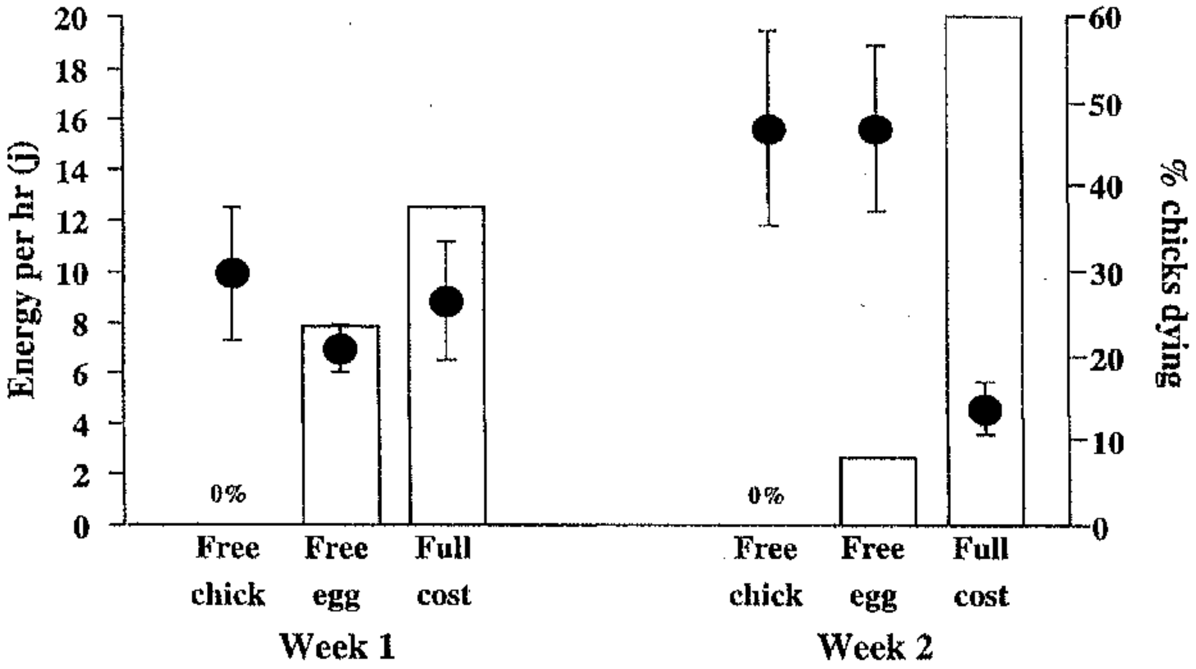


Figure 2. The mean energy per chick per hour (solid circles, ± s.e.) delivered to the brood by pairs in each treatment group during the first and second weeks after complete hatching of the brood. There was no significant difference between the groups in the first week, but a highly significant difference in the second week, with the distribution of values among the groups following that predicted by the degree of cost incurred with the Free Chick Group tending to have the highest and the Full Cost Group the lowest delivery rates (Kruskal Wallis ANOVA, based on all data week 1 $X^2_2 = 0.19$, n.s.; week 2 $X^2_2 = 11.04$, $p = 0.004$; if based on means per nest $X^2_2 = 0.10$, n.s. and $X^2_2 = 6.69$, $p = 0.035$; Jonckheere Test for Ordered Alternatives $p = 0.025$ and $p = 0.029$). The histograms show the percentage of second-hatched chicks dying in each group in each week.

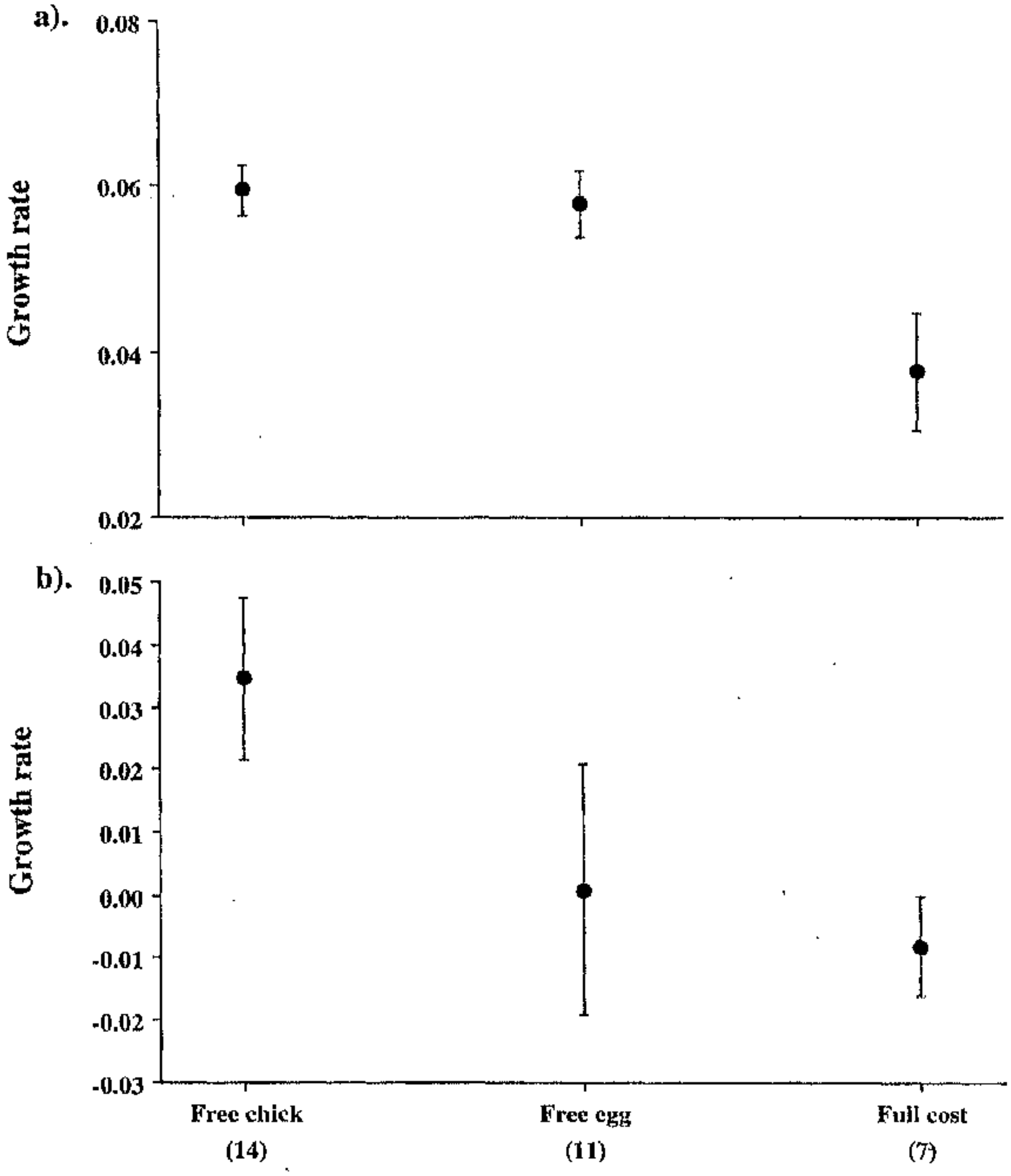


Figure 3. The brood mean instantaneous growth rate (*a*) wing length; and (*b*) body mass (± s.e.; see methods for calculation details) in each of the treatment groups shortly before fledging (17-20d). There was a significant difference between the groups (one-way ANOVA wing $F_{2,29} = 6.18$, $p = 0.006$ and mass Kruskal Wallis ANOVA $X^2_2 = 6.30$, $p = 0.042$), and the distribution of values among the groups followed that predicted by the degree of cost incurred, with the Full Cost Group tending to have the lowest and the Free Chick Group the highest growth rates for both parameters (Jonckheere Test for Ordered Alternatives $p = 0.001$ wing, $p = 0.021$ mass).

Discussion

These results clearly show that the way in which broods are enlarged has an important effect on the extent to which parents can rear additional young. Only when laying and incubation costs were excluded did the common terns in this study successfully rear a larger brood. The greater the degree of additional cost, and hence the closer the experimental protocol mimicked the natural situation the birds would face in producing more chicks, the poorer the breeding success of the parents.

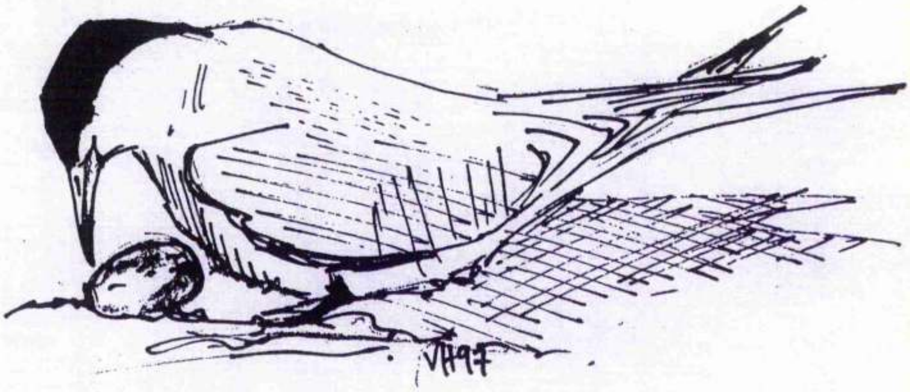
This relatively poor performance of the full-cost and free-egg groups appears to be mediated by a reduced capacity of the parents to provision the brood, rather than through any effect on the quality of the additional egg. There was no evidence that the extra egg produced was of a reduced quality, which is in contrast to a previous study in the lesser black-backed gull *Larus fuscus* (Monaghan *et al.* 1995). However, in the latter study birds were induced to lay a fourth egg which resulted in a smaller hatchling whose survival as the third-hatched chick in a brood of three was much less than the third-hatched chicks in control broods of three, and most of the mortality occurred less than five days after hatching (Monaghan *et al.* 1995). Because the typical maximum clutch in both common terns and lesser black-backed gulls is three, the production of additional eggs outside this range may have a greater impact on egg quality.

The difference in the performance of the common tern groups lay in the fate of the second-hatched chick. That there was no survival difference of this chick among the groups in the first week of life further argues against any egg or chick quality effect. Rather the survival difference coincided with a difference in parental provisioning rates, which was most marked in the full-cost group. Even for surviving chicks, growth rates close to fledging in the full-cost group were lower than in the other two groups, presumably again reflecting a lower parental provisioning rate. However, it was not possible to examine this in detail due to the very small sample of visible nests remaining in that group by this stage. The way in which performance declined in relation to the degree of costs incurred suggests that the incubation and chick rearing costs have a cumulative negative effect on the foraging capacity of parents and hence on the growth and survival of their chicks.

Thus the within-clutch cost of egg production demonstrated in this study appears to be mediated by a negative effect on parental condition, resulting in a reduced capacity to provision the young. Because the study used birds laying a clutch of two for the experimental manipulation, it is possible that these individuals are towards the lower end of the quality spectrum and therefore those most likely to show such an effect. Their central nesting position in the colony makes it unlikely that they were largely young birds (Nisbet *et al.* 1984). It was not possible to distinguish between male and female parents in this study, but it is possible that both are affected, as courtship feeding of females by males plays an important part in egg production (Nisbet 1973).

Life-history theory assumes that reproduction is costly and elucidating the nature of these costs is a prime focus of research (Roff 1992, Stearns 1992). It has generally been assumed from previous avian brood enlargement studies that the main costs in producing additional young operate as a between- rather than within-clutch trade-off, via a reduction in residual reproductive value (Smith *et al.* 1987, Gustafsson & Sutherland 1988, Pettifor *et al.* 1988, Gustafsson & Part 1990, Roff 1992, Stearns 1992). However this study provides the first demonstration of a within-clutch trade-off between producing and rearing extra eggs; when parents incur the full cost of producing as well as rearing additional young, their apparent capacity to rear an enlarged brood is negated. It is clear from this study that the exclusion of costs associated with egg production has been a serious omission in previous brood enlargement studies, and these findings cast doubt on the evidence that the most common clutch size is less than the Lack value.

Chapter 4 : Optimal Allocation of Effort Between Reproductive Phases: The Trade-Off Between Incubation Demand and Subsequent Brood Rearing Capacity



The data presented in this chapter were published in

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Introduction

Investigation of the ways in which animals partition their reproductive investment within and between breeding attempts is a key component of life history theory. A prime focus of study has continued to be the elucidation of the factors that determine the optimal clutch size. Theory concerned with the evolution of clutch size is now generally applied to a wide variety of animals and plants that produce embryos in batches (Godfray *et al.* 1991). For species that show parental care, the main emphasis has been on the constraints imposed by brood rearing costs and on between-brood trade-offs mediated through effects of increased effort on parental survival and fecundity (Williams 1966, Dijkstra *et al.* 1990, Roff 1992, Stearns 1992). While it has been recognised that trade-offs operating within a breeding cycle may also play a part in determining clutch size, how the need to optimise effort between different phases of the reproductive process influences the number of embryos produced has received relatively little attention (Winkler & Walters 1983, Martin 1987, Partridge 1989, Lessells 1991).

Avian reproduction is a useful model for studies of the partitioning of investment during reproduction since it involves three distinct phases: egg production, incubation and chick rearing. While the relative demands of each phase will vary between species and between individuals, the success of a particular breeding attempt will depend on individuals optimising their allocation of effort between phases. Investigation of this process requires independent manipulation of the demands incurred in each phase. Avian brood manipulation studies have concentrated on the last two phases, increasing or decreasing the brood by giving the parents extra (or removing), eggs or chicks. The effects of increased incubation demand on the success of the breeding attempt have not been examined independently of the chick rearing effort, and demands associated with egg production have been largely ignored. Egg production in many bird species is difficult to manipulate experimentally. However, previous experiments with gulls and terns where birds were induced to lay one extra egg in addition to their intended clutch, have shown that increased effort during egg production has important consequences for the outcome of the breeding attempt. Reduced quality of the additional egg has negative effects on offspring survival (Monaghan *et al.* 1995) and the inclusion of egg production costs removes the capacity of the parents to rear an enlarged brood (chapter 3), thereby highlighting the importance of the early stages of reproduction.

The incubation phase has often been assumed to be a relatively undemanding period of the breeding cycle, (e.g. King 1973, Walsberg & King 1978), particularly in bi-parental incubators like gulls and terns where the off-duty parent has the opportunity to replenish its reserves. Thus, provided that the parent can actually cover the clutch with brood patch, the increased demand of heating more eggs might not be expected to affect parental performance after the brood hatches. However, recent measures of the energetic effort associated with heating eggs have shown that these can be relatively high (Moreno *et al.* 1991, Tatner & Bryant 1993). Furthermore, the summation of even a small increase in effort across the whole incubation period may have significant effects. Various experimental studies have reported a reduction in the efficiency of incubation following an increase in the number of eggs incubated, including a prolonged incubation period (e.g. Baltz & Thompson 1988, Coleman & Whittall 1988, Smith 1989, Moreno & Carlson 1989, Székely *et al.* 1994, Siikamaki 1995), reduced hatching success (e.g. Briskie & Sealey 1989, Moreno *et al.* 1991, Siikamaki 1995) and increased hatching asynchrony (Moreno & Carlson 1989). While these findings suggest that parental effort during the incubation phase is subject to constraints, whether an increase in incubation demand alone can have negative consequences for the chick rearing capacity of the parents, independent of any effects on the efficiency of incubation itself, has not yet been established. This is because the key experiment, which involves isolating the increased incubation effort from the demands of rearing an enlarged brood, has hitherto not been carried out. This paper reports the results of such an experiment in common terns *Sterna hirundo*, in which incubation effort was manipulated independently of that of egg production and chick rearing.

Methods

The study was conducted on common terns breeding on Coquet Island, Northumberland, in 1995. We compared the breeding performance of birds given an extra egg during the incubation phase only (experimental group, 21 pairs), with that of unmanipulated control pairs subjected to the same level of disturbance (control group, 20 pairs). Common terns lay 1-3 eggs. Pairs laying a clutch of two were used in this experiment, so no pair was made to incubate a super-normal clutch. To obtain an equal spread of laying dates between experimental and control groups, and to minimise any effects due to differences between groups in parental age or other qualities (Nisbet *et al.* 1984), study pairs were selected from the centre of the colony during the peak of laying and one pair commencing laying at the same time (measured to the nearest half day) was randomly assigned to each of the two groups. The overall spread of the initiation of laying in the study birds was 9d (23-31 May) and the mean date of initiation of laying did not differ significantly between groups (laying date, measured as days from 1 May: mean laying date of controls group 27.4 ± 0.50 s.e., n = 20 nests; experimental group 27.5 ± 0.52 s.e., n = 21 nests; $t_{39} = 0.14$, $p = 0.89$, n.s.).

Experimental pairs laying a clutch of two eggs were given an additional egg (a third-laid egg produced by another female laying at the same time) 2d after their own second egg was laid. This additional egg was removed just prior to hatching (i.e. as soon as the second chick hatched, or 2d after the first hatched if their second egg did not hatch) and returned to its original nest, where it was not monitored further. All eggs were measured (volume and fresh mass) on the day of laying and all chicks measured (mass and wing length) within 24h of hatching. Chick growth was monitored at approximately 3-day intervals until they either fledged or died, which was known for all chicks. Fledging mass was taken as the mass at 20d, which was within 1-2d of the chicks departing from the nesting area. Fledging mass was not obtained for a small number of chicks that eluded capture at this stage. Instantaneous growth rates over the period of linear growth were calculated using the formula: $R = (LnW2 - LnW1)/(t2 - t1)$, where R = instantaneous growth rate, W = mass and t = time.

Since not all pairs fledged two chicks in either control or experimental groups, the sample sizes for chick parameters vary with chick survival, and are as indicated in the results. Parental nest attendance was studied during incubation and the first week after hatching during watches of 3h randomised over the daylight hours on those nests within 25m of the hides (24 watches on 10 control nests and 18 watches on 9 experimental nests during incubation; 19 watches on each during the first week after hatching).

Results

There was no significant difference between experimental and control pairs in the duration of the incubation period for the first or second egg (with all chicks hatching according to laying order), and thus the hatching date of the chicks in the two groups did not differ significantly (see Table 1), nor did the hatching interval between the first and second chicks (control 0.94 ± 0.81 s.e., $n = 17$; experimental 0.94 ± 0.71 s.e., $n = 17$; $t_{32} = 0.00$, $p = 1.0$, n.s.).

Table 1. *Hatchling parameters (measured on the day of hatching) for chicks in Control and Experimental nests. Data are compared using t-tests.*

Parameter	Experimental, mean ± s.e.(*n*)	Control, mean ± s.e.(*n*)	*p*
Duration of incubation			
a chick	22.50 ± 0.18 (19)	22.47 ± 0.17 (19)	0.92
b chick	21.24 ± 0.14 (17)	21.47 ± 0.15 (17)	0.28
Hatching date (days after 1 May)			
a chick	49.90 ± 0.56 (19)	49.90 ± 0.48 (19)	1.00
b chick	50.53 ± 2.48 (17)	50.91 ± 2.56 (17)	0.64
Hatchling mass (g)			
a chick	15.40 ± 0.45 (19)	14.45 ± 0.28 (19)	0.08
b chick	14.71 ± 0.28 (17)	14.30 ± 0.38 (17)	0.38
Hatchling wing length (cm)			
a chick	1.65 ± 0.03 (19)	1.63 ± 0.02 (19)	0.50
b chick	1.64 ± 0.02 (17)	1.67 ± 0.02 (17)	0.28

There was no significant difference in parental nest attendance between experimental and control pairs during incubation (the percentage time the nest was left unattended during incubation: control median 1.3%, Quartile deviation (QD) 2%, $n = 10$ nests; experimental median 2.67 %, QD 2%, $n = 9$ nests; Mann Whitney U-test $U_{17} = 42.5$, $p = 0.83$, n.s.) or during the first week after hatching when chicks are brooded by their parents (control median 22.73%, QD 19%, $n = 8$ nests; experimental median 11.29 %, QD 17%, $n = 9$ nests; Mann Whitney U-test $U_{15} = 28.5$, $p = 0.47$, n.s.). Hatching success of the original clutch did not differ between the two groups, and was relatively high in both groups (number of young hatched: control mean 1.80 ± 0.12 s.e., $n = 20$ nests; experimental 1.71 ± 0.14 s.e., $n = 21$ nests; proportions hatching zero, one and two chicks were as follows: control 5%, 10%, 85%; experimental 10%, 10%, 80%; $X^2{}_2 = 1.31$, $p = 0.80$, n.s.).

There was no significant difference between the groups in hatching mass or size in the first or second hatched chicks (see **Table 1**). Thus, there is no evidence that the increased incubation demand affected the efficiency of incubation itself.

There was no difference in the number of chicks fledged between the control and experimental groups, and the pattern of chick mortality did not differ between the two groups (examined using Kaplan-Meier survival functions for first and second hatched chicks, and by comparing the mean age at death for chicks in the two groups: control mean 11.79 ± 2.80 days, $n = 7$; experimental mean 8.17 ± 2.33 days, $n = 6$; $t_{11} = 0.97$, $p = 0.35$, n.s.). However, since the potential variability in the number of chicks surviving per nest is low, this is likely to be a relatively insensitive measure of the effects of increased costs (Ricklefs 1984). The growth and fledging mass of chicks, particularly that of the second chick, is likely to be most influenced by any depression of adult performance. The overall growth rate of the second hatched chick was significantly lower in the group that experienced increased incubation demand, as was the fledging mass (see **Figure 1**).

Table 2. *The proportion of pairs fledging zero, one and two chicks did not differ significantly between the two groups ($X^2_2 = 0.41$, p = 0.75, n.s.).*

	NUMBER FLEDGED			
TREATMENT	0	1	2	Mean ± s.e. (*n*)
Control	1 (5%)	9 (45%)	10 (50%)	1.45 ± 0.14 (20)
Experimental	2 (10%)	8 (38%)	11 (52%)	1.43 ± 0.14 (21)

This reduced growth rate of the second chicks in experimental pairs is likely to be mediated through an effect on adult provisioning capacity, which will be most evident in lower quality pairs. Since this study used pairs producing two rather than three eggs, overall these birds will tend to be at the lower end of the quality spectrum (Nisbet *et al.* 1984, Coulson & Porter 1985). (In an unmanipulated sample of 178 pairs at the study colony in 1995, 3% laid one egg, 28% laid two egg clutches and 69% laid three egg clutches). However, even within pairs laying two eggs, there is likely to be variation in adult quality, therefore the extent to which the effect of increased incubation demand on the parent's capacity to rear the brood was greater in lower quality pairs, was examined. Laying date is a good indicator of quality in common terns, with higher quality pairs laying earlier (Nisbet *et al.* 1984). Since the spread of laying was similar in the two groups, a comparison of the relationship between the laying date and the fledging mass of the second chicks in the experimental and control groups was carried out, to see if the degree of difference between them varied with adult quality. There was a significant relationship between laying date and second chick fledging mass in the experimental but not in the control group; in other words, the difference between experimental and control pairs in the fledging mass of second chicks was, as predicted, most marked in the poorer quality pairs (see **Figure 2**).

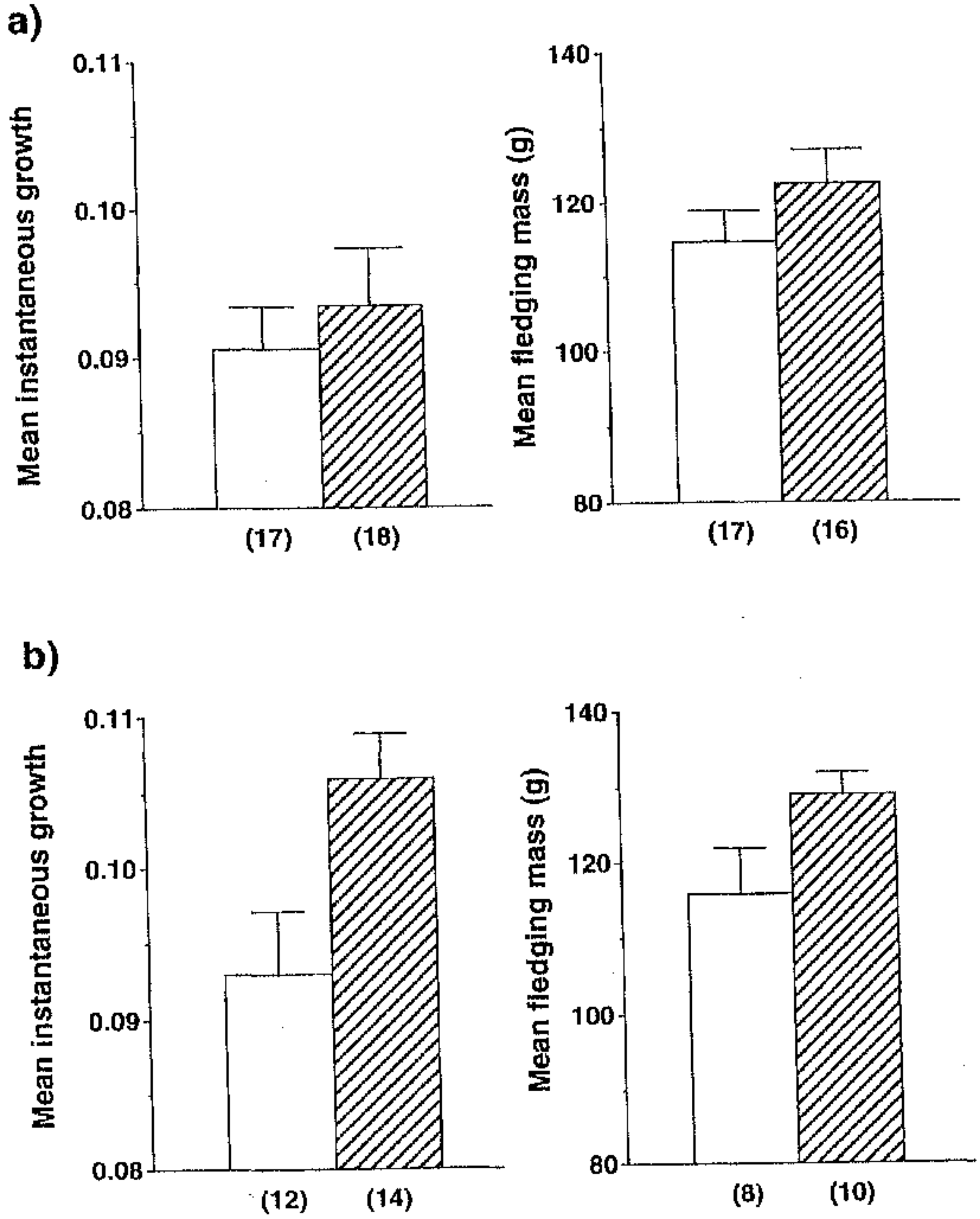


Figure 1. Mean (+ s.e.) instantaneous growth rate (expressed as the mean instantaneous growth rate of body mass over the period 2-20d) and mean fledging mass of (*a*) first and (*b*)second hatched chicks in the control (hatched) and experimental (open) groups. The numbers of chicks in each group are given below the histograms. In second hatched chicks, there was a significant difference between the two groups in both parameters, (instantaneous growth rate t_{24} = 2.53, p = 0.02; fledging mass t_{16} = 2.24, p = 0.04). The same trend was present in the first hatched chicks, but the differences were not significant (instantaneous growth rate t_{33} = 0.55, p = 0.58; fledging mass t_{31} = 1.25, p = 0.22).

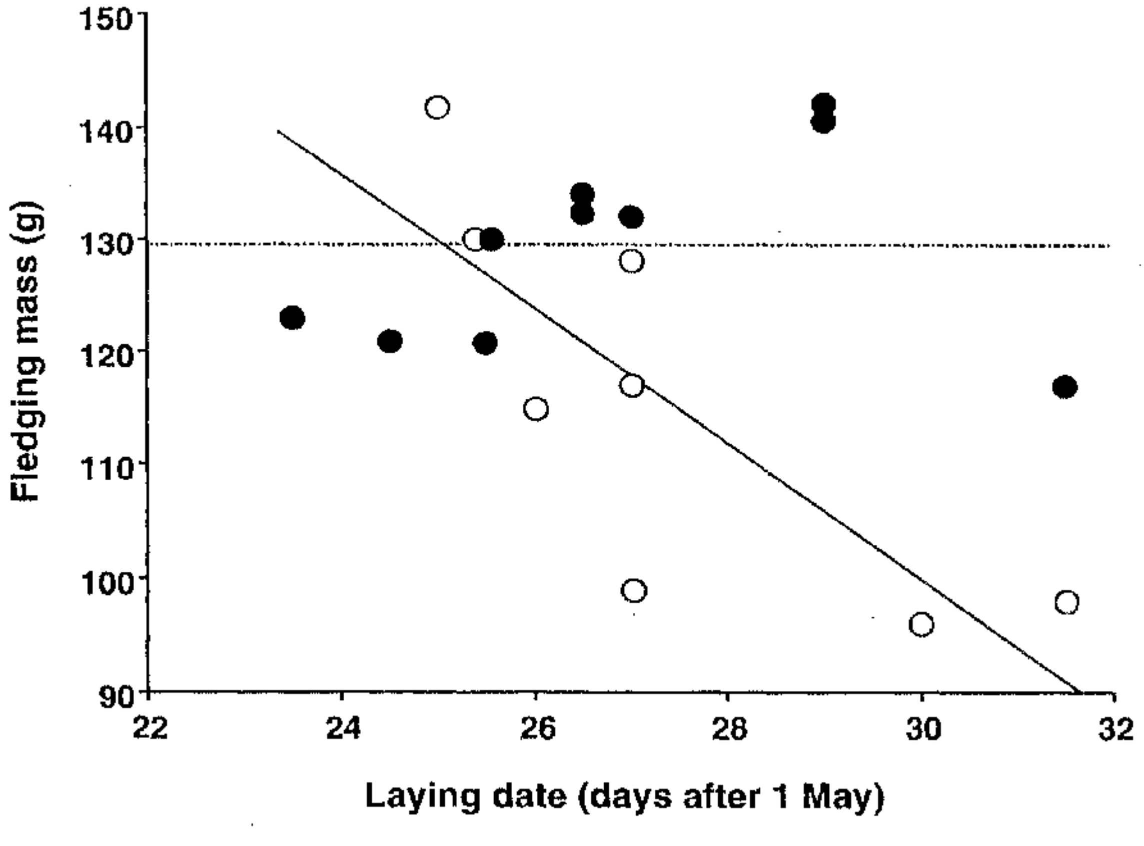


Figure 2. The relationship between parental quality (indicted by laying date) and the fledging mass of the second hatched chick in the control (solid circles, stippled line through mean value) and experimental (open circles, solid line) groups. The relationship was significant in the experimental group ($r_6 = 0.89$, $p = 0.003$, $y = -5.98x + 279.58$) but not in the control group ($r_8 = 0.04$, n.s., $y = 0.85x + 106.68$). This difference between experimental and control groups was highly significant (covariance analysis, difference in slopes $F_{1,16} = 9.84$, $p = 0.007$).

Discussion

The results of this study clearly demonstrate that an increase in the number of eggs incubated can significantly depress the capacity of the parents to sustain the growth of their brood during the chick rearing phase. The observed lower growth rate and fledging mass of second hatched chicks of experimental pairs in comparison with controls was presumably mediated through changes in the capacity of the parents to provision the brood as a consequence of the increased incubation demand imposed. The growth rate of the first hatched chick may have been maintained by selective provisioning by the parent and/or as a consequence of its superior competitive ability. Since first hatched chicks have a developmental and size advantage over second hatched chicks (Nisbet & Cohen 1975, Bollinger *et al.* 1990), the latter seems the most likely explanation. The survival chances of slower growing chicks which fledge at a lighter mass are generally lower in Larids (e.g. Ward 1973, Parsons 1976, Coulson & Porter 1985), and thus the increased incubation demand is likely to have reduced parental reproductive success. Furthermore, while in this study no difference between the experimental and the control groups was found in the proportion of chicks surviving to fledging, that breeding conditions were relatively good is indicated by the fact that relatively few chicks died; under harsher environmental conditions, effects of increased incubation demands on chick survival may be more pronounced.

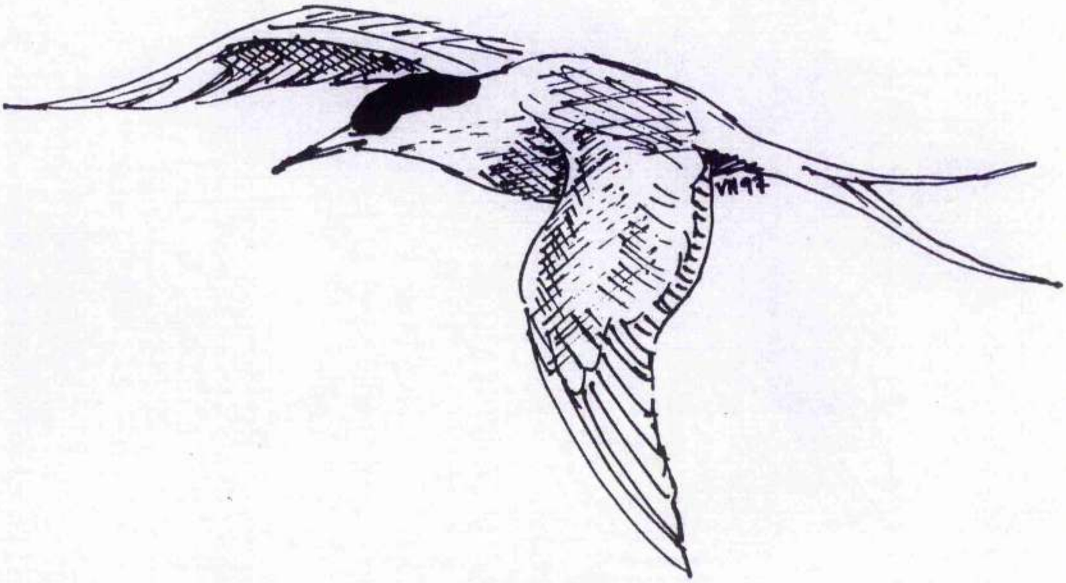
In contrast to other studies which have found that increasing the number of eggs incubated reduces the efficiency of incubation itself (e.g. Coleman & Whittall 1988, Briskie & Sealy 1989, Smith 1989, Moreno & Carlson 1989, Moreno *et al.* 1991, Székely *et al.* 1994, Siikamaki 1995), no such effects were found in this study; the duration of incubation, parental attendance, hatching success, chick size and body mass and the hatching interval between the two chicks in the original brood did not differ between the experimental and control pairs. While the hatching success of the extra egg was not monitored directly after it was returned to its original nest, it is unlikely that this egg could have been selectively subjected to a different incubation regime from the other two. Common terns turn their eggs frequently (Hume 1993), and all eggs in the clutch would therefore receive the same share of the incubation effort. The lack of an effect on incubation itself is not surprising, since clutches of three eggs are frequent in common terns, and the birds have three incubation patches.

Since each egg requires an input of heat to maintain a constant temperature, the heat output required to incubate the clutch will increase with clutch size where ambient temperature is below the thermoneutral zone. Such environmental conditions will be experienced frequently by birds breeding in temperate and higher latitudes. Increases in the respiration rate of incubating birds with increased clutch size have been found in several studies (Biebach 1981, 1984, Haftorn & Reinertsen 1985, Moreno & Carlson 1989, Moreno *et al.* 1991), and the consequent increased energy demand has been linked to an increase in food intake by incubating birds (Coleman & Whittall 1988). In bi-parental incubators like terns, loss of mass during incubation is likely to be much less than in uniparental incubators, since incubating birds have the opportunity to forage for themselves, albeit for a reduced time, and generally do not have to re-heat the clutch. However, the magnitude of the change in the number of eggs incubated, though still within the normal clutch size was increased by 50% from two to three eggs. Since in terns females may do up to 70% of the incubation and most of the early brooding of the chicks after the hatching, the increased incubation costs may not have been borne equally by both members of the pair (Uttley 1992, Hume 1993). In addition, since the study pairs were likely to be relatively low quality individuals (in that their initial clutch was two rather than the modal three), such an increase in the energetic costs may have substantially reduced the adults' body condition.

That individuals have varied, but limited, capacities to compensate for the deviations from their individual allocation of effort which the experimental protocol imposed is further illustrated in the variation observed within the experimental group. The difference between the experimental and control groups was the greatest in the late-laying, low quality individuals, who would be least able to compensate for an increase in the demands of incubation. Wright and Cuthill (1989) similarly found that later laying starlings appeared less able to compensate for an experimental increase in breeding effort, in this case that required in provisioning offspring. Such a state-dependant variation in response to experimental increases in costs is to be expected where individuals differ in phenotypic quality (McNamara & Houston 1996).

In experimental studies of the adaptive significance of life history decisions, the emphasis has largely been on between-brood trade-offs. However, as shown in this study, within-brood trade-offs in the allocation of effort to different phases of the reproductive cycle also occur, and will play an important role in determining key life history parameters such as the optimal clutch size. Furthermore, it cannot be assumed, (as it has been in many studies (see Roff 1992, Stearns 1992)) that manipulation of effort during the chick rearing phase alone represents an adequate experimental protocol for manipulation of the cost of producing the brood, since the important reproductive costs of the earlier phases are omitted. The exclusion of such costs may explain why the most common clutch size is often found to be less than the calculated optimum (Lessells 1991, Godfray *et al.* 1991, chapter 3).

Chapter 5 : Variation in Response to Egg Removal, Both Within and Between Years



An abridged version of the data presented in this chapter is to be submitted to Ardea

Introduction

Bird species can be broadly classified as determinate or indeterminate layers with respect to the control of clutch size and laying pattern. Laying patterns are a product of the mechanisms that control follicle growth and ovulation. Determinate layers are defined as species in which extrinsic factors perceived by the female, such as eggs present in the nest, are not involved in determining the number of large yolky follicles produced by the ovary or the number of follicles ovulated (Haywood 1993a), (e.g. albatrosses, auks and pigeons). Among indeterminate layers, both the number of large yolky follicles produced by the ovary and the number of follicles ovulated, depend on extrinsic factors. Larids (Paludan 1951), in common with many other bird species (Klomp 1970), produce more developing follicles than eggs, and are indeterminate layers. Tactile contact between the female's brood patch and the eggs stimulates the cessation of egg laying. Several studies on different gull species (Paludan 1951, Weidman 1956, Parsons 1976, Monaghan *et al*. 1995), show that larids can, in fact, be further classified as tactile indeterminate Type S layers, where contact with a single egg is sufficient to stop laying (Haywood 1993a). This means that egg removal leaving no egg in the nest is required for the female to extend the laying period and lay extra 'replacement' eggs.

Small seabirds such as terns have less leeway in their annual energy budgets than do larger species, and are considered to be working near the limits of their physiological capacity (Pearson 1968). They are iteroparus, showing a low annual reproductive output and relatively high adult survival. We should therefore expect them to be especially prone to nest desertion as the costs of reproduction increase (Monaghan *et al*. 1989). Having to lay more eggs increases the demand at this first stage of the breeding cycle, which may also have knock-on effects on the capacity to incubate and rear the clutch (see chapters 3 & 4, Monaghan & Nager 1997). Differences in the capacity of individuals to obtain resources for egg production, due either to changes in food availability or differences in foraging performance, will influence the extent to which replacement eggs can be laid (Monaghan & Nager 1997). Egg removal studies on larids have been mainly restricted to the larger gull species, with only a handful of studies on terns (Feare 1976, Rawson *in* Burns 1900, Nisbet pers. comm.). This study investigates the response of common terns, *Sterna hirundo*, to experimental egg removal during laying.

Since egg production is relatively expensive, (Monaghan *et al.* 1995, Perrins 1996, Monaghan & Nager 1997), and individuals differ in state and in quality (McNamara &

Houston 1996, Daan *et al.* 1990, Pettifor *et al.* 1988), we would expect the ability of individual birds to replace a removed egg to differ. The ability to replace the lost egg is likely to be related to the condition of the bird prior to and during laying. This 'condition factor' of individual birds will have a genetic component, combined with experience, but will also be modified by local environmental factors, such as food availability. This paper then, sets out to examine the inter-pair variation in response to egg removal in common terns, both within years and between years at the same colony.

Methods

The study was conducted on common terns breeding on Coquet Island, Northumberland in 1994 and 1995. Common terns lay between 1 and 3 eggs at intervals of approximately two days. At the time of nest initiation in each year, scrapes were checked twice daily and the first laid egg was removed from experimental nests within 12 hours of laying.

In 1994 first laid *a* eggs were removed from 30 pairs, within 12 hours of laying, and from 55 pairs in 1995. In some cases the removed egg was subsequently returned to the nest, to examine the effect of increased egg production and incubation on subsequent chick rearing capacity (see chapters 3 & 7). Unmanipulated control pairs were subject to the same level of disturbance as the experimental birds (i.e. eggs were handled), but laying was not manipulated. In 1994 the control group consisted of 164 unmanipulated pairs, and in 1995, 173 unmanipulated pairs. Birds were not marked during egg laying, because of the increased desertion risk (Nisbet 1981), but they were watched closely for any possible change-overs and considered to be the same birds if they continued to lay in exactly the same scrape after egg removal. Unmarked experimental pairs that deserted the nest site altogether after egg removal could not be followed, and are considered not to have replaced the removed egg.

To obtain an equal spread of laying dates between experimental and control groups, and to minimise any effects due to differences between the groups in parental age or other qualities (Nisbet *et al.* 1984), the study birds in both years were selected from a number of adjacent plots within the central part of the colony, over the week of early to peak laying. One or two pairs commencing laying at the same time (measured to the nearest half day), were randomly assigned to the experimental group and all other birds in the study area, laying at that time, were assigned to the control group. The overall spread of initiation of laying in the study pairs in both years was nine days (1994 27 May - 4 June; 1995 23 - 31 May).

In both control and experimental groups all eggs were measured (volume (cc) - length x breadth^2 x 0.000478, after Dunn 1972, and fresh mass) on the day of laying, and nesting success monitored (see chapter 2). Fresh mass and egg volume are typically highly correlated (Williams 1994). For example Reid & Boersma (1990), working on penguins found a correlation between the two of $r = 0.95$, $n = 1446$, $p < 0.001$, and in the two years of this study the correlation was similarly strong (1994 $r = 0.92$, $n = 418$, $p < 0.001$; 1995 $r = 0.91$, $n = 460$, $p < 0.001$). However the relationship between mass and volume in this study differed between the two years (ANCOVA of volume on mass, difference in slopes $F_{1,877} = 8.17$, $p = 0.004$). Subsequent investigations suggest that the egg mass data obtained in 1994 may have been influenced by the balance used, making between year comparisons difficult. Volume is therefore used as a measure of egg size when comparing between years.

Dates of first arrival, first laying, total breeding numbers and average clutch size were collected for the colony as a whole in both years. Data on wind speed, average daily temperature and total daily rainfall, during the months of the study, were obtained from the meteorological office at RAF Boulmer (6 miles NNW of Coquet Island). Breeding density was calculated for the study plots in both years (see chapter 2).

For true protracted laying, the interval between removed eggs and subsequent eggs in the clutch should be approximately the same as in a normal clutch (Parsons 1976). In this study the normal laying interval in control pairs, between *a* and *b* eggs (mean ± s.e.), was 1.92 ± 0.07 days, $n = 96$. Therefore only birds which continued to lay additional eggs in the same nest scrape, within 3 days of removal are considered to have replaced the removed egg. In 1995, 5 pairs continued to lay in the same nest scrape after a delay of 5 or more days, during which they were observed 'loafing' at the nest site. These birds are not considered to have directly replaced the lost egg, by continuing the clutch with no delay. The procrastination in laying of the 5 pairs in 1995, probably corresponds to the time needed to recommence courtship and stimulate ovulation of a new clutch (Feare 1976). The average delay between egg removal and subsequent egg laying in these pairs, was 11.4 ± 1.83 (mean ± s.e., days). This is comparable to a previous study, conducted on common terns by Becker & Anlauf (1988), in which they found that it took pairs 9-14 days to relay whole clutches lost during flooding. These birds will presumably have had time to replenish their reserves and are thus in a different category, since the eggs laid after experimental egg removal do not represent a continuation of the same clutch, but a new replacement clutch.

Results

Variation within years

There was no reduction in clutch size with season in control birds, within the laying dates during which this study took place (see **Table 1**). Of the 30 pairs from which eggs were removed in 1994, 22 pairs (73%), continued to lay additional eggs in the same nest scrape. The remaining 8 pairs (27%), deserted the nest site. Of the 22 that laid additional eggs, 11 (50%), laid a further three eggs, 9 (41%), a further two eggs, and 2 (9%), one more egg. This was not significantly different from the ratio of three-, two- and one-egg clutches laid over the same period in the control group ($X^2_2 = 0.53$, n.s.). Experimental pairs laid 0.85 ± 0.129 (mean difference ± 95% C.I. for s.e. of difference) eggs more than control pairs laying in the same time period, (number of eggs laid in total, mean ± s.e.: control 2.56 ± 0.05, $n = 164$; experimental 3.41 ± 0.14, $n = 22$; $t_{184} = 6.07$, $p < 0.0005$).

Table 1. *Number of 'early', 'middle' and 'late' nesters in the control group, laying clutches of 1, 2 and 3 eggs, within the dates that study nests were selected in 1994 (number of eggs laid:* $X^2_4 = 4.78$, *n.s.).*

	CLUTCH SIZE			
Laying date of *a* egg	**1**	**2**	**3**	**mean ± s.e. (*n*)**
Early (27/5 - 29/5)	2 (5%)	19 (44%)	22 (51%)	2.47 ± 0.09 (43)
Middle (30/5 - 1/6)	4 (6%)	16 (25%)	45 (69%)	2.63 ± 0.07 (65)
Late (2/6 - 4/6)	4 (7%)	17 (30%)	35 (63%)	2.55 ± 0.08 (56)

In order to examine the effect of parental quality on the response to egg removal, birds in the experimental group and control groups were compared with respect to both the laying date of the first egg and its size; both of these parameters have been related to parental quality (Nisbet *et al.* 1984, Coulson & Porter 1985). The 22 pairs that continued to lay after egg removal laid a significantly larger first egg than the birds which deserted the nest site (see **Figure 1**). They also had a significantly earlier laying date than the eight which deserted (laying date, days after 1st May, mean ± s.e.: replaced 30.32 ± 0.40, $n = 22$; deserted 33.13 ± 0.73, $n = 8$; $t_{28} = 3.54$, $p = 0.001$). To take into account the effect of laying date, a paired comparison between experimental birds and daily means for all control pairs starting laying on the same day, was carried out. There was no difference in first laid egg size between birds that replaced the removed egg and date-matched controls (see **Figure 2**). However, the eight pairs that deserted the nest site after egg removal laid a significantly smaller first egg than date-matched control pairs (see **Figure** 3).

In 1995, as in 1994, there was no reduction in clutch size in control nests over the laying dates within which the study took place (see **Table 2**). Eggs were removed from 55 pairs in total. Twenty-eight pairs (51%), continued to lay additional eggs in the same nest scrape. Five pairs (9%) laid a replacement clutch after a delay of 5 or more days and the remaining 22 pairs (40%) deserted the nest site altogether. Of the 28 pairs that laid additional eggs, 7 (25%), laid a further three eggs; 18 (64%), a further two eggs; and 3 (11%), one more egg. In contrast to 1994, this is significantly different from the ratio of three-, two- and one-egg clutches laid over the same period in the control group (X^2_1 = 17.93, $p < 0.0001$). Experimental pairs laid 0.47 ± 0.109 (mean difference ± 95% C.I. for s.e. of difference) eggs more than control pairs laying in the same time period (number of eggs laid in total, mean ± s.e.: control 2.67 ± 0.04, $n = 173$; experimental 3.14 ± 0.11, $n = 28$; $t_{199} = 4.43, p < 0.0005$).

Table 2. *Number of 'early', 'middle' and 'late' nesters in the control group, laying clutches of 1, 2 and 3 eggs, within the dates that study nests were selected in 1995 (number of eggs laid:* $X^2_2 = 4.66$, *n.s.).*

	CLUTCH SIZE			
Laying date of *a* egg	**1**	**2**	**3**	**mean ± s.e. (*n*)**
Early (23.5-25.5/5)	0 (0%)	10 (21%)	38 (79%)	2.79 ± 0.06 (48)
Middle (26-28/5)	3 (3%)	26 (29%)	61 (68%)	2.64 ± 0.06 (90)
Late (28.5-30.5/5)	1 (3%)	14 (40%)	20 (57%)	2.54 ± 0.09 (35)

There was no difference between the 28 pairs that continued to lay after egg removal, the 22 that deserted and the 5 pairs laying a replacement clutch, in either the size of the first laid egg (see **Figure** 4), or in laying date (days after 1st May, mean ± s.e.: replaced 27.16 ± 0.44, n = 28; deserted 27.32 ± 0.43, n = 22; replacement clutch 25.30 ± 0.66, n = 5; Kruskal Wallis ANOVA $X_2^2 = 4.54$, $p = 0.10$, n.s.). As in 1994, we carried out paired comparisons between daily means for experimental birds and date-matched control means. We found no difference in first laid egg size between birds that continued to lay after egg removal and date-matched controls (see **Figure 5**). There was also no difference in the size of the first laid egg between the 22 pairs that deserted the nest site after egg removal and date-matched control pairs (see **Figure** 6). There was no difference in the size of the first laid egg between the 5 pairs that

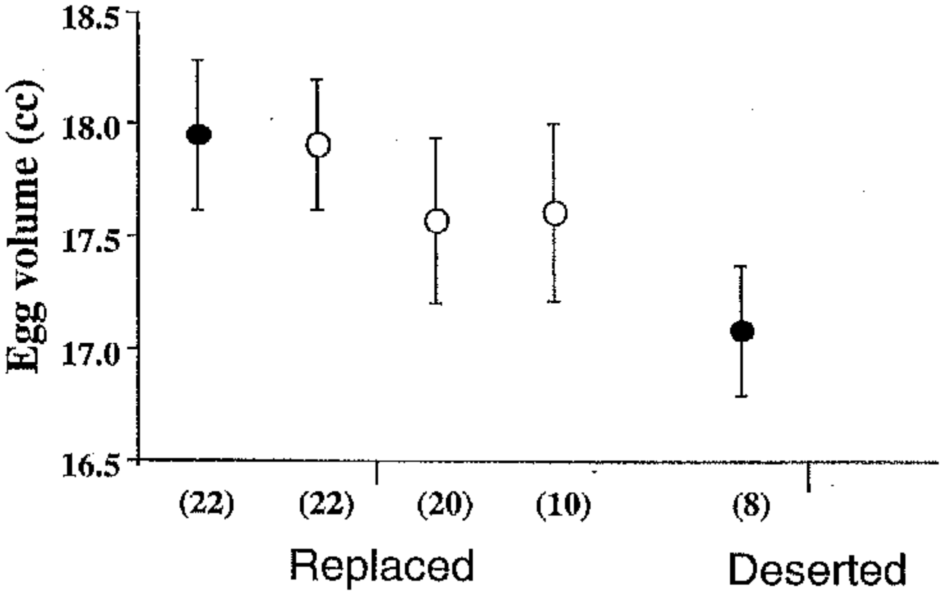


Figure 1. Mean (solid circles ± s.e.) volume of the first laid egg (mm^3) for experimental birds that replaced and those which deserted their nest site after egg removal in 1994. The sample sizes are given in brackets on the *x*-axis under the corresponding means. There was a significant difference between the two groups in the size of the first laid egg (volume of *a* egg: $t_{28} = 2.15$, $p = 0.04$). Also shown are the mean sizes of the eggs subsequently laid by the birds that replaced eggs (open circles ± s.e.).

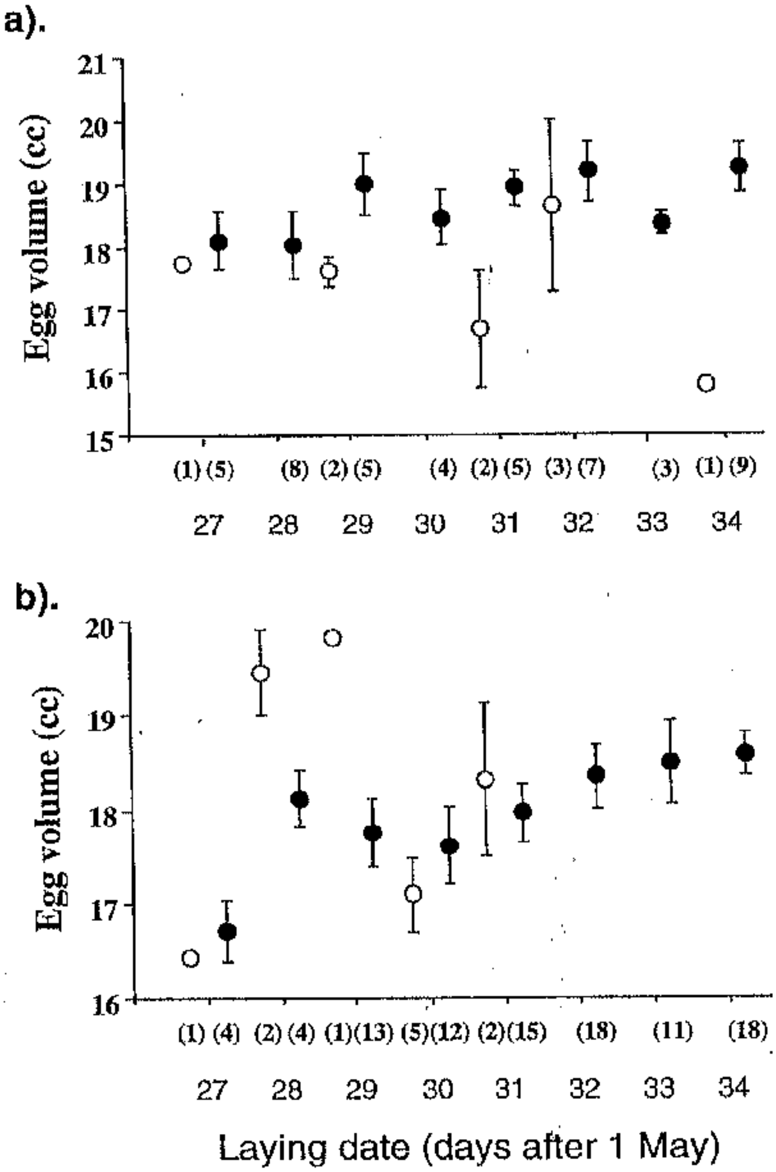


Figure 2. Daily mean (± s.e.) first laid egg volume (mm^3) for (*a*) experimental birds that continued to lay two eggs after removal (open circles) and date-matched controls birds laying two eggs (solid circles); and (*b*) experimental birds that continued to lay three eggs after removal (open circles) and date-matched controls birds laying three eggs (solid circles) over the study period in 1994. The sample sizes are given in brackets on the *x*-axes under the corresponding means. There was no difference between the experimental and control groups in the size of the first laid egg (volume of *a* egg: birds intending a clutch of two eggs; Wilcoxon's matched pairs test, $z_8 = 1.84$, $p = 0.07$, n.s.; birds intending a clutch of three eggs; Wilcoxon's matched pairs test, $z_{10} = 0.71$, $p = 0.48$, n.s.).

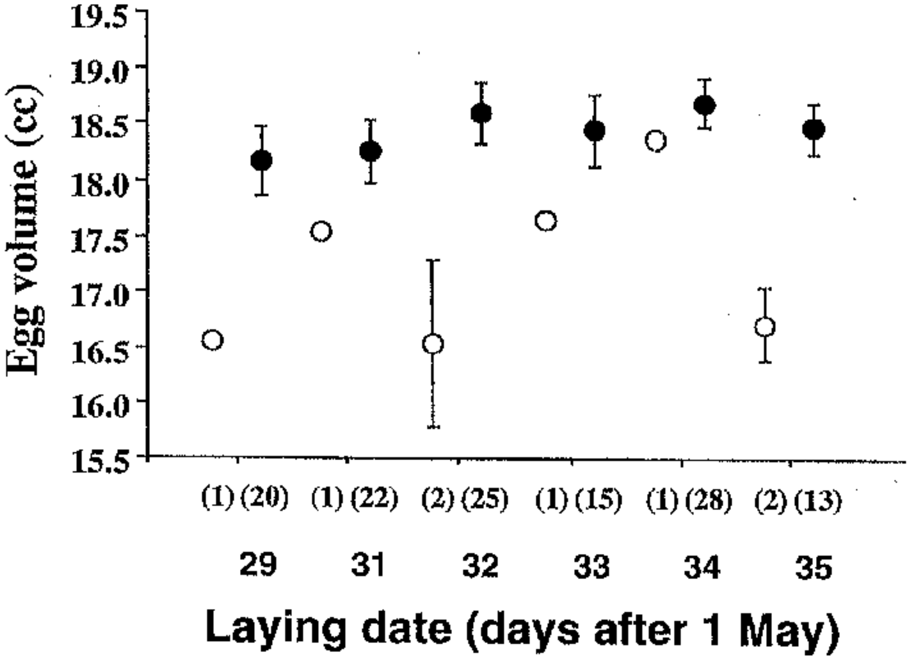


Figure 3. Daily mean (± s.e.) first laid egg volume (mm^3) for experimental birds that deserted the nest site after egg removal (open circles) and date-matched controls (closed circles), over the study period in 1994. The sample sizes are given in brackets on the x-axis under the corresponding means. There was a significant difference between the two groups in the size of the first laid egg (volume of *a* egg: Wilcoxon's matched pairs test, $z_7 = 2.52$, $p = 0.012$).

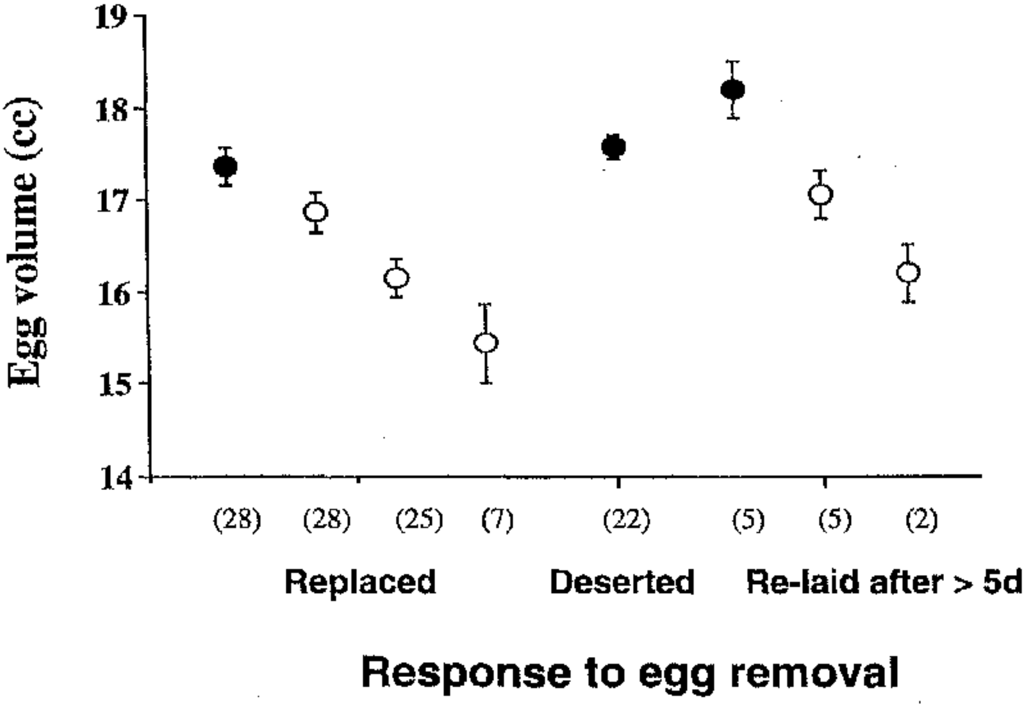


Figure 4. Mean (solid circles ± s.e.) volume of the first laid egg (mm^3) for experimental birds that replaced, deserted and re-laid a new clutch after > 5 days, after egg removal in 1995. Also shown are the mean sizes of the eggs subsequently laid by the birds that replaced and re-laid eggs (open circles ± s.e.). The sample sizes are given in brackets on the *x*-axis under the corresponding means. There was no difference between the three groups in the size of the first laid egg (volume of *a* egg: Kruskal Wallis ANOVA $X_2^2 = 3.45$, $p = 0.18$, n.s.).

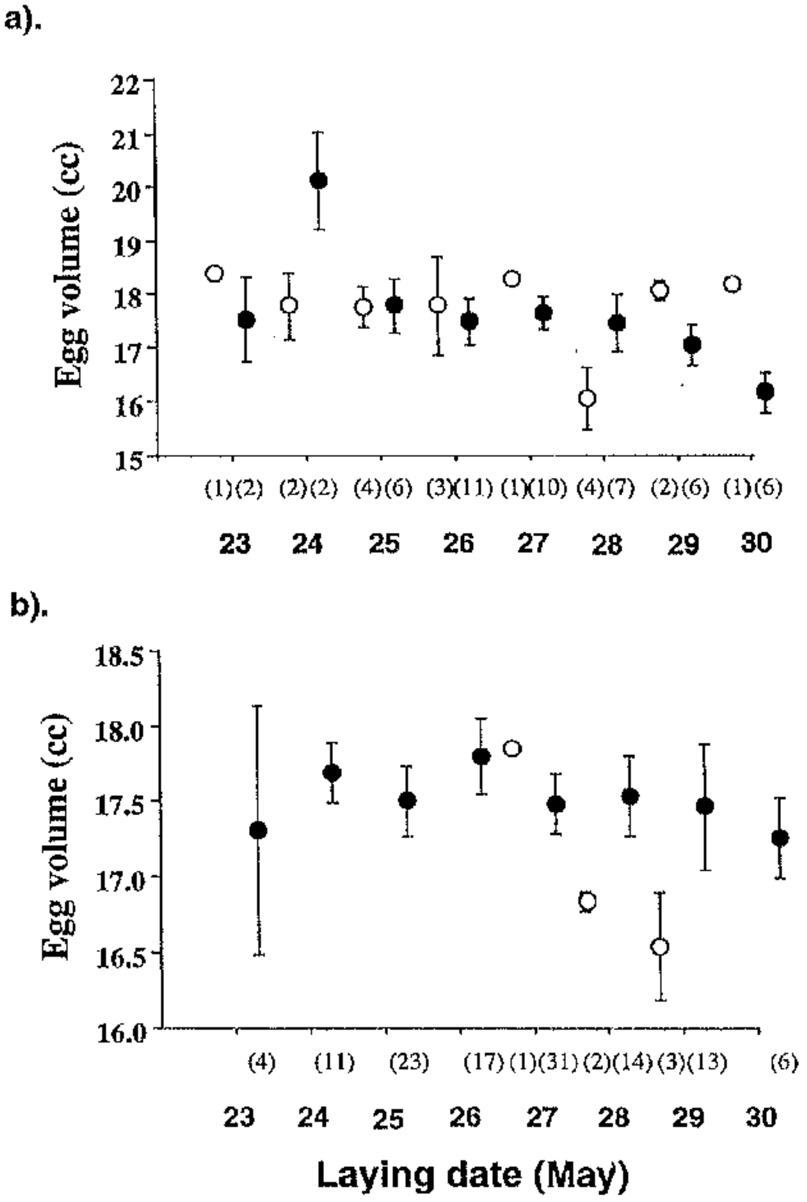


Figure 5. Daily mean (± s.e.) first laid egg volume (mm^3) for (*a*) experimental birds that continued to lay two eggs after removal (open circles) and date-matched controls birds laying two eggs (solid circles); and (*b*) experimental birds that continued to lay three eggs after removal (open circles) and date-matched controls birds laying three eggs (solid circles) over the study period in 1995. The sample sizes are given in brackets on the *x*-axes under the corresponding means. There was no difference between the experimental and control groups in the size of the first laid egg (volume of *a* egg: birds intending a clutch of two eggs; Wilcoxon's matched pairs test, $z_{17} = 0.50$, $p = 0.62$, n.s.; birds intending a clutch of three eggs; Wilcoxon's matched pairs test, $z_5 = 1.57$, $p = 0.12$, n.s.).

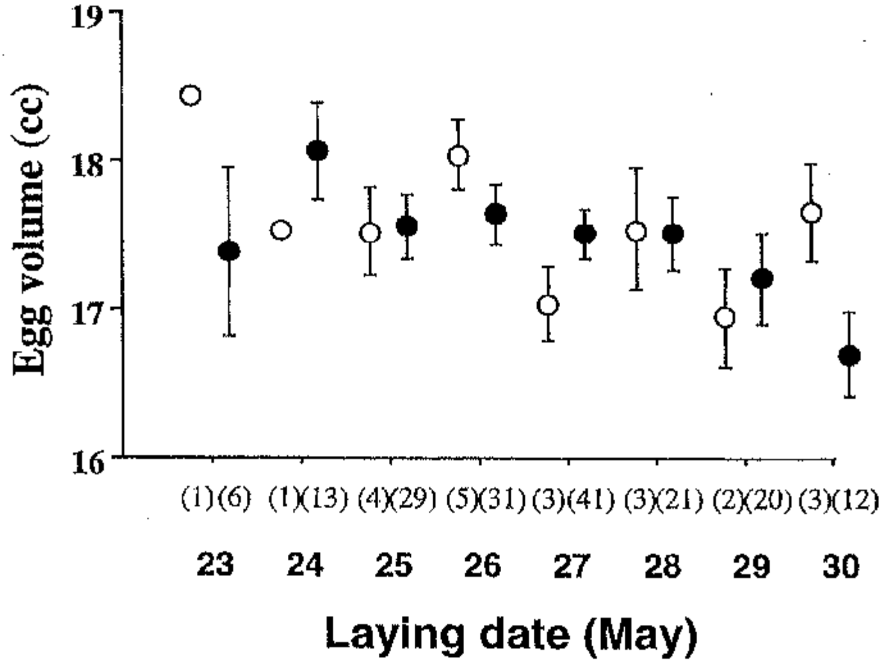


Figure 6. Daily mean (± s.e.) first laid egg volume (mm^3) for experimental birds that deserted after egg removal (open circles) and date-matched controls (solid circles), over the study period in 1995. The sample sizes are given in brackets on the x-axis under the corresponding means. There was no difference between the two groups in the size of the first laid egg (volume of a egg: Wilcoxon's matched pairs test, $z_{21} = 0.80$, $p = 0.43$, n.s.).

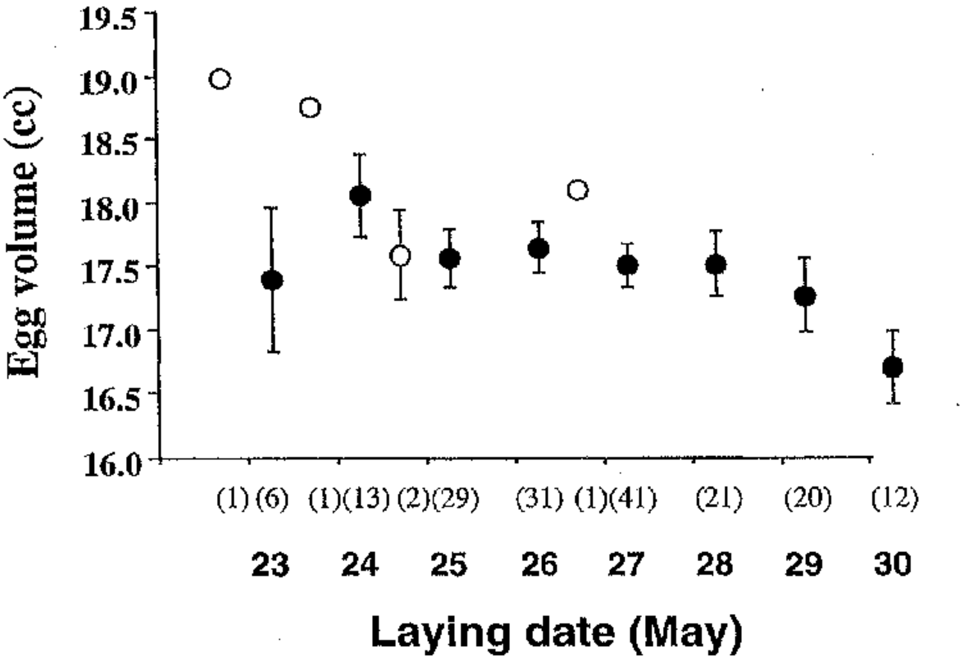


Figure 7. Daily mean (± s.e.) first laid egg volume (mm^3) for experimental birds that re-laid a replacement clutch after 5 or more days (open circles) and date-matched controls (solid circles), over the study period in 1995. The sample sizes are given in brackets on the x-axis under the corresponding means. There was no difference between the two groups in the size of the first laid egg (volume of *a* egg: Wilcoxon's matched pairs test, $z_4 = 1.75$, $p = 0.08$, n.s.).

laid a replacement clutch after 5 or more days delay and date-matched controls (see **Figure 7**).

Variation between years

There was no significant difference between 1994 and 1995 in the proportion of birds continuing to lay in a protracted manner after experimental egg removal (see **Table 3**).

Table 3. *The response of experimental pairs to egg removal in 1994 and 1995 ($X^2_1 = 3.15$, n.s.).*

	RESPONSE TO EGG REMOVAL	
YEAR	Continued to lay in same nest scrape	Deserted the nest site
1994 ($n = 30$)	22 (73%)	8 (27%)
1995 ($n = 55$)	28 (51%)	27 (49%)

However of the birds that continued to lay, there was a significant difference between years in the number of 'extra' eggs they produced compared to unmanipulated controls (number of extra eggs laid, mean ± s.e.: 1994 0.85 ± 0.07, $n = 22$; 1995 0.47 ± 0.06, $n = 28$; $t_{48} = 4.35$, $p < 0.01$). It would appear that although the majority of birds continuing to lay eggs after experimental egg removal in 1994 are replacing the lost egg, less than half of the experimental birds in 1995 are doing so. Of the birds that laid two eggs after removal (three eggs in total) in 1995, it was not possible to separate the birds that had originally intended a clutch of two eggs and replaced the lost egg, from those that were simply finishing a clutch of three eggs in a determinate manner. However, since a natural clutch size of 4 eggs is extremely rare in common terns (Winkler & Walters 1983, Conover 1984, Reid 1987, Salzer & Larkin 1990), we may assume that all birds laying four eggs, intended a clutch size of three and replaced the removed egg. There was a significant difference between years in the proportion of these 'unequivocal' replacers, with a larger proportion of the experimental group intending a clutch of three and replacing the lost egg in 1994 than in 1995 (see **Table 4**).

In 1994 there were more pairs of common terns attempting to breed on Coquet than in 1995 (see **Table 5**), and breeding density in the central area of the colony was 0.28 nests per m^2 in 1994 compared with 0.25 nests per m^2 in 1995. These breeding densities exceed those previously reported for common terns on Coquet Island (Langham 1968: 0.06 mean number of nests per m^2, n = 113), but are still considerably less than reported for common terns nesting on Bird Island, Massachusetts (Nisbet pers. comm.: 1996 average nest density exceeding 1 nest per m^{-2}). The breeding densities recorded in this study can be compared between years using a matched pairs test, for the 10 central plots used in both years. There was no difference in breeding density within the plots between years, (number of nests per plot, mean ± s.e.: 1994 26.8 ± 3.70, n = 10; 1995 22.4 ± 3.33, n = 10; Wilcoxon's matched pairs $z_9 = 1.02$, $p = 0.31$, n.s.).

Table 4. *The number of experimental birds laying four eggs in total as a proportion of all the experimental birds in 1994 and 1995 ($X^2_1 = 5.32$, $p < 0.05$).*

	RESPONSE TO EGG REMOVAL	
YEAR	Laid four eggs in total	Laid less than four eggs
1994 (n = 30)	11 (37%)	19 (63%)
1995 (n = 55)	7 (13%)	48 (87%)

Table 5. *Breeding data from the entire common tern colony on Coquet Island (Rob Scott pers. comm.).*

	1994	**1995**
Birds first seen in colony	24 April	30 April
First egg laid in colony	17 May	19 May
Number of breeding pairs (date)	809 (15 June)	763 (12 June)
Number of Late-breeders/Re-lays (date)	43 (8 July)	45 (8 July)
Average clutch size	2.54 eggs	2.49 eggs

Common terns arrived at the study site a week earlier in 1994 and first egg laying was 2 days earlier than in 1995 (see **Table 5**). Despite this early start, egg laying overall was significantly later in 1994 than in 1995 (see **Figure 8**). In 1994 there was a small gap in laying after the earliest nests were started, and these were mostly deserted. However once nesting was resumed, laying was highly synchronous and there is no difference in the slopes of the cumulative percentage lines over the linear phase of nest initiation between years (cumulative % of nests initiated per day: 1994, 23 - 31 May, n = 230; 1995, 27 - 4 June, n = 250; difference in slope $t_{476} = 0.834$, $p > 0.05$, n.s.).

In the whole population mean clutch size was slightly larger in 1994 than in 1995 (see **Table 5**). However there was no difference in average clutch size between years in the study area (see **Table 6**). In 1994 all eggs in control clutches of two and three were significantly larger than their counterparts in 1995 (see **Figure 9**). Also, the second and third eggs in clutches of three were relatively larger in proportion to the rest of the clutch in 1994 than in 1995 (see **Figure 10**), but this was not true for relative egg sizes within control clutches of two eggs, (*b* egg volume as % of *a* egg volume, mean ± s.e.: 1994 96.61 ± 0.78, n = 52; 1995 96.87 ± 0.89, n = 50; t_{100} = 0.23, p = 0.82, n.s.).

Table 6. *Clutch sizes within the study area for 1994 and 1995 (number of eggs laid:* X^2_2 = *3.69, n.s.).*

	CLUTCH SIZE			
YEAR	**1**	**2**	**3**	**mean ± s.e. (*n*)**
1994	10 (6%)	52 (32%)	102 (62%)	2.56 ± 0.05 (164)
1995	4 (2%)	50 (29%)	119 (69%)	2.67 ± 0.04 (173)

The eggs produced by experimental birds continuing to lay in the same nest scrape within three days of removal in 1994 were significantly larger than those laid by experimental birds in 1995 (see **Figure 11**). There was no difference in the size of the first laid egg between years, in experimental birds that deserted their nest site after egg removal (see **Figure 12**).

Weather data were compared for the two years over the periods from the 17 May - 4 June in 1994 and the 13 - 31 May in 1995. These dates correspond to the period from 10 days preceding laying, to the end of nest initiation in the study birds; this period is therefore when the study birds would have been collecting most of the necessary materials for egg production (Nisbet 1973 & 1977, Taylor 1979, Mills 1973, Brown 1967). Data are compared using paired t-tests, matching daily means standardised in relation to the initiation of laying (day 0: 27 May 1994; 23 May 1995). Windspeed was significantly stronger prior to and during initiation of the study nests in 1994 than in 1995 (daily mean windspeed ± s.e. (knots): 1994 9.34 ± 0.42, n = 20; 1995 6.94 ± 0.33, n = 20; t_{19} = 2.91, p = 0.009), but there was no

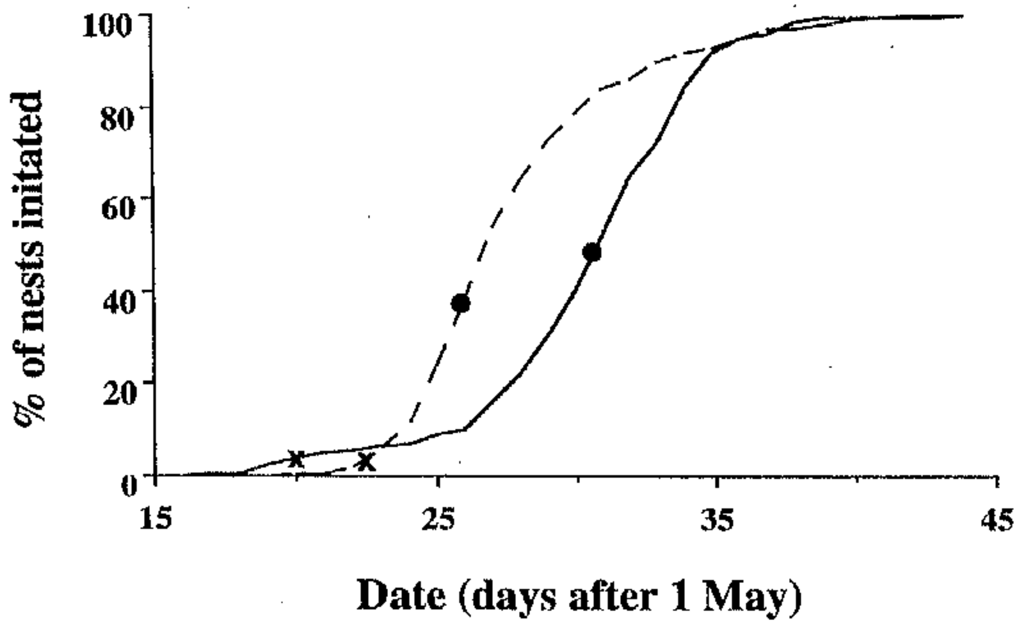


Figure 8. Cumulative plot of the percentage of nests initiated against date for 1994 (solid line) and 1995 (dotted line). In 1994 egg laying on average was significantly later than in 1995 (laying date, days after 1 May: 1994 median = 31, Quartile Deviation 29-34, n = 284; 1995 median = 27, QD 26-30, n = 305; Mann Whitney U-Test, U = 1466.5, $p < 0.001$). The dates by which 5% (crosses) and 50% (circles) of nests were initiated are shown for each year. The time taken between these two points was significantly different between years (number of days between 5% & 50% nests initiated in the study area: 1994 11 days, n = 135; 1995 5 days, n = 158). The overall pattern of laying differed between the two years (Kolmogorov-smirnov D = 0.89, $p < 0.001$).

difference in the mean daily temperature between years (daily mean temperature ± s.e. (^{0}C): 1994 9.52 ± 0.50, $n = 20$; 1995 9.40 ± 0.72, $n = 20$; $t_{19} = 0.26$, $p = 0.80$, n.s.).

There was a significant difference between years in the amount of rainfall prior to and during initiation of the study nests, with 1995 being the wetter year (total daily rainfall, mean ± s.e. (mm): 1994 0.37 ± 0.14, $n = 20$; 1995 2.02 ± 0.51, $n = 20$; $t_{19} = 3.50$, $p = 0.002$). There was also a significantly larger number of actual days with appreciable rainfall in 1995 than 1994 (days with total rainfall > 2 mm: 1994 0 of 20; 1995 9 of 20; $X^2_1 = 9.18$, $p < 0.01$). In the week preceding the initiation of egg laying in study birds, there were significantly more favourable foraging hours available to birds in 1994 than 1995, because the low tide was occurring at either end of the day (daily foraging time available, mean ± s.e. (hours): 1994 9.14 ± 0.36 hours, $n = 7$; 1995 6.61 ± 0.32, $n = 7$; Wilcoxon's matched pairs test, $z_6 = 2.2$, $p = 0.028$). The number of favourable foraging hours available to the terns and the daily rainfall totals for the study egg laying periods in 1994 and 1995 are presented in **Figure 13** (*a*) & (*b*), respectively.

The weather data were also examined according to actual date, from the 13 - 22 May, the time of egg formation in the year of earlier laying (1995). There was no difference between years in the average temperature (daily mean temperature ± s.e. (^{0}C): 1994 8.25 ± 0.30, $n = 10$; 1995 6.90 ± 0.75, $n = 10$; Wilcoxon's matched pairs test, $z_9 = 1.27$, $p = 0.20$, n.s.), or in the amount of rainfall (total daily rainfall, mean ± s.e. (mm): 1994 0.42 ± 0.19, $n = 10$; 1995 1.54 ± 0.67, $n = 10$; Wilcoxon's matched pairs test, $z_9 = 1.78$, $p = 0.08$, n.s.). However in 1994 the average windspeed over this 10 day period was much stronger than in 1995 (see **Figure 14**).

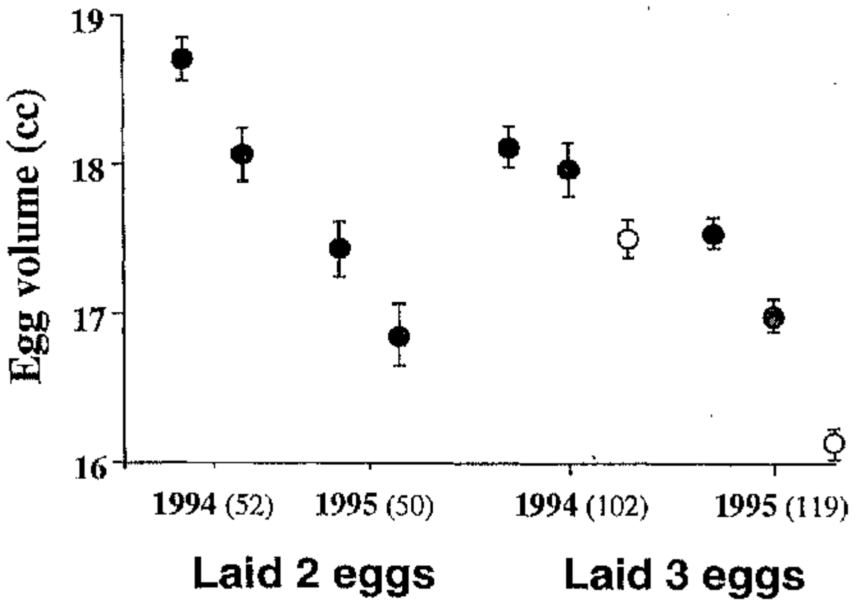


Figure 9. Mean (± s.e.) egg volume (mm^3) of control birds laying different clutch sizes in 1994 and 1995 (first laid eggs, solid circles; second eggs, grey circles; third eggs, open circles). The sample sizes are given in brackets on the *x*-axis under the corresponding means. In 1994 all eggs in the clutch were significantly larger than their counterparts in 1995 (absolute egg sizes: birds laying two eggs, 2-way ANOVA, laying order effect $F_{1, 200} = 11.41$, $p = 0.001$, year effect $F_{1, 200} = 47.04$, $p < 0.0001$, interaction $F_{1, 200} = 0.05$, $p = 0.83$, n.s.; birds laying three eggs, 2-way ANOVA, laying order effect $F_{1, 438} = 8.92$, $p = 0.003$, year effect $F_{1, 438} = 45.33$, $p < 0.0001$, interaction $F_{1, 438} = 2.89$, $p = 0.09$, n.s.).

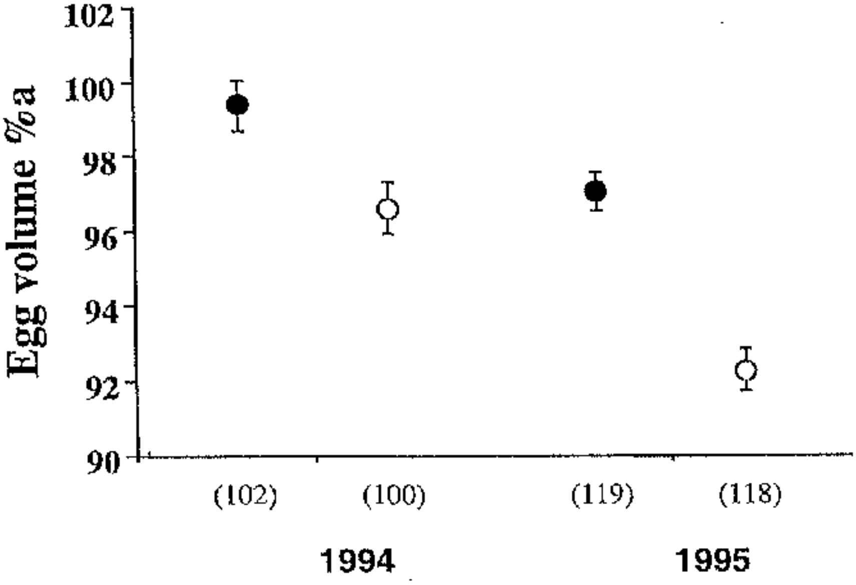


Figure 10. Relative sizes (mean ± s.e., volume as a percentage of first egg volume) of second (solid circles) and third laid (open circles) eggs in control clutches of three in 1994 and 1995. The sample sizes are given in brackets on the *x*-axis under the corresponding means. In 1994 all eggs in the clutch were significantly relatively larger in proportion to the rest of the clutch, than their counterparts in 1995 (relative egg sizes: 2-way ANOVA, laying order effect $F_{1,435} = 38.30$, $p < 0.0001$, year effect $F_{1,435} = 30.41$, $p < 0.0001$, interaction $F_{1,435} = 2.61$, $p = 0.11$, n.s.).

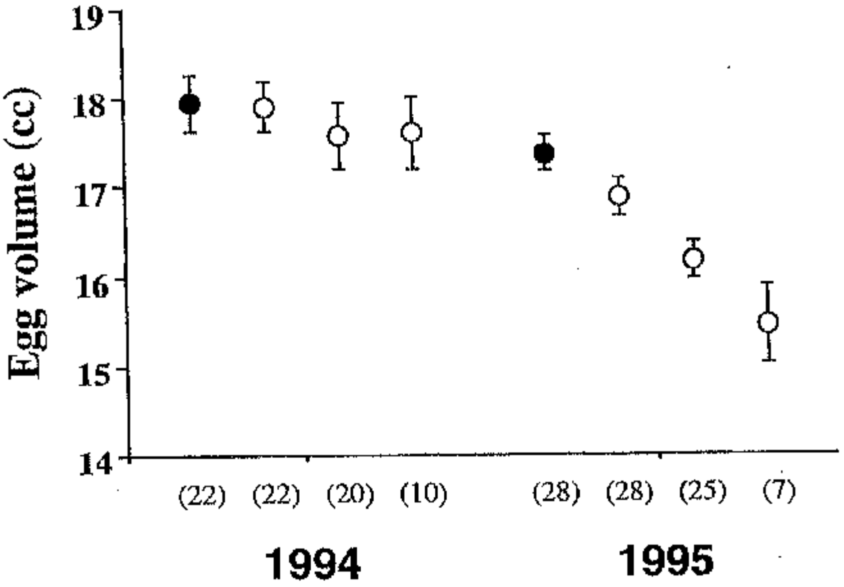


Figure 11. Mean (± s.e.) egg volume (mm^3) for experimental birds that continued to lay in the same nest scrape within three days of egg removal in 1994 and 1995. The sample sizes are given in brackets on the *x*-axis under the corresponding means. The eggs laid by the experimental birds in 1994 were significantly larger than those laid by the experimental birds in 1995 (absolute egg sizes: birds laying two eggs after removal, 2-way ANOVA, laying order effect $F_{2, 175} = 1.20$, $p = 0.31$, n.s., year effect $F_{1, 175} = 6.09$, $p = 0.02$, interaction $F_{2, 175} = 2.15$, $p = 0.12$, n.s.; birds laying three eggs after removal, 2-way ANOVA, laying order effect $F_{3, 62} = 1.27$, $p = 0.29$, n.s., year effect $F_{1, 62} = 24.25$, $p < 0.0005$, interaction $F_{3, 62} = 0.54$, $p = 0.65$, n.s.).

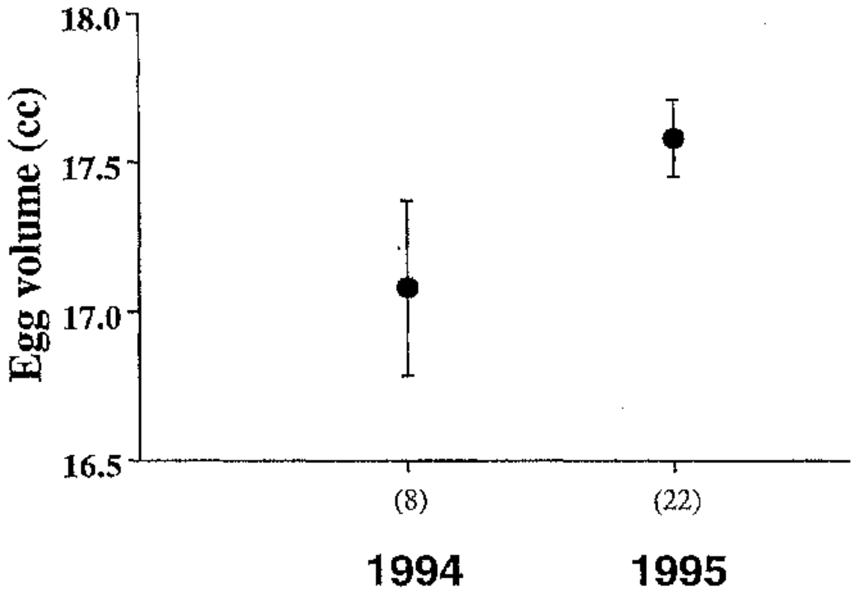


Figure 12. Mean (solid circles ± s.e.) egg volume (mm^3) for experimental birds that deserted the nest site altogether after egg removal in 1994 and 1995. The sample sizes are given in brackets on the *x*-axis under the corresponding means. There was no difference between the two groups in the size of the first laid egg (volume of *a* egg: Mann Whitney U-test, $U_{28} = 55$, $p = 0.12$, n.s.).

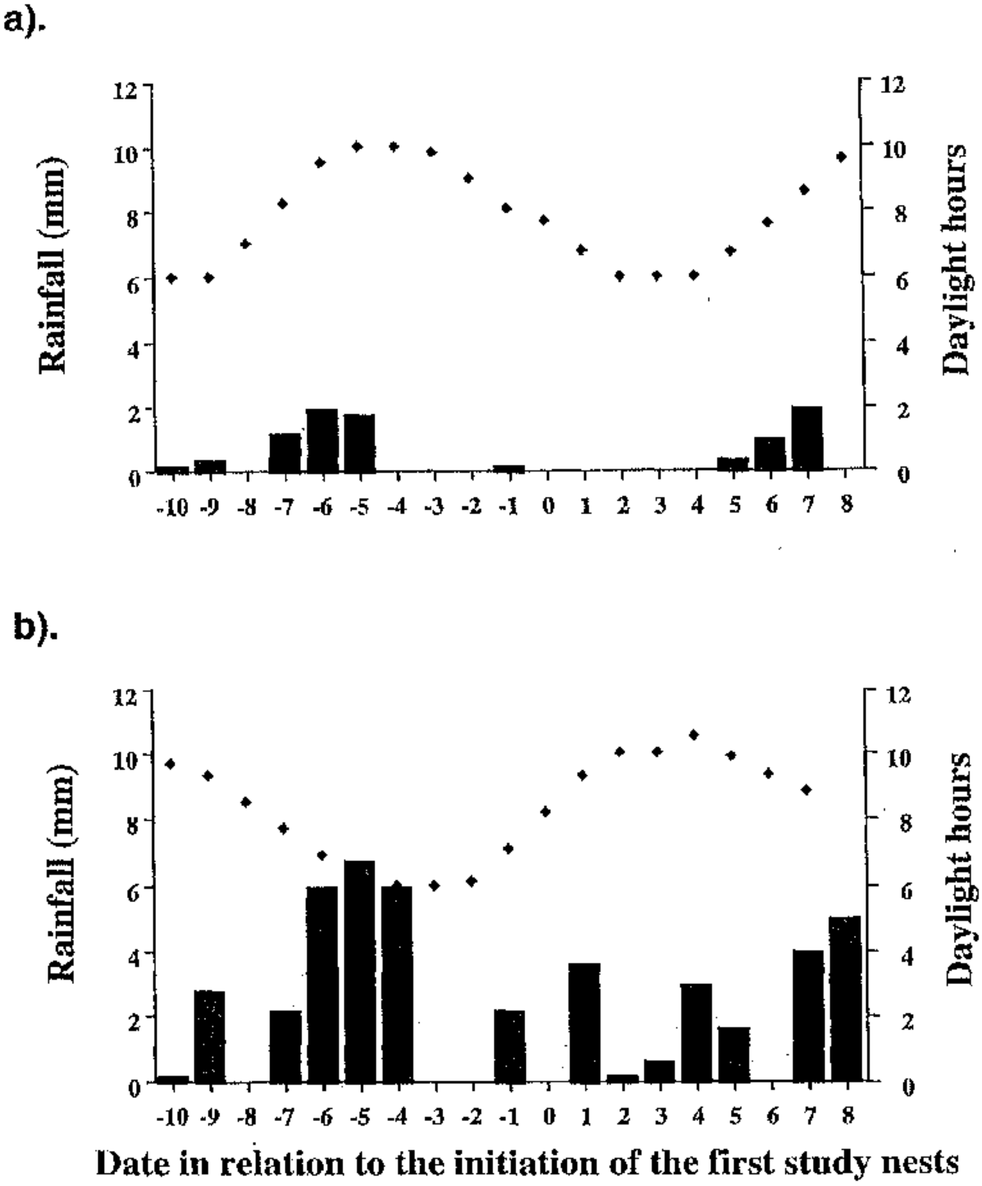


Figure 13. The number of favourable daylight foraging hours available (solid diamonds) and the daily rainfall totals (shaded histograms) during the egg laying period of study birds in (*a*) 1994; and (*b*) 1995.

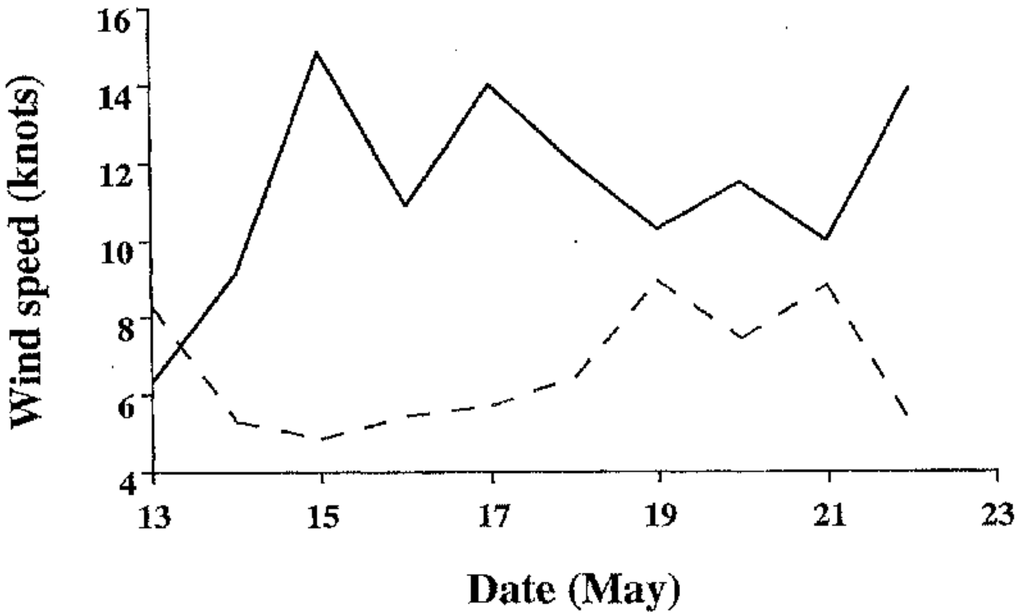


Figure 14. Daily mean (± s.e.) windspeed records between 13 - 22 May in both 1994 (solid line) and 1995 (dotted line). The average windspeed over this 10 day period was much stronger in 1994 than in 1995 (daily mean windspeed ± s.e., (knots); Wilcoxon's matched pairs test, $z_9 = 2.50$, $p = 0.01$).

Discussion

Variation within years

From the results of this experiment we can classify common terns as indeterminate tactile layers, Type S, (after Haywood 1993a). However not all experimental birds displayed the ability to replace an egg removed from the nest at the start of laying. The capacity to do so differed both within and between years.

In 1994, 73% of the birds that had their first egg removed continued to lay in the same nest scrape after removal, and appear to have replaced the egg that was removed. The remaining 27% of the experimental birds deserted their nest site. In 1995 only 51% of the experimental birds continued to lay after removal, and only half of these birds appear to have actually replaced the lost egg, with experimental birds laying an average of only half an egg more than unmanipulated controls. Forty percent of the experimental group in 1995 deserted the nest site altogether, and 9% of pairs resumed laying after a delay of 5 or more days (presumably spent building up reserves for this replacement clutch).

Thus, within a year where all the study birds will be experiencing roughly the same breeding conditions (food supply, temperature etc.), the individual pairs differ in their ability to replace a lost egg. In 1994, the birds that replaced the removed egg laid a significantly larger first egg and had a significantly earlier laying date than those which deserted. We can eliminate the possibility that this difference in *a* egg size is just a seasonal effect, since experimental birds that deserted their nest site after removal laid a significantly smaller *a* egg than date-matched controls.

Both egg size and laying date can be used as an index of parental quality in gulls (Coulson & Porter 1985), and terns (Nisbet *et al.* 1984). There thus appears to be a relationship between parental quality and the ability to replace eggs lost during the early stages of the laying cycle. There may in fact be a 'threshold condition' (perhaps related to the reserves of pectoral muscle protein used in egg production, Selman & Houston 1996, Bolton *et al.* 1993, Houston *et al.* 1995a), which must be reached by the female, prior to or during laying, for her to be able to produce the replacement egg. Below this threshold, the female either fails to replace the removed egg, continuing laying in a determinate manner, or deserts the nesting site altogether. The condition of the female will be related to the quality of both herself and her mate (common terns tend to select mates of a similar age and quality, Nisbet *et al.* 1984), and the females of higher quality pairs are presumably more likely to reach the threshold condition for replacement than those of lesser quality pairs, through superior reserves, foraging ability and courtship feeding (Nisbet 1973).

Within the group of experimental birds continuing to lay two more eggs in the same nest scrape after removal in 1995, we were not able to distinguish between those showing true replacement and those continuing to lay in a determinate manner after removal. Only birds continuing to lay three eggs after removal can be described as 'unequivocal' replacers. However, there was no difference in *a* egg size between either experimental birds laying a total of three or a total of four eggs and date-matched controls. Within the group of experimental birds which did not replace the removed egg in 1995, those that deserted the nest site altogether laid a slightly smaller first egg than those which re-laid after a delay of 5 or more days. However the sample size in the second category is small and this result is not significant. There is a suggestion that the birds opting to relay a replacement clutch after a delay are better birds than those deserting the nest site, which would follow since investing in this second clutch will be costlier to the parents than abandoning the years' breeding attempt altogether. However this idea is confounded by the fact that birds deserting their nest site after egg removal were not marked and could therefore have laid subsequent eggs elsewhere in the colony in 1995 without detection (Nisbet pers. comm.). There was little difference between the size of eggs laid by birds continuing to lay in the same nest scrape with no delay and those relaying after 5 days or more (again confounded by small sample sizes). However, we might expect the first group to be in better condition, since it is presumably more costly to continue laying in a true protracted manner, than to take a short break in order to replenish reserves for laying a second clutch.

Variation between years

The response to egg removal was markedly different between the two years of the study. Although there was no significant difference between 1994 and 1995 in the proportion of experimental birds continuing to lay in a protracted manner after egg removal, the desertion rate in 1995 (40%) was much higher than in 1994 (27%). Of the experimental birds that continued to lay at the same nest site, only half actually replaced the lost egg in 1995, compared to the majority in 1994. Since we cannot distinguish the 'true' replacers within the group laying two eggs after removal, we compared the number of unequivocal replacers between years. We found that a significantly larger proportion of the experimental pairs definitely replaced the removed egg (laid four eggs in total) in 1994 than in 1995.

The study birds in the two years were an equivalent subset of the same colony (selected from the centre of the colony at peak laying), yet, overall, they were less able to replace lost eggs in 1995 than 1994. Common terns are reasonably site faithful (Austin 1949, Nisbet *et al.* 1984), so that it is possible that a few birds may have been studied in both years and there may have been a roll-over effect. However since only 30 egg removals were done in 1994 and the control group alone, in 1995, consisted of 173 pairs, this could not fully explain the differences, and there appears to be a difference between the years in local conditions, affecting the overall capacity of individuals to replace eggs.

In long-lived iteroparus species, like the common tern, the decision to breed in a certain year will be related to a trade-off between the probability of successfully raising a brood and the residual reproductive value of the parent; fewer individuals should attempt to nest in a year with poorer breeding conditions (Williams 1966). This was demonstrated by Langham (1968) for common terns on Coquet, with 17% fewer birds breeding in 1966, a year associated with poor food availability, than in either 1965 or 1967, when food was more abundant. In this study, there were 6% less pairs overall attempting breed in 1995 than in 1994, suggesting that 1994 provided better breeding conditions than 1995 for the terns on Coquet. In further support of this, birds breeding in 1994 laid a higher average clutch size and significantly larger eggs, both absolutely and relatively than in the following year. This difference in egg size is also apparent within the experimental birds, with pairs that replaced the removed egg in 1994, laying significantly larger eggs than pairs that continued to lay within three days of removal in 1995. These differences in breeding numbers and egg size may in part be due to differences in weather conditions for foraging, prior to, and during the time of laying in 1994.

Many studies have shown that both clutch and egg size can be related to foraging conditions during laying, with bottlenecks in food availability affecting egg size in particular (for review see Perrins 1996). Nisbet (1973) showed that in common terns, egg size was significantly correlated to the males' courtship feeding performance in the week prior to laying. Mills (1973) found in red-billed gulls that peak courtship feeding occurred in the 10 days preceding egg laying, this corresponds to the period of accelerated growth in the ovary (Brown 1967). Becker *et al.* (1985) recorded courtship feeding in common terns, for 5-10 days close to the colony and 1-6 days at the nest, and Taylor (1979) found that the female could gain up to 50% of the extra weight needed to produce eggs during this time.

The influence of weather on tern foraging success is mediated mainly through effects on sea surface conditions and the ability of the terns to locate and dive for prey beneath the surface. In strong winds, when the sea surface is rough, tern fishing success is much reduced (Taylor 1983, Dunn 1975, Frank & Becker 1992). However Dunn (1973a) found that within a certain range increasing windspeed produces conditions which facilitate fish capture. He reported that fishing the success of terns was better in moderate than in calm seas, since prey were less likely to spot the hovering tern and take evasive action. Becker *et al.* (1985) found that a reduction in clutch size and subsequently breeding success was correlated with heavy rainfall in the 5-10 days preceding egg laying. This has also been observed in arctic terns (*Sterna paradisaea*) (Lemmetyinen 1973). They suggest that rainfall probably has an effect on clutch size and breeding success in much the same way as strong winds; by churning up the water surface and reducing foraging success. This is further supported by the fact that tern chicks tend to receive less food on rainy days (LeCroy & LeCroy 1974, Feare 1976).

Weather data were compared for the two years of the study over the period from 10 days preceding laying, to the end of study nest initiation. There were no differences in average temperature between years, but 1995 received significantly more rainfall than 1994 around the time of egg formation and laying. Common terns mainly use the hours before and after low tide for fishing (Boecker 1967). If we consider the time between 3 hours before and after low tide as the best time (Becker *et al.* 1985), the available time for favourable foraging during the daylight period could vary between 6 and almost 11 hours per day.[1] In 1995 there were fewer favourable foraging hours in the week prior to laying by the study pairs, so it is possible that the adverse effect of rainfall in 1995 may have been accentuated by the interaction of the tidal cycle with the daylight hours (Becker *et al.* 1985). Mean windspeeds preceding and during laying, however, were stronger in 1994 than in 1995, although only by a couple of knots, and average windspeeds did not exceed 11 knots. Although these speeds recorded are in the less favourable range (Dunn 1975) for foraging, sea surface conditions were not monitored in this study. It is therefore possible that there was local shelter which reduced the impact of the windspeed on surface conditions.

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[1] As visual feeders it is possible that terns may feed on a clear night; for example Coulson & Johnson (1993) recorded kittiwakes feeding at night. However, no observations to test this were possible.

A slight anomaly occurs with respect to the laying dates between years. In the apparently better year, 1994, peak laying was a week later than in 1995, although the birds arrived at the study site a week earlier and the first eggs in the colony were laid two days earlier than in 1995. It is difficult to compare the laying dates recorded in this study to other studies, since the data I collected are restricted to the birds laying in the central area of the colony, and not the colony as a whole. However, Langham (1968) in a previous study on common terns on Coquet did record median laying dates differing between years by as much as a week.

Looking at the spread of laying within the study area between years, we can see that the birds seemed ready to lay earlier in 1994, but then took significantly longer to reach peak laying. Although the foraging conditions in relation to peak laying were more favourable in 1994 than in 1995, this is not the case if we compare weather data by actual date. In the period from 13 - 22 May winds were significantly stronger in 1994 than in 1995. This suggests that birds in 1994 may have laid earlier, but were prevented from doing so by a period of considerable (> 12 knots) Northerly winds (15 - 18 May). The earliest laid nests were deserted and the main thrust of nest initiation in the study area (although congruous in the rate of initiation to 1995), was delayed by over a week. Consequently, it is possible that birds in 1994 had longer to collect materials (despite unfavourable foraging conditions in the high winds) and were able to lay bigger eggs (Drent pers. comm.). In 1995, weather conditions were more favourable in the middle weeks of May, so that birds were able to lay earlier. Although this may have been advantageous later in the season (see Perrins 1996 for review), at the time of egg laying this left them less opportunity to collect materials for egg production, especially since they arrived at the colony slightly later than in 1994.

Relating this difference between years to the condition threshold hypothesis for egg replacement, we find that in a less favourable breeding year, fewer birds appear able to attain the threshold, and replace the lost egg. The egg replacement condition threshold stays the same (there was no difference between years in the size of first laid egg of experimental birds that deserted their nest site after egg removal), yet fewer individuals are able to reach it. This effect may be accentuated by the fact that the relative costs of egg production will be increased in a poorer foraging situation (Perrins 1996), and these costs will be of greater significance to individuals in poorer condition (chapter 4, McNamara & Houston 1996). In a poorer year, only the very highest quality birds will be able to replace the removed egg, and more experimental birds will either desert or continue laying in a determinate manner, after egg removal.

Differences between studies

There have been many egg removal studies carried out (for review see Haywood 1993a), and many more, particularly ones where there was no egg replacement, that have not been reported in the literature. Different experiments on the same species have produced varying results. In this section I would like to look in detail at other egg removal studies in the common tern and also in other larids and a passerine species, to highlight some of the possible reasons for the differences in response to egg removal between studies.

Other than this study I know of only two removal experiments in common terns. The first study by Rawson (*in* Burns 1900), reports inducing one pair of common terns to lay as many as 11 eggs by sequential removal of these eggs as they were laid, but is published with little information on the exact method and timing of the egg removal. In the second study, Nisbet (pers. comm.) removed first laid eggs from common terns at a colony on Bird Island, Massachusetts, USA. He found that only half of his experimental pairs replaced the removed egg and over three-quarters of the experimental birds moved nest site. Removal experiments in lesser black-backed gulls (*Larus fuscus*) on Walney Island have also produced varying results. In 1996, Nager *et al.* (in prep.) manipulated study birds into producing as many as 17 eggs in a row by the sequential removal of these eggs as they were laid; whereas Griffith (pers. comm.) was less successful in inducing gulls to lay additional eggs in 1992, with many birds moving nest site after egg removal.

In this study I found a difference between years and between individuals within years, in the response to egg removal. Certainly within the studies on common terns and lesser black-backed gulls, there was a range of responses to egg removal, from the birds within each study. Nisbet (pers. comm.) found that only half his study birds replaced the removed egg, the rest either deserting the nesting area or continuing to lay in a determinate manner. In Nager *et al.*'s study although the majority of birds laid replacement eggs, they differed in the actual number of 'extra' eggs laid. This difference between individuals within a year in response to egg removal will be found in virtually all removal studies. For example Haywood (1993b) working on blue tits (*Parus caeruleus*), a tactile indeterminate layer type S, found that some females responded to egg removal by laying larger clutches and others did not, she also found that some birds deserted the breeding attempt altogether. Parsons (1976), working on herring gulls (*Larus argentatus*), found a range of responses in study birds to egg removal. He was also able to relate this to differences in individual quality, with birds that laid the greatest number of 'extra' eggs, in response to continuous removal of eggs as they were laid, on average, laid the heaviest *a* eggs. This is similar to the finding of this study where birds that deserted the nesting attempt after egg removal in 1994 had laid a smaller first egg than those that continued to lay.

Differences between studies in overall response of experimental birds to removal, could again be explained by differences between years in breeding conditions. For example in Nager *et al.*'s study we might expect a high replacement rate, since the egg removal was part of an experiment relating egg laying capacity to food supply prior to and during laying, and these birds were given supplementary egg protein. However he still found a relatively high replacement rate in non-fed controls. Nisbet, who found a relatively poor response to removal in common terns, reports that in the year of the study (1996), the colony at Bird Island appears to have been severely food-limited. This may have been related to the very high breeding densities he recorded (Perrins 1996, Coulson *et al.* 1982).

Eggs are produced sequentially. Each egg that is laid originates from a cohort of small follicles in the ovary that are recruited into growth. Due to atresia, which results in the removal and reabsorption of follicles, the number of follicles in each follicular cohort decreases with increasing size of the follicles (Gilbert *et al.* 1983). Large yolky follicles, selected through atresia from the successive cohorts of small yolky follicles, complete the rapid-growth phase (during which the yellow yolk is deposited) and are normally ovulated, that is the ovum breaks out of its ovarian follicle (Gilbert *et al.* 1983, Perry *et al.* 1983). The ovum then passes down the oviduct where the albumen, membranes and shell are successively laid down. It has been suggested that the high concentrations of prolactin found during incubation (Bailey 1952), could be responsible for the disruption of ovarian follicular growth in gulls, causing developing follicles to atrophy (Eisner 1958 & 1960), and ovulation to cease (Mead & Morton 1985). This is because high levels of prolactin inhibit follicle-stimulating hormone, which promotes follicle growth, and luteinizing hormone, which is released from the anterior pituitary and peaks with progesterone (released from the mature follicle) to produce ovulation (Mead & Morton 1985). Thus at the onset of incubation, increases in the concentration of prolactin, control the number of large yolky follicles produced by the ovary and the number of these follicles ovulated (Parsons 1976).

If this is true for larids in general, it would explain why the exact timing of egg removal is so critical if experimental birds are to respond by replacing the lost egg. The first laid egg must be removed as soon as possible after laying, since soon after, and certainly around the time of *b* egg deposition, the female may have begun incubation behaviour. The tactile stimulation of eggs on brood patch may cause the concentration of prolactin to increase, promoting atresia of any potential 'extra' replacement egg follicles. Paludan (1951) found that in the lesser black-backed gull, laying a modal clutch of three eggs, follicular disruption occurred between the laying of the first and second eggs. This may have been of relevance in Nisbet's study where, due to problems with access to the breeding colony, it seems possible that in some cases as much as 24 hours may have passed between the laying of the first egg and its removal.

The timing of egg removal in relation to peak laying in the colony is also crucial to the probability of replacement. In common terns (Nisbet *et al.* 1984), and the majority of bird species studied (for reviews see Daan *et al.* 1988, Fowler 1995), there is a relationship between parental quality and laying date, with better quality birds laying earlier in the season. Average clutch size tends to decline with season partly as a consequence of this relationship, and partly due to external influences such as food availability (Nisbet *et al.* 1984, Daan *et al.* 1988). These factors combine to reduce the probability of egg replacement as the season progresses, since the birds laying later in the season are more likely to be poorer quality (usually younger) individuals (Nisbet *et al.* 1984), that are less able to replace the lost egg. The seasonal timing of egg removal may therefore also explain some of the differences between egg removal studies. Haywood (1993b) reports that blue tits, were more likely to respond to egg removal by laying in a determinate manner as the season progressed. This she related to ambient temperature which dictated the peak of caterpillar food abundance, and therefore the best time to be raising young. Parsons (1976) also reports that in herring gulls, the ability to relay waned as the season progressed, however he was not able to separate the variation in replacement due to the interval of incubation prior to removal and to the lateness of season.

Another difficulty may arise with respect to keeping track of relaying birds. Nisbet (pers. comm.) reported a high percentage (*ca.* 85%) of experimental birds moving nest site after egg removal. Of the birds that moved nest site, many (56%) continued to lay at another site in the colony (as much as 50m away) after only a short delay (mean interval between first and second eggs about one day longer in the experimental group than in the controls). Griffiths, who reported a high desertion rate in lesser black-backed after egg removal, also found that many birds laid again only a short distance from their original attempt (Griffiths pers. comm.). In this study experimental birds were not marked at egg laying and were considered not to have replaced the removed egg if they moved nest site, because in general we could not relocate them. Thus, we may in fact be underestimating the number of birds responding in an indeterminate manner to egg removal. However, in order to mark the birds, Nisbet trapped them on the nest on the day of egg removal. The additional disturbance of capture may be crucial at this time and greatly increase the probability of desertion (Nisbet 1981).

Kennedy (1991) in his review on determinate and indeterminate egg laying patterns, identified the difference in response between individuals and classified a species as indeterminate only if at least 20% of the experimental birds that did not desert after egg removal had exhibited an indeterminate response. He cites one particular example as mew (or common) gulls (*Larus canus*), which lay between 1 and 3 eggs, and are often labelled as indeterminate layers on the basis of von Torne's 1940 study (cited in Kennedy 1991) where 1 out of 33 gulls responded to egg removal in an indeterminate way. According to Kennedy we should view this species as determinate on the basis of this result. This then, highlights the importance of standardising techniques to assess laying patterns, with removal of *a* eggs within 12 hours of laying, early in the breeding season and if possible in more than one season. It would also be useful to develop a relatively unobtrusive technology for marking individuals at the time of egg laying, so that we can follow individuals that desert the nest site after egg removal, whilst also making this response less likely. Alternatively a tracking method that can be used from one season to the next, such as the transponders used by Becker *et al.* (1997), may be most practical.

Adaptive significance

We must consider the adaptive significance of tactile indeterminate laying of the type displayed in the common tern and larids in general. Incubation does not begin in earnest before the second egg of a modal clutch of three is laid. As a result the first laid egg is often left unattended in the nest and most vulnerable to predation. For example in a study on herring gulls (Parsons 1976), it was found that the *a* egg suffered significantly higher loss than the *b* egg ($p < 0.01$), and this occurred, in the main part, when it was the sole occupant of the nest. It has been suggested therefore that it would help limit the impact of early egg loss on breeding success, by replacing eggs that have disappeared (Rinkel 1940, Gwynn 1953, Kendleigh *et al.* 1956). Thus the breeding pair by laying extra eggs will eventually end up incubating and raising the clutch size they intended.

This may be particularly important in larids where selection for the modal clutch size of three seems particularly strong. For example, herring gulls lay on average 2.9 eggs, with 91% of clutches containing three eggs, and both sexes invariably developing three discrete brood patches (Drent 1970). Previous studies have found, that any deviation from a clutch size of three causes an alteration in incubation behaviour (Baerends *et al.* 1970, Coulter 1973), resulting in reduced hatching success (Paynter 1949, Baerends *et al.* 1970) and increased predation (Paynter 1949, Baerends *et al.* 1970), although these results are not separated from any confounding effects of parental quality.

In order for indeterminate laying to have a significant positive effect on reproductive success, the breeding success of an individual would have to be increased by the potential of eggs lost during laying, effectively being realised as a result of extra egg production. For example in birds intending a clutch of three eggs, the responding birds must realise a greater fitness raising the *b*, *c* and *d* eggs than if they had just raised the *b* and *c* left after the loss. There will be selection for the indeterminate response to be flexible in relation to parental condition prior to and during laying. If birds are in poor condition prior to laying, whether it be due to year effects or a combination of these and individual quality, it may not actually be advantageous to replace an egg lost in the early stages of laying. This would be the case if the cost of producing this extra egg reduced the subsequent breeding success below the level that would have been achieved if the egg had not been replaced.

Summary

Common Terns can be classified as tactile indeterminate layers Type S, according to Haywood (1993a), but with some qualifications. The ability to replace a lost egg may be dictated by the ability to reach a certain condition prior to or during laying, which will depend on individual quality combined with environmental conditions. This ability of birds to lay extra eggs in response to egg removal provides a very important tool for use in experimental studies into the evolution of clutch size using brood manipulation. If experimental birds can be made to lay additional eggs as well as incubate and rear them, then the full cost of an enlarged brood can be investigated (chapter 3).

Chapter 6 : The Effect of Increased Egg Production on Egg Composition

An abridged version of the data presented in this chapter has been accepted for publication in Ibis (V. Heaney, P. Monaghan, R. Nager)

Introduction

Larids, in common with most seabirds, hatch at a relatively late stage of development, are downy and able to thermoregulate within days of hatching, but are nutritionally dependent on their parents for an extended period. This semiprecocial mode of development requires energy to support the metabolic costs of a relatively long period of embryonic growth (Astheimer & Grau 1990, Carey 1996), and the raw materials for synthesis of feathers, muscles and other advanced tissues required by precocial hatchlings (Carey 1996). In order to facilitate this characteristic, seabirds lay proportionately larger eggs in relation to adult mass, with the energy rich (*cf.* albumen) yolk making up a larger proportion of the egg contents than in most other non-passerines (Boersma 1982, Rahn *et al.* 1976, Carey 1996). In addition, many seabirds hatch with a large quantity of residual yolk, in fact as much as 40% of the total yolk may still be available to the chick at the time of hatching (Herring Gull *Larus argentatus*, Dunn 1972 calculated from figures in Parsons 1970, 1971). This lipid remaining in the yolk sac is utilised by the growing chick during the first few days of life (Dunn 1972), and, when resorbed into the gut, can permit survival without feeding for a short time after hatching (Astheimer & Grau 1990).

The 'quality' of eggs has been defined in terms of their relative size, weight, and composition (Ricklefs 1977a). The relative amounts of constituent parts of the egg can have important fitness consequences related to their general function in embryonic development and early chick life. The lipids contained in the yolk are vital to the maintenance and development of the chick embryo, functioning as an energy source and constituent of body cells (Dunn 1972, Carey 1996). Consequently, any variation in the size of the initial and residual (post-hatching) lipid reserve is of considerable importance to chick survival; if initial feeding conditions are not ideal for the hatchling, the size of fat reserves inherited could tip the balance between survival or death from starvation and exposure (Parsons 1970, Dunn 1972, Langham 1972, Sotherland & Rahn 1987). The protein content of the egg, roughly 46% of which is found in the albumen (Carey *et al.* 1980), is vital for structural development and size at hatching (Hill 1993, Williams 1994). The albumen is entirely used up by the time of hatching, suggesting that it is the amount of protein in the albumen in particular that limits structural growth of the chick (Freeman & Vince 1974, Boersma 1982). Water content of precocial eggs is roughly 75% (Carey 1996); this is mainly contained in the albumen. If a high water content is retained by the neonate this may be adaptive in species such as seabirds, which have a high salt content in their diet (Ricklefs *et al.* 1978). As well as lipid, protein and water avian eggs also require relatively large amounts of calcium for shell formation. An egg shell that is too thick or too thin can lead to the death of the embryo through, inability to respire or hatch, and shell breakage or excessive water loss, respectively (Carey 1996, Perrins 1996).

Regardless of the relation between egg mass and yolk or albumen content, relative egg size is a useful measure of egg quality, since larger eggs will contain more absolute amounts of nutrients than smaller eggs (Williams 1994, Carey 1996). Williams (1994) reviewed 27 studies on precocial species and found that on average egg size explained 65.3% of variation in hatchling mass (range 21-94%). Larger eggs will tend to give rise to heavier hatchlings with more nutrient reserves (Parsons 1970, Lundberg & Väisänen 1979, Birkhead and Nettleship 1984, Ricklefs 1984a, Grant 1991, Bollinger *et al.* 1990, Amundsen *et al.* 1996), and with a higher probability of survival, independent of laying sequence (Parsons 1970, 1975, Lundberg & Väisänen 1979, Sydeman & Emslie 1992) and parental quality (Nisbet 1978, Thomas 1983, Bolton 1991, Magrath 1992, Amundsen *et al.* 1996). Large eggs may also give rise to hatchlings that are structurally larger (Ricklefs *et al.* 1978, Alisauskas 1986, Bolton 1991, Amundsen *et al.* 1996) and better able to compete with their siblings (Parsons 1971, Nisbet 1973, Birkhead & Nettleship 1984). This will be particularly important in larids with three chicks in the nest, where a considerable size discrepancy is likely to occur as a result of asynchronous hatching (Nisbet & Cohen 1975, Bollinger *et al.* 1990, Salzer & Larkin 1990). Larger chicks also require relatively less energy to maintain homeothermy at ambient temperatures (Alisauskas 1986, Rhymer 1988), and may have fewer problems dealing with relatively large and robust prey items such as fish (Perrins 1996, pers. obs.). Egg size can also have a positive effect on hatching success (Croxall *et al.* 1992, Magrath 1992, Amundsen *et al.* 1996, Perrins 1996, but see Reid & Boersma 1990). To counterbalance selection for even larger eggs, a number of factors have been suggested; a trade-off between laying date and egg size, would allow adults laying smaller eggs to lay earlier (Birkhead & Nettleship 1982, Furness 1983, Perrins 1996), small chicks may require less food than larger ones, and so survive better if food availability was low (Furness 1983, Perrins 1996), also egg size may be proximately constrained by rate-limiting steps during the different stages of egg production (Shaw 1985, Williams 1990, Bolton 1991).

Through these effects on size and reserves at hatching, the most important effect of variation in egg quality is determining probability of survival in the first few days of chick life (Williams 1994). A smaller chick less well endowed with reserves is more likely to succumb to either starvation or exposure, following a failure to elicit an appropriate feeding response from its parents (Langham 1972, Dunn 1972, Bollinger *et al.* 1990). After the first critical days, parental quality becomes more important in determining chick survival (Parsons 1970, Nisbet 1973, 1977, Amundsen & Stokland 1990, Reid & Boersma 1990, Bolton 1991, Magrath 1992, Williams 1994).

Early egg loss can induce Common Terns (*Sterna hirundo*) like most other larids (Parsons 1970, Bolton 1991) to lay more eggs then their usual clutch size (i.e. they are indeterminate layers, Haywood 1993a). However, examination of the probability of such 'additional' eggs giving rise to fledged chicks suggests that both the quality of the additional eggs, and the performance of the parents during later stages of the same breeding attempt, can be reduced as a consequence of increased egg production demands (chapter 3, Monaghan & Nager 1997). For example, Monaghan *et al.* (1995) found that the viability of chicks from additional eggs in Lesser Black-backed Gulls (*Larus fuscus*) is greatly reduced, and suggested that this may, in part, be due to additional eggs being of lower quality. In view of the possibility that a reduction in egg quality might contribute to post-hatching survival of chicks hatched from additional or 'forced' eggs, it was decided to investigate further certain aspects of the physical attributes and nutritional composition of these eggs in common terns. This paper therefore compares the composition of *c* eggs from unmanipulated control birds, with the forced *d* egg from birds that intended a clutch of three, but were experimentally induced to lay four eggs.

Methods

Field collection and measurement

Fieldwork was carried out on Coquet Island, Northumberland in 1995, under licence from English Nature (no. SB:36:95). Common Terns lay between one and three eggs, and the modal clutch size in our study colony was three (mean ± s.e., 2.67 ± 0.04, $n = 173$, mode = 3; 2.3% of pairs laid 1 egg, 28.9% 2 eggs and 68.8% 3 eggs). The first-laid *a* egg was removed from seven pairs within twelve hours of laying. These birds went on to produce a further three eggs, therefore laying four eggs in total (termed *a*, *b*, *c* and *d*), at approximately 2 day intervals (laying interval between eggs, mean ± s.e. (days): *a-b* 2.07 ± 0.25, *b-c* 1.93 ± 0.13, *c-d* 2.07 ± 0.13, $n = 7$). The fourth laid *d* eggs were collected for composition analysis, together with 10 *c* eggs from unmanipulated control pairs initiating laying a clutch of three eggs at the same time. All eggs were collected on the day of laying, weighed to the nearest 0.1g using a Salter spring balance, and marked with a fine-tipped pen. Maximum length and breadth were measured to the nearest 0.1 mm using dial callipers and volume (cc), calculated from the equation taken from Dunn (1972):

$$\text{Breadth}^2 \times \text{Length} \times 0.000478$$

(0.000478 is an adjusted correction factor which allows for the imperfect ellipsoid form of the egg). The eggs were then hard-boiled (approx. 10 minutes), sealed in paraffin wrap and frozen until compositional analysis could take place back in the laboratory at Glasgow University.

Laboratory egg composition analysis

The eggs were thawed and the solid yolk separated from the surrounding albumen. The yolks were then dried in an oven at 60°C to a constant weight and the lipid extracted in petroleum ether for 2 hours using a modified Soxhlet technique (Dobush *et al.* 1985). The fat-free yolk residue was dried and the original lipid content found by subtracting weights. The separated albumen was also oven-dried at 60°C to constant weight, and since the dried albumen samples were so small, no fat extraction was performed and they are considered to be mainly protein (Romanoff & Romanoff 1949, Ricklefs 1977b). The water content of the egg may change as a result of boiling, so the fresh weights of components (shell, albumen, yolk) were not determined (Bolton *et al.* 1992). Shell thickness was measured to the nearest 0.002mm, using micro-callipers with specially modified ends. Five measurements were taken along the equator of the egg, where thickness is least variable (Tyler & Geake 1961), and an average recorded. A shell mass index was calculated from the following equation:

$$(\text{Shell dry mass} \times 1000) / \text{Egg fresh mass}$$

Results

There was no significant difference between the forced and control eggs in either fresh weight or volume (**Table 1**). The dry yolk to dry albumen ratio did not differ between forced *d* and control *c* eggs, neither was there a difference between them in the proportion of lipid in the yolk (see **Table 1**). However there was a significant difference in the egg shell component. The *d* eggs had a thinner and relatively lighter shell than the Control *c* eggs (**Table 1**).

Table 1. *Egg composition parameters for the experimentally forced* d *eggs and control* c *eggs of pairs of Common Terns laying at the same time (*n *= 7 and 10 respectively). Probability values are based on Mann Whitney* U*-tests. Using the modified sequential Bonferroni technique (Rice 1989), test statistics denoted by an asterisk should be considered significant table-wide.*

Parameter	*c* (mean ± s.e.)	*d* (mean ± s.e.)	*p*
EGG SIZE			
Fresh mass (g)	19.65 ± 0.20	19.43 ± 0.47	0.69
Volume (cc)	15.74 ± 0.21	15.44 ± 0.43	0.59
EGG CONTENTS			
Dry yolk: albumen ratio	1.76 ± 0.14	1.60 ± 0.13	0.33
% Yolk lipid	68.03 ± 1.48	67.05 ± 1.14	0.75
SHELL			
Shell thickness (mm)	0.151 ± 0.003	0.136 ± 0.004	0.02
Shell mass index	54.14 ± 1.14	49.86 ± 0.79	0.008*

This result is even more significant than the table would suggest due to the effects of allometry (the study of size and its consequences). The 'simple-ratio' thickness index used in this study assumes isometry. However, since shells comprise the 'surface' of an egg's volume, they must change allometrically with egg volume. Because *c* eggs were slightly bigger than *d* eggs they would tend to have a lower shell mass index due to the effects of allometric scaling. Thus, the finding that the *d* eggs in fact have a significantly lower shell mass index than *c* eggs is even more important since it goes against this effect.

Statistical techniques derived from allometry customarily are used to examine the relation between egg size and egg composition (Reiss 1989, Hill 1995). 'Log:log regressions of egg components on egg size are examined. With this method of analysis slopes with a value significantly greater than or less that 1 indicate a proportional increase or decrease, respectively, in the egg component with increasing egg size; values not significantly different from 1 indicate that components change in direct proportion (isometrically) to variation in egg size' (from Williams 1994). In this study, probably as a result of the small sample sizes, log:log functions provided only weak correlation between egg components and egg size, and usually only in one or other of the *c* or *d* eggs, if at all. This coupled with the small range of sizes, particularly of *d* eggs, makes conclusions from any allometric relationships somewhat questionable. However, two are presented here.

Although there was no absolute difference in the percentage of fresh egg mass that was made up of water between forced *d* and control *c* eggs, in the control *c* eggs the percentage water declined with egg mass, but this was not the case in the forced *d* eggs (see **Figure 1**). Thus, a larger *d* egg will contain relatively more water, but relatively less dry matter, than a *c* egg of the same overall size. There was no difference between control *c* eggs and forced *d* eggs in albumen or yolk content, both in absolute terms or relative to egg size. However, in the forced *d* eggs the amount of dry albumen increased with egg mass, but this was not the case in the control *c* eggs (see **Figure 2**). Thus, a larger *d* egg will contain relatively more dry albumen than a *c* egg of the same size.

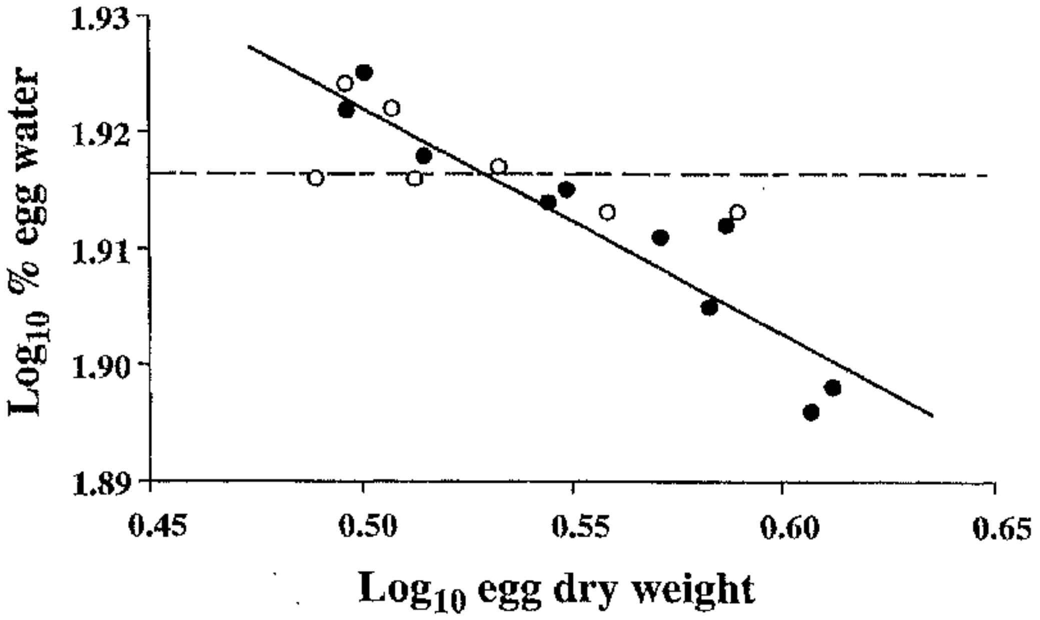


Figure 1. The relationship between egg mass ($\log_{10}$ total egg dry weight) and egg water content ($\log_{10}$ % egg is water), in the control *c* eggs (solid circles, solid line) and experimental *d* eggs (open squares, stippled line through mean value). The relationship was significant in the control *c* eggs ($r_8 = 0.70$, $p = 0.023$, $y = 0.45x - 1.07$), but not in the forced *d* eggs ($r_5 = 0.16$, $p = 0.73$, $y = 0.16x - 0.95$). The difference between forced and control eggs was significant (covariance analysis, difference in slopes $F_{1,16} = 0.52$, $p = 0.48$, n.s., difference in elevations $F_{1,16} = 5.33$, $p = 0.037$).

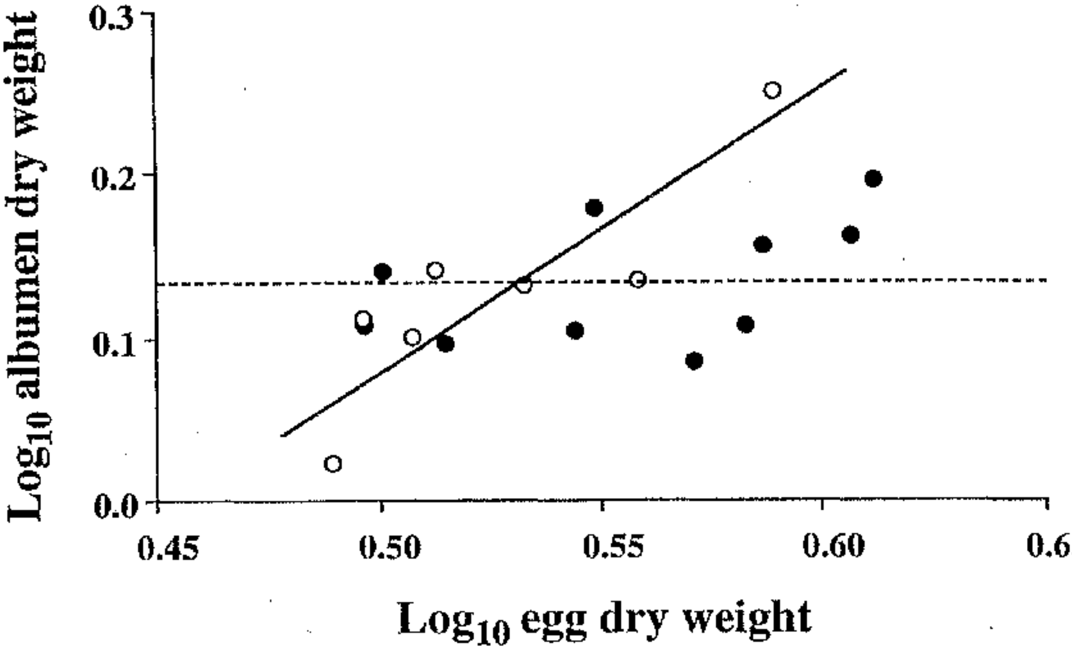


Figure 2. The relationship between egg size ($\log_{10}$ egg volume) and albumen content ($\log_{10}$ albumen dry weight), in the control *c* eggs (solid circles, solid line through mean value) and experimental *d* eggs (open squares, stippled line). The relationship was significant in the forced *d* eggs ($r_5 = 0.71$, $p = 0.07$, $y = 0.70x - 0.85$), but not in the control *c* eggs ($r_8 = 0.49$, $p = 0.15$, $y = 0.89x - 1.04$). The difference between forced and control eggs was significant (covariance analysis, difference in slopes $F_{1,16} = 0.09$, $p = 0.77$, n.s., difference in elevations $F_{1,16} = 6.05$, $p = 0.028$).

Discussion

The main difference between control *c* and forced *d* eggs lay in the thickness of the egg shell. Control *c* eggs had significantly thicker and relatively heavier egg shells than forced *d* eggs. Dunn (1972) recorded eggshell thickness for common terns on Coquet Island, and found that in clutches of 3, the shells of *c* eggs were significantly thinner than *a* eggshells. However he recorded egg shell thickness ranging from 0.102 - 0.163 mm, with *c* egg shell thickness mean 0.138 ± 0.003, $n = 11$, a value more similar in fact to that recorded for the *d* egg shells in this study, and significantly thinner than the mean value for *c* egg shells in this study ($p < 0.01$).

There is evidence that many insectivorous and granivorous birds have difficulty in obtaining sufficient calcium for shell formation, taking snail shells, calcareous grit or bones during egg laying to meet the increased demands, (MacLean 1974, Ankney & Scott 1980, Graveland & Drent 1997, Perrins 1996). Piscivorous terns taking vertebrate prey may be expected to have little or no difficulty in obtaining the necessary calcium (Perrins 1996, Brenninkmeijer *et al.* 1997). However recent studies suggest that this is not the case. Calculations of the calcium in their diet and that needed for shell formation in a 2 or 3 egg clutch added to the body maintenance requirement, suggest that female terns may well experience a short term calcium deficit during egg laying (Nisbet 1997), especially in areas where acidification has reduced vertebrate prey populations (Beintema *et al.* 1997). This is further supported by observations of female birds seeking extra dietary sources of calcium during the egg laying period, for example molluscs and shell fragments (Common Terns, Nisbet 1997), and crabs and shell fragments (Sandwich Terns *Sterna sandvicensis*, Brenninkmeijer *et al.* 1997). Dunn (1972) found that the shell thickness of the terminal egg in Common Terns is most variable and concluded that there was probably a smaller more variable amount of material available. Thus it would appear as the laying sequence progresses calcium may quite simply be running out.

The shell of an egg serves as a barrier between the embryo and the external environment. It must be sufficiently thick and strong to support the mass of the contents of the egg and the incubating adult, yet thin and porous enough to allow gas exchange and perforation by the embryo's egg tooth at hatching (Carey 1996). Shell thickness and overall quality may be related to the amount of calcium the nesting birds can find during the laying period (Perrins 1996). Beintema *et al.* (1997) report that Black Terns (*Chlidonias niger*) experiencing a calcium shortage showed a tendency for late nesting and a higher incidence of incomplete clutches, with relatively thin egg shells. These suffered lower hatching success in comparison with a control population having no calcium deficit. An egg shell lacking in calcium may also cause problems for the developing embryo since approximately 78-82% of the calcium needed by the embryo for skeleton formation and regulation of cellular processes is derived from the shell, with the remainder largely from the yolk (Simkiss 1975). A deficit of calcium has been linked with rickets in young terns (Beintema *et al.* 1997). Water loss from avian eggs during incubation has been estimated at an average of 15% of the initial fresh egg weight (Drent 1970, Rahn & Ar 1974, Ar & Rahn 1978). It is possible that eggs with thinner shells may allow a greater loss of water during incubation although they may have a lower functional pore area, that is fewer pores in the egg shell, to counter the loss (Whittow 1980). Water loss may also be regulated by cycling reserves around the system of fluid compartments (subgerminal, allantoic and amniotic) in the egg (Simkiss 1980b). Incubation water loss was increased experimentally from 15 to 30% in Domestic Fowl (*Gallus domesticus*) eggs, and no apparent effect on hatchability was found, although the chicks hatched from experimental eggs were lighter than those from control eggs of the same size (Simkiss 1980a). From this result Simkiss (1980a) concluded that the critical role of egg shell porosity in avian development has been over-emphasised

There was no difference in size between the control *c* and forced *d* eggs, and composition analysis revealed no significant differences between them in the relative contributions of the constituent parts of the egg. There was no difference between *c* and *d* eggs in the water content of the eggs, although the values obtained were slightly higher than those obtained in other larid studies (75.4% Laughing Gull *Larus atricilla* Ricklefs 1977a, 69% Ring-billed Gull *Larus delawarensis* Meathrel & Ryder 1987, 72% Herring Gull Meathrel *et al.* 1987), and for semiprecocial eggs in general (70-75% Ricklefs 1977b, 76.5% Carey *et al.* 1980). However these differences are likely to be due to variation in technique. There was no difference between *c* and *d* eggs in the relative contribution of the yolk to the dry weight of the egg and the values obtained are very similar to those found in other studies (mean relative yolk content of semiprecocial eggs is 33% Carey *et al.* 1980, Ring-billed Gull 35%, Meathrel & Ryder 1987, 30% Herring Gull Meathrel *et al.* 1987). Within the yolk itself, there was no difference between *c* and *d* eggs in the relative contribution of lipid to yolk dry weight, although the values obtained are slightly higher than those found in other studies (60.3% for *c* eggs of Common Tern Dunn 1972, 64% Laughing Gull Ricklefs 1977a, 60% Ring-billed Gull Meathrel & Ryder 1987, 59% Herring Gull Meathrel *et al.* 1987), but nearer to some of the values obtained by Nisbet (63.5-68.5% for *a* eggs of Common Tern, calculated from tables in Nisbet 1978).

We might have expected to find differences between the control *c* and forced *d* eggs in both size and composition for two reasons. Firstly, individual optimisation (Drent & Daan 1980, Pettifor *et al.* 1988) suggests that clutch and egg size will be related to a females reserves and food intake (Nisbet 1973, Jones & Ward 1976, Houston *et al.* 1983, Winkler & Walters 1983, Bolton *et al.* 1993), as well as to her ability to incubate and rear the clutch. The females in this study intended a clutch of 3 eggs; in laying a fourth egg they have invested beyond their supposed optimum (the forth egg represents a 33% increase in the cost of egg production) and thus we might expect a drop in quality in the unplanned/forced egg (Monaghan *et al.* 1995). However, the effect of the increased investment in the current breeding attempt may also be evident in a reduction in residual reproductive value i.e. in future reproduction.

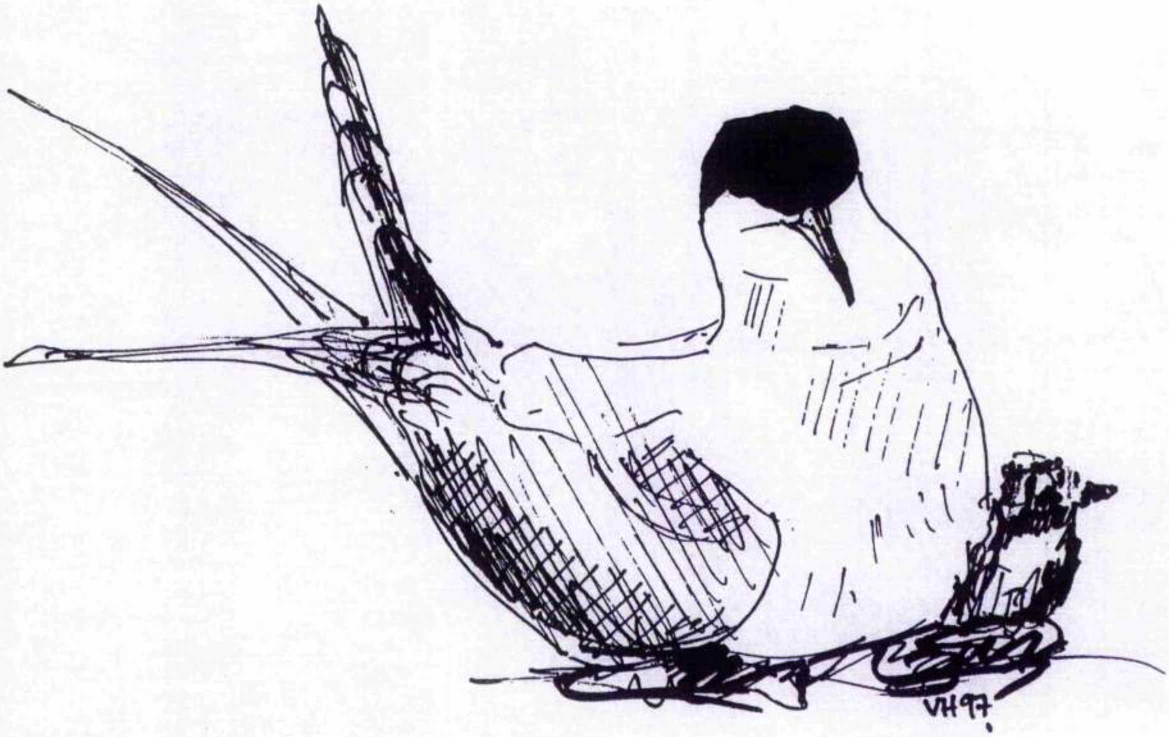
The second reason we might have expected the forced *d* egg to be of lesser quality than the control *c* egg, is because it is the fourth egg in the clutch sequence. Egg quality has been found to be related to female body condition and reserves at the time of laying in a number of species (Lesser Black-backed Gull Houston *et al.* 1983, Ring-billed Gull Meathrel *et al.* 1987, American Kestrel *Falco sparverius* Wiebe & Bortolotti 1995). If body condition is depressed through the laying sequence in response to the stresses of egg laying and food acquisition (Jones & Ward 1976, Bolton *et al.* 1993, Cooke *et al.* 1995), we might expect that egg quality would deteriorate as subsequent eggs are laid (Pierotti & Belrose 1986, Houston *et al.* 1995a, 1995b). This has indeed been shown to be the case in many larids, where the last egg is usually smaller than the preceding eggs in the clutch (Paludan 1951, Gemperle & Preston 1955, Dunn 1972, Nisbet 1973, Nisbet & Cohen 1975, Parsons 1972, Gochfeld 1977, Pierotti & Belrose 1986, Salzer & Larkin 1990, Sydeman & Emslie 1992, Bollinger 1994).

In addition to the differences in the size of eggs within the clutch, many studies have found differences in composition. There appears to be a relative uniformity in actual yolk size through the laying sequence (Domestic Hen Romanoff & Romanoff 1949, Common Tern Dunn 1972, Herring Gull Parsons 1972), with the reduced size of the *c* egg owing primarily to reduced albumen deposition around yolk (Parsons 1970, 1976, Coulter 1977, Ricklefs *et al.* 1978, Bolton 1991). However the third laid *c* egg tends to contain (relatively and absolutely) less lipid than the eggs preceding it in the laying sequence (Herring Gull Parsons 1970, Common Tern Dunn 1972).

Although they should be treated with caution (see methods), covariance analyses revealed that as egg size increased, forced *d* eggs contained relatively more water and relatively larger albumen contribution, than control *c* eggs. Allometric studies in larids have revealed that most of the difference in size between small and large eggs is due to increases in relative albumen and water content (Parsons 1970, Ricklefs *et al.* 1978, Carey *et al.* 1980, Bolton 1991). In fact Nisbet (1978) found that the difference in water content between eggs accounted for 84% of the size difference between large and small Common Tern eggs. That a positive relationship between egg size and offspring survival has been found in many larids (e.g. Parsons 1970, Bolton 1991) suggests that these changes in the wet albumen or water component of eggs are adaptive (Williams 1994). This could occur through effects on hatchling size (particularly important in this youngest chick) and chick water content (Parsons 1970, Meathrel & Ryder 1987, Bolton 1991, Williams 1994).

That there are no significant differences between the control *c* and forced *d* eggs, apart from shell thickness, and possibly albumen content with size, is perhaps not so surprising. Studies on other larids (Herring Gull Paludan 1951, Parsons 1975, Black-headed Gull *Larus ridibundus* Weidman 1956), have demonstrated the existence of an important adaptive mechanism which limits clutch size and so prevents the production of progressively smaller eggs, that would give rise to runted chicks, assuming they hatched at all. The mechanism is triggered by the onset of incubation which leads to the cessation of egg-laying by inhibiting follicle growth. Thus follicles degenerate providing they have not reached a certain stage of maturity and this limits the number of eggs to be laid after the gull has started to incubate. This 'switch-off' mechanism prevents ovulation if a follicle does not reach a minimum size, resulting in a terminal egg of roughly the same size whether it be a *b*, *c* or forced *d* egg (Parsons 1975, 1976). This study can, necessarily, only investigate the quality of *d* eggs that were laid. In birds where the fourth follicle had not reached the critical size at the time of experimental egg removal, and therefore would have produced a poorer quality egg, no *d* egg was laid. These females, who intended a clutch of three eggs, either abandoned the breeding attempt (49% of pairs), or just laid and raised the remaining *b* and *c* eggs of the clutch (approximately 32%), (see chapter 5). Thus, it is likely that the experimental birds that laid a fourth *d* egg are a biased sub-set of higher quality birds, that were able to incur the increased egg production demand whilst maintaining the quality of this egg. Although the *d* egg is the officially forced egg, it would be interesting to look at the quality of the *b* and *c* eggs in these experimental clutches also, since previous studies have reported an increase in relative egg size following removal (Parsons 1976, Salzer & Larkin 1990, chapter 7).

Chapter 7 : Does Increased Egg Production Alone Influence the Capacity to Rear a Normal Brood, and if so How?



Introduction

Egg production is a costly time for breeding birds since they must obtain all the nutrients for the egg contents and also the energy required for collecting this extra food and for its metabolism into the egg (Perrins 1996, Carey 1996). They may finance this demand either using stored reserves or a combination of these and their daily intake of resources (see Drent & Daan 1980, Perrins & Birkhead 1983). Recent correlative and experimental studies in wild birds, where clutch and egg size, timing of laying and laying intervals are closely linked to variation in food supply, support the assumption that egg production is costly (Bolton *et al.* 1992, Nager & van Noordwijk 1992, Nilsson & Svensson 1993, for review see Daan *et al.* 1990). An organism will have a finite amount of energy available, and will be expected to tailor its breeding effort according to this (Stearns 1992, Roff 1992). An experimental increase in egg production (above the supposed optimum) might, therefore, be expected to have a negative effect on subsequent parental fitness; with an increase at this stage of the breeding attempt necessarily effecting a decrease in the amount of energy available for subsequent components of reproductive effort or parental somatic effort (Martin 1987).

Previous avian brood enlargement studies have generally assumed that the main costs of an increase in current reproductive effort (producing or rearing additional young) operate as a between- rather than within-clutch trade-off, via a reduction in residual reproductive value (Smith *et al.* 1987, Gustafsson & Sutherland 1988, Pettifor *et al.* 1988, Gustafsson & Part 1990, Roff 1992, Stearns 1992, Daan *et al.* 1996). However, it is also possible that the consequences of an experimental increase in current reproductive effort (for example extra egg production) may be evident within the same breeding attempt (chapter 3, Monaghan *et al.* 1995). This paper aims to investigate the possibility of the latter, a within-clutch trade-off between egg production and the later stages of the reproductive attempt.

There are two main routes by which increased egg production could affect within-brood success; either by lowering subsequent parental performance (see chapter 3), or by lowering the quality of additional eggs (Monaghan *et al.* 1995). In order to separate these two scenarios it is necessary to cross-foster clutches between control and experimental nests (that have had the additional egg production).

To investigate the possible effects of increased cost early in the breeding attempt on parental performance later in the same attempt, experimental birds laying an extra egg as a result of experimental manipulation were given a normal clutch to incubate and rear. This differs from the experiment presented in chapter 3, in that the experimental birds were not made to raise the enlarged clutch size resultant from the additional egg, but raised a control clutch of the size they had originally intended. Thus in this study experimental birds incurred the additional egg production costs only (not incubation and chick-rearing). In order to investigate the quality of additional eggs in terms of egg and resultant chick size, chick growth and survival, the entire clutches produced by experimental birds were cross-fostered into appropriate control nests, and followed until fledging.

The effects of increased egg production on experimental birds laying two and three eggs after removal of their first laid *a* egg, are studied here. Since these two sets of birds are likely to differ in quality, originally intending clutches of two and three eggs respectively, they may show different relative effects (McNamara & Houston 1996, Wright & Cuthill 1989, chapter 4), and are therefore presented separately with a joint summary.

Methods

The experiment was carried out on common terns *Sterna hirundo* nesting on Coquet Island, Northumberland. Common terns lay between 1-3 eggs. To manipulate parents into producing an additional egg, the first laid egg was removed shortly after laying (Haywood 1993a). In 1995 the first laid (*a*) egg was removed from 55 pairs within 12 hours of laying. Twenty-eight pairs continued to lay subsequent eggs in the same nest scrape; 7 laid a further three eggs; 18 a further two eggs; and 3 one more egg. Only the experimental birds with an apparent intended clutch of two or three eggs (laying a total of three or four eggs respectively), are dealt with in this paper.

In the 28 nests where experimental birds continued to lay after removal, the *a* egg was returned to the nest as soon as the second (*b*) egg was laid. This *b* egg was removed and kept in storage and either swapped for the *c* egg when the latter was laid, or returned to the nest after two days if no *c* egg was produced. This was repeated where applicable, swapping the *c* egg for the *d* egg, so that the nest contained the *a*, *b*, and *c* eggs, maintaining the normal hatching pattern, both in terms of hatching interval between the chicks and hatching order of the egg. Between removal and replacement eggs were sealed in a plastic bag to conserve moisture and stored at 11-14 ^{0}C (see chapter 2). The seven *d* eggs laid, were not returned to the nest, but boiled and frozen for laboratory analysis of composition (see chapter 6).

Clutches were swapped between experimental and unmanipulated control nests, in order to investigate the effects of extra egg production on additional egg quality and subsequent parental performance independently. In these experiments it is important that foster parents and control clutch donors are of roughly equal quality. Thus, any differences in the resulting success of the broods can be attributed with certainty to egg quality or parental performance effects. For this reason all the study pairs were selected from the centre of the colony during peak laying. Study nests were matched by the clutch size they intended and by the laying date of their first egg. Clutch swaps were carried out as soon as egg laying was complete in the nests involved; that is, no new eggs had been laid for 3 days.

All eggs were measured (volume and fresh mass) on the day of laying and the chicks were measured within 36 hours of hatching. Nests and chicks were marked and breeding success, duration of the incubation period, chick growth and fledging size, were recorded using standard methods (see chapter 2). Chick fledging size was measured at 20 days of age and brood fledging weight was calculated as the sum of the weights of the surviving chicks in a brood when the *a* chick reached (or would have reached) 20 days of age. Instantaneous growth rates over the period of linear growth were calculated using the formula:

$R = (\ln W_2 - \ln W_1) / (t_2 - t_1)$,

where R = instantaneous growth rate, W = mass and t = time.

Observations were made on a subset of experimental and control nests within 25m of hides, during an average of three or four 3h watches per day, randomised over the daylight hours. Attendance at the nest was recorded during the first week of chick life (0-8 days from hatching of the first chick), and the rate of provisioning during the first and second weeks of chick life (0-8 days and 9-15 days respectively from hatching of the first chick) were recorded using standard methods (see chapter 2). Non-parametric statistical tests have been used in comparisons where variances between groups were non-homogeneous, or distributions non-normal (Sokal & Rohlf 1981, Siegel & Castellan 1988).

Experiment 1

In this first experiment the effect of increased egg production in birds intending a clutch of three eggs was investigated. The seven pairs in 1995, intending a clutch of three and made to lay a total of four eggs were studied. Three is the modal and maximum natural clutch size in common terns (in an unmanipulated sample of 178 pairs at the study colony in 1995, 3% laid one egg, 28% laid two egg clutches and 69% laid three egg clutches) and so these birds are likely to be from the higher end of a quality spectrum, and thus may show a lower relative effect of increased cost than poorer quality individuals (McNamara & Houston 1996, Wright & Cuthill 1989, chapter 4).

In these seven experimental nests where a fourth *d* egg was produced the *a*, *b* and *c* eggs of the clutch were swapped with a control clutch of three (*a, b, c*) initiated at the same time. Thus, the parents incurred the demand of increased egg production but were only made to incubate and raise the clutch size of three that they had intended. The eggs they raised were a normal clutch of three eggs from an unmanipulated control pair that initiated laying in the centre of the colony at the same time. Thus any differences in hatching success, chick growth or fledging success, between experimental and controls nests, will be as a result of reduced parental performance. This experimental group is referred to as the Parental Effect Group.

The second group in this first experiment consisted of seven pairs that laid an unmanipulated clutch of three eggs and were made to raise the *a*, *b* and *c* eggs (the *d* egg having been collected for analysis), laid by the seven birds in the Parental Effect Group above. By cross-fostering the *a*, *b*, and *c* eggs of the 'forced' clutch into the nest of a control pair initiating laying at the same time, we can investigate the quality of these eggs, independent of any parental effects. This second experimental group is referred to as the Egg Effect Group.

The control group for both the Parental Effect and Egg Effect groups consisted of 20 pairs initiating laying of an unmanipulated clutch of three eggs at the same time as the experimental pairs and raising another control clutch of 3 eggs (*a*, *b*, *c*) also initiated at the same time. By raising a clutch that was not their own, this group controlled for the effect of swapping eggs between nests. The experimental set-up is summarised in **Figure 1.**

Provisioning data for the Egg Effect and Control groups are presented as an average over the first two weeks of chick life (18 and 54 watches on 4 and 13 nests respectively). However, in order to extract a bit more detail on the performance of the experimental parents, feeding data for the Parental Effect and Control groups are split into the first and second weeks of chick life (18, 28 and 12, 26 watches on 6 and 13 nests in weeks 1 and 2 respectively).

Results

i). Parental effect

There was no significant difference in the date of initiation of laying of the original clutch between Parental Effect and Control pairs (laying date of *a* egg (days after 1 May), mean ± s.e.: Parental Effect 27.57 ± 1.29, $n = 7$; Control 28.68 ± 0.39, $n = 20$; Mann Whitney U-test $U_{25} = 69.5$, $p = 0.98$, n.s.), and both intended a clutch of three eggs. Their original clutches were removed and the pairs in both groups were given an unmanipulated clutch of three eggs (*a*, *b*, *c*), laid at the same time as their original clutch, to incubate and raise. The only difference between the experimental and control groups was, therefore, that the Parental Effect group had laid four eggs. There were no differences in the size of the eggs in the clutches they raised (2-Way ANOVA on egg volume, laying order effect $F_{2,75} = 4.61$, $p = 0.013$, group effect $F_{1,75} = 0.006$, $p = 0.94$, interaction $F_{2,75} = 2.25$, $p = 0.11$, n.s.).

There was no significant difference in hatching success between Control and Parental Effect pairs, which was very high in both groups, with only one nest in each group failing to hatch all three eggs, (number of eggs hatched, mean ± s.e.: Parental Effect 2.86 ± 0.14, $n = 7$; Control 2.95 ± 0.05, $n = 20$; Fisher exact test $p = 0.46$, n.s.).

Table 1. *Hatchling parameters (measured on day hatched) for Parental Effect and Control groups. Data are compared using Mann Whitney U-tests.*

Parameter	Parental Effect, mean ± s.e.(n)	Control, mean ± s.e.(n)	p
Duration of incubation			
a chick	22.50 ± 0.19 (7)	22.33 ± 0.13 (20)	0.45
b chick	21.64 ± 0.45 (7)	21.32 ± 0.11 (19)	0.83
c chick	21.17 ± 0.21 (6)	20.97 ± 0.09 (19)	0.44
Hatchling mass (g)			
a chick	15.29 ± 0.51 (7)	15.55 ± 0.40 (20)	0.76
b chick	14.14 ± 0.53 (7)	14.90 ± 0.46 (20)	0.42
c chick	14.50 ± 0.53 (6)	13.47 ± 0.31 (19)	0.12
Hatchling wing length (cm)			
a chick	1.71 ± 0.04 (7)	1.72 ± 0.02 (20)	0.86
b chick	1.71 ± 0.05 (7)	1.65 ± 0.04 (20)	0.10
c chick	1.77 ± 0.06 (6)	1.66 ± 0.02 (19)	0.16

Chicks are identified according to their hatching order, with the *a* chick hatching first, the *b* chick second and the *c* third. In all cases in Control and Parental Effect groups the eggs hatched in the order they were laid. There was no significant difference in the duration of incubation, hatchling weight or wing length for *a*, *b* or *c* chicks between the two groups (see **Table 1**).

There was no difference in the number of chicks fledged per nest, between Parental Effect and Control groups, and no nests failed completely (see **Table 2**); nor was there any difference between groups in the percentage of chicks surviving to fledging according to hatching order (see **Figure 2**).

Table 2. *Number of chicks fledged per nest by Parental Effect and Control pairs (Fisher exact test* p *= 0.16, n.s.).*

	NUMBER FLEDGED			
TREATMENT	1	2	3	Mean ± s.e. (*n*)
Parental Effect	0 (0%)	5 (71%)	2 (29%)	2.29 ± 0.18 (7)
Control	2 (10%)	17 (85%)	1 (5%)	1.95 ± 0.09 (20)

Table 3. *Growth and fledging parameters for fledging chicks in Parental Effect and Control groups. Mean Instantaneous Growth Rate wing 3-21d, weight 1-16.5d. Data are compared using Mann Whitney U-tests.*

Parameter	Parental Effect, mean ± s.e.(*n*)	Control, mean ± s.e.(*n*)	*p*
Instantaneous Growth Rate (weight)			
a chick	0.115 ± 0.009 (7)	0.115 ± 0.006 (19)	0.89
b chick	0.125 ± 0.007 (7)	0.117 ± 0.006 (19)	0.67
c chick	0.126 ± 0.001 (2)	0.148 - (1)	-
Instantaneous Growth Rate (wing)			
a chick	0.127 ± 0.003 (7)	0.124 ± 0.003 (19)	0.75
b chick	0.129 ± 0.006 (7)	0.128 ± 0.003 (19)	0.93
c chick	0.126 ± 0.002 (2)	0.152 - (1)	-
Fledging mass (g)			
a chick	123.43 ± 3.06 (7)	119.05 ± 5.53 (19)	0.98
b chick	115.00 ± 6.74 (7)	119.37 ± 4.67 (19)	0.35
c chick	85.00 ± 12.00 (2)	-	-
Fledging wing length (cm)			
a chick	15.84 ± 0.21 (7)	15.23 ± 0.40 (19)	0.49
b chick	14.44 ± 0.32 (7)	14.45 ± 0.29 (19)	0.84
c chick	11.80 ± 0.20 (2)	-	-

Too few *c* chicks survived to fledging in either group to allow statistical comparison of growth rates and fledging size between them. However, of the *a* and *b* chicks that fledged, there was no difference in the overall growth rates, between Parental Effect and Control groups (see **Table 3**). There was also no difference between the control and experimental nests in the fledging size (measured at 20 days of age) of the surviving chicks (see **Table 3**). The brood fledging weight did not differ between Parental Effect and Control nests (brood fledging weight (g), mean ± s.e.: Parental Effect 262.71 ± 15.52, $n = 7$; Control 224.80 ± 11.38, $n = 20$; Mann Whitney U-test $U_{25} = 54.5$, $p = 0.39$, n.s.).

There was no difference between the Parental Effect and Control groups in attendance at the nest in the first week of chick life (percentage time nest left unattended, mean ± s.e.: Parental Effect 0.19 ± 0.03, $n = 6$; Control 0.28 ± 0.06, $n = 14$; Mann Whitney U-test on arcsin transformed values $U_{18} = 35$, $p = 0.56$, n.s.). There was also no difference in the provisioning rate between the two groups in the first and second weeks after hatching of the brood (see **Figure 3**).

ii). Egg effect

There was no significant difference between Egg Effect and Control birds in the date of initiation of laying of their original clutch (laying date of *a* egg (days after 1 May), mean ± s.e.: Egg Effect 29.50 ± 0.48, $n = 7$; Control 28.68 ± 0.39, $n = 20$; Mann Whitney U-test $U_{25} = 47$, $p = 0.19$, n.s.), and birds in both groups intended and laid unmanipulated clutch of three eggs. There was also no significant difference in the size of these eggs that they originally laid (2-Way ANOVA on egg volume, laying order effect $F_{2,73} = 3.73$, $p = 0.03$, group effect $F_{1,73} = 2.91$, $p = 0.09$, interaction $F_{2,73} = 1.12$, $p = 0.33$, n.s.).

In the experimental protocol birds in the Egg Effect and Control groups were given a clutch of three eggs that was not their own to incubate and raise. The Egg Effect group raising the *a*, *b* and *c* eggs laid by birds manipulated into laying an extra fourth egg, and the Control group raising a normal clutch of three eggs (*a*, *b*, *c*). There was no significant difference in the absolute size of the eggs raised by Egg Effect and Control groups, however the eggs differ in relative size between the two groups (see **Figure 4**). The size of the *b* and *c* eggs, relative to the *a* egg, increases after experimental removal of the *a* egg, and therefore in the clutch raised by the Egg Effect group in comparison to the Controls (2-way ANOVA *b* & *c* eggs as a of % *a* egg volume, laying order effect $F_{1,50} = 6.47$, $p = 0.01$, treatment effect $F_{1,50} = 11.04$, $p = 0.002$, interaction $F_{1,50} = 0.23$, $p = 0.64$).

Chicks are identified according to the egg they hatched from, so that any differences according to laying order in the Egg Effect and Control clutches can be identified. There was no difference in hatching success between the two groups (number of eggs hatched, mean ±

s.e.: Egg Effect 3.00 ± 0.00, $n = 7$; Control 2.95 ± 0.05, $n = 20$; Fisher exact test $p = 1.0$, n.s.), which was very high in both, with only one nest failing to hatch all three eggs in the Control group, and 100% hatching success in the Egg Effect group. There was also no difference in hatchling size between Control and Egg Effect nests of the *a*, *b* or *c* chicks (see **Table 4**). However in the Egg Effect group although there were no differences in the hatching date of the *a* chick, the *b* and *c* chicks both hatched significantly later than the *b* and *c* chicks in Control nests (see **Table 4**).

Table 4. *Hatchling parameters (measured on day of hatching) for Egg Effect and Control groups. Data are compared using Mann Whitney U-tests.*

Parameter	Egg Effect, mean ± s.e.(n)	Control, mean ± s.e.(n)	p
Hatching date (days after 1/5)			
a egg	52.36 ± 0.84 (7)	50.88 ± 0.35 (20)	0.07
b egg	53.50 ± 0.61 (7)	51.60 ± 0.38 (20)	0.02
c egg	55.14 ± 0.45 (7)	53.13 ± 0.38 (19)	0.01
Hatchling mass (g)			
a egg	14.64 ± 0.52 (7)	15.55 ± 0.40 (20)	0.28
b egg	14.64 ± 0.42 (7)	14.90 ± 0.46 (20)	0.89
c egg	13.80 ± 0.69 (7)	13.47 ± 0.31 (19)	0.34
Hatchling wing length (cm)			
a egg	1.67 ± 0.04 (7)	1.72 ± 0.02 (20)	0.38
b egg	1.70 ± 0.04 (7)	1.65 ± 0.04 (20)	0.15
c egg	1.73 ± 0.03 (7)	1.66 ± 0.02 (19)	0.18

Table 5. *Number of chicks fledged per nest by Egg Effect and Control pairs ($X^2_1 = 3.26$, n.s.).*

	NUMBER FLEDGED			
TREATMENT	**1**	**2**	**3**	Mean ± s.e. (n)
Egg effect	1 (14%)	3 (43%)	3 (43%)	2.29 ± 0.29 (7)
Control	2 (10%)	17 (85%)	1 (5%)	1.95 ± 0.09 (20)

There was no difference in the number of chicks fledged per nest, between Egg Effect and Control groups (see **Table 5**), and no nests failed completely. There was also no difference in the percentage of chicks surviving to fledging in each group according to hatching order (see **Figure 5**).

Table 6. *Growth and fledging parameters for the chicks from* a, b *and* c *eggs raised by Egg Effect and Control groups. Mean Instantaneous Growth Rate wing 3-21d, weight 1-16.5d. Data are compared using Mann Whitney U-tests.*

Parameter	Egg Effect, mean ± s.e.(*n*)	Control, mean ± s.e.(*n*)	*p*
Instantaneous Growth Rate (weight)			
a egg	0.110 ± 0.014 (6)	0.115 ± 0.006 (19)	0.66
b egg	0.135 ± 0.008 (7)	0.117 ± 0.006 (19)	0.26
c egg	0.076 ± 0.022 (3)	0.148 - (1)	-
Instantaneous Growth Rate (wing)			
a egg	0.125 ± 0.005 (6)	0.124 ± 0.003 (19)	0.95
b egg	0.115 ± 0.006 (7)	0.128 ± 0.003 (19)	0.08
c egg	0.122 ± 0.001 (3)	0.152 - (1)	-
Fledging mass (g)			
a egg	123.50 ± 3.96 (6)	119.05 ± 5.53 (19)	0.95
b egg	118.40 ± 3.60 (7)	119.37 ± 4.67 (19)	0.34
c egg	108.00 - (1)	-	-
Fledging wing length (cm)			
a egg	15.77 ± 0.15 (6)	15.23 ± 0.40 (19)	0.87
b egg	14.36 ± 0.09 (7)	14.45 ± 0.29 (19)	0.25
c egg	12.50 - (2)	-	-

Too few *c* chicks survived to fledging in either group to allow statistical comparison of growth rates and fledging size between Control and Egg Effect groups. However, of the *a* and *b* chicks that survived, there was no significant difference in the overall growth rates or fledging size, between the two groups (see **Table 6**). The brood fledging weight also did not differ between Egg Effect and Control nests (brood fledging weight (g), mean ± s.e.: Egg Effect 277.14 ± 33.85, $n = 7$; Control 224.80 ± 11.38, $n = 20$; Mann Whitney U-test $U_{25} = 45$, $p = 0.17$, n.s.).

There was no difference between Egg Effect and Control groups in attendance at the nest in the first week of chick life (percentage time nest left unattended, mean ± s.e.: Egg Effect 0.14

± 0.04, $n = 5$; Control 0.28 ± 0.06, $n = 14$; Mann Whitney U-test on arcsin transformed values $U_{17} = 22$, $p = 0.23$, n.s.). There was also no difference between the two groups in the provisioning rate, measured as an average over the first two weeks of chick life (energy (j) delivered to the nest per living chick per hour, mean ± s.e.: Egg Effect 4.93 ± 0.96, $n = 4$; Control 6.20 ± 0.84, $n = 13$; Mann Whitney U-test $U_{15} = 22$, $p = 0.65$, n.s.).

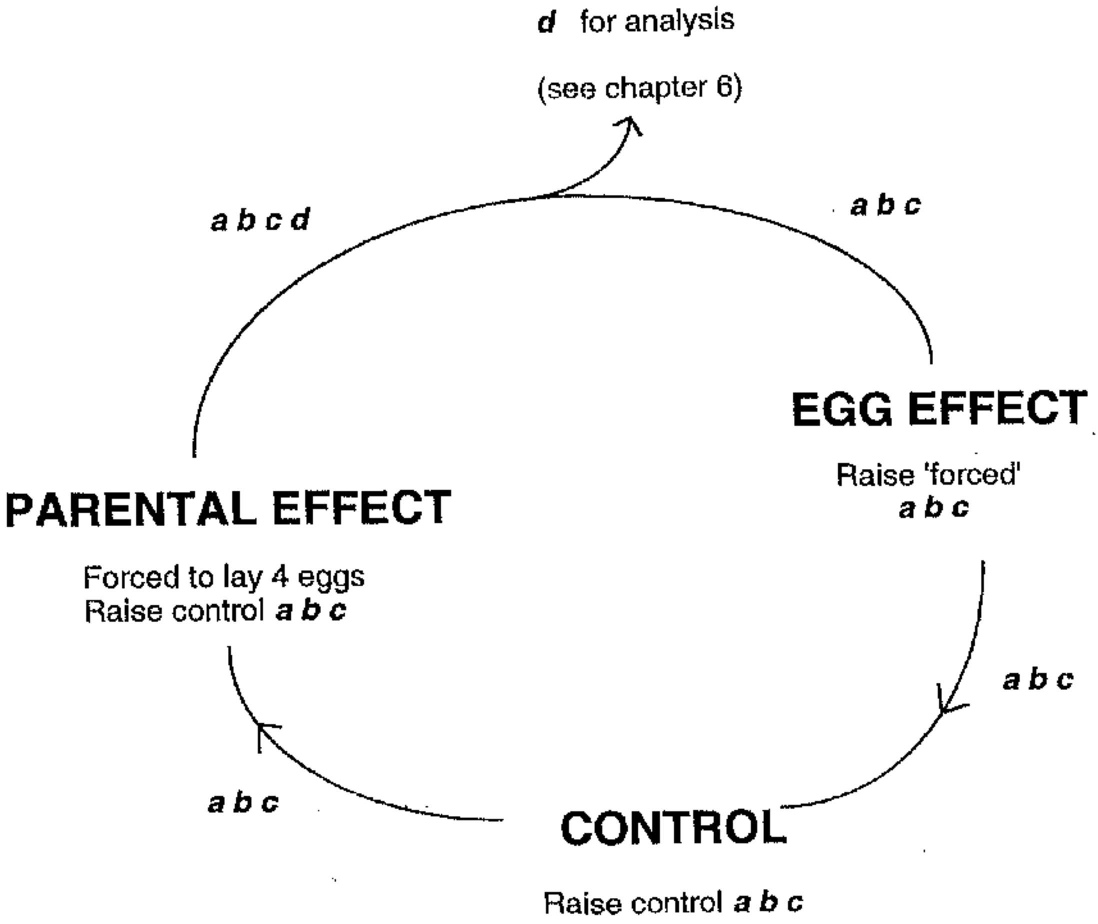


Figure 1. The set-up for experiment 1. The arrows indicate the directions of the experimental clutch movements between nests. The Parental Effect birds laying a total of four eggs, raised an unmanipulated clutch of three eggs. The *d* eggs from the experimental clutches were collected for composition analysis, and the remaining eggs of the clutch raised by the Egg Effect group. The control group raised a clutch of three eggs that was not their own.

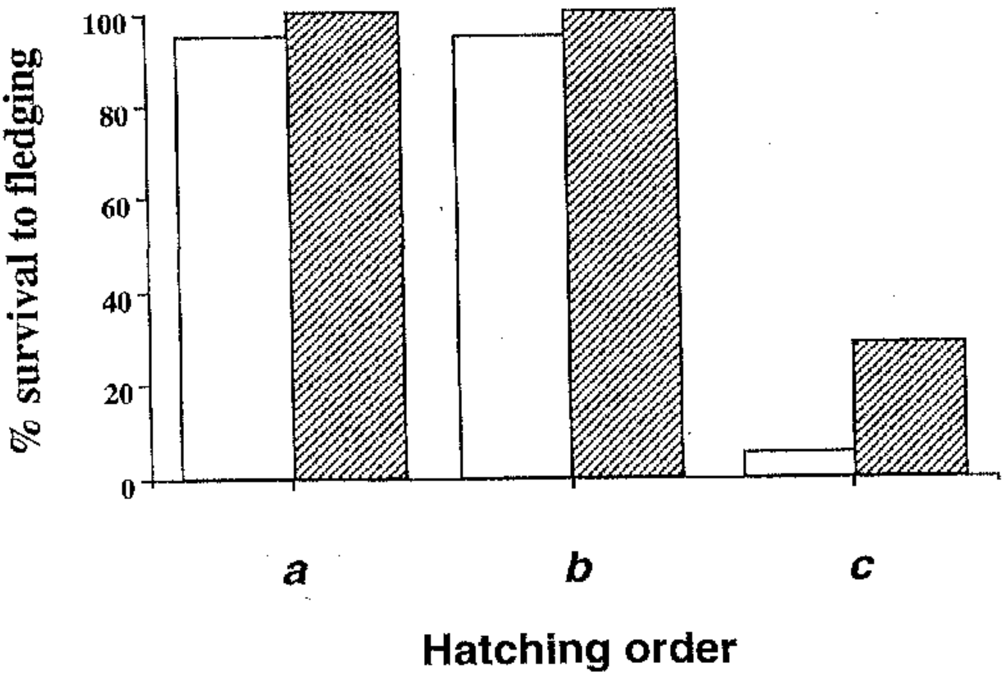


Figure 2. The percentage of chicks surviving to fledging in the Control (open, *n* = 20) and Parental Effect (hatched, *n* = 7) groups in relation to hatching order. There was no difference between the two groups in the survival of the first, second or third hatched chicks (see text for details).

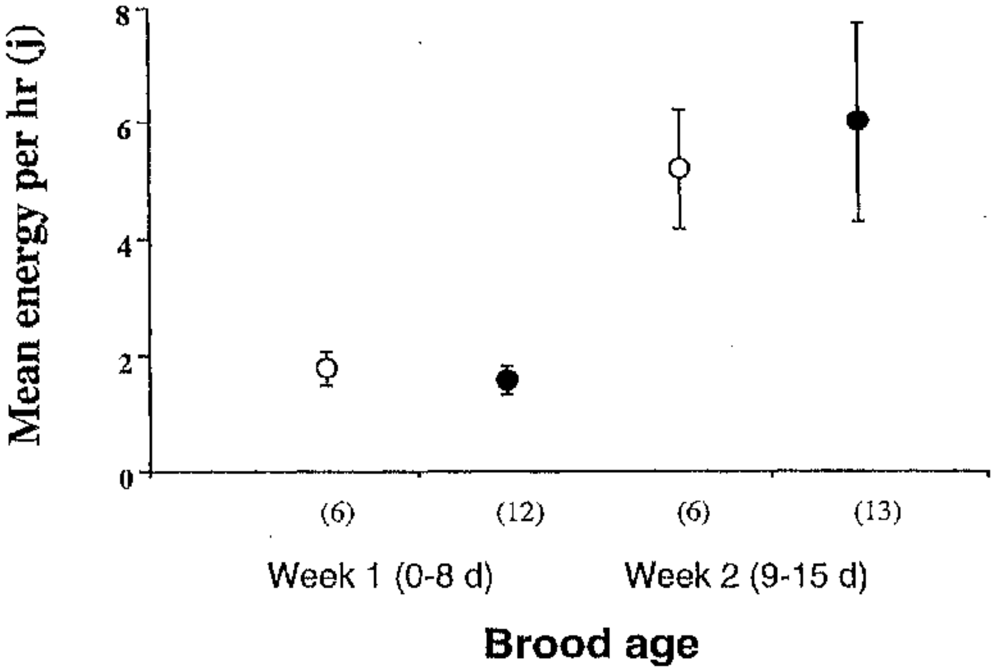


Figure 3. The mean energy per chick per hour (± s.e.) delivered to the brood by control (solid circles) and Parental Effect (open circles) groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the x-axis. There was no significant difference between the groups in the first (Mann Whitney U-test $U_{16} = 28$, $p = 0.45$, n.s.) or the second week (Mann Whitney U-test $U_{17} = 33$, $p = 0.60$, n.s.).

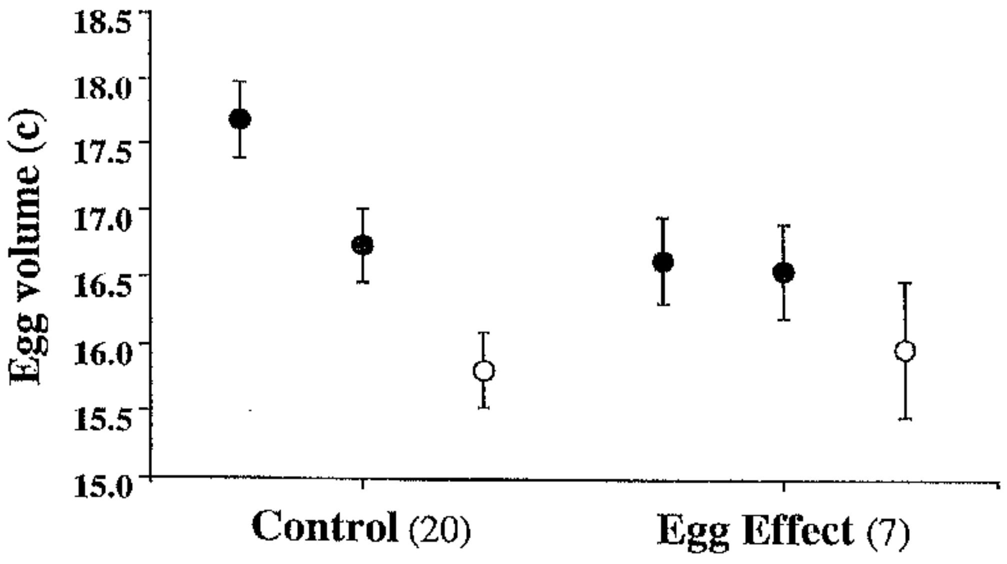


Figure 4. Mean (± s.e.) egg volume (cc) of eggs raised by Egg Effect and Control groups, (first egg, solid circle; second egg, shaded circle; third egg, open circle). The sample sizes are given in brackets on the x-axis. There was no difference in the absolute size of the eggs between the two groups (2-Way ANOVA on egg volume, laying order effect $F_{2,75} = 5.80$, $p = 0.005$, treatment effect $F_{1,75} = 1.37$, $p = 0.25$, interaction $F_{2,75} = 1.42$, $p = 0.25$). However, they differed in relative size (see text for details).

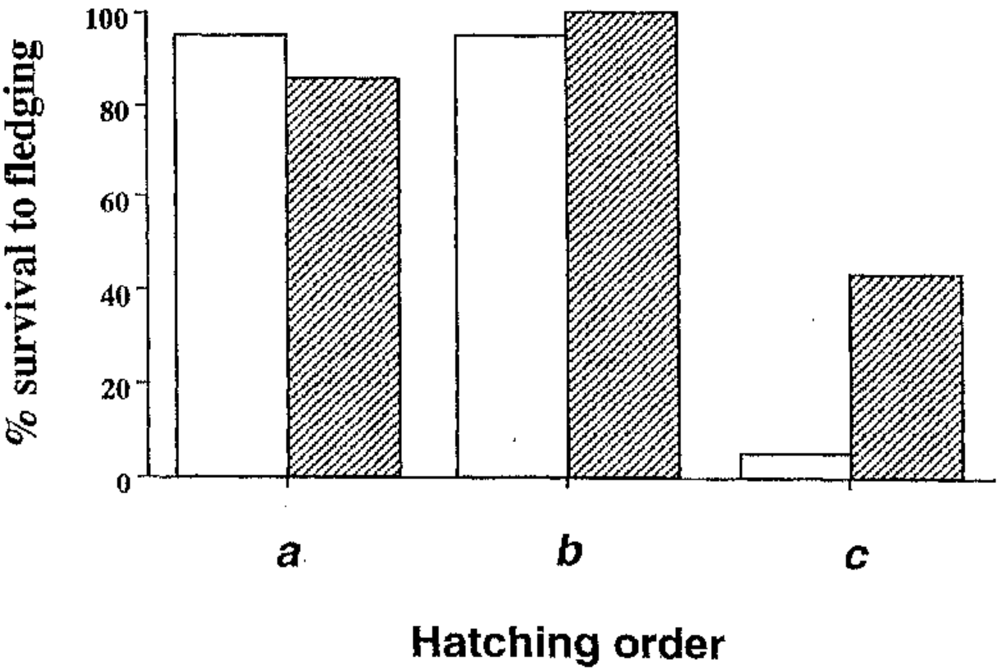


Figure 5. The percentage of chicks surviving to fledging in the Control (open, n = 20) and Egg Effect (hatched, n = 7) groups in relation to hatching order. There was no difference between the two groups in the survival of the first, second or third hatched chicks (see text for details).

Discussion

i). Parental Effect

The experimental birds in the Parental Effect group incurred a 33% increase in egg production costs, but were only made to incubate and rear a control clutch of three, the size that they had intended. We might expect this increase in effort at the egg production stage to effect a decrease in investment in the later stages of incubation and chick rearing as reserves fall short (see chapters 3 & 4, Martin 1987, Monaghan & Nager 1997). However this does not appear to be the case. There were no differences between control and experimental birds in the duration of incubation or in hatching success (which was very high in both groups) and there was no significant difference in the hatching size of chicks.

There also appears to be no difference between experimental and control birds in subsequent chick rearing ability. There was no significant difference between the control and experimental groups in attendance at the nest during the first week of chick life, when chicks are most vulnerable to death from exposure (Langham 1972, Dunn 1972, Bollinger *et al.* 1990). There was also no significant difference between the two groups in provisioning effort. There was correspondingly no significant difference between experimental and control nests in the overall growth rates of the surviving *a* or *b* chicks and their size at fledging. In fact the experimental birds fledged slightly more young (2.29) than controls (1.95), although this result is not significant. The resultant brood fledging weight, although still not significant, is on average 38g more in experimental nests (263g) than in controls (225g).

This result would seem to be in contrast to that found in chapter 3, where an increase in egg production demand caused a reduction in overall fledging success, mainly through reduced provisioning capacity. However, in 1994 the experiment was conducted on birds intending a clutch size of two eggs, whereas in this study the experimental birds intended the maximum and modal clutch size of three eggs, and may thus show relatively less effect of the increase in demand (Wright & Cuthill 1989, McNamara & Houston 1996, chapter 4). In addition, in the 1994 study, the experimental birds with the increased egg production demand were also made to incubate and rear the enlarged brood size. In this study the experimental birds only incubated and raised the clutch size they had originally intended. Thus, although the ability to raise an enlarged brood is negated by the inclusion of egg production costs, this is not the case with the intended or normal brood size.

That the increased egg production demand in the experimental birds does not appear to effect a significant reduction in the subsequent chick rearing ability, may in fact be explained if we further consider the quality of the experimental birds. Of the birds that had their first laid egg removed in 1995, only half continued to lay further eggs in the same nest scrape, and only 12.7% of the total group laid three subsequent eggs (four eggs in total). Thus, the experimental group are in some ways 'pre-selected' for high quality birds, by definition of their being the subset of birds able to lay a fourth egg. In order for the indeterminate response to be adaptive (see chapter 5), the birds laying four eggs in total need only achieve a higher breeding success raising their own *b*, *c* and 'forced' *d* eggs after loss of the *a* egg, than if they raised the *b* and *c* eggs only. In this study, we compare the experimental group to control birds intending and raising a clutch of three eggs, and the experimental pairs are made to raise an unmanipulated clutch of three eggs (*a*, *b*, *c*) which is possibly of higher quality than the *b*, *c*, *d* clutch they would have raised in the wild. Thus, we might expect a roughly similar breeding success in the Parental Effect and Control groups, despite the extra egg production demand incurred.

In summary therefore, while the capacity to rear an enlarged clutch was found to be reduced in low quality birds made to lay an extra egg (chapter 3), in these higher quality birds increasing egg production by one egg does not appear to have affected their capacity to rear their intended brood size. Whether their capacity to rear an enlarged brood would have been affected is not known.

ii). Egg Effect

The aim of this section of the first experiment, was to investigate the quality of the eggs laid by the birds in part i) above, that intended a clutch of three eggs and were made to lay four. However, only the *a*, *b* and *c* eggs are raised by the Egg Effect group, since the *d* egg was collected for composition analysis (see chapter 6). Any reduction in egg quality is most likely to be found in the official 'forced' *d* egg (Monaghan *et al.* 1995), and so this section is not a full test. Also, it may also have been more important to investigate the success of the *b*, *c*, and *d* eggs raised by a control group, since this is the clutch the experimental birds would have raised in the wild had they replaced their first egg after natural loss. The success of 'additional' eggs, independent of parental effects, was however investigated in Experiment 2 (see below).

As in previous studies (e.g. Parsons 1976) an increase in relative, but not absolute, size was found in the *b* and *c* eggs laid after removal, which may have positive survival effects for the resulting chicks (for reviews see Williams 1994, Carey 1996). However, there were no significant differences in hatching success, or in the size of hatchlings from the eggs in experimental and control nests. The lack of difference in hatching success and hatchling size suggests that the limited egg storage time (no more than three days, and usually less) had no adverse effects on viability (see appendix 2).

There were, however, differences in hatching date. Both the *b* and *c* eggs hatched significantly later in experimental than control nests. This is most likely to be a result of the experimental protocol, which involved removal and storage of the eggs before return to the nest, in order to maintain the normal hatching order. This had the effect of delaying the onset of effective incubation for each egg in the experimental brood, by roughly two days (the average egg-laying interval). This however, mimics the situation of natural egg loss more closely, since a bird that has replaced its first egg lost through predation, will find the clutch it subsequently incubates and raises, effectively delayed by the laying interval between the first and second egg.

Despite the possible disadvantages due to delayed hatching date in the experimental nests (see Perrins 1996), the subsequent chicks, identified according to the eggs they hatched from, did not show any significant differences in growth or fledging size, from the chicks in control nests, and there was no difference in fledging success between the two groups by egg. Experimental pairs raising the forced clutch raised slightly more young per nest to fledging (2.29) than control pairs (1.95), although the difference was not significant. They also had a heavier brood fledging weight (277g) by on average over 50g heavier than controls (225g), although this was also not significant and possibly due to the small sample size.

Experiment 2

In the second experiment the effect of an increase in egg production costs in birds intending a clutch of two eggs is investigated. In 1995, eighteen pairs laid a further two eggs after removal of their first laid egg. Thus, they intended a clutch of two eggs but were experimentally manipulated into producing three. Their intended clutch size is lower than the mode of three for common terns and so these birds are likely to be toward the lower end of a quality spectrum, and thus might be expected to show a greater relative effect of increased cost than higher quality individuals (Wright & Cuthill 1989, McNamara & Houston 1996, chapter 4).

The entire clutch produced by the experimental birds was swapped with a control clutch of two (*a*, *b*), laid by an unmanipulated pair that initiated laying in the central area of the colony at the same time. The experimental pairs then, incurred an increased egg production demand, but were only made to incubate and raise the clutch size of two that they had originally intended. This group of 18 pairs is referred to as the Parental Effect Group. The Control group consisted of 15 pairs initiating laying of an unmanipulated clutch of two eggs at the same time as the experimental nests, and raising another control clutch of two eggs (*a*, *b*) laid by a pair that also initiated laying on the same date. Any differences between the experimental and control nests, in hatching success, chick growth and fledging success, will be as a result of differences between the two groups in parental performance.

The second experimental group consisted of 18 pairs that laid an unmanipulated clutch of three eggs in the central area of the colony, and were made to raise the *a*, *b* and *c* eggs (the *c* egg being the official additional egg), laid by the birds in the Parental Effect group above. By cross-fostering this clutch to be raised by unmanipulated control parents, we can investigate the possibility of reduced egg quality, especially in the 'forced' *c* egg, independent of any effect of increased egg production on parental performance. This second experimental group is referred to as the Egg Effect group.

The control group for the Egg Effect Group consisted of the 20 pairs (from experiment 1) laying an unmanipulated clutch of three eggs and raising another control clutch of three eggs (*a*, *b*, *c*) laid by a pair that initiated laying on the same date. This second experimental set-up is summarised in **Figure 6**.

As in experiment 1, provisioning data are examined in more detail in the Parental Effect and Control groups; split into the first and second weeks of chick life (29, 23 and 20, 14 watches on 12 and 9 nests in weeks 1 and 2 respectively). Feeding data for the Egg Effect and Control groups are presented as an average over the first two weeks of chick life (39 and 54 watches on 10 and 13 nests respectively).

Results

i). Parental Effect

There was no significant difference between Parental Effect and Control groups in the date they initiated laying of their original clutch (laying date of *a* egg (days after 1 May), mean ± s.e.: Parental Effect 26.94 ± 0.47, $n = 18$; Control 28.43 ± 0.52, $n = 15$; Mann Whitney U-test $U_{31} = 83.5$, $p = 0.06$, n.s.), and both groups intended a clutch of two eggs.

The original clutches laid by the Parental Effect and Control pairs were removed and both groups were given an unmanipulated clutch of two eggs (*a*, *b*) to incubate and raise. There was no significant difference in the size of the eggs in the clutches they raised (2-Way ANOVA on egg volume, laying order effect $F_{1,58} = 2.12$, $p = 0.15$, group effect $F_{1,58} = 1.07$, $p = 0.30$, interaction $F_{1,58} = 1.40$, $p = 0.24$, n.s.).

Table 7. *Hatchling parameters (measured on the day of hatching) for Parental Effect and Control groups. Data are compared using t-tests*

Parameter	Parental Effect, mean ± s.e.(*n*)	Control, mean ± s.e.(*n*)	*p*
Duration of incubation			
a chick	22.42 ± 0.12 (18)	22.89 ± 0.29 (14)	0.25
b chick	21.34 ± 0.11 (16)	21.63 ± 0.26 (12)	0.48
Hatchling mass (g)			
a chick	15.22 ± 0.33 (18)	14.70 ± 0.32 (15)	0.27
b chick	14.84 ± 0.47 (16)	14.27 ± 0.28 (16)	0.33
Hatchling wing length (cm)			
a chick	1.66 ± 0.03 (18)	1.67 ± 0.03 (15)	0.73
b chick	1.68 ± 0.02 (16)	1.64 ± 0.03 (12)	0.39

There was no significant difference in hatching success, which was very high in both groups, with only two *b* eggs from each group failing to hatch, (number of eggs hatched, mean ± s.e.: Parental Effect 1.89 ± 0.08, *n* = 18; Control 1.87 ± 0.09, *n* = 15; $X^2_2 = 0.118$, n.s.). Chicks are identified according to the order they hatched, with the *a* chick hatching first and the *b* chick hatching second. There was no significant difference in the duration of incubation of the *a* or *b* eggs, or in the size of the chicks hatched from these eggs in the Parental Effect and Control groups (see **Table 7**).

Table 8. *Growth and fledging parameters for chicks in Parental Effect and Control groups. Mean Instantaneous Growth Rate wing 3-21d, weight 1-16.5d. Data are compared using Mann Whitney U-tests.*

Parameter	Parental Effect, mean ± s.e.(*n*)	Control, mean ± s.e.(*n*)	*p*
Instantaneous Growth Rate (weight)			
a chick	0.123 ± 0.004 (15)	0.127 ± 0.004 (13)	0.66
b chick	0.124 ± 0.006 (14)	0.117 ± 0.005 (8)	0.22
Instantaneous Growth Rate (wing)			
a chick	0.130 ± 0.003 (15)	0.129 ± 0.003 (13)	0.63
b chick	0.137 ± 0.005 (14)	0.127 ± 0.004 (8)	0.20
Fledging mass (g)			
a chick	126.60 ± 3.68 (15)	118.92 ± 4.69 (12)	0.16
b chick	126.55 ± 4.77 (11)	107.43 ± 6.76 (7)	0.04
Fledging wing length (cm)			
a chick	15.50 ± 0.21 (15)	15.04 ± 0.22 (12)	0.14
b chick	14.85 ± 0.21 (11)	13.67 ± 0.60 (7)	0.06

There was no significant difference in the number of chicks fledged per nest, in the Parental Effect and Control groups (see **Table 9**), or in the percentage of chicks surviving to fledging in each group according to hatching order (see **Figure 7**). Of the chicks that fledged, there was no difference in the overall growth rates of *a* or *b* chicks (see **Table 8**). There was also no difference between the two groups in the fledging weight or wing length of *a* chick or in the fledging wing length of the *b* chick. However the *b* chick fledged at a significantly heavier weight in the Parental Effect group than in the Controls (see **Table 8**). The brood fledging weight did not differ between the two groups (brood fledging weight (g), mean ±

s.e.: Parental Effect 188.72 ± 14.53, $n = 18$; Control 176.92 ± 15.19, $n = 13$; Mann Whitney U-test $U_{29} = 98.5$, $p = 0.46$, n.s.).

Table 9. *The number of chicks fledged per nest by Parental Effect and Control pairs ($\chi^2_1 = 0.01$, n.s.).*

	NUMBER FLEDGED			
TREATMENT	0	1	2	Mean ± s.e. (n)
Parental Effect	0 (0%)	7 (39%)	11 (61%)	1.61 ± 0.12 (18)
Control	1 (7%)	6 (40%)	8 (53%)	1.47 ± 0.17 (15)

There was no significant difference between Parental Effect and Control groups in attendance at the nest in the first week of chick life, (percentage time nest left unattended, mean ± s.e.: Parental Effect 0.31 ± 0.08, $n = 12$; Control 0.24 ± 0.11, $n = 9$; Mann Whitney U-test on arcsin transformed values $U_{19} = 44$, $p = 0.48$, n.s.). There was also no difference in the provisioning rate of the two groups in the first or second weeks after hatching of the brood (see **Figure** 8).

ii). Egg Effect

There was no significant difference between Egg Effect and Control groups in the date they initiated laying of their original clutch (laying date of *a* egg (days after 1 May), mean ± s.e.: Egg Effect 27.97 ± 0.48, $n = 18$; Control 28.68 ± 0.39, $n = 20$; $t_{36} = 1.15$, $p = 0.26$, n.s.), and birds in both groups intended and laid unmanipulated clutch of three eggs. There was also no difference between the two groups in the size of the eggs in the original clutches they laid (2-Way ANOVA on egg volume, laying order effect $F_{2,106} = 20.86$, $p < 0.0005$, group effect $F_{1,106} = 0.01$, $p = 0.92$, interaction $F_{2,106} = 0.43$, $p = 0.65$, n.s.).

In the experimental protocol birds in the Egg Effect and Control groups were given a clutch of three eggs that was not their own to incubate and raise. The Egg Effect group raising the *a*, *b* and *c* eggs laid by birds manipulated into laying an extra third egg, and the Control group raising a normal clutch of three eggs (*a*, *b*, *c*). There was no significant difference in the absolute size of the eggs raised by Egg Effect and Control groups, however the eggs differ in relative size between the two groups (see **Figure** 9). The size of the *b* and *c* eggs relative to the *a* egg increases after removal and therefore in the clutch raised by the Egg Effect group in comparison to the Controls (2-way ANOVA *b* & *c* eggs as a of % *a* egg volume, laying order effect $F_{1,72} = 15.97$, $p < 0.0005$, treatment effect $F_{1,72} = 10.86$, $p = 0.002$, interaction $F_{1,72} = 0.11$, $p = 0.75$).

In the following analyses, the chicks are identified according to the egg they hatched from, so that any differences according to laying order, especially in the official 'forced' *c* egg chick, can be identified. There was no difference in hatching success between Egg Effect and Control groups (number of eggs hatched, mean ± s.e.: Egg Effect 2.78 ± 0.13, $n = 18$; Control 2.95 ± 0.05, $n = 20$; $X^2_2 = 0.403$, n.s.), and no difference between the 'forced' *c* and control *c* eggs in viability (Fisher exact test $p = 1.0$, n.s.). There was also no significant differences in hatching date or in hatchling size between the two groups in the chicks hatched from the *a*, *b* or *c* eggs (see **Table 10**).

Table 10. *Hatchling parameters (measured on the day of hatching) for a, b, and c egg chicks in Egg Effect and Control nests. Data are compared using t-tests.*

Parameter	Egg Effect, mean ± s.e.(*n*)	Control, mean ± s.e.(*n*)	*p*
Hatching date (days after 1/5)			
a egg	50.97 ± 0.48 (16)	50.88 ± 0.35 (20)	0.87
b egg	52.35 ± 0.45 (17)	51.60 ± 0.38 (20)	0.21
c egg	54.24 ± 0.46 (17)	53.13 ± 0.38 (19)	0.07
Hatchling mass (g)			
a egg	15.16 ± 0.44 (16)	15.55 ± 0.40 (20)	0.51
b egg	14.91 ± 0.29 (17)	14.90 ± 0.46 (20)	0.98
c egg	13.82 ± 0.33 (17)	13.47 ± 0.31 (19)	0.44
Hatchling wing length (cm)			
a egg	1.67 ± 0.03 (16)	1.72 ± 0.02 (20)	0.13
b egg	1.71 ± 0.02 (17)	1.65 ± 0.04 (20)	0.14
c egg	1.72 ± 0.02 (17)	1.66 ± 0.02 (19)	0.10

There was no significant difference in the number of chicks fledged per nest, between Egg Effect and Control nests (see **Table 11**), with no nests failing completely, and no difference in the percentage of chicks surviving to fledging in each group according to hatching order (see **Figure 10**).

Table 11. *Number of chicks fledged per nest by Egg Effect and Control pairs ($X^2_2 = 0.96$, n.s.).*

	NUMBER FLEDGED			
TREATMENT	1	2	3	Mean ± s.e. (n)
Egg Effect	3 (17%)	13 (72%)	2 (11%)	1.94 ± 0.13 (18)
Control	2 (10%)	17 (85%)	1 (5%)	1.95 ± 0.09 (20)

Table 12. *Growth and fledging parameters for chicks in the Egg Effect and Control groups. Mean Instantaneous Growth Rate wing 3-21d, weight 1-16.5d. Data are compared using t-tests.*

Parameter	Egg Effect, mean ± s.e.(n)	Control, mean ± s.e.(n)	p
Instantaneous Growth Rate (weight)			
a egg	0.125 ± 0.004 (16)	0.115 ± 0.006 (19)	0.20
b egg	0.123 ± 0.012 (16)	0.117 ± 0.006 (19)	0.64
c egg	0.123 ± 0.021 (3)	0.148 - (1)	-
Instantaneous Growth Rate (wing)			
a egg	0.126 ± 0.004 (16)	0.124 ± 0.003 (19)	0.60
b egg	0.126 ± 0.003 (16)	0.128 ± 0.003 (19)	0.66
c egg	0.124 ± 0.014 (3)	0.152 - (1)	-
Fledging mass (g)			
a egg	122.94 ± 3.68 (16)	119.05 ± 5.53 (19)	0.58
b egg	123.00 ± 4.95 (15)	119.37 ± 4.67 (19)	0.60
c egg	122.00 - (1)	-	-
Fledging wing length (cm)			
a egg	15.38 ± 0.23 (16)	15.23 ± 0.40 (19)	0.78
b egg	14.15 ± 0.30 (15)	14.45 ± 0.29 (19)	0.48
c egg	13.40 - (2)	-	-

Unfortunately too few of the chicks hatched either from the 'forced' *c* or the control *c* eggs fledged to allow statistical comparison of their growth rates and fledging sizes. However, of the *a* and *b* chicks that fledged, there was no significant difference in the overall growth rates or in the fledging size between the Egg Effect and Control groups (see **Table 12**). The brood fledging weight did not differ between the two groups (brood fledging weight (g), mean ± s.e.: Egg Effect 226.78 ± 13.65, $n = 18$; Control 224.80 ± 11.38, $n = 20$; $t_{36} = 0.11$, $p = 0.91$, n.s.).

There was no difference between the Egg Effect and Control groups in nest attendance during the first week of chick life (percentage time nest left unattended, mean ± s.e.: Egg Effect 0.27 ± 0.07, $n = 10$; Control 0.28 ± 0.06, $n = 14$; Mann Whitney U-test on arcsin transformed values $U_{22} = 69$, $p = 0.95$, n.s.). Neither was there a difference in the provisioning rate, expressed as an average over the first two weeks of chick life (energy (J) delivered to the nest per living chick per hour, mean ± s.e.: Egg Effect 5.10 ± 1.15, $n = 10$; Control 6.20 ± 0.84, $n = 13$; Mann Whitney U-test $U_{21} = 60$, $p = 0.76$, n.s.).

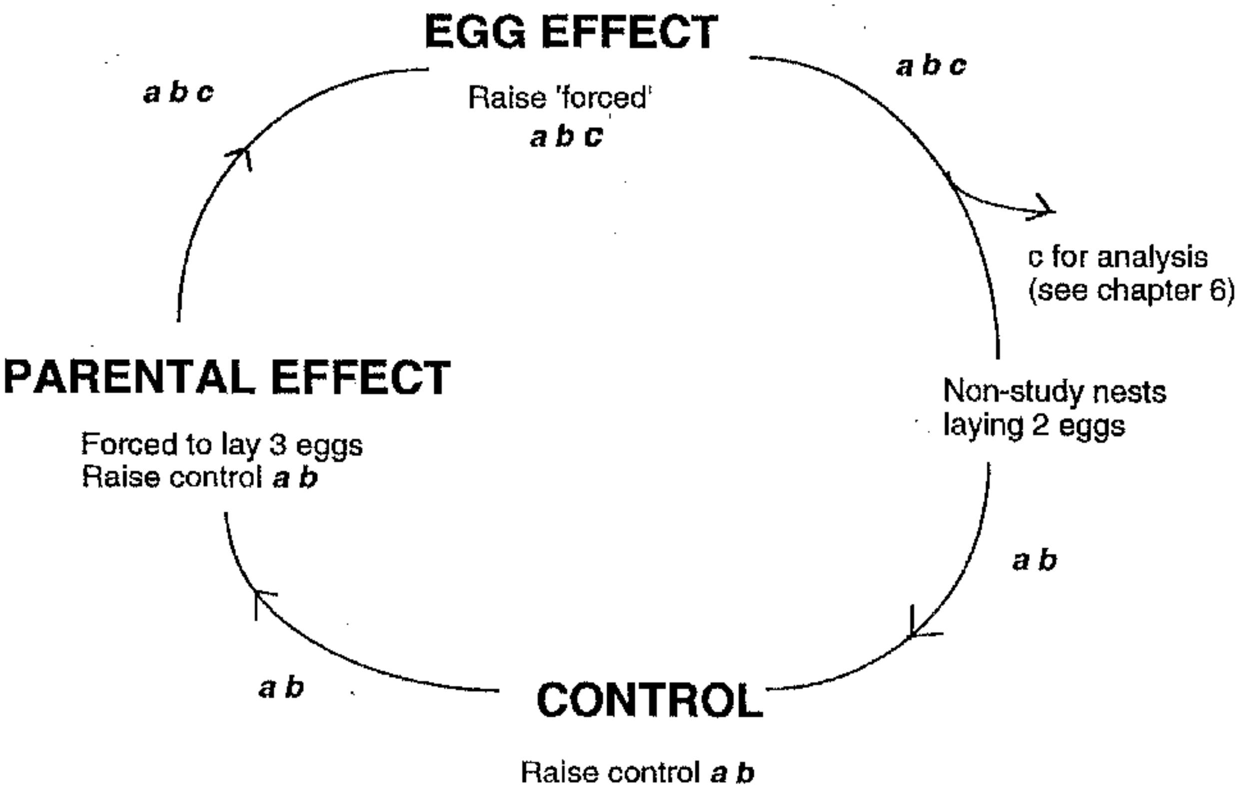


Figure 6. The set-up for experiment 2. The arrows indicate the directions of the experimental clutch movements between nests. The Parental Effect birds laying a total of three eggs, raised an unmanipulated clutch of two eggs. The eggs of the experimental clutch were raised by the Egg Effect group (who intended a clutch of three eggs), and the Control group raised a normal clutch of two eggs that was not their own.

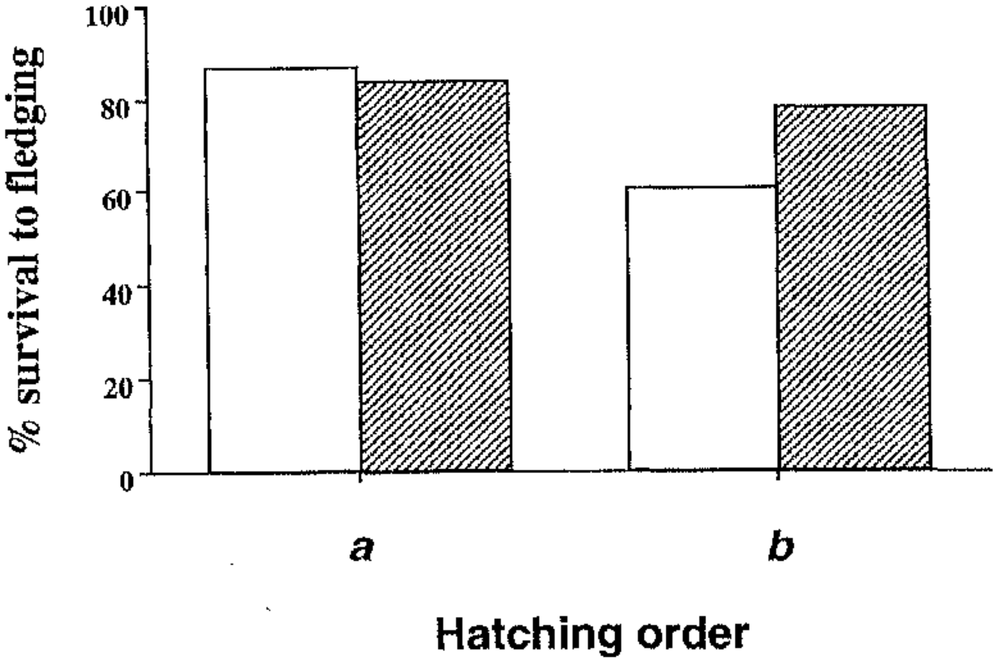


Figure 7. The percentage of chicks surviving to fledging in the Control (open, n = 15) and Parental Effect (hatched, n = 18) groups in relation to hatching order. There was no difference between the two groups in the survival of the first or second hatched chicks (see text for details).

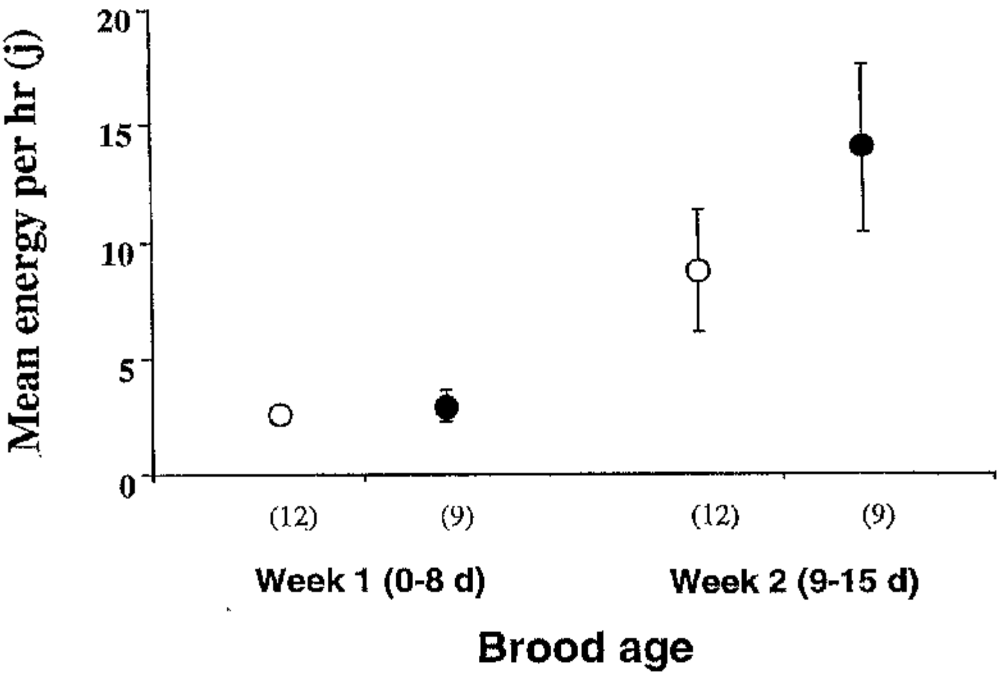


Figure 8. The mean energy per chick per hour (± s.e.) delivered to the brood by Control (solid circles) and Parental Effect (open circles) groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the x-axis. There was no significant difference between the groups in the first (Mann Whitney U-test $U_{19} = 53$, $p = 0.94$, n.s.) or the second week (Mann Whitney U-test $U_{19} = 38$, $p = 0.26$, n.s.).

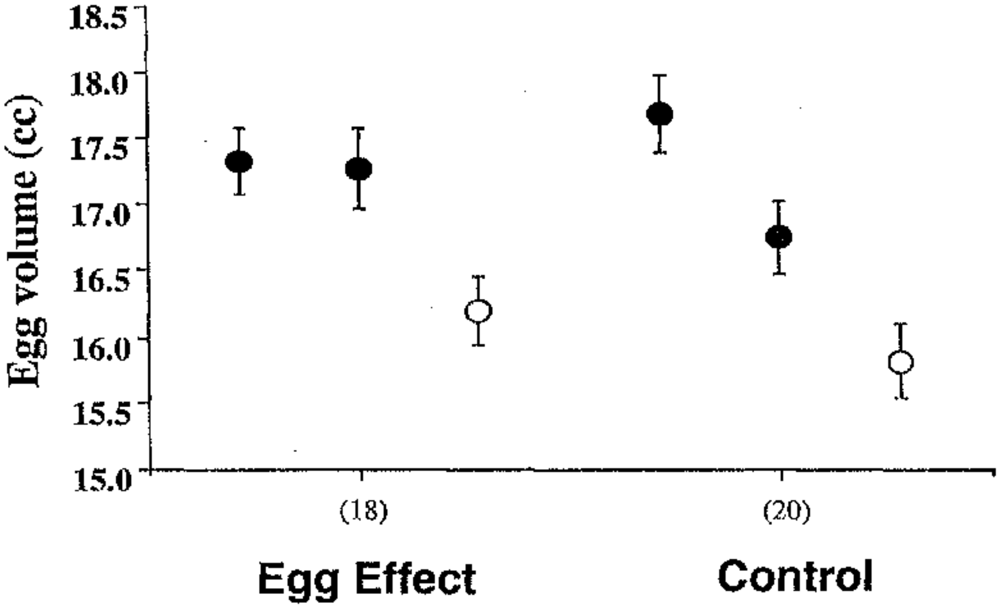


Figure 9. Mean (± s.e.) egg volume (cc) of eggs raised by Egg Effect and Control groups, (first egg, solid circle; second egg, shaded circle; third egg, open circle). The sample sizes are given in brackets on the x-axis. There was no difference in the absolute size of the eggs between the two groups (2-Way ANOVA on egg volume, laying order effect $F_{2,108}$ = 15.10, $p < 0.0005$, treatment effect $F_{1,108} = 0.62$, $p = 0.43$, interaction $F_{2,108} = 1.56$, $p = 0.22$). However, the eggs differed in relative size (see text for details).

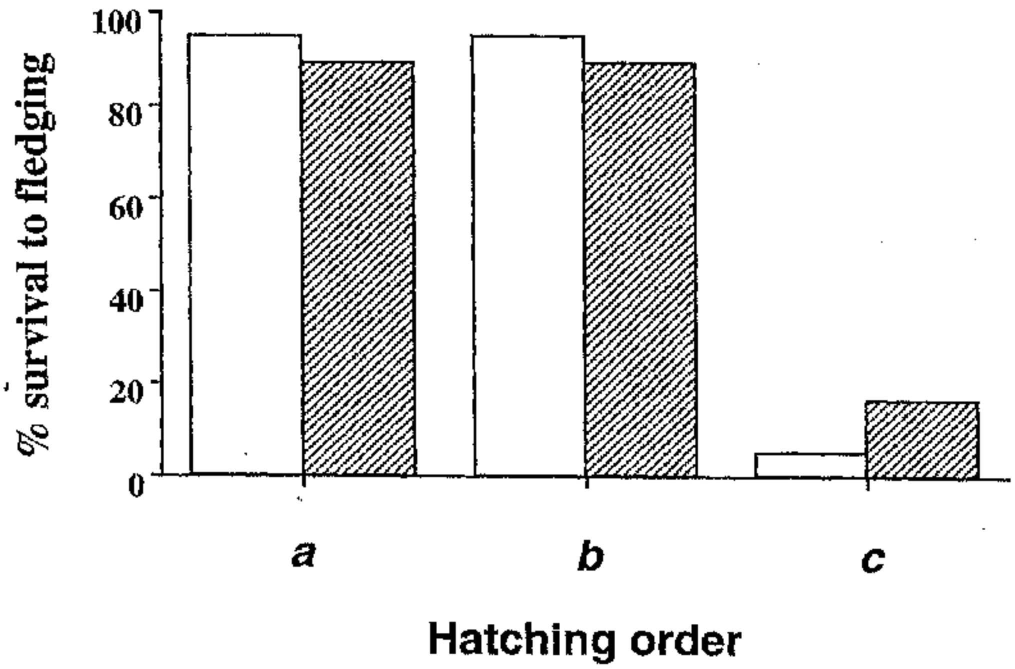


Figure 10. The percentage of chicks surviving to fledging in the Control (open, n = 15) and Egg Effect (hatched, n = 18) groups in relation to hatching order. There was no difference between the two groups in the survival of the first, second or third hatched chicks (see text for details).

Discussion

i). Parental Effect

The birds in the experimental Parental Effect group incurred a 50% increase in egg production demand, but were only made to incubate and rear a control clutch of two, the size that they had originally intended. Again we might have expected this forced increase in demand in the early stage of reproduction to cause a trade-off reduction in effort later in the reproductive attempt, especially since these were lower quality birds intending a clutch of two eggs only (Wright & Cuthill 1989, McNamara & Houston 1996, chapter 4).

There were no significant differences between control and experimental pairs, in the duration of incubation, or in hatching success, and no differences in the hatching size of the chicks. There also appears to have been no reduction in parental effort during chick rearing in the experimental birds compared to controls, with no differences in attendance or provisioning. There were, correspondingly, no significant differences in the overall growth rates of the chicks in experimental and control nests, and no differences in the fledging size (measured at 20 days of age) for the *a* chick. There was also no significant difference in the brood fledging weight between experimental (188g) and controls (176g) nests. In fact, the experimental group appear to be doing slightly better than the controls, with the *b* chick fledging at a significantly heavier weight, which is likely to have a positive effect on future survival prospects (Perrins 1965, Coulson & Porter 1985). However, this is only a weak effect and may be due to multiple comparisons (Rice 1989).

A number of reasons could be put forward to explain why the experimental group, despite the increased egg production demand incurred, have a similar breeding success to the control group. Firstly, in the normal situation with replacement of the *a* egg lost through natural causes, the experimental birds would raise the *b* and 'extra' *c* eggs. Thus, in this experiment they are raising artificially high quality eggs (*a*, *b*), in the natural situation they would only need to do better raising the *b* and *c* eggs than raising *b* egg alone).

Secondly, and perhaps most importantly, not all of the birds laying two eggs after removal may have originally intended a clutch of two eggs. Experimental pairs on average laid only 0.47 eggs more than controls. In Experiment 1 all the birds laying four eggs can be classed as 'unequivocal' replacers since natural four egg clutches are virtually absent in larids (Winkler & Walters 1983, Conover 1984, Reid 1987, Salzer & Larkin 1990). However, in this

Experiment 2 not all the birds may be 'true replacers' (see chapter 5). Since we cannot distinguish between those birds that replaced the lost egg and those who simply laid two eggs to complete the clutch of three eggs they intended, we must continue to class all 18 pairs continuing to lay after egg removal as replacing. Thus, the experimental group is diluted with non-replacers that have incurred no additional egg production cost to their intended clutch size. They intended and laid a clutch size of three eggs and thus we would expect them to have a higher fitness than the controls intending and laying a clutch of two (Nisbet *et al.* 1984, Coulson & Porter 1985, Pettifor 1993).

ii). Egg Effect

In this experiment the Egg Effect group raised the entire clutch laid by the experimental birds intending a clutch of two eggs and made to lay a third. Thus we can look in detail at the quality of the 'forced' *c* egg and its resultant chick. Previous studies have found a reduction in quality in additional eggs, for example Monaghan *et al.* (1995), found that the chick hatched from an additional *d* egg was significantly lighter at hatching than control *c* chicks and as a result showed lower survival.

In this study we found no obvious reduction in quality in the 'forced' *c* eggs in comparison to control *c* eggs. There was no difference between the two in absolute size, in fact the 'forced' *c* eggs were relatively larger in comparison to the *a* egg of the clutch than the control *c* eggs, a phenomenon found in previous studies following egg removal (Parsons 1976). However, there were no differences between the experimental and control *c* eggs in hatching success, hatching date or in the size of the chicks hatched from them. The fledging success of these chicks was low, but did not differ between the two groups. Unfortunately too few chicks hatching from the 'forced' and control *c* eggs in the experimental and control groups respectively survived to fledging to allow statistical analysis of the growth rates and fledging sizes and this may have been an important component.

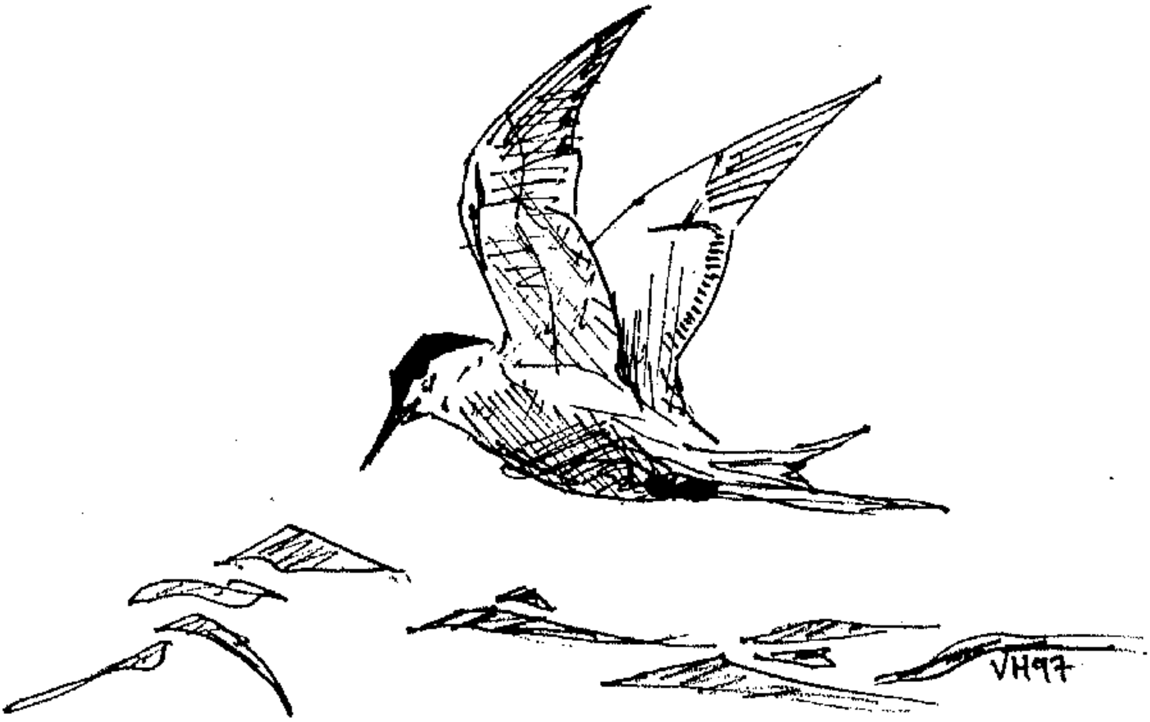
The quality of the experimental clutch overall does not appear to be less than the control clutches of three, and the eggs appear again to incur no loss in viability due to temporary storage. There were no differences between the Egg Effect and Control groups in hatching success (over 92% of all eggs hatching successfully), and no difference in the hatching date or in the size of the hatchling from either the *a*, or *b* eggs. There was also no difference in the number of chicks fledged overall in control and experimental nests, or in the brood fledging weight. Of the *a* and *b* chicks that survived, the chicks in the experimental group showed no significant differences in growth or fledging size to those in control nests.

That we found no apparent reduction in quality in the experimental clutch and in particular in the additional egg, could be explained by the adaptive significance of egg replacement, and the adaptive 'switch-off' mechanism identified in other larids (Herring Gull Paludan 1951, Parsons 1975; Black-headed Gull *Larus ridibundus* Weidman 1956). Where follicles that have not reached a certain stage of maturity at the onset of incubation are not ovulated, preventing the production of progressively smaller eggs, that would give rise to runted chicks, assuming they hatched at all, and resulting in a terminal egg of roughly the same size whether it be a *b* or forced *c* egg (Parsons 1976, see chapter 6). This study can, necessarily, only investigate the quality of *c* eggs that were laid. In birds where the third follicle had not reached the critical size at the time of experimental egg removal, and therefore would have produced a poorer quality egg, no *c* egg was laid. This may well be the case for the 49% of pairs that deserted the breeding site after egg removal in 1995 (see chapter 5).

Summary

In summary, this experiment was complicated by the variation in response of pairs to egg removal in 1995, with roughly only half of the experimental pairs examined in Experiment 2 apparently responding in a indeterminate manner. However what does become clear from this experiment is the apparent lack of a cost of increasing egg production by one egg. Experimental pairs with this increased egg production demand and the clutches they produce were not less successful than control clutches. The reason for this result may lie in the experimental technique. Although eggs were removed from a random sample of pairs in the centre of the colony, necessarily only those pairs in a high enough condition prior to and during laying were able to replace the lost egg and can be investigated for costs of increased egg production demand (see chapter 5). Thus the experimental pairs responding to egg removal by laying an extra egg (51%), will be a pre-selected higher quality subset of the population. This pre-selection will operate against the likelihood of detecting a difference, therefore if a difference is found it is likely to represent a relatively substantial effect. The methodology mimics the situation in the wild where extra egg production can limit the impact of early egg loss on breeding success. Therefore, in order for laying indeterminacy to be adaptive, birds intending a clutch of three eggs and laying an extra *d* egg as a result of egg loss (Experiment 1), need realise a higher reproductive success raising the *b*, *c* and later *d* egg, than birds raising the *b* and *c* eggs only. Similarly, birds intending two eggs and laying an extra *c* egg as a result of egg loss (Experiment 2), need only realise a higher reproductive success raising the *b*, and later *c* egg, than birds raising the *b* egg only.

Chapter 8 : The Effects of Increased Egg Production in Birds Intending a Clutch of Three Eggs



Introduction

In order to investigate the optimal allocation of effort to the different stages within a reproductive attempt, it is necessary to experimentally manipulate the energetic demands incurred by parents (Parker & Maynard Smith 1990, Monaghan & Nager 1997). To isolate the effects of increased demand at the different phases of the attempt (egg production, incubation and rearing), effort must be independently augmented at each stage (see chapter 4). This experiment aims to investigate the effect of an increase in egg production demand alone on subsequent reproductive performance.

The experiment was conducted on the common tern (*Sterna hirundo*), a small larid that lays between one and three eggs in an indeterminate manner (Haywood 1993a). Experimental pairs intending a clutch of three eggs were induced to lay a fourth 'additional' egg by removal of their first laid (*a*) egg from the nest (see chapter 5). The removed egg was not replaced into the nest and the experimental pairs were subsequently made to incubate and rear the original clutch size of three that they had intended, incurring increased egg production demand only. The experimental protocol, however, differs from the study presented in the previous chapter (Experiment 1) in that there was no cross fostering of experimental and control clutches. The experimental pairs with an increased egg production demand incubated and raised their own eggs, including the 'additional' *d* egg. Thus, any effect on the parents (chapter 3) or in egg quality (Monaghan *et al.* 1995) will be combined in the experimental group. To investigate any possible within-clutch manifestation of the cost of the extra egg production in experimental nests, the subsequent incubation and chick rearing capacity of the parents was recorded. It was not possible to record adult body condition or future survival and reproduction, and so possible between-clutch effects were not examined.

Previous studies suggest that the effects of an increase in reproductive demand may be state dependent, with poorer quality birds less able to compensate for deviations from their allocation of effort to different reproductive phases (chapter 4, Wright & Cuthill 1989, McNamara & Houston 1996). The individuals in this study intended a clutch of three eggs; the modal and maximum natural clutch size in common terns. Thus, they may be better able to cope with an experimentally increased egg production demand, than for example birds intending a clutch of only two eggs.

Methods

The experiment was carried out on common terns nesting on Coquet Island, Northumberland, in 1994. The first laid *a* egg was removed from 7 pairs within 12 hours of laying to induce them to produce an additional egg. These experimental pairs continued to lay subsequent eggs in the same nest scrape, producing a further three eggs. Thus they intended a clutch of three, but were made to lay a clutch of four eggs as a result of the experimental manipulation. The *a* egg was not returned to the nest and the experimental pairs hatched their own *b*, *c* and *d* eggs in that order.

The control group consisted of 15 pairs laying an unmanipulated clutch size of three eggs, initiating laying at the same time as the experimental pairs. To further minimise any differences between treatment groups due to the effects of differences in parental age (Nisbet *et al.* 1984), study pairs were selected from the centre of the colony, during the peak of laying. The overall spread of initiation of laying in the study birds was seven days.

All eggs were measured (volume and fresh mass) on the day of laying, and chicks (mass and wing length) within 24 hours of hatching. Nests and chicks were marked and breeding success, chick growth and provisioning were recorded using standard methods (see chapter 2). Observations of parental provisioning effort were made on nests within 25m of hides and the frequency of trips and the energy delivered was recorded. Observational data were grouped into the first (0-8d) and second (9-15d) weeks after complete hatching of the brood (control and experimental groups: 21, 15 and 17, 17 watches on 9 and 6 nests in weeks 1 and 2 respectively).

Results

There was no significant difference between the control and experimental group in hatching success, and all seven of the 'forced' *d* eggs hatched (number of eggs hatched, mean ± s.e.: control 2.60 ± 0.24, $n = 15$; experimental 3.00 ± 0.00, $n = 7$; Fisher exact test $p = 0.53$ n.s.). There was also no significant difference between the two groups in the number of young fledged (see **Table 1**). In both groups the majority of third hatched chicks died within the first week of hatching, and most of the first hatched chicks fledged. Although there was no significant difference between the two groups in the survival to fledging of the second hatched chick (see **Figure 1**), only 40% of these *b* chicks in the control group fledged, less than half the proportion surviving in the experimental group (85.7%).

Table 1. *The number of chicks fledged per nest in the control and experimental groups* ($X^2_1 = 3.34$, *n.s.*).

Treatment	0	1	2	3	mean	s.e.	*n*
Control	1	9	5	0	1.27	0.15	15
Experimental	0	1	5	1	2.00	0.22	7

Taking into account the phenomenon of increased relative egg size after removal (Parsons 1976, chapter 7) and the manipulations of hatching order in the experimental group, it is necessary to compare the quality of this second egg in the two groups. In the experimental nests this second egg was in fact the third laid *c* egg (hatching *b*, *c*, *d*), and in control nests, with no manipulations of hatching order, it was the second laid *b* egg. There was no significant difference between the two groups in the size of this second egg, either absolute (see **Table 2**), or relative (as % *a* volume, mean ± s.e.: control 99.17 ± 1.39, $n = 15$; experimental 95.31 ± 4.29, $n = 7$; Mann Whitney U-test, $U_{20} = 43$, $p = 0.50$, n.s.). There was also no significant difference in the size of the chicks that hatched from this egg (see **Table 2**).

Despite the universally poor survival of the third hatched chick (see **Figure 1**), it is important to investigate the quality of the egg it emanated from, since this was the unmanipulated *c* egg in control nests, and the 'forced' *d* egg in experimental nests. However, there was no difference between the two groups in the size of the third egg (egg volume, mean ± s.e.(cc): control *c* egg 17.29 ± 0.27, $n = 15$; experimental *d* egg 17.42 ± 0.49, $n = 7$; Mann Whitney U-test, $U_{20} = 51$, $p = 0.92$, n.s.), or in the size of the hatchling produced from it (hatchling wing length (cm), mean ± s.e.: *c* egg 1.69 ± 0.03, $n = 13$; *d* egg 1.67 ± 0.05, $n = 7$; Mann Whitney U-test, $U_{18} = 42$, $p = 0.78$, n.s.; hatchling mass (g), mean ± s.e.: *c* egg 13.65 ± 0.47, $n = 13$; *d* egg 14.57 ± 0.49, $n = 7$; Mann Whitney U-test, $U_{18} = 31.5$, $p = 0.26$, n.s.).

Table 2. *Egg and hatchling parameters (mean ± s.e.,* n*) for second eggs in control and experimental nests (probability values are based on Mann Whitney U-tests).*

Parameter	Control	Experimental	*p*
Egg volume (cc)	17.81 ± 0.29 (15)	17.11 ± 0.85 (7)	0.86
Egg mass (g)	19.60 ± 0.29 (15)	19.36 ± 0.45 (7)	0.75
Hatchling mass (g)	16.35 ± 0.58 (13)	16.14 ± 0.57 (7)	0.91
Hatchling wing (cm)	1.76 ± 0.04 (13)	1.81 ± 0.05 (7)	0.37

The laying and hatching dates of the eggs in experimental nests tended to be roughly a day later than in control nests especially for second and third eggs. However, the differences were not significant (see **Table 3**).

Table 3. *Laying and hatching dates (mean ± s.e.,* n*) for eggs in the control and experimental groups, (probability values are based on Mann Whitney U-tests, and dates are recorded as days after 1 May).*

Parameter	Control	Experimental	*p*
Laying date			
First egg	31.00 ± 0.52 (15)	32.14 ± 0.39 (7)	0.14
Second egg	32.57 ± 0.37 (15)	33.64 ± 0.40 (7)	0.09
Third egg	34.30 ± 0.37 (15)	35.43 ± 0.39 (7)	0.07
Hatching date			
First egg	53.50 ± 0.45 (14)	54.43 ± 0.53 (7)	0.26
Second egg	54.46 ± 0.45 (13)	55.29 ± 0.36 (7)	0.31
Third egg	56.00 ± 0.39 (12)	56.86 ± 0.40 (7)	0.16

There was no significant difference in growth rates or fledging size (measured at 20d) of the chicks that survived, identified by hatching order (see **Table 4**). There was also no significant difference in the brood growth rates between control and experimental nests (Instantaneous Growth Rate, wing length, mean ± s.e.: control 0.104 ± 0.004, $n = 14$; experimental 0.102 ±

0.005, n = 7; Mann Whitney U-test, U_{19} = 42, p = 0.60, n.s.; Instantaneous Growth Rate, mass, mean ± s.e.: control 0.112 ± 0.007, n = 14; experimental 0.124 ± 0.008, n = 7; Mann Whitney U-test, U_{19} = 39, p = 0.46, n.s.).

Table 4. *Growth and fledging parameters (mean ± s.e.,* n*), for chicks in control and experimental groups (mean Instantaneous Growth Rate wing 3-21d; weight 1-16.5d). Probability values are based on Mann Whitney U-tests.*

Parameter	Control	Experimental	p
Instantaneous Growth Rate (mass)			
a chick	0.116 ± 0.006 (12)	0.112 ± 0.004 (7)	0.55
b chick	0.119 ± 0.005 (6)	0.125 ± 0.010 (6)	0.63
c chick	0.091 - (1)	0.123 - (1)	-
Instantaneous Growth Rate (wing)			
a chick	0.110 ± 0.003 (12)	0.104 ± 0.004 (7)	0.31
b chick	0.112 ± 0.005 (6)	0.100 ± 0.007 (6)	0.15
c chick	0.088 - (1)	0.111 - (1)	-
Fledging mass (g)			
a chick	120.83 ± 3.43 (12)	126.29 ± 4.83 (7)	0.47
b chick	122.83 ± 3.18 (6)	114.60 ± 2.84 (5)	0.12
c chick	-	-	-
Fledging wing length (cm)			
a chick	15.23 ± 0.34 (12)	15.30 ± 0.22 (7)	0.73
b chick	14.07 ± 0.71 (6)	13.84 ± 0.34 (5)	1.00
c chick	-	-	-

There was no apparent difference between the control and experimental groups, in provisioning of the brood in the first or second weeks after complete hatching of the brood, in terms of energy delivered to the nest per living chick. However since the experimental pairs fledged slightly more chicks they were delivering more energy overall, and in fact made significantly more deliveries of food to the nest in the first week of chick life than control parents (see **Figure 2**).

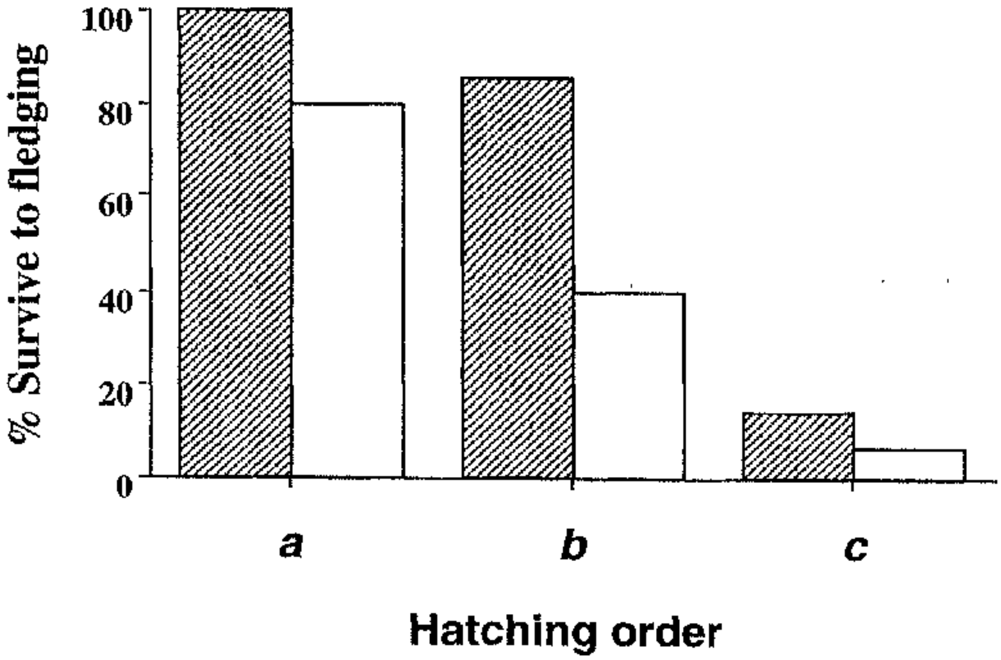


Figure 1. The percentage of chicks in control (open, $n = 15$); and experimental (hatched, $n = 7$) groups surviving to fledging in relation to hatching order. There was no difference between the two groups in survival of the first or third hatched chicks, and although survival of the second hatched chicks was lower in control than experimental nests, the difference was not significant ($X^2_1 = 2.39$, n.s.).

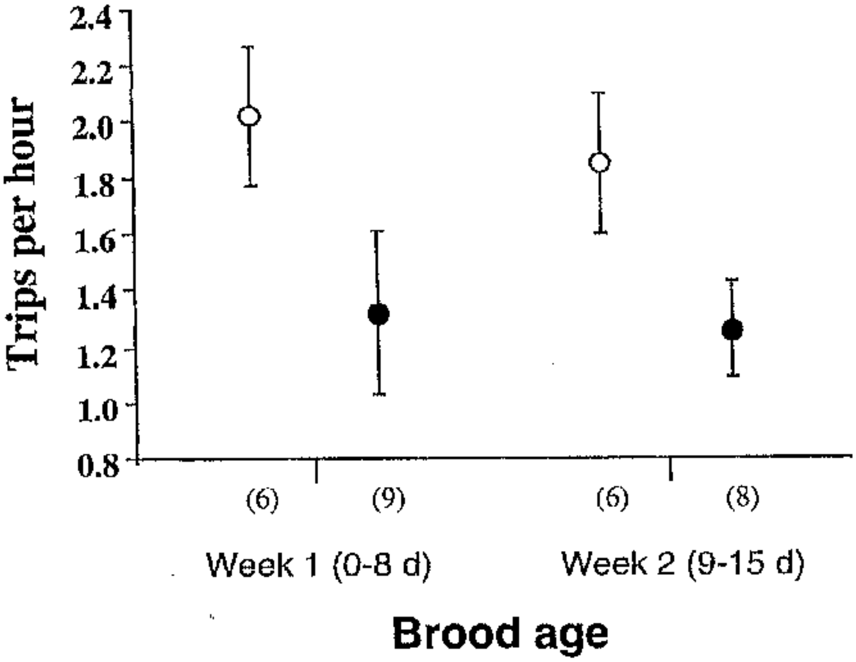


Figure 2. The mean (± s.e.) number of food deliveries per hour brought to the nest by pairs in the control (solid circles) and experimental (open circles) groups, in the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the x-axis. There was no difference in provisioning by pairs in the two groups in the second week, but in the first week the experimental pairs made significantly more food deliveries to the nest than did pairs in the control group (week 1: Mann Whitney U-test $U_{13} = 10.5$, $p = 0.05$; week 2: Mann Whitney U-test $U_{12} = 11.5$, $p = 0.10$, n.s.).

Discussion

In this study, the experimental group incurred a 33.3% increase in egg production demand over the controls. Since many previous studies have shown that egg production is relatively costly (Carey 1996, Perrins 1996, Houston *et al.* 1995a, Van Es 1980), we might have expected this increase in demand early in the breeding attempt to have a knock-on effect on effort as laying progressed (Monaghan *et al.* 1995), or in the later stages of incubation and chick rearing (chapter 3 & 4). However, experimental pairs appear to be doing just as well if not slightly better than control pairs. There was no difference in hatching or fledging success between the two groups, and no difference in the growth rates or fledging weights of surviving chicks. Survival of the second hatched chicks in the experimental group (85.7%) was over twice that of *b* chicks in the control group (40%), although this result is not significant.

In the control group there were no manipulations of hatching order and the *b* chick hatched from the *b* egg. In the experimental group the order of hatching was manipulated, with the *b* chick hatching from the *c* egg laid after removal. Previous studies have shown that an increase in the relative size of subsequent eggs often results from removal of the first egg (Parsons 1976, Salzer & Larkin 1990, chapter 7). This may have implications for the probability of the subsequent eggs giving rise to successful chicks (for reviews see Williams 1994, Carey 1996, Perrins 1996). However, the (non-significant) increased survival of the *b* chick does not appear to be as a result of differences in egg quality, since there was no difference between the two groups in the size at hatching of the *b* chick, or in the size of the egg it hatched from.

There was also no apparent reduction in quality in the 'forced' *d* egg. This is in contrast to a previous study on egg production in lesser black-backed gulls (Monaghan *et al.* 1995), where the increase in egg production demand resulted in a decrease in the quality of the additional egg. Although the majority of the chicks hatching from both experimental *d* and control *c* eggs died within the first week, there was no difference in the size of the eggs or the size of the hatchlings produced from them, all good indications of egg quality (see Williams 1994, Carey 1996 for reviews). This result is in agreement with the findings in chapter 6 that the composition of the egg contents of the 'forced' *d* and control *c* eggs did not differ. However, this analysis revealed that the 'forced' *d* eggs had a lower calcium content than control *c* eggs, but this does not appear to have adversely affected hatching success in the additional eggs, with all seven of the *d* eggs in this study hatching successfully.

In fact, the experimental pairs appear to retain a greater ability to provision the brood than controls, despite the increased egg production demand. This may have contributed to the increased survival of the *b* chick in the experimental group, with superior provisioning in the this group compared to the control group during the first week of chick life which is a critical time for the survival of marginal chicks (Langham 1972, Dunn 1972, Bollinger *et al.* 1990).

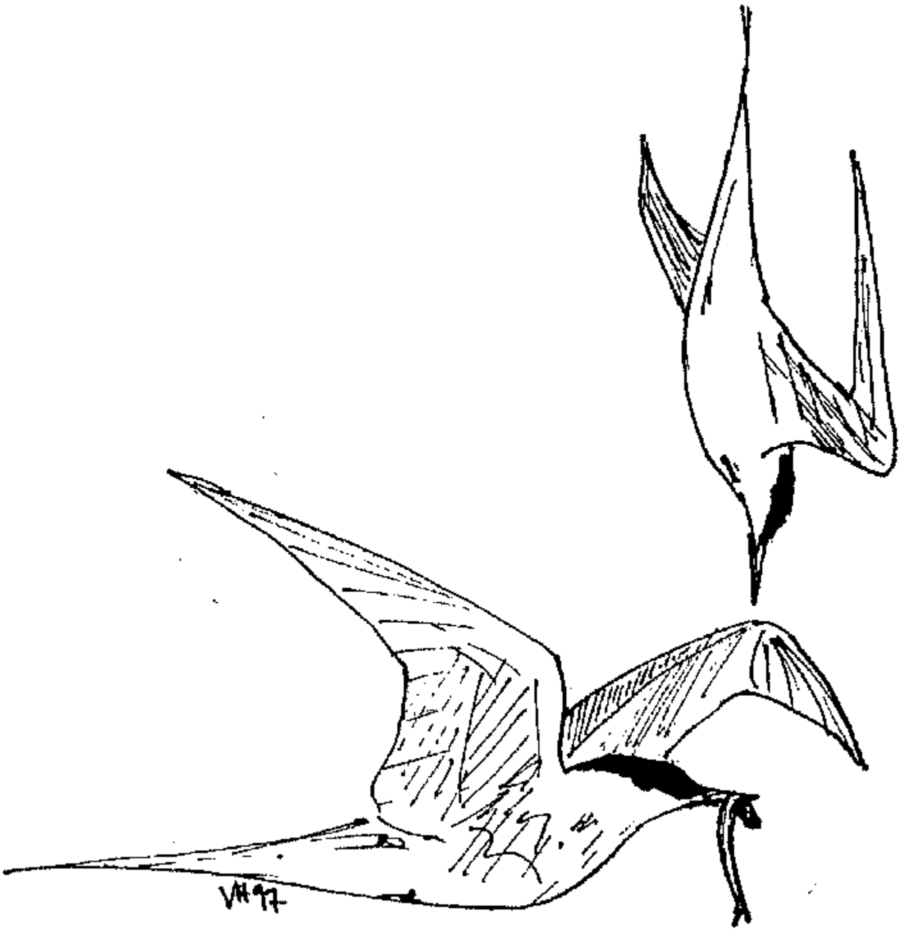
This result is in contrast to previous studies which suggest that an increase in egg production demand, may be met using protein reserves (Carey 1996) mainly stored in the flight muscles (Houston *et al.* 1995a), with increased depletion of these muscles possibly affecting flight performance and the ability to provision the brood (Monaghan & Nager 1997, chapter 3). Also a number of previous studies have suggested such a within-clutch trade-off, with increased demand in the early stages of the reproductive attempt being 'shunted' onto the offspring in the later stages of the attempt, possibly through an impairment of provisioning performance (Mauck & Grubb 1995, chapters 3 & 4). However, this lack of agreement between studies may lie primarily in the experimental protocol.

In manipulating the number of eggs laid, by removal of the first laid *a* egg within 12 hours, we are mimicking a situation not too uncommon in the wild. That is, when as a result of inattention at the nest before clutch completion, the first laid egg is lost to predation (Parsons 1976, Morris & Wiggins 1986, Bollinger *et al.* 1990). In many cases (see chapter 5), the female will lay a replacement egg, and the pair incubate and raise the clutch size they intended, thus limiting the impact of early egg loss (Rinkel 1940, Gwynn 1953, Kendleigh *et al.* 1956, chapter 5). In this situation, the pair will end up incubating and raising the additional egg among the clutch, and the brood will necessarily be delayed by the equivalent of one laying interval (approximately 2 days). Thus, the inclusion of the *d* egg to the exclusion of the *a* and the resultant delay of one day found in experimental nests is in fact an integral part of the investigation. In order for the indeterminacy of laying to be adaptive, the potential of eggs lost early in the breeding attempt must be effectively realised through the production of replacement eggs (Haywood 1993a, Kennedy 1991, chapter 5). The pair, having lost their *a* egg, must realise a greater success from raising the clutch of three, with the late hatching 'forced' *d* egg included, than they would from raising the remaining *b* and *c* eggs only (see chapter 5).

Differences in foraging performance between individuals will influence their ability to lay replacement eggs in any one breeding season (Monaghan & Nager 1997), and only the higher quality individuals, in better condition prior to and during laying, will be in a position to respond to egg removal by replacing the lost egg (Parsons 1976, chapter 5). That is, only the higher quality individuals, will be likely to realise a higher success through laying a replacement egg and raising the resultant clutch. Pairs unable to produce a high quality additional egg and maintain sufficient reserves for the later stages of the reproductive attempt are likely not to replace the lost egg at all and continue laying in a determinate manner or desert the nest site after egg removal. This range of ability or quality is demonstrated by the range of response of experimental pairs to egg removal; in 1994, of the 30 pairs which had their *a* egg removed, only 11 pairs (36.7%) laid a further three eggs, with 27% of birds deserting the nest site altogether (possibly to re-lay elsewhere, Nisbet pers. comm.), and the fact that the overall response from year to year also differs depending on environmental conditions (see chapter 5).

Thus, although both control and experimental pairs intended a clutch of three eggs, the crude integer steps of clutch size increase (Ricklefs 1984b) mean that even within a selection of birds intending the same clutch size, there will be a range of quality. The control birds were selected at random from the centre of the colony at peak laying. As a result of the protocol of egg removal, the experimental birds were in some ways 'pre-selected' for quality in being the subset of birds, also selected from the central area, that responded to egg removal by laying three more eggs. The experimental pairs laying a total of four eggs are likely to be from the higher end of a quality spectrum of the subset of birds intending the maximum and modal clutch size of three, in that they were able to lay an additional high quality egg. They may be expected to have a relatively high capacity to compensate for the deviations from their individual allocation of effort which the experimental protocol imposed, and the relative cost of the increase in egg production demand may be lower (than for pairs lower on the spectrum) (chapter 4, Wright & Cuthill 1989, McNamara & Houston 1996). Some pairs may be able to incur the cost of laying an extra egg and still have further 'buffering capacity' to exceed the control group in provisioning effort. However, they will not have been able to incur the full cost of an extra young (chapter 3) in order to have laid a clutch of four in the first place. This chapter has concentrated on possible within-clutch trade-offs in reproductive cost and effort, it is possible that the increase in egg production demand in this current breeding attempt, may result in a between-clutch trade-off, with reduced success in subsequent broods (Pettifor *et al.* 1988, Gustafsson & Part 1990, Roff 1992, Stearns 1992), and this was not investigated.

Chapter 9 : Do Experimental Manipulations of Reproductive Effort Affect Prey Choice and Kleptoparasitic Attack?



Introduction

Kleptoparasitism is the stealing of already procured food by individuals of one species from individuals of the same or another species (Rothschild & Clay 1952, Brockmann & Barnard 1979). Seabird colonies are ideal venues for food stealing and meet many of the prerequisites for the development of this behaviour (Brockmann & Barnard 1979); they produce a considerable number of hosts predictably bringing large quantities of visible food to a fixed location. The number of active parasites is positively correlated with the availability of hosts carrying fish (Dunn 1973b), and hosts are most vulnerable as they try to feed their chicks (Hays 1970). Dense 'air traffic' in colonies means that hosts are less able to detect and anticipate aerial threats from parasites, which thereby gain a greater degree of surprise and success in their attacks (Dunn 1973b). The aim of this study was to investigate the pattern of kleptoparasitism in a colony of common terns (*Sterna hirundo*). Common terns are particularly vulnerable to kleptoparasitism because they carry fish cross-wise in the bill, making them an easy and preferred target (Dunn 1973b). This study also aims to investigate the effect of experimental manipulations of reproductive effort on the susceptibility of birds to kleptoparasitic attack when provisioning their young. It has previously been found that increases in reproductive demand can affect the subsequent chick rearing ability of experimental birds (chapters 3 & 4), and we sought to discover if this was in part due to changes in provisioning behaviour or ability affecting the attractiveness of experimental birds to, and/or their ability to evade, kleptoparasites.

Methods

The study was conducted on a colony of common terns (*c.* 800 pairs) breeding on Coquet Island, Northumberland in 1994 and 1995. Coquet is a small, low island; roughly 200 by 400 metres and not more than 10 metres above sea level. During the summer it is home to as many as 30 000 pairs of breeding birds (mainly puffins, gulls and terns). Thus it is an ideal habitat for kleptoparasites (Rand 1954).

Provisioning data were collected for study nests in both years within 25 m of hides during an average of four 3h watches per day randomised over the daylight hours. In common terns fish brought to the chicks are carried in the adults' bill, and thus prey species could be identified (see chapter 2) and size estimated with reference to the bill. Prey items were grouped according to length; size class 1 (0-4 cm), size class 2 (>4-8 cm), size class 3 (>8-12 cm), size class 4 (>12 cm). Energy content was estimated from conversion factors given in Harris & Hislop (1978). The eventual fate of each fish delivered to the nest by the parents was recorded as either consumed by the chick, the adult itself or its mate, or by a kleptoparasite. A small additional number of prey items was either dropped or taken away, usually as a result of a kleptoparasitic attack. In this way only successful kleptoparasitic attacks were recorded and it was not possible to estimate what percentage of overall attacks this constituted. Provisioning data were split into the first (0-8 days from hatching date of first chick) and second (9-15 days) weeks after hatching of the full brood. This was done because we might expect to see more kleptoparasitism later in the chick rearing phase when chicks are being fed larger fish (Uttley 1991, Boecker 1967) and at a higher rate (Uttley 1991).

In order to investigate the possibility of an effect of experimental increase in reproductive cost on the probability of kleptoparasitic attack, provisioning data from the treatment groups within two separate experiments in 1994 and 1995 were examined. In 1994 provisioning data for three experimental groups with varying degrees of increased reproductive demand and an unmanipulated control group, (free-chick, free-egg and full-cost experimental groups, plus control group: 20, 22, 11, 19 and 15, 18, 8, 15 nest watches on 7, 8, 3 and 6 nests in weeks 1 and 2 respectively), were examined. The four treatment groups are summarised in **Table 1**, (for further details of the experimental protocol, see chapter 3).

Table 1. *The brood manipulation treatments used in the 1994 experiment.*

	Number of young			
Treatment (*n*)	**Intended**	**Laid**	**Incubated**	**Hatchlings**
Free-chick (14)	2	2	2	3
Free-egg (11)	2	2	3	3
Full-cost (7)	2	3	3	3
Unmanipulated (12)	2	2	2	2

In 1995 provisioning data for the experimental group with an increase in incubation demand and an unmanipulated control group, were compared (incubation cost and control groups: 17, 18,and 25, 18 nest watches on 9 and 8 nests in weeks 1 and 2 respectively). The treatment groups are summarised in **Table 2** (for further details of the experimental protocol, see chapter 4).

Table 2. *The brood manipulation treatment used in the 1995 experiment.*

	Number of young			
Treatment (*n*)	**Intended**	**Laid**	**Incubated**	**Raised**
Incubation cost (21)	2	2	3	2
Unmanipulated (20)	2	2	2	2

Results

In the years of the study the prey delivered to the colony by the common tern parents were almost entirely fish; Ammodytidae (mainly *Ammodytes marinus*, sandeel) and Clupeidae (mainly *Sprattus sprattus*, sprat); comprising 71% and 28% respectively of all prey items. The majority of prey items (93%) that were delivered were successfully consumed by the chicks. However a number of prey items brought to the nest by study birds were stolen by kleptoparasites; in fact 4.2% of all prey items were stolen, comprising as much as 13% of the total energy delivered over the two years, with no significant difference between years (see **Figure 1**). The fish stolen by kleptoparasites was found to be highly dependent on both size class (see **Table 3**), and species of fish (see **Table 4**). Successful kleptoparasitic attacks were concentrated in the larger size classes of both fish species (virtually non existent in fish less than 4 cm in length), and within size classes more common for sprats than sandeels, with over 10% of all sprats delivered to the study nests being stolen.

Table 3. *Fate of prey items delivered to the nest, according to size class. The proportion of fish kleptoparasitised differed significantly between the four size classes* ($X^2_3 = 166.57$, $p < 0.0001$), *calculated from 3564 prey items delivered to study nests during chick rearing in 1994 and 1995.*

	Size class of prey item			
Fate of prey item	1	2	3	4
Consumed by chick	415 (98%)	2362 (98%)	608 (89%)	26 (70%)
Kleptoparasitised	7 (2%)	58 (2%)	77 (11%)	11 (30%)

Table 4. *Fate of the two main prey species delivered to the nest, according to species. The proportion of fish kleptoparasitised differed significantly between the two species* ($X^2_1 = 120.85$, $p < 0.001$), *calculated from 3533 prey items delivered to study nests during chick rearing in 1994 and 1995.*

	Fish prey item species	
Fate of prey item	**Sprat**	**Sandeel**
Consumed by chick	885 (89.6%)	2495 (98.0%)
Kleptoparasitised	103 (10.4%)	50 (2%)

In the first experiment in 1994, the rate of total energy delivered per chick per hour (this includes all prey brought to the nest area, regardless of its subsequent fate) did not differ among the three experimental groups during the first week after hatching, but in the second week the rate of provisioning of the brood in the full-cost group was less than a third of that in the other experimental groups (see **Figure 2**, taken from chapter 3).

The percentage of this energy delivered to the nest that was successfully consumed by the chicks does not differ significantly between the three experimental groups, but there is a non-significant trend for kleptoparasitic losses to decrease as the relative experimental demand increases. That is, birds in the free-chick group suffer the highest loss of energy to kleptoparasites and birds in the full-cost group the least, particularly in the second week of chick life (see **Figure 3**).

Table 5. *Choice of prey item (number of each type taken) by the three experimental groups in 1994. In simple terms of numbers of each class, prey choice does not differ significantly between the three experimental groups (*$X^2_{10} = 5.95$*, n.s.).*

	Sandeel				**Sprat**			
Group	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Free-chick	49 (16%)	156 (51%)	34 (11%)	0 (0%)	20 (7%)	37 (12%)	7 (2%)	2 (1%)
Free-egg	44 (15%)	161 (53%)	33 (11%)	1 (0%)	18 (6%)	39 (13%)	8 (3%)	0 (0%)
Full-cost	15 (19%)	41 (51%)	3 (4%)	0 (0%)	6 (8%)	12 (15%)	3 (4%)	0 (0%)

There was no significant difference in prey choice between the three groups in simple terms of the numbers of sandeel and sprat of each size class (see **Table 5**). However when this is translated into the amount of energy derived by each treatment from the different prey classes, there are significant differences between them (see **Figure 4**). Birds in the free-chick group are relying more on prey of the larger size classes for energy than birds in the full-cost group, with free-egg birds intermediate ($X^2_4 = 54.05$, $P < 0.001$). The treatment groups also differ in the amount of the total energy delivered that is derived from the two main prey species ($X^2_2 = 95.7$, $P < 0.001$). However the relationship between the degree of cost and prey species choice is not so clear, with full-cost birds deriving most energy from sprats (59% total), free-egg birds least (40%), and birds from the free-chick group intermediate (50%).

I have also compared the free-chick group (with an increase in demand at a single phase of the reproductive attempt) with the control group in 1994. This may be roughly equivalent to a comparison between the control and experimental group (also with a single phase increase in reproductive demand) in the 1995 study, and allow a comparison of the patterns of kleptoparasitism in study groups between years.

There was no significant difference between the free-chick group and the unmanipulated control group in 1994 in the total amount of energy brought to the nest per chick per hour in the first or second weeks after hatching (see **Figure** 5). However, the percentage of this energy that was stolen by kleptoparasites differs between the two groups, with the free-chick group losing significantly more energy to kleptoparasites than the control group in the first week, but not the second week after hatching (see **Figure** 6). Despite significantly greater losses of energy in the free-chick group, there is still no significant difference between the free-chick and control groups in the amount of energy successfully consumed by the chicks in the first or second weeks (energy consumed per chick jhr^{-1}, based on means per nest, mean ± s.e.(n); week 1, free-chick 4.63 ± 0.81 (7), control 7.30 ± 1.87 (6), Mann Whitney U-test $U_{11} = 14$, p = 0.32, n.s.; week 2, free-chick 7.90 ± 0.88 (7), control 14.07 ± 6.60 (6), Mann Whitney U-test $U_{11} = 18$, p = 0.67, n.s.).

Table 6. *Choice of prey item (number of each type taken) by the Control and Free-chick groups in 1994. In simple terms of numbers of each class, prey choice does not differ significantly between the two groups* ($X^2_6 = 5.92$, *n.s.*).

	Sandeel				Sprat			
Group	1	2	3	4	1	2	3	4
Control	25 (11%)	129 (55%)	35 (15%)	1 (0%)	12 (5%)	26 (11%)	4 (2%)	1 (0%)
Free-chick	49 (16%)	156 (51%)	34 (11%)	0 (0%)	20 (7%)	37 (12%)	7 (2%)	2 (1%)

The prey choice of the two groups does not differ when measured in terms of the numbers of each prey type (see **Table** 6). However when the possible energy from each prey item is considered, the free-chick birds are apparently targeting more valuable prey items, relying on sprats ($X^2_1 = 88.85$, $p < 0.001$), and the larger size classes overall ($X^2_3 = 12.35$, $p < 0.01$), for a greater portion of the total energy delivered to the nest than the control group (**Figure 7**).

In 1995 there was no significant difference between the experimental group with increased incubation demand and the control group in the total amount of energy brought to the nest per living chick per hour, in either the first or second weeks of chick life (see **Figure 8**). However, the *b* chicks in this group have a lower growth rate and fledge at a lighter weight than the second hatched chicks in control nests (see chapter 4).

Although the percentage of the total energy brought to the nest that was actually consumed by the chicks does not differ significantly between control and experimental birds, it can be seen that the latter tend to suffer higher losses to kleptoparasitism, especially in the second week after hatching (see **Figure 9**). The overall prey choice of experimental and control birds does not differ significantly in simple terms of numbers of each prey species and size delivered to the nest (see **Table 7**). However when this is translated into the amount of energy derived from each prey item, the two groups differ significantly in their reliance on the different species and size classes for the total amount of energy delivered to the nest (see **Figure 10**). Experimental birds are relying more on sprats, ($X^2_1 = 18.20$, $P < 0.01$), and more on the larger size classes, for the percentage of total energy brought to the nest, than the controls ($X^2_3 = 459.56$, $P < 0.001$, **Figure 10**).

Table 7. *Choice of prey item (number of each type taken) by Control and Experimental groups in 1995. In simple terms of numbers of each class, prey choice does not differ significantly between the two groups ($X^2_6 = 6.97$, n.s.).*

	Sandeel				**Sprat**			
Group	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Control	9 (3%)	173 (63%)	17 (6%)	0 (0%)	2 (1%)	38 (14%)	34 (12%)	2 (1%)
Experimental	9 (3%)	171 (56%)	31 (10%)	0 (0%)	4 (1%)	46 (15%)	40 (13%)	7 (2%)

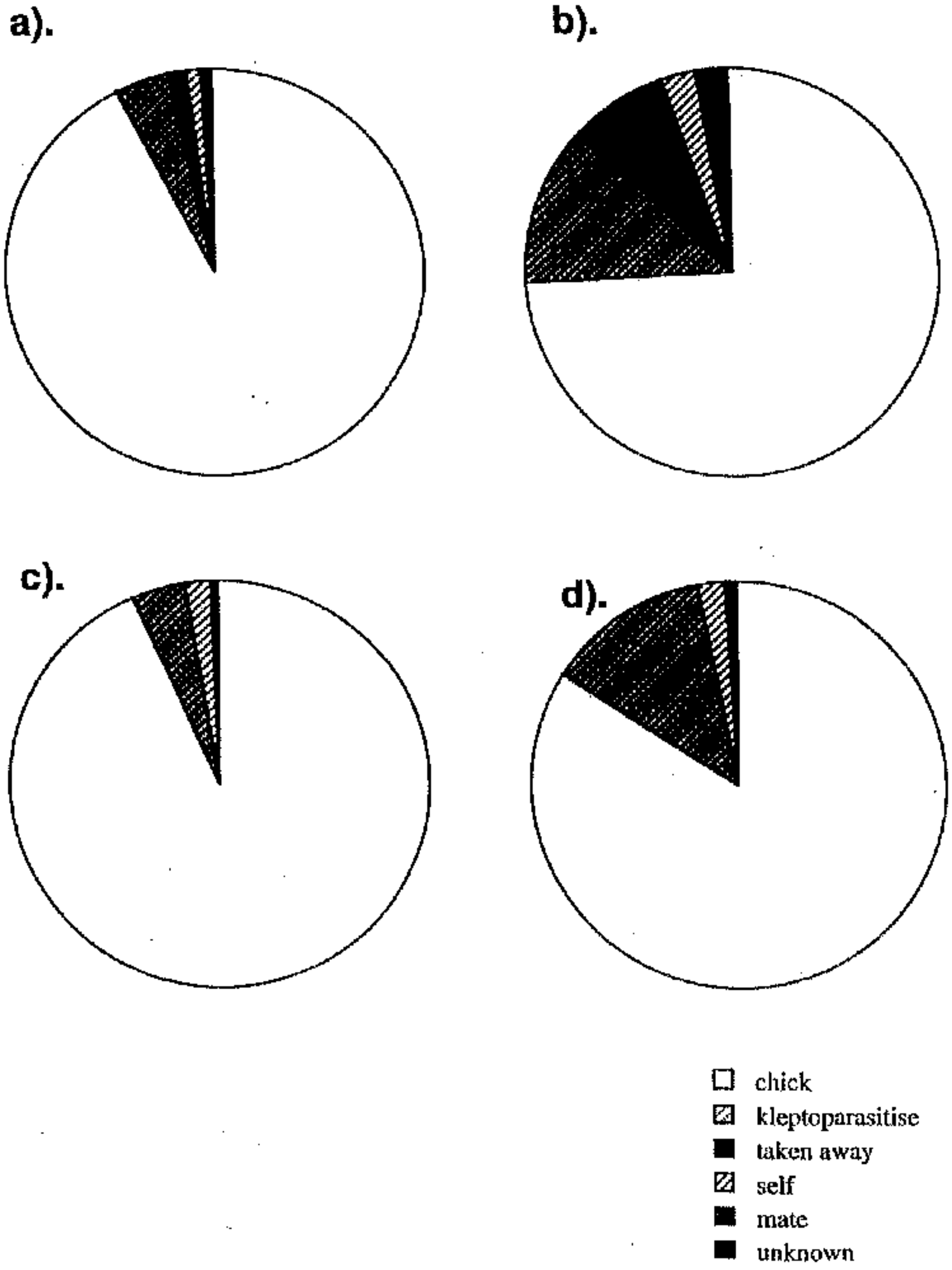


Figure 1. The fate of prey items brought to the study nests in 1994, (*a*) in terms of numbers, (*b*) in terms of energy; and in 1995, (*c*) in terms of numbers, (*d*) in terms of energy.

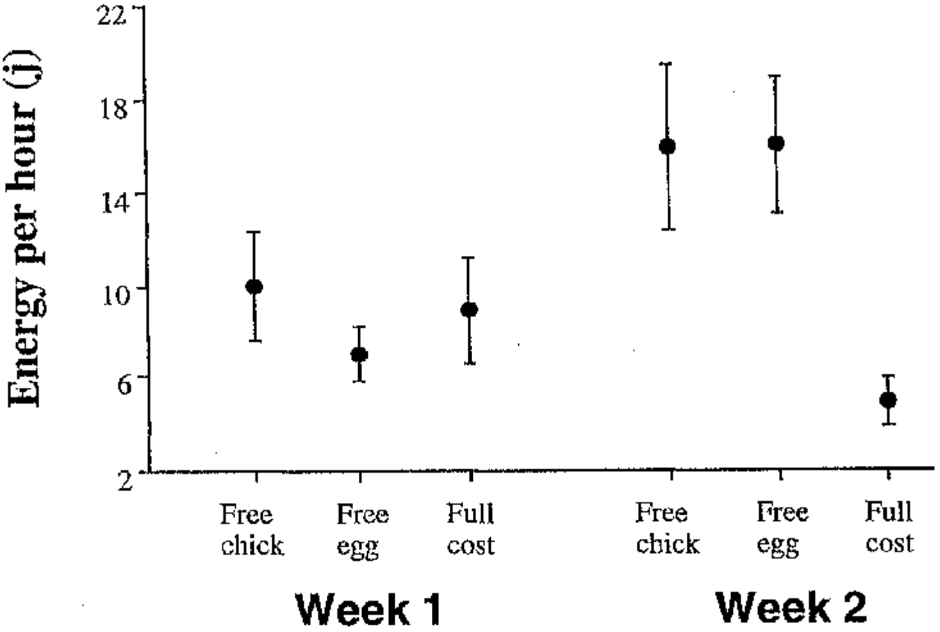


Figure 2. The mean energy per chick per hour (solid circles, ± s.e.) delivered to the brood by pairs in each treatment group during the first and second weeks after complete hatching of the brood. There was no significant difference between the groups in the first week, but a highly significant difference in the second week, with the distribution of values among the groups following that predicted by the degree of cost incurred with the Free Chick Group tending to have the highest and the Full Cost Group the lowest delivery rates (Kruskal Wallis ANOVA, based on all data week 1 $X^2_2 = 0.19$, n.s.; week 2 $X^2_2 = 11.04$, $p = 0.004$; if based on means per nest $X^2_2 = 0.10$, n.s. and $X^2_2 = 6.69$, $p = 0.035$; Jonckheere Test for Ordered Alternatives $p = 0.025$ and $p = 0.029$).

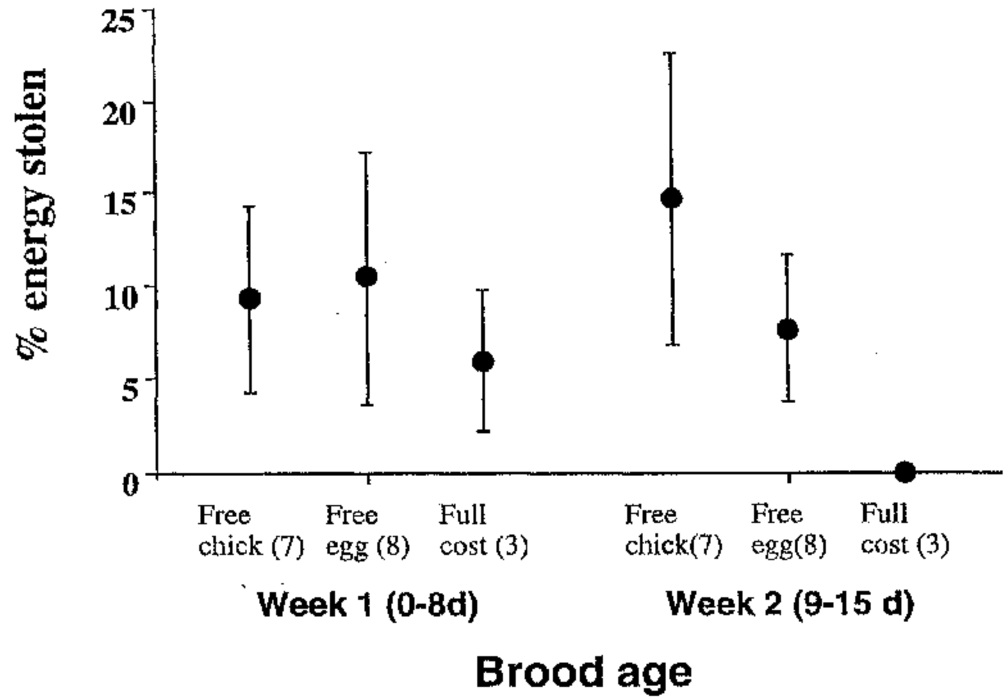


Figure 3. The mean percentage of energy stolen (± s.e.) from nests in the Free chick, Free egg, and Full cost groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the x-axis. There was no significant difference between the groups in the first (Kruskal Wallis ANOVA $X^2_2 = 0.94$, $p = 0.63$, n.s.) or the second week (Kruskal Wallis ANOVA $X^2_2 = 1.86$, $p = 0.40$, n.s.).

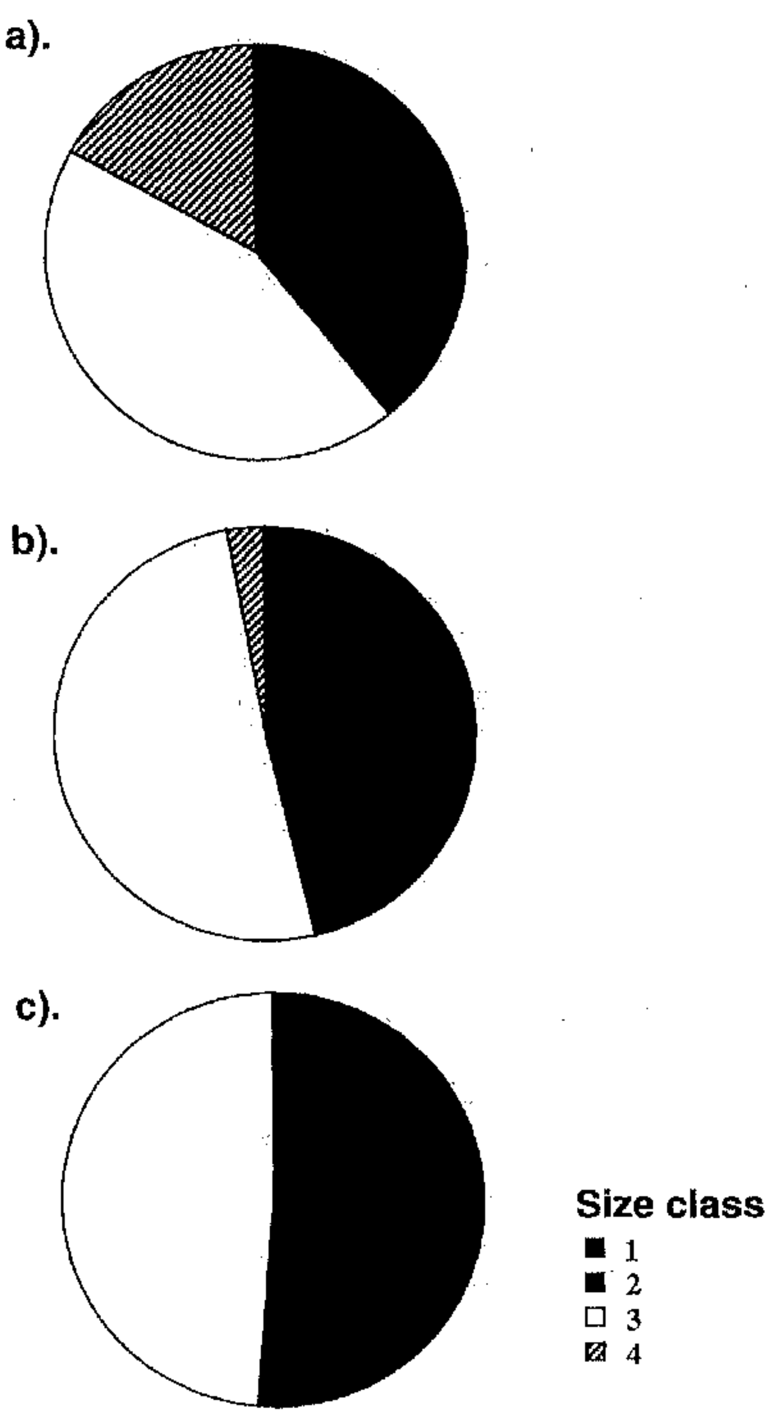


Figure 4. The proportion of energy derived from different prey sizes in (*a*) Free chick, (*b*) Free egg and (*c*) Full cost groups. The differences between the three experimental groups are highly significant when treated overall (see text for details), but not when treated on a means per nest basis (% total energy derived from size class 1: Kruskal Wallis ANOVA $X^2_2 = 0.19$, $p = 0.91$, n.s.; % derived from size class 2: $X^2_2 = 0.17$, $p = 0.92$, n.s.; % derived from size class 3: $X^2_2 = 0.26$, $p = 0.88$, n.s.; % derived from size class 4: $X^2_2 = 0.46$, $p = 0.79$, n.s.).

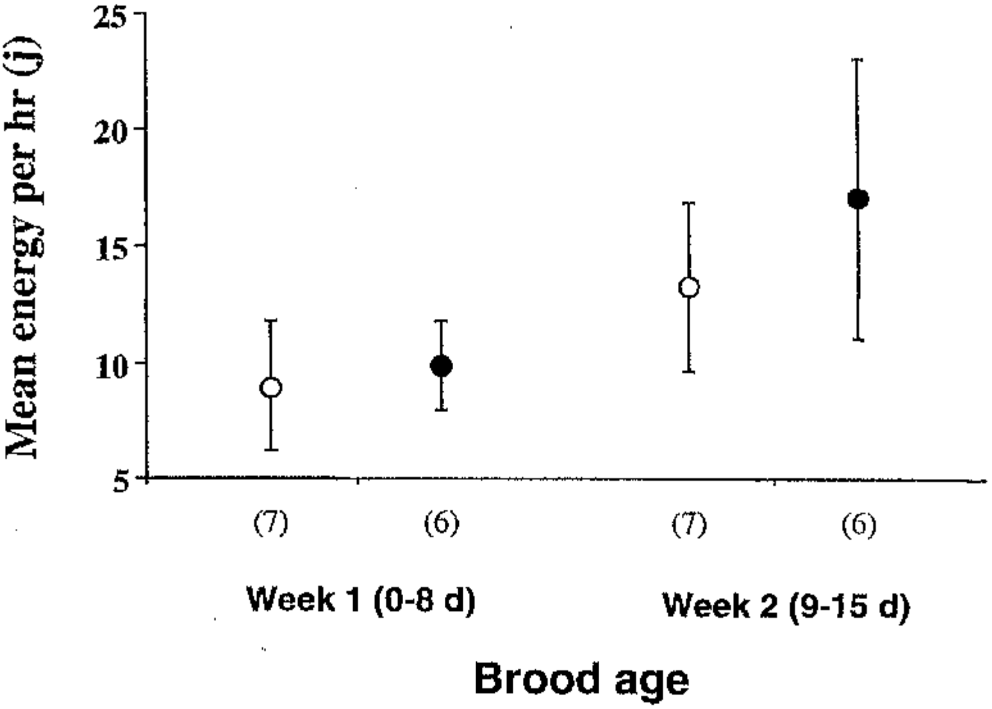


Figure 5. The mean energy per chick per hour (± s.e.) delivered to the brood by Control (solid circles) and Free chick (open circles) groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the *x*-axis. There was no significant difference between the groups in the first (Mann Whitney U-test $U_{11} = 16$, $p = 0.48$, n.s.) or the second week (Mann Whitney U-test $U_{11} = 18$, $p = 0.67$, n.s.).

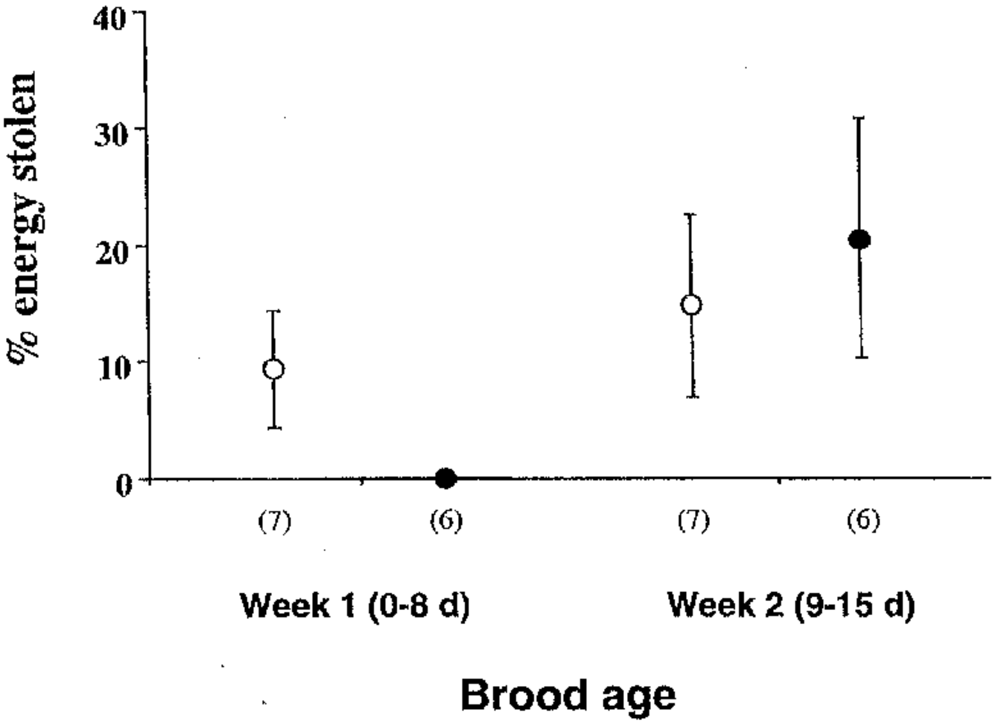


Figure 6. The mean percentage of energy stolen (± s.e.) from nests in the Control (solid circles) and Free chick (open circles) groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the x-axis. There was a significant difference between the two groups in the first week, with birds in the Free Chick group losing a larger percentage of energy to (Mann Whitney U-test $U_{11} = 9$, $p = 0.036$). There was no difference between the two groups in the second week (Mann Whitney U-test $U_{11} = 18$, $p = 0.64$, n.s.).

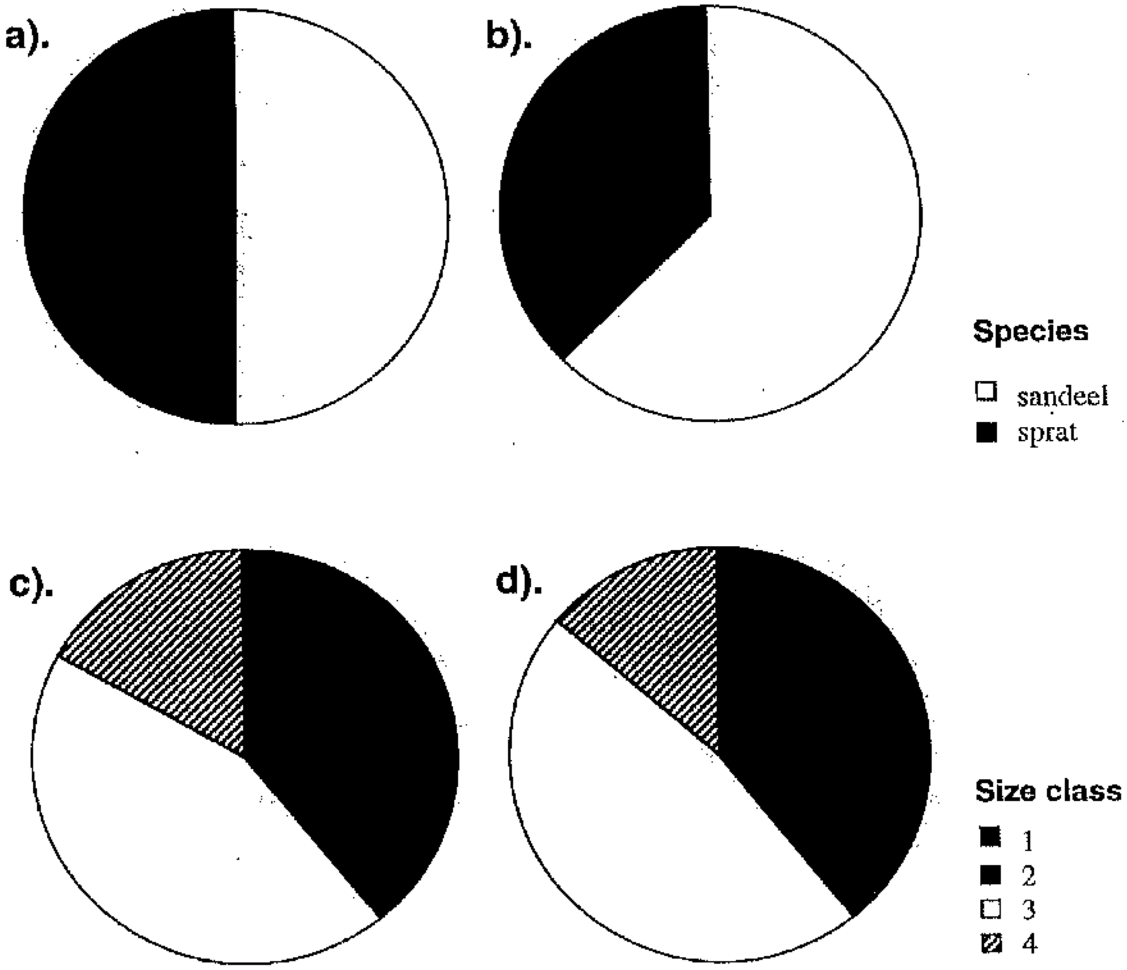


Figure 7. The proportion of energy derived from different prey species in (*a*) the Free chick and (*b*) the Control group, and from different prey species in (*c*) the Free chick and (*d*) the Control group. The differences between the control and Free chick groups are highly significant when treated overall for both species and size class choice (see text for details), but not when treated on a means per nest basis (% total energy derived from sandeel: Mann Whitney U-test $U_{11} = 16$, $p = 0.48$, n.s.; % derived from sprats: $U_{11} = 17$, $p = 0.57$, n.s.; % derived from size class 1: $U_{11} = 18$, $p = 0.67$, n.s.; % derived from size class 2: $U_{11} = 17$, $p = 0.57$, n.s.; % derived from size class 3: $U_{11} = 18$, $p = 0.67$, n.s.; % derived from size class 4: $U_{11} = 18$, $p = 0.56$, n.s.).

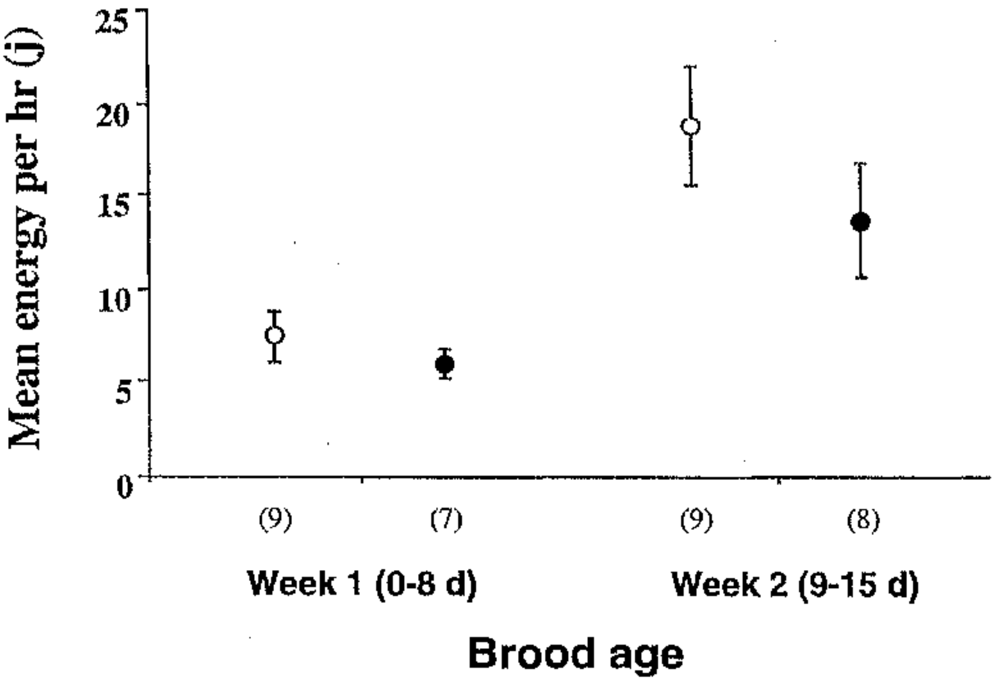


Figure 8. The mean energy per chick per hour (± s.e.) delivered to the brood by Control (solid circles) and Experimental (open circles) groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the *x*-axis. There was no significant difference between the groups in the first (Mann Whitney U-test $U_{14} = 26$, $p = 0.56$, n.s.) or the second week (Mann Whitney U-test $U_{15} = 26$, $p = 0.34$, n.s.).

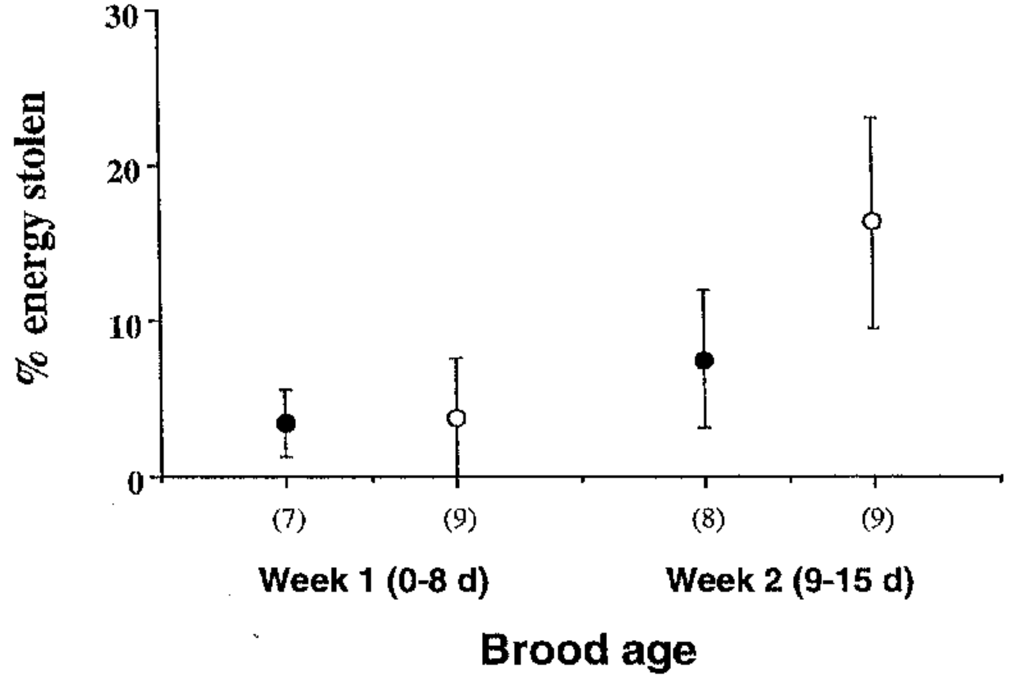


Figure 9. The mean percentage of energy stolen (± s.e.) from nests in the Control (solid circles) and Experimental (open circles) groups during the first and second weeks after complete hatching of the brood. The sample sizes are given in brackets on the x-axis. There was no significant difference between the groups in the first (Mann Whitney U-test $U_{14} = 27$, $p = 0.49$, n.s.) or the second week (Mann Whitney U-test $U_{15} = 26$, $p = 0.32$, n.s.).

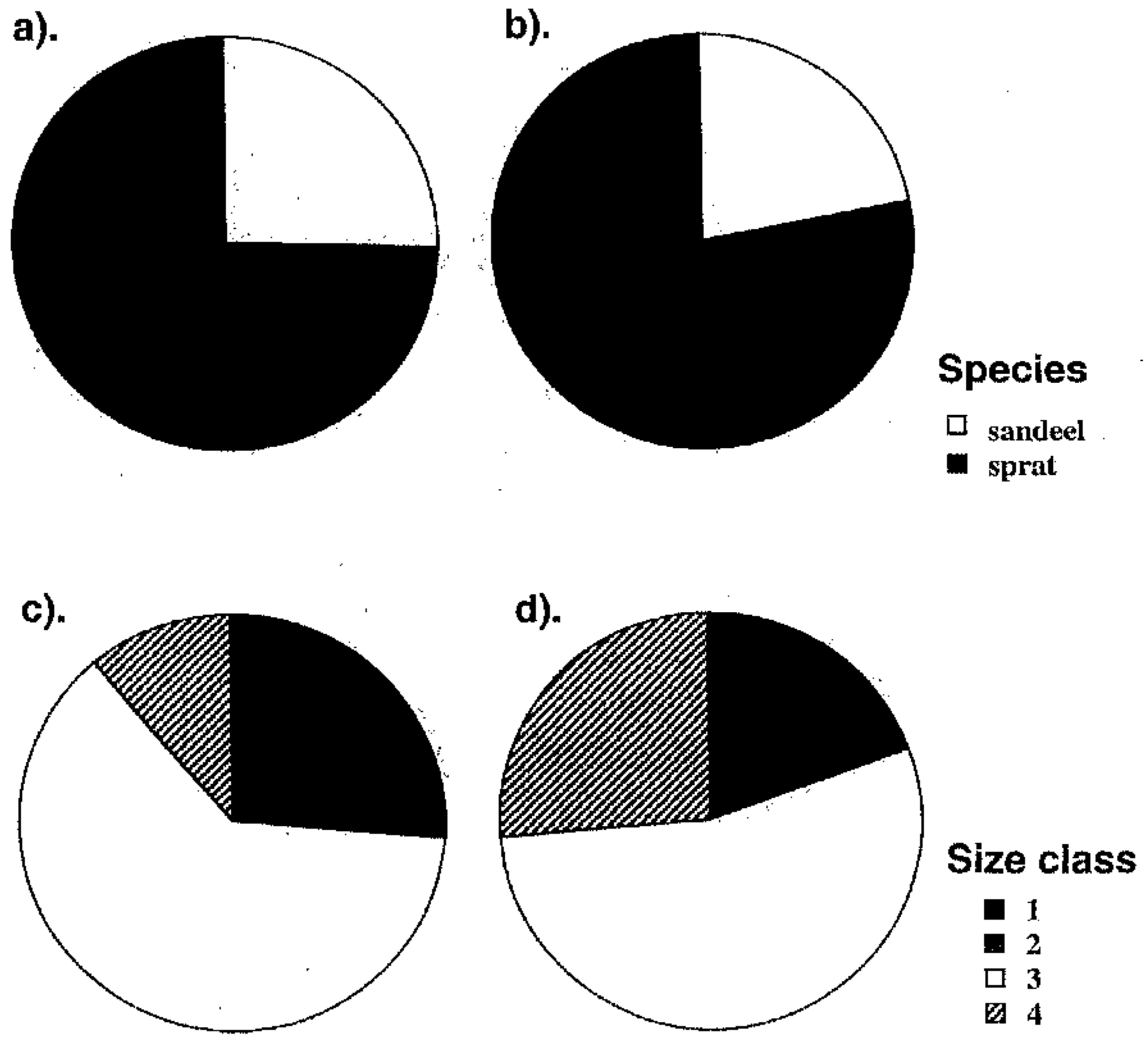


Figure 10. The proportion of energy derived from different prey species in (*a*) the Control and (*b*) the Experimental group, and from different prey species in (*c*) the Control and (*d*) the Experimental group. The differences between the Control and Experimental groups are highly significant when treated overall for both species and size class choice (see text for details), but not when treated on a means per nest basis (% total energy derived from sandeel: Mann Whitney U-test $U_{15} = 31$, $p = 0.63$, n.s.; % derived from sprats: $U_{16} = 31$, $p = 0.42$, n.s.; % derived from size class 1: $U_{16} = 29$, $p = 0.31$, n.s.; % derived from size class 2: $U_{16} = 24$, $p = 0.16$, n.s.; % derived from size class 3: $U_{16} = 39$, $p = 0.93$, n.s.; % derived from size class 4: $U_{16} = 26.5$, $p = 0.15$, n.s.).

Discussion

Kleptoparasitism was clearly an important phenomenon within the colony of breeding terns on Coquet Island in both 1994 and 1995, with over 13% of the total energy delivered to the nests over the two years being stolen by conspecifics. This figure may not even represent the true extent of food stealing since only attacks in the vicinity of the nest site were recorded, and it is likely that piracy will also occur at the feeding grounds (Hulsman 1976), or on the journey back to the colony. A few attacks were made by roseate terns (*Sterna dougallii*), but the majority of the kleptoparasites on both control and experimental birds were other common terns.

Although mixed tern colonies are ideal venues for the development of kleptoparasitic behaviour, it is often only recorded in what are (Uttley 1991) or were presumed to be (Hays 1970), years of poor food availability. Thus, kleptoparasitic behaviour has been associated mainly with a food-stressed population (Brockmann & Barnard 1979). In this study we recorded levels of kleptoparasitism in both years (4% of all prey items delivered to the nest by study birds being stolen) similar to those found in a food stressed population (3.6% stolen, Uttley 1991). However 1994 and 1995 did not appear to be particularly poor years on Coquet Island in overall terms of breeding success (Scott 1994, 1995).

In this study kleptoparasites showed a highly significant preference for attacking hosts carrying prey of the larger size classes. They also showed a strong preference for sprats, which contain more energy than sandeels for a given size class (Harris & Hislop 1978, Hislop *et al.* 1991). Thus, in accordance with previous literature, kleptoparasites targeted hosts carrying larger fish with a higher calorific content in preference to smaller less valuable prey (Hopkins & Wiley 1972, Dunn 1973b, Ens *et al.* 1990, Dunbrack 1979, Uttley 1991 & Thompson 1986). Thompson (1986) produced a profitability model to predict the optimal prey choice of kleptoparasites. The model is based on a simple hypothesis of energy maximisation, and takes into account, prey availability and energy value, the likelihood of success and the energetic costs of the attack and associated handling costs. He concluded that although attacks for larger, more valuable prey items were likely to incur more competition from other pirates and more time in flight (as hosts were more reluctant to give up their prey), attacks on a bigger target were likely to be more successful and prove more profitable. Thus, parasites should, as found in this study, target a mixture of larger prey and show a strong avoidance of smaller prey classes.

In 1994, although there was no difference between the three experimental groups in the first week in the amount of energy delivered to the nest per living chick, in the second week deliveries in the full-cost group were less than a third of that in the free-chick and free-egg groups. It is necessary, however, to look at this parameter in greater detail, investigating the fate of food items delivered to the nest, since this provisioning effort by the parent will not be translated into chick maintenance and growth unless the food is actually consumed by the chick. Looking at the fate of items delivered to the nest we find that the free-chick birds tend to suffer greater kleptoparasitism than the full-cost birds, with the free-egg group intermediate. This trend however is not significant and does not affect the overall result, with chicks in the full-cost group still receiving less food compared to the free-chick and free-egg nests in the second week after hatching. The free-chick group also suffer significantly greater losses of energy to kleptoparasites in the first week than the unmanipulated control group, although there is no difference in the remaining amount of energy that is successfully consumed by the chicks. In 1995 there was no significant difference in provisioning in terms of the amount of energy delivered to the nest per living chick between the control and experimental group, in either the first or second weeks. However the experimental group with the increased incubation cost tend to suffer greater kleptoparasitism than the controls. This result again is not significant, though some of the experimental nests are being robbed of as much as 40 - 50 % of the energy delivered to the nest in the second week after hatching.

There are two possible explanations (which are not mutually exclusive) as to why some treatments may be suffering higher kleptoparasitic losses than others;

i). They may be exhibiting a shift in prey selection - picking larger fish, particularly sprats, and this is making them more attractive targets to kleptoparasites.

ii). Through a loss in condition and flight muscle (Bolton *et al.* 1993, Houston *et al.* 1995a, Carey 1996) due to experimentally increased reproductive cost, they may have impaired manoeuvrability and speed in flight, and consequently be less able to evade parasitic attacks, making them an easy and preferred target.

Examination of the prey choice of the different study groups reveals that the increased kleptoparasitic losses suffered by some treatment groups are likely to be partly as a result of a shift in prey selection. In 1994 the trend for increased kleptoparasitism from the full-cost birds, through free-egg to the free-chick group, mirrors the increasing reliance of these groups on energy derived from prey of the larger size classes. The free-chick group is also suffering significantly greater losses of energy to kleptoparasites than the control group, and again free-chick parents are relying more heavily on the energetically valuable prey than the controls. Similarly, in 1995, the experimental birds suffering higher kleptoparasitic losses are delivering more energy from fish of a larger size and more from sprats than the birds in the control group. Thus greater kleptoparasitic losses do appear, to some extent, to be due to shifts in prey choice. The birds in groups relying on energetically valuable prey items for a significantly larger amount of the energy delivered to the nest, are suffering a greater loss of energy to kleptoparasites, while the birds relying more on low value prey items, are attracting less kleptoparasitic attention. That kleptoparasitic losses decrease through the experimental groups in 1994 as the reproductive demand increases, suggests that impaired avoidance ability is not an important factor. However, once the differences in prey choice have been taken into account, it is possible that reduced evasion ability has a secondary role in the vulnerability of some groups to kleptoparasitism. A more detailed study of the attack, and associated success rate of kleptoparasites, would be needed to test this.

Host prey selection will vary according to the overall profitability of the different prey selections. Just as hosts carrying more valuable prey items are more profitable targets from the kleptoparasites point of view, the presence of kleptoparasites affects the profitability of different prey selections of their hosts, and therefore optimal prey choice (Barnard & Stephens 1981, Barnard *et al.* 1982). The hosts' risk of being targeted by a kleptoparasite will be influenced by prey choice, with the probability of a tern losing its fish increasing with the length of the fish (Hulsman 1976). The increased risk from kleptoparasites suggests that hosts should select smaller prey that are actively avoided by the parasites. However small fish, yielding less energy, will mean that a parent must make more trips to provide the same amount of food to the chicks. Therefore parents should select intermediate sized fish to maximise their efficiency ratio (Hopkins & Wiley 1972). Uttley (1991) produced a model based on the observed probability of a fish of size class x being stolen and the net amount of energy provided to the young if the fish was successfully delivered. The model suggested even at the observed (high) levels of kleptoparasitism large fish (sandeels), despite being stolen at a much higher frequency, would result in a higher net energy gain by broods than smaller fish, per fish caught. In this model the probability of kleptoparasitism needed to be considerably higher than observed levels for the profitability of a larger fish to drop below that of a lesser size class. However, by only recording the energy loss of the food item itself, the model may be grossly underestimating the full cost of kleptoparasitic attacks, and as a result the profitability of a large fish in a population where food piracy is rife may well fall below the level predicted by the model, and consequently that of the next size class down.

It is important to realise that the cost of kleptoparasitism can be quite high, and the associated costs may be more important than the loss of the food item *per se* (Uttley 1991). Most of the kleptoparasites on the study birds were conspecifics, although there was some harassment by a few individual roseate terns in the area. Common terns' main parasitic strategy is fast, energetic chases of hosts carrying fish. Thus the main demand is an energetic one, with high flight costs involved in the chases which may be quite lengthy (Dunn 1973b, Hulsman 1976, pers. ob.). As the value of the prey items increase, the host is more vigilant (Dunn 1973b), and increasingly reluctant to give up the food, while parasites become more persistent (Hulsman 1976). There is a disproportionate increase in time taken to land the larger fish, and host birds may be forced to make up to 15 or even 20 attempts at landing a fish, before it is eventually fed to the chick, or stolen (pers. obs.). This can result in a feeding delay of between 20 (Arctic terns *Sterna paradisaea*, Uttley 1991) and 45 minutes (crested terns *Sterna bergii*, Hulsman 1976). Victims of chases are constantly harassed until forced into error (Hulsman 1976). So that often, even if the prey item is not successfully stolen (success rates of parasitic chases have been recorded from 10%, Hopkins & Wiley 1972, to 18%, Dunn 1973b), it may be dropped or a desperate attempt is made to swallow it by the host to avoid losing it (Hopkins & Wiley 1972, Hulsman 1986).

Kleptoparasitism also involves a physical risk to both the host and its brood. The physical risk to the adult arises during the chase, especially, as often occurs, if the chase involves more than one pursuer (Hopkins & Wiley 1972), where the initial attacker was attracted by the size of prey item and the subsequent attackers by the chase itself (Hatch 1970 & 1975, Hulsman 1976). If the adult does manage to land a larger fish, the chick will take longer to handle it (Hopkins & Wiley 1972). At this time the chick is highly vulnerable to attack by a kleptoparasite intent on getting the fish. If the fish is stolen while protruding from the gape, the chick may accidentally be carried off with it and dropped from a height of a couple of metres, often at some distance from the nest (Hays 1970, Uttley 1991, pers. obs.).

The relationship between experimental increases in reproductive effort and susceptibility to kleptoparasitic attack is not straight-forward. Although shifts in prey selection go some way to explaining the observed pattern in kleptoparasitic losses, the relationship between experimental increases in reproductive demand and the observed shifts in diet are not immediately clear. In 1995, the experimental birds with an increased reproductive demand (33% increase in incubation demand) shift to a selection of more energy rich prey with a higher kleptoparasitic risk. In 1994 the free-chick birds with the smallest increase in reproductive cost (33% increase in chick rearing only) also switch to a more risky energy rich diet in comparison to the control group. However, as the experimental demand is increased through the free-egg (increased incubation and rearing) and full-cost groups (increased egg production, incubation and rearing), the birds rely less on the large energy rich prey items and the attendant kleptoparasitic losses are reduced.

It is possible that the initial increase in reproductive demand causes the experimental birds to shift to a risk prone diet. Risk sensitive decision making in optimal foraging theory (Stephens & Charnov 1982, Pulliam & Millikan 1982), suggests that the presence of kleptoparasites will cause individuals to adjust their diet selection. However, the condition or state of the individual forager must be included in the equation. The consumption of *N* units by a near starving animal could increase the individual's survivorship more than the same number of units increases the survivorship of an animal near satiation. Thus a forager's potential responses to risk are likely to vary with its total net intake, depending on the comparison of energetic intake with energetic requirement (Caraco 1980, Caraco *et al.* 1980).

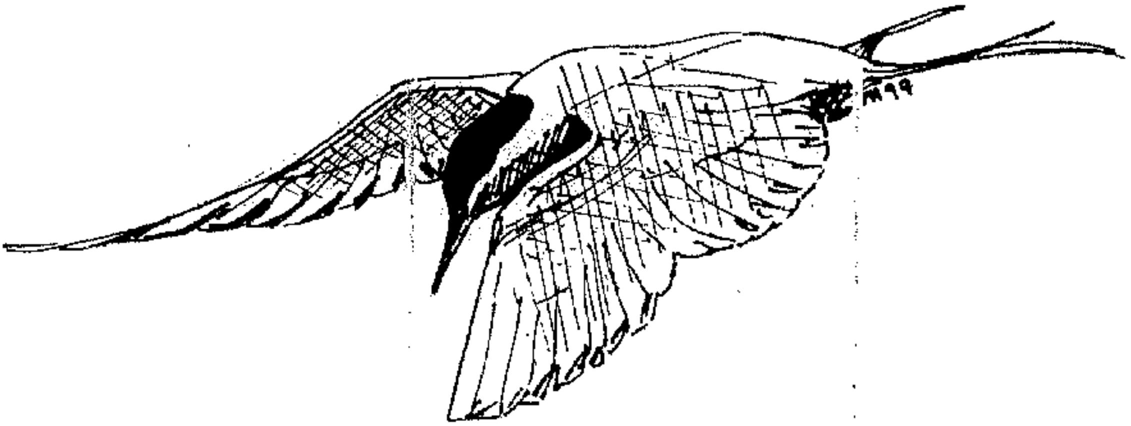
In the context of this study, the condition of the individual may also be seen in terms of the brood that the adult is provisioning, and the relative value of *N* units of energy to a chick which is either satiated or near starvation. The experimental birds, whose broods are likely to be in a lower energetic condition because of the increased reproductive demand, are seeking greater average energetic benefits than the risk-avoiding controls, but they are doing so at the expense of a greater probability of starvation of their chicks. In favouring risk, and selecting larger more energy rich prey items, the experimental birds may be accepting the chance of losing the fish (resulting in a net energy loss), in order to capitalise on the possibility of obtaining relatively larger energetic rewards if they deliver it to the young successfully (Caraco 1980). The control birds are showing more risk aversion, avoiding resources with relatively high variation (large sprats), and favouring exploitation of resources with small variation (smaller sandeels), even though the average reward is less than the means of the more variable food resource (Caraco 1980). Thus, the experimental birds in 1995 and the free-chick group in 1994 suffer higher losses of energy to kleptoparasites, but the net energy intake of the chicks is not reduced below the levels in the respective control groups.

Initially the experimental birds adopt a risk prone foraging strategy, selecting larger prey with an attendant higher kleptoparasitic risk. The greater average energetic gains per item received by the risk prone experimental birds means that they are ultimately able to provision their young with similar amounts of energy as the control birds. In 1995, the experimental group (with increased incubation demand only), achieves the same fledging success as the control group. However, the foraging strategy adopted by these birds does not appear to wholly compensate for the experimental increase in cost, with the second hatched *b* chicks showing a slower growth rate and lighter fledging weight than in control broods (see chapter 4). In 1994, birds in the free-chick group which also adopted a risk prone foraging strategy in response to a limited increase in reproductive cost (increased chick rearing only), seem able to compensate for the extra cost quite successfully. The free-chick group in fact fledge significantly more young than the control group, although this result is somewhat artificial since they have not had to pay the full cost (egg production and incubation) of the third potential fledgling in the nest (see chapter 3).

With the important factor of the condition or state of the individual introduced into the model, we may begin to explain what is occurring in the free-egg and full-cost groups in 1994. As the experimental demand increases the profitability of the larger prey items will be further reduced. A loss in muscle condition, as a result of the extra experimental demand (Bolton *et al.* 1993, Houston *et al.* 1995a, Carey 1996), may mean that the birds are less able to evade attacking kleptoparasites, and the probability of losing large prey items is increased. The increased capture and transportation costs and search time involved in obtaining the larger fish (Uttley 1991), may also be relatively more costly to the experimental birds in poorer condition due to the increases in reproductive demand (chapter 4, McNamara & Houston 1996), so much so that they are just not worth pursuing. The free-egg and full-cost group in particular then, rely more on the smaller prey size classes for delivering energy to their chicks, and although they are harassed less, they must make more trips to supply the same amount of energy. As a result the birds are unable to provision their young adequately, and the free-egg and full-cost groups fledge progressively less young than the free-chick group; and even the chicks that survive grow less well in the full-cost group (see chapter 3).

The results of this study show that kleptoparasitism is an important factor in prey choice in tern colonies, even in years when food availability does not appear particularly low. Increases in reproductive demand can affect the probability of kleptoparasitic attack in experimental groups, mainly through shifts in prey selection. Initially the experimental birds adopt a risk prone foraging strategy, which does seem to compensate to some extent for the effects of increased effort. However, as the costs of selecting the larger prey rise for the birds presumably in poorer condition (from increased reproductive demand), they rely less on the energetically valuable prey items, so that they are delivering less energy overall, and as a result fledging success decreases.

Chapter 10 : General Discussion



Individual Optimisation and the Lack Clutch Size

Life history theory assumes that reproduction is costly and elucidating the nature of these costs is a prime focus of research (Roff 1992, Stearns 1992). This thesis has been particularly concerned with some of the trade-offs in reproductive effort and cost involved with the evolution of clutch size. Lack (1947) suggested that altricial birds should lay the clutch size that fledges the most offspring, and that avian clutch size is set by the number of young parents can adequately provision;

> *I believe that in nidiculous species, the average clutch size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and at the season in question.*
>
> David Lack 1947

This most productive clutch size is known as the Lack value or Lack clutch size, and will be shaped by evolution to maximise fitness.

It is generally accepted that individuals differ in quality and in state, and that this will effect their reproductive effort and success (Drent & Daan 1980, Pettifor *et al.* 1988, Daan *et al.* 1990, Roff 1992, Stearns 1992, McNamara & Houston 1996). We must therefore put the Lack Clutch Size into the context of phenotypic variation among individuals. The Individual Optimisation Hypothesis, first proposed by Perrins & Moss (1975), attempts to do this. The theory states that in general each female is laying that size of clutch that maximises the number of offspring subsequently recruited from that clutch into the breeding population. Thus, the '*optimal clutch size is* n *for birds that choose to lay* n *eggs*' (Hogstedt 1980). The number of eggs laid will reflect the ability of the female (and/or her mate) to rear offspring, so that this number may be less or more than the population average (Drent & Daan 1980).

The crucial question is whether parents setting out to rear a certain brood size, but then having young added to or removed from their nests, fare any better than if they had reared their natural brood size. The central point of the Individual Optimisation Hypothesis is that they do not, their intended clutch size producing the maximum number of surviving offspring (hence recruits) (Perrins & Moss 1975, Hogstedt 1980, Pettifor 1993a).

Previous Brood Augmentation Studies

Traditionally the period of nestling care is viewed as the main bottleneck in the reproductive cycle (Drent & Daan 1980, Stearns 1992). Lack's proposal and the majority of manipulation studies have focused on this presumed all important chick rearing phase as the major constraining period, with previous brood enlargement being almost exclusively effected by the addition of eggs or chicks taken from another pair (see **Table 1**). These experiments have shown that in many bird species parents can apparently rear more young than the number of eggs they lay, and this is taken as empirical evidence that observed clutch sizes are less than the Lack value (Lindén & Møller 1989, Partridge 1989, Dijkstra *et al.* 1990, Godfray *et al.* 1991, Lessells 1991, Roff 1992, Stearns 1992, Vander Werf 1992). The protocol used in the manipulations is presumed to mimic realistically the cost of producing additional young with the major reproductive constraints operating after the young hatch. However, such experiments have failed to include the full cost of an increased brood, since through the method of brood augmentation, they tend to omit the process of egg production and much of the incubation cost also.

Table 1. *Numbers of experiments on birds in which a brood manipulation was effected at different stages of the breeding cycle (from 97 studies that manipulated reproductive effort in at least one breeding phase, although a few manipulated effort in two or more phases causing non-independence of results at the different stages), (reproduced from Monaghan & Nager 1997, updated from Stearns 1992).*

	Manipulation		
	No. Chicks after hatching	No. Eggs during incubation	No. Eggs laid per clutch
Number of studies	78 (80.4%)	24 (25.7%)	3 (3.1%)

Egg production, apart from being relatively difficult to manipulate, is often considered a relatively inexpensive phase. This is because birds will often replace eggs that are lost during laying, and replace entire clutches if they are lost after completion. For example the American coot *Fulica americana*, which lays a normal clutch size of 10 eggs, produced a remarkable 35 eggs in 37 days in response to continual egg removal (Arnold 1992), and the lesser black-backed gull *Larus fuscus*, which normally lays 3 eggs, has been made to produce 19 or more eggs by continuous removal of the eggs as they were laid (Paludan 1951, Nager pers. comm.). The incubation phase has also been assumed to be relatively undemanding (e.g. King 1973, Walsberg & King 1978), with apparent inactivity at the nest and the opportunity in biparental incubators such as terns, to replenish reserves between incubation bouts. However, these arguments fail to consider the need to maintain reserves for later stages (Winkler & Walters 1983, Martin 1987, Partridge 1989, Lessells 1991). Parents must produce and incubate the eggs, whilst also maintaining sufficient reserves for the later stages of the reproductive attempt.

More recent studies suggest that the costs of both egg production and incubation may have been underestimated (Carey 1996, Perrins 1996, Monaghan & Nager 1997). Larids lay relatively large clutches for their body weight, with egg production imposing energy and protein demands far above maintenance levels (Salzer & Larkin 1990). Ricklefs (1974) estimated the energy costs of egg laying in gulls and terns to represent 170% basal metabolic rate (BMR). This was the second highest value of the 6 birds groups he listed, with the highest value recorded in ducks (180% BMR) and the lowest in owls (39% BMR). Robbins (1981) estimated the protein costs of eggs production in larids to be 232% of maintenance costs, this was the highest of any of the 5 groups he compared (the lowest value he recorded was 86%, in raptors). However, assessments of the energy required for egg production must take into account not only the composition of the end product but also the cost of acquiring and manufacturing the material, especially since eggs are often formed before peak food abundance (Perrins 1996, Carey 1996). A study of laying barn swallows (*Hirundo rustica*) using doubly labelled water, recorded daily levels of energy expenditure that were not significantly different from those during chick-rearing (Ward 1996). Also, direct measurements of the energy consumption of uni-parental incubators have revealed levels of expenditure as high as those in birds feeding young, with energy requirements increasing with increasing clutch size (Haftorn & Reinertsen 1985, Moreno & Carlson 1989, Moreno *et al.* 1991, Tatner & Bryant 1993, Ward 1996, Williams 1996).

Experimental studies manipulating these parameters also suggest that they are costly and subject to constraints. For example, lesser black-backed gulls manipulated into laying an extra egg showed a reduction in quality in this additional egg with negative effects on offspring survival (Monaghan *et al.* 1995). Other experimental studies have reported a reduction in the efficiency of incubation following an increase in the number of eggs incubated, including a prolonged incubation period (e.g. Baltz & Thompson 1988, Coleman & Whittall 1988, Smith 1989, Moreno & Carlson 1989, Székely *et al.* 1994, Siikamaki

1995), reduced hatching success (e.g. Briskie & Sealey 1989, Moreno *et al.* 1991, Siikamaki 1995) and increased hatching asynchrony (Moreno & Carlson 1989).

This Study

In light of the more recent estimations of the costs of egg production and incubation, it seems possible that the inclusion of these costs could have influenced the outcome of previous brood enlargement experiments, so rendering many of the interpretations invalid (Partridge 1989, Dijkstra *et al.* 1990, Godfray *et al.* 1991, Lessells 1991, Monaghan *et al.* 1995). In this thesis I have aimed to redress the balance of brood manipulation studies somewhat, emphasising the importance of the earlier stages of egg production and incubation in the reproductive attempt. In doing this I also aim to emphasise the importance of within-brood trade-offs on reproductive success and the allocation of reproductive effort.

The Free Chick group presented in chapter 3 followed the protocol of previous brood manipulation studies, adding a chick from another pair to the nest at hatching. In accordance with many of these studies the experimental birds raised significantly more young to fledging than controls. However, in this chapter I also investigated the breeding performance of experimental birds that were made to lay, incubate and rear the additional young. These birds fledged less young than the control broods raising the intended clutch size. Thus, when the experimental birds incurred the full cost of an additional young to their intended clutch size, their ability to raise an enlarged brood was negated. The way in which performance declined in relation to the degree of cost incurred (Free Chick through Free Egg and Full Cost groups) suggested that the incubation and chick rearing demands had a cumulative negative effect on fitness. In order to separate the relative effects of manipulations of these early stages in the reproductive attempt they were also studied in isolation.

In chapter 4 I examined the effect of incubation alone. The results of this experiment demonstrated that an increase in demand at the incubation phase can effect an important fitness cost in terms of chick condition, with the second hatched chick growing at a slower rate and fledging at a lighter weight than in control nests. Lack's argument discussed productivity in terms of the number of fledging young. However, it is important to take into consideration the condition of these young (Martin 1987), since slower growth rates and lighter fledging weights are likely to have ultimate fitness costs, influencing the probability of survival and subsequent breeding success (Ward 1973, Parsons 1976, Coulson & Porter

1985). As predicted this cost was more marked in lower quality pairs which would be expected to be less able to compensate for a deviation from their intended reproductive effort (Drent & Daan 1980, Clutton-Brock 1984, Wright & Cuthill 1989, Pettifor *et al.* 1988, Partridge 1990, McNamara & Houston 1996).

Examination of the differences in response to egg removal between individuals and between years, suggest that egg production is costly since only a subset of individuals in good condition prior to and during laying appear able to replace the lost egg. In fact a significant proportion of the experimental birds (27% 1994, 40% 1995) respond to egg removal with the ultimate behavioural response, opting in the face of the increase in demand (or perhaps a perceived predation risk) to desert the breeding attempt altogether. The experimental birds that are successfully manipulated to lay an extra egg, incurring an increase in egg production demand only, appear to show no apparent fitness costs. Although the birds may incur between-brood costs as a result of reduced condition, no within-brood trade-offs were identified. The increase in egg production results in no changes in parental performance (chapters 7 & 8). The additional egg shows no apparent reduction in quality (chapter 6), apart from a reduced shell calcium content. However, this effect does not appear to have adversely affected the hatching success or survival of additional eggs (chapters 7 & 8). Possible reasons for these findings are discussed further under the heading of Laying Indeterminacy.

It has generally been assumed from previous avian brood enlargement studies that the main costs in producing additional young operate as a between- rather than within-clutch trade-off, via a reduction in residual reproductive value (Smith *et al.* 1987, Gustafsson & Sutherland 1988, Pettifor *et al.* 1988, Gustafsson & Part 1990, Roff 1992, Stearns 1992), and that this then is the main constraint on clutch size. This would be expected in a long-lived iteroparus species, where lifetime reproductive success depends primarily on survival rather than seasonal fecundity (Lindén & Møller 1989). An intergenerational trade-off between parental and offspring traits has been demonstrated in many studies, where parents shunt the experimental costs to their young (e.g. Mauck & Grubb 1995, see review Dijkstra *et al.* 1990), and in general the increase in feedings by the parents is not proportional to the experimental brood increase (von Hartmann 1954, Drent & Daan 1980). In a summary of over 50 studies involving enlarged broods, in 82% of the cases reported that costs were found in offspring traits, in only 44% of the cases were they identified in parental traits; a significant difference (*G*-test, $p < 0.025$, Stearns 1992, see also figure 1, Lindén & Møller

1989, for the relative frequency of experimentally demonstrated trade-offs of between adult survival and fecundity and between adult and offspring survival).

A physiological basis for these costs can be envisaged, with the total amount of energy available to a breeding bird (to allocate between survival and reproduction and between the different phases within reproduction) providing a qualitative framework within which to examine the various trade-offs (Calow 1979). For example an increase in reproductive effort denies resources from other functions such as growth, somatic repair or maintenance. The optimal trade-off between reproductive effort and survival has been described as the Optimal Working Capacity (Royama 1966, von Hartmann 1954, Drent & Daan 1980). This has been estimated at roughly 4 x BMR (Drent & Daan 1980, *cf.* Bryant & Tatner 1991). Above this level of exertion parents suffer increasing risks from dangers (physical, fatigue, predation) which begin to have a negative effect on lifetime reproductive performance. This evokes a ceiling on cost for the current reproductive attempt (Goodman 1974).

In this study no direct measurements of adult condition or subsequent survival and reproduction were taken, and it is possible that increased reproductive effort may have reduced the Residual Reproductive Value of the experimental parents. However, the results of the study emphasise the importance of the current breeding attempt. The within-brood trade-offs identified in this study lend support to the Individual Optimisation Hypothesis and cast doubt on the evidence that the most common clutch size is less than the Lack Value. The effects of the experimentally increased reproductive demand appear to be mediated through an impact on the foraging capacity of the parents and hence the growth and survival of the chicks. The manipulations also appear to influence prey choice in the experimental parents as explored in chapter 9, with birds under stress initially adopting a more risk prone foraging strategy. Then, as the reproductive demand increases, the costs of selecting larger prey with a high energetic content rises. The birds, presumably in poorer condition, rely more on the smaller less valuable prey items and deliver less energy overall. These within clutch trade-offs can also be understood using the same physiological basis or framework as before, with increased demand at an early stage of the reproductive effort leaving less energy for the subsequent stages. The birds may be able to increase their work rate aboye the above the Optimal Working Capacity to a certain extent (Bryant & Tatner 1991) allowing some buffering capacity against a poor situation. However, they cannot sustain this level of effort on a daily basis and survive, they will be forced to cut back drastically later to recover (Hamer *et al.* 1993). This appears to be the case with the experimental birds in this study. As a result of increasing their reproductive effort in response to the experimental manipulations they have created a resource deficit. This short-fall is not/ cannot effectively be repaid from the allocation for parental survival and future reproduction, and their capacity to rear the chicks successfully is reduced. They incur an ultimate fitness cost in the current attempt (and possibly future also).

There is no *a priori* reason to assume that a certain level of parental investment has already been fixed for the current breeding attempt and that trade-offs in size and number of offspring must occur within this. It may be more useful to view the relationships between all traits using a more descriptive term such as Dynamic Linkage (Stearns 1989). For example in the Free Chick group, where the experimental parents incurred increased chick rearing demand only, they were able to successfully fledge more chicks than the controls. An increase in reproductive effort at this end stage of the reproductive attempt cannot by definition be paid from the allocation to later stages and must come from the maintenance budget. The propensity of the adults to increase their effort, in spite of possible reductions in residual reproductive value, will be increased as the hatched chicks in the nest represent a relatively large investment at stake (Williams 1966).

Mechanisms of Trade-Offs

In order to understand the manifestation of reproductive costs, we need to consider the mechanism underlying an organism's response to the manipulation and the degree to which it can compensate for the imposed change in its life history (Reznick 1985). When considering the trade-off between current reproductive effort and future parental survival and reproduction, a useful distinction can be drawn between ecological and physiological costs (Calow 1979). For example, reproduction may increase the level of exposure to external hazards such as disease, predation or accidents (e.g. frogs calling for mates attract predatory bats, Tuttle & Ryan 1981) or in defending a brood parents may suffer physical damage or death (Magnhagen 1991). These can be classed as ecological costs.

In this thesis we have been concerned mainly with the physiological basis for the cost of increases in reproductive effort. Physiological costs result if an increase in reproductive effort denies resources from other functions such as growth, somatic repair or maintenance (Calow 1979, Partridge & Harvey 1985). The consequences for mortality of experimentally increased effort might then be measurable only several months after the experiment, when weather conditions and food availability have deteriorated (Reid 1987, Daan *et al.* 1996). It may be expressed under subsequent periods of stress; for example Reid (1987) recorded increased mortality after the breeding season associated with the period of moult in August and September. He suggested that the increased energetic stress may result in the death of the stressed birds, especially if moult was delayed until later when the costs of thermal homeostasis would be higher. Cave (1968) originally suggested that increased brood size may aggravate a 'risk of death by exhaustion' in kestrels, however more precise mechanisms have been proposed.

A number of studies suggest that reproductive effort may interfere with the resistance of animals to disease and parasites, with increased parasitism observed in birds with experimentally increased brood sizes (Møller 1993, Norris *et al.* 1994, Gustafsson *et al.* 1994, Oppliger *et al.* 1996). This may be due to either increased rates of transmission and exposure with increased reproductive effort, or alternatively endocrine changes associated with reproduction, which can cause immunosuppression (Grossman 1984, Bhalla 1989, Marsh 1992).

Deerenberg *et al.* (1997) propose a third most plausible mechanism for the negative effect of increased reproductive effort on subsequent parental survival. Immunological response relies primarily on stored reserves (Beisel 1977), drawing particularly on protein reserves (protein malnutrition has been shown repeatedly to impair immune function e.g. Lochmiller *et al.* 1993). They suggest that parents may suffer reduced immunocompetence as a consequence of the adaptive reallocation of resources in times of increased energetic demand. They found that antibody responsiveness was reduced in birds raising manipulated broods of increasing size. Furthermore, they found that non-breeding birds with experimentally increased rates of physical activity (manipulated hop rate) also showed negative effects on antibody responsiveness. They suggest the immune effect is, therefore, not due hormones associated with reproduction (e.g. corticosteroids), but because of the increased physical activity associated with parental effort. The increased workload requires that the parents reallocate resources between various somatic compartments (e.g. experimental birds show body mass reductions and major reductions in maintenance energy, Deerenberg 1996). Thus there is a trade-off between maintenance and immune function and both of these are traded-off against demands due to reproduction. This redirection of parental resources may be a significant causal component of the cost of reproduction phenomenon, with a temporary suppression of vitality occurring due to interference of the rate of work with the functioning of the immune system (Apanius 1993, Deerenberg 1996, Daan *et al.* 1996).

A direct physiological basis can be found for the mechanism of the within-clutch trade-off between egg production and rearing capacity. Birds use stored protein in egg formation (Carey 1996, Houston *et al.* 1995a), showing increased depletion with increased egg production (Cooke *et al.* 1995, Bolton *et al.* 1993). Most of the protein reserve is stored in the flight muscles (Jones & Ward 1974, Houston *et al.* 1995b). Experimental increase in egg production may therefore cause further depletion of the flight muscle protein, directly affecting flight performance and foraging efficiency (Monaghan & Nager 1997). This provides a direct link between the increased egg production demand and the subsequently reduced provisioning performance and chick rearing ability.

Laying Indeterminacy

In manipulating birds to lay additional eggs, this thesis made use of the indeterminate laying capacity of common terns. The adaptive significance of this response is explored in chapter 5. When using the ability to replace eggs to examine the costs of egg production in isolation (see chapters 6, 7 & 8) no within-brood fitness costs were identified. This is likely to be a result of an integral part of this methodology.

In chapter 5 the response of individuals within a population and between years was examined, and it was concluded that only those birds in a good enough condition prior to laying would be in a position to respond to egg removal by producing an additional egg. Thus within any year, although eggs were removed from a random sample of birds, only a subset of the higher quality individuals actually replaced the lost egg. The difficulty with the methodology is that birds cannot be forced to lay an additional egg. Birds in a poor condition, unable to produce a high quality additional egg and maintain sufficient reserves for the later stages of the reproductive effort, can opt not to replace the lost egg and to desert the nesting attempt altogether or to continue to lay in a determinate manner. These birds then will not be included in the experimental group. Thus, while providing further evidence that egg production is costly, this results in an experimental group that are in a sense 'pre-selected' for quality. These birds may be expected to have a relatively high capacity to compensate for the deviations from their individual allocation of effort which the experimental protocol imposed, and the relative cost of the increase in egg production demand may be lower (than for pairs lower on the spectrum) (chapter 4, Wright & Cuthill 1989, McNamara & Houston 1996).

This contrasts to the protocol for an increase in incubation demand (chapter 4) [or chick rearing], since in this case the experimental birds effectively have no choice in the matter. The entire random selection of birds intending a particular clutch size will be included in the experimental group and are not in any way 'pre-selected' for those that can cope. They have the option to desert the nesting attempt after manipulation, but as they are already included in the experiment, this is now recorded as a response. In conclusion, indeterminate laying is a useful mechanism for the experimental manipulation of egg laying, however, the results must be treated with some caution. It is an adaptive response only shown by birds that are in a good enough condition to incur the extra demand. As a result the overall effect of an increase in egg production may be underestimated.

APPENDIX 1. The relative effects of hatching order and egg size variation in determining chick survival

Many avian studies have shown systematic differences in the characteristics of eggs according to their laying order within the clutch (reviewed by Slagsvold *et al.* 1984, Reid 1987). As with most Larids (Parsons 1970 & 1975, Lundberg & Väisänen 1979, Pierotti & Belrose 1986, Salzer & Larkin 1990, Sydeman & Emslie 1992) this is true for common terns, *Sterna hirundo*, where the last (*c*) egg of modal clutches of three is usually smaller than the preceding *a* and *b* eggs of the clutch (Gemperle & Preston 1955, Dunn 1972, Nisbet & Cohen 1975, Gochfeld 1977, Bollinger *et al.* 1990, Bollinger 1994), with lower yolk reserves (Dunn 1972, Nisbet 1978), and shows a lower survival rate (Langham 1972, Dunn 1972, Quinn & Morris 1986, Bollinger *et al.* 1990). This reduced survival may be partly due to the inferior quality of the third egg, in terms of size and reserves available to the developing embryo and newly hatched chick (for reviews see Williams 1994, Carey 1996), but is also influenced by the degree of hatching asynchrony and by the hatching order. In common terns (Nisbet & Cohen 1975), as with other larids (Parsons 1972), partial incubation begins with the laying of the first of the three eggs so that the chicks hatch asynchronously over 1.5 - 3 days (Courtney 1979, Nisbet 1973). Thus combined in the third-hatched *c* chick is lower egg quality and hatching last. At hatching it may already be a couple of days in growth behind its larger siblings, substantially reducing its competitive ability and chances of survival (Nisbet 1973, Pierotti & Belrose 1986, Sydeman & Emslie 1992, Bollinger *et al.* 1990, Bollinger 1994). This phenomenon of intrabrood age and size asymmetry of the chicks attributable to variation in egg size and asynchronous hatching, and the resulting nestling mortality, has been termed the 'third-chick disadvantage' (Pierotti & Belrose 1986, Sydeman & Emslie 1992).

Thus the relative importance of laying order (presumed to reflect egg quality) and hatching order in the survival of common tern chicks are confounded in unmanipulated clutches. In 1994 the protocol in an experiment to study the effects of an increase in reproductive costs involved a manipulation of the hatching order of the clutch (chapter 3). Five experimental nests hatched all their eggs in the order *b*, *c*, *a*, with the normal hatching asynchrony between chicks maintained. While the experiment was not designed to address the issue of hatching order, by analysing the survival of the experimental chicks hatching in a different order to that in which they were laid, we may gain some insight into the effect of hatching order on fledging success.

However, the protocol is not ideal for three main reasons:

i). The eggs in the experimental clutches do not follow the usual pattern of size distribution. Egg size data for the experimental nests and also for 105 unmanipulated control clutches of three initiated in the central area of the colony in the same year are presented in **Figure 1a & 1b** respectively. The eggs laid after manipulation (especially the *b* egg) in the experimental clutches are relatively larger (with respect to the first laid egg) than the *b* and *c* eggs in control nests. This effect of egg removal on the size of subsequent eggs has also been demonstrated in gulls (Parsons 1976). Thus, the *a* egg while hatching last is not the largest of the clutch and the second hatching *c* egg is not significantly smaller than the other eggs in the clutch, therefore the effects of size and hatching order are complicated. This however has some advantages, since to some extent it allows us to examine the effects of hatching order in the absence of significant size differences between the eggs.

ii). In the experimental nests the normally high correlation between egg size and hatchling size (for review see Williams 1994) is absent in the *a* egg/chick. Although the three eggs in the experimental clutch were of roughly similar size, there was a highly significant difference in the size of fledglings produced from these eggs, with the chick hatched from the *a* egg, although not significantly skeletally smaller (see **Figure 2a**), significantly lighter than the chicks hatched from the *b* and *c* eggs (see **Figure 2b**). In the 5 experimental nests this *a* egg, which had been removed from the nest on laying, was only returned to the nest 2 days after the *c* egg had been laid. The average laying interval between the *a* and *c* eggs for control clutches of 3 eggs in 1994, was 3.54 ± 0.07d (mean ± s.e., $n = 105$), and thus the average time the *a* egg was kept in storage between removal and replacement was 6.00 ± 0.42d, $n = 5$. Although this did not affect the hatching success of this egg (which was 100%), the mass of the hatchling it produced appears to be diminished as a result (see appendix 2).[1]

iii). There is no direct control for the experimental group, since the clutch was raised by parents incurring the extra costs of egg production, incubation and rearing; the 'forced' *c* egg

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[1] This reduced hatchling quality after egg storage does not affect the outcome of chapter 3. The difference between the experimental and control groups lay in the survival to fledging of the second hatched chick which as not from a stored egg.

having remained in the nest (see chapter 3). Also, the experimental birds, made to raise a brood of three, only intended a clutch of two eggs, so that comparisons with control birds also raising a brood of three will be confounded by the fact that the latter birds actually intended a clutch of three eggs and are likely therefore to be of a better quality than the birds in the experimental group. Despite these difficulties it is probably still possible to use unmanipulated clutches of three for qualitative comparison.

In unmanipulated nests hatching all three eggs according to laying order in 1994, survival decreased significantly with laying and therefore hatching order (see **Table 1**). In these nests while the majority of the *a* chicks fledged, most of the *c* chicks died within the first week of hatching. Survival of the *b* chick was intermediate, but closer to the *a* than the *c* (53% of *b* chicks fledged). Of the *b* and *c* chicks that died, the *c* chicks died at a significantly younger age (age at death, mean ± s.e. (days): *b* chicks 9.13 ± 2.00, $n = 8$; *c* chicks 4.13 ± 0.52, $n = 16$; Mann Whitney U-test, $U_{22} = 22.5$, $p = 0.01$).

Table 1. *Fledging success by egg in control nests hatching all three eggs according to laying order. Fledging success varied significantly with laying order* ($X^2_2 = 23.22$, $p < 0.01$).

Egg (Laying order)	**Hatching order**	**Number fledged**	**Number died**	*n*
a	First	15 (88%)	2	17
b	Second	9 (60%)	8	17
c	Third	1 (6%)	16	17

However, the pattern of mortality in the experimental nests differed greatly from that in the control nests (see **Table 2**).

Table 2. *Fledging success by egg in experimental nests hatching all three eggs in the order* b, c, a. *Fledging success varied significantly with laying order* ($X^2_2 = 10.18$, $p < 0.01$).

Egg (Laying order)	**Hatching order**	**Number fledged**	**Number died**	*n*
a	Third	0 (0%)	5	5
b	First	5 (100%)	0	5
c	Second	2 (40%)	3	5

When the *a* egg hatched as a *c* chick, its usually high fledging success (when hatching as an *a* chick in a control nest) was totally negated, with all 5 chicks dying within 7 days. They were also generally the first chicks to die, dying at a significantly younger age than the unsuccessful *c* egg chicks (age at death, mean ± s.e. (days): *c* egg chicks 10.33 ± 1.76, $n = 3$; *a* egg chicks 3.00 ± 0.63, $n = 5$; Mann Whitney U-test, $U_6 = 0.0$, $p = 0.022$). The fledging prospects of the *b* and *c* egg chicks in the experimental broods, were consequently raised (relative to control nests) as they hatched first and second respectively, with all of the *b* egg chicks fledging and the *c* egg chick showing intermediate success (equivalent to that of *b* chicks in control three egg broods).

Previous studies suggest that the relative (rather than absolute) size of a chick to that of its siblings at brood completion is the decisive factor in survival (Gibbons 1987, Bollinger *et al.* 1990, Bollinger 1994). Thus, in naturally asynchronous broods, hatching order will be more influential in determining chick survival than egg size (see appendix 3). These results support this assumption to some extent, with the fledging prospects of the *b* and *c* egg chicks promoted with hatching order. However, as discussed before, the lack of difference in egg size within the clutch and the abnormally small size of the *a* egg hatchling confound any firm conclusions.

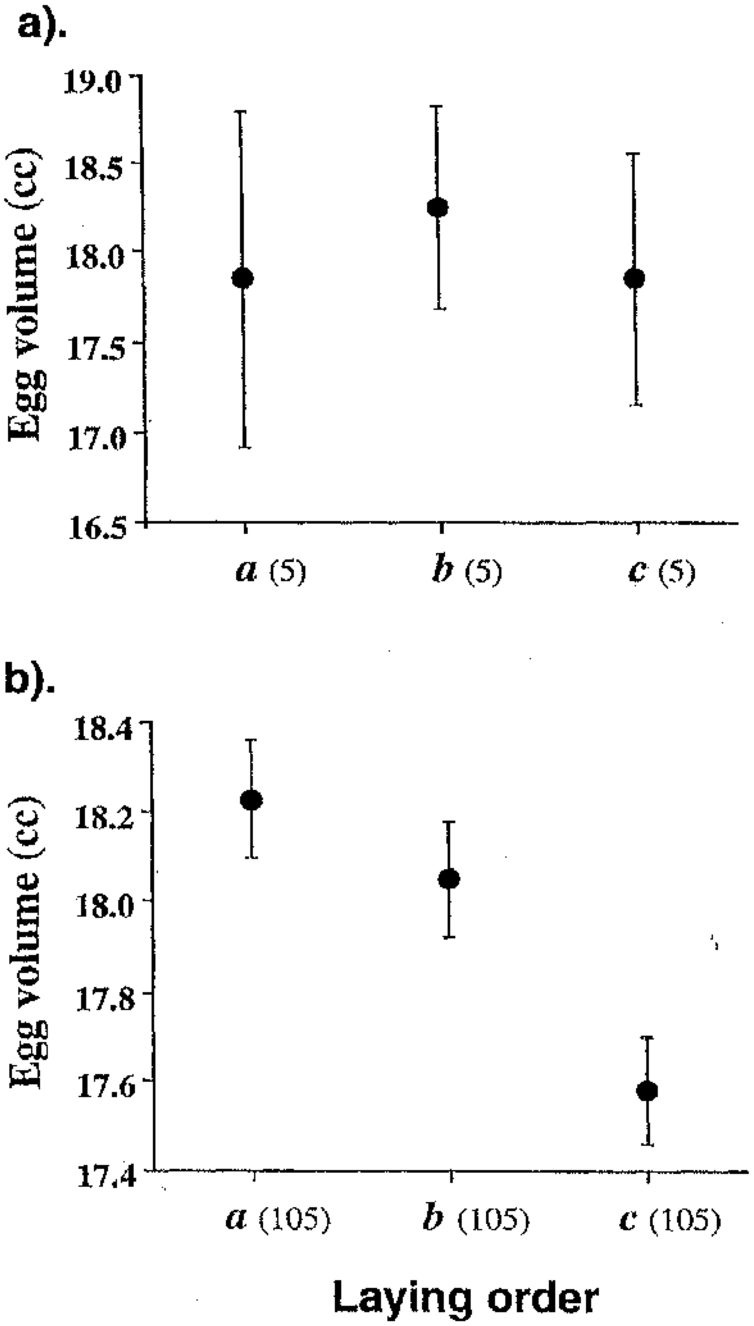

Figure 1. Mean egg size (solid circles ± s.e.) for (*a*) experimental clutches and (*b*) pairs laying an unmanipulated clutch of three eggs in 1994. The sample sizes are given in brackets on the *x*-axis under the corresponding means. There was no significant difference in egg size with laying order in the experimental clutches (Kruskal Wallis ANOVA $X^2_2 = 0.18$, $p = 0.91$, n.s.), but in the control nests egg size decreased significantly with laying order (ANOVA $F_{2,312} = 7.17$, $p = 0.001$).

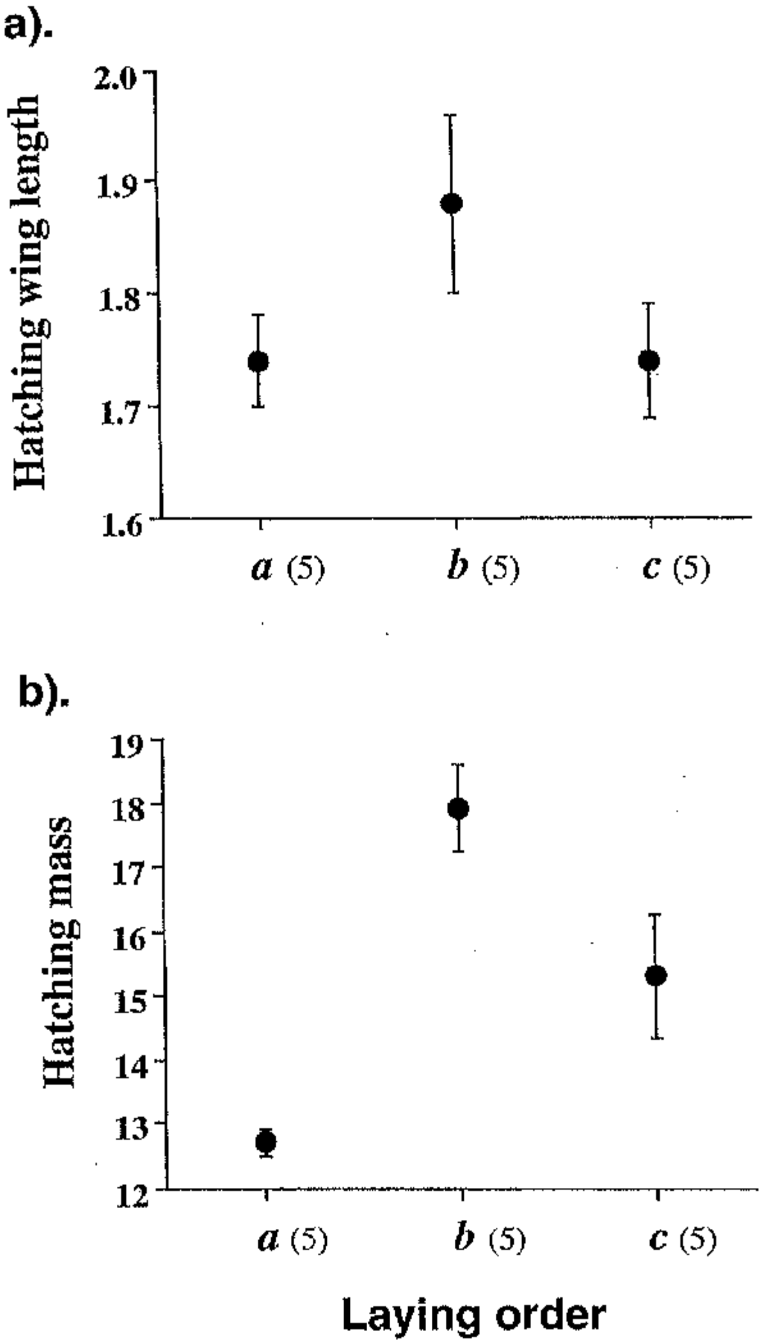

Figure 2. Mean (solid circles ± s.e.) (*a*) wing length; and (*b*) mass at hatching in relation to laying order of each chick in experimental broods of three hatched in the order *b*, *c*, *a*. The sample sizes are given in brackets on the *x*-axis under the corresponding means. There was no difference in wing length (Kruskal Wallis ANOVA $X^2_2 = 3.77$, $p = 0.15$, n.s.), however, hatching mass differed significantly with laying order (Kruskal Wallis ANOVA $X^2_2 = 10.27$, $p = 0.006$).

APPENDIX 2: The effects of egg storage

Information from studies on the storage of eggs before incubation is almost exclusively limited to commercial chicken hatcheries. However, it may be possible to gain some useful insights for effective storage of tern eggs from the findings.

Most studies agree that egg storage depresses hatchability (Hodgetts 1991). However, numerous studies have shown that normal fertile eggs can be stored for several days without a major problems, providing optimal storage conditions are maintained (Wilson 1991). Hatchability does not appear to decline until after about 8-10 days of storage (Hodgetts 1991). It must not be forgotten that the fertile egg contains an extremely delicate organism and care should be taken that the egg receives the minimum amount of 'environmental insults' (Hodgetts 1991). During the pre-incubation storage period temperature, humidity, gaseous environment, egg turning and egg orientation are all likely to affect the subsequent hatchability of the egg (Wilson 1991). The relative influence of each of these factors and how this can be controlled is considered below.

Proudfoot & Hulan (1983) recommend that fertile eggs should be stored below 'physiological zero' (25-27 °C, see review Lundy 1969) to maintain dormancy of the embryo (physiological zero being the temperature above which embryogenesis starts). It has been concluded that the shorter the storage period, the higher the optimum storage temperature for maximum hatching will be (Mayes & Takeballi 1984). Suggested storage temperatures for chicken eggs were 18-30 °C for less than 3 days, 16-17 °C for 3-7 days, and 10-12 °C for more than 7 days storage. There are indications that when the embryo is in the pre- or early gastrula stage chilling causes increased abnormalities and reduces hatch (Hutt and Pilkey 1930, Hays & Nicolaides 1934). Since not all embryos are at this stage at laying (Hays & Nicolaides 1934, Mather & Laughlin 1979) a beneficial effect of some degree of pre-storage warming on hatchability can be seen, especially for storage periods in excess of 7 days (e.g. Becker & Bearse 1958, Butler 1991). Periods of discrete warming may also be beneficial throughout a storage period to reduce the degradation of the blastoderm (Kosin 1956, Arora & Kosin 1966).

Moisture loss from eggs during storage is influenced by temperature and humidity (Butler 1991). The optimal relative humidity levels during egg holding are within the range of 75-

90% (Reinhart & Hurnik 1982). Studies of eggs subjected to extended holding periods (12-28 days) suggest that hatchability may be improved by the use of low permeability plastic wrapping (Becker 1964, Proudfoot 1964a, 1964b, Gordon & Siegel 1966), although storage unwrapped at very high humidities (90-92%) has a similar effect (Reinhart & Hurnik 1980). Some studies suggest beneficial effects from nitrogen flushing of stored eggs (Proudfoot 1964*b*, Gowe 1965), but in general the optimum gaseous environment, in respect of carbon dioxide, nitrogen and oxygen, remains undefined (Butler 1991). Bacteria can also affect the hatchability of eggs once inside the eggs, and whilst bacterial penetration will be influenced primarily by the egg shell and cuticle, the hygienic status of the environment into which the egg is laid is thought to play an important part in increasing the likelihood of this occurring (Tullett 1990, Bruce & Drysdale 1991).

The turning of eggs can be beneficial when the eggs are stored for more than two weeks (Farnsworth & Warren 1962, Proudfoot & Hulan 1983). However, storing eggs small-end-up without turning results in increased hatch which is not further improved by turning (Proudfoot & Hulan 1983, Mayes & Takeballi 1984). Mayes and Takeballi (1984) suggest that the effect of small-end-up storage may be due to centering of the yolk in the albumen giving the embryo greater protection from dehydration and adhesion. Eggs held small-end-down should be turned daily through 90° if stored for more than 7 days (Butler 1991).

In this study eggs were removed from the nest on the day of laying. In an attempt to conserve moisture they were stored in re-sealable plastic bags, and in egg trays in a cool box. The eggs were turned daily and the ambient temperature maintained at approximately 11 °C. In 1995 no eggs were kept in storage longer than 3 days, although duration of storage for some eggs in 1994 was considerably longer (mean ± s.e., 6.00 ± 0.42d, max. = 8d, *n* = 5, see appendix 1).

Storage did not appear to affect hatchability in either year (see chapters 3, 7 & 8). However, the prolonged storage of the experimental *a* eggs in 1994 appears to have had an adverse effect on chick viability through reduced hatching weight. The normally high correlation between egg size and hatchling size (for review see Williams 1994) is inconsistent, with chicks from the stored *a* eggs, although not significantly skeletally smaller, significantly lighter than other chicks from similarly sized eggs (see appendix 1). This effect is probably mediated through a significant increase in water loss, despite the eggs being sealed in plastic bags during storage (possibly water was deposited as condensation on the inside of the bags).

Avian embryos are capable of some osmotic control of fluid distribution among compartments under varying hydric conditions (Hoyt 1969, Simkiss 1980b), however at the time of egg storage, little embryonic development would have occurred, and so regulatory capacities to limit water loss, may be poorly established (Simkiss 1980b). Previous experiments to investigate the tolerance of avian embryos to variation in water loss during incubation, have found that quite considerable increases can be tolerated (e.g. 100% increase in water loss, Simkiss 1980a) with no effect on hatchability, but with a significant effect on hatching mass, which is reduced in water deprived hatchlings (Simkiss 1980a, Tullett & Burton 1982, Carey 1986, Davis *et al.* 1988), although dry masses of control and experimental hatchlings do not vary significantly (Simkiss 1980a, Tullett & Burton 1982). Thus avian embryos have evolved a mechanism for regulating growth so as to match the metabolite supplies (water, respiratory gases, and nutrients) available (Simkiss 1980a), and this appears to be what has happened in the experimental *a* egg chicks with increased water loss, resulting in chicks emerging 4 or 5g lighter at hatching than might have been expected.

In conclusion, although pre-incubation egg storage may be a useful tool particularly in experimental studies of laying patterns, the length of pre-incubation storage time should be kept to an absolute minimum, preferably less than a week. Eggs should be stored small-end-up at a temperature perhaps slightly higher than used in this study, and water loss reduced as much as possible. An initial period of warming or discreet warming periods during storage may also be useful (Butler 1991).

APPENDIX 3. Why does the *b* chick sometimes do better than the *a*?

Closer examination of the results presented in figure 1, chapter 4 (*p*45), reveal that in 2 chick broods the *b* chick is doing just as well if not better than the *a* chick. In the control group that laid an unmanipulated clutch of 2 eggs, of the 17 nest that hatched both of these eggs, the *b* chicks grew significantly faster than the *a* chicks and fledged at a heavier weight (although this difference was not significant) (see **Figure 1** below).

Many avian studies have shown systematic differences in the characteristics of eggs and the chicks hatched from them according to their laying and hatching order within the clutch (reviewed by Slagsvold *et al.* 1984, Reid 1987). However, in general investigations into this phenomenon study modal clutches of three eggs. In common terns the last-laid *c* egg is usually smaller than the preceding *a* and *b* eggs of the clutch (Gemperle & Preston 1955, Dunn 1972, Nisbet & Cohen 1975, Gochfeld 1977, Bollinger *et al.* 1990, Bollinger 1994), with lower yolk reserves (Dunn 1972, Nisbet 1978), and shows a lower survival rate (Langham 1972, Dunn 1972, Quinn & Morris 1986, Bollinger *et al.* 1990). The *a* and *b* eggs tend to be roughly similar in size, and many studies report no differences in mortality rates between the chicks hatched from them (e.g. Lundberg & Väisänen 1979). In fact some studies have found that the *b* egg is larger than the *a*, especially when egg size variation within the clutch is reduced (Pierotti & Belrose 1986, Meathrel *et al.* 1987, Kilpi *et al.* 1996). Bollinger (1994) reports in natural clutches of two in common terns that there is little difference in mass between the *a* and *b* chicks at hatching (on average 1.2 days apart, $n = 29$), and that survival rates are similar for both chicks.

In natural asynchronously hatching broods, although egg mass is a contributory factor, it is the relative (rather than absolute) size of the chick on brood completion, to that of its siblings, that is the decisive factor in survival (Gibbons 1987, Bollinger *et al.* 1990, Bollinger 1994). A later hatching chick will already be at a size disadvantage at hatching. The extent of this difference will depend on the length of the hatching interval during which its older sibling(s) will have gained a head-start in growth often as the sole occupant in the nest. As a result its competitive ability and chances of survival may be substantially reduced (Nisbet 1973, Pierotti & Belrose 1986, Sydeman & Emslie 1992, Bollinger *et al.* 1990, Bollinger 1994). Chick mass at brood completion will diverge in direct relation to hatching order which will reflect the pattern and degree of hatching asynchrony (Morris *et al.* 1991).

In the two chick broods presented here there were no difference in size between the *a* and *b* eggs (egg mass (g), mean ± s.e. (*n*): *a* egg 20.27 ± 0.29 (17); *b* egg 20.00 ± 0.24 (17); t_{32} = 0.70, p = 0.49, n.s.) nor was there a difference in the mass of the chick that hatched from them (hatchling mass (g), mean ± s.e. (*n*): *a* egg chick 14.59 ± 0.28 (17); *b* egg chick 14.29 ± 0.38 (17); t_{32} = 0.63, p = 0.54, n.s.). Furthermore, in 8 of the 17 nests the chicks hatched on the same day, so that there would be little or no size disparity. Since it is the initial size hierarchy at brood completion that usually determines chick survival, it appears that in these broods it is more arbitrary who gets the largest share of the initial feedings and does well in the first critical days (Langham 1972, Dunn 1972, Bollinger *et al.* 1990). Food will be divided among nest-mates according to nestling competition and relative ability to obtain food, giving larger chicks a clear advantage (Malacarne *et al.* 1994, Ostreiher 1997). Thus, once a disparity is established it will tend to be maintained and the gap widened and enhanced, and in some cases the *b* chick will be the stronger.

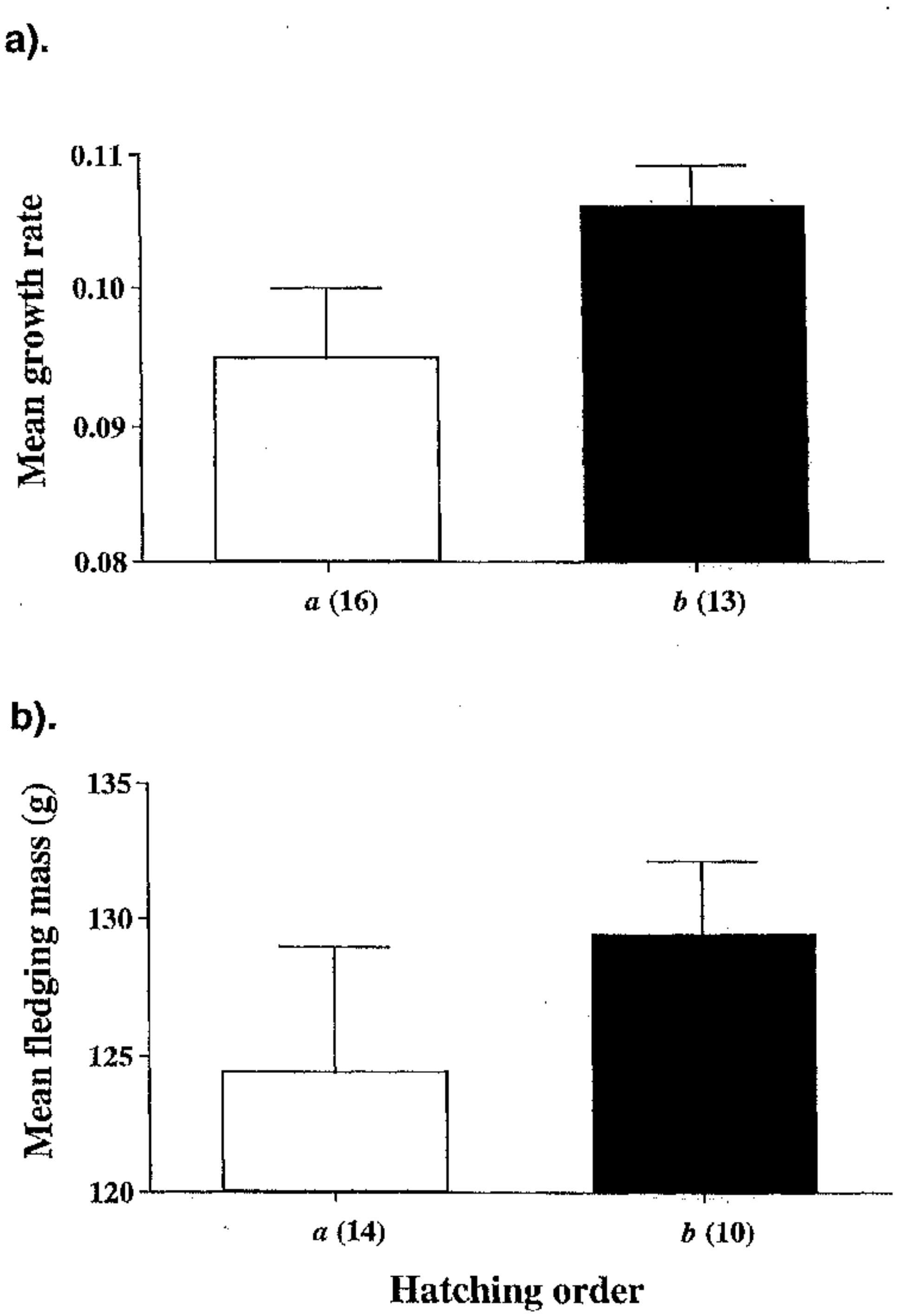

Figure 1. (*a*) Mean (+ s.e.) instantaneous growth rate (expressed as the mean instantaneous growth rate of body mass over the period 2-20d) and (*b*) the mean fledging mass (mass at 20d) of the first (open) and second (shaded) hatched chicks in control clutches of two that hatched both chicks in 1995. The numbers of chicks in each group are given below the histograms. There was a significant difference between the two groups with the *b* chicks growing significantly faster than the *a* chicks (instantaneous growth rate $t_{27} = 2.24$, $p = 0.03$). The same trend was present in the fledging weights but the difference was not significant (fledging mass $t_{22} = 0.84$, $p = 0.41$, n.s.).

APPENDIX 4. Egg composition raw data

The raw data on egg composition of the control *c* and forced *d* eggs collected in 1995 are presented in **Table 1**. The wet weights measured in the laboratory are presented in **Table 2.** These data on the fresh weights of the egg components (shell, albumen, yolk) should be treated with some caution, since the water content of the egg may have change as a result of boiling and freezing (Bolton *et al.* 1992). In fact the fresh weights for the three components do not quite add up to the fresh weight of the egg as measured in the field. The deficit is water lost presumably from the albumen so that a revised albumen fresh weight is also presented in table 2 (albumen wet weight 2).

Table 1. *Data on composition of control* c *and forced* d *eggs, collected on Coquet in 1995 (see chapter 6).*

Egg	Laying date (May)	Fresh weight	Length	Breadth	Shell Thick	Shell dry weight	Albumen dry weight	Yolk dry weight	Yolk lean weight	Yolk fat weight
Control *c*	26.5	19.5	39.8	28.2	0.146	1.06	1.27	1.17	0.39	0.78
Control *c*	26.5	21.0	40.0	30.0	0.152	1.10	1.43	1.33	-	-
Control *c*	26.5	20.0	39.7	29.3	0.144	1.11	1.38	0.68	0.16	0.52
Control *c*	26.5	20.0	40.0	29.2	0.160	1.11	1.51	0.92	0.29	0.63
Control *c*	27.0	19.5	40.8	28.1	0.144	1.02	1.28	1.53	0.56	0.97
Control *c*	28.0	20.0	39.1	28.8	0.158	1.08	1.22	1.42	0.57	0.91
Control *c*	28.0	19.0	39.1	28.9	0.154	1.08	1.45	1.52	0.51	1.01
Control *c*	29.0	19.0	39.6	28.6	0.140	0.95	1.25	1.07	0.31	0.76
Control *c*	29.0	19.0	38.7	28.4	0.142	0.93	1.28	0.93	0.26	0.67
Control *c*	30.0	19.5	37.9	29.3	0.170	1.20	1.57	1.32	0.48	0.84
Forced *d*	27.5	19.5	39.5	28.1	0.140	0.97	1.29	0.88	0.32	0.56
Forced *d*	28.5	17.5	36.9	28.0	0.144	0.91	1.05	1.13	0.35	0.78
Forced *d*	28.5	21.5	40.5	29.8	0.150	1.12	1.78	0.99	0.29	0.70
Forced *d*	28.5	19.5	39.8	28.6	0.120	0.92	1.26	1.04	0.38	0.66
Forced *d*	29.5	20.0	40.4	28.9	0.130	0.99	1.36	1.27	0.41	0.86
Forced *d*	29.5	19.5	40.5	28.7	0.126	0.92	1.35	1.14	0.40	0.74
Forced *d*	29.5	18.5	38.1	28.2	0.144	0.95	1.38	0.93	0.28	0.65

Table 2. *Fresh weight measurements for egg components as measured in the laboratory after boiling and freezing.*

Egg	Laying date	Shell wet weight	Yolk wet weight	Albumen wet weight	Albumen wet weight 2
Control *c*	26.5	1.30	5.50	9.74	12.70
Control *c*	26.5	1.38	6.18	10.62	13.44
Control *c*	26.5	1.42	6.67	10.18	11.91
Control *c*	26.5	1.57	5.82	10.87	12.61
Control *c*	27.0	1.36	6.68	8.73	11.46
Control *c*	28.0	1.36	7.72	8.04	10.92
Control *c*	28.0	1.38	6.86	9.33	10.76
Control *c*	29.0	1.59	6.16	8.80	11.25
Control *c*	29.0	1.19	5.75	10.07	12.06
Control *c*	30.0	1.48	6.44	11.44	11.58
Forced *d*	27.5	1.23	4.97	10.14	13.30
Forced *d*	28.5	1.18	5.57	8.27	10.75
Forced *d*	28.5	1.49	5.69	12.40	14.32
Forced *d*	28.5	1.29	6.50	9.93	11.71
Forced *d*	29.5	1.26	5.69	11.23	13.05
Forced *d*	29.5	1.18	5.87	9.71	12.45
Forced *d*	29.5	1.30	4.93	10.29	12.27

APPENDIX 5. Adult weights

In 1994 seventeen adult birds were trapped on the nest with chicken wire drop traps and various measurements taken, including weight. One bird was captured on two occasions. These data are presented in **Table 1** overleaf. No birds displayed any feather moult.

For birds that formed part of experimental study groups the laying date of the first egg and the current brood size is recorded (brood size reads zero if the bird was still incubating and no eggs had hatched yet). The brood age was recorded as the number of days that had passed since the first chick hatched. The location of the nest is recorded with reference to the plot numbers detailed in chapter 2, figure 4, p.19). The plastic colour ring codes are as follows; *DB* dark blue, *LB* light blue, *DG* dark green, *LG* light green, *Wh* white, *Y* yellow, *St* black and white stripe, *Sta* pink and black stripe, *Bl* black; *M* refers to the positioning of the BTO metal ring. Birds with BTO ring numbers not starting with SX had been ringed previously by another researcher (numbers starting XR by Wylie Horn, pers. comm.).

Seven of the birds were non-study birds for which the laying date is not known. They were all nesting in the area between plots 11 and 4 (see page p.19). For these birds the current brood size was recorded. The brood age column in **Table 1** either reads A if the birds were still incubating a full clutch or B if the clutch had begun to hatch and contained a mixture of eggs and chicks (no non-study nests had hatched fully when the adults were trapped).

Table 1. *Data for common tern adults trapped on the study site in the breeding season of 1994.*

Date	Plot number	Laying date	Treatment	Brood size	Brood age	Weight (g)	Wing (mm)	Head & Bill (mm)	BTO ring number	Coulour rings Right leg	Coulour rings Left leg
01.07.94	2	27.05.94	Control 2	1	12d	122	276	79	SX67505	*Wh/Wh*	*DB/M*
01.07.94	2	28.05.94	Control 2	2	12d	102	267	74	SX67507	*Y/Wh*	*DB/M*
01.07.94	8	27.05.94	Control 2	2	13d	121	281	78	XR49931	*DB/M*	*DB/DB*
17.06.94	8	27.05.94	Free chick	0	-	140	270	75	SX67501	*DB/M*	*LB/LB*
01.07.94	8	27.05.94	Free chick	2	12d	125	274	75	SX67501	*DB/M*	*LB/LB*
01.07.94	8	29.05.94	Free chick	2	10d	113	275	77	SX67504	*LG/LG*	*DB/M*
01.07.94	4	28.05.94	Free chick	2	12d	113	266	80	XR59636	*DB/M*	*St/St*
01.07.94	9	27.05.94	Free egg	1	12d	113	276	75	SX67503	*DG/DG*	*DB/M*
01.07.94	2	31.05.94	Free egg	2	9d	119	270	78	SX67506	*Y/Y*	*DB/M*
01.07.94	2	28.05.94	Free egg	2	10d	121	269	78	SX67508	*DB/M*	*DB/Wh*
17.06.94	8	27.05.94	Full cost	0	-	122	278	80	SX67502	-	-
01.07.94	-	-	Non-study	3	A	136	264	75	SX67509	*DB/LG*	*DB/M*
01.07.94	-	-	Non-study	3	B	121	265	78	SX67510	*DG/LB*	*DB/M*
01.07.94	-	-	Non-study	2	A	119	277	76	SX67511	*DG/Wh*	*DB/M*
01.07.94	-	-	Non-study	2	A	120	276	84	SX67512	*DB/Y*	*DB/M*
01.07.94	-	-	Non-study	3	A	114	265	76	XR72847	*DB/M*	*DB/Y*
01.07.94	-	-	Non-study	3	B	111	263	81	XR89263	*DB/M*	*DB/LG*
01.07.94	-	-	Non-study	3	B	111	251	77	CX20215	*Sta/M*	*Bl*

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