Sex-specific breeding ecology of common terns in N. E. England.

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Bi-parental care is necessary in a wide range of avian species to successfully raise offspring. I investigated a range of topics relating to sex-specific breeding ecology in common terns *Sterna hirundo*, a monogamous seabird with negligible sexual size dimorphism.

Subtle size differences can be utilised to identify the sex of terns, enhanced by within-pair comparisons which increased the accuracy and simplified computational procedures. Under natural conditions, parental contributions were found to be flexible with respect to adult quality and body condition. Males were also found to provision more efficiently and to deliver more energy to offspring than females. Therefore there was no evidence for females investing more than males during a breeding attempt. Parental favouritism with respect to offspring sex was found, although why this should have occurred is uncertain.

Experimentally increased egg production highlighted adult quality as an important factor in determining clutch size. Experimentally increasing male body mass did not result in lower provisioning rates or chick condition, suggesting that this species has a greater buffering capacity than previously thought. Environmental sensitivity of male and female offspring was examined under natural conditions. Mothers produced more female offspring at the end of the laying sequence, and male chicks from these eggs had higher mortality than females. This suggests that gender influences environmental sensitivity, even without sexual size differences.

Declaration

I declare that the material contained in this thesis has not been previously submitted for a degree in this or any other university. All the work recorded in this thesis is entirely my own, unless otherwise stated.

Statement of Copyright

Table of Contents

List of Tables

List of Figures

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Chapter 1: General introduction.

1.1. General introduction

In all bird species with the exception of megapodes (Family Megapodiidae, del Hoyo *et al.* 1994a), parental care is essential to raise young to independence. The majority of species are socially monogamous with both parents providing care. However there may be asymmetry in the amount of care provided by each sex (Lack 1968, Clutton-Brock 1991). In comparison to other mating systems, the roles of the sexes are relatively rarely investigated within monogamous species, with the exception of sexually size dimorphic species (Burger 1981, Pierotti 1981). However even within species with little size dimorphism each sex should seek to minimise its effort whilst still ensuring that the maximum number of offspring survive (Trivers 1972). In addition, factors influencing decisions about the trade-off between current reproduction and future survival and reproduction may differ between the sexes, and may also be influenced by the sex of their offspring. Seabirds include many species with marked sexual size dimorphism, but other species such as terns (family Sternidae) show smaller differences between the sexes.

1.2. Sexual differences in parental care

In seabirds, parental care from both sexes is normally required for acquisition and maintenance of territories, incubation of eggs and chick rearing (Lack 1968). Chicks may also require care long after fledging (Burger 1980). If a species is genetically, as well as socially, monogamous then both parents have the same fitness benefits in raising the young. Extra pair paternity has been found in some seabird species (Graves *et al.* 1992, Huyvaert *et al.* 2000), but it is relatively rare (Gilbert *et al.* 1998, Moreno *et al.* 2000, Gonzalez-Solis *et al.* 2001).

As the male gamete is smaller than the female gamete, early researchers assumed that by the start of incubation, the female had invested more than the male in reproduction (Wilson & Pianka 1963, Trivers 1972, Alexander 1974). However males may take a more prominent role than females in territory defence (Montevecchi & Porter 1980, Burger 1981, 1986) and in the families Laridae and Sternidae, the males also provide food for the female in the form of courtship feeding (Nisbet 1973, Salzer & Larkin 1990, Wendeln 1997, Neuman *et al.* 1998, Gonzalez-Solis *et al.* 2001). This is likely to reduce the sexual difference in reproductive effort during the egg production stage.

In addition to shared costs of territory acquisition and egg production, bi-parental incubation is also a feature of seabirds, with the proportion of incubation undertaken by each sex varying in some species with environmental conditions (Pierotti 1981, Uttley 1992). Recent work has shown that incubation can be costly and that experimentally increased incubation effort can reduce breeding success (Heaney & Monaghan 1996, Thomson *et al.* 1998, Reid *et al.* 2000). It is therefore important to include incubation when considering sexual differences in parental care.

Once the eggs have hatched, chicks are usually brooded until they attain thermal independence. Hence parental care can be in the form of time and effort spent brooding as well as providing food. Sexual differences in foraging location and efficiency have primarily been investigated in sexually size dimorphic species (Croxall *et al.* 1991, Sagar & Weimerskirch 1996, Gonzalez-Solis *et al.* 2000) and are generally attributed to asymmetric competition or to sexual differences in foraging efficiency resulting from differences in body size (Weimerskirch *et al.* 1997, Gonzalez-Solis *et al.* 2000). Few studies, however, have examined whether or not the same differences occur in species with negligible sexual size dimorphism (but see Gray & Hamer 2001, Lewis *et al.* 2002).

When studying sexually dimorphic species, identification of males and females is relatively simple to achieve using external measurements. In monomorphic species, behavioural observations during copulation and courtship feeding are often used, but can be time-consuming. To facilitate identification of the two sexes, more subtle size and shape differences in external measurements can be examined, but this often involves complex computational procedures and requires a sample of individuals of known sex. Statistical procedures may be greatly simplified by comparing individuals within breeding pairs, but the usefulness of this potential refinement has seldom been examined.

1.3. Seabird life-histories

Seabirds are a diverse group of species with a more or less global breeding range (Schreiber & Burger 2001). They have in common the need to forage primarily in the marine environment, beyond the tide line (Furness & Monaghan 1987). Seabirds also share, in comparison to many other birds, extreme life history traits (Ricklefs 1990). Seabirds delay reproduction until at least the second year of life, with some Procellariiformes breeding for the first time at 12 years old (Warham 1990). High adult survival (longevity record currently stands at over 60 years; Warham 1990) is offset by low annual reproductive output: many seabird species produce only a single-egg clutch with slow chick development (Ricklefs 1983). There is a general trend for inshore feeders (such as Sternidae) to have less extreme life history traits than offshore or pelagic species. For example, inshore feeders have larger, faster developing broods and lower adult survival (Lack 1968, Hamer *et al.* 2001). Within seabirds there is also a wide range of foraging trip durations, with marine terns returning to the nest often within minutes, whereas some pelagic species can be away many days on a single foraging trip (Becker *et al.* 1997, Weimerskirch *et al.* 2000). Regardless of the foraging range, the energy gathered during foraging bouts has to be allocated by parents between present reproduction and future reproduction and survival, so as to maximise inclusive fitness (Williams 1966). The reserves stored by the animal are likely to play an important role on these foraging and allocation decisions (Drent & Daan 1980, McNamara & Houston 1996). Long-lived species increase fitness more by spending energy on self-allocation to limit the risk of increasing mortality and therefore not jeopardise future reproduction (Charlesworth 1980). Indeed when adult body condition deteriorates, birds have been found to abandon their breeding attempt (Pugesek 1987, Monaghan *et al.* 1989).

The question of how individuals achieve a balance between current and future reproduction has been examined experimentally by presenting pairs with additional offspring and by handicapping adults. Studies experimentally increasing the brood size of seabirds have found that, in many cases, adults have little problem increasing effort to successfully rear an additional chick (for review see Ydenberg & Bertram 1989). However, the addition of a chick does not mimic all the costs of an increased number of offspring, because it omits egg production and incubation (Heaney & Monaghan 1995, 1996, Monaghan *et al.* 1998, Reid *et al.* 2000). An alternative approach is to induce birds to lay additional eggs, by experimental removal of all or part of the clutch (e.g. Nager *et al.* 2001). However, it is not known what determines how many additional eggs are laid in such circumstances and the long-term costs of extra egg production have also seldom been examined (but see Nager *et al.* 2001). More recent attempts at increasing costs for adults have directly increased the work load required by adults to forage successfully (Moreno *et al.* 1999). However for seabirds at least, no consensus has yet emerged from these studies (Table 6.1). Although the experimental approach has been strongly advocated (Partridge & Harvey 1988, Partridge 1989), experimental manipulations of reproductive effort can be confounded by variation in adult quality: for instance in studies of egg production adults of higher quality may be both more likely to lay additional eggs and less affected by increased costs than lower quality individuals (McNamara & Houston 1996), although this has rarely been investigated in field studies.

In addition to the number of offspring produced, female birds also have some physiological control over the sexes of their offspring. Sex allocation theory predicts that parents will bias their brood sex ratio when they can enhance their fitness by preferentially producing, or allocating resources to, one sex (Trivers & Willard 1973, Charnov 1982). Following recent developments in DNA-based techniques (Griffiths *et al.* 1998, Fridolfsson & Ellegren 1999), evidence has recently emerged that female birds, the heterogametic sex, can adaptively adjust sex ratios prior to laying in relation to a number of different factors, including territory quality (Komdeur *et al.* 1997), mate quality (Ellegren *et al.* 1996, Sheldon *et al.* 1999), food availability (Dijkstra *et al.* 1990, Torres & Drummond 1999, Velando *et al.* 2002, but see Radford & Blakey 2000) and female body condition (Nager *et al.* 1999, Hornfeldt *et al.* 2000, Kalmbach *et al.* 2001, Velando *et al.* 2002). However offspring sex ratios have primarily been examined in sexually size dimorphic species (Nager *et al.* 1999, Torres & Drummond 1999, Kalmbach *et al.* 2001, Velando *et al.* 2002). In these species, inherent sex effects are masked or amplified by differences in body size, so it is important to study species without sexual size differences, in order to examine the effects of gender *per se*.

1.4. Study species

The common tern *Sterna hirundo* is a member of the family Sternidae, which is sometimes included within the closely related family Laridae. There are 44 species of tern, of which one third belong to the genus *Sterna* (del Hoyo *et al.* 1994b). Common terns breed in northern temperate zones of Europe, North America and Asia (Nisbet 2002). The European distribution has a northerly bias, with birds breeding irregularly as far south as North Africa, but only regularly north of the Mediterranean and as far north as the north coast of Finland (Cramp 1985). Common terns are one of the few tern species that breeds on both fresh and salt waters, often in large colonies on inshore islands, beaches and marshes (Nisbet 2002). The common tern is also migratory, travelling from northern European colonies to winter offshore in sub-equatorial Africa (Cramp 1985).

Common terns are one of the smaller seabirds, with an average body mass of 130g (Cramp 1985). They are generalist feeders, foraging by plunge-diving, surface dipping and occasionally hawking for insects in the air (Nisbet 2002). They can forage in mixed species feeding flocks or individually (Becker *et al.* 1993, Frick & Becker 1995).

Within Britain, adults return to their breeding sites at the end of April, with the first egg laid mid-May, first chicks in early June and they leave, often in family groups, in late July (Cramps 1985, pers. obs.). Most birds return as first time breeders at age three or four and occasionally when two years old (Cramp 1985). The nests are shallow depressions, sometimes with a lining made up of nearby debris and vegetation (Burger & Lesser 1978, Robinson *et al.* 2001a). The modal clutch size is three eggs, although clutches of two eggs are also laid, and very occasionally one or four eggs (Cramp 1985). Incubation lasts 20 to 23 days (Harrison & Castell 1998) and eggs hatch asynchronously. The fledging period is 21 to 26 days (Pearson 1968). During this period the young show semi-precocial development, in that they are mobile but are totally dependent on their parents for food (Langham 1983). Parents generally deliver single fish (rarely up to five small fish) to their offspring, carrying the fish sideways in the bill (Nisbet 2002). Each year pairs only rear a single brood, but may lay replacement clutches if eggs or chicks are lost early in the season (Nisbet 2002).

As with other seabirds, common terns normally have high annual adult survival (e.g. 89-91%; Nisbet 2002), with the oldest breeding individual currently recorded being 26 years old (Nisbet & Cam 2002). They are generally considered to be socially monogamous with pair bonds persisting between breeding seasons (Cramp 1985). However divorce rates have been found to reach almost 20%, due to asynchronous arrival of partners at the colony (Gonzalez-Solis *et al.* 1999). In addition to high mate fidelity, common terns are also known to have strong site fidelity (Cramp 1985, Gonzalez-Solis *et al.* 1999).

1.5. Aims

The aim of this thesis is to investigate a range of topics related to sex-specific parental care in a species with virtually no sexual size dimorphism. Chapter 2 describes general methods used in two or more of the following chapters. Chapter 3 examines the potential of using within-pair comparisons to determine sexes of common terns and closely related Arctic terns *Sterna paradisaea* from biometrics. Chapter 4 describes sexual differences in provisioning behaviour and which chick is fed by which parent (parental favouritism).

Chapter 5 investigates which proximate factors determine a females' annual egg production capacity. In addition, I assess the impact of additional egg production on both the current and subsequent breeding events. Having manipulated female reproductive effort, the impact of increasing the males' effort by increasing body mass during chick rearing is then examined in chapter 6.

Chapter 7 investigates the sex ratio of embryos produced and sexual differences in chick growth and survival. In particular the focus was directed to asking whether or not males have lower survival than females even in a species with negligible sexual size dimorphism. Chapter 8 provides a general discussion of the results from earlier chapters in the context of sexual differences in breeding ecology in species with negligible sexual size dimorphism.

Chapter 2: Methods and materials.

2.1. Study site

Fieldwork was undertaken on Coquet Island (55°20′N, 1°32′W). The island is small and low-lying, approximately 1km off the coast of Northumberland, N.E. England (Figure 2.1). The land above high water is no more than 10m above sea level and covers an area of approximately 400m by 200m.

The island has been declared a Special Protection Area under EC Directive 79/409. Although owned by the Duke of Northumberland the island has been managed by the Royal Society for the Protection of Birds (RSPB) since 1970.

In addition to the tern species (common tern *Sterna hirundo*, Arctic tern *S. paradisaea*, Sandwich tern *S. sandvicensis* and roseate tern *S. douglaii*), another seven seabird species breed on the island (black-headed gull *Larus ridibundus*, herring gull *Larus argentatus*, lesser black-backed gull *Larus fuscus*, eider *Somateria mollisima*, puffin *Fractercula artica*, fulmar *Fulmaris glacialis* and kittiwake *Rissa tridactyla*). Other regular breeders include shelduck *Tadorna tadorna*, oystercatcher *Haematopus ostralegus*, rock pipit *Anthus spinoletta*, starling *Sturnus vulgaris*, feral pigeon *Columba livia* (domest.) and jackdaw *Corvus monedula*.

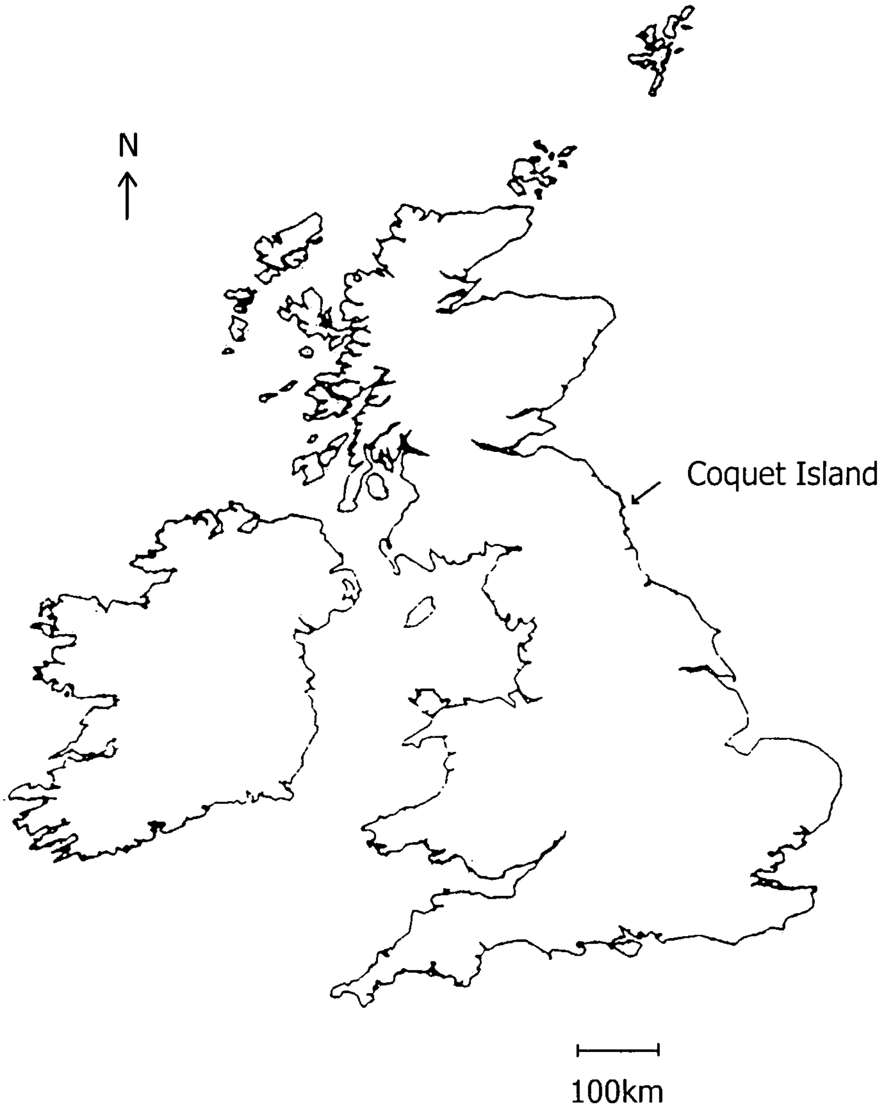

Figure 2.1: Map of the British Isles showing the location of Coquet Island.

The island has a lighthouse, which has been automated since 1989, requiring few maintenance visits from Trinity House staff. During the breeding season only RSPB staff, approved researchers and Trinity House personnel have permission to land, so the seabirds encounter relatively little human disturbance. In addition to breeding birds, the island has fewer than 100 rabbits *Oryctolagus cunniculus* (the only terrestrial mammal). These occasionally kill young tern chicks (Robinson & Hamer 1998, pers. obs. in 1999) but the overall risk of predation of chicks is low due to the absence of other vertebrate predators. Herring and lesser black-backed gulls are present in small numbers but rarely prey on the tern colony, possibly due to the large colony of black-headed gulls that nest between the terns and the larger gulls. Birds of prey have occasionally been observed on the island, but have minimal impact during the height of the breeding season. Coquet Island therefore provides a breeding site with low levels of disturbance and predation for terns.

The area immediately surrounding the lighthouse buildings (Figure 2.2) is managed to provide short grassy areas (mainly *Holcus lanatus*), surrounded by strips of taller vegetation dominated by *Urtica dioica, U. urens, Sonus sp.* and *Lycopsis arvensis*. This is achieved by a combination of strimming and herbicide applications (more details can be found in Coquet Island annual reports, RSPB). Common, Sandwich and roseate terns and black-headed gulls make use of these plots. Arctic terns breed primarily in the grass areas within the walls of the lighthouse compound (helipad and garden in Figure 2.2) and have some peripheral colonies on

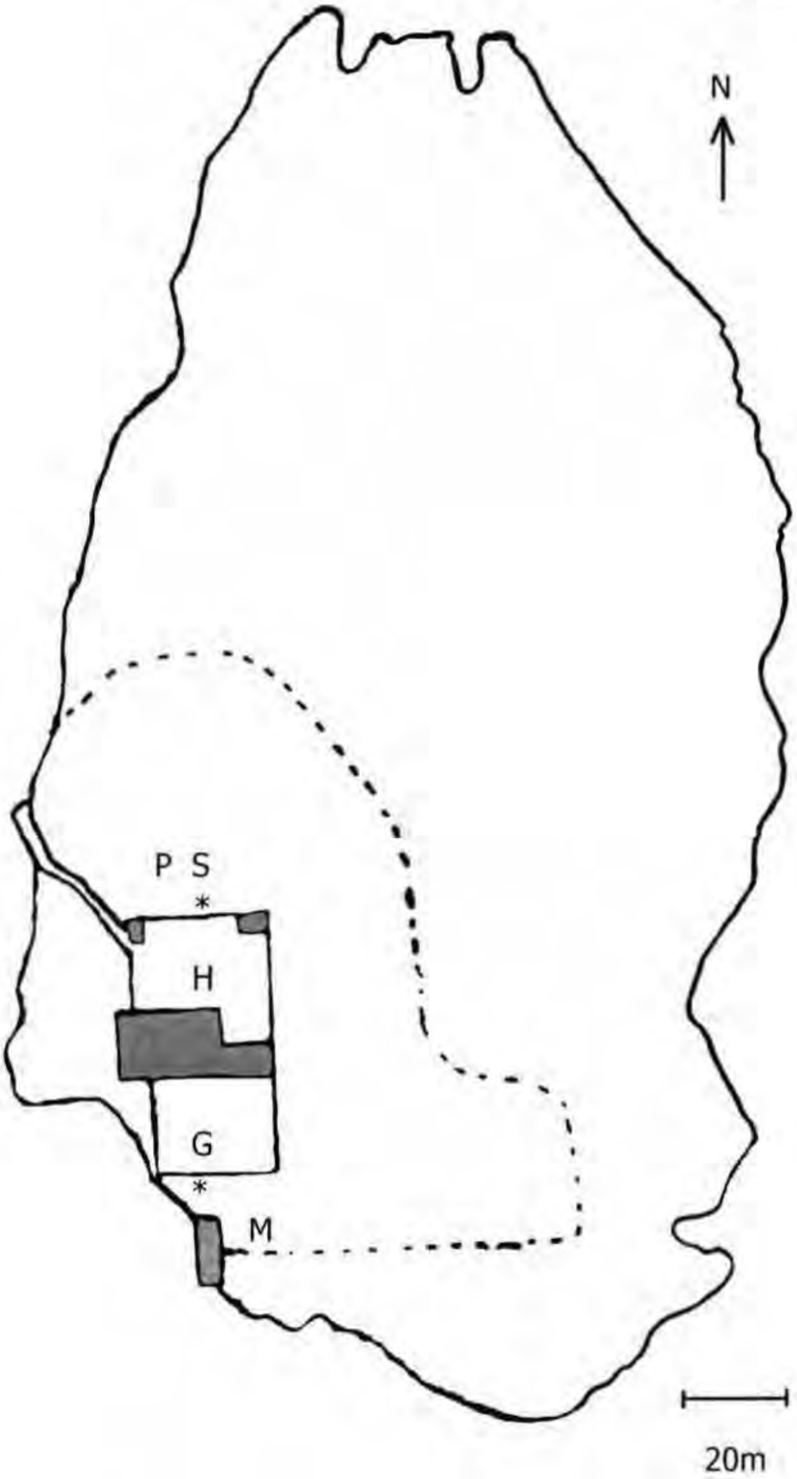

Figure 2.2: Outline of the island above the high water mark, with the buildings shaded and the area managed for terns enclosed within the broken line. The letters denote the study areas used (common tern plots: P = plot 10, S = shed, M = magazine; Arctic tern plots: H = helipad, G = garden). * marks the locations of common tern observation hides.

the pebble beaches along the east side of the island. The number of breeding pairs and the productivity of common terns fluctuates between years, although since 1997 the peak timing of breeding has changed little (Table 2.1).

Table 2.1: Breeding statistics for common terns at Coquet Island from 1996 – 2001 (data collated from RSPB annual reports).

	1996	1997	1998	1999	2000	2001
Nest count	611	806	805	1049	1033	977
First egg date	26/5	17/5	17/5	14/5	12/5	12/5
Modal lay date	31/5	21/5	26/5	23/5	21/5	23/5
First chick date	17/6	6/6	7/6	8/6	3/6	8/6
Mean clutch size	2.0	2.5	2.0	2.3	2.5	2.5
Productivity (chicks/nest)	1.6	0.9	0.3	1.1	2.2	1.8

2.2. Study plots

The study plots were chosen with the aim of finding a representative sample of nests. The edge of the common tern breeding area was therefore avoided (Coulson 1968). For common terns, three study plots were used as indicated on Figure 2.2. Plot 10 was used to increase the sample of nests for chapter 7, whereas the shed and magazine plots were used in all years. There were no differences in nest density, mean clutch size or laying date between the plots in any year, so data were combined.

The Arctic terns used in chapter 3 were nesting in the helipad (Figure 2.2).

The nettle beds surrounding the grassy areas defined the boundaries of the study plots. The plots were checked daily from 10 May to determine accurate laying dates. The laying date for individual nests always refers to the first laid egg and for simplicity refers to the number of days after the first egg of the season in the colony. The modal laying date was determined by combining all nests from the shed and magazine plots. For studies requiring incubation, brooding and food provisioning data, the nests were chosen at random, providing they were within line of sight of the hides. In addition these nests were within seven days either side of the modal laying date to avoid the extremes of adult quality (Burger *et al.* 1996)

2.3. Nest identification and egg monitoring

When a new nest was found a nest marker was put in the ground approximately 30cm behind the nest. Each marker consisted of a 60cm long bamboo cane with a piece of cardboard attached to one end, covered in masking tape. A two-digit number or a number and letter were painted on the masking tape and markers were angled so that the number could be seen from the observation hides.

Each egg was marked with the nest number using non-toxic waterproof marker pens, with different colours denoting laying position.

Egg volume was calculated from (length * breadth^2 * 0.502) / 1000 (cm^3 Moore *et al.* 2000), where length and breadth were measured to the nearest 0.1mm using Vernier callipers on the day of laying. All measurements were taken by a single person to ensure no inter-observer variation.

Nests chosen for the study of parental care during chick rearing had a wire enclosure erected around the nest prior to hatching (Pearson 1968, Langham 1972, Nisbet & Drury 1972). The $1^1/_2$ inch mesh enclosure was approximately 30cm high and had a diameter of 1m if around a single nest, or larger if nests were adjacent. Within the enclosure the grass was kept short so that the chick being fed could be identified. Long grass usually provides protection for the chicks, so a shelter was provided for each brood (Burness & Morris 1992).

2.4. Chick size and growth

All marked nests were checked daily to determine an accurate hatch date. At hatching all chicks were ringed with BTO metal rings and those within enclosures were dyed in relation to hatch order with a waterproof dye (Marksman®, Net-Tex Agricultural Ltd, Kent). The dye was sprayed on the white breast and had no discernible detrimental effects. The dye was reapplied as the down was shed and new feathers grew.

All chicks within enclosures were measured within three days of hatching. Body mass was measured to the nearest 1g with a Pesola balance, head plus bill length to the nearest 0.1mm with Vernier callipers and wing length (maximum flattened chord including down) to the nearest 1mm using a stopped ruler (further details in Redfern & Clark 2001). Following recommendations in Barrett *et al.* (1989), all chick measurements were made by the author to reduce sampling error. To correct for the age of measuring (1 - 3 days), the standardised residuals of the linear regression of body mass, head plus bill or wing length against age were calculated.

In addition to size at hatching, chicks within enclosures were measured, at a consistent time of day, twice in consecutive four day periods until fledging (nine four day periods in 1999 and 2001, eight four day periods in 2000). From these data instantaneous growth rates (R) were calculated using equation 1 (following Heaney & Monaghan 1995).

$$R = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \qquad \text{equation 1.}$$

where W = body mass (g) or head plus bill (mm) or wing (mm), t = age (days). Growth rates were calculated during the linear growth phase (5 – 14 days inclusive; Coulson & Horobin 1976, Robinson 1999) and a mean rate calculated for each chick.

Chicks practised flying more often in windy conditions (pers. obs.), so the age chicks were first seen flying was not a good indicator of fledging age. Instead, when asymptotic body mass was reached, head plus bill length and wing length were recorded as the fledging size and this was also noted as the age of fledging. Fledging condition was taken to be the asymptotic body mass corrected for age (approximately 20 days). All enclosed nests were checked daily to obtain precise ages of death for chicks that did not fledge. When the chicks were first seen flying or found outside their enclosure, the enclosures were removed and chick measuring ended. All nests outside enclosures were also checked daily to record the death of any ringed chicks.

2.5. Identifying individual adults

Incubating adults were caught at the nest using walk-in traps. This became easier as hatching approached, but attempts were stopped once hatching was underway because adults may be more likely to desert at this time (Nisbet 1981). To avoid excessive disturbance catching was undertaken for no more than two hours before moving to a different plot. No eggs were broken during trapping and only one pair deserted out of 352 catches.

Size measurements were recorded for each adult as detailed in chapter 3. Throughout the rest of the thesis, body mass is used as an index of body condition during the breeding attempt (following Monaghan *et al.* 1989, Wendeln 1997 and because body mass was not significantly correlated with body size measurements, laying date, time of capture, or the number of days between capture and egg laying).

Every bird caught was individually colour-ringed with 4mm high darvic rings (seven colours). Each bird was fitted with two colour rings on one leg and a metal BTO ring and a colour ring on the other leg. Colour-rings allowed identification of birds in subsequent breeding seasons, but were difficult to see later in the season when the grass was taller. Hence, to facilitate identifying which of the two adults was returning to the nest during observations, the birds were also marked with picric dye. The first caught bird was marked on the back and the second on the breast. Birds undergo post-breeding body moult (Baker 1993) when the dye will be lost. The picric also enabled un-marked individuals to be targeted more efficiently.

The adults were sexed primarily from observations of multiple mate provisioning and copulation behaviour. Males pass fish to females during courtship (Uttley 1992, I.C.T. Nisbet pers. comm.) and males are always on top of females during copulation (P.H. Becker pers. comm.). As the adults were not marked until incubation most birds were sexed in the following year. In the final season (2001) blood was taken from the wing vein in the same way as taken from the chicks (section 2.6). Blood from a sample of birds of known sex was also taken to verify the DNA-based technique (section 2.6).

The Arctic terns used in chapter 3 were caught and measured in the same way as the common terns. Arctic terns were also fitted with individual colour ring combinations. Their smaller legs allowed only one ring per leg, however two-colour celluloid rings (A.C. Hughes, Middlesex) were used to increase the number of possible combinations. As with common terns the colour rings facilitated sexing from behaviour in the following years.

2.6. Sexing using DNA

The sex of embryos', and therefore chicks, produced is utilised in chapters 4, 5 and 7. To avoid repetition the full details of the methods are recorded below.

If the egg did not hatch by five days after the maximum known incubation period (23 days; Harrison & Castell 1998), these were opened and if an embryo could be detected (68% of opened eggs), a small amount of tissue was removed. If the chick died during hatching then tissue from the brain was taken. All tissue was stored in identical conditions as the blood (see below).

For chicks, blood was taken from the leg vein on the day of hatching (or soon after if conditions were cold or wet), with no discernible ill effects. The leg vein was punctured just below the knee with a sterile needle (19GA) and the blood was taken from the surface using a 50μl capillary tube. Approximately 30μl of blood was collected. The blood was then blown from the capillary tube into a 2ml Eppendorf tube that already contained 1.5ml of 100% ethanol. The Eppendorfs were labelled and stored at room temperate, away from direct sunlight, prior to analysis at the Sheffield Molecular Genetics Facility. Blood from the adults, taken from the wing vein in 2001 was stored in the same way.

DNA was extracted using an ammonium acetate salt extraction procedure (as detailed in Richardson *et al.* 2001) and individuals were PCR sex-typed using the 2550F and 2718R sexing primers (Fridolfsson & Ellegren 1999). PCR amplification was performed in a Hybaid Touchdown thermal cycler following the thermal profile of Fridolfsson & Ellegren (1999) in 2mM $MgCl_2$ solution. The solution also included 1µl Buffer IV, 1µl dNTP's, 0.05µl *Taq* DNA polymerase (Thermoprime^{Plus}, Advanced Biotechnologies) and 1µl of each of the primers per sample. The PCR products were scored on standard 2% agarose gel (SeaKemLE agarose) visualised with ethidium bromide staining. In both common and Arctic terns, the presence of two products indicated a female and a single product indicated a male.

To check sex allocations, we also took blood samples, from 23 adult common terns (11 females and 12 males) and 12 adult Arctic terns (six of each sex) that had been sexed from behavioural observations. The sexes assigned using primers agreed with those assigned from behavioural data for all 35 birds.

2.7. Parental care

2.7.1. Incubation

During incubation in 2000 (chapter 5) and 2001 (chapter 4 and 6) nests were observed, from the hides, over at least eight hours to determine how much of the time each sex incubated. Every fifteen minutes each adult was identified to ensure that no change-overs had been missed. In 2000 the length of incubation, in days, was also determined.

2.7.2. Brooding

Watches, randomised during daylight hours, were undertaken to record the proportion of time spent brooding by each adult in 2000 (chapter 5) and 2001 (chapter 4 and 6). This was a measure of how much time was spent brooding and not how much time was spent on the territory.

2.7.3. Provisioning

In 1999 observations of food delivered to the chicks were undertaken from dawn to dusk (approximately 04:00 to 22:00) by two observers so that every nest was watched for a full day once within consecutive four day periods. In 2000 and 2001, when only the author undertook observations, they were in two hour blocks, ensuring no bias with respect to time of day, over a four day period. During a four day period each nest was watched for an average of eight hours (range seven to 10 hours). The four day periods continued until the majority of the chicks were flying (nine periods in 1999 and 2001, eight periods in 2000).

During observations all arrivals and departures were recorded. Occasionally an adult arrived without a fish and these arrivals were not used to calculate trip duration. Also fish species was recorded as clupeid (herring *Clupea harengus* or sprat *Sprattus sprattus*), sandeel (*Ammodytes tobianus* or *Hyperoplus lanceolatus*), other (saithe *Pollachius virens*,

2.8. Statistical methods

When data were normally distributed the mean (s.d.) were calculated, however when data were not normally distributed median (inter-quartile range) were quoted.

In all chapters with provisioning data, the number of fish delivered per hour and energy delivered per hour was averaged for each chick age period, square root transformed and the factor under investigation compared by fitting linear mixed models. The models used were repeated measures residual maximum likelihood models (repeated measures REML; Patterson & Thompson 1971) using GenStat® (5th Edition). Chick age was divided into three periods: 1-7 days, 8-15 days and 16-23 days or six periods of four days each depending on available sample sizes. Trip duration was not averaged but all the data were used in repeated measures REML, with the corresponding chick age codes. Analysing the data with REML's enabled the inclusion of nest identity as a random factor to control for individual effects, thereby accounting for the problem of pseudoreplication. In all REML's the significance of each variable or interaction was determined by comparing Wald statistics with percentiles of chi-squared or F-distributions (Elston *et al.* 2001). Other statistics used are detailed within each chapter.

Chapter 3: Sexing terns using biometrics.

Data from this chapter is in press as Fletcher, K. L. & Hamer, K. C. Sexing terns using biometrics: the advantage of within-pair comparisons. *Bird Study*

3.1. Abstract

In species with monomorphic plumage and soft-tissue colouration, sexing birds using biometrics is often the simplest and most cost-effective method available. However the effectiveness of statistical methods for sexing birds using biometrics can be limited if males and females overlap in size or if birds mate assortatively with respect to body size. We examined the extent to which these problems could be overcome by sexing common and Arctic terns using measurements obtained for both members of breeding pairs. Within-pair comparisons, when compared to individual-based analysis, improved the accuracy of sexing from 73% to 86% in common terns and from 72% to 84% in Arctic terns. Comparing birds within pairs can also eliminate the need to calculate cut points or discriminant functions from a sample of birds of known sex for each particular study. In most studies there exists a trade-off between obtaining a large sample size, which is best achieved using individual-based analysis, and obtaining a high level of accuracy, which is best achieved using within-pair comparisons. However I strongly advocate the use of within-pair comparisons wherever possible, as a means of increasing accuracy and of simplifying computational procedures for predicting sex and so reducing associated sources of error. This is particularly important in species such as terns, where differences between the sexes are subtle and involve only a single body component rather than overall body size.

3.2. Introduction

Sexing of individuals can greatly enhance the interpretation of behavioural and ecological data, but sexing birds with monomorphic plumage and soft-tissue colouration presents a serious problem, especially if differences between the sexes in body size are small. During the breeding season, sexing can be achieved in some cases by using observations of copulation and courtship behaviour (Catry *et al.* 1999) or by cloacal examination (Boersma & Davies 1987, Gray & Hamer 2001) or brood patch (Cowley 1999). However these methods are restricted to narrow time periods and the birds may need to be caught during early incubation, when trapping is more likely to lead to nest desertion. More recently, DNA-based techniques have also been used to determine sex in a variety of species (e.g. Ellegren & Sheldon 1997, Jodice *et al.* 2000), but these require taking of blood samples and access to appropriate laboratory facilities.

An alternative approach is to sex birds using externally measured biometrics: either single measurements (e.g. Coulson *et al.* 1983) or discriminant multivariate analysis (e.g. van Franeker & ter Braak 1993). In many cases this is likely to be the simplest and most cost-effective method available. However its usefulness depends heavily on the accuracy and repeatability of body measurements (Hamer & Furness 1991). Moreover the power of the technique decreases markedly with decreasing differences in means between sexes and with increasing variability within each sex (Weidinger & van Franeker 1998). Analyses can also be confounded if individuals mate assortatively by size i.e. large males mate with large females and small males mate with small females (Burley 1983, Coulter 1986). For instance in species where the sexes overlap in size, but males are on average larger than females, assortative mating would lead to an increased likelihood of males in small pairs being sexed as females and females in large pairs being sexed as males.

These problems may be greatly reduced by using within-pair comparison of relative size to sex individuals. Such within-pair comparisons resulted in improved sex determination in south polar skuas *Catharacta maccormicki* (Ainley *et al.* 1985) and cape petrels *Daption capense* (Weidinger & van Franeker 1998). However the usefulness of this technique, as compared to individual-based analysis, has not been widely evaluated.

Common terns *Sterna hirundo* and Arctic terns *S. paradisaea* are small ground-nesting seabirds with monomorphic plumage and soft-tissue colouration. Males of both species are slightly larger on average than females, at least in terms of bill measurements (Coulter 1986, Craik 1999), but there is considerable overlap in body size between sexes. Here we describe the sexual size dimorphism and variability in a variety of external measurements of both species, and assess their usefulness in determining the sexes of birds at two scales; individual level and within pairs. As part of this process, we examined whether or not there was assortative mating with respect to body size.

3.3 Methods

Data were collected during summer 1999 and 2000 for common and Arctic terns breeding on Coquet Island. As detailed in chapter 2, adults were caught, marked and sexed using behavioural observations during the following breeding season. For every bird caught the following measurements were recorded:

- body mass to the nearest 1g using a Pesola balance
- wing (maximum flattened chord) to the nearest 1mm using a stopped ruler (400mm long)
- tail length (from the base to the tip of the longest (outermost) feather to the nearest 1mm using a reversed stopped ruler
- tail fork (difference in length between central and outermost feathers to the nearest 1mm using a reversed stopped ruler
- tarsus to the nearest 0.1mm using Vernier callipers
- head plus bill (head-bill) length to the nearest 0.1mm using Vernier callipers

If the outermost tail feather was abraded (5% of individuals) then no tail or tail fork was recorded. The author measured all birds, in keeping with the procedure recommended by Barrett *et al.* (1989), and within-observer variability was investigated by repeating (during a single capture event) each biometric in a sample of 92 birds for body mass and 51 birds for all other measurements. Coefficients of repeatability (COR) were then calculated following equation 4, where higher COR values indicate higher repeatability.

$$\mathrm{COR} = \frac{1}{\{[(\Sigma|x_i - y_i|)/\mathrm{n}]/[(\bar{x} + \bar{y})/2]\} * 100} \qquad \text{equation 4.}$$

where x_i and y_i are the values of the n pairs of measurements made and $\bar{x}$ and $\bar{y}$ are the means of the x_i and y_i values respectively (adapted from Summers *et al.* 1988). The maximum and mean differences between repeated measurements were also determined.

Thirteen common terns and 18 Arctic terns were caught in consecutive years enabling between-year variability of each measurement to be assessed using paired *t*-tests and COR values. In view of the number of paired *t*-tests performed, probabilities were corrected using the sequential Bonferroni technique (Rice 1989).

To determine the accuracy of individual biometrics in sexing adults, a cut point was calculated and, following Weidinger & van Franeker (1998), birds with measurements $\geq$ the cut point were classified as males. The cut point was the point mid-way between the mean value for females and the mean value for males. This technique was then compared to within-pair comparisons, where the larger bird in each pair was classified as male. Females were on average heavier than males in both species, and so birds with body masses $\geq$ the cut point were classified as females and for within pair comparisons, the lighter bird was classified as male.

For all measurements, coefficients of variation ([standard deviation / mean] *100) were calculated for each sex and averaged within a species to indicate the degree of variability. Sexual size dimorphism (SSD) values were also calculated for each biometric using equation 5 (after Weidinger & van Franeker 1998).

$$\text{SSD \%} = [(\text{male mean} / \text{female mean}) - 1] * 100 \qquad \text{equation 5.}$$

Biometrics were then combined in a stepwise discriminant analysis for each species (for details of method see Norusis 2000) using mean values for birds caught in both years. The proportion of birds correctly sexed when considering individuals was compared with the accuracy achieved if within a pair, where the bird with the higher discriminant score was classified as male.

3.4. Results

3.4.1. Repeatability: within-observer and between-year variation

Within observer differences were very small (<1% on average) for all biometrics (Table 3.1). Tail fork length was the least repeatable measurement and also differed significantly between years for individuals of both species (Table 3.2). Body mass of an individual also differed between years in Arctic terns (Table 3.2).

3.4.2. Sexing using biometrics

Males were larger than females in all variables except body mass (Table 3.3). In both species, head plus bill length and wing length had the lowest within-sex variation whilst tail fork length had the highest (Table

Table 3.1: Within-observer variation in body measurements. All measurements are in mm, except body mass in g.

Biometric	n	difference between repeated measurements max.	mean	s.d.	COR
Tail fork	51	4	0.51	0.98	0.8
Tarsus	51	1.4	0.18	0.55	1.2
Head-bill	51	2.2	0.48	0.49	1.6
Tail	51	4	0.98	0.71	2.2
Wing	51	2	0.33	0.79	8.3
Body mass	92	3	0.10	0.76	10.0

Table 3.2: Between-year variation in body measurements, with coefficients of repeatability (COR). All measurements are in mm, except body mass in g.

	mean (s.d.) 1999	2000	*t*	d.f.	*p*	COR
Common tern						
Body mass	125 (9.5)	125 (6.5)	0.11	12	0.9	5.4
Wing	272 (4.1)	270 (5.2)	1.93	12	0.08	1.8
Tarsus	20.8 (1.10)	21.2 (1.16)	-1.55	12	0.1	0.5
Head-bill	78.2 (2.61)	78.3 (2.98)	-0.25	12	0.8	11.3
Tail	154 (7.0)	154 (7.3)	0.16	12	0.9	10.0
Tail fork	78 (7.1)	82 (6.9)	-4.56	12	0.001**	0.3
Arctic tern						
Body mass	104 (5.5)	111 (6.4)	-6.22	17	<0.001**	0.2
Wing	272 (7.3)	272 (7.4)	-0.14	17	0.9	24.5
Tarsus	16.7 (0.94)	17.2 (0.76)	-2.41	17	0.03	0.3
Head-bill	71.2 (2.26)	70.9 (3.14)	0.44	17	0.7	3.1
Tail	181 (13.1)	176 (13.3)	2.31	15	0.04	0.5
Tail fork	107 (13.4)	101 (13.2)	3.03	15	0.008*	0.2

After Bonferroni corrections, *p* values with * are significant at the 5% and ** at 1% level.

Table 3.3: Body measurements of male and female birds plus coefficients of variation (CV), sexual size dimorphism (SSD) and accuracy levels (see methods). Based on 124 birds (62 pairs) for common terns and 74 birds (37 pairs) for Arctic terns.

	mean (s.d.)		CV	SSD	accuracy (%)	
	male	female	(%)	(%)	individuals	pairs
Common tern						
Body mass	124 (7.7)	128 (7.7)	5.6	3.7	60.5	67.8
Wing	273 (5.6)	270 (5.5)	2.1	0.9	61.3	53.2
Tarsus	21.4 (1.11)	21.2 (1.08)	5.0	1.2	56.5	61.3
Head-bill	79.6 (1.81)	77.0 (2.18)	2.5	3.4	72.6	85.5
Tail	156 (7.9)	152 (8.2)	6.2	2.7	60.7	66.6
Tail fork	81 (7.1)	78 (7.9)	9.3	2.8	53.3	60.0
Arctic tern						
Body mass	105 (7.2)	106 (6.9)	6.4	1.5	59.5	45.9
Wing	274 (5.9)	270 (6.4)	2.2	1.4	59.5	67.6
Tarsus	16.8 (1.06)	16.6 (1.12)	6.3	0.07	48.6	51.4
Head-bill	72.7 (1.68)	70.2 (2.51)	2.9	3.4	71.6	78.4
Tail	185 (9.1)	177 (11.4)	5.7	4.0	60.6	58.1
Tail fork	111 (8.5)	104 (11.3)	9.4	7.3	64.8	80.6

3.3). For common terns, head plus bill length also had high sexual size dimorphism, and this was the best single variable for sexing birds (73% sexed correctly; Table 3.3). For Arctic terns, the two tail measurements had greater sexual size dimorphism than head plus bill length but the latter was the best single variable for sexing birds (72% sexed correctly; Table 3.3). Removing those individuals that were <1mm away from the cut point for head plus bill length, increased the number of birds classified correctly by 6% in each species (from 72.6% to 79.3% in common terns, from 71.6% to 77.5% in Arctic terns), but the number of individuals sexed was reduced to 92 birds (74% of the sample) and 49 birds (66% of the sample) in common and Arctic terns respectively.

To determine whether or not greater accuracy could be gained by using several variables simultaneously, all variables were combined in a stepwise discriminant analysis for each species (birds with abraded tails were excluded: 2 female common terns, 2 male and 1 female Arctic terns). For common terns head plus bill in conjunction with body mass sexed 95 out of 122 individuals (77.8%) correctly according to their scores on the following discriminant function, where $D > 0$ were classified as males:

$$D = 0.48 * \text{head plus bill length (mm)} - 0.07 * \text{body mass (g)} - 28.2$$

For Arctic terns, the analysis was able to correctly classify 52 of 71 individuals (73.2%) according to their scores on the following discriminant function, where $D > 0$ were classified as males:

$$D = 0.41 * \text{head plus bill length (mm)} + 0.05 * \text{tail fork length (mm)} - 35.2$$

Both head plus bill length and tail fork length contributed significantly to this function ($p < 0.05$ for significance of improvement of model) but the accuracy achieved using both variables was only slightly greater than that achieved using head plus bill length alone (71.6%; Table 3.3).

3.4.3. Within-pair comparisons

For common terns, all variables except wing length had higher success in sexing birds within pairs (60% - 86% correct) than in the sample as a whole (53% - 73% correct; Table 3.3). The degree of improvement gained by sexing birds within pairs was highly correlated with the degree of sexual size dimorphism in each variable ($r_S = 0.94$, $n = 6$, $p < 0.01$) and head plus bill length was the most accurate single biometric for sexing within pairs. In Arctic terns, all variables except body mass and tail length had higher success in sexing birds within pairs (51% - 81% correct) than in the sample as a whole (49% - 72% correct; Table 3.3). There was no correlation between the degree of improvement gained by sexing birds within pairs and the degree of sexual size dimorphism in each variable ($r_S = 0.3$, $n = 6$, $p = 0.6$) but tail fork length was the most sexually dimorphic measurement and was also the most accurate measurement for sexing within pairs (Table 3.3).

The accuracy of within-pair comparisons was highest in those cases where there was agreement between each of the three variables that were best able to sex pairs in isolation (96% of cases correct in common terns using head plus bill length, tail length and body mass; 100% of cases correct in Arctic terns using head plus bill length, tail fork length and wing length). However these cases comprised only 39% of the original sample of common terns and only 45% of the original sample of Arctic terns. Male common terns had higher discriminant function scores than their partners in 49 out of 62 pairs (79.0%). For Arctic terns discriminant function scores of males were higher than those of their partners in 26 of 31 pairs (83.9%).

3.4.4. Assortative mating

There was no within-pair correlation between wing, tarsus, head plus bill, tail or tail fork lengths of males and females for either species (*p* > 0.1 in all cases). Thus there was no evidence of assortative mating by body size. However in Arctic terns, but not common terns, body masses of males and females were significantly correlated within a pair ($r_S = 0.35$, n = 37, *p* = 0.03; Figure 3.1 data from both years combined).

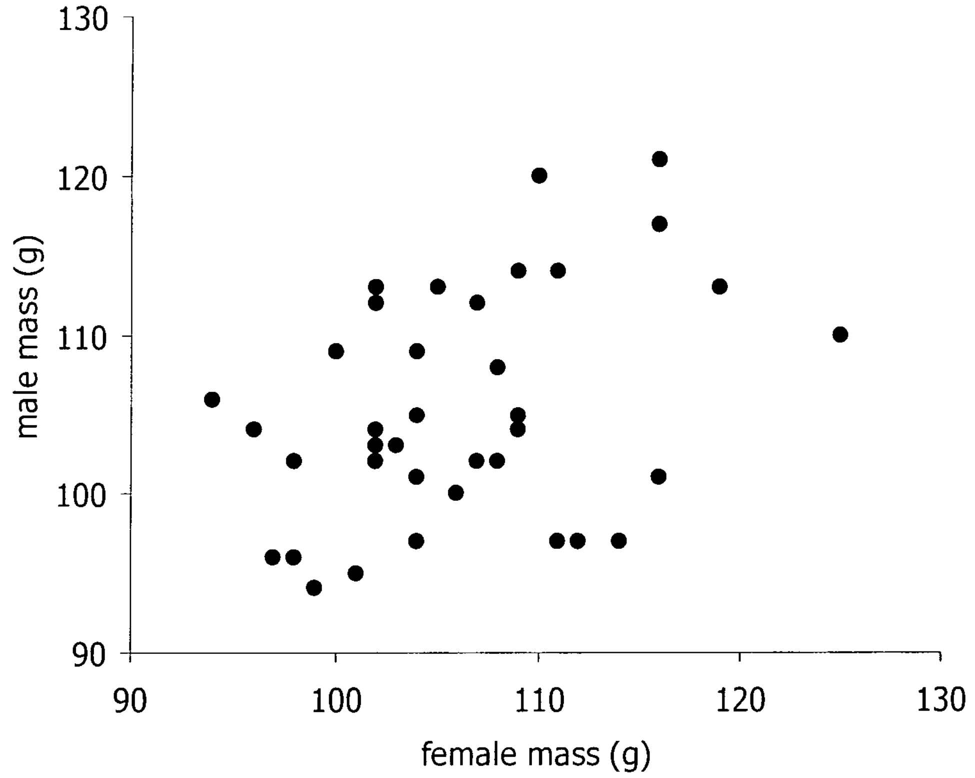

Figure 3.1: Relationship between female and male body mass for 37 pairs of Arctic terns (data combined from 1999 and 2000).

3.5. Discussion

3.5.1. Collection of data

All birds were sexed from behavioural observations. These were considered to be reliable indicators of sex because males predominantly perform mate provisioning (Uttley 1992, Moore *et al.* 2000) and to our knowledge reverse copulation does not occur in common or Arctic terns (pers. obs. and P.H. Becker pers. comm.). In this study, all pairs where both birds were marked contained a male, as indicated from multiple behavioural observations, and so female-female pairs were unlikely to have presented a problem (e.g. Nisbet & Hatch 1999).

Within-observer variability was negligible (Table 3.1) but the lowest repeatability was in tail fork length and this measurement also differed significantly between years (Table 3.2). This raises the possibility that tail fork length was measured differently in the two years of the study. However this is unlikely, because whereas tail fork length increased between years for common terns, it decreased for Arctic terns (Table 3.2). Thus differences between years were probably due to variation in feather growth and abrasion rather than measurement technique.

3.5.2. Individual-based analysis

Head plus bill length had relatively high sexual size dimorphism and relatively low variability within each sex for both common and Arctic terns. As a result, this was the best single variable for predicting sex in both species (Table 3.3). Coulter (1986) also found that the most accurate combination of variables for sexing common terns was a discriminant function incorporating bill length, depth and width. In other larids, head plus bill length alone or in combination with other bill measurements also achieved higher levels of accuracy than other measures in sexing birds (e.g. Coulson *et al.* 1983, Mawhinney & Diamond 1999, Jodice *et al.* 2000).

There was a correlation between body masses of male and female Arctic terns during incubation (Figure 3.1), probably indicating a common impact of male foraging success on male and female body mass, as a result of mate provisioning by the male. There was however no evidence of assortative mating by body size in either species. Despite this, only 78% of common or Arctic terns were sexed correctly from external measurements, either alone or in combination with other measurements. Coulter (1986) similarly found that only 70% of common terns could be sexed correctly from a combination of bill measurements. These classification rates are lower than those obtained for a variety of gull species (generally >85%; Coulson *et al.* 1983, Hanners & Patton 1985, Bosch 1996, Mawhinney & Diamond 1999, Jodice *et al.* 2000), and may indicate a lower degree of sexual dimorphism in size and shape in terns than in gulls.

3.5.3. Within-pair comparisons

The ability to measure both birds from mated pairs improved the discriminatory power of most variables and allowed us to sex 86% of common terns and 78% of Arctic terns correctly from head plus bill length alone (Table 3.3). For Arctic terns, the discriminant function also performed conspicuously better within pairs (84% sexed correctly) than in the sample as a whole (73% correct). Within-pair comparisons also resulted in higher classification rates in a variety of other seabirds (Ainley *et al.* 1985, Weidinger & van Franeker 1998, Jodice *et al.* 2000). Moreover within-pair comparisons eliminate the need to calculate cut points or discriminant functions from a sample of birds of known sex for each particular study. Thus within-pair comparisons are not only more powerful but also much more flexible than individual-based analysis for sexing birds from biometrics.

The most accurate technique of all in this study was to restrict within-pair classification to those pairs where three or more variables all indicated the same sexes. This achieved >95% accuracy, but resulted in <50% of pairs being sexed. In most studies there exists a trade-off between obtaining a large sample size, which is best achieved by measuring only one bird from each pair and using individual-based analysis, and obtaining a high level of accuracy, which is best achieved using within-pair comparisons. How this trade-off is best resolved will depend on the circumstances of each particular study. However I strongly advocate the use of within-pair comparisons wherever possible, as a means of increasing accuracy and of simplifying computational procedures for predicting sex and so reducing associated sources of error.

Chapter 4: Sexual differences in parental care during incubation and chick rearing.

4.1. Abstract

Sexual differences in parental care and parental favouritism with respect to offspring size and sex were examined in common terns *Sterna hirundo*. The sexes varied in the proportion of incubation undertaken in nests with different clutch sizes. This suggests that parental contributions are flexible, at least during incubation.

During early chick rearing females brooded chicks more than males, while males provided a greater proportion of food. Later in chick rearing, females delivered more fish than males, but not more energy. This was due to males delivering a greater proportion of longer and energy-rich species of fish. There was no evidence that a more equal division of food provisioning resulted in higher breeding success. Data from incubation and chick rearing suggest that the sexes provided near equal care, or that males provided more than females, which disagrees with Trivers' (1972) prediction that in monogamous species, females should invest more than males.

There was some evidence of mothers favouring sons when chicks were young and of fathers favouring daughters when chicks were older. Evidence for this type of parental favouritism has not, to my knowledge, been found before. However the reasons why common terns should show parental favouritism needs investigating further.

4.2. Introduction

Bi-parental monogamy occurs in over 90% of avian species (Lack 1968) and in many cases the effort of both sexes is necessary to successfully raise offspring. Nonetheless conflict can still arise over the precise contributions that each parent makes (Houston & Davies 1985, Parker 1985). In some cases, parents have specialised roles during incubation and chick rearing (for instance in many passerine species, only females incubate). In other cases, parents may have similar roles but contribute differently. In the past, it was predicted that because females produce larger gametes they should go on to invest more than males later in the breeding attempt (Trivers 1972). However an alternative hypothesis, that conflicts of interest between the sexes should result in equal investment (Winkler 1987), has been corroborated by field studies (Burger 1981, Pierotti 1981, Fasola & Saino 1995). Parental investment usually refers to the fitness costs of parental care (as discussed in Clutton-Brock 1991), however this is difficult to quantify. Parental care refers to any form of parental behaviour that increases the fitness of a parent's offspring and is useful when comparing the sexes, with the assumption that the costs of behaviours will be similar to each sex.

The role and contribution of the sexes in parental care has previously been investigated in the common tern *Sterna hirundo*, a small seabird with negligible sexual size dimorphism (Wiggins & Morris 1987, Wagner & Safina 1989, Fasola & Saino 1995). Nevertheless certain aspects have been omitted and for some aspects of parental care, no general pattern has emerged. Females have been found consistently to undertake more incubation than males (Wiggins & Morris 1987, Fasola & Saino 1995), but the effect of clutch size on the division of labour is unknown. Brooding has been combined with incubation (Fasola & Saino 1995) or recorded as time on territory (Wiggins & Morris 1987), so the contribution of each sex requires clarification. No general pattern has been found for food provisioning rates of males and females: males have been found to provision at a faster rate in some cases (Wiggins & Morris 1987, Fasola & Saino 1995) whilst in others, the sexes have been found to have similar provisioning rates (Wagner & Safina 1989). Food provisioning rate has usually been recorded as the number of fish delivered to a brood per unit time. However the sexes have also been found to differ in the sizes and species of fish delivered (Wagner & Safina 1989, Fasola & Saino 1995) and different fish species and sizes also vary in caloric density (Hislop *et al.* 1990). It is therefore important to investigate the energy delivered by each parent, which is rarely done. Previous studies of food provisioning rates have also focussed on peak foraging times (Wiggins & Morris 1987, Wagner & Safina 1989), ignoring other times of the day when the sexes may differ.

In addition to sexual differences in overall contributions to chick-rearing, males and females may also differ in their allocation of care to particular offspring. Such parental favouritism would occur if different parents benefited by caring for a given offspring. The majority of studies on parental favouritism with respect to size of offspring have focussed on passerines with large asynchronous clutches. The result have been varied, with different studies showing females favouring small chicks (Stamps *et al.* 1985, Leonard & Horn 1996, Slagsvold 1997), males favouring small chicks (Harper 1985, Westneat *et al.* 1995) and no evidence for favouritism (Byle 1990, Smiseth *et al.* 1998, Kloskowski 2001). The reason for these differences is unclear, and so more data are required covering a wider range of species.

Parental favouritism with respect to offspring sex has been investigated but no evidence has been found that it occurs (Stamps *et al.* 1987, Teather 1992, Leonard *et al.* 1994, Westneat *et al.* 1995). In sexually size dimorphic species and in species where sexes differ in variance of reproductive success (e.g. due to extra pair paternity opportunities) the benefits of the sexes may differ (Howe 1977). As common terns have negligible sexual size dimorphism and negligible extra pair paternity (Gonzalez-Solis *et al.* 2001), parental favouritism with respect to offspring sex would not be predicted. However, this has not previously been examined. It has also been suggested that pairs that share parental care equally have higher breeding success than those that do not (Burger 1986). This would however only be true if an equal division of labour resulted in increased food provisioning, and further data are needed to address this point.

4.3. Methods

Data were collected in 1999 and 2001. Adults from 25 nests in 1999 and 74 nests in 2001 were caught, marked and sexed as detailed in section 2.5. Incubation watches in 2001 (section 2.7.1.) observed 18 two-egg nests and 56 three-egg nests, over at least eight hours, spread over the incubation period. As eggs were incubated continuously, only the proportion of time incubated by the female was analysed. To determine if females undertook more incubation than males, the proportion of time that females spent incubating was compared to 0.5 using a one sample t-test. Brooding watches in 2001 (section 2.7.2) observed 20 nests where three eggs hatched. As brooding was not continuous, especially as chicks grew older, the proportion of time spent brooding by each adult was investigated.

Data from food provisioning observations were split into trip duration, diel pattern, delivery rate and meal size (25 nests in 1999 and 21 nests in 2001). Data for each year were treated separately. In 1999 observations were undertaken from dawn to dusk; in 2001 they were in two-hour blocks. Watches (as detailed in section 2.7.3) recorded all departures, arrivals and the fish species and size delivered. Sexual differences in trip duration were examined using repeated measures residual maximum likelihood models (repeated measures REML; section 2.8), using chick ages (1 - 4 days, 5 - 8 days etc. until 21 – 24 days) as the time point, nest identity as the random factor, adult sex and brood size as fixed factors and with trip duration data square root transformed.

The same data were then used to investigate diel patterns with time of day (04:01 – 07:00h, 07:01 – 10:00h, etc. until 19:01 - 22:00h) as an additional fixed factor. The number of fish and energy delivered per hour were also examined using repeated measures REML using the same time points, random and fixed factors as for the trip duration analysis. Energy delivery was estimated from fish lengths in relation to adult bill length and using energy conversion equations (Hislop *et al.* 1990; section 2.7.3). The proportion of each fish species (clupeid or sandeel) and fish lengths (3cm, 6cm or 11cm) delivered were also analysed using repeated measures REML (using the same time points and factors as for the trip duration analysis) with the proportion data arcsine transformed.

Nineteen nests were used to examine sexual differences in food provisioning from the chicks' perspective. The absolute number of fish and energy delivered to chicks by each parent were analysed using repeated measures REML as for trip durations except that I used larger age classes (1 - 7 days, 8 – 15 days, 16 – 23 days) in order to maximise the number of nests included in the analysis.

To examine whether male and female parents differed in their provisioning with respect to brood size, chicks aged 16 – 23 days were considered: at this stage brood size had stabilised and time spent brooding was negligible. Food delivery by each sex was compared between broods of one and two chicks using Mann Whitney U tests as the data were not normally distributed.

To examine the division of labour between parents, I used the proportion of fish or energy delivered by males as a measure of equitability. This was then compared to breeding success and the total number of fish or energy delivered using linear regressions. Breeding success was measured in terms of both the number of chicks fledged and their fledging condition (standardised residuals of the linear relationship between asymptotic body mass and chick age).

Parental favouritism was examined with respect to chick hatching order (i.e. older / larger chick versus younger / smaller chick) and sex of offspring determined from DNA-based techniques using blood (full details in section 2.6). The proportion of fish or energy delivered (arcsine transformed) to older and to male chicks were analysed using repeated measures REML, with time point as chick ages 1 – 7 days, 8 – 15 days and 16 – 23 days, nest identity as a random factor and adult sex as a fixed factor. Brood size was constant with two chicks in all nests. Nineteen nests were used when investigating favouritism with respect to hatch order. Thirteen nests with one male and one female chick were used when investigating favouritism with respect to offspring sex. Of these, male chicks were older in eight nests and female chicks were older in five nests. As the proportion of fish / energy delivered to male chicks was mirrored by the proportion delivered to females, only male chicks were included in this analysis.

4.4. Results

4.4.1. Incubation and Brooding

In two-egg clutches females incubated significantly less than males (proportion of time spent incubating by females = 0.44 (0.09); $t_{17} = -2.7$, $p = 0.02$), but in three-egg clutches, the sexes shared the incubation more equally (proportion of time spent incubating by the female = 0.53 (0.12); $t_{55} = 1.9$, $p = 0.06$). Therefore when comparing clutch sizes, females incubated significantly more in three-egg clutches ($t_{72} = 2.8$, $p = 0.006$).

In nests that hatched three-eggs, chicks were brooded for at least 50% of the time up to age five days (data from 20 nests, chick age = 5.0 (1.1) days). During this period, females spent a significantly greater proportion of their time brooding when compared to males (proportion of time spent brooding by males = 0.32 (0.10); by females = 0.52 (0.10); $t_{19} = 5.1$, $p < 0.001$). Parents may brood occasionally until the chicks are much older, usually in inclement weather (chick age when last brooded = 14.5 (4.7) days). If all brooding is examined, females still spent a greater proportion of time brooding (proportion of time spent brooding by males = 0.17 (0.07); by females = 0.31 (0.08); $t_{19} = 6.3$, $p < 0.001$).

4.4.2. Food provisioning

4.4.2.1. Trip duration

There was no significant sexual difference in trip duration (1999: male = 41.7 (45.8) min, female = 45.1 (51.2) min, Wald (χ^2) = 0.6, d.f. = 1, p =

0.4, 25 nests, 4018 trips; 2001: male = 17.4 (17.2) min, female = 17.2 (16.9) min, Wald (χ^2) = 1.4, d.f. = 1, $p = 0.2$, 21 nests, 1514 trips).

4.4.2.2. Diel pattern of foraging

In both years, time of day had a significant influence on trip duration (1999: Wald (χ^2) = 172.0, d.f. = 5, $p < 0.001$, 25 nests, 4018 trips; 2001: Wald (χ^2) = 20.5, d.f. = 5, $p < 0.001$, 21 nests, 1514 trips), with shorter trips undertaken before 07:00h. There was no interaction between time of day and adult sex (1999: Wald (χ^2) = 4.9, d.f. = 5, $p = 0.4$; 2001: Wald (χ^2) = 10.6, d.f. = 5, $p = 0.06$), indicated that males and females had similar diel patterns of food provisioning.

4.4.2.3. Delivery rate and meal size

Provisioning rate was strongly influenced in 1999 and less so, but still significantly, in 2001 by the sex of the adult (Table 4.1). This sexual difference was higher in both years when energy delivery rate was considered (Table 4.1). This was because females in addition to having a lower provisioning rate also delivered a higher proportion of smaller fish and a lower proportion of energy-rich clupeids (Table 4.1). Therefore males were provisioning more efficiently than females by selecting prey with higher energy content. Energy delivery rate varied with chick age, increasing up to 9 – 16 days post-hatching, then declining towards fledging (Figure 4.1; 1999: Wald (χ^2) = 38.2, d.f. = 5, $p < 0.001$; 2001: Wald (χ^2) = 30.5, d.f. = 5, $p < 0.001$). There was no difference between

Table 4.1: Sexual differences in food provisioning (1999 25 nests; 2001 21 nests.

		mean (s.d.)		influence of adult sex	
		male	female	Wald (χ^2)	*p*
Provisioning rate (fish hr^{-1})	1999	0.87 (0.4)	0.63 (0.4)	40.5	<0.001
	2001	1.40 (0.9)	1.21 (0.9)	5.2	0.02
Energy ($kJ\ hr^{-1}$)	1999	8.22 (7.1)	4.55 (4.5)	54.1	<0.001
	2001	12.6 (12.2)	7.54 (9.7)	23.3	<0.001
Diet: proportion of each fish species:					
Clupeid	1999	0.20 (0.1)	0.15 (0.1)	9.2	0.002
	2001	0.30 (0.1)	0.20 (0.1)	14.7	<0.001
Sandeel	1999	0.80 (0.1)	0.83 (0.1)	9.9	0.002
	2001	0.70 (0.1)	0.80 (0.1)	16.9	<0.001
Diet: proportion of each fish length:					
3cm	1999	0.32 (0.1)	0.36 (0.1)	13.4	<0.001
	2001	0.16 (0.1)	0.25 (0.1)	4.2	0.04
6cm	1999	0.46 (0.1)	0.45 (0.1)	0.001	0.9
	2001	0.73 (0.1)	0.70 (0.1)	1.2	0.3
11cm	1999	0.22 (0.1)	0.19 (0.1)	13.8	<0.001
	2001	0.10 (0.1)	0.05 (0.1)	-	

the sexes in the pattern of energy delivery with respect to chick age (adult sex * chick age interaction: 1999: Wald (χ^2) = 5.6, d.f. = 5, p = 0.3; 2001: Wald (χ^2) = 3.1, d.f. = 5, p = 0.7).

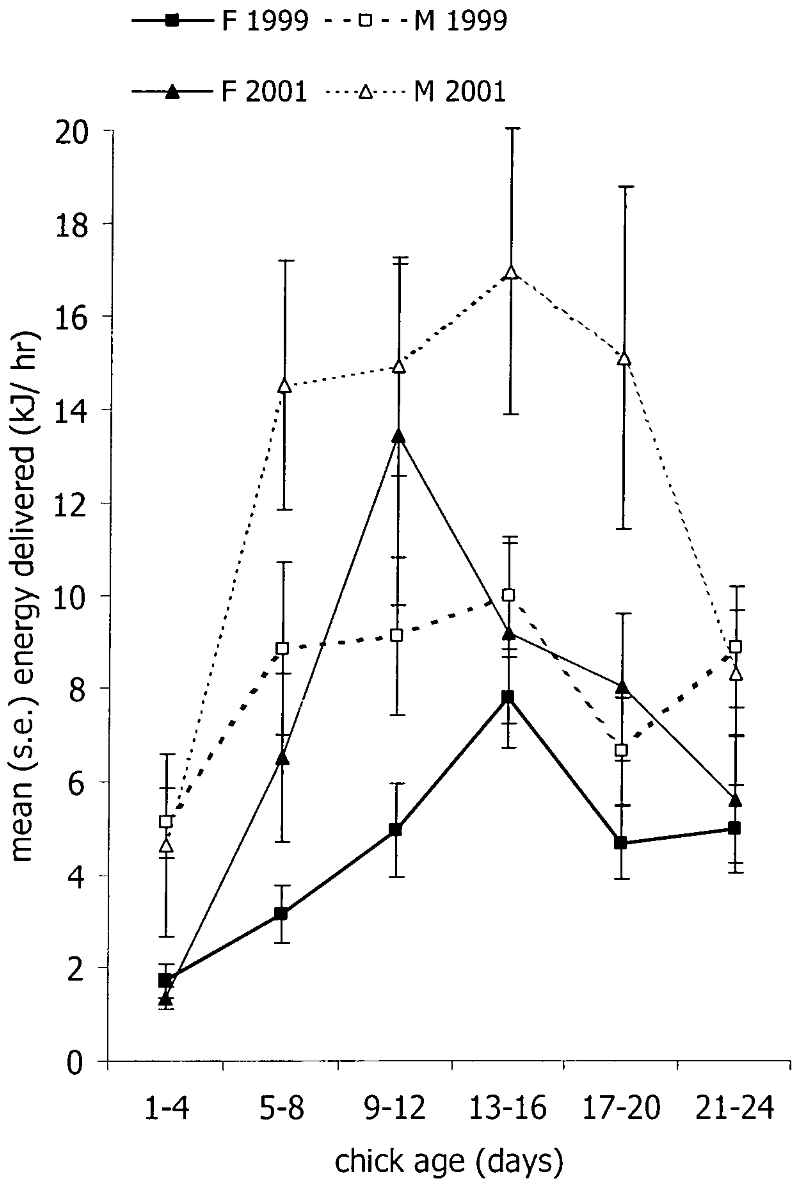

Figure 4.1: Energy delivery rates by females (F) and males (M) at different chick ages in 1999 and 2001.

The proportion of fish received by chicks from males decreased as chicks grew (proportion of fish delivered by males: chicks 1 - 7 days = 0.73 (0.2), chicks 8 - 15 days = 0.53 (0.2), chicks 16 – 23 days = 0.42

(0.2) data from 19 nests). This means that overall, males and females delivered a similar number of fish to individual chicks (proportion delivered by male = 0.53 (0.2) Wald statistic (χ^2) = 1.3, d.f. = 1, $p = 0.3$). Males did however contribute more energy than females to individual chicks (proportion delivered by male = 0.66 (0.3) Wald statistic (χ^2) = 11.7, d.f. = 1, $p < 0.001$).

Provisioning rates of males and females for different brood sizes are displayed in Table 4.2. In both 1999 and 2001, females had significantly higher provisioning rates when feeding broods of two-chicks, but only in 2001 was this translated into an energy difference. For males in 1999, provisioning rate was not significantly higher for two-chick broods, but there was a significant difference in energy delivered. In 2001, males delivered on average fewer fish per hour, but more energy per hour, to two-chick broods.

4.4.3. Equitability and breeding success

The proportion of fish delivered by males ranged from 0.36 to 0.71 (mean (s.d.) = 0.54 (0.13)), and the proportion of energy delivered ranged from 0.34 to 0.94 (mean (s.d.) = 0.65 (0.16)). There were no significant relationships between the proportion of fish delivered by males and breeding success as measured either by number of chicks or by condition of chicks at fledging (linear regressions $p > 0.2$). There was also no significant relationship between proportion of fish delivered by males and the total number of fish delivered ($p = 0.2$). In addition there were no

Table 4.2: Comparison of provisioning rates and energy delivery rates for one and two-chick broods when chicks were aged 16 – 23 days old. (Mann-Whitney U tests: 1999: 15 one-chick nests and 9 two-chick nests, 2001: 7 one-chick nests and 14 two-chick nests).

			one-chick	two-chicks	Z	*p*
Provisioning rate (fish hr^{-1})	1999	male	0.56 (0.2)	0.97 (0.4)	1.8	0.08
		female	0.55 (0.2)	0.88 (0.4)	2.0	0.05
	2001	male	1.46 (0.6)	0.89 (0.5)	-2.3	0.02
		female	0.96 (0.4)	1.46 (0.4)	2.4	0.02
Energy rate (kJ hr^{-1})	1999	male	5.55 (2.2)	10.94 (4.8)	3.0	0.003
		female	4.53 (2.7)	6.19 (4.3)	0.8	0.4
	2001	male	6.92 (2.9)	16.09 (12.1)	2.2	0.03
		Female	2.87 (2.3)	9.30 (6.9)	2.46	0.01

significant relationships between the proportion of energy delivered by males and the total energy delivered ($p > 0.06$) or breeding success ($p > 0.9$).

4.4.4. Parental favouritism

The sexes did not differ in the proportion of fish they delivered to the oldest or the largest chick (all ages combined: proportion of fish delivered to oldest chick by males = 0.53 (0.10), by females = 0.50 (0.10); Wald statistic (χ^2) = 0.5, d.f. = 1, *p* = 0.5). There were also no sexual difference in the proportion of energy delivered to the oldest chick (all ages combined: proportion of energy delivered to oldest chick by males = 0.57 (0.14), by females = 0.52 (0.16); Wald statistic (χ^2) = 0.4, d.f. = 1, *p* = 0.5).

The proportion of fish delivered to male chicks by each parent did not differ between fathers and mothers (all ages combined: proportion of fish delivered to male chick by fathers = 0.49 (0.12), by mothers = 0.50 (0.07); Wald statistic (χ^2) = 1.0, d.f. = 1, *p* = 0.3). However the proportion of energy delivered to male chicks was significantly higher by mothers than by fathers (Figure 4.2; Wald statistic (χ^2) = 10.0, d.f. = 1, *p* = 0.002). The greatest deviation from feeding the sexes equally occurred in young chicks (1 – 7 days) when females biased energy delivery in favour of sons and in older chicks (16 – 23 days) when males biased energy delivery in favour of daughters.

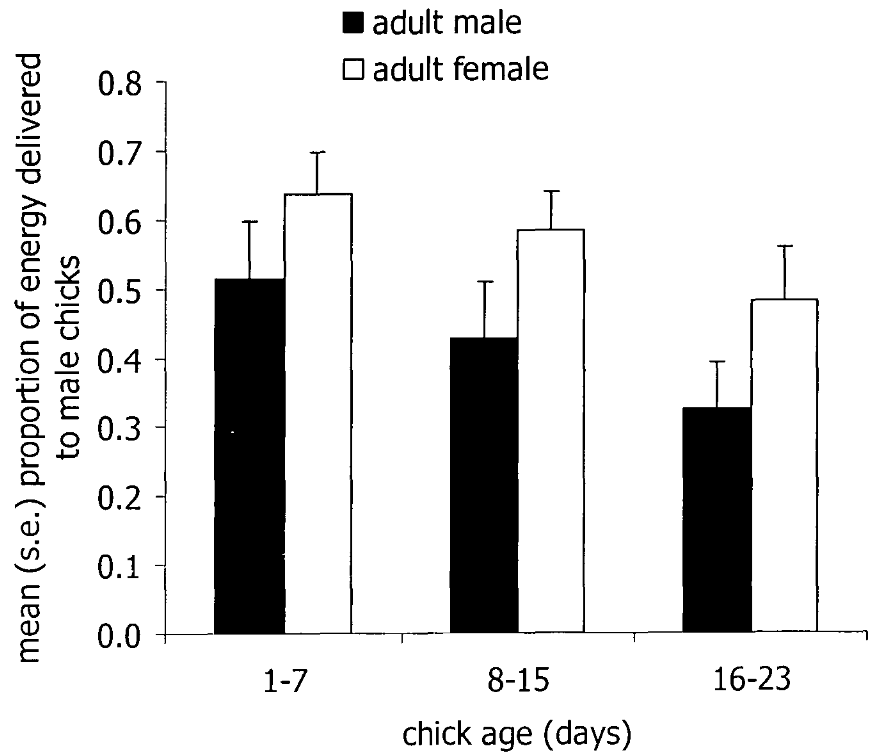

Figure 4.2: Proportion of energy delivered to male chicks by each parent (data from 13 nests with a chick of each sex).

4.5. Discussion

4.5.1. Sexual differences in parental care

Previous studies of common terns found that females undertook more incubation than males (Wiggins & Morris 1987, Fasola & Saino 1995). In this study I found differences in the division of labour during incubation with respect to clutch size. Pairs laying sub-modal clutches are thought to be of lower quality (Heaney & Monaghan 1995, Wendeln & Becker 1999) and in chapter 7 I found that the occurrence of two-egg clutches was related to low maternal condition. Females with low body condition may incubate less than females with high body condition. Maternal condition was not recorded in this or previous common tern studies, but this could explain the differences between studies. This suggests that parental contributions during incubation can be flexible with respect to prevailing environmental conditions, body condition or adult quality, as also found in other seabirds (Pierotti 1981, Uttley 1992).

Females undertook more brooding than males. Energy expenditure during brooding is thought to be between two and three times basal metabolic rate (BMR, Adams *et al.* 1991, Nagy & Obst 1992) and can be slightly higher than during incubation (Bevan *et al.* 1995). However this is still lower than energy expenditure during foraging (e.g. 6.5*BMR, Adams *et al.* 1991; 5.4*BMR, Nagy & Obst 1992).

There was no evidence of sexual differences in foraging trip duration, and thus no support for the suggestion by Wagner & Safina (1989) that males and females foraged in different areas. These authors made this suggestion because they recorded sexual differences in the fish species delivered to chicks, which was also found in the Coquet birds. Sexual differences in foraging location could be masked when considering trip duration if the sexes have different time budgets within a foraging trip (Burger & Gochfeld 1991). This may also explain why provisioning rates, but not trip duration differed significantly between the sexes. Differences in foraging location are usually found in seabird species with sexual size dimorphism (Weimerskirch & Jouventin 1987, Sagar & Weimerskirch 1996, Gonzalez-Solis *et al.* 2000, but see Lewis *et al.* 2002) so would not necessarily be expected to occur in common terns. There was also no sexual difference in diel pattern of food provisioning in common terns, although such a pattern has been found in some sexually size dimorphic species (Wanless *et al.* 1995, Kato *et al.* 2000).

The data presented in this chapter agree with Wiggins & Morris (1987) and Fasola & Saino (1995) that males deliver fish at a faster rate than females. Males also provided a higher proportion of longer and energy-rich fish than females. Sexual differences in foraging efficiency are usually attributed to size differences (Weimerskirch *et al.* 1997, Gonzalez-Solis *et al.* 2000), which is not the case in common terns. Further research is therefore necessary to determine why, even in species with negligible sexual size dimorphism, the sexes vary in foraging efficiency.

Even though the sexes differed in foraging efficiency, both sexes did increase their delivery of energy as chicks grew and provided more energy to larger broods. Previous work has suggested, when looking at fish delivery, that only males increase deliveries as chicks grow (Wiggins & Morris 1987). This highlights the need for sexual differences in food provisioning to be monitored using energy delivered, because the results can differ from number of fish delivered. This is also the case when examining the proportion of fish and energy delivered by each sex to individual chicks. The proportion of fish delivered by each sex was similar over the whole chick-rearing period, but the males contributed more than the females when energy was considered.

There was no evidence that a more equal division of labour during chick rearing led to greater breeding success, as found by Burger (1986). This was probably because in my study, a more equal division of labour did not result in more fish or energy being delivered to the brood.

Within this chapter I have examined parental care by recording incubation, brooding, and food provisioning. However I present no data on mate provisioning or territory defence. Territory defence is generally shared equally in terns (reviewed in Fasola & Saino 1995) but mate provisioning (i.e. fish delivered to the female by the male) makes an important nutrient contribution prior to egg laying (Nisbet 1973, Moore *et al.* 2000, Wendeln *et al.* 2000). Added to the data presented here, there is thus strong evidence to refute the idea (Trivers 1972) that female common terns provide more parental care than males. However parental care has been examined and not parental investment. Investment is the extent to which any parental care given to an offspring reduces the parent's residual reproductive value (reviewed Clutton-Brock 1991).

Hence in order to examine investment, the costs and benefits of behaviours to each sex need to be estimated. Mate provisioning compensates, at least partially, for the cost to the female of egg production. The costs of incubation, in birds that lay the modal clutch size, are presumably similar for each sex. The costs of brooding are greater than BMR, but not as great as food provisioning. During early chick rearing, males are thus undertaking the more costly activity, although later in chick rearing, females make a similar contribution to food provisioning as males. Although superficial, these estimates suggest that the sexes have equal investment, or if anything that males invest more due to greater overall contribution to food provisioning. This agrees with earlier seabird studies which found no support for Trivers' (1972) argument that in monogamous species, females should invest more than males (Burger 1981, Pierotti, 1981, Fasino & Saino 1995).

4.5.2. Parental favouritism

In asynchronously hatching species, parents and chicks may be in conflict as to which chick is fed (Trivers 1974, Parker *et al.* 1989). The oldest chick will favour feeding itself, whereas the parents will not want to totally ignore the youngest chick leading to its death and hence a reduced number of fledged chicks. When compared to the passerines studied, the modal brood size of two in this study (third-hatched chicks usually died within a few days of hatching so were not included) is likely to result in less parent-offspring conflict. As parental favouritism enables parents to counteract the chicks' influence on which chick is fed (Gottlander 1987), this may explain why no favouritism with respect to offspring size was found here.

In contrast to the results for offspring size, parental favouritism was found with respect to offspring sex. However, it is not clear why parents would differ in the benefits of feeding one particular sex. In poor environmental conditions, male offspring have lower survival (chapter 7), which suggests that males are inherently more costly to produce than females. Even though male and female offspring may differ in their benefits to parents due to a difference in survival, it is unclear why male and female parents should differ in this benefit. In territorial species with limited territory availability, future competition with offspring of the same sex may be a cost (Gowaty 1993). However as common terns are nest-site faithful and do not use the nesting territory for foraging, it does not seem likely that this could be a driving factor. More research is therefore necessary to determine why parental favouritism occurs in common terns.

Chapter 5: Determinants of egg production capacity and resulting short and long-term costs.

5.1. Abstract

Egg production costs, until recently, have rarely been included as determinants of clutch size. I set out to elucidate, in a small, long-lived seabird, the common tern *Sterna hirundo*, what were the major determinants of the total number of eggs laid when the first egg was removed. I compared pairs that laid four eggs and those that laid three eggs in total (the modal clutch size under normal conditions) and also pairs that had natural three-egg and two-egg clutches. The pattern of changes in egg volume during the laying sequence for replacement three-egg and two-egg clutches (resulting from birds laying a total of four eggs and three eggs respectively) was the same pattern as found when comparing natural three-egg and two-egg clutches. Moreover females that laid four eggs had no lower body condition after clutch completion than females that laid three eggs, even though the former had laid an extra egg. These data support the notion that egg production is determined mainly by the body reserves available to females during clutch completion.

Pairs that laid fewer eggs had lower return rates the following year, and were less mate faithful, supporting the idea that pairs that laid fewer eggs were of lower quality than those that laid more eggs. Moreover, pairs that had laid different number of eggs did not differ in behaviour or breeding success in the current breeding attempt. These data suggest that the requirements of egg production had less of an impact on high quality pairs than on low quality pairs, and highlight the importance of considering adult quality when examining egg production.

5.2. Introduction

Birds are useful models for studying life histories because their breeding cycle is split in to three distinct phases; egg production, incubation and chick rearing, that can be independently manipulated. The fact that egg loss can induce birds to lay more eggs led Lack (1947) to assume that egg production was an inexpensive part of the breeding cycle. More recently, researchers have highlighted the need for egg production to be examined more closely (Partridge & Harvey 1985, Monaghan & Nager 1997). Energetics studies have found similar energy expenditure during egg production as during chick rearing (Tinbergen & Dietz 1994, Ward 1996, Bryan & Bryant 1999, Stevenson & Bryant 2000, Nilsson & Raberg 2001). In addition to energy requirements, birds may also be limited by the need to acquire specific nutrients for egg production (Bolton *et al.* 1992, Ramsay & Houston 1997), which may require more demanding foraging strategies than during chick rearing (Monaghan & Nager 1997, Heaney *et al.* 1998). Moreover egg production can reduce the parents' ability to raise chicks (Heaney & Monaghan 1995, Monaghan *et al.* 1998) and may also reduce female survival (Visser & Lessells 2001).

Parental quality has been highlighted as a major determinant of clutch size under natural conditions (Coulson & Porter 1985, Wendeln & Becker 1999). However it is not known if parental quality is still a major determinant of how many eggs are laid when birds incur additional egg production costs. I investigated the common tern *Sterno hirundo*, a small, long-lived, semi-precocial seabird, with a modal clutch size of three eggs.

Common terns are indeterminate layers with the proportion of birds replacing lost eggs varying between years and colonies (Arnold *et al.* 1998, Heaney *et al.* 1998). In this study, after the removal of the first egg, the pairs that laid a replacement modal clutch ("four-egg") were compared with the pairs that laid a replacement two-egg clutch size ("three-egg"). Pairs that laid natural three-egg and two-egg clutches were also compared. Adult body condition, laying date, egg volume and offspring sexes were all compared between clutch sizes, in both manipulated and natural conditions. If clutch size were predetermined (i.e. related mainly to intrinsic adult quality) then the relationships between clutch sizes in manipulated and natural conditions should be similar. If, however, clutch size were determined primarily by extrinsic factors, then the relationship between clutch sizes in manipulated and natural conditions would differ.

The extent to which egg production demands translate into fitness costs may well depend on the state or quality of the parent (McNamara & Houston 1996). To examine this, the impact of extra egg production on both male and female effort during the remainder of the breeding event, was compared between four-egg and three-egg pairs. Both sexes are necessary to successfully rear offspring (chapter 4) and by monitoring both sexes, the occurrence of compensation behaviour could also be examined. The impact of extra egg production was also examined with respect to chick size, growth and survival. If birds of higher quality were affected less by additional cost of increased egg production than birds of lower quality, within the current breeding effort there should be few differences in adult behaviour or success.

In a long-lived species, such as the common tern, the impact of extra egg production may not be borne in the current breeding attempt. Therefore to assess long-term costs, the following breeding attempt was also monitored. Pairs that lay more eggs are expected to show characteristics of high quality birds (mate and site fidelity; Pyle *et al.* 2001) although there may not be differences in breeding success.

5.3. Methods

5.3.1. Inducing extra egg production

During 2000 the first laid egg (a-egg) was removed, within 12 hours of laying, in a sample of common terns (n = 72) nesting close to the centre of the colony. In some pairs (35%), egg removal caused the parents to relocate. Of the birds that re-laid, only those within sight of the observation hides, were monitored further. Within this sample some laid four eggs in total (four-egg, n = 16), whereas some laid three (three-egg, n = 14). In the four-egg clutches the last egg (d-egg) was removed soon after laying and in all nests the a-egg was replaced so the birds were incubating their own three-egg clutch. Hence although pairs differed in the number of eggs produced, the number of eggs incubated was the same for pairs in both groups.

5.3.2. Proximate factors that may influence egg production capacity

Adults from the 30 manipulated nests were caught and body mass was recorded as an index of body condition (section 2.5). In addition, laying date was recorded as the number of days since the first egg in the colony was laid. Egg volume (cm^3; section 2.3) was measured on the day of laying. The sexes of embryos were determined from DNA-based techniques, either by taking tissue from dead embryos or chicks or from taking blood from chicks soon after hatching (full details in section 2.6). Normally distributed data are quoted as mean (s.d.) and analysed using t-tests, whereas data that were not normal are quoted as median (inter-quartile range, IQR) and analysed with Mann-Whitney U tests. To avoid repeated t-tests on the volume of eggs from different laying orders, the data were analysed using residual maximum likelihood models (REML; section 2.8), with laying order and number of eggs laid as fixed factors and nest identity as a random factor.

Data from manipulated nests in 2000 were compared with unmanipulated two-egg and three-egg clutches laid in 2001. The same methods were used in 2001 to collect data on adult condition.

5.3.3. Comparing adult behaviour, chick size, growth and survival between three-egg and four-egg pairs

Incubation, brooding and provisioning data were collected as detailed in section 2.7. As incubation is continuous, only the proportion of time spent incubating by females was compared between groups using a Mann-Whitney U test. The number of days that clutches were incubated (date of first hatched chick minus date of first laid egg) was compared between groups using a t-test.

As chicks were not brooded continually, the proportion of time spent brooding by each sex was compared between groups using REML, with total number of eggs laid (three eggs or four eggs) and brood size as fixed factors (not all eggs hatched and so brood size was variable) and nest identity as a random factor, with the proportion data arcsine transformed. This analysis was restricted to the early chick-rearing period when chicks were brooded for at least 50% of the observation period (see chapter 4). Behaviour of males and females during incubation and brooding were also compared to data presented in chapter 4, from natural pairs.

As in the previous chapter, food provisioning was considered for each sex in terms of trip duration (square root transformed), rate of fish delivery and rate of energy delivery. The methodology for randomised watches is detailed in section 2.7.3. All three variables were analysed using repeated measures REML, with nest identity as a random factor, chick ages (1 – 4 days, 5 – 8 days, etc. until 20 – 24 days) as time points, and with number of eggs laid and brood size as fixed factors.

Chick size (head plus bill length in mm, wing length in mm and body mass in g) were measured at hatching and at fledging (full details in section 2.4). Fledging size and age were recorded when asymptotic body mass was reached, because age of first flight is often associated with weather conditions and so is not a reliable measure of age at fledging. An average chick growth rate for body mass, wing length and head plus bill length was calculated from measurements taken approximately every two days during the linear growth phase (5 – 14 days). To analyse the differences between groups in chick size, growth and age of fledging, REMLs were used with nest identity as a random factor, and with brood size, chick hatch order and number of eggs laid as fixed factors. If brood size or chick hatch order were not significant in the model they were removed and the analysis was repeated. Chick survival was compared between groups using G-tests.

5.3.4. Comparing return rates, mate-fidelity and breeding success the following year between three-egg and four-egg pairs

During the 2001 breeding season, the study plots and adjacent areas were searched for colour-ringed adults and both members of pairs were identified. The laying date, clutch size and number of chicks fledged by colour-ringed adults was also recorded. Site and mate fidelity were compared between three-egg and four-egg pairs using G-tests, as was breeding success for each sex. Laying dates were compared using Mann-Whitney U tests for each sex.

5.4. Results

5.4.1. Factors influencing egg production capacity

In manipulated conditions, maternal body condition did not differ between birds that laid four eggs and those that laid three eggs (three-egg = 132.5 (123-135) g; four-egg = 131.5 (126-137) g; Mann-Whitney U test: Z = -0.2, n = 30, $p = 0.8$) . Maternal condition in 2001, when clutch size was not manipulated, showed a marginally significant difference, with females that laid three-eggs being heavier than those which had laid two (two-egg = 124.8 (7.7) g; three-egg = 128.4 (9.5) g; $t_{114} = -2.0$, $p = 0.05$).

Paternal body condition in manipulated conditions showed no difference between three-egg and four-egg pairs (three-egg = 127 (121-133) g; four-egg = 123 (118-128) g; Z = -1.4, n = 30, $p = 0.2$). This was also the case when two-egg and three-egg males were compared in natural conditions (two-egg = 123.6 (6.2) g; three-egg = 123.2 (7.4) g; $t_{107} = 0.3$, $p = 0.8$).

In the manipulated groups, there was no difference between three-egg and four-egg nests in laying date (three-egg = 9.5 (5.5-14) days; four-egg = 9 (7-12) days; Z = -0.5, n = 30, $p = 0.6$). In natural conditions there was also no difference between two-egg and three-egg nests (two-egg = 13.3 (6.5) days; four-egg 12.0 (6.1) days; $t_{178} = 1.3$, $p = 0.2$).

The volume of the first laid egg was similar in three-egg and four-egg groups (three-egg = 19.7 (1.0) cm^3; four-egg = 18.9 (1.5) cm^3; $t_{28} = 1.6$, $p = 0.1$). This was the same when comparing natural two-egg and three-egg clutches (two-egg = 19.4 (1.3) cm^3; three-egg = 19.0 (1.5) cm^3; $t_{114} = 1.3$, $p = 0.2$). However in manipulated clutches there was a significant interaction between laying order and group when the volume of a-, b- and c-eggs were considered (Figure 5.1; Wald statistic (χ^2) = 11.1, d.f. = 2, $p = 0.004$): the third laid egg was similar in volume to the second laid in four-eggs clutches, whereas the third egg was smaller than the second in three-eggs clutches. This is the same pattern as seen in natural two-egg and three-egg clutches (Figure 5.2).

In all laying positions, there were fewer male eggs in the four-egg group (proportion male a-egg, b-egg, c-egg: three-egg group = 0.58, 0.46, 0.46; four-egg group = 0.30, 0.20, 0.38; G-tests all $p > 0.1$). This sexual difference was close to significant when a-, b- and c- eggs were considered together (proportion male: three-egg = 0.50, four-egg = 0.29; $G_1 = 3.5$, $p = 0.06$). In natural clutches, the overall sex ratio showed no such difference between clutch sizes (proportion male: two-egg (n= 47) = 0.47; three-egg (n = 111) = 0.44). The sex ratio of the perceived two-egg clutch, laid after the a-egg was removed, was also no different to natural two-egg clutches (proportion male: manipulated = 0.43, natural = 0.47; $G_1 = 0.2$, $p = 0.7$). However the sex ratio of the perceived three-egg clutch, laid after the a-egg was removed, contained marginally more female embryos than natural three-egg clutches (proportion male: manipulated = 0.30, natural = 0.44; $G_1 = 3.3$, $p = 0.07$).

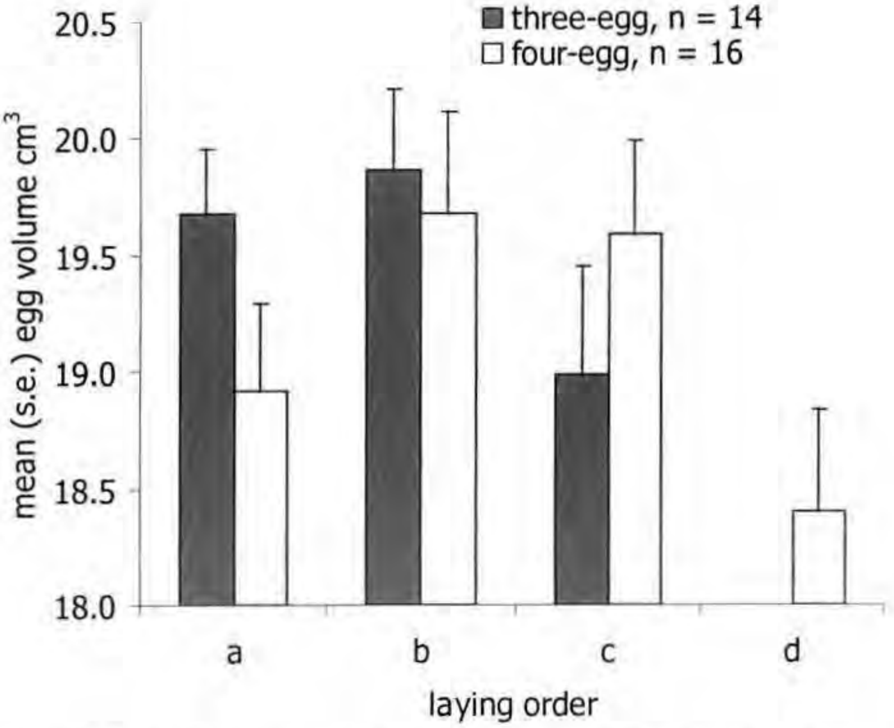

Figure 5.1: Egg volumes in clutches where the a-egg was removed.

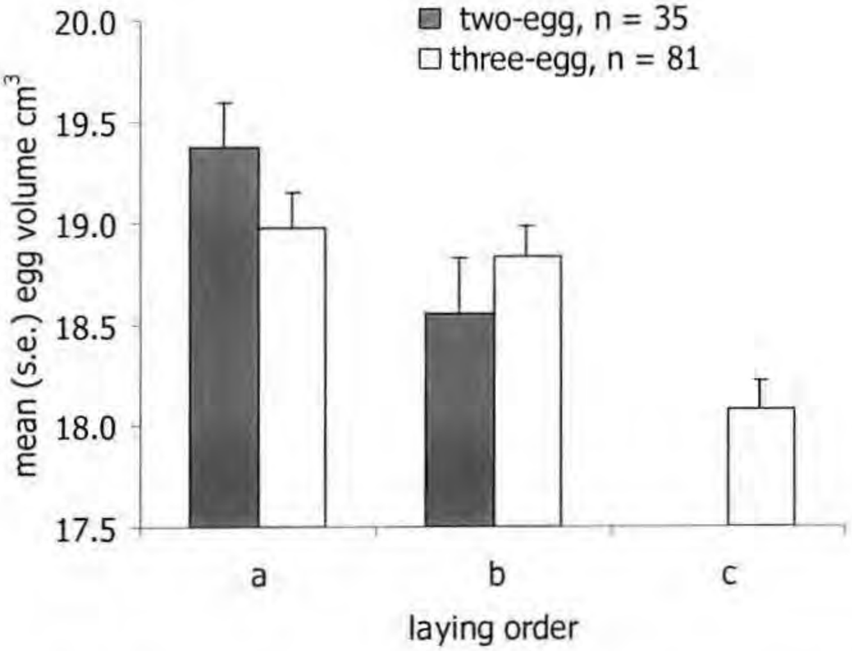

Figure 5.2: Egg volumes in natural two and three egg clutches.

5.4.2. Impact of extra egg production on adult behaviour

The length of incubation and the proportion of incubation carried out by females showed no significant difference between groups (Table 5.1). The proportion of incubation undertaken by females was similar to natural pairs in 2001 (proportion by female = 0.53 (0.12)). There was also no difference between groups in the number of chicks hatched (three-egg = 2.6 (0.6) chicks; four-egg = 2.3 (0.8) chicks; Z = 1.5, $p = 0.1$) or in the proportion of time spent brooding by males or females (Table 5.1). However when compared to data collected from natural pairs in 2001 (males = 0.32 (0.10), females = 0.52 (0.10)), males in manipulated pairs appear to have increased brooding effort, and females to have decreased effort.

There were no significant differences for either sex between the groups in the trip duration (Table 5.2; repeated measures REML $p > 0.3$), fish delivery rate ($p > 0.3$) and energy delivery ($p > 0.1$).

Table 5.1: Comparison of incubation and brooding behaviour in three-egg and four-egg pairs.

	three-egg pairs (14)	four-egg pairs (16)	$Z^{§}$ or Wald (χ^2)	*p*
Incubation length (days)	24.1 (1.1)	24.9 (1.7)	$1.5^{§}$	0.1
Prop. incubation by female	0.54 (0.10)	0.51 (0.07)	1.2	0.2
Prop. brooding by male	0.45 (0.13)	0.47 (0.12)	0.1	0.7
Prop. brooding by female	0.44 (0.13)	0.42 (0.10)	0.1	0.7

Table 5.2: Comparison of food provisioning behaviour in three-egg and four-egg pairs.

		mean (s.d.)	
		three-egg pairs (14)	four-egg pairs (16)
Trip duration (min)	male	18.8 (17.3)	19.4 (19.7)
	female	17.3 (18.0)	17.8 (18.0)
No. fish delivered	male	1.14 (0.42)	1.08 (0.43)
(fish hr^{-1})	female	0.82 (0.30)	0.84 (3.6)
Energy delivered	male	5.6 (1.4)	5.8 (2.5)
(kJ hr^{-1})	female	4.3 (2.2)	3.2 (2.7)

5.4.3. Impact of extra egg production on chick size, growth and survival

At hatching and at fledging, body mass and wing length did not differ significantly between groups (REML all $p > 0.4$). Head plus bill length at fledging was longer in the three-egg group (REML $p = 0.02$), which was consistent with the higher proportion of male chicks at fledging in the three-egg group (proportion of male chicks (*n*) in hatch order a-, b-, and c-: three-egg = 0.50 (*14*), 0.44 (*8*), 1.0 (*1*); four-egg = 0.19 (*16*), 0.42 (*12*), 1.0 (*1*): $G_1 = 11.3$, $p = 0.003$). The growth rates of all biometrics did not differ between groups (REML $p > 0.5$), nor did the age of fledging (REML $p = 0.5$). Breeding success (number of chicks fledged divided by number of eggs incubated) was no different between the groups (three-egg = 0.67 (0.33-0.67), four-egg = 0.67 (0.33-0.67); $G_1 = 0.08$, $p = 0.8$).

Fledging success (number of chicks fledged divided by the number of chicks hatched) was also not significantly different between groups (three-egg = 0.67 (0.42-0.67), four-egg = 1.0 (0.67-1.0); $G_1 = 0.4$, $p = 0.5$).

5.4.4. Impact of extra egg production on subsequent breeding attempt

Of the 16 pairs that laid four-eggs in 2000 (Table 5.3), 13 pairs (81%) returned in 2001, stayed with the same partners and laid a modal clutch. Of the remainder, one pair was not seen on the plot and the other two pairs changed partners. Of the 14 pairs that laid three-eggs in 2000, only two pairs (14%) returned in 2001, with the same partner and laid a modal clutch. Another pair laid a two-egg clutch with the same partner, a further six pairs changed partners and the final five pairs were not seen on the plot. When the number of pairs not returning, staying with the same partner and changing partners was compared between groups there was a significant difference ($G_2 = 10.7$, $p = 0.005$). Neither the number of chicks fledged nor laying date differed between groups when females and the males were considered separately (Table 5.4).

Table 5.3: The number of pairs remaining site and mate faithful after extra egg production.

	Number of pairs	
	three-egg n = 14	four-egg n = 16
Same partner, modal clutch	2	13
Same partner, two-egg clutch	1	0
Divorced partners	6	2
Not returned	5	1

Table 5.4: The number of females and males raising one or two chicks the year following additional egg production and the timing of laying by these birds (also two males from the three-egg pairs raised no fledglings).

Breeding in 2001	three–egg pairs (14)	four-egg pairs (16)	U or G§	*p*
Females: median laying date	13	10	27.0	0.2
Males: median laying date	9	9	52.5	<1.0
Females: with one fledgling	3	3	2.1§	0.1
Females: with two fledglings	2	11		
Males: with one fledgling	2	4	0.08§	0.8
Males: with two fledglings	4	11		

5.5. Discussion

5.5.1. Determinants of egg production capacity

In manipulated birds, the third-laid egg was similar in volume to the second-laid egg in four-eggs clutches, whereas the third egg was smaller than the second in three-eggs clutches. This was the same pattern as that seen in natural two-egg and three-egg clutches (Figure 5.1 and 5.2) and provides strong support for the notion that egg production capacity was influenced by the body reserves available to females during clutch completion. Maternal condition under natural conditions was greater in females that had laid three eggs, when compared to those that had laid two, but there was no difference in maternal condition after clutch completion between females that had laid four and three eggs. However, since females that laid four eggs had no lower body condition after clutch completion than those that laid only three, then females in the four-egg group probably had higher body condition prior to egg laying. In a similar experiment, female lesser black-backed gulls *Larus fuscus* that laid more eggs were lighter and had less pectoral muscle after egg laying than did females that had laid fewer eggs (Monaghan *et al.* 1998). These data suggest that maternal body condition may have strongly influenced egg production capacity in the current study, although this can not be confirmed without data on maternal condition prior to egg laying, which is difficult to obtain in common terns.

5.5.2. Relationship between number of eggs and sexes of offspring

The sexes of embryos are rarely considered in egg production studies, except when supernumary eggs are produced (Nager *et al.* 1999, Kalmbach *et al.* 2001). The data presented here suggest a tendency for more female embryos to be produced when four eggs are laid, which is consistent with the notion that male chicks are more vulnerable than female chicks in poor environments (chapter 7).

5.5.3. Impacts of extra egg production

Increased egg production did not alter the proportion of incubation undertaken by each sex. However in both manipulated groups, males undertook more brooding and females less than under natural conditions. Terns are known to be flexible in terms of their relative contributions to brooding in different environmental conditions (Uttley 1992). In poor conditions, male and female Arctic terns were found to share brooding more equally, which is what the manipulated pairs did in the current study. This could be as a result of females, and maybe also males, having fewer reserves after extra egg production, as suggested in previous studies (Heaney & Monaghan 1995, Monaghan *et al.* 1998).

Food provisioning and chick growth showed no differences between manipulated groups. Although this shows that birds laying four eggs did not have reduced chick-rearing capacity when compared to birds that laid three eggs, it does not show that egg production had no cost, since the provisioning and chick growth rates of natural clutches in the same year are not known. Parents in the four-egg group had higher mate and site fidelity the following season than pairs that laid fewer eggs and this suggests that the pairs from four-egg and three-egg groups may have been of different quality. Previous studies found that producing supernumerary eggs leads to lower return rates in the next breeding season in females (Nager *et al.* 2001) and in passerines it has also been found that female survival can be reduced when egg production is increased (Visser & Lessells 2001). However in the current study, the pairs that laid more eggs had higher mate and site fidelity, which suggests that variation in parental quality overrode any impact of extra egg production. Moreover the results of this study suggest that pairs of high quality that laid four eggs were as capable of raising chicks as were lower quality pairs that laid three eggs. This supports the idea that increased costs will be manifested less in high quality birds (McNamara & Houston 1996) and indicates the importance of including a range of quality phenotypes when examining egg production requirements.

Chapter 6: Effects of experimentally increased body mass on breeding performance of males during chick rearing.

6.1 Abstract

For seabirds, as long-lived species, life history theory predicts that adults should not jeopardise their future survival, but that fewer offspring or offspring in poorer condition should be produced in years of low food availability. However if parents have some capacity to buffer themselves against the impacts of low food availability, then they may be able to absorb the costs of increased foraging effort without passing them on to their offspring. Such natural buffering capacity would be beneficial to seabirds under circumstances were food availability has high inter-year variability.

The common tern, a small seabird, has traditionally been believed to have little buffering capacity. In this study male body mass was increased by 10%, by attaching a weight to the trachael pit. Males in this species deliver more energy to offspring than females. These birds did not reduce food provisioning effort and their offspring were of similar number and condition as controls. These data suggest that common terns have a greater buffering capacity than previously thought.

6.2. Introduction

Iteroparous species must achieve a balance between investment in current reproduction and investment in future reproduction and survival (Williams 1966, Stearns 1992). Seabirds forage in unpredictable patchy environments, where prey availability may show large inter-year variation (Monaghan *et. al.* 1992, Weimerskirch *et. al.* 1999, Hamer *et. al.* 2001). Therefore seabirds, as long-lived iteroparous species, must make decisions about current investment when the future is unpredictable. Long-term fitness benefits are highest if adult survival is not jeopardised. Hence in years of low food availability seabirds are expected to fledge fewer offspring or offspring in poorer condition, rather than increase their own foraging effort to the extent that it reduces resources available for the future investment (Drent & Daan 1980, Wooller *et. al.* 1992).

However evidence is emerging that some seabird species have flexible time budgets and behavioural plasticity to enable increased foraging effort in years of low food availability (Burger & Piatt 1990, Falk & Moller 1997, Davoren 2000). Some species even continue chick provisioning to the detriment of their own body mass over the short-term (Weimerskirch & Lys 2000). Natural inter-year variation in food availability may be associated with other factors, such as weather, making quantification of increased cost to the adult difficult. Therefore experimental manipulations of increased cost to the parent are advocated (Partridge & Harvey 1988). Marine food availability is difficult to experimentally manipulate directly, so instead researchers have increased adult effort by handicapping (e.g. Saether *et al.* 1993, Mauck & Grubb 1995). This is preferential to removing one of the partners as it retains the natural bi-parental care (Wright & Cuthill 1989). Studies attempting to mimic moult found that handicapping adults had no effect on the chicks (Verbeek & Morgan 1980, Weimerskirch *et al.* 1995), possibly because adults can alter their flight pattern to cope with the altered wing structure. In contrast, the majority of seabird handicapping studies found that the current offspring suffer from the costs incurred by the handicap, supporting life history theory (Table 6.1). However these studies were all of Procellariiformes, which leave their chicks unattended while they undertake long foraging trips (Schreiber & Burger 2001) and therefore have little capacity to increase their foraging effort.

Terns are small seabirds, which are also thought to have little leeway in their time and energy budget (Pearson 1968 and cited many times e.g. Monaghan *et al.* 1989, Uttley *et al.* 1989, Wendeln & Becker 1996, Robinson *et al.* 2001b). However compared to Procellariiformes, terns have high provisioning rates and forage close to the colony (Becker *et al.* 1997). This may enable them to be more flexible and have a greater buffering capacity than previously thought.

By handicapping male common terns *Sterna hirundo*, the sex which delivers the greater proportion of energy to the offspring (chapter 4), I aimed to determine whether, as life history predicts for long lived species, parental effort would not be increased and the offspring would suffer. If the number and condition of offspring was not diminished then this would

Table 6.1: Previous studies handicapping long –lived species during chick-rearing.

Type and size of handicap		Species	Outcome	Supports life history theory:
Reduced wing area	9%	*Oceanodroma leucorhoa*	Adult condition not changed, chicks grew slower and fed less frequently	YES [3]
Mimic moult		*Larus glaucescens*	Increased forage trip duration, but no reduction in chick growth, no compensation detected in unmanipulated partner	NO [1]
		Pachyptila belcheri	Handicapped birds unable to maintain body condition while feeding chicks at same rate as controls	NO [4]
Added weight to legs	6%	*Thalassoica antarctica*	Handicapped birds reduced food loads, increased trip duration, no change in adult mass, no compensation by partner	YES [2]
	7%	*Pachyptila desolata*	Increased duration of self-feeding trips, but did not decrease food loads, or own body mass	YES [5]
	6%	*Pachyptila belcheri*	Handicapped bird decreased feeding rate, kept body mass constant, no change in survival	YES [6]
Added weight to base of tail	6.4%	*Diomedea chlororhynchos*	Increased time foraging, smaller food loads delivered	YES [7]

References: [1] Verbeek & Morgan 1980, [2] Saether *et al.* 1993, [3] Mauck & Grubb 1995, [4] Weimerskirch *et al.* 1995, [5] Weimerskirch *et al.* 1999, [6] Duriez *et al.* 2000, [7] Weimerskirch *et al.* 2000.

suggest that the increase in foraging cost incurred as a result of increased body mass must be within the buffering capacity of this species. Handicapping may affect foraging efficiency by altering the centre of gravity, decreasing stability and increasing drag, as well as the energetic cost of flight. Previous handicapping experiments have attached weights to legs (Weimerskirch *et al.* 1999, Duriez *et al.* 2000) or the base of the tail (Wright & Cuthill 1989, Markman *et al.* 1995). As I wanted to increase only energetic flight costs, weights were attached in the tracheal pit where fat normally builds up prior to migration (Redfern & Clark 2001).

6.3. Methods

6.3.1. Weight attachment

Data were collected from May to July 2001. A total of 39 nests, with the modal clutch size of three eggs and with laying dates ±7 days of the modal laying date were assigned at random to handicapped (18) and control (21) treatments.

Lead weights of approximately 10% of adult body mass (12mm * 14mm * 5mm; 13g) were attached to 18 males (handicapped treatment). This was on average 10.2 (0.64)% of the body mass of males (range 9.4% - 11.7%). This size of increase in body mass was chosen to fall at the top range of previous handicap studies. The weight was added on average 4.5 (1.7) days before the first chick hatched at each nest (range 2 - 8 days before). The weights were attached to the underside of the feathers covering the tracheal pit using Saltair Ostomy Adhesive Solution (Salts Healthcare, UK).

6.3.2. Elimination of confounding variables

The following variables were measured to examine the possibility of confounding differences between treatments prior to weight attachment. Laying date was recorded as the number of days since the first egg in the colony was laid. Egg volume (cm^3; section 2.3) was measured on the day of laying, the volume of each egg within a clutch was summed to give a clutch volume. Data on incubation by each parent were collected as detailed in section 2.7.3. As incubation is continuous only the proportion of time spent incubating by females was compared between treatments. The number of days clutches were incubated (date of first hatched chick

Table 6.2: Data collected during incubation, before manipulation, at control and handicapped nests (n = 21 and 18 respectively).

	mean (s.d.) or median (IQR)			
	control	handicap	t or Z§	*p*
Laying date (days after first egg in colony)	12 (8-13.5)	11.5 (7-13)	-0.18§	0.9
Clutch egg volume (cm^3)	55.9 (5.06)	55.4 (3.65)	0.4	0.7
Length of incub. (days)	22.5 (22-23)	23 (22-23)	0.2§	0.9
Prop. incub. by female	0.52 (0.14)	0.55 (0.10)	-0.7	0.5
Male body mass (g)	118.9 (8.0)	122.9 (5.6)	-1.8	0.08
Female body mass (g)	129.3 (12.7)	129.4 (6.6)	-0.02	<1.0

minus date of first laid egg) was compared between treatments. Both adults from the 39 nests were caught prior to weight attachment, sexed and body mass recorded as index of body condition (details in section 2.5). The number of days after egg laying when the adults were caught and measured did not differ between experimental and control group (male: $t_{37} = 0.8$, p = 0.9; female: $t_{37} = 0.6$, p = 0.6).

Normally distributed data are quoted as mean (s.d.) and analysed using t-tests, whereas data that were not normally distributed are quoted as median (inter-quartile range, IQR) and analysed with Mann-Whitney U tests. As detailed in Table 6.2. there were no significant differences between treatments in any of the above variables. The hatching success also did not vary between treatments (number of chicks hatched divided by number of eggs: median (IQR), control = 1.0 (1.0-1.0), handicap = 1.0 (0.67-1.0): $G_1 = 0.2$, $p = 0.6$).

6.3.3. Comparing adult behaviour, chick size, growth, and survival between treatments

The methodology for randomised watches to record brooding and food provisioning is detailed in section 2.7.3. As brooding was not continuous the proportion of time spent brooding by each sex was compared between treatments using residual maximum likelihood model (REML; section 2.8), with treatment and brood size as fixed factors and nest identity as a random factor, with the proportion data arcsine transformed. Brooding focussed on the early chick-rearing period when chicks were brooded for at least 50% of the observation period. As in the previous chapters, food provisioning was considered for each sex in terms of trip duration, rate of fish delivery and rate of energy delivery. All three variables were analysed using repeated measures REML, with nest identity as the random factor, chick ages (1 – 4 days, 5 – 8 days, etc. until 20 – 24 days) as time points, brood size and treatment as fixed factors (trip duration data was square root transformed).

All chicks that hatched, fifty-five chicks from 21 control nests and 44 chicks from 18 handicapped nests, were monitored from hatching to fledging (or death) as detailed in section 2.4. Chick size (head plus bill length in mm, wing length in mm and body mass in g) was measured at hatching and at fledging. Fledging size and age was recorded when asymptotic body mass was reached. An average chick growth rate for body mass, wing length and head plus bill length was calculated from measurements taken approximately every two days during the linear growth phase (5 – 14 days).

To analyse the differences between treatments in chick size, growth and age of fledging REMLs were used with nest identity as a random factor, brood size, chick hatch order and treatment (control or handicapped) as fixed factors. If brood size or chick hatch order were not significant in the model they were removed and the analysis repeated. Chick survival was recorded as breeding and fledging success (medians (IQR)) and compared between treatments using G tests.

6.4. Results

There were no differences in size between chicks from control and handicapped nests either at hatching or at fledging (Table 6.3). There were also no differences between treatments in growth rates of chicks during the linear growth phase for head plus bill length, wing length or body mass. The sexes were also investigated separately (control = 19 males and 21 females; handicap = 17 males and 15 males) but showed no differences between groups (all $p > 0.05$). Age at fledging also did not differ between treatments (control = 21.5 (20-25) days; handicap = 23 (19-25.5) days: Mann Whitney U test : $Z = -1.0$, $n = 55$, $p = 0.3$).

Fledging success (number of fledged chicks divided by number of chicks hatched) did not differ between treatments (control = 0.42 (0.33-0.67), handicap = 0.67 (0.5-0.67), $G_1 = 0.2$, $p = 0.6$) and nor did overall breeding success (number of fledged chicks divided by number of eggs: both treatments = 0.33 (0.33-0.67), $G_1 = 0.02$, $p = 0.9$).

There was no difference between treatments in the proportion of time either sex spent brooding chicks during the early chick rearing period when chicks were brooded for at least 50% of the time (Table 6.4). There were also no differences, in either sex, in food provisioning, in terms of trip duration, rate of fish delivery and rate of energy delivery (Table 6.4).

Table 6.3: Chick size and growth statistics for control (c) and handicapped (h) chicks.

		Mean (s.d.)		Wald	
		control	handicap	(χ^2)	*p*
Hatching (55c / 44h)	Head-bill (mm)	32.3 (1.1)	32.5 (0.9)	0.8	0.4
	Wing (mm)	17.8 (0.9)	17.8 (1.1)	0.0	1.0
	Body mass (g)	13.8 (2.2)	14.1 (1.2)	0.3	0.6
Growth rate (40c / 32h)	Head-bill (mm day^{-1})	0.04 (0.01)	0.04 (0.01)	0.4	0.5
	Wing (mm day^{-1})	0.13 (0.03)	0.14 (0.03)	0.2	0.6
	Body mass (g day^{-1})	0.11 (0.04)	0.09 (0.04)	3.2	0.08
Fledging (26c / 26h)	Head-bill (mm)	63.6 (2.1)	64.2 (2.6)	0.7	0.4
	Wing (mm)	157.4 (18)	162.1 (23)	2.1	0.1
	Body mass (g)	119.6 (9.5)	120.5 (8.2)	0.3	0.6

Table 6.4: Adult behaviour statistics at control and handicapped nests.

		mean (s.d.)		t_{37}§ or	
		control	handicap	Wald (χ^2)	*p*
Brooding					
Prop. by male		0.17 (0.08)	0.18 (0.11)	0.06§	0.9
Prop. by female		0.30 (0.09)	0.31 (0.06)	-0.3§	0.7
Food Provisioning					
Trip duration (min)	male	22 (15)	24 (15)	1.2	0.3
	female	21 (13)	20 (10)	0.2	0.7
Fish delivered (fish hr^{-1}).	male	1.37 (0.9)	1.22 (0.7)	0.9	0.4
	female	1.15 (0.9)	1.07 (0.7)	0.5	0.5
Energy delivered (kJ hr^{-1})	male	3.15 (2.8)	3.18 (3.0)	0.01	0.9
	female	1.95 (2.3)	2.05 (2.2)	0.02	0.9

6.5. Discussion

6.5.1. Collection of data

Decisions about future investment may differ between birds of different ages. The exact age of the males used in this study were not known. However laying date in terns is correlated with age and adult quality, with young poorer quality birds breeding later (Nisbet *et al.* 1984, Wendeln 1997), and by only using nests with laying dates near the modal laying date, the extremes of the age spectrum were avoided. There were also no differences between the treatments in clutch size or egg volume, which are also indicators of age and quality (Saether 1990). Investment decisions may also be influenced by nutrient reserves (McNamara & Houston 1996). However as there were no differences between treatments in body condition for either sex, no bias occurred.

6.5.2. Impact of increased body mass

Handicapping male common terns, by increasing their body mass by 10%, did not cause them to raise fewer offspring or fledge offspring in poorer condition. If males had decreased their effort, their partners may have compensated at least partially (Wright & Cuthill 1989, 1990, Markman *et al.* 1995, Takahasi *et al.* 1999). However this was not the case.

As male common terns did not reduce investment in current offspring they appear to have been able to absorb the cost of increased body mass themselves. Another study on common terns attached a dummy transmitter weighing 8g (6% of body mass) which did not increase daily energy expenditure, or increase mass loss during incubation (Klaassen *et al.* 1992). Yet a 6% increase in body mass elicited a response from other seabirds (Table 6.1). It does therefore appear that in relation to Procellariiformes, terns have a greater buffering capacity.

As daily energy expenditure was not measured, the increase in effort produced by a 10% increase in body mass is unknown. Other species have been found to react to increased body mass by increasing the efficiency of their flight muscles (Kvist *et al.* 2001) or by strategically regulating their muscle mass to reduce flying costs without compromising performance (Swaddle & Biewenner 2000, Lind & Jakonsson 2001). If common terns can also regulate their muscle mass in response to an experimental increase in body mass, then the increase in effort produced by the experiment may have been minimal. However it is unlikely that terns can decrease their body reserves to a great extent, as Arctic terns *Sterna paradisaea* with low body masses were found to abandon their breeding attempt (Monaghan *et al.* 1989).

The cost of increased body mass may also be absorbed through behavioural plasticity (Davoren 2000). In other seabirds, high offspring output has been achieved by reducing time at the colony (Falk & Moller 1997, Bryant *et al.* 1999). Territorial attendance was not monitored directly in this study, but is reflected in trip duration. However there were no differences between treatments in trip duration. While away from the nest, common terns may also spend time at communal sites (Burger &

Gochfeld 1991). If this activity was replaced by more time spent foraging to self-feed, this may not have been detected in this study.

This study adds to the evidence from natural inter-year variation in food availability that many seabirds do have buffering capacity. This means that in years of high food availability parents may not be working as hard as previously suggested (Pearson 1968).

Chapter 7: The primary sex ratio and sexual differences in eggs, chick growth and chick survival.

7.1. Abstract

In many vertebrates, male offspring are more affected than female offspring by adverse conditions during growth. This is generally attributed to sexual size dimorphism, although greater sensitivity to poor environmental conditions could be more closely related to negative effects of steroids on males' physiology. To control for sexual differences in body size, I examined the sex ratio variation of offspring in common terns, a species with only slight sexual size dimorphism. In this species, the last-laid egg (termed the c-egg) is smaller than the first two and hatches last, so that the chick obtains relatively little food, due to low competitive ability, and therefore has a low probability of survival to fledging. This provides a powerful model for examining sex-linked mortality and sex ratio variation under natural conditions. I found that the sex ratio of c-eggs, but not of earlier-laid eggs, was significantly biased in favour of females. Maternal body condition was positively related to male, but not female, c-egg volume. Chicks from c-eggs had low survival compared to those from earlier-laid eggs and female c-chicks had significantly higher survival than male c-chicks. These data provide correlative evidence that factors other than sexual size dimorphism are involved in producing greater environmental sensitivity among male offspring.

7.2. Introduction

Recent studies of birds and mammals have provided strong evidence that parents can adjust the sex ratio of their offspring in relation to the social and environmental conditions experienced during breeding (e.g. Clutton-Brock & Iason 1986, Emlen 1997, Bradbury & Blakey 1998, Nager *et al.* 1999, Badyaev *et al.* 2002, Velando *et al.* 2002). A common factor favouring sex ratio adjustment is that in many species, male offspring are more vulnerable than females to adverse environmental conditions, with the result that postnatal mortality of males is often higher than that of females, particularly when environmental conditions are poor (review in Clutton-Brock 1991, Griffiths 1992). Males are typically larger than females at maturity, and male offspring have been reported to have greater energy requirements and food consumption than females in a number of species of mammals (Wolff 1988, Ono & Boness 1996) and birds (Slagsvold *et al.* 1986, Teather & Weatherhead 1994). Thus one likely explanation for greater environmental sensitivity among males is that males require more resources than females in order to sustain higher rates of development. This effect of body size is supported by studies of species with reversed sexual size dimorphism, which reported that parents produced more males during adverse environmental conditions (Appleby *et al.* 1997, Kalmbach *et al.* 2001), and that postnatal mortality was higher among females (Torres & Drummond 1997).

Taken together, these studies appear to provide strong evidence that differences in body size and growth rate are the major cause of sexual differences in the environmental sensitivity of offspring in a wide range of species. However this notion can be challenged on the grounds that in many species, growth is only a relatively minor component of the total energy budget (Ricklefs *et al.* 1998). About half the respiratory rate of young chicks reflects the costs of growing (Drent & Klaassen 1989) but this proportion declines steadily during growth, especially in non-altricial species, as energy expenditures for basal metabolism, thermoregulation and activity increase (Ricklefs *et al.* 1998). Thus only large differences in growth rate would be expected to have appreciable consequences for offsprings' food requirements, especially in non-altricial species. In blue-footed boobies *Sula nebouxii*, females grow faster than males and are about 32% heavier than males at the end of development, yet there is no difference between sexes in nestling food consumption (Torres & Drummond 1999). Rather, males grow more slowly than females for the same intake of food. Similar effects have been reported in sparrowhawks *Accipiter nisus*, where females grow to be more than 70% heavier than males without any greater food consumption (Newton 1978). Sexual size dimorphism could also not fully explain the differences in food consumption by male and female offspring in marsh harriers *Circus aeginosus* (Krijgsveld *et al.* 1998).

These data suggest that there must be other factors that act independently of body size to make males inherently more sensitive than females to environmental conditions during development. For instance greater sensitivity could result from the action of steroids such as testosterone, which are required to produce sexual differentiation of males from females but may have negative impacts on other aspects of male physiology that may lead to elevated mortality of males during adverse conditions (for instance by compromising immune function; Grossman 1985, Saino *et al.* 1995, Nolan *et al.* 1998). In species where males are larger, this would exaggerate the effects of differences in body size; in species with reversed sexual size dimorphism, it would reduce the impact of body size so that higher postnatal mortality of females under adverse conditions might occur only in species with rapid growth, altricial development and/or pronounced dimorphism. In support of this idea, the most convincing evidence to date of higher postnatal mortality among females is for blue-footed boobies, which are altricial and markedly dimorphic (Torres & Drummond 1997).

One way to disentangle the potentially confounding effects of body size and gender, is to examine species with negligible sexual size dimorphism. Any sex-linked differences in environmental sensitivity would then indicate the effects of possessing a male phenotype without any confounding influence of differences in body size. Sheldon *et al.* (1998) adopted this approach and found no sex-linked differences in environmental sensitivity of nestling collared flycatchers *Ficedula albicollis*, an altricial species with rapid postnatal growth. However data for other monomorphic species are lacking, particular for species with different modes of development and lower mass-specific growth rates.

In many species of bird, eggs hatch asynchronously in the order in which they are laid. Older earlier-hatched chicks are thus able to monopolise food provided by their parents with the result that younger later-hatched chicks are comparatively poorly fed (Mock & Ploger 1987, Stoleson & Beissinger 1995). In general, in birds that lay three-egg clutches, the effects of asynchronous hatching are exacerbated by the last-laid egg (termed the c-egg) being typically about 10% smaller than the first two, so that the chick is relatively small at hatching and has fewer reserves remaining from the yolk sack (Nisbet 1973, Meathrel *et al.* 1987, Williams 1994). In these species, chicks from c-eggs often experience elevated mortality (Sydeman & Morris 1992, Royle & Hamer 1998), which should produce strong selection for females to bias c-eggs in favour of the less sensitive sex. This provides a powerful model for examining sex-linked mortality and sex ratio adjustment under natural conditions.

Common terns *Sterna hirundo* have little sexual size dimorphism (chapter 3 data; difference between sexes in body mass < 3%, head plus bill length < 4%, which agrees with other authors Coulter 1986, Wendeln & Becker 1996, Craik 1999). Common terns also have asynchronous hatching and semiprecocial development (Bollinger *et al.* 1990); chicks have relatively high mass-specific costs of maintenance and activities compared to altricial species and are completely dependent on their parents for provision of food until they are fully grown. I examined sex ratios and survival of common tern offspring in relation to egg volume, clutch size, position within the laying sequence and maternal body condition. In particular, I tested three predictions that arise from the hypothesis that male offspring have greater environmental sensitivity than females, unrelated to sexual size dimorphism: (1) common terns should show no sexual differences in growth rates or food consumed; (2) female common terns should bias c-eggs in favour of females; (3) last-hatched female chicks should have lower postnatal mortality than last-hatched males.

7.3. Methods

Data were collected from May to July 2001. On the day of laying egg volume (cm^3; section 2.3) was measured for 47 two-egg clutches, and 111 three-egg clutches that covered the full range of laying dates for the colony. During incubation, 118 females (35 from two-egg clutches, 81 from three-egg clutches) were caught and body mass recorded as an index of body condition (details in section 2.5).

The sex of the embryos was determined from DNA analysis, either by taking tissue from dead embryos or chicks or from taking blood from chicks soon after hatching (full details section 2.6). All nests were checked daily to ascertain chick survival. A sample of chicks from 21 nests were measured (head plus bill length in mm, wing length in mm and body mass in g) approximately every other day and the data from the linear growth phase (5 - 14 days) used to calculate average growth rates (section 2.4). When asymptotic body mass was reached, size at fledging was recorded (section 2.4).

Randomised watches, throughout the chick-rearing period, recorded the food delivered to each chick. The number of fish and the fish size and species, as detailed in section 2.7.3 were recorded, enabling calculations of number of fish hr^{-1} and energy hr^{-1} for male and female offspring.

Sexual differences in egg volume were examined using residual maximum likelihood model (REML; section 2.8), with clutch size, egg laying order and embryo sex as fixed factors. Chick growth and fledgling size were also examined using REMLs, with brood size, chick hatching order and offspring sex as fixed factors. Food and energy consumption were analysed using repeated measures REML, chick ages (1 – 4 days, 5 – 8 days, etc. until 20 – 24 days) as time points, brood size, chick hatch order and offspring sex as fixed factors. Chick survival was examined using general linear mixed models with binomial error distributions (Schall 1991, Kalmbach *et al.* 2001), clutch size, chick hatch order and offspring sex were used as fixed factors. In all models nest identity was added as a random factor and non significant fixed factors were removed (except embryo or offspring sex) from the models.

7.4. Results

7.4.1. Egg volume and primary sex ratio

Primary sex ratio (numbers of male and female embryos) did not differ from the expected binomial distributions for two-egg clutches (16 of two females, 18 of one female plus one male, 13 of two males; $G_2 = 1.4$, $p = 0.5$) or for three-egg clutches (21 of three females, 44 of two females plus one male, 37 of one female plus two males, 9 of three males; $G_3 = 2.8$, $p = 0.4$; data include hatched and unhatched eggs). However c-eggs in three-egg clutches showed a significant bias in favour of females (39 male, 72 female; $G_1 = 5.0$, $p = 0.02$). There were also significantly more all female than male three-egg clutches (binomial test, $p = 0.04$), but there was no such difference in two-egg clutches ($p = 0.7$).

When eggs of all laying orders were considered, there was no overall difference in the sizes of eggs containing male and female embryos (mean ± s.d. (n); male = 18.7 ± 1.4cm^3 (189); female = 18.7 ± 1.5cm^3 (238)). However there was a significant interaction between embryo sex and laying order in three-egg clutches (Wald statistic (χ^2) = 9.6, d.f. = 2, $p = 0.008$), suggesting that smaller c-eggs were more likely to contain female embryos (Figure 7.1).

Adult females that laid three eggs were marginally significantly heavier during incubation than those that laid two eggs (128.4 ± 9.5g (81) and 124.8 ± 7.7g (35) respectively; $t_{114} = 2.0$, $p = 0.05$). There was also a positive relationship between maternal body condition and clutch volume for three-

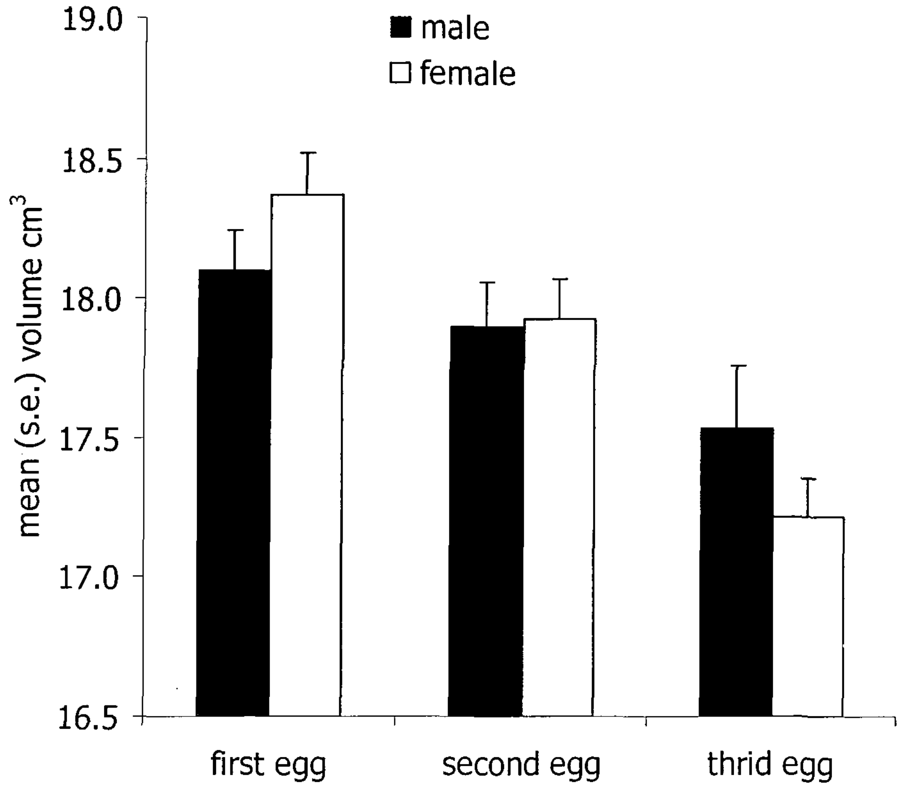

Figure 7.1: Egg volume with respect to sex and laying order. Number of male/female eggs in sample: first egg = 52/59, second egg = 54/57, third egg = 39/72.

egg clutches (linear regression; $F_{1,79}$ = 11.1, p = 0.001, R^2 = 0.1) but not for two-egg clutches ($F_{1,33}$ = 1.9, p = 0.2). When sexes of embryos in three-egg clutches were considered, maternal body condition was positively related to the volume of male c-eggs ($F_{1,28}$ = 12.1, p = 0.002, R^2 = 0.3) but not of female c-eggs eggs ($F_{1,49}$ = 0.9, p = 0.3).

7.4.2. Chick growth, fledging size and provisioning rates

Growth rates (head plus bill length, wing length and body mass) during the linear growth did not differ between the sexes (Table 7.1). The only significant sexual differences were in fledging head plus bill length and wing length (Table 7.1). The sexual size dimorphism (SSD calculated as in section 3.3) for head plus bill length was less than in adults (fledgling = 2.7%, adults = 3.4%) whereas SSD in wing length was greater in fledglings (fledgling = 2.4%, adults = 0.9%). There were no sexual differences in the rate of food or energy delivery to offspring (Table 7.2).

7.4.3. Hatching and fledging success

Overall hatching success was high (96% of male eggs; 95% of female eggs) and was not related to sex or egg volume ($p > 0.4$ in all cases). There was a significant interaction between the effects of laying order and sex on chick survival (three-egg clutches only: Wald statistic (χ^2) = 7.2, d.f. = 2, $p = 0.03$); chicks from c-eggs had low survival but this effect was ameliorated if the chick was female (Figure 7.2). There was some indication of a similar pattern in the second chicks from two-egg clutches, but with only marginal significance ($G_1 = 3.4$, n = 46, $p = 0.06$).

Table 7.1: Growth indices for male and female chicks and results of linear mixed models examining sexual differences in growth and fledging size.

	mean (s.d.) *n*				Wald (χ^2)	*p*
	male		female		d.f. = 1	
Growth rates						
Head –bill (mm day^{-1})	0.04 (0.008)	*23*	0.04 (0.007)	*23*	0.0	1.0
Wing (mm day^{-1})	0.13 (0.03)	*23*	0.14 (0.02)	*23*	1.6	0.2
Body mass (g day^{-1})	0.10 (0.04)	*23*	0.11 (0.04)	*23*	0.2	0.6
Fledging size						
Head-bill (mm)	64.74 (1.54)	*13*	63.05 (2.56)	*17*	7.6	0.006
Wing (mm)	159.5 (16.3)	*13*	155.8 (16.9)	*17*	7.5	0.006
Body mass (g)	119.8 (7.5)	*13*	117.2 (12.1)	*17*	0.04	0.8

Table 7.2: Food and energy consumption of male and female chicks

	mean (s.d.) *n*				Wald (χ^2)	*p*
	male		female		d.f. = 1	
No. of fish consumed (fish hr $^{-1}$)	1.17 (0.4)	*22*	1.26 (0.5)	*19*	3.2	0.07
Energy consumed (kJ hr $^{-1}$)	9.57 (8.2)	*22*	10.20 (8.5)	*19*	1.7	0.2

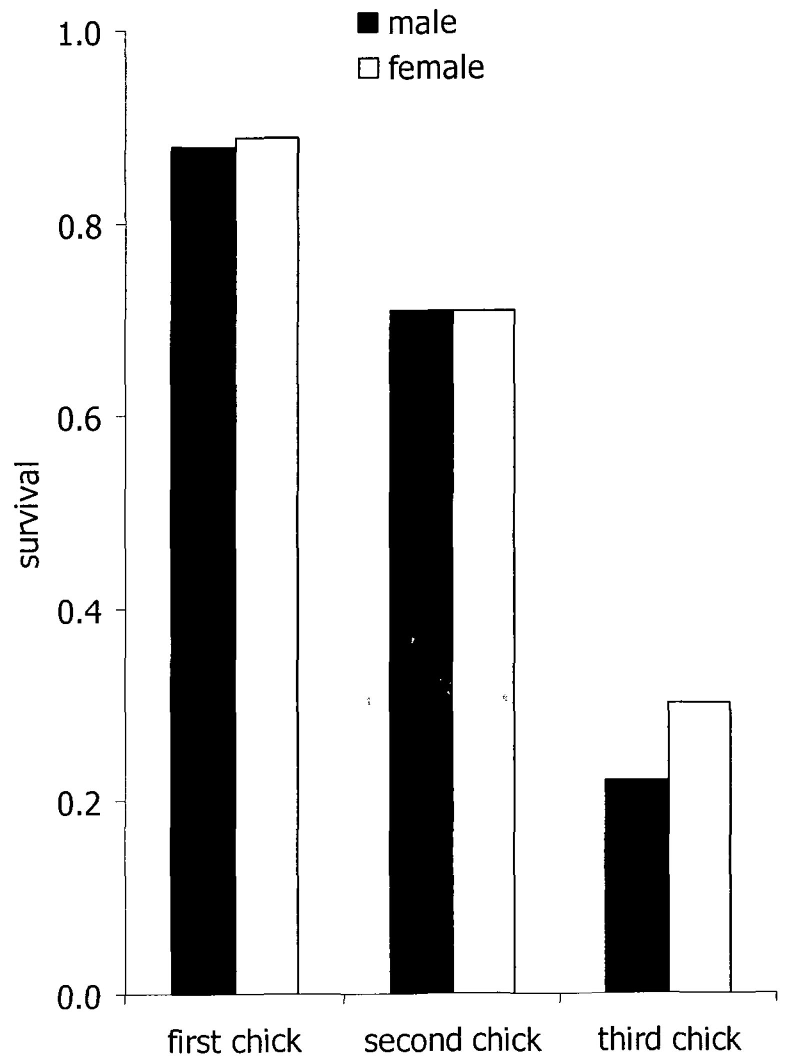

Figure 7.2: Chick survival to fledging of three-egg clutches, as a proportion of number of chicks hatched, with respect to sex and laying order. Number of male/female chicks hatched: first chick = 49/56, second chick = 51/55, third chick = 37/69.

7.5. Discussion

7.5.1. Sexual differences in growth and food consumption

As predicted there were no differences between the sexes in chick growth rates or in food and energy consumed. Therefore any difference in environmental sensitivity of male and female offspring could not simply be a function of differences in growth rate. Growth rates measured here covered the linear phase of growth up to 14 days post-hatching. In some sexually dimorphic species, growth rates are similar but the larger sex continues to grow for a longer period (Krijgsveld *et al.* 1998). This could be the same for the common tern and explain the small but significant difference between the sexes in size at fledging. However this was not detected in food consumption which covered this later period.

7.5.2. Sex ratio variation and the influence of maternal body condition

If size were acting alone, in species with negligible sexual size dimorphism there would be no sex bias in the embryos. However as predicted, in c-eggs there was a bias towards female embryos, providing evidence of sex-ratio adjustment in response to greater environmental sensitivity among male offspring, even when size is not a factor. In mammals, possession of heterologous sex chromosomes could also make males vulnerable to the expression of deleterious sex-linked recessive alleles. However this cannot be a universal explanation for greater environmental sensitivity among males because in bird females are the heterogametic sex (Charnov 1982).

An apparent female bias among c-eggs could result from differential mortality of male and female embryos. However this was not the case in this study, because hatching success of male and female eggs was very high ($\geq$ 95%) and the analysis of primary sex ratios included embryos from unhatched eggs. The bias in the last laid egg is consistent with the results of experimental manipulations of egg production, where there was a similar female bias in supernumerary eggs (Nager *et al.* 1999) indicating facultative sex ratio adjustment.

Experimental studies have also indicated a strong influence of maternal body condition (Nager *et al.* 1999, Kalmbach *et al.* 2001). In this study, under natural conditions, the strongest effect of maternal condition was on clutch size rather than sex ratio. Maternal condition was also positively related to the egg volume in male, but not female, c-eggs. This suggests that males benefit more than females from higher egg volume. This adds to the evidence that males are more sensitive to poor environmental conditions than females. The significant interaction between laying order and sex in egg volume also suggests that male c-eggs were larger than female c-eggs. Some studies have also found that paternal condition and quality influence offspring sex ratios (Svensson & Nilsson 1996, Sheldon *et al.* 1999), and in common terns, paternal quality is reflected in maternal condition through mate provisioning (Wendeln 1997).

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7.5.3. Environmental sensitivity

In common terns and related species, chicks from c-eggs are in poorer physical condition at hatching (Magrath 1992; Kilpi 1995; Blount *et al.* 2002) and receive less parental care than chicks from earlier-laid eggs (Langham 1972; Nisbet *et al.* 1995). Thus unless food supply is very good, c-chicks have relatively poor survival to fledging (Sydeman & Morris 1992; Royle & Hamer 1998; Robinson & Hamer 2000) as was found in this study (Figure 7.2). Under these poor environmental conditions female c-chicks had significantly higher survival than male c-chicks and this was not due to any sexual differences in growth rates or energy delivery rate.

There have been few other studies of gender and environmental sensitivity in species with negligible sexual size dimorphism. Sheldon *et al.* (1998) found no evidence that male collared flycatchers had poorer growth than females in artificially enlarged broods, which may suggest that there was no difference in environmental sensitivity of males and females in this species. However males may have competed more effectively than females for food provided by the parents (chicks with higher androgen levels have higher competitive ability; Eising *et al.* 2001). Moreover there was no difference in growth rates of chicks in enlarged and reduced broods, suggesting that parents may have compensated to some extent for changes in brood size by altering their rates of food supply to the nest (as found in pied flycatchers *Ficedula hypoleuca*; Moreno *et al.* 1995).

Sexual differences in growth rate should have a stronger effect on food requirements of offspring in rapidly-growing altricial species than in non-altricial species. Great skuas *Catharacta skua* have reversed sexual size dimorphism, and Kalmbach *et al.* (2001) found that female great skuas in poor body condition produced male-biased sex ratios at the end of an experimentally extended laying sequence. This was interpreted as strong evidence that larger size *per se* reduces offspring value under poor conditions. Yet great skuas are non-altricial and males are only 1-3% smaller than females as adults in a variety of morphological measurements (Hamer 2001). It is thus unlikely that there are substantive differences between sexes in nestlings' food requirements for growth. One possible advantage of a male-biased sex ratio is that females could have greater energy requirements than males for activity, but this also seems unlikely. Moreover Kalmbach *et al.* (2001) presented no evidence that chick survival to fledging was related to sex. Thus there are probably factors involved other than sex-specific differences in food requirement during growth. For instance during the breeding season, female great skuas have a specialised role defending the offspring from predation by conspecifics, for which large body size and heavy body mass are advantageous (Hamer & Furness 1993). Assuming that the long-term consequences of poor growth continue into adulthood (Hamer *et al.* 1991), then females reared under adverse environmental conditions would have an impaired ability to defend their own offspring. Hence, females whose chicks are likely to grow relatively poorly could benefit from rearing males in this species as a result of differential consequences of poor growth for the future reproductive potential of males and females.

7.5.4. Factors other than body size that may influence variation in sex ratios and sexual differences in survival

In common terns, recruitment of males but not females into the breeding population increases with advancing hatching date (P.H. Becker unpublished data), which suggests that recruitment of males may be more affected, than recruitment of females, by conditions experienced during growth, as also suggested for other species (Horak 1994; Albrecht & Johnson 2002). However this would be most likely to cause seasonal variation in the sex ratio (Dijkstra *et al.* 1990).

Differential variances in reproductive success (Howe 1977) could also lead to sexual differences in fitness benefits. While variance in reproductive success is typically most pronounced in polygamous mating systems, variation can occur in monogamous systems when extra pair fertilisations are prevalent (Kempenaers *et al.* 1997). However common terns have been found to be socially and genetically monogamous (Gonzalis-Solis *et al.* 2001), so variance in reproductive success is unlikely to cause sexual differences.

Although levels of maternal testosterone can increase from first to last laid egg, regardless of the embryo sex (Schwabl 1993), it has also been found that male eggs are provided with more steroids than female eggs (Petrie *et al.* 2001). Testosterone is known to increase growth rates

(Schwabl 1996) and competitive ability (Schwabl 1993) but also has a negative impact on immune function (Grossman 1985, Folstad & Karter 1992, Saino *et al.* 1995, Nolan *et al.* 1998). The higher levels of steroids could be reducing survival of male c-chicks. To test if higher levels of steroids are responsible for reduced survival in male chicks in poor condition, manipulation of steroid levels would be advantageous. Evidence to support sexual differences in immunity was found in kestrels *Falco tinnunculus,* where after correcting for body size males had lower immunity than females in poor conditions (Fargallo *et al.* 2002).

From this study, the cause of greater environmental sensitivity in male common terns can not be determined. However it is clear that gender, and not just size, can influence environmental sensitivity.

Chapter 8: General discussion.

8.1. General discussion

For most avian species reproduction is the most energetically expensive part of their life cycle. It has therefore been the focus for many researchers, pioneered by Lack (1947, 1968). The role of gender in reproduction, at least in monomorphic species, was largely ignored until recent advance in DNA-based technology (e.g. Griffiths *et al.* 1998) made sexing adults and offspring easier. Studies of species without sexually dimorphic plumage or size are therefore lagging behind studies of dimorphic species. This has led to many findings about sexual differences in parental care and offspring survival being explained in relation to sexual size differences. If size differences are the sole cause of sexual differences then in monomorphic species the same sexual differences would not be expected to occur. However this is not always the case, as was found in this study. Within this thesis I have also examined the ability of females to lay extra eggs and the ability of males to carry extra body mass during chick rearing. These topics will be discussed in relation to buffering capacity.

8.2. Size and adult common terns

Throughout this thesis I have maintained that common terns have negligible sexual size dimorphism. However in chapter 3, I attempted to identify the sex of adult terns using biometrics. Body mass is generally used to describe how much difference there is between the sexes; in common terns males were lighter than females (<3%). In the biometric that showed the greatest sexual difference, males had longer head plus bill lengths than females, with a difference of <4%. So although males have larger head plus bill lengths they are lighter in body mass. This makes common terns a difficult species to sex on size (only 73% accuracy if sexing individuals; 86% accuracy if comparing members of a pair), with neither sex being much larger than the other. I therefore feel justified in using common terns as an example of a seabird with negligible sexual size dimorphism.

8.3. Parental care

In common with most seabirds, common terns are monogamous with both parents contributing to egg production (males through mate provisioning), incubation and chick provisioning (Wiggins & Morris 1987, Fasola & Saino 1995, Moore *et al.* 2000). Although bi-parental care is common, effort is not always divided equally between the sexes (Lack 1968, Clutton-Brock 1991). In many instances, sexual differences have been attributed to size. For example, in crested auklets *Aethia cristatella* males brood more than females as they are larger, thereby providing better protection against predators (Fraser *et al.* 2000). Also the fact that larger males forage closer to the colony than smaller females has been attributed to asymmetric competition (Gonzalez-Solis *et al.* 2000). The larger size of males is also thought to enable them to carry larger food loads

(Weimerskirch *et al.* 1997). By foraging closer to the colony and delivering larger food loads, males provision with greater efficiency and provide more energy to offspring than females.

Male common terns were also found to have greater efficiency and to provide more energy to offspring than females (chapter 4), even though males are no larger in body size than females. This sexual difference in food provisioning appears to be a general pattern in terns (Fasola & Saino 1995 and references therein), although it is not immediately obvious why males should be more efficient or provide more energy than females. Terns often feed in flocks (Becker *et al.* 1993), where males may out-compete females for the larger fish. However the sexes also differ in the proportion of fish species they deliver. This may be due to the sexes foraging in different areas, which could also be related to competition, but I found no evidence for this from the lengths of foraging trips. In many Procellariiformes longer foraging trips are undertaken to replenish body reserves (Chaurand & Weimserskirch 1994, Weimerskirch *et al.* 1994, 1997, Booth *et al.* 2000). However in terns, males provide energy for females prior to egg laying and during incubation when body mass was measured, females were heavier than males. It therefore seems unlikely that females would need to replenish body reserves more than males, and this conclusions is supported by the lack of a sexual difference in the durations of trips.

Although provisioning rates and quantity of food delivered are relatively easy to measure, it is the energetic costs to each sex that are more important. As common terns are monogamous with low extra pair paternity (Gonzalez-Solis *et al.* 2001), the benefits of successfully raising offspring should be the same for both members of the pair. Therefore both members of a pair would be expected to contribute equally. Energetic costs of foraging are known to be greater than brooding (Adams *et al.* 1991, Nagy & Obst 1992), so if chick rearing alone is considered in common terns, it appears that males have a greater energetic cost than females. However if males remain lighter than females, then the cost of flight may be less for them (Freed 1981, Norberg 1981, Pennycuick 1989). It is generally thought that males provide more care during chick rearing as females incur greater costs during egg production. Although males provide nutrients for the females (up to 76%; Moore *et al.* 2000), it has not been determined how the sexes vary in energetic costs at this stage. Once this has been ascertained the effort provided by males and females over the whole breeding attempt may be quantified, and may indeed be the same as predicted if size causes sexual differences in dimorphic species.

Another aspect of parental care is parental favouritism, which may occur if the parents differ in benefits of providing care for different offspring. Common terns showed parental favouritism with respect to offspring sex, with mothers favouring sons early in chick rearing and fathers favouring daughters late in chick rearing (chapter 4). Previous studies that have looked for favouritism with respect to offspring have often found no evidence (Stamps *et al.* 1987, Teather 1992, Leonard *et al.*

1994, Westneat *et al.* 1995) or have found non-significant trends ($p < 0.1$, Harper 1985, Gowaty & Droge 1991). These trends also suggested that mothers fed sons and fathers fed daughters. However some theoretical models predict that if parents differ in benefits then they should show large biases (Lessells 2002), which have not been found. The direction of the biases is logical for species where the sexes differ in philopatry, and species defend territories which include their food supply as well as nest site (Harper 1985), but this is not the case for common terns. Therefore it is not immediately obvious why parental favouritism would occur. Research into issues such as inter-generational conflicts, and sexual differences in the relationship between fledging condition and future reproductive success, may shed light on why common terns show favouritism.

8.4. Sexes of embryos produced in monomorphic species

Trivers & Willard (1973) suggested that under certain environmental conditions, adjusting the primary sex ratio in favour of the sex with the greater reproductive value could enhance parental fitness. Manipulating offspring sex ratio is one way parents can fine-tune reproductive output to resource availability (Williams 1979). There is abundant evidence in invertebrates that females manipulate the sex ratio of offspring, but evidence has been more equivocal in birds (Clutton-Brock 1986, Krackow 1999). Evidence has been found that the sex ratio can be detected and manipulated by females before laying (Anderson *et al.* 1997, Heinsohn *et al.* 1997, Kilner 1998). Early work on the sex of offspring focused on species that could be sexed by plumage or size differences by the age of fledging. This could lead to biased data, if there were sexual differences in survival during early chick rearing (Clutton-Brock 1986, Hasselquist & Kempenaers 2002). Advances in DNA-based technology have enabled researchers to sex offspring as soon as they hatch and also to sex embryos from unhatched eggs. This technology also enables studies on species with little sexual difference in plumage or size, of which there have been few to date (Sheldon *et al.* 1998).

Benefits of producing males and females most usually differ in co-operative breeders, where one sex provides help for future broods (Komdeur *et al.* 1997, Arnold *et al.* 2001), or in polygamous breeding systems, where sexual differences in variation of reproductive success exist (Howe 1977). The overall sex ratio should not differ from unity in a monogamous species (reviewed in Sheldon 1998), as I found in common terns (chapter 7). When food availability is low the cheaper sex to produce is predicted to outnumber the more expensive sex (Myers 1978). In great tits *Parus major*, males are slightly larger than females, and therefore might initially be expected to be more expensive to raise than females. However a male bias was found in the sex ratio in poor environmental conditions (Dhondt 1970, Smith *et al.* 1989, Lessells *et al.* 1996). Yet more recently Oddie (2000) discovered that males were more competitive and gained more food within large broods and were more likely to survive when food availability was low. Therefore in great tits the cheaper sex to produce was males, which agrees with the sex ratios found. Low food availability in common terns occurs for the last hatched chick, therefore it would also be predicted that more of the cheaper sex would be produced. Indeed more females were produced (chapter 7). It is not immediately obvious why females should be cheaper to produce than males, when there are negligible size differences. However evidence is emerging of a link between steroid levels and immunological function (Grossman 1985), which could result in differential survival and therefore benefits from producing sons and daughters.

The sexes of embryos have also rarely been investigated in relation to clutch size, although sex has been investigated in studies where females produce supernumary eggs (Nager *et al.* 1999, Kalmbach *et al.* 2001). Data within chapter 5 suggest a tendency for more female embryos to be produced when larger clutches were laid. This may imply that female embryos require fewer nutrients or less energy during production, thereby enabling more of them to be produced. Although composition of eggs has been studied in many contexts (Williams 1994, Heaney *et al.* 1998, Jager *et al.* 2000, Nager *et al.* 2000a, Badzinski *et al.* 2001) the nutrient content in relation to embryo sex has not been determined. An alternative explanation would be that in producing more eggs the mother is unable to provide as much parental care later (Heaney & Monaghan 1995) and under conditions of reduced parental care female offspring may have better chances of survival than males. In lesser black backed gulls *Larus fuscus* male survival was reduced, in all male broods, when parental condition was also low (Nager *et al.* 2000b). This suggests that offspring requiring more parental care may have lower survival when parental condition is low. This may be because higher circulating testosterone concentrations mean males require more food to grow at the same rate as females, but this has yet to be confirmed.

8.5. Size and offspring growth and survival

In species with sexual size dimorphism the larger sex has been found to grow at a faster rate (Newton 1978, Collopy 1986, Fiala & Congdon 1983, Roskaft & Slagsvold 1985). The larger sex has also been found to have higher mortality than the smaller sex (Wegge 1980, Roskaft & Slagsvold 1985, Sayce & Hunt 1987, Griffiths 1992). However in species with little sexual size dimorphism no sexual differences in growth (Gowaty & Lennartz 1985, Nisbet & Szczys 2001) or mortality (Lombardo 1982, Gowaty & Lennartz 1985) have been found. In common terns, when all hatching orders were considered there were also no sexual differences in growth or survival (chapter 7). Clutton-Brock (1986) commented that for several species the differences between sexes in mortality only became clear when food availability was low. This was also the case for common terns, where for c-chicks, which suffer low food availability due to competition with older siblings; males had higher mortality than females.

If poor conditions were investigated in other monomorphic species, then sexual differences in survival may also be found.

8.6. Ability to increase effort: buffering capacity

Seabirds have to cope with fluctuating food availability. In years of low food availability, as long-lived species, seabirds are expected to produce fewer offspring, offspring in poorer condition or abandon the breeding attempt. However evidence is emerging that some species have the ability to increase foraging effort (Burger & Piatt 1990, Falk & Moller 1997). As demonstrated experimentally, male common terns can cope with increased body mass, without reducing provisioning effort or chick condition. Evidence for buffering is primarily from seabirds that forage relatively near to their breeding colonies (Burger & Piatt 1990, Falk & Moller 1997). These are also the species with lower adult survival than pelagic species (Hamer *et al.* 2001). Therefore species with lower adult survival may be more inclined to maximise current reproductive output rather than investing resources in the future.

The experiment increasing egg production (chapter 5) also showed that females that laid four eggs raised as many offspring, in similar fledging condition, to those that laid three eggs. This lack of difference between the females that laid four and three eggs may have been due to individual quality, with high quality birds being capable of absorbing the cost of extra egg production better than low quality birds (McNamara &

Houston 1996). Buffering capacity therefore may vary with individual quality within a species, and may not be an option for all individuals.

The contribution of the sexes during incubation showed differences between pairs that had laid two and three eggs (chapter 4). In three-egg pairs the males undertook a greater proportion of incubation than the males of four-egg pairs. As incubation in terns is continuous an adult must be able to stay incubating until its partner returns. This may require some flexibility, as weather conditions can affect terns' foraging effort (Taylor 1983) and therefore how long the mate may be away foraging for itself.

Ydenberg & Bertram's (1989) review of brood size manipulations in seabirds highlights that many species can raise more offspring than their modal clutch size. Within seabirds more species from Charadriiformes, which include terns, were able to raise extra offspring than from Procellariiformes. Although more recent studies have found egg production and incubation costs to be an important omission in brood enlargement experiments (Monaghan & Nager 1997, Thomson *et al.* 1998), these experiments may be another instance of greater buffering capacity in the seabirds that forage nearer the breeding colony.

8.7. Influence of environmental conditions on this work

The mean clutch size between 1996 and 2002 only fluctuated between 2.0 and 2.5 eggs per nest, whereas productivity ranged from 0.3 to 2.2 chicks per nest (Table 2.1). It therefore appears that productivity is a more sensitive measure of prevailing food availability and weather conditions than clutch size. The data presented in this thesis were collected between 1999 and 2001 when common tern productivity on Coquet Island was relatively high (1.1 to 2.2 chicks per nest, Table 2.1). This suggests that during experimental manipulations food availability was high and weather conditions not detrimental to chick survival. If food availability had been lower, then males with increased body mass may have been less able to maintain provisioning rates and fledge as many offspring.

References.

Adams, N. J., Abrams, R. W., Siegfried, W. R., Nagy, K. A. & Kaplan, I. R. 1991. Energy expenditure and food consumption by breeding cape gannets *Morus capensis*. *Marine Eco. Prog. Ser.* **70**: 1-9.

Albrecht, D. J. & Johnson, L. S. 2002. Manipulation of offspring sex ratio by second-mated female house wrens. *Proc. R. Soc. Lond. B* **269**: 461-465.

Alexander, R. D. 1974. The evolution of social behaviour. *Ann. Rev. Ecol. Syst.* **5**: 325-383.

Ainley, D.G., Spear, L.B. & Wood, R.C. 1985. Sexual colour and size variation in the south polar skua. *Condor* **87**: 427-428.

Anderson, D. J., Reeve, J. & Bird, D. M. 1997. Sexually dimorphic eggs, nestling growth and sibling competition in American kestrels *Falco sparverius*. *Func. Ecol.* **11**: 331-335.

Appleby, B. M., Petty, S. J., Blakey, J. K., Rainey, P. & Macdonald, D. W. 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls *Strix aluco*? *Proc. R. Soc. Lond. B* **264**: 1111-1116.

Arnold, J. M., Nisbet, I. C. T. & Hatch, J. J. 1998. Are common terns really indeterminate layers? Responses to experimental egg removal. *Col. Waterbirds* **21**: 81-86.

Arnold, K. E., Griffith, S. C. & Goldizen, A. W. 2001. Sex-biased hatching sequences in the cooperatively breeding noisy miner. *J. Avian Biol.* **32**: 219-223.

Badzinski, S. S., Ankney, C. D., Leafloor, J. O. & Abraham, K. F. 2001. Composition of eggs and neonates of Canada geese and lesser snow geese. *Auk* **118**: 687-697.

Baker, K. 1993. *Identification guide to European non-passerines.* British Trust for Ornithology, Thetford.

Badyaev, A. V., Hill, G. E., Beck, M. L., Dervan, A. A., Duckworth, R. A., McGraw, K. J., Nolan, P. M. & Whittingham, L. A. 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. *Science* **295**: 316-318.

Barrett, R.T., Peterz, M., Furness, R.W. & Durinck, J. 1989. The variability of biometric measurements. *Ringing & Migr.* **10:** 13-16.

Becker, P. H., Frank, D. & Sudmann, S. R. 1993. Temporal and spatial pattern of common tern *Sterna hirundo* foraging in the Wadden Sea. *Oecologia* **93**: 389-393.

Becker, P. H., Frank, D. & Wagener, M. 1997. Luxury in freshwater and stress at sea? The foraging of the common tern *Sterna hirundo. Ibis* **139**: 264-269.

Bevan, R. M., Butler, P. J., Woakes, A. J. & Prince, P. A. 1995. The energy expenditure of free-ranging black-browed albatrosses. *Phil. Trans. R. Soc. Lond. B* **350**: 119-131.

Blount, J.D., Surai, P.F., Nager, R.G., Houston, D.C., Moller, A.P., Trewby, M.L. and Kennedy, M.W. 2002. Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplementary feeding study of maternal effects. *Proc. R. Soc. Lond. B* **269**: 29-36.

Boersma, P.D. & Davies, E.M. 1987. Sexing monomorphic birds by vent measurements. *Auk* **104**: 779-783.

Bollinger, P. B., Bollinger, E. K. & Malecki, R. A. 1990. Tests of three hypotheses of hatching asynchrony in the common tern. *Auk* **107**: 696-706.

Bolton, M., Houston, D. C. & Monaghan, P. 1992. Nutritional constraints of egg formation in the lesser black-backed gull: an experimental study. *J. Anim. Ecol.* **61**: 521-532.

Booth, A. M., Minot, E. O., Fordham, R. A. & Imber, M. J. 2000. Co-ordinated food provisioning in the little shearwater *Puffinus assimilis hauakiensis*: a previously undescribed foraging strategy in the Procellariidae. *Ibis* **142**: 139-158.

Bosch, M. 1996. Sexual size dimorphism and determination of sex in yellow-legged gulls. *J. Field Ornithol.* **67:** 534-541.

Bradbury, R. B. & Blakey, J. K. 1998. Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*. *Proc. R. Soc. Lond. B* **265**: 895-899.

Bryan, S. M. & Bryant, D. M. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. *Proc. R. Soc. Lond. B* **266**: 157-162.

Bryant, R., Jones, I. L. & Hipfner, J. M. 1999. Responses to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador. *Can. J. Zool.* **77**: 1278-1287.

Burger, J. 1980. The transition to independence and post-fledging parental care in seabirds. in: *Behaviour of marine animals - vol 4 marine birds.* pp367-448 (eds. J. Burger, B. L. Olla & H. E. Winn), Plenum Press, New York.

Burger, J. 1981. Sexual differences in parental activities of breeding black skimmers. *Am. Nat.* **117**: 975-984.

Burger, J. 1986. Selection for equitability in some aspects of reproductive investment in herring gulls *Larus argentatus. Ornis Scand.* **18**: 17-23.

Burger, J. & Gochfeld, M. 1991. Reproductive vulnerability: parental attendance around hatching in roseate (*Sterna dougallii*) and common (*S. hirundo*) terns. *Condor* **93**: 125-129.

Burger, J. & Lesser, F. 1978. Selection of colony sites and nest sites by common terns *Sterna hirundo* in Ocean County, New Jersey. *Ibis* **120**: 433-449.

Burger, A. E. & Piatt, J. F. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Stud. Avian Biol.* **14**: 71-83.

Burger, J., Nisbet, I. C. T., Safina, C. & Gochfeld, M. 1996. Temporal patterns in reproductive success in the endangered roseate tern (*Sterna dougallii*) nesting on Long Island, New York and Bird Island, Massachusetts. *Auk* **113**: 131-142.

Burley, N. 1983. The meaning of assortative mating. *Ethol. & Sociobiol.* **4**: 191-203.

Burness, G. P. & Morris, R. D. 1992. Shelters decrease gull predation on chicks at a common tern colony. *J. Field Ornithol.* **63**: 186-189.

Byle, P. A. F. 1990. Brood division and parental care in the period between fledging and independence in the dunnock (*Prunella modularis*). *Behaviour* **113**: 1-20.

Catry, P., Ruxton, G.D., Ratcliffe, N., Hamer, K.C. & Furness, R.W. 1999. Short-lived repeatabilities on long-lived great skuas: implications for the study of individual quality. *Oikos* **84**: 473-479.

Charlesworth, B. 1980. *Evolution in age-structured populations.* Cambridge University Press, Cambridge.

Charnov, E. L. 1982. *The theory of sex allocation.* Princeton University Press, Princeton.

Chaurand, T. & Weimerskirch, H. 1994. Incubation routine, body mass regulation and egg neglect in the blue petrel *Halobaena caerulea. Ibis* **136**: 285-290.

Clutton-Brock, T. H. 1991. *The evolution of parental care.* Princeton University Press, Princeton.

Clutton-Brock, T. H. 1986. Sex ratio variation in birds. *Ibis* **128**: 317-329.

Clutton-Brock, T. H. & Iason, G. R. 1986. Sex ratio variation in mammals. *Q. Rev. Biol.* **61**: 339-374.

Collopy, M. W. 1986. Food consumption and growth energetics of nestling golden eagles. *Wilson Bull.* **98**: 445-458.

Coulson, J. C. 1968. Difference in the quality of birds nesting in the centre and on the edge of a colony. *Nature* **217**: 478-479.

Coulson, J. C. & Horobin, J. 1976. The influence of age on the breeding biology and survival of the Arctic tern *Sterna paradisaea. J. Zool. Lond.* **178**: 247-260.

Coulson, J. C. & Porter, J. M. 1985. Reproductive success of the kittiwake *Rissa tridactyla* : the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**: 450-466.

Coulson, J.C., Thomas, C S., Butterfield, J E L., Duncan, N., Monaghan, P. & Shedden, C. 1983. The use of head and bill length to sex live gulls *Laridae. Ibis* **125**: 549-557.

Coulter, M.C. 1986. Assortative mating and sexual dimorphism in the common tern. *Wilson Bull.* **98**: 93-100.

Cowley, E. 1999. Sand martin *Riparia riparia* - male or female? *Ringing & Migr.* **19:** 205-209.

Craik, J. C. A. 1999. Sexual dimorphism of common terns *Sterna hirundo* and Arctic terns *S. paradisaea. Ringing & Migr.* **19**: 311-312.

Cramp, S. (ed.) 1985. *The birds of the Western Palearctic.* Oxford University Press Oxford.

Croxall, J. P., Naito, Y., Kato, A. & Rothery, P. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps. J. Zool. Lond.* **225**: 177-199.

Davoren, G. K. 2000. Variability in foraging in response to changing prey distributions in rhinoceros auklets. *Marine Ecol. Prog. Ser.* **198**: 283-291.

del Hoyo, J., Elliot, A. & Sorgatal, J. (eds) 1994a. *Handbook of the birds of the world, vol 2: new world vultures to guineafowl.* Lynx Edicions, Barcelona.

del Hoyo, J., Elliot, A. & Sorgatal, J. (eds) 1994b. *Handbook of the birds of the world, vol 3: hoatzin to auks.* Lynx Edicions, Barcelona.

Dhondt, A. A. 1970. The sex ratio of nestling great tits. *Bird Study* **17**: 282-286.

Dijkstra, C., Daan, S. & Buker, J. B. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. *Func. Ecol.* **4**: 143-147.

Drent, R. H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 225-252.

Drent, R. & Klaassen, M. 1989. Energetics of avian growth: the causal link with bmr and metabolic scope. in: *Physiology of cold adaptation in birds.* (eds. C. Bech and R. E. Reinertsen), Plenum Press, London.

Duriez, O., Weimerskirch, H. & Fritz, H. 2000. Regulation of chick provisioning in the thin-billed prion: an inter-annual comparison and maipulation of parents. *Can. J. Zool.* **78**: 1275-1283.

Eising, C. M., Eikenaar, C., H, S. & Groothuis, T. G. G. 2001. Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. *Proc. R. Soc. Lond. B* **268**: 839-846.

Ellegren, H. & Sheldon, B.C. 1997. New tools for sex identification and the study of sex allocation in birds. *Trends Ecol. Evol.* **12**: 255-259.

Ellegren, H., Gustafsson, L. & Sheldon, B. C. 1996. Sex ratio adjustment in relation to paternal attractiveness in wild bird popualtions. *Proc. Natl Acad. Sci. USA* **93**: 11723-11728.

Elston, D. A., Horgan, G. W. & Hunter, E. A. 2001. *Introduction to REML for scientists*. BioSS, Edinburgh.

Emlen, S. 1997. When mothers prefer daughters over sons. *Trends Ecol. Evol.* **12**: 291-292.

Falk, K. & Moller, S. 1997. Breeding ecology of the fulmar *Fulmarus glacialis* and the kittiwake *Rissa tridactyla* in high-arctic northeastern Greenland, 1993. *Ibis* **139**: 270-281.

Fargallo, J. A., Laaksonen, T., Poyri, V. & Korpimaki, E. 2002. Inter-sexual differences in the immune response of Eurasian kestrel nestlings under food shortage. *Ecol. Letters* **5**: 95-101.

Fasola, M. & Saino, N. 1995. Sex-biased parental-care allocation in three tern species (Laridae, Aves). *Can. J. Zool.* **73**: 1461-1467.

Fiala, K. L. & Congdon, J. D. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* **64**: 642-647.

Folstad, I. & Karter, A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* **139**: 603-622.

Fraser, G. S., Jones, I. L. & Hunter, F.M. 2002. Male-female differences in parental care in monogamous crested auklets. *Condor* **104**: 413-423.

Freed, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation ? *Ecology* **62**: 1179-1186.

Frick, S. & Becker, P. H. 1995. Different feeding strategies of common tern and Arctic tern (*Sterna hirundo* and *S. paradisaea*) in the German Wadden Sea. *J. fur Ornithol.* **136**: 47-63.

Fridolfsson, A. K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**: 116-121.

Furness, R. W. & Monaghan, P. 1987. *Seabird ecology.* Blackie, Glasgow.

Gilbert, L., Burke, T. & Krupa, A. 1998. No evidence for extra pair paternity in the western gull. *Mol. Ecol.* **7**: 1549-1552.

Gonzalez-Solis, J., Becker, P. H. & Wendeln, H. 1999. Divorce and asynchronous arrival in common terns *Sterna hirundo. Anim. Behav.* **58**: 1123-1129.

Gonzalez-Solis, J., Croxall, J. P. & Wood, A. G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* **90**: 390-398.

Gonzalez-Solis, J., Sokolov, E. & Becker, P. H. 2001. Courtship feedings, copulations and paternity in common terns, *Sterna hirundo. Anim. Behav.* **61**: 1125-1132.

Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca. Ornis Scand.* **18**: 269-276.

Gowaty, P. A. 1993. Differential dispersal, local resource competition and sex ratio variation in birds. *Am. Nat.* **141**: 263-280.

Gowaty, P. A. & Droge, D. L. 1991. Sex ratio conflict and the evolution of sex biased provsioning in birds. *Proc. 20th Int. Ornithol. Congr.,* 932-945.

Gowaty, P. A. & Lennartz, M. R. 1985. Sex ratio of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. *Am. Nat.* **126**: 347-353.

Graves, J., Hay, R. T., Scallan, M. & Rowe, S. 1992. Extra pair paternity in the shag *Phalacrocorax aristotelis* as determined by DNA fingerprinting. *J. Zool.* **226**: 399-408.

Gray, C.M. & Hamer, K.C. 2001. Food provisioning behaviour of male and female Manx shearwaters *Puffinus puffinus. Anim. Behav.* **62**: 117-121.

Griffiths, R. 1992. Sex-biased mortality in the lesser black-backed gull *Larus fuscus* during the nestling stage. *Ibis* **134**: 237-244.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7**: 1071-1075.

Grossman, C. J. 1985. Interactions between the gonodal sterioids and the immune system. *Science* **227**: 257-261.

Hamer, K.C. 2001. Great skua *Catharacta skua. Birds of the Western Palearctic Update* **3**: 91-110.

Hamer, K.C. & Furness, R.W. 1991. Sexing great skuas *Catharacta skua* by discriminant analysis using external measurements. *Ringing & Migr.* **12**: 16-22.

Hamer, K.C. & Furness, R.W. 1993. Parental investment and brood defence by male and female great skuas *Catharacta skua*: the influence of food supply, laying date, body size and body condition. *J. Zool. Lond.* **230**: 7-18.

Hamer, K.C., Furness, R.W & Caldow, R.W.G. 1991. The effects of changes in food supply on the breeding ecology of great skuas *Catharacta skua* in Shetland. *J. Zool. Lond.* **223**: 175-188.

Hamer, K. C., Schreiber, B. A. & Burger, J. 2001. Breeding biology, life histories and life history - environmental interactions in seabirds. in: *Biology of marine birds*. pp215-259 (eds. B. A. Schreiber and J. Burger), CRC Press, Florida.

Hanners, L.A. & Patton, S.R. 1985. Sexing laughing gulls using external measurements and discriminant analysis. *J. Field Ornithol.* **56**: 158-164.

Harper, D. G. C. 1985. Brood division in robins. *Anim. Behav.* **33**: 466-480.

Harrison, C. & Castell, P. 1998. *Bird nests, eggs and nestlings of Britain and Europe*. Harper Collins Publishers, London.

Hasselquist, D. & Kempenaers, B. 2002. Parental care and adaptive brood sex ratio manipulation in birds. *Phil. Trans. R. Soc. Lond. B* **357**: 363-372.

Heaney, V. & Monaghan, P. 1995. A within-clutch trade-off between egg production and rearing in birds. *Proc. R. Soc. Lond. B* **261**: 361-365.

Heaney, V. & Monaghan, P. 1996. Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. *Proc. R. Soc. Lond. B* **263**: 1719-1724.

Heaney, V., Nager, R. G. & Monaghan, P. 1998. Effect of increased egg production on egg composition in the common tern *Sterna hirundo*. *Ibis* **140**: 693-696.

Heinsohn, R., Legge, S. & Barry, S. 1997. Extreme bias in sex allocation in *Eclectus* parrots. *Proc. R. Soc. Lond. B* **264**: 1325-1329.

Hislop, J. R. G., Harris, M. P. & Smith, J. G. M. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J. Zool. Lond.* **224**: 501-517.

Horak, P. 1994. Effect of nestling history on adult size and reproduction in the great tit. *Ornis Fennica* **71**: 47-54.

Hornfeldt, B., Hipkiss, T., Fridolfsson, A. K., Eklund, U. & Ellegren, H. 2000. Sex ratio and fledging success of supplementary-fed tengmalm's owl broods. *Mol. Ecol.* **9**: 187-192.

Houston, A. I. & Davies, N. B. 1985. The evolution of cooperation and life history in the dunnock *Prunella modularis*. in: *Behavioural ecology. Ecological consequences of adaptive behaviour.* pp471-487 (eds. R. M. Sibley & R. H. Smith), Blackwell, Oxford.

Howe, H. F. 1977. Sex ratio adjustment in the common grackle. *Science* **198**: 744-746.

Huyvaert, K. P., Anderson, D. J., Jones, T. C., Duan, W. R. & Parker, P. G. 2000. Extra pair paternity in waved albatrosses. *Mol. Ecol.* **9**: 1415-1419.

Jager, T. D., Hulscher, J. B. & Kersten, M. 2000. Egg size, egg composition and reproductive success in the oystercatcher *Haematopus ostralegus*. *Ibis* **142**: 603-613.

Jodice, P.G.R., Lanctot, R.B., Gill, V.A., Roby, D.D. & Hatch, S.A. 2000. Sexing adult black-legged kittiwakes by DNA, behaviour, and morphology. *Waterbirds* **23**: 405-415.

Kalmbach, E., Nager, R. G., Griffiths, R. & Furness, R. W. 2001. Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism. *Proc. R. Soc. Lond. B* **268**: 2175-2179.

Kato, A., Watanuki, Y., Nishiumi, I., Kuroki, M., Shaughnessy, P. & Naito, Y. 2000. Variation in foraging and parental behaviour of king cormorants. *Auk* **117**: 718-730.

Kempenaers, B., Verheyen, G. R. & Dhondt, A. A. 1997. Extra pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**: 481-492.

Kilner, R. 1998. Primary and secondary sex ratio manipulation by zebra finches. *Anim. Behav.* **56**: 155-164.

Kilpi, M. 1995. Egg size asymmetry within herring gull clutches predicts fledging success. *Col. Waterbirds* **18**: 41-46.

Klaassen, M., Becker, P. H. & Wagener, M. 1992. Transmitter loads do not affect the daily energy expenditure of nesting common terns. *J. Field Ornithol.* **63**: 181-185.

Kloskowski, J. 2001. Temporal patterns of parental resource distribution in the red-necked grebe: equalising the share of the survivors. *Behaviour* **138**: 1355-1370.

Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. 1997. Extreme adaptive modification in sex ratios of the Seychelles warblers eggs. *Nature* **385**: 522-525.

Krackow, S. 1999. Avian sex ratio distortions: The myth of maternal control. *Proc. 22 Int. Ornithol. Congr.* 425-433.

Krijgsveld, K. L., Dijkstra, C., Visser, G. H. & Daan, S. 1998. Energy requirements for growth in relation to sexual size dimorphism in marsh harrier *Cirus aeruginosus* nestlings. *Phys. Zool.* **71**: 693-702.

Kvist, A., Lindstrom, A., Green, M., Piersma, T. & Visser, G. H. 2001. Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* **413**: 730-732.

Lack, D. 1947. The significance of clutch-size. *Ibis* **89**: 302-352.

Lack, D. 1968. *Ecological adaptations for breeding in birds.* Methuen, London.

Langham, N. P. E. 1972. Chick survival in terns (*Sterna* spp.) with particular reference to the common tern. *J. Anim. Ecol.* **41**: 385-395.

Langham, N. P. E. 1983. Growth strategies in marine terns. *Stud. Avian Biol.* **8**: 73-83.

Leonard, M. & Horn, A. 1996. Provisioning rules in tree swallows. *Behav. Ecol. Sociobiol.* **38**: 341-347.

Leonard, M. L., Teather, K. L., Horn, A. G., Koenig, W. D. & Dickinson, J. L. 1994. Provisioning in western bluebirds is not related to offspring sex. *Behav. Ecol.* **5**: 455-459.

Lessells, C. M. 2002. Parentally biased favouritism: why should parents specialize in caring for different offspring ? *Phil. Trans. R. Soc. Lond. B* **357**: 381-403.

Lessells, C. M., Mateman, A. C. & Visser, J. 1996. Great tit hatchling sex ratios. *J. Avian Biol.* **27**: 135-142.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S. & Hamer, K. C. 2002. Sex specific foraging behaviour in a monomorphic seabird. *Proc. R. Soc. Lond. B.* **269**: 1687-1693.

Lind, J. & Jakobsson, S. 2001. Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proc. R. Soc. Lond. B* **268**: 1915-1919.

Lombardo, M. P. 1982. Sex ratios in the eastern bluebird. *Evolution* **36**: 35-51.

Magrath, R. D. 1992. Roles of egg mass and incubation pattern in establishment of hatching hierarchies in the blackbird (*Turdus merula*). *Auk* **109**: 474-487.

Markman, S., Yom-Tov, Y. & Wright, J. 1995. Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Anim. Behav.* **50**: 655-669.

Mauck, R. A. & Grubb, T. C. 1995. Petrel parents shunt all experimental increased reproductive costs to their offspring. *Anim. Behav.* **49**: 999-1008.

Mawhinney, K. & Diamond, T. 1999. Sex determination of great black-backed gulls using morphometric characters. *J. Field Ornithol.* **70**: 206-210.

McNamara, J. N. & Houston, A. I. 1996. State-dependent life histories. *Nature* **380**: 215-221.

Meathrel, C. E., Ryder, J. P. & Termaat, B. M. 1987. Size and composition of herring gull eggs: relationship to position in the laying sequence and the body condition of females. *Col. Waterbird* **10**: 55-63.

Mock, D. W. & Ploger, B. J. 1987. Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. *Anim. Behav.* **35**: 150-160.

Monaghan, P. & Nager, R. G. 1997. Why don't birds lay more eggs? *Trends Ecol. Evol.* **12**: 270-274.

Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. & Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea. J. Anim. Ecol.* **58:** 261-274.

Monaghan, P., Uttley, J. D. & Burns, M. D. 1992. Effect of changes in food availability on reproductive effort in Arctic terns *Sterna paradisaea. Ardea* **80**: 71-81.

Monaghan, P., Nager, R. G. & Houston, D. C. 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. *Proc R. Soc. Lond. B* **265**: 1731-1735.

Montevecchi, W. A. & Porter, J. M. 1980. Parental investment by seabirds at the breeding area with emphasis on northern gannets (*Morus bassanus*). in: *Behaviour of marine animals - vol 4 marine birds.* (eds. .J. Burger, B. L. Olla and H. E. Winn), Plenum Press, New York.

Moore, D. J., Williams, T. D. & Morris, R. D. 2000. Mate provisioning, nutritional requirements for egg production, and primary reproductive effort of female common terns *Sterna hirundo. J. Avian Biol.* **31**: 183-196.

Moreno, J., Cowie, R. J., Sanz, J. J. & Williams, R. S. R. 1995. Differential responses by males and females to brood manipulations in the pied flycatcher: energy expenditure and nestling diet. *J. Anim. Ecol.* **64**: 721-732.

Moreno, J., Merino, S., Potti, J., de Leon, A. & Rodriguez, R. 1999. Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. *Behav. Ecol. Sociobiol.* **46**: 244-251.

Moreno, J., Boto, L., Fargallo, J. A., de Leon, A. & Potti, J. 2000. Absence of extra pair fertilisations in the chinstrap penguin *Pygoscelis antarctica. J. Avian Biol.* **31**: 580-583.

Myers, J. H. 1978. Sex ratio adjustment under food stress: maximization of quality or numbers of offspring ? *Am. Nat.* **112**: 381-388.

Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson, R. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proc. Natl. Acad. Sci. USA* **96**: 570-573.

Nager, R. G., Monaghan, P. & Houston, D. C. 2000a. Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. *Ecology* **81**: 1339-1350.

Nager, R. G., Monaghan, P. & Houston, D. C. 2000b. Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). *Behav. Ecol. Sociobiol.* **48**: 452-457.

Nager, R. G., Monaghan, P. & Houston, D. C. 2001. The cost of egg production: increased egg production reduces future fitness in gulls. *J. Avian Biol.* **32**: 159-166.

Nagy, K. A. & Obst, B. S. 1992. Food and enery requirements of adelie penguins *Pygoscelis adeliae* on the Antarctic peninsula. *Physiol. Zool.* **65**: 1271-1284.

Neuman, J., Chardine, J. W. & Porter, J. M. 1998. Courtship feeding and reproductive success in black-legged kittiwakes. *Col. Waterbirds* **21**: 73-80.

Newton, I. 1978. Feeding and development of sparrowhawk *Accipiter nisus* nestlings. *J. Zool. Lond.* **184**: 465-487.

Nilsson, J. A. & Raberg, L. 2001. The resting metabolic cost of egg laying and nestling feeding in great tits. *Oecologia* **128**: 187-192.

Nisbet, I. C. T. 1973. Courtship feeding, egg size and breeding success in common terns *Sterna hirundo*. *Nature* **241**: 141-142.

Nisbet, I. C. T. 1981. Behaviour of common and roseate terns after trapping. *Col. Waterbirds* **4**: 44-46.

Nisbet, I. C. T. 2002. Common tern *Sterna hirundo. The Birds of North America no.618.* (eds. A. Poole and F. Gill), The Birds of North America, Inc., Philadelphia.

Nisbet, I. C. T. & Cam, E. 2002. Test for age-specificity in survival of the common tern. *J. Appl. Statist.* **29**: 45-83.

Nisbet, I. C. T. & Drury, W. H. 1972. Measuring breeding success in common and roseate terns. *Bird Band.* **43**: 97-106.

Nisbet, I.C.T. & Hatch, J.J. 1999. Consequences of a female-biased sex-ratio in a socially monogamous bird: female-female pairs in the roseate tern *Sterna dougallii. Ibis* **141**: 307-320.

Nisbet, I. C. T. & Szczys, P. 2001. Sex does not affect early growth or survival in chicks of the roseate tern. *Waterbirds* **24**: 45-49.

Nisbet, I. C. T., Winchell, J. M. & Heise, A. E. 1984. Influence of age on the breeding biology on common terns. *Col. Waterbirds* **7**: 117-126.

Nisbet, I. C. T., Spendlow, J. A. & Hatfield, J. S. 1995. Variations in growth of roseate tern chicks. *Condor* **97**: 335-344.

Nolan, P. M., Hill, G. E. & Stoehr, A. M. 1998. Sex, size, and plumage redness predict house finch survival in an epidemic. *Proc. R. Soc. Lond. B* **265**: 961-965.

Norberg, R. A. 1981. Optimal flight speed in birds when feeding young. *J. Anim. Ecol.* **50**: 473-477.

Norusis, M.J. 2000. *SPSS 10.0 Guide to Data Analysis.* Prentice Hall, London.

Oddie, K. R. 2000. Size matters: competition between male and female great tit offspring. *J. Anim. Ecol.* **69**: 903-912.

Ono, K. A. & Boness, D. J. 1996. Sexual dimorphism in sea lion pups: differential maternal investment or sex specific differences in energy allocation ? *Behav. Ecol. Sociobiol.* **38**: 31-41.

Parker, G. A. 1985. Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.* **33**: 519-533.

Parker, G. A., Mock, D. W. & Lamey, T. C. 1989. How selfish should stronger sibs be? *Am. Nat.* **133**: 846-868.

Partridge, L. & Harvey, P. H. 1985. Costs of reproduction. *Nature* **316**: 20.

Partridge, L. & Harvey, P. 1988. The ecological context of life history evolution. *Science* **241**: 1449-1455.

Partridge, L. 1989. An experimentalist's approach to the role of costs of reproduction in the evolution of life-histories. in: *Toward a more exact ecology.* pp231-248 (eds. P. Grubb and J. B. Whittaker), Blackwell Scientific Publications, Oxford.

Patterson, H. D. & Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**: 545-554.

Pearson, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. *J. Anim. Ecol.* **37**: 521-552.

Pennycuick, C. J. 1989. *Bird flight performance: a practical calculation manual.* Oxford University Press, Oxford.

Petrie, M., Schwabl, H., Brande-Lavridsen, N. & Burke, T. 2001. Maternal investment: sex differences in avian yolk hormone levels. *Nature* **412**: 498.

Pierotti, R. 1981. Male and female parental roles in the western gull under different environmental conditions. *Auk* **98**: 532-549.

Pugesek, B. H. 1987. Age-specific survivorship in relation to clutch size and fledging success in California gulls. *Behav. Ecol. Sociobiol.* **21**: 217-221.

Pyle, P., Sydeman, W. J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *J. Anim. Ecol.* **70**: 1088-1097.

Radford, A. N. & Blakey, J. K. 2000. Is variation in brood sex ratios adaptive in the great tit (*Parus major*)? *Behav. Ecol.* **11**: 294-298.

Ramsay, S. L. & Houston, D. C. 1997. Nutritional constraints on egg production in the blue tit: a supplementary feeding study. *J. Anim. Ecol.* **66**: 649-657.

Redfern, C. P. F. & Clark, J. A. 2001. *Ringers' manual.* British Trust for Ornithology, Thetford.

Reid, J. M., Monaghan, P. & Ruxton, G. D. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proc. R. Soc. Lond. B* **267**: 37-41.

Rice, W.R. 1989. Analysing tables of statistical tests. *Evolution* **43**: 223-225.

Richardson, D. S., Jury, F. L., Blaakmeer, K., Komdeur, J. & Burke, T. 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Mol. Ecol.* **10**: 2263-2273.

Ricklefs, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* **8**: 84-94.

Ricklefs, R. E. 1990. Seabird life histories and the marine environment: some speculations. *Col. Waterbirds* **13**: 1-6.

Ricklefs, R. E., Starck, J. M. & Konarzewski, M. 1998. Internal constraints on growth in birds. in: *Avian Growth and Development. Evolution within the Altricial-Precocial Spectrum.* (eds. J. M. Starck and R. E. Ricklefs), Oxford University Press, Oxford.

Robinson, J. A. 1999. *The comparative breeding ecology of sympatric common and Arctic terns in N. E. England.* Ph.D. thesis, University of Durham.

Robinson, J. A. & Hamer, K. C. 1998. Predation of Arctic tern chicks by rabbits in northeast England. *Seabird* **20**: 41-43.

Robinson, J.A. & Hamer, K.C. 2000. Brood size and food provisioning in common terns *Sterna hirundo* and Arctic terns *S. paradisaea*: consequences for chick growth. *Ardea*, **88**: 51-60.

Robinson, J. A., Chivers, L. S. & Hamer, K. C. 2001a. A comparison of Arctic tern *Sterna paradisaea* and common tern *S. hirundo* nest-site characteristics on Coquet Island, north-east England. *Atlantic Seabird* **3**: 49-58.

Robinson, J. A., Hamer, K. C. & Chivers, L. S. 2001b. Contrasting brood sizes in common and Arctic terns: the role of food provisioning rates and parental brooding. *Condor* **103**: 108-117.

Roskaft, E. & Slagsvold, T. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. *J. Anim. Ecol.* **54**: 261-266.

Royle, N. J. & Hamer, K. C. 1998. Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. *J. Avian Biol.* **29**: 266-272.

Saether, B.-E. 1990. Age specific variation in reproductive performance of birds. *Current Ornithol.* **7**: 251-283.

Saether, B.-E., Andersen, R. & Pedersen, H. C. 1993. Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antarctica. Behav. Ecol. Sociobiol.* **33**: 147-150.

Sagar, P. M. & Weimerskirch, H. 1996. Satellite tracking of southern buller's albatrosses from the Snares, New Zealand. *Condor* **98**: 649-652.

Saino, N., Moller, A. P. & Bolzern, A. M. 1995. Testosterone effects on the immune system and parasite infestations in the barn swallow (*Hirundo rustica*): an experimental test of the immunocompetence hypothesis. *Behav. Ecol.* **6**: 397-404.

Salzer, D. W. & Larkin, G. J. 1990. Impact of courtship feeding on clutch and third-egg in glaucous-winged gulls. *Anim. Behav.* **40**: 1149-1162.

Sayce, J. R. & Hunt, G. L. J. 1987. Sex ratios of prefledging western gulls. *Auk* **104**: 33-37.

Schall, R. 1991. Estimation of generalised linear models with random effects. *Biometrika* **78**: 719-727.

Schreiber, E. A. & Burger, J. (eds) 2001. *Biology of marine birds.* CRC Press, Florida.

Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. *Proc. Natl. Acad. Sci. USA* **90**: 11446-11450.

Schwabl, H. 1996. Maternal testosterone in the avian egg enhances postnatal growth. *Comp. Phys. Biochem.* **A114**: 271-276.

Sheldon, B. C. 1998. Recent studies of avian sex ratios. *Heredity* **80**: 397-402.

Sheldon, B. C., Merila, J., Lindgren, G. & Ellegren, H. 1998. Gender and environmental sensitivity in nestling collared flycatchers. *Ecology* **79**: 1939-1948.

Sheldon, B. C., Andersson, S., Griffiths, S. C., Ornborg, J. & Sendecka, J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**: 874-876.

Slagsvold, T. 1997. Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Anim. Behav.* **54**: 1357-1368.

Slagsvold, T., Roskaft, E. & Engen, S. 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scand.* **17**: 117-125.

Smiseth, P. T., Amundsen, T. & Hansen, L. T. T. 1998. Do males and females differ in the feeding of large and small siblings? An experiment with the bluethroat. *Behav. Ecol. Sociobiol.* **42**: 321-328.

Smith, H. G., Kallander, H. & Nilsson, J. A. 1989. The trade-off between offspring number and quality in the great tit *Parus major*. *J. Anim. Ecol.* **58**: 383-401.

Stamps, J., Clark, A. B., Arrowood, P. & Kus, B. 1985. Parent-offspring conflict in budgerigars. *Behaviour* **94**: 1-40.

Stamps, J., Clark, A., Kus, B. & Arrowood, P. 1987. The effects of parent and offspring gender on food allocation in budgerigars. *Behaviour* **101**: 177-199.

Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press Oxford.

Stevenson, I. R. & Bryant, D. M. 2000. Avian phenology: climate change and constraints on breeding. *Nature* **406**: 366-367.

Stoleson, S. H. & Beissinger, S. R. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? *Curr. Ornithol.* **12**: 191-270.

Summers, R.W., Nicoll, M., Underhill, L.G. & Petersen, A. 1988. Methods for estimating the proportions of Icelandic and British redshanks *Tringa totanus* in mixed populations wintering on British coasts. *Bird Study* **35**: 169-180.

Svensson, E. & Nilsson, J.-A. 1996. Mate quality affects offspring sex ratio in blue tits. *Proc. R. Soc. Lond. B* **263**: 357-361.

Swaddle, J. P. & Biewenner, A. A. 2000. Exercise and reduced muscle mass in starlings. *Nature* **406:** 585-586.

Sydeman, W. J. & Morris, R. D. 1992. Effects of parental age on hatching asynchrony, egg size and third-chick disadvantage in western gulls. *Auk* **109**: 242-248.

Takahasi, A., Niizuma, Y. & Watanuki, Y. 1999. Regulation of food provisioning and parental body condition in Leach's storm petrel, *Oceanodroma leucorhoa*: experimental manipulation of offspring food demand. *Ecol. Res.* **14**: 155-164.

Taylor, I. R. 1983. Effect of wind on foraging behaviour of common and Sandwich terns. *Ornis Scand.* **14**: 90-96.

Teather, K. L. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. *Behav. Ecol. Sociobiol.* **31**: 81-87.

Teather, K. & Weatherhead, P. J. 1994. Allometry, adaptation, and growth and development of sexually dimorphic birds. *Oikos* **71**: 515-555.

Thomson, D. L., Monaghan, P. & Furness, R. W. 1998. The demands of incubation and avian clutch size. *Biol. Rev.* **73**: 293-304.

Tinbergen, J. M. & Dietz, M. W. 1994. Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Func. Ecol.* **8**; 563-572.

Torres, R. & Drummond, H. 1997. Female-biased mortality in nestlings of a bird with size dimorphism. *J. Anim. Ecol.* **66**: 859-865.

Torres, R. & Drummond, H. 1999. Does large size make daughters of the blue footed booby more expensive than sons ? *J. Anim. Ecol.* **68**: 1133-1141.

Trivers, R. L. 1972. Parental investment and sexual selection. in: *Sexual selection and the descent of man 1871-1971.* pp136-179 (ed. B. Campbell), Aldine Publishing Company, Chicago, Illanois.

Trivers, R. L. 1974. Parent-offspring conflict. *Am. Zool.* **14**: 249-264.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**: 90-92.

Uttley, J. D. 1992. Food supply and allocation of parental effort in Arctic terns *Sterna paradisaea. Ardea* **80**: 83-91.

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

van Franeker, J.A. & ter Braak, C J.F. 1993. A generalized discriminant for sexing fulmarine petrels from external measurements. *Auk* **110**: 492-502.

Velando, A., Graves, J. & Ortega-Ruano, J. E. 2002. Sex ratio in relation to timing of breeding, and laying sequence in a dimorphic seabird. *Ibis* **144**: 9-16.

Verbeek, N. A. M. & Morgan, J. L. 1980. Removal of primary remiges and its effect on the flying ability of glaucous-winged gulls. *Condor* **82**: 224-226.

Visser, M. E. & Lessells, C. M. 2001. The costs of egg production and incubation in great tits (*Parus major*). *Proc. R. Soc. Lond. B* **268**: 1271-1277.

Wagner, R. H. & Safina, C. 1989. Relative contribution of the sexes to chick feeding in roseate and common terns. *Wilson Bull.* **101**: 497-500.

Ward, S. 1996. Energy expenditures of female barn swallows *Hirundo rustica* during egg formation. *Physiol. Zool.* **69**: 930-951.

Wanless, S., Harris, M. P. & Morris, J. A. 1995. Factors affecting daily activity budgets of south-georgian shags during chick rearing at Bird Island, South Georgia. *Condor* **97**: 550-558.

Warham, J. 1990. *The Petrels. Their ecology and breeding systems.* Academic Press, London.

Wegge, P. 1980. Distorted sex ratios and small broods in a declining capercaillie population. *Ornis Scand.* **11**: 106-109.

Weidinger, K. & van Franeker, J.A. 1998. Applicability of external measurements for sexing of the cape petrel *Daption capense* at within-pair, within-population and between-population scales. *J. Zool. Lond.* **245**: 473-482

Weimerskirch, H. & Jouventin, P. 1987. Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet islands: cause and consequences of the population decline. *Oikos* **49**: 315-322.

Weimerskirch, H. & Lys, P. 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biol.* **23**: 733-744.

Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeyer, X. & Judus, J. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Anim. Behav.* **47**: 472-476.

Weimerskirch, H., Chastel, O. & Ackermann, L. 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav. Ecol. Sociobiol.* **36**: 11-16.

Weimerskirch, H., Cherel, Y., Cuenor-Chaillet, F. & Ridoux, V. 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* **78**: 2051-2063.

Weimerskirch, H., Fradet, G. & Chevel, Y. 1999. Natural and experimental changes in chick provisioning in a long-lived seabird. *J. Avian Biol.* **30:** 165-174.

Weimerskirch, H., Price, P. A. & Zimmerman, L. 2000. Chick provisioning by the yellow-nosed albatross *Diomedea chlororhynchos*: response of foraging effort to experimentally increased costs and demands. *Ibis* **142**: 103-110.

Wendeln, H. 1997. Body mass of female common terns (*Sterna hirundo*) during courtship: relationships to male quality, egg mass, diet, laying date and age. *Col. Waterbirds* **20**: 235-243.

Wendeln, H. & Becker, P. H. 1996. Body mass change in breeding common terns *Sterna hirundo*. *Bird Study* **43**: 85-95.

Wendeln, H. & Becker, P. H. 1999. Effects of parental quality and effort on the reproduction of common terns. *J. Anim. Ecol.* **68**: 205-214.

Wendeln, H., Becker, P. H. & Gonzalez-Solis, J. 2000. Parental care of replacement clutches in common terns *Sterna hirundo*. *Behav. Ecol. Sociobiol.* **47**: 382-392.

Westneat, D. F., Clark, A. B. & Rambo, K. C. 1995. Within-brood patterns of paternity and paternal behaviour in red-winged blackbrds. *Behav. Ecol. Sociobiol.* **37**: 349-356.

Wiggins, D. A. & Morris, R. D. 1987. Parental care of the common tern *Sterna hirundo*. *Ibis* **129**: 533-540.

Williams, G. C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* **100**: 687-690.

Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. *Proc. R. Soc. Lond. B* **205**: 567-580.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev.* **69**: 35-59.

Wilson, M. F. & Pianka, E. R. 1963. Sexual selection, sex ratio and mating system. *Am. Nat.* **97**: 405-406.

Winkler, D. W. 1987. A general model for parental care. *Am. Nat.* **130**: 526-543.

Wolff, J. O. 1988. Maternal investment and sex ratio adjustment in American bison calves. *Behav. Ecol. Sociobiol.* **23**: 127-133.

Wooller, R. D., Bradley, J. S. & Croxall, J. P. 1992. Long-term population studies of seabirds. *Trends Ecol. Evol.* **7**: 111-114.

Wright, J. & Cuthill, I. 1989. Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* **25**: 171-181.

Wright, J. & Cuthill, I. C. 1990. Manipulation of sex difference in parental care: the effect of brood size. *Anim. Behav.* **40**: 462-471.

Ydenberg, R. C. & Bertram, D. F. 1989. Lack's clutch size hypothesis and brood enlargement studies on colonial seabirds. *Col. Waterbirds* **12**: 134-137.