REPRODUCTIVE DECISIONS IN MONOGAMOUS BIRDS

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Presented in candidature for the Degree of Doctor of Philosophy, to the
Faculty of Biomedical and Life Sciences, Glasgow University.
April 2001

CANDIDATE’S DECLARATION

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

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April 2001

ACKNOWLEDGEMENTS

The completion of this thesis would not have been possible without the support and help of many people. Thanks go, especially, to my supervisors Pat Monaghan and Graeme Ruxton. It can't be that easy having me as a PhD student and I think they did a fine job of keeping me on the straight and narrow. Thank you, also, to the Cumbrian Wildlife Trust for permission to work on Walney Island, Bill Makin, the warden, Rebecca Lewis for help in the field and Mertixell Genovart who sexed the gulls in the lab. The work on the zebra finches would not have been possible without John Laurie, Alister Kirk and Graham Adam who looked after them so well, Bill Stewart who made the mate-choice arenas and Andrew Ferguson who designed and built the electronic perches. I would like to thank the little beasties themselves, who chirruped so happily while I worked.

NERC gave me the opportunity to do this PhD by providing the funding and were very kind in allowing me to take three months out in the middle to do an Environmental Education project in Bolivia. Various people read through manuscripts and chapters, including long-suffering Ruedi Nager (who will probably be incredibly relieved now it is finally finished), Hanna Kokko and Nick Davies.

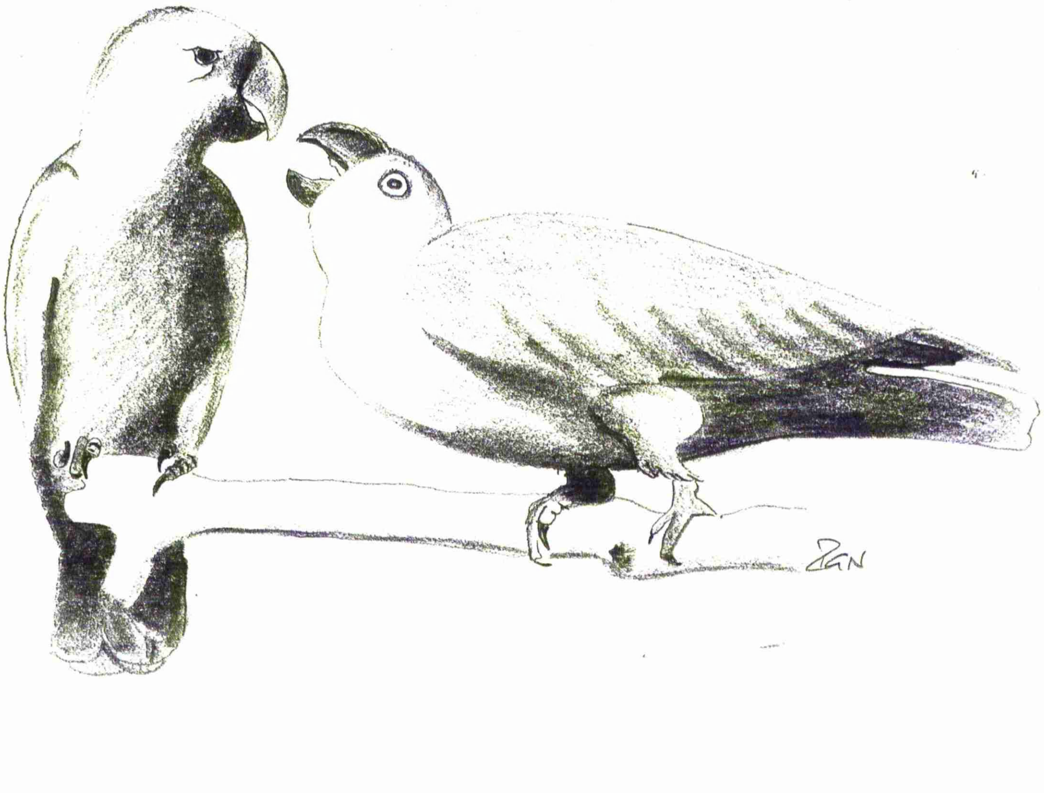
My friends and colleagues, both within and outwith D.E.E.B. have been great fun over the last few years but, in the interests of keeping this to one page, I cannot mention them all. However, special thanks go to those people who have had to share an office with me and put up with my incessant chatter: Suki Finney, Francis Daunt, Jane Reid, Steve Arnott, Elvira Polchanzka, Tom van-Pelt, Geoff Hilton, Mark Cook, Tom Sawyer, Darren Evans. Thanks, too, to my parents Lyn and Amanda (and my sister Jules too) for being great.

Lastly I would like to thank Ruedi, who has been absolutely wonderful over the last three and a half years. Not only was he official cake maker, hot-water bottle and moral supporter, he also gave me invaluable advice and help during both fieldwork and analysis, drew the fantastic pictures for each chapter and, most importantly of all, encouraged me to believe that I would finish this thesis … .eventually.

CONTENTS

Chapter 1

GENERAL INTRODUCTION



DECISION MAKING AND TRADE-OFFS

'You can't have your cake and eat it'

Anon.

As we were constantly reminded as children, we cannot both have our cake, and eat it. This is the basic argument behind the concept of trade-offs in life history theory (Fig. 1). Resources can often be used in different ways, but investment in one way often prohibits the investment of that same resource in another way. Therefore, individuals must consider this trade-off when deciding on an investment strategy (Fig. 2).

Figure 1. Trade-offs: Garfield wants to have his cake and eat it.

Every living organism faces trade-offs due to limited resources such as energy, time, space and nutrients. For example an individual that increases its investment in current reproduction may face reduced survival and/or ability to invest in future reproduction (Stearns 1992; Roff 1992; Daan et al. 1996; Nager et al. in press). Individuals are generally expected to act in ways that maximise their fitness, that is the representation of their genes in future generations, given the limited resources that are available to them.

One of the most basic decisions is the question of how to divide resources amongst growth, self-maintenance and reproduction. Investing in one will compromise an individual's ability to invest in the others. Many studies have looked into the trade-off between growth and reproduction (reviewed in Stearns 1992, and see Ernsting et al. 1993; Heino & Kaitala 1999) and the trade-off between self-maintenance and reproduction (reviewed in Stearns 1992, and see also Weimerskirch 1995; Rogowitz 1996).

Figure 2. Garfield has a difficult allocation decision to make

REPRODUCTIVE DECISIONS IN BIPARENTAL SPECIES

In this thesis, I concentrate on investment decisions made by individuals of species that provide biparental care. Biparental care is a relatively rare strategy, with birds being the only group in which it is common, occurring in 90% of known species (Lack 1968). It is, however, also found in some fish (Balshine-Earn & Earn 1998; Annett et al. 1999;

Lavery & Reebes 1994; Mrowka 1982), insects (Scott 1998; Rosengaus & Traniello 1991), amphibians (Jungfer & Weygolt 1999; Caldwell & de Oliveria 1999) and mammals (Lonstein & de Vries 1999; Wynne-Edwards 1995). Systems of biparental care tend to be associated with social monogamy, due to the constraints put on the parents if both are needed to raise the offspring, although in some biparental bird-species, other breeding systems such as polygyny and, more rarely, polyandry also occur (Clutton-Brock 1991). The simplest situation of biparental care to study, and the one that I examine in the following chapters, is that of monogamy. This is because decisions made within the pair will not be complicated by investments that one or both of the partners have made outside the partnership in terms of extra pair copulations (EPCs) or a second mate, which may affect that partner's willingness to care for the young.

In order to examine the reproductive decisions made by biparental species in more detail, I have chosen two monogamous species of birds to study empirically. Firstly, to study mate choice I used zebra finches (*Taeniopygia guttata*), which easily form pair bonds and breed in laboratory conditions. Secondly, to examine decisions made during breeding and parental care, I carried out a field study on the lesser black-backed gull (*Larus fuscus*), which nests in large open colonies that are easy to access and observe. The third approach I use involves theoretical models to look at reproductive decisions over allocation of parental care. The use of models allows me to investigate the elements of conflict and co-operation that favour the evolution of biparental care.

INTRODUCING THE CHAPTERS

If an individual provides substantial breeding resources or parental care it would pay that individual to be choosy when looking for a partner (Burley 1977; Jones & Hunter 1993; Andersson 1994; Amundsen 2000). In general, females are considered to be the choosy sex (Andersson 1994; Amundsen 2000). However, in biparental, monogamous species, the males invest considerably in the breeding event and have very few, if any, other opportunities to breed that season (for example by EPCs). We would therefore expect such males to choose to mate with females that will give them a higher reproductive success. In **chapter 2,** I investigate whether males make a decision to pair with more fecund females in an experiment using captive zebra finches.

Laying a replacement clutch when the first has been predated can mitigate the effects of loosing a clutch. Gulls also have the ability to replace the first egg if it is lost in the first few hours after laying. The benefits of this are not known, since egg production may, itself carry costs (Monaghan & Nager 1997). In **chapter 3**, I report an experiment designed to investigate whether replacing a lost egg, as indeterminate layers do, is beneficial in terms of reproductive performance.

The period of caring for the offspring is covered in chapters 4 and 5. The decisions become more complex in this period because each individual has the behaviour of their partner to consider along with the trade-offs in the allocation of resources between self-maintenance and reproduction. There will be both co-operation, as partners have a shared interest in the offspring, and also conflict, as each partner tries to preserve its own condition for future reproductive attempts. The co-operation between the sexes of the lesser black-backed gull is examined in **chapter 4**, where I describe an experiment in which I manipulated female investment during egg laying. I observed how the manipulation of investment changed the female's own pattern of parental behaviour, and that of her partner, over the rest of the breeding period. In **chapter 5**, I explore conflict theoretically, taking a situation where one parent must always be present at the nest. I present a graphical model to illustrate this and discuss how the conflict can be resolved.

Decisions of where to establish a territory and how individual quality affects this decision is tackled in **chapter 6**, using a field study on the lesser black-backed gull. Individuals with higher quality breeding sites generally have a higher breeding success (Newton 1991; Rees et al. 1991; Hatchwell et al. 1996; Côté 2000). This could be due to the good habitat itself, which may offer food resources or a protected nest site, or due to the quality of the individuals settling on the breeding site. In this chapter I test each of these hypotheses and look at decisions of timing of breeding and investment into the clutch.

The current state of an individual (e.g. age, condition, immunocompetence, parasite load) is known to affect reproductive decisions (McNamara & Houston 1996). In **chapter 7**, I investigate whether decisions of timing of laying and egg size can also be affected by one important aspect of state - body-size. Finally, in **chapter 8**, I draw together the findings of the preceding chapters and discuss them in a wider context.

REFERENCES

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **264**, 1579-1586.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Priceton.

Annett, C. A., Pierotti, R. & Baylis, J. R. 1999. Male and female parental roles in the monogamous cichlid, *Tilapia mariae*, introduced in Florida. *Environmental Biology of Fishes*, **54**, 283-293.

Balshine-Earn, S. & Earn, D. J. D. 1998. On the evolutionary pathway of parental care in mouth-brooding cichlid fish. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 2217-2222.

Burley, N. 1977. Parental investment, mate choice, and mate quality *Proceedings of the National Academy of Sciences U.S.A.*, **74,** 3476-3479.

Caldwell, J. P. & de Oliveira, V. R. L. 1999. Determinants of biparental care in the spotted poison frog, *Dendrobates vanzolinii* (Anura : Dendrobatidae). *Copeia*, 565-575.

Clutton-Brock, T. H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton.

Côté, S. D. 2000. Aggressiveness in king penguins in relation to reproductive status and territory location. *Animal Behaviour*, **59**, 813-821.

Daan, S., Deerenberg, C. & Dijkstra, C. 1996. Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology*, **65**, 539-544.

Ernsting, G., Zonneveld, C., Isaaks, J. A. & Kroon, A. 1993. Size at maturity and patterns of growth and reproduction in an insect with indeterminate growth. *Oikos*, **66**, 17-26.

Hatchwell, B. J., Chamberlain, D. E. & Perrins, C. M. 1996. The demography of blackbirds *Turdus merula* in rural habitats: Is farmland a sub-optimal habitat? *Journal of Applied Ecology*, **33** , 1114-1124.

Heino, M. & Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, **12**, 423-429.

Jones, I. L. & Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**, 238-239.

Jungfer, K. H. & Weygoldt, P. 1999. Biparental care in the tadpole-feeding Amazonian treefrog *Osteocephalus oophagus*. *Amphibia-Reptilia*, **20**, 235-249.

Lack, D. 1968. Ecological Adaptation for Breeding in Birds. Methuen & Co., London.

Lavery, R. J. & Reebs, S. G. 1994. Effect of mate removal on current and subsequent parental care in the convict cichlid (Pisces, Cichlidae). *Ethology*, **97**, 265-277.

Lonstein, J. S. & De Vries, G. J. 1999. Sex differences in the parental behaviour of adult virgin prairie voles: Independence from gonadal hormones and vasopressin. *Journal of Neuroendocrinology*, **11**, 441-449.

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

Monaghan, P. & Nager, R. G. 1997. Why don't birds lay more eggs? *Trends in Ecology and Evolution,* **12**, 270-274.

Mrowka, W. 1982. Effect of removal on the parental care behaviour of the biparental cichlid *Aequidens paraguayensis*. *Animal Behaviour*, **30**, 295-297.

Nager, R. G., Monaghan, P. & Houston, D. C. in press. The cost of egg production: increased egg production reduces future fitness in gulls. *Journal of Avian Biology*.

Newton, I. 1991. Habitat variation and population regulation in sparrowhawks. *Ibis* **133**, 76-88.

Rees, E. C., Black, J. M., Spray, C. J. & Thorisson, S. 1991. Comparative-study of the breeding success of whooper swans *Cygnus cygnus* nesting in upland and lowland regions of Iceland. *Ibis* **133**, 365-373.

Roff, D. A. 1992. The Evolution of Life Histories. Chapman & Hall, London.

Rogowitz, G. L. 1996. Trade-offs in energy allocation during lactation. *American Zoologist*, **36**, 197-204.

Rosengaus, R. B. & Traniello, J. F. A. 1991. Biparental care in incipient colonies of the dampwood termite *Zootermopsis angusticollis hagen* (Isoptera, Termopsidae). *Journal of Insect Behavior*, **4**, 633-647.

Scott, M. P. 1998. The ecology and behavior of burying beetles. *Annual Review of Entomology*, **43**, 595-618.

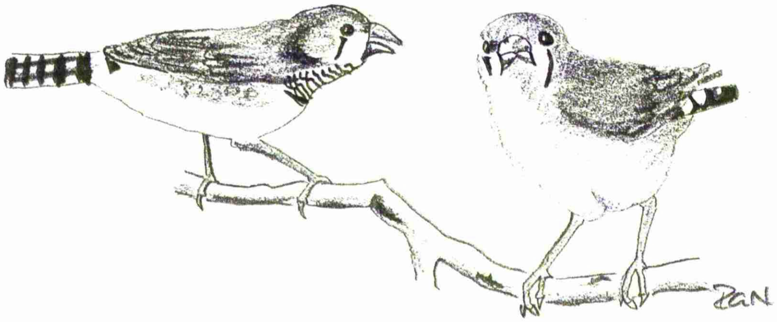
Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

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*. *Behavioral Ecology and Sociobiology*, **36**, 11-16.

Wynne-Edwards, K. E. 1995. Biparental care in Djungarian but not Siberian dwarf hamsters (Phodopus). *Animal Behaviour*, 50, 1571-1585.

Chapter 2

MALE MATE CHOICE AND FEMALE FECUNDITY



ABSTRACT

Studies of sexual selection have mostly focused on female choice and male-male competition. However, when a male contributes substantially to a breeding attempt, he would benefit from choosing a female whose reproductive potential is high in order to maximize his reproductive success. We examined male mate choice in zebra finches, *Taeniopygia guttata*, with respect to experimental manipulation of female fecundity. This was enhanced by a dietary supplement prior to contact with the males. When housed with females of differing fecundity, male zebra finches preferentially direct their courtship towards more fecund females. This outcome could be a consequence of female-female interactions or direct male preference. In this experiment, we gave males a choice between standard and supplemented females in an experimental arena where the females were spatially segregated, and could not interact with each other, thereby excluding the possibility of female-female competition. Males spent significantly more time with the more fecund female, they hopped more times on the perch opposite that female and were twice as likely to choose her than the standard female. The standard females were not, however, unreceptive to males, nor did they appear to differ in their activity patterns in response to the male. These results show that males are able to distinguish females that have higher fecundity, and that this is not the result of relative female competitiveness or dominance status.

INTRODUCTION

The main focus of studies of mate choice has been on females choosing males, since both theoretical and empirical studies of reproductive investment lead us to expect that females will generally be the choosier sex (Andersson 1994; Amundsen 2000). However, it is widely acknowledged that, in situations where females vary substantially in fecundity and/or where males provide breeding resources or parental care, males are also expected to be choosy (Burley 1977; Jones & Hunter 1993; Andersson 1994; Amundsen 2000). In ectothermic animals, there is generally considerable variation in the body size of mature females, and female size is closely related to the number or size of eggs she can lay (Côte & Hunte 1989; Honeka 1993; Merrett 1994; Kiorboe & Sabatini 1995; Clobert et al. 1998; Kraak & Bakker 1998; Garcia-Barros 2000). In such species, female size is therefore a good indicator of fecundity. Many studies of invertebrates, fish, reptiles and amphibians, both correlational (e.g. Côte & Hunte 1989; Wang & Millar 1997; Gage 1998; Arntzen 1999) and experimental (e.g. Olsson 1993; Capone 1995; Verrell 1995; Ptacek & Travis 1997; Kraak & Bakker 1998; Van Dongen et al. 1998; Harari et al. 1999), have shown that males discriminate between females by size when choosing a mate. In endotherms however, female size is generally not a reliable predictor of fecundity (but see Saether et al. 1997; Barbraud 2000). Any assessment of female reproductive potential is therefore likely to be based on more complex indicators of quality.

The majority of studies of mate choice in endotherms have been concerned with birds. However, studies of male mate choice in birds are relatively few (Amundsen

METHODS

The mate choice experiments took place in June and July 2000. Twenty males and 16 females were bought from several different breeders in spring 1999. In addition to these 12 males and 14 females in breeding age (> 9 months) that were raised in our lab were used. In all trials test individuals were presented with unfamiliar birds, avoiding previous breeding partner, parents, offspring or siblings.

The zebra finches were housed in cages (61 x 41 cm and 46 cm high) in single-sex pairs and had previously been fed on a 'standard diet'. The standard diet consisted of ad libitum mixed millet daily, containing pearl white, yellow, panicum, red, Japanese and Canadian canary millets (foreign finch seed, supplied by Haith's, Cleethorpes, Lincolnshire, U.K.) and in addition greens and a protein supplement containing egg-biscuit, poppy seeds (blue maw) and vitamins (rearing and condition soft food, also supplied by Haith's) once a week. At all times birds from both groups had access to water, cuttlefish bone and grit. Two weeks before taking part in the experiment females were split into two groups with different dietary regimes; one group continued to receive only the standard diet (standard group) while the other received the standard diet plus the protein supplement ad libitum daily (supplemented group). Females from such a supplemented group subsequently lay both larger eggs and larger clutches (Monaghan et al. 1996; Selman & Houston 1996). Males remained on the standard diet throughout the experiment.

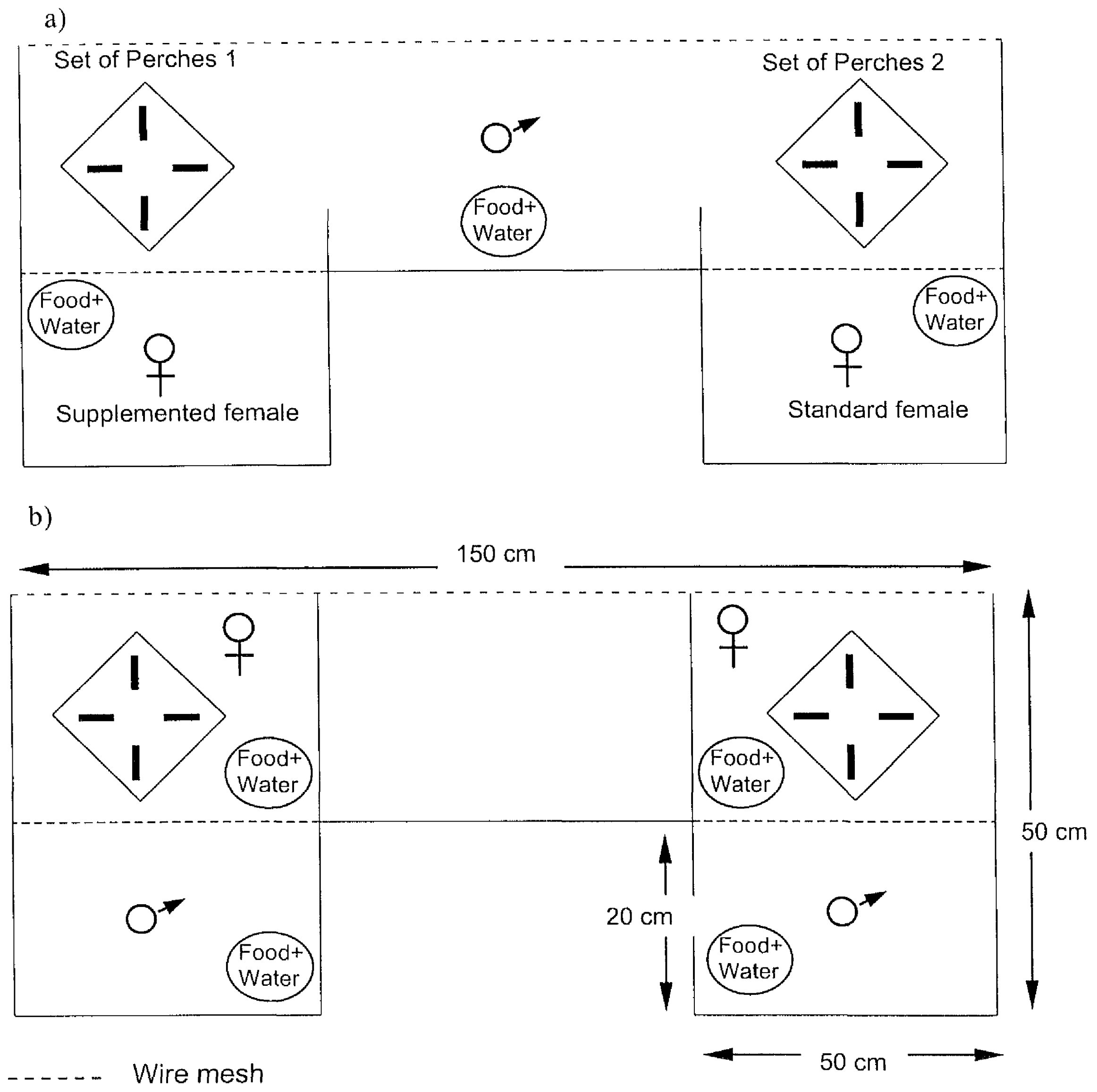


Figure 1. Diagrams of the arena used in the experiments. The lower half of the mesh was covered so that birds could only see each other when standing on the perches. a) The experimental set-up for the male mate-choice experiment b) a modification used to assess females' responsiveness to males.

perch within the array and the length of time he spent on it directly on to a PC. This gave a measure of how long the male was in visual contact with each female, and how active he was, as indicated by the extent to which he hopped between the perches.

We put a male and two females (one from each diet group) into the arena in the morning. The position of the females in the apparatus was randomized, and the female pairs used in each test were matched for colour (there were three colour morphs: wild-type, N = 14; fawn, N = 13; white, N = 2) and were also matched as far as possible by tarsus length and age (less than 1 year/more than 1 year). We gave the finches 30 min to settle in the apparatus and then recorded the males' behaviour on the perches for the next 7.5 h. We included in the analysis only males that spent at least 10 min on the perch array and therefore had seen the females. The cut-off point of 10 min was suggested by the distribution of total time spent on perches (Fig. 2). We took the proportion of time that the test male associated with the supplemented females as a measure of the preference for this female (e.g. Burley & Coopersmith 1987; Hill 1993; Swaddle & Cuthill 1994; Hansen et al. 1999; Johnsen et al. 2000). We tested this preference against an equal distribution of time between the two females (50%) using a Wilcoxon signed-ranks test. We also tested whether more males associated with the supplemented female against the null hypothesis that there is no preference for supplemented females (one-tailed binomial test, Zar 1984).

We could not use this experimental protocol to compare the behaviour of standard and supplemented females, because males spent little time with the standard females and male behaviour is likely to have influenced female behaviour. Therefore, to assess whether females on the two dietary regimes showed any difference in their behaviour towards males, in experiment 2 we used slightly modified arenas (Fig.1b) to quantify the behaviour of all the females in each treatment group in the continued presence of a male. Females had access to the electronic perches in one of the cage sections. Each had an unfamiliar male in the adjacent compartment and female activity levels were recorded by the apparatus in trials similar to the male mate choice experiments. One hour after the birds had been put into the arena, an observer hidden behind a screen took more detailed measurements of female behaviour. During this 1-h observation period, a time sampling protocol was used. Every 3 min (21 times in all) the female was assigned to a category on an increasing scale describing the degree of her interaction with the male: 0 = on ground; 1 = on a perch other than the perch closest to the male, 2 = on the closest perch to the male but inactive; 3 = communicating with the male; 4 = displaying (flights/ hopping side to side). To obtain measures of female activity and receptivity from these data, we used three measurements: perch-hops/min, taken from the electronic perch data, a total activity score (the sum of the activity scores taken during the observation period) and a communication score (the number of times the observer recorded the female communicating with, or displaying to the male during the 1-h observation period). The recorded activity of standard and supplemented females was compared with *t* tests.

Finally, in experiment 3, we examined whether males considered the standard females to be as acceptable as mates in the absence of a supplemented female. Males were tested again in the same apparatus, but this time with a choice between a standard female, which they had not encountered before, and an empty cage. We were able to use only 14 of the 23 males that had previously accepted the apparatus to ensure that they were matched with an unfamiliar female. Preferences and activity levels were recorded with the electronic perch arrays.

For proportional information, untransformed data are presented in the figures and tables but we arcsine transformed proportions before carrying out statistical tests. Means are given ± SE. Statistical tests are two-tailed unless otherwise stated.

RESULTS

Female body mass did not differ between the treatment groups either at the beginning of the supplemented dietary regime, or 2 weeks later at the time of the mate choice tests (repeated measures ANOVA: stage: $F_{1,25} = 0.006$, $P = 0.94$; diet: $F_{1,25} = 0.005$, $P = 0.943$; stage x diet interaction: $F_{1,25} = 0.728$, $P = 0.402$). Nor was there any difference in the mass of the standard and supplemented females presented to individual males in each test (paired samples t test: $t_{22} = 0.930$, $P = 0.362$).

Table 1. Behaviour of standard (*N* = 13) and supplemented (*N* = 11) zebra finch females in a 1-h observation period in experiment 2. Median values (25, 75 % quartile) are given for total activity score describing the intensity of the interaction of the female with the male and communication & display representing the number of incidences the female communicates with and displays to the male (see Methods)

Behaviour	**Standard**	**Supplemented**	***U***	***P***
Perch hops/min	1.20 (0.66, 3.08)	0.91 (0.48, 2.50)	63.0	0.622
Total activity score	42 (21, 45)	40 (21, 47)	67.5	0.816
Communication & Display	3 (2, 4)	2 (0, 5.5)	52.5	0.264

Behaviour tests were carried out in the modified arena (see Fig. 1b). Statistics are from Mann-Whitney *U* tests.

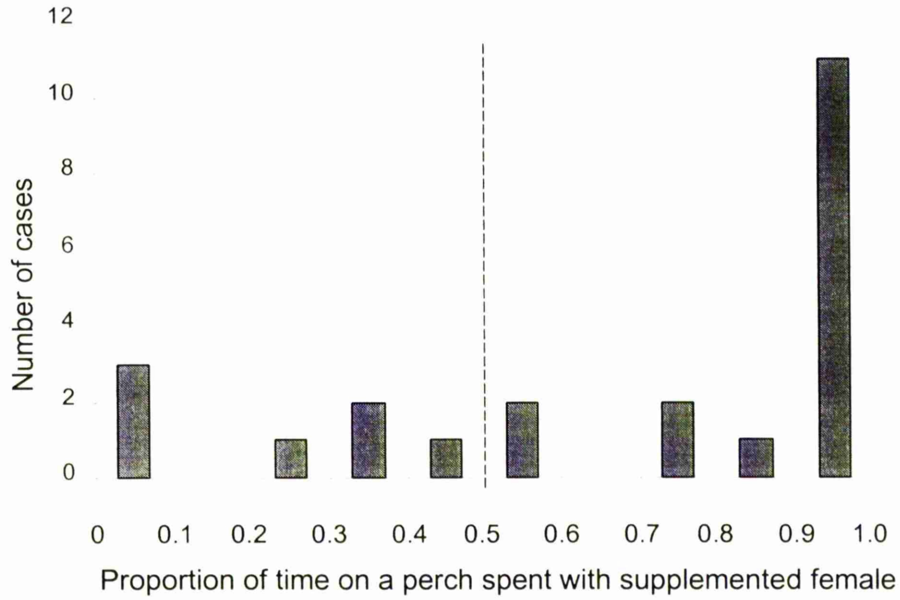


Figure 2. Frequency distribution of the number of males spending different proportions of time with the female that had been fed the protein supplement for 2 weeks prior to testing. The dotted line shows equal preference for the two females.

When presented with a standard and a supplemented female (experiment 1) nine of the 32 males used did not accept the perches i.e. spent less than 10 minutes on the perches (Fig. 2). Thus these males could not view the females and were excluded from further analysis. Males spent a significantly higher percentage of time with the supplemented female (67.8 ± 7.58 %) than would be expected by chance (50 %; Wilcoxon signed-ranks test: $Z = 2.11$, $N = 23$, $P = 0.035$; Fig. 3). Males also performed more hops on the perches in front of the supplemented female (median values (25, 75 % quartile), supplemented females: 27 (5, 135) hops, standard females: 11 (0, 67) hops;

standard and a supplemented female (29.4 ± 7.7 %, $N = 14$, paired t test: $t_{14} = 3.448$, $P = 0.004$).

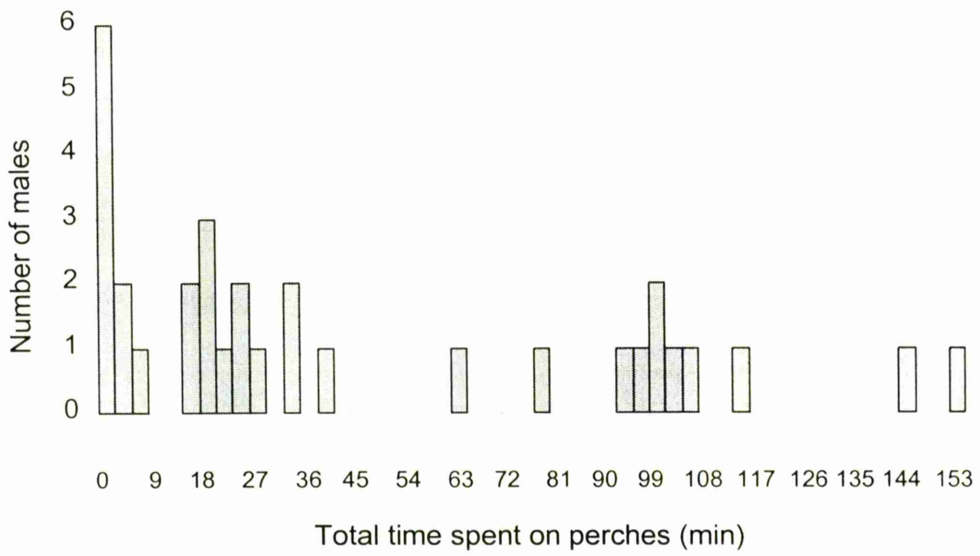


Figure 3. Frequency distribution of the number of males spending different proportions of time with the female that had been fed the protein supplement for 2 weeks prior to testing (experiment 1). The median (25, 75 % quartile) time males spent with supplemented females was 30.5 (16.5, 71.2) min and with standard females was 18.1 (0, 30.8) min. The dotted line shows the point of no male preference for either female

standard female may, however, not resolve the problem because the male may prefer to sit closer to a conspecific than a heterospecific partner, independent of sexual preference.

Although mate choice is a complex behavioural process, sexual mate preference has been measured regularly in the laboratory using similar choice apparatus to ours. Following the previous studies, we measured the amount of time males spent with each bird (e.g. Burley & Coopersmith 1987; Johnson 1988; Hill 1993; Swaddle & Cuthill 1994; Amundsen et al. 1997; Hansen et al. 1999; Johnsen et al. 2000) and the number of hops performed (e.g. Hunt et al. 1999) in front of each test female. Zebra finches usually form stable pair bonds within hours and then remain close to each other (Silcox & Evans 1982). Therefore, the measured association is likely to reflect sexual preference in zebra finches. Males also performed more hops in front of the supplemented female and this was a consequence of the increased time spent with her since male hopping rate was no different with the two females. There was no difference in hop frequency and males were not more active towards either of the females.

Our finding that male zebra finches can discriminate between females in the absence of any female interactions shows that males can assess current female condition. In ectotherms, differences in fecundity are related to body size (Côte & Hunte 1989; Honeka 1993; Merrett 1994; Kiorboe & Sabatini 1995; Clobert et al. 1998; Kraak & Bakker 1998; Garcia-Barros 2000), but endotherms, such as birds and mammals, show considerably less variation in mature body size, and there is little evidence that size of endotherms is related to fecundity (Roff 1992; Stearns 1992; Visman et al. 1996). Size is unlikely to be involved in the choice made in our experiment as females were matched for body size in the tests and dietary treatment did not affect females' mass. We did not find any gross behavioural differences between the two groups of females; supplemented females were no more active than the standard females, nor did they display or communicate more often with a male. It is possible, however, that more subtle behavioural differences between the females occurred.

Female quality may also be related to physical attributes other than size and behaviour. In this experiment, such attributes must have effectively signalled an individual's current condition, since the females were randomly allocated to an experimental treatment that had taken place during the 2 weeks preceding the choice test. Various plumage ornaments have been suggested as signals for displaying female quality and a number of studies have found that these correlate with fitness (Møller 1993; Johnsen et al. 1996; Potti & Merino 1996; Amundsen et al. 1997; Linville et al. 1998; Roulin et al. 2000; but see Rohde et al. 1999). The plumage of our experimental females, however, was formed well before the experimental treatment and is therefore unlikely to reflect short-term changes in a bird's condition, unless it relates to differences in preening behaviour, or preen gland condition. Coloration of the nonfeathered parts of the bird, such as legs and bill, often depend on carotenoids and may be better candidates for providing cues to short-term changes in condition as carotenoid levels are relatively mobile and the coloration they cause can change quickly (Burley et al. 1992; Cottam 1998; Negro et al. 1998; Saino et al. 2000). Bill colour of female zebra finches on protein-supplemented diets becomes more yellow (Cottam 1998) and males tend to choose females with more yellow-orange bill coloration (Burley & Coopersmith 1987). However, this needs to be tested by further experiments where bill coloration is manipulated independently of female condition. Whatever the mechanism males use to identify differences in female fecundity, it is obvious that this ability has a selective advantage.

REFERENCES

Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution*, **15**, 149-155.

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B,* **264**, 1579-1586.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Arntzen, J. W. 1999. Sexual selection and male mate choice in the common toad, *Bufo bufo*. *Ethology, Ecology and Evolution*, **11**, 407-414.

Barbraud, C. 2000. Natural selection on body size traits in a long-lived bird, the snow petrel, *Pagodroma nivea*. *Journal of Evolutionary Biology*, **13**, 81-88.

Burley, N. 1977. Parental investment, mate choice, and mate quality. *Proceedings of the National Academy of Sciences U.S.A.*, **74,** 3476-3479.

Burley, N. T. & Coopersmith, C. B. 1987. Bill color preferences of zebra finches. *Ethology*, **76**, 133-151.

Burley, N. T., Price, D. K. & Zaan, R. A. 1992. Bill color, reproduction and condition effects in wild and domesticated zebra finches. *Auk*, **109**, 13-23.

Capone, T. A. 1995. Mutual preference for large mates in green stink bugs, *Acrosternum hilare* (Hemiptera: Pentatomidae). *Animal Behaviour*, **49**, 1335-1344.

Clobert, J., Garland, T. & Barbault, R. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *Journal of Evolutionary Biology*, **11**, 329-364.

Côte, I. M. & Hunte, W. 1989. Male and female mate choice in the redlip blenny: why bigger is better. *Animal Behaviour*, **38**, 78-88.

Cottam, M. P. 1998. Selection, storage and utilization of protein in the zebra finch (*Taeniopygia guttata*). Ph.D. thesis, University of Glasgow.

Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. *Animal Behaviour*, **56**, 1311-1321.

Gage, M. J. G. 1998. Influences of sex, size, and symmetry on ejaculate expenditure in a moth. *Behavioral Ecology*, **9**, 592-597.

Garcia-Barros, E. 2000. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society*, **70**, 251-284.

Hansen, L. T. T., Amundsen, T. & Forsgren, E. 1999. Symmetry: attractive not only to females. *Proceedings of the Royal Society of London, Series B*, **266**, 1235-1240.

Harari, A. R., Handler, A. M. & Landolt, P. J. 1999. Size-assortative mating, male choice and female choice in the curculionid beetle *Diaprepes abbreviatus*. *Animal Behaviour*, **58**, 1191-1200.

Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*, **47**, 1515-1525.

Honeka, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483-492.

Hunt, S., Cuthill, I. C., Bennett, A. T. D. & Griffiths, R. 1999. Preferences for ultraviolet partners in the blue tit. *Animal Behaviour*, **58**, 809-815.

Johnsen, A., Fiske, P., Amundsen, T., Lifield, J. T. & Rohde, P. A. 2000. Colour bands, mate choice and paternity in the bluethroat. *Animal Behaviour*, **59**, 111-119.

Johnsen, T. S., Hengeveld, J. D., Blank, J. L., Yasukawa, K. & Nolan, V. 1996. Epaulet brightness and condition in female red-winged blackbirds. *Auk*, **113**, 356-362.

Johnson, K. 1988. Sexual selection in pinyon jays. 2. Male choice and female- female competition. *Animal Behaviour*, **36**, 1048-1053.

Jones, I. L. & Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**, 238-239.

Kiorboe, T. & Sabatini, M. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. *Marine Ecology Progress Series*, **120**, 285-298.

Kraak, S. B. M. & Bakker, T. C. M. 1998. Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Animal Behaviour*, **56**, 859-866.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Chapman & Hall.

Langmore, N. E. & Davies, N. B. 1997. Female dunnocks use vocalizations to compete for males. *Animal Behaviour*, **53**, 881-890.

Linville, S. U., Breitwisch, R. & Schilling, A. J. 1998. Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour*, **55**, 119-127.

Merrett, N. R. 1994. Reproduction in the North Atlantic oceanic ichthyofauna and the relationship between fecundity and species sizes. *Environmental Biology of Fishes*, **41**, 207-245.

Monaghan, P., Metcalfe, N. B. & Houston, D. C. 1996. Male finches selectively pair with fecund females. *Proceedings of the Royal Society of London, Series B*, **263**, 1183-1186.

Møller, A. P. 1993. Sexual selection in the barn swallow *Hirundo rustica.* 3. Female tail ornaments. *Evolution*, **47**, 417-431.

Negro, J. J., Bortolotti, G. R., Tella, J. L., Fernie, K. J. & Bird, D. M. 1998. Regulation of integumentary colour and plasma carotenoids in American kestrels consistent with sexual selection theory. *Functional Ecology*, **12**, 307-312.

Olsson, M. 1993. Male-preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). *Behavioral Ecology and Sociobiology*, **32**, 337-341.

Owens, I. P. F., Burke, T. & Thomson, D. B. A. 1994. Extraordinary sex-roles in the Eurasian dotterel: female mating arenas, female-female competition, and female mate choice. *American Naturalist*, **144**, 76-100.

Potti, J. & Merino, S. 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proceedings of the Royal Society of London, Series B*, **263**, 1199-1204.

Ptacek, M. B. & Travis, J. 1997. Mate choice in the sailfin molly, *Poecilia latipinna. Evolution*, **51**, 1217-1231.

Roff, D. A. 1992. *The Evolution of Life Histories*. London: Chapman & Hall.

Rohde, P. A., Johnsen, A. & Lifjeld, J. T. 1999. Female plumage coloration in the bluethroat: no evidence for an indicator of maternal quality. *Condor*, **101**, 96-104.

Roulin, A., Jungi, T. W., Pfister, H. & Dijkstra, C. 2000. Female barn owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London, Series B*, **267**, 937-941.

Saether, B. E., Lorentsen, S. E., Tveraa, T., Andersen, R. & Pedersen, H. C. 1997. Size-dependent variation in reproductive success of a long-lived seabird, the Antarctic petrel (*Thalassoica antarctica*). *Auk*, **114**, 333-340.

Saino, N., Ninni, P., Calza, S., Martinelli, R., De Bernardi, F. & Møller, A. P. 2000. Better red than dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings. *Proceedings of the Royal Society of London, Series B*, **267**, 57-61.

Selman, R. G. & Houston, D. C. 1996. The effect of pre-breeding diet on reproductive output in zebra finches. *Proceedings of the Royal Society of London, Series B*, **263**, 1585-1588.

Silcox, A. P. & Evans, S. M. 1982. Factors affecting the formation and maintenance of pair bonds in the zebra finch, *Taeniopygia guttata. Animal Behaviour*, **30**, 1237-1243.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Swaddle, J. P. & Cuthill, I. C. 1994. Preference for symmetric males by female zebra finches. *Nature*, **367**, 165-166.

Van Dongen, S., Matthysen, E., Sprengers, E. & Dhondt, A. A. 1998. Mate selection by male winter moths *Operophtera brumata* (Lepidoptera, Geometridae): adaptive male choice or female control? *Behaviour*, **135**, 29-42.

Verrell, P. A. 1995. Males choose larger females as mates in the salamander *Desmognathus santeelah*. *Ethology*, **99**, 162-171.

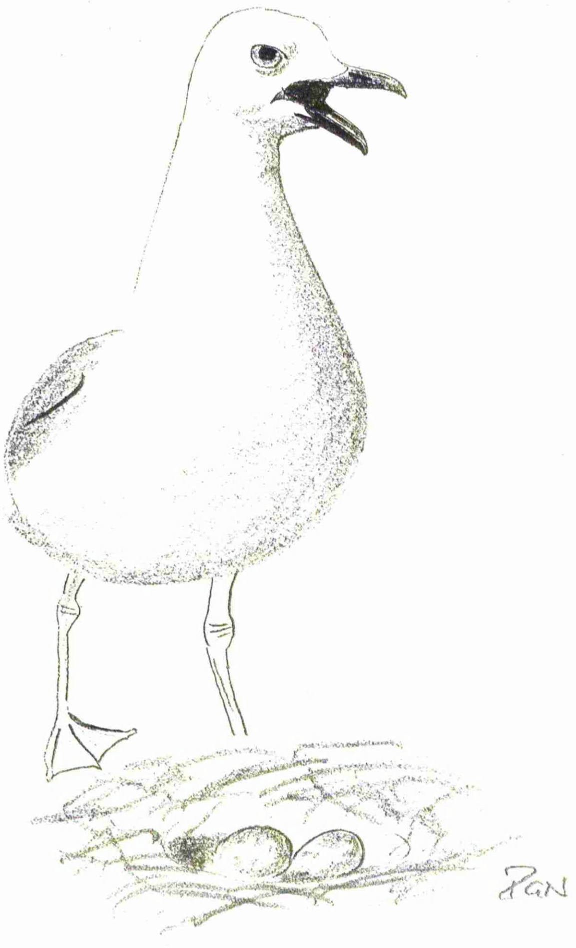
Visman, V., Pesant, S., Dion, J., Shipley, B. & Peters, R. H. 1996. Joint effects of maternal and offspring sizes on clutch mass and fecundity in plants and animals. *Ecoscience*, **3**, 173-182.

Wang, Q. & Millar, J. G. 1997. Reproductive behavior of *Thyanta pallidovirens* (Heteroptera: Pentatomidae). *Annals of the Entomological Society of America*, **90**, 380-388.

Zar, J. H. 1984. *Biostatistical Analysis*. 2nd edn. Englewood Cliffs, New Jersey: Prentice-Hall.

Chapter 3

REPLACEMENT EGG LAYING IN THE LESSER BLACK-BACKED GULL: ADAPTIVE BEHAVIOUR OR PHYSIOLOGICAL CONSTRAINT?



ABSTRACT

Predation is an almost universal risk in nature. Colonial nesting birds, especially, suffer from intense predation pressure on eggs and chicks at the time of breeding. Laying a replacement clutch when the first has been predated is one way that birds, such as gulls, can mitigate the effects of loosing a clutch. Gulls also have the ability to replace the first egg if it is lost in the first few hours after laying. This chapter describes an experiment to test whether laying a replacement egg is an adaptive strategy for lesser black-backed gulls (*Larus fuscus*). I found that females that lay a replacement egg did not fare any better than an experimental group created to emulate a group of non-replacers. Due to poor conditions in the year of study, replacing a lost egg may not have been adaptive, as nests containing fewer chicks seemed to be more successful because of less competition for food in the nest. I cannot rule out the possibility that replacing a lost egg is adaptive under good environmental conditions. I discuss the advantages and disadvantages of laying a replacement egg.

INTRODUCTION

Predation of young has an enormous effect on an individual's breeding success. It is, therefore, not surprising that most species of animal have adapted their life history in various ways to deal with it. Some organisms, for example many species of fish and insects, produce large numbers of offspring and invest very little in each in the hope that some will survive to adulthood. Others, like birds and mammals, have few offspring but invest more in terms of parental care and brood protection. Even though these animals are careful to protect their offspring, some still suffer predation and the parent/s must be able to change their strategy in order to maximise their reproductive success during what remains of the breeding season. Many birds will lay a replacement clutch if the first is predated, which means that they will still have the possibility of producing offspring during that breeding season. However, this is costly in terms of time and energy and is often risky as the young may not survive if they are brought up late in the season (Sorci et al. 1997). Indeed we find that birds are more likely to replace clutches towards the beginning of a season (Arnold 1993; Barba et al. 1995; Hegyi & Sasvari 1998), or if they are good quality females or in good body condition (Rooneem & Robertson 1997; Hipfner et al. 1999). Some species of bird also have the ability to replace eggs lost within a short period of laying (Haywood 1993). It is thought that this strategy may act to limit the impact of predation that occurs during laying, although less is known about its adaptive significance.

Many colonial birds experience a high predation pressure on eggs and chicks. In seabirds, especially, eggs are often lost soon after laying (Ewins 1991; Holloway 1993;

Regehr & Montevecchi 1997; Bukacinski et al. 1998; Blight et al. 1999) and many have the ability to replace these losses (Haywood 1993). Gulls, for example, can be classified as 'tactile indeterminate layers' (Haywood 1993). This means that tactile stimulation of the brood patch by eggs causes the cessation of laying. Many gulls normally lay a clutch of three eggs and if the first egg is lost within 12 hours of laying, then it is replaced with a further egg (Parsons 1976).

Replacement egg laying has possible costs and it is therefore unclear whether it is better to replace a lost egg or not. Egg removal experiments in the lesser black-backed gull have shown that birds laying one additional egg are significantly less successful breeders than birds laying and raising three (Monaghan et al. 1995; 1998). A reduced breeding success in experimental nests suggests that replacement egg laying may not, in fact, be adaptive. There are other theories as to why some birds are indeterminate egg layers. It may be an adaptation by species that experience brood parasitism to prevent them ending up with too many eggs in the nest (Power et al. 1989; Kennedy & Power 1990). Haywood (1993) suggests that indeterminate laying could be a mechanism by which birds living in unpredictable environments can regulate their clutch size. However he also points out that, for some species where this has evolved, this may no longer be an advantage under the prevailing environmental or ecological conditions.

In this experiment I investigated the adaptive significance of replacing a lost egg in lesser black-backed gulls. It is not possible simply to compare birds that do replace a removed egg with those that do not as these may be qualitatively different. Instead I created experimental groups to look at the adaptive value of replacing a lost egg.

METHODS

The study was conducted in 1998 at South Walney Nature Reserve, Cumbria, UK, a colony of c. 24 000 pairs of lesser black-backed gulls nesting on sand dunes with a cover of grass and low vegetation. Lesser black-backed gulls lay a modal clutch of three eggs but can be induced to lay additional eggs if fresh eggs are removed within twelve hours of laying (Parsons 1976; Haywood 1993; Monaghan et al. 1995; 1998). Each egg in the sequence is given a letter, starting with A for the first-laid egg. The D-egg refers to the extra egg laid in nests where the A-egg is removed shortly after laying.

We selected a small plot near the centre of the colony. The average date of the first egg in all nests studied (7th May ± 0.60 days $N = 103$) was early compared with all other nests studied at the colony that year (16.5 May ± 0.36, $N = 962$) and these birds are therefore likely to be relatively high quality birds (Hipfner et al. 1997). There was no difference in lay-date of the A-egg (ANOVA: $F_{3,60} = 0.243$, $P = 0.866$) or mass of the A-egg (ANOVA: $F_{3,59} = 1.035$, $P = 0.384$) between the experimental groups.

To simulate clutches where the female had decided not to lay a replacement egg (non-replacers) I set up two alternative situations. In one group I removed (under licence from English Nature) the first egg laid to produce AB clutches, and in the other group I

Table 1 number of nests that laid the 'full clutch' (three eggs for non-replacers and four for replacers).

GROUP	A-Removed	C-Removed	Control	Replacers
Laid the 'full clutch'	16	19	14	15
Laid less than the 'full clutch'	4	6	7	9

In each nest, eggs were weighed and measured along the long and the short axis with a pair of callipers within one day of laying. Some eggs were not weighed due to error or predation after clutch completion (one A-egg, four B-eggs, three C-eggs and three D-eggs).

We followed the nests that did not suffer predation during laying through incubation and hatching and recorded the number of chicks hatched in each nest. Five nests suffered predation during incubation in the replacer group; four in the control group; five in the A-removed group and six in the C-removed group. Not all of these nests had every egg predated and seven replacer, six control, nine A-removed and ten C-removed nests remained in the experiment. To determine breeding success I followed the chicks for five weeks after hatching. At 35 days of age the chicks are close to fledging and I assumed that they survived to independence. Within the context of this chapter I define breeding success as the number of chicks surviving to 35 days of age. Nests were surrounded by a low fence of chicken wire to facilitate finding the chicks, following Bolton (1991) and Monaghan et al. (1998). Eggs that failed to hatch were opened to determine whether they contained an unhatched embryo.

Chicks were weighed and their tarsus and wing measured at hatching, three days old and then every eight days. The final measurement was taken at age 35 days and also included a head-bill measurement. If the gulls are behaving adaptively by replacing a lost egg, birds that laid four eggs should have a higher breeding success than the 'non-replacers' (pairs raising two eggs).

For proportional information, original data are presented in the figures and tables but proportions were arcsine transformed before carrying out statistical tests. All averages given are the mean plus and minus the standard error

RESULTS

Figure 1 shows the within-clutch pattern of egg masses. In nests unmanipulated during laying, A and B-eggs are of similar size and the C-egg is smaller. In nests where the first egg was removed, A and B-eggs were similar in size to the first two eggs of unmanipulated females and the third-laid C-egg (now in second position) was significantly bigger than the C of unmanipulated females. The final egg in both groups was similar in size (t-test: $t_{57} = 1.245$, $P = 0.218$).

There was no significant difference in the number of nests which had eggs predated during incubation ($\chi^2_3 = 0.078$, $P = 0.994$) between the treatments. There was no difference in hatching success between the groups (proportion of eggs that hatched: ANOVA on arcsine transformed data: $F_{3,60} = 0.029$, $P = 0.993$). As expected, pairs

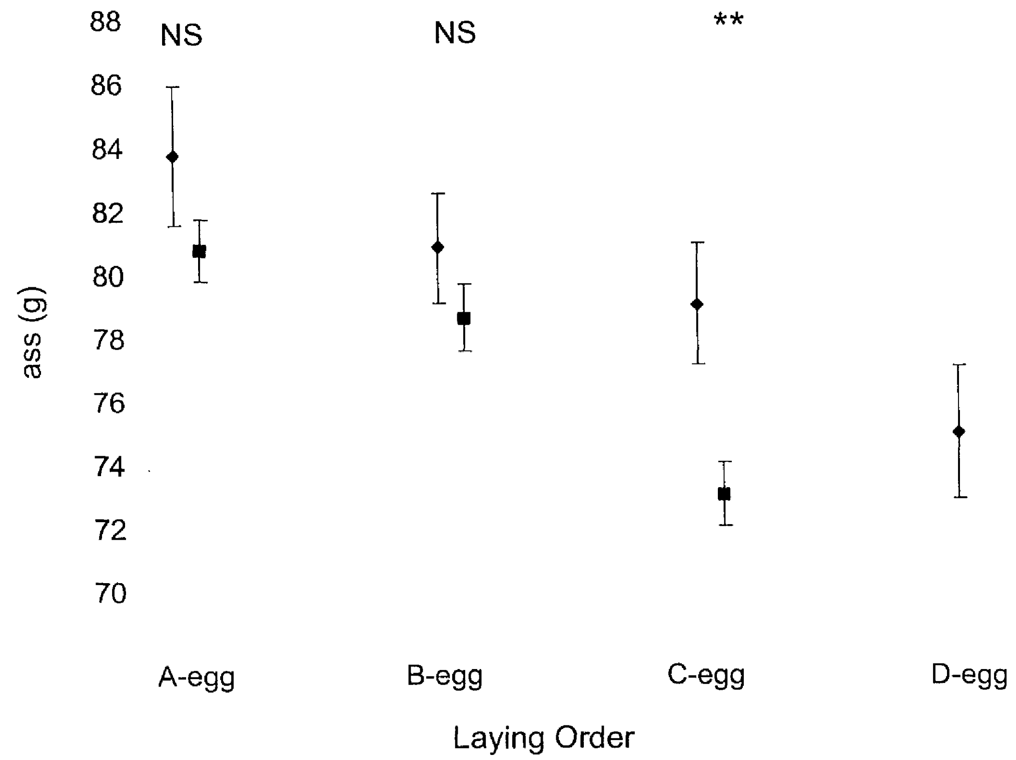


Figure 1. Mean egg masses ± SE in relation to laying order in females whose first egg was removed within 12 hours of laying (diamonds) and females who were unmanipulated during laying (squares). Egg size at the same position in the sequence were compared and the results are given at the top of the figure (NS denotes $P > 0.05$, ** denotes $P < 0.01$). In birds that had the first egg removed, the A and B-eggs were not statistically different in size from the first two eggs of unmanipulated females (t-test: for A-eggs, $t_{61} = 1.77$, $P = 0.082$; for B-eggs, $t_{58} = 1.322$, $P = 0.191$). C-eggs, however, are significantly bigger than those from unmanipulated clutches (t-test: $t_{59} = -3.277$, $P = 0.002$).

raising two eggs had significantly fewer hatchlings (1.03 ± 0.16, *N* = 35) than those that were allowed to raise three eggs (1.69 ± 0.24, *N* = 29; t-test: $t_{62} = 2.391$, *P* = 0.02) meaning that mortality during incubation did not affect the treatments differently.

Comparing the two-egg groups

The two groups raising two eggs had significantly different breeding success. Although there was no significant difference between them in number of fledglings (t-test, equal variances not assumed, $t_{33} = 1.034$, *P* = 0.309; Fig. 2), the total brood-mass of the C-removed group was significantly higher (t-test, $t_{17} = 2.433$, *P* = 0.026; Fig. 3). Comparing the breeding success of replacer birds with that of the C-removed group would give us a more conservative result of whether it is adaptive to replace a lost egg.

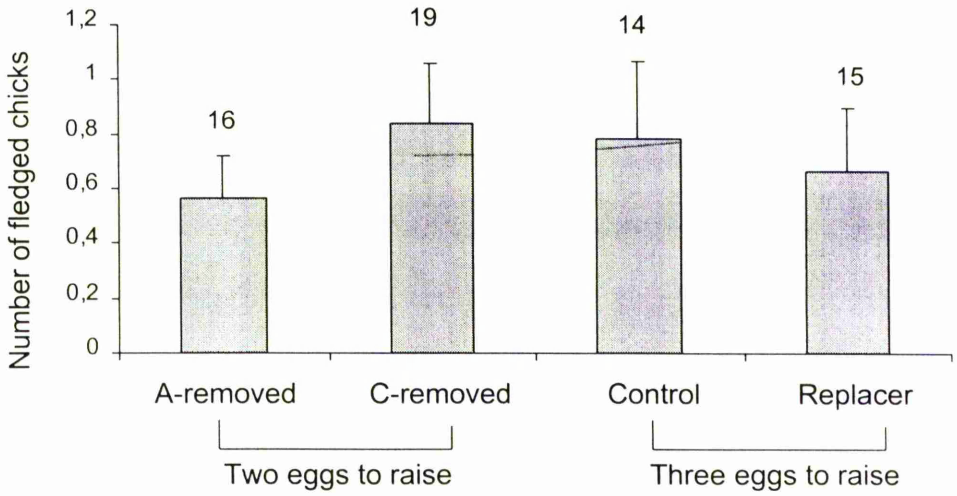


Figure 2. Mean number of chicks fledged from nests in each treatment group ± SE

Comparing two-egg and replacer nests.

There was no difference between the number of fledglings raised (t-test, $t_{32} = 0.544$, $P = 0.59$; Fig. 2) or the brood mass at fledging (t-test, $t_{15} = 1.227$, $P = 0.239$; Fig. 3) between the C-removed and replacer groups. Neither was there a difference between the number of fledglings raised (t-test, $t_{29} = 0.376$, $P = 0.710$; Fig. 2) or the brood mass at fledging (t-test, $t_{14} = 0.747$, $P = 0.467$; Fig. 3) between the A-removed and replacer groups.

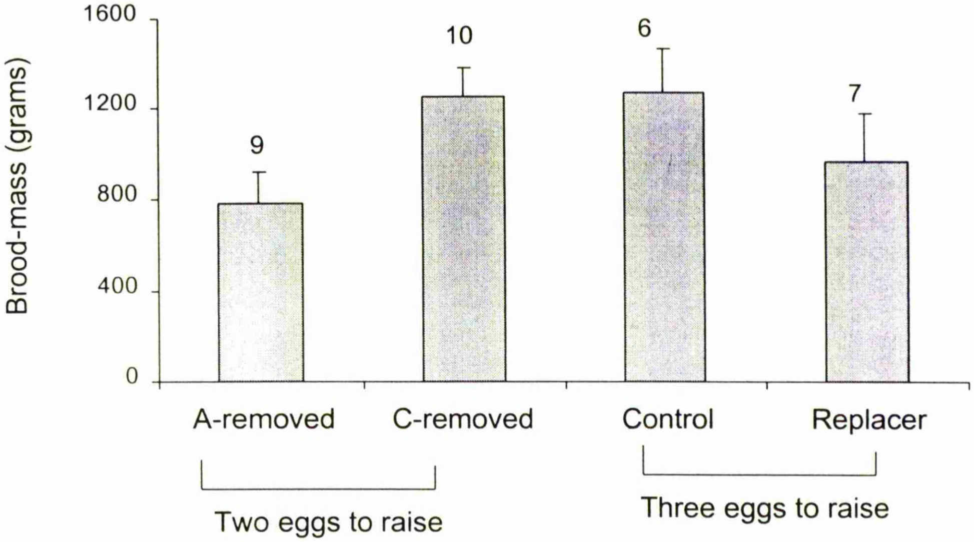


Figure 3. Mean brood mass at fledging in each treatment group ± SE

The survival graph in Figure 4 shows the number of chicks from each nest remaining alive over the period of chick rearing. A repeated measures ANOVA on number of chicks surviving in replacer and C-removed groups shows that the survival curves for the two groups are different. Multivariate tests of significance were used as

Mauchly's test for sphericity was significant, time (days since hatching) was the within subject factor, experimental group was the between subjects factor. There was a significant effect of time since hatching ($F_{5,14}$ = 4.568, P = 0.011); group × time interaction was approaching significance ($F_{5,14}$ = 2.828, P = 0.057). Although the replacer group started with more hatchlings, there were no differences in the number of fledglings between the groups, meaning that chicks from C-removed nests survive better. There was no difference between survival curves of chicks from A-removed nests and C-removed nests (group × time interaction, $F_{5,13}$ = 0.567, P = 0.724) although time since hatching had a significant effect on number of chicks remaining ($F_{5,13}$ = 6.643, P = 0.003).

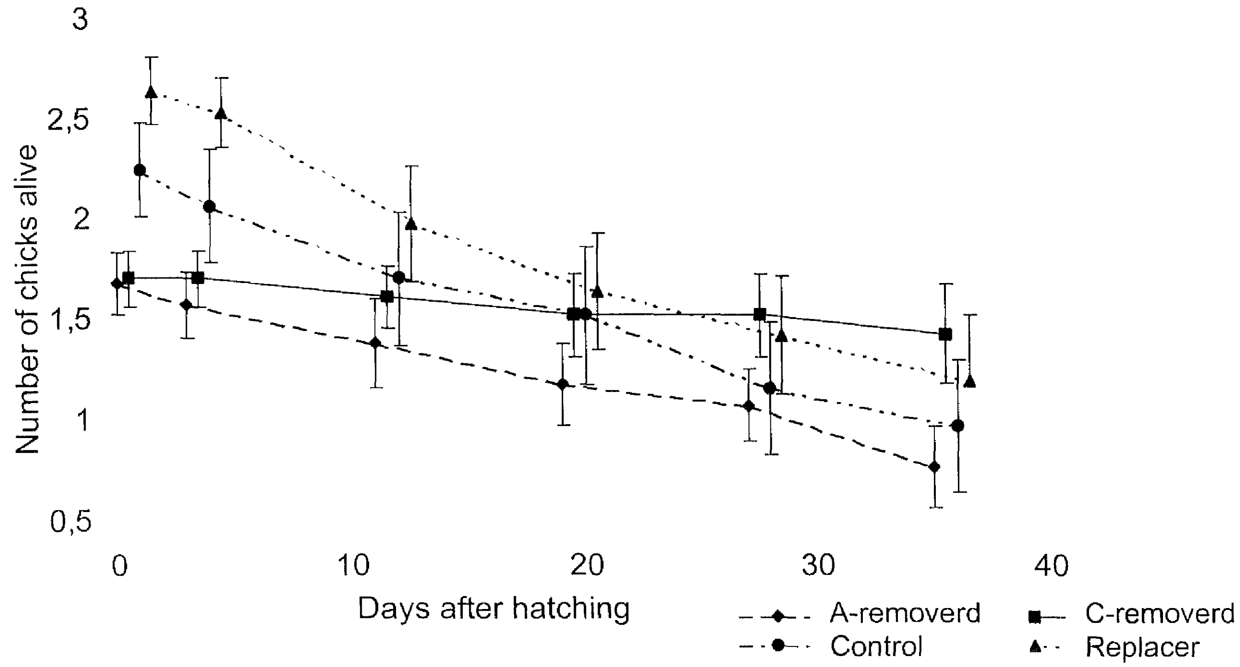


Figure 4. Cumulative survival curves for chicks in the four experimental groups.

DISCUSSION

The aim of this experiment was to compare the success of gulls that replaced a lost egg with a group of gulls that did not. I found no significant difference in the number of fledglings or brood-mass at fledging between replacers and non-replacers. There was, however, a difference in breeding success between the two groups of experimentally created non-replacers depending on which eggs they were given to raise. Birds raising the A and B-eggs achieved a significantly higher brood-mass at fledging than those raising the B and C-eggs. The non-replacers lost less chicks between hatching and fledging so, although they started with less hatchlings than the replacers, they finished with the same number of fledged chicks. This result suggests that, under the conditions during the year of study, there was no advantage in laying an extra egg.

It is important to note, that the small sample sizes in this study mean that the tests are not very powerful. A power analysis, showed that the power of the t-test between broodmass in A-removed and replacer groups is only 10.3% and that of the test of number of fledged chicks is only 5.9%. In order to obtain a power of 70% in the test to find whether there is a difference between the two groups in numbers of fledged chicks, with the same magnitude of effect we would have needed 122 nests in each group. To undertake the power analyses I used G*Power, an MS-DOS tool found at, http://www.pycho.uni-duesseldork.de/dap/projects/gpower.

We also found that there was no difference between the success of control nests and nests in which the female had laid four eggs to obtain a clutch of three. This result is in contrast to studies by Monaghan et al. (1995; 1998) which showed that females who laid an extra egg had a significantly reduced breeding success. The difference between this study and the two previous ones may have been due to the very poor conditions for breeding present during the study season. In the year of study, 1998, there was a low productivity (fledglings per egg) over the colony as a whole (30.3% over 962 nests) which is low for lesser black-backed gulls in general (range 38.5% to 69%, Cramp & Simmons 1983). The poor conditions for breeding may explain the fact that laying an extra egg did not give nests an advantage over those that were raising only two eggs. In nests containing two eggs there would have been less competition between the chicks during the vital few days after hatching and, in a situation of limited food, they would be more likely to survive, as is shown by the survival curves. This raises the question, then, of why females do replace an egg lost early in laying, even when conditions are bad.

It may be that females are unable to predict the conditions during chick rearing in advance of laying and so replacement laying will be selected for given that the pay-off for laying a replacement egg in a good year outweighs the risk of doing worse in a bad year.

It has also been suggested that laying an extra egg could be a physiological constraint of the laying process. Haywood (1993) speculates that indeterminate laying could be a mechanism by which birds in an unpredictable environment can regulate their clutch size. Gulls, however, have little variation in their clutch sizes, despite being indeterminate layers, (75% of birds laid 3 eggs Monaghan et al. 1998) and Haywood (1993) interprets this as being a relic from a time when ecological conditions were such that it was advantageous to lay indeterminately.

There is little doubt, however, that laying one extra egg is a costly activity. It has been shown to compromise, not only breeding success in the year of manipulation (Monaghan et al. 1995; 1998), but also local return rate and egg size the following year (Nager et al. in press). Many birds will continue to lay extra eggs as long as they are regularly removed and, although this would rarely happen under natural conditions, it is unlikely to be beneficial to them if it did. Laying a long run of eggs will have other detrimental effects: lesser black-backed gulls will continue to lay up to 21 eggs (Nager pers. com.) and since eggs are produced with at least two days' gap between them, the breeding attempt could be very significantly delayed.

Lesser black-backed gulls have been found to be able to maximise their breeding success by selecting the sex of their offspring (Nager et al. 1999). This enables the female to finely adjust success of the reproductive event within the constraints of her clutch size. So female gulls may be able to use changes in the sex ratio of her brood to fine-tune the competitiveness of the chicks in order to maximise the success of her breeding attempt within the constraints of the egg laying process.

In conclusion, I found that, under poor rearing conditions, there is no advantage to a female in replacing an egg lost early in laying. It seems that, under some conditions, it would be more beneficial to avoid laying the extra egg, especially since laying an extra egg may have consequences for subsequent breeding seasons. Why the females lay this egg, even under the poor conditions pertaining during the season of study, needs to be further investigated. It would be interesting to carry out the same experiment under different environmental conditions or to manipulate feeding conditions using supplementary food. Decisions on egg laying could be investigated by following the breeding success of all birds by studying the birds that lay only one or two eggs as well as the modal class. Further work is also needed to quantify how common egg loss and replacement is under natural conditions and to investigate the long-term consequences of continual egg removal for individuals (e.g. Nager et al. in press).

REFERENCES

Arnold, T. W. 1993. Factors affecting renesting in American coots. *Condor*, **95**, 273-281.

Barba, E., Gildelgado, J. A. & Monros, J. S. 1995. The costs of being late - consequences of delaying great tit *Parus major* first clutches. *Journal of Animal Ecology*, **64**, 642-651.

Blight, L. K., Ryder, J. L. & Bertram, D. F. 1999. Predation on Rhinoceros Auklet eggs by a native population of Peromyscus. *Condor*, **101**, 871-876.

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull - relative contributions of egg size and parental quality. *Journal of Animal Ecology*, **60**, 949-960.

Bukacinski, D., Bukacinska, M. & Spaans, A. L. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the lesser black-backed gull *Larus fuscus*. *Ibis*, **140**, 422-430.

Cramp, S. & Simmons, K. E. C. 1983. Birds of the Western Palearctic Vol III Waders to Gulls. Oxford University Press, Oxford.

Ewins, P. J. 1991. Egg predation by corvids in gull colonies on Lake Huron. *Colonial Waterbirds*, **14**, 186-189.

Haywood, S. 1993. Sensory and hormonal-control of clutch size in birds. *Quarterly Review Of Biology*, **68** , 33-60.

Hegyi, Z. & Sasvari, L. 1998. Components of fitness in Lapwings *Vanellus vanellus* and black- tailed godwits *Limosa limosa* during the breeding season: Do female body mass and egg size matter? *Ardea*, **86**, 43-50.

Hipfner, J. M., Gaston, A. J. & deForest, L. N. 1997. The role of female age in determining egg size and laying date of thick-billed Murres. *Journal of Avian Biology*, **28**, 271-278.

Hipfner, J. M., Gaston, A. J., Martin, D. L. & Jones, I. L. 1999. Seasonal declines in replacement egg layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? *Journal of Animal Ecology*, **68**, 988-998.

Holloway, M. 1993. The variable breeding success of the little tern, *Sterna albifrons,* in south-east India and protective measures needed for its conservation. *Biological Conservation*, **65**, 1-8.

Kennedy, E. D. & Power, H. W. 1990. Experiments on indeterminate laying in House Wrens and European Starlings. *Condor*, **92**, 861-865.

Monaghan, P., Bolton, M. & Houston, D. C. 1995. Egg-production constraints and the evolution of avian clutch size. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, **259**, 189-191.

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. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1731-1735.

Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson, R. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 570-573.

Nager, R. G., Monaghan, P. & Houston, D. C. in press. The cost of egg production: increased egg production reduces future fitness in gulls. *Journal of Avian Biology*.

Parsons, J. 1976. Factors determining the number and size of eggs laid by the herring gull. *Condor*, **78**, 481-492.

Power, H. P., Kennedy, E. D., Romagnano, L. C., Lombardo, M. P., Hoffenberg, A. S., Stouffer, P. C. & McGuire, T. R. 1989. The parasitism insurance hypothesis: why starlings leave space for for parasitic eggs. *Condor*, **91**, 753-765.

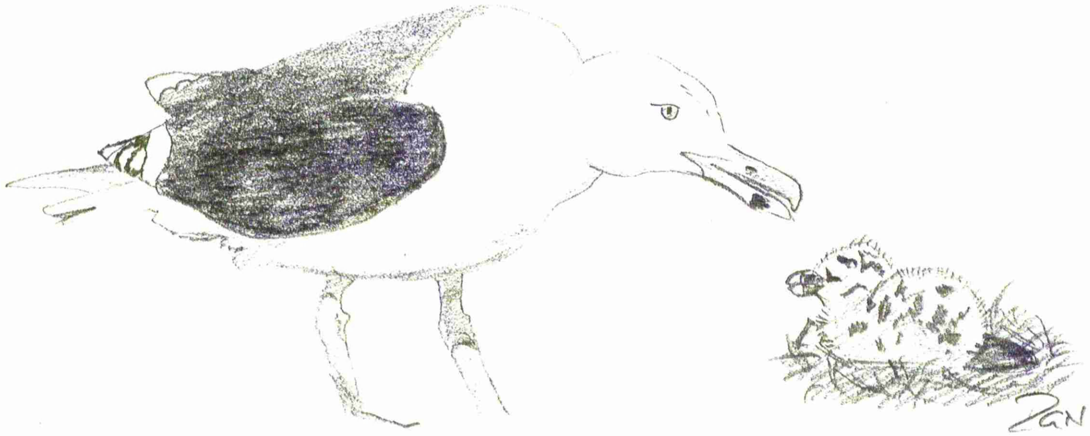
Regehr, H. M. & Montevecchi, W. A. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. *Marine Ecology-Progress Series*, **155**, 249-260.

Rooneem, T. M. & Robertson, R. J. 1997. The potential to lay replacement clutches by Tree Swallows. *Condor*, **99**, 228-231.

Sorci, G., Soler, J. J. & Moller, A. P. 1997. Reduced immunocompetence of nestlings in replacement clutches of the European magpie (*Pica pica*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **264**, 1593-1598.

Chapter 4

MALES COMPENSATE BEHAVIOURALLY FOR A MANIPULATION OF THEIR PARTNER'S CONDITION AT EGG LAYING



ABSTRACT

Models of parental investment show that biparental care is an evolutionarily stable strategy (ESS) when each parent only partially compensates for decreases in care by the other. We used a manipulation of female condition that affected her parental investment to investigate compensation behaviour by the male partner. Female lesser black-backed gulls were made to lay an extra egg, which decreases their protein condition compared to that of control females. Manipulated females were found to decrease their parental investment during incubation, brooding and chick rearing compared to controls. Males fully compensated for changes in female behaviour during incubation and brooding. High predation risk for the brood during incubation and early chick rearing may constrain males to full compensation as partial compensation is likely to lead to the loss of the eggs or chicks.

INTRODUCTION

According to life-history theory, since individuals have limited resources to allocate to reproduction, growth and self-maintenance, they should allocate resources amongst these components so as to maximise lifetime reproductive success (Stearns 1992). In iteroparus breeders such as birds, the level of investment in a reproductive event will determine current reproductive success as well as the probability of survival to the next breeding period (e.g. Gustafsson & Sutherland 1988; Nilsson & Svensson 1996; Siikimaki et al. 1997; Nager et al. in press). Within a discrete reproductive event, too, there will be trade-offs in the amount of resources individuals can allocate to different phases within the breeding cycle (Heaney & Monaghan 1995; Monaghan et al. 1998). All these trade-offs need to be considered in understanding how parents allocate resources so as to maximise lifetime reproductive success.

In species with biparental care, any reproductive decision taken by an individual will have to take into account the behaviour of the partner (Houston & Davies 1985; Mock et al. 1996). Houston and Davies (1985) demonstrated that biparental care is an evolutionarily stable strategy (ESS) when each parent only partially compensates for decreases in effort by its partner. If individuals fully compensated for changes in the levels of parental care by their partner, then the situation would be vulnerable to cheating and biparental care would become unstable.

Many experimental approaches have been used to test the partial compensation model. Mate removal experiments (e.g. Mrowka 1982; Sasvari 1986; Transue & Burger

1989; Fetherston et al. 1994; Pinxten et al. 1995; Markman et al. 1996) have been used extensively but, as pointed out by Wright and Cuthill (1989) and tested by Whittingham et al. (1994), the reaction of a widowed individual may differ from that of one whose partner has decreased its parental contribution. Other experimenters have manipulated foraging ability during chick feeding by adding weights (Wright & Cuthill 1989; Markman et al. 1995), or feather clipping (Whittingham et al. 1994; Sanz et al. 2000). Manipulations of male testosterone levels have also been used to influence behaviour (Ketterson et al. 1992; Saino & Moller 1995; Hunt et al. 1999).

These manipulations may have a more complex effect on the individual than simply affecting the level of parental care. Weighting a bird will increase the mass-dependent risk of injury and the mass-dependent predation risk as well as flight costs (Witter & Cuthill 1993). Individuals may compensate in unexpected ways for such a manipulation, for example weighted individuals may carry lighter food loads in order to reduce flight costs (Cuthill & Kacelnik 1990). Sanz et al. (2000) found that a manipulation using wing clipping could alter the shape of the bird's survival-effort curve, i.e. the individual's probability of survival with a given amount of effort. Manipulations of hormones increase male investment in extra-pair copulations (Ketterson et al. 1992; Saino & Moller 1995; Hunt et al. 1999), but it may also have other effects, for example on the male's metabolism. Cuckoldry by the male may elicit a change in behaviour from the female unrelated to the male's decrease of investment in parental care. More direct manipulations of an individual's condition, and thereby of its capacity to invest in a reproductive event may overcome some of these difficulties.

In the following experiment we induced a group of female lesser black-backed gulls, *Larus fuscus*, to lay one extra egg by removing their first egg (Monaghan et al. 1995; 1998) within 12 hours of laying. This procedure increases her investment in egg production and reduces female condition at the end of laying (Monaghan et al. 1998), and therefore enabled us to examine the effects on the pattern of investment of females and males during both incubation and chick rearing, unlike previous studies which have concentrated only on the latter.

METHODS

This study was undertaken on Walney Island, Cumbria in a colony comprising c. 24 000 pairs of lesser-black backed gulls and c. 8 000 pairs of herring gulls nesting on sand dunes covered with low vegetation.

Lesser black-backed gulls replace the first-laid egg if it is removed shortly after laying (Monaghan et al. 1995; 1998). Nests were allocated at random to either the control (25 nests) or manipulated (27 nests) groups. We weighed, measured and removed (under licence from English Nature) the first egg in manipulated nests within 12 hours of laying and measured, but did not remove any eggs from the controls (one A-egg was not weighed due to an error).

Fifteen out of the 27 manipulated females did not suffer predation during laying and laid a further 3 eggs following removal of the first laid eggs; this did not differ from the proportion (14 out of 25) producing a three-egg clutch in the control group (χ^2_1 = 0.06, P = 0.805). To ensure a comparable quality between control and experimental birds, nests containing clutches of less than three were not included in either group. There was no difference between number of nests that experienced predation during incubation in control (4 out of 14) nests and manipulated (5 out of 15) nests (Fishers exact test, $P = 0.55$).

To identify males and females we caught birds using a walk-in trap two days after the clutch was complete and colour ringed one of the pair. A droplet of blood was collected (under Home Office licence) and used to identify sex using the CHD gene (Griffiths et al. 1996). Nests were checked once in the morning and once in the afternoon during incubation and early chick rearing to note the sex of the attendant bird. These observations stopped when the chicks were seven days old and were thremoregulating and therefore no-longer needed constant brooding. For analysis, we divided the data into two periods: stage 1: incubation of the eggs and stage 2: brooding of the chicks. The average number of observations per nest was 18.2 ± 2.1 $N = 15$ for the incubation stage and 5.2 ± 0.56 $N = 13$ for the brooding stage. In the nests in which there were at least three observations for each stage we calculated a proportion of times that the female was seen at the nest. Nests were left unattended very seldom (4 instances in 390 observations of 16 nests).

During the late chick-rearing period (with chicks between 20 and 35 days of age) we carried out 24 two-hour observation periods on six control and three manipulated nests, all nests being observed on between two and seven occasions (an average of 4.4 ± 0.5 times), all starting between 14:00 and 16:00. Not all nests in the experiment were visible from the hides and so could not be observed. We recorded which parent was present and for how long, whether any feeds took place and any chick begging. We recorded the age of the chicks and how many were present. Gulls regurgitate food to the chicks and so it is not possible to ascertain how much food an adult brings to the chicks in a feeding visit by observation as it is with seabirds that carry prey in their bills. We weighed chicks at the beginning and end of each observation period, however, there were not enough feeds during the observation periods to provide enough data to analyse.

For nests that were followed during the experiment there were no differences in laying date of the first egg (controls: 7th May ± 1.5 days, $N = 14$; manipulated: 6th May ± 1.7 days, $N = 15$; t-test: $t_{27} = 0.52$, $P = 0.607$) or of the last egg (t-test: $t_{27} = 0.572$, $P = 0.572$). There was no difference in egg mass of the first egg (controls: 80.6 ± 1.8 g, $N = 13$; manipulated: 84.3 ± 2.1 g, $N = 15$; t-test: $t_{26} = 1.304$, $P = 0.204$). There was no difference in hatching date (controls: 4th June ± 2 days, $N = 10$; manipulated: 6th June ± 2 days, $N = 10$; t-test: $t_{18} = -0.679$, $P = 0.506$). For the nests that were observed during chick rearing, there was no significant difference in the ages of the chicks between control (26.7 days ± 2.4, $N = 6$) and experimental nests (28.0 days ± 2.8, $N = 3$; t-test: $t_7 = -0.342$, $P = 0.742$).

Nests were surrounded by a low fence of chicken wire to facilitate finding the chicks following Bolton (1991). Chicks were weighed and their tarsus and wing measured at hatching, three days old and then every eight days. The final measurement was taken at age 35 days and also included a head-bill measurement.

Instantaneous growth rates were calculated for chicks that reached at least 11 days of age using the formula:

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

Where R = instantaneous growth rate, W = mass and t = time measured at chick hatching (t_1) and 27 days of age, or date it was last measured (t_2).

Proportional data were arcsine transformed before carrying out statistical tests but original data are represented in the figures and tables. Incubation data were normal (Kolmogorov-Smirnov test for normality) but the chick rearing data, although it passed the test of normality had a small sample size and so non-parametric tests were used on these data. All averages given in the methods and results are the mean plus and minus the standard error.

RESULTS

Figure 1 shows the average proportion of times that the female was seen at the nest during incubation and brooding (here taken as the period between hatching of the chick and seven days old). A two-way ANOVA shows a significant difference between the experimental and control groups ($F_{1,23} = 6.453$, $P = 0.018$) with no significant interaction between stage of breeding (incubation/brooding) and treatment group ($F_{1,22} = 3.066$, $P = 0.092$).

Nests in both the experimental and control groups were so seldom left unattended during brooding and incubation (1% of observations) that male behaviour almost perfectly mirrors that of the female.

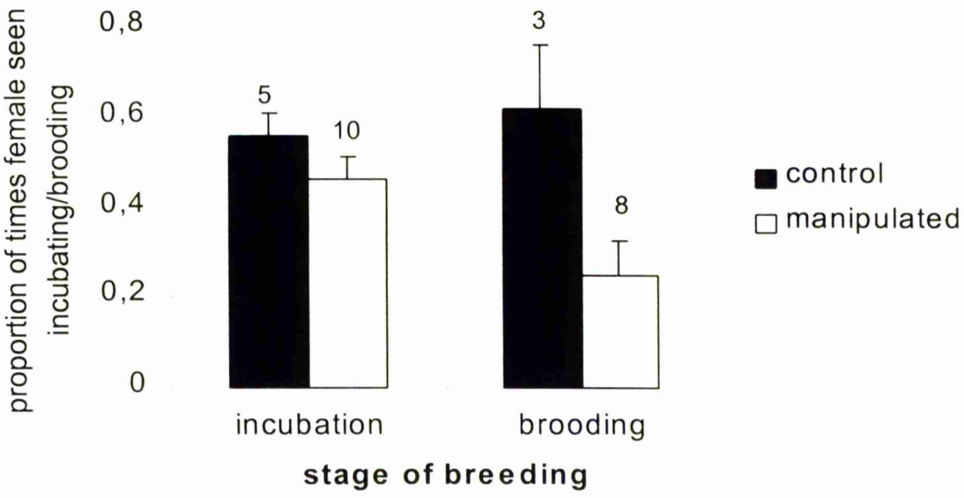


Figure 1. The proportion of times that the female was seen at the nest during incubation and brooding (the first week when chicks are in the nest). Nests are seldom left unattended so male behaviour complements that of the female.

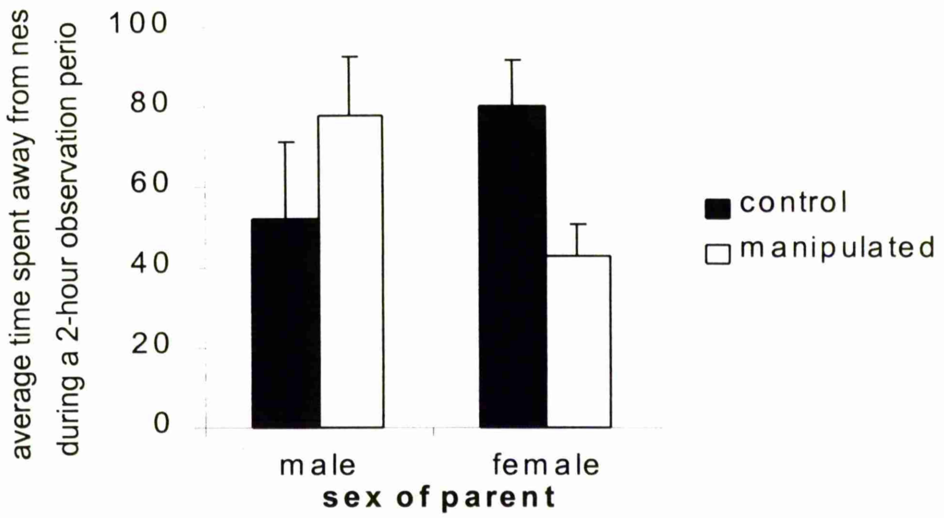


Figure 2. Average time away from the nest by males and females in control (*N* = 6) and manipulated (*N* = 3) nests when chicks are thermally independent and large enough not to be predated by other gulls.

Figure 2 shows that during late chick-rearing, the parents behaved differently according to experimental treatment. Females spent more time away from the territory in the control group and males spent more time away from the territory in the manipulated group. There was a significant interaction between sex and experimental group (repeated measures ANOVA: $F_{1,7} = 7.78$, $P = 0.027$). However there was no difference in the treatments between the proportion of time the territory was unattended, the proportion of time both parents were there together and the total time the nest was unattended (Table 1).

Table 1. Parental behaviour in control (*N* = 6) and manipulated (*N* = 3) nests.

	Control	**Manipulated**	**t**	**df**	**p**
Percent of time territory unattended	11.5 ± 6.3	14.4 ± 2.3	-0.29	7	0.783
Percent of time male and female attend together	10.4 ± 3.3	8.3 ± 4.3	0.36	7	0.727
Total time parents away from nest during observation period (minutes)	114.8 ± 11.4	130.7 ± 6.1	-0.925	7	0.386

Numbers given in table are means ± SE.

During the two-hour nest observations during late chick-rearing, very few adults were observed to feed chicks and so it was not possible to compare feeding rates between the two groups.

In order to control for brood size when examining the chick rearing performance of the parents, we used only those nests where three chicks hatched. We found no difference in hatching or fledging success between the treatments from these nests (Table 2). The total brood mass at fledging of control nests (1266 ± 201 g, *N* = 6) was greater, though not significantly so, than manipulated nests (1053 ± 220 g, *N* = 7; Mann-Whitney U test: *Z* = -0.480, *P* = 0.631). Average instantaneous growth rates of chicks in the nest did not differ significantly between control (0.89 ± 0.032, *N* = 7) and manipulated (0.80 ± 0.082, *N* = 9) nests (Mann-Whitney U test: *Z*= -0.265, *P* =0.791).

Table 2. The number of chicks hatched and fledged in each group.

	No. of chicks hatched from nest				Number of chicks fledged from nest			
	3	**2**	**1**	**0**	**3**	**2**	**1**	**0**
Control	5	4	1	0	1	3	2	4
Manipulated	6	3	1	0	1	1	4	4

There are no differences between control and manipulated nests in hatching data (Fisher's Exact: *P* = 0.763) or for fledging data (Fisher's Exact: *P* = 0.314). In order to be able to analyse these data, we combined categories due to the small sample sizes: nests which hatched/fledged 3 chicks were combined with those that hatched/fledged 2, and nests that hatched/fledged 1 chick with those that hatched/fledged none.

DISCUSSION

In this experiment we studied behavioural compensation by males for reduced parental care by their manipulated partner. We found that a manipulation of female condition had a significant effect, both on her own behaviour and that of her partner.

During incubation, and during the first week after the chicks hatched (the brooding period), the manipulated females were seen incubating / brooding significantly less than control females. Incubation has recently been shown to have a significant cost (Heaney & Monaghan 1995; Thomson et al. 1998; Reid et al. 1999; Conway & Martin

2000). The first week of chick life is also thought to be a time when energy stress is highest because the chicks must be constantly brooded as they are not yet able to thermo-regulate, and the parents must also feed them (Moreno & Hillstrom 1992; Uttley 1992; Salamolard & Weimerskirch. 1993; Pearson 1994; Heaney & Monaghan 1995). Experimental females, which are in a poorer condition due to laying an extra egg (Monaghan et al. 1998), decrease their parental investment in these costly activities.

Males fully compensated for the time spent away from the nest by the manipulated female to ensure nests were never left unattended. This is vitally important, as any unattended nests are very prone to predation by neighbours (Bukacinski et al. 1998). This means that the male has no choice but to compensate fully for the absence of his female as re-nesting after predation would be unsuccessful in most cases due to the time constraints of the breeding season.

During the chick-rearing period, the control females spent a significantly larger proportion of time away from the territory than did manipulated females. This suggests that manipulated females have shorter feeding trips than controls and are putting less effort into feeding the chicks. The chicks were all over 20 days old when they were observed and therefore fully thermo-regulating and big enough to make predation difficult. This removes the necessity for a parent to be present at the nest all the time.

Males of manipulated females spent more time foraging than controls and, although this was not significant, it was enough to compensate for the reduced foraging by experimental females. The small number of nests retaining chicks to 20 days of age means that the number of nests observed during this period is very small. This means that it is not possible to distinguish between partial compensation for the female or full compensation late in the breeding event. Small sample sizes are a problem in this study due to heavy predation and nest loss so it would be useful to rerun the experiment using larger sample sizes to allow for this large loss of nests.

Consistent with the result that males were able to compensate for the females' change in behaviour we found no difference in predation during incubation, hatching success or breeding success between treatment groups. However, another study using a similar manipulation found a decrease in breeding success in the manipulated group (Monaghan et al. 1995). This effect was due, both to a decrease in parental care (Monaghan et al. 1998) and the fact that the fourth egg was poorer in quality (Nager et al. 2000). Even when egg quality was eliminated by cross fostering eggs (Monaghan et al. 1998), the manipulated parents were not able to provide the same level of care as controls and their chicks had a lower survival. The differences between these two studies and the current one may be explained by the high level of predation and the poor rearing conditions during the year of this study. From 962 nests sampled throughout the colony in 1998, only 30.3% of eggs resulted in fledged chicks and many pairs were raising only one chick (unpublished data). The normal range for lesser black-backed gulls is 38.5% to 69% success (Cramp & Simmons 1983). This meant pairs in this study were raising a reduced brood size and therefore experienced a lower chick demand that was more easily compensated for by the male. Males may not be able to make up for the deficit of care left by the manipulated females when there is a full brood of chicks so when there is little chick mortality chicks grow more slowly and have poorer fledging success in manipulated pairs.

Houston and Davies' model of parental care (1985) stresses the importance of partial compensation for changes in the behaviour of a partner in producing an evolutionarily stable strategy (ESS) for biparental care. Previous studies which set out to test whether parents do, indeed, only partially compensate for a lower level of effort from the partner have come up with varying results. Some studies have found that the partner of the manipulated individual partially compensates (e.g. Markman et al. 1995), while others find full, or nearly full, compensation (Hunt et al. 1999; Saino & Moller 1995) and others find no evidence of compensation (Whittingham et al. 1994). Some experiments, which involved handicapping both males and females in different trials found the same response for each sex (Wright & Cuthill 1989-partial compensation), or different responses from each sex (Sanz et al. 2000).

In this study the males were able to fully compensate for the female's drop in parental effort during incubation and brooding. Males also compensated for a drop in female effort during chick rearing, although the number of nests observed was not large enough to ascertain whether this was full or partial compensation. All the other studies of compensation have looked only at the chick stage, when the amount of care given by the parents can be variable. However, during incubation and brooding in a species with a high predation risk, partial compensation will result in predation of eggs or chicks.

When the costs of partial compensation far outweigh the benefits to the individual of increased survival, as in a gull colony where cannibalism is rife (Bukacinski et al. 1998) then we would not expect to see partial compensation. During the later chick-rearing period, however, the chicks were large enough to deter most predators and were able to run and hide more effectively so partial compensation at this stage may be less costly. The high predation and chick loss that the nests in this study suffered resulted in a much lower demand on parents. This means that the costs to the male of compensating for the reduction in female care are much lower and therefore he may be able to compensate more for the reduced female care. Also, since the manipulated females were putting in less effort in the incubation and chick-rearing stages in order to compensate for the increased investment during laying, her overall investment in the breeding event may not be reduced. This is a different situation from one in which an individual has reduced their parental effort for purely selfish reasons. The manipulation used in this experiment may, therefore, not have altered the male's perception of female parental effort and he may be prepared to work harder in incubation and chick-rearing because she worked harder in egg laying.

REFERENCES

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull - relative contributions of egg size and parental quality. *Journal of Animal Ecology* **60**, 949-960.

Bukacinski, D., Bukacinska, M. & Spaans, A. L. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the lesser black-backed gull *Larus fuscus*. *Ibis* **140**, 422-430.

Conway, C. J. & Martin, T. E. 2000. Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution*, **54**, 670-685.

Cramp, S. & Simmons, K. E. C. 1983. Birds of the Western Palearctic Vol III Waders to Gulls. Oxford University Press, Oxford.

Cuthill, I. & Kacelnik, A. 1990. Central place foraging - a reappraisal of the loading effect. *Animal Behaviour*. **40**, 1087-1101.

Fetherston, I. A., Scott, M. P. & Traniello, J. F. A. 1994. Behavioral compensation for mate loss in the burying beetle, *Nicrophorus orbicollis*. *Animal Behaviour*. **47**, 777-785.

Griffiths, R., Daan, S. & Dijkstra, C. 1996. Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**, 1251-1256.

Gustafsson, L. & Sutherland, W. J. 1988. the costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature* **335**, 813-815.

Heaney, V. & Monaghan, P. 1995. A within-clutch trade-off between egg-production and rearing in birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* **261**, 361-365.

Houston, A. I. & Davies, N. B. 1985. The evolution of co-operation and life history in the dunnock, *Prunella modularis*. In: Behavioural Ecology (Sibly, R.M. & Smith, R. H. eds). Blackwell Scientific Publications, Oxford, pp. 471-487

Hunt, K. E., Hahn, T. P. & Wingfield, J. C. 1999. Endocrine influences on parental care during a short breeding season: testosterone and male parental care in Lapland longspurs (*Calcarius lapponicus*). *Behavioral Ecology and Sociobiology* **45**, 360-369.

Ketterson, E. D., Nolan, V., Wolf, L. & Ziegenfus, C. 1992. Testosterone and avian life histories - effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *American Naturalist* **140**, 980-999.

Markman, S., YomTov, Y. & Wright, J. 1995. Male parental care in the orange-tufted sunbird – behavioral adjustments in provisioning and nest guarding effort. *Animal Behaviour*. **50**, 655-669.

Markman, S., YomTov, Y. & Wright, J. 1996. The effect of male removal on female parental care in the orange-tufted sunbird. *Animal Behaviour*. **52**, 437-444.

Mock, D. W., Schwagmeyer, P. L. & Parker, G. A. 1996. The model family. In: Partnerships in Birds (Black, J. M. ed). Oxford University Press, Oxford, pp. 53-71.

Monaghan, P., Bolton, M. & Houston, D. C. 1995. Egg-production constraints and the evolution of avian clutch size. *Proceedings of the Royal Society of London Series B-Biological Sciences* **259**, 189-191.

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. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 1731-1735.

Moreno, J. & Hillstrom, L. 1992. Variation in time and energy budgets of breeding wheatears. *Behaviour* **120**, 11-39.

Mrowka, W. 1982. Effect of removal of the mate on the parental care behavior of the biparental cichlid *Aequidens paraguayensis. Animal Behaviour.* **30**, 295-297.

Nager, R. G., Monaghan, P. & Houston, D. C. 2000. 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. in press. The cost of egg production: increased egg production reduces future fitness in gulls. *Journal of Avian Biology.*

Nilsson, J. A. & Svensson, E. 1996. The cost of reproduction: A new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**, 711-714.

Pearson, J. T. 1994. Oxygen consumption rates of adults and chicks during brooding in king quail (*Coturnix chinensis*). *Journal of Comparative Physiology [B]* **164**, 415-424.

Pinxten, R., Eens, M. & Verheyen, R. F. 1995. Response of male European starlings to experimental removal of their mate during different stages of the breeding cycle. *Behaviour* **132**, 301-317.

Reid, J. M., Monaghan, P. & Ruxton, G. D. 1999. The effect of clutch cooling rate on starling, *Sturnus vulgaris*, incubation strategy. *Animal Behaviour*, **58**, 1161-1167.

Saino, N. & Moller, A. P. 1995. Testosterone induced depression of male parental behavior in the barn swallow - female compensation and effects on seasonal fitness. *Behavioral Ecology and Sociobiology* **36**, 151-157.

Salamolard, M. & Weimerskirch, H. 1993. Relationship between foraging effort and energy requirement throughout the breeding-season in the wandering albatross. *Functional Ecology* **7**, 643-652.

Sanz, J. J., Kranenbarg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *Journal of Animal Ecology* **69**, 74-84.

Sasvari, L. 1986. Reproductive effort of widowed birds *Journal of Animal Ecology*. **55**, 553-564.

Siikamaki, P., Hovi, M. & Ratti, O. 1997. Low male return rate due to clutch enlargements in the pied flycatcher (*Ficedula hypoleuca*). *Ecoscience* **4**, 24-28.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Thomson, D. L., Monaghan, P. & Furness, R. W. 1998. The demands of incubation and avian clutch size. *Biological Reviews of the Cambridge Philosophical Society*, **73**, 293-304.

Transue, G. J. & Burger, J. 1989. Responses to mate loss by herring gulls *Larus argentatus* and great black-backed gulls *Larus marinus*. *Ornis Scandinavica* **20**, 53-58.

Uttley, J. D. 1992. Food-supply and allocation of parental effort in arctic terns *Sterna paradisaea*. *Ardea*, **80**, 82-91.

Witter, M. S. & Cuthill, I. C. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London Series Biological* **340**, 73-92.

Whittingham, L. A., Dunn, P. O. & Robertson, R. J. 1994. Female response to reduced male parental care in birds - an experiment in tree swallows. *Ethology* **96**. 260-269.

Wright, J. & Cuthill, I. 1989. Manipulation of sex-differences in parental care. *Behavioral Ecology and Sociobiology* **25**, 171-181.

Chapter 5

Limits to laziness: Is Full Compensation for Reduced Partner Effort Compatible with Stable Biparental Care?

ABSTRACT

Previous models have suggested that biparental care will only be evolutionarily stable when each parent only partially compensates for decreases in effort by their partner. We investigated a system where breeding success is a concave-up function of parental effort. This could occur in species with a high predation level, for example in a dense sea-bird colony or in species where eggs or young are very prone to cooling. In this case parents will fully compensate for decreased partner effort, or else they will abandon the breeding attempt altogether. This full compensation will lead to unstable biparental care. We use a second, graphical, model to show that biparental care can exist under a situation of full compensation for reduced partner effort if neither parent can do all the care alone. Each parent will abandon the breeding attempt if his or her condition goes below a certain threshold. If the participation of both parents is necessary for the breeding attempt to be successful, then neither parent will want to force their partner to abandon by making him/her work so hard that s/he passes below the condition threshold. Since abandonment by one partner means the failure of the breeding attempt, each individual will do at least enough work (its 'laziness threshold') so that the partner will not abandon, resulting in biparental care. There will be a region of conflict between the parents, within which the conflict can be resolved in various ways. Possible resolutions of this conflict, and the consequences and applications of the model, are discussed.

INTRODUCTION

In species where both parents care for the offspring, there will often be a conflict of interest between the male and the female over the division of labour. Each individual has limited resources to divide between reproduction, growth and self-maintenance (Lessells 1991; Stearns 1992), and this generally results in a trade-off between current and future reproduction. In order to maximise lifetime reproductive success, individuals should maximise the success of the current breeding attempt, while minimising the cost to their future reproductive potential. Therefore each parent wants its partner to do more of the work. Houston and Davies (1985) showed that biparental care is an evolutionarily stable strategy (ESS) when each parent only partially compensates for any decrease in effort by the partner. Full compensation for reduced partner effort is expected to lead to the evolution of uniparental care. A number of empirical studies have looked at compensation in biparental systems using mate removal experiments (Sasvari 1986; Transue & Burger 1989; Davies 1992; Dunn & Robertson 1992; Fetherston et al. 1994; Lavery & Reebs 1994; Pinxten et al. 1995; Markman et al. 1996); handicapping, through the addition of weights or by feather clipping, (Wright & Cuthill 1989; Whittingham et al. 1994; Markman et al. 1995; Sanz et al. 2000) and testosterone manipulations (Hegner & Wingfield 1987; Saino & Møller 1995; Hunt et al. 1999). Some of these studies have observed partial compensation. However others have demonstrated that full compensation can occur (Table 1), therefore going against the prediction of the ESS model.

Table 1. Review of experiments that investigate parental compensation.

Study	Species	Manipulation	Result
Mrowka 1982	Cichlid (Aequidens paraguayensis)	Mate removal (male and female)	Full compensation
Sasvari 1986	Great tit and blue tit	Mate removal (male and female)	Not full compensation before 7 days old, full compensation afterwards †
Hegner & Wingfield 1987	House sparrows	Testosterone manipulation	Partial / no compensation by female ‡
Wright & Cuthill 1989	Starling	Weighted (male and female)	Partial compensation by both sexes
Transue & Burger 1989	Herring gull and great black-backed gull	Mate removal (male and female)	Both sexes desert but males desert earlier than females
Dunn & Robertson 1992	Tree swallows	Mate removal (male)	Partial / no compensation by female ‡
Davies 1992	Dunnock	Mate removal (male) *	In pairs, female partially compensated, in trios she did not compensate. Beta males partially compensated for removal of an alpha male but alpha males did not compensate for loss of a beta male.
Featherston et al. 1994	Burying beetle	Mate removal (male and female)	Partial compensation in both sexes
Lavery & Reebs 1994	Convict cichlid	Mate removal (male and female)	Both sexes increase fanning frequency. This is not strictly compensation by females as control males rarely fan
Whitingham et al. 1994	Tree swallows	Mate removal (male)	full compensation by female
		Feather clipped (male)	no/partial compensation by female
Markman et al. 1995	Orange tufted sunbird	Tail-weighted (male)	Partial compensation by female
Saino & Møller 1995	Barn swallow	Testosterone manipulation	Almost full compensation by females
Pinxten et al. 1995	Starling	Mate removal at various stages during incubation and chick-rearing (female)	Partial compensation in broods where chicks were more than 5 days old **
Markman et al. 1996	Orange tufted sunbird	Mate removal (male)	Partial compensation by female
Annett et al. 1999	Cichlid (*Tilapia mariae*)	Mate removal (males)	Partial compensation in both sexes
Hunt et al. 1999	Lapland longspur	Testosterone manipulation	Full compensation by females
Sanz et al. 2000	Great tit	Feather-clipping (males and females)	Full compensation by females for male behaviour change
Stoehr & Hill 2000	House finch	Testosterone manipulation	Full compensation
Jones (Chapter 4)	Lesser black-backed gull	Female laid extra egg	Full compensation by male through incubation & brooding

† both parents increased frequency of feeds but level of compensation inferred from growth rates and survival of the chicks.

‡ inferred from reduced breeding success, no observations of female parental behaviour

* males removed from dunnock pairs and trios (female, alpha male and beta male)

** eggs/chicks were removed or abandoned if female was removed before the chicks were 5 days old.

Most models of biparental care (Houston & Davies 1985; Winkler 1987; Mock et al. 1996; Ratnieks 1996; McNamara et al. 1999) assume that breeding success is a continuously increasing but saturating function of parental effort (Fig. 1a). That is, above a certain level of care, chick survival increases (by diminishing amounts) as combined parental effort increases. However, for ecological situations where there is a high risk of losing success from a breeding attempt with a small decrease in parental effort, then the shape of the parental survival curve would become steeper or even concave-up (Fig. 1b). This situation could occur in species with a very high predation level, for example in a dense sea-bird colony (Burger & Gochfeld 1991; Bukancinski et al. 1998; Bukacinski & Bukacinska 2000), in a mouth brooder (Mrowka 1982) or in species where unattended eggs or young are subject to intense cooling, for example in the king penguin (Challet et al. 1994). In an extreme situation (e.g. when eggs are predated if ever the nest is left unattended) the curve will tend towards a step function (Fig. 1c). In this case breeding success will be zero unless at least one parent is present at all times. However, the simultaneous attendance of both parents does not increase success above that where one parent is present at a time (e.g. only one parent can incubate at a time).

In the following paper we describe a model of biparental care with such a concave-up function for current reproductive success. We look at the consequences of this breeding success function for compensation for decreased partner effort, and the subsequent effect on the evolutionarily stable investment strategies of both parents.

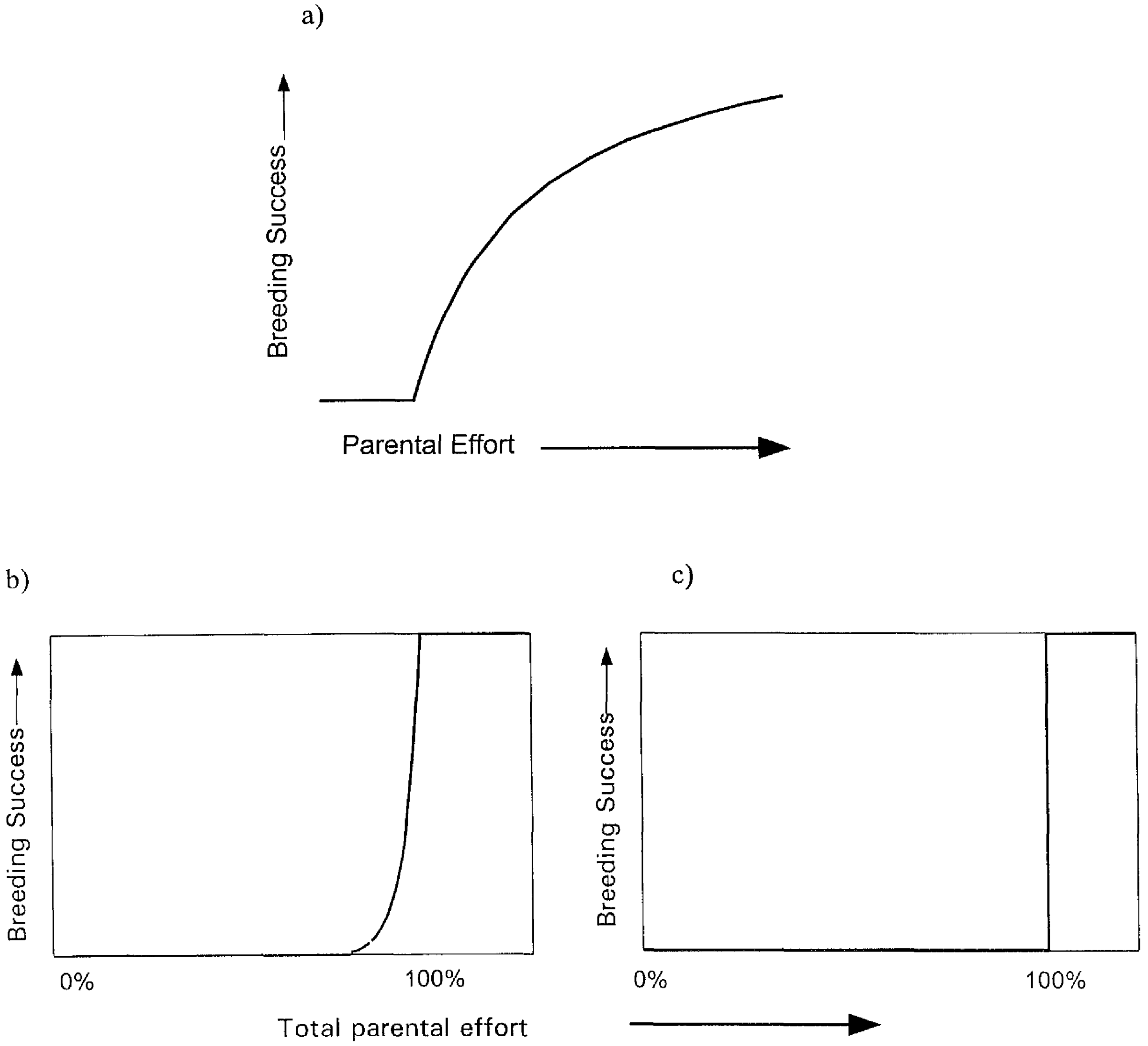


Figure 1. The relationship of breeding success to total parental investment: a) the relationship assumed in models of chick rearing, b) concave-up function where a small decrease in parental effort results in a large decrease in breeding success c) where a breeding attempt is forfeited as parental effort is decreased.

MODEL I: COMPENSATION FOR DECREASED PARTNER EFFORT

In the extreme case (Fig. 1c), where the breeding attempt fails as soon as a parent leaves the nest unattended, it is obvious that, if the parents are to breed successfully, they need to fully compensate for the absence of their partner. Partners will fully compensate for each other (if they can sustain the effort) because the costs of not fully compensating for a decrease in partner nest attendance greatly outweigh the costs of the extra nest attendance in terms of decreased residual reproductive value. It is less clear, however, what should happen when the loss of the reproductive attempt is not a forgone conclusion i.e. if the breeding success function is similar in shape to figure 1b.

In order to answer this question we have used, as an example, a gull colony during incubation. This is because incubation offers a simple situation where all investment into the breeding event takes place at the nest, in the form of incubation and nest defence, and all investment in self-maintenance takes place away from the nest. Secondly, there is intense predation pressure in large gull colonies (Brown 1967; Davis & Dunn 1976; Burger 1977; Brouwer et al. 1995; Bukacinski et al. 1998) and eggs are stolen very soon after they are left unattended, thus demonstrating the breeding success function illustrated in figure 1b. We used an approach following Houston and Davies (1985), but replaced their convex-up breeding success function with the curve illustrated in figure 2. The equation of this curve is:

$$S_e = (p_f + p_m)^n$$

where S_e is the probability that the eggs will survive the incubation period, p_f is the proportion of time the nest is attended by the female and p_m is the proportion of time that the nest is attended by the male. In the simulations we used various values for the shape parameter n, which describes the steepness of the curve. We assume that the birds partition their time such as to avoid the inefficiency of both guarding the nest simultaneously.

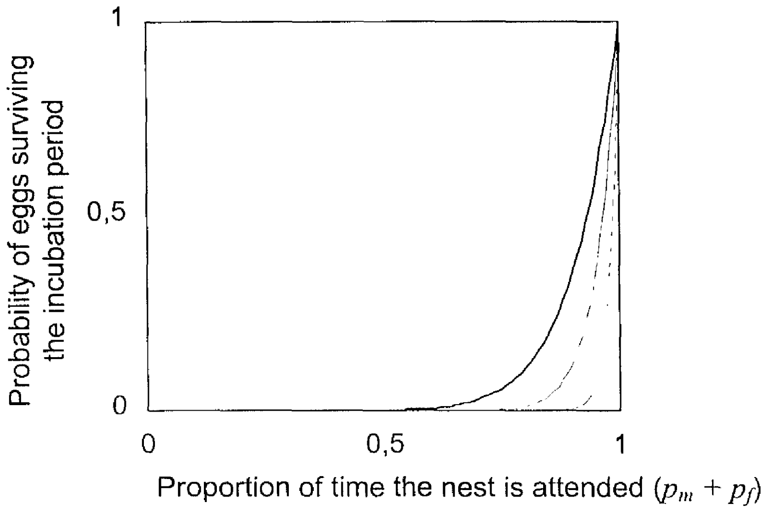


Figure 2. Graph showing how the probability of eggs surviving the incubation period relates to the proportion of time the nest is attended. Three values of n are shown: thick line $n = 10$, thin line $n = 20$ and broken line $n = 50$.

This function was substituted into the ESS model of Houston & Davies (1985), and the best response lines for male and female found using a Visual Basic program. That is, for each potential level of investment by one partner, we plotted the value of the other partner's investment that allowed it to maximise fitness from this reproductive event and from future events. In each case, this predicted that the best response is full compensation. This was not dependent on the shape of the individual parents' survival-effort curves or on the value of n, providing n was large (generally over ten). When n was small, so that the steepness of figure 2 was reduced, a region of full compensation remained but a low effort of either parent will lead to abandonment being the best response by the partner.

The above model shows that parents in biparental species should fully compensate for changes in their partner's behaviour when current breeding success is an accelerating function of parental care. In contrast, Houston and Davies (1985) stressed the importance of partial compensation in maintaining stable biparental care. Given that some of the experimental studies have found parents fully compensating (Mrowka 1982; Hunt et al. 1999; Sanz et al. 2000) and we have shown here that, in theory, full-compensation is a necessity under certain conditions, we now go on to explore how biparental care is maintained in such circumstances.

MODEL II: MODELLING BIPARENTAL CARE IN A FULLY-COMPENSATING SYSTEM

In this model we continue with the example of incubation in a large gull colony. Incubation is costly, both energetically (Williams 1996; Thomson *et al.* 1998), and because time spent incubating cannot be spent feeding (Moreno & Hillstrom 1992). An increasing proportion of time allocated to incubation by a parent will result in a decrease in their survival (and therefore residual reproductive value) due to the trade-off between investment in self-maintenance and in reproduction. The shape of this decrease in survival will be determined by the individual's condition: a parent in good condition will be able to spend more time incubating than a parent in poor condition while retaining the same residual reproductive value; this is described graphically in Fig. 3a. The equation for adult survival used in this model is;

$$S = \frac{(q - q_{min})}{(q - q_{min} + c)}$$

where S *is* the survival probability of the parent, q is the proportion of time not spent incubating by the parent (i.e. $[1- p_m]$ for the male and $[1- p_f]$ for the female), q_{min} is the minimum proportion of time for which the parent must forage in order to have any chance of survival, and the parameter c controls the rate at which feeding beyond this minimum value increases survival probability. If q is less than q_{min}, then adult survival is defined to be zero. A parent in poorer condition would need to forage for longer in order to survive: i.e. q_{min} is greater in individuals with poorer body condition.

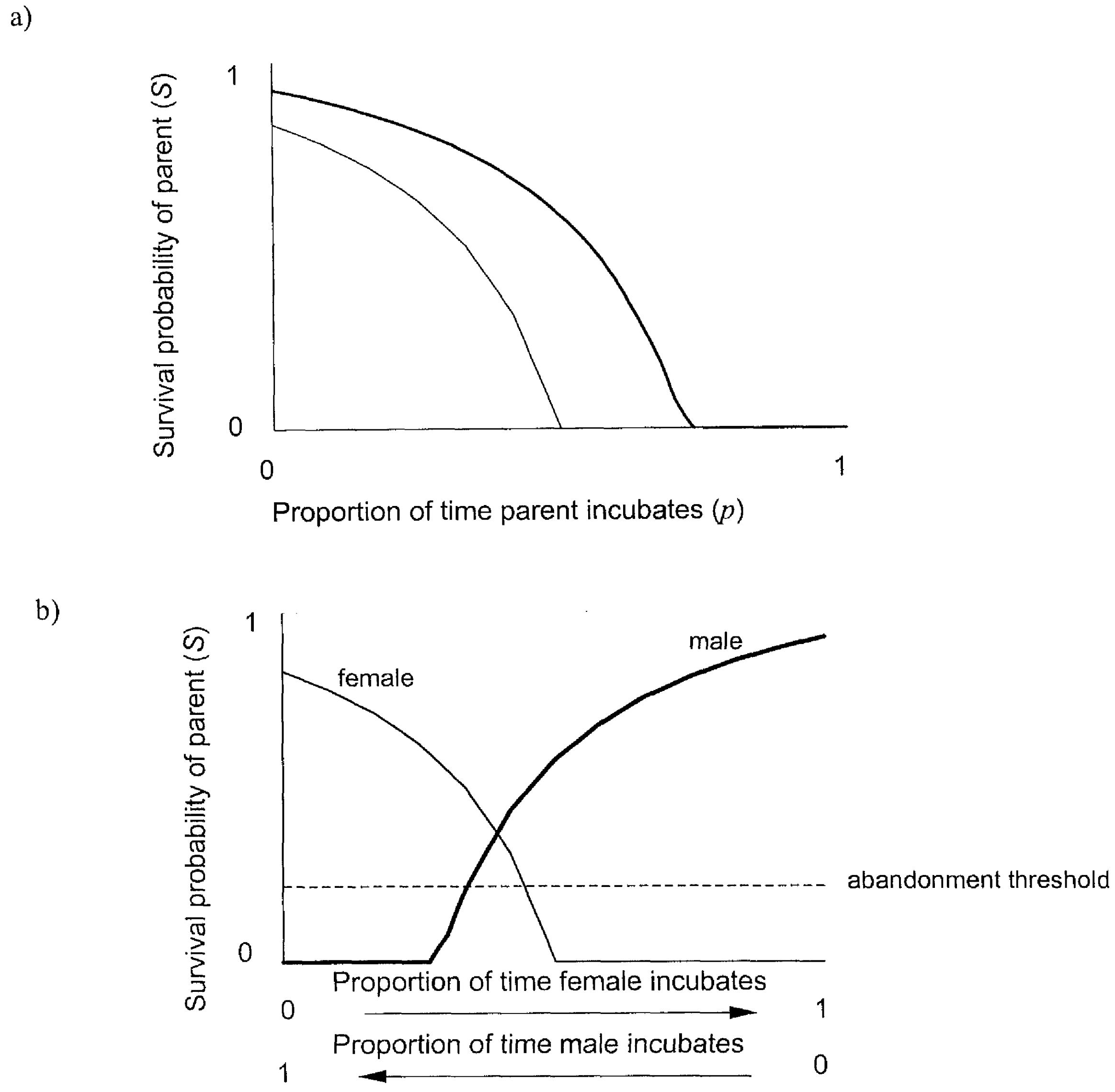


Figure 3. a) Graphical model showing how the survival probability (S) of the parent (and therefore residual reproductive potential) changes with increased investment into incubation (p) in a parent in good condition (bold line) and poor condition (thinner line). b) The male's survival curve (bold line with the axis inverted) is superimposed on to the female survival curve (thinner line) to form this graph. The abandonment threshold, below which the parents will give up on their current breeding attempt in order to preserve residual reproductive value, is marked as a dotted line. In this graph the female is illustrated as being in a poorer condition than the male.

Since we are assuming full compensation for a decrease in partner effort, the survival curves for male and female can be superimposed with an inverted axis for one sex (Fig. 3b). In iteroparus species, lifetime reproductive success is a function of both current and future reproductive success. Individuals need to partition resources efficiently between the current breeding attempt and future opportunities. Several studies have found evidence that there is a threshold of body condition, or level of environmental conditions, below which individuals will not initiate breeding (Naulleau & Bonnet 1996; Madsen & Shine 1999; Mand et al. 2000) or will abandon a breeding attempt (e.g. Monaghan et al. 1992; Lorentsen & Rov 1995; Olsson 1997). Hence, in the following model we have included an 'abandonment threshold', a probability of survival below which the individual will terminate the breeding attempt in order to preserve their residual reproductive value. The level of the threshold will depend on the importance of future reproductive success to the individual (e.g. it will generally be higher for long-lived species and lower for short-lived ones).

FINDING THE SOLUTION

If the abandonment threshold is above the intersection of the two survival curves (Fig. 4a), then the minimum level of care cannot be reached without one or both parents going below their abandonment threshold. This means that the optimal strategy for both parents will be to abandon the breeding attempt. If one parent's curve never crosses the abandonment threshold (Fig. 4b), then that individual will be able to do all the parental care alone and their partner will be completely freed from such duties. An example of this would be the female common eider (*Somateria mollissima*), which does all the incubation without ever leaving the nest. If the lines cross exactly on the abandonment threshold (Fig. 4c) there will be no conflict between the parents, and the ideal strategies for the male and the female will be exactly complementary.

If, however, the two curves cross above the threshold (Fig. 4d) there will be conflict between the parents. When neither parent can do all the work alone there is no ESS, because each will be able to exploit the other by slacking off and obliging the partner to fully compensate. There will, however, be limits to the laziness of each partner. These limits function to maintain biparental care. Neither parent will want to do so little work that their partner is pushed over its abandonment threshold, thereby ruining the breeding attempt for both parents. This means there is a threshold for each parent, beyond which exploiting their partner does not pay, as they would forfeit the current breeding attempt when the partner abandoned (Fig. 5). The ideal level of investment for each individual will be just more than his or her 'laziness threshold'. Unless the abandonment threshold is above the intersection of the two curves (when both parents abandon) or it goes through the intersection (when both parents agree on strategy), the ideal investment levels are different for the male (σ_m) and for the female (σ_f). This means that there will be a region of conflict between the laziness thresholds. Within this region of conflict, there is no ESS, and we would predict that observed strategies should drift between these limits.

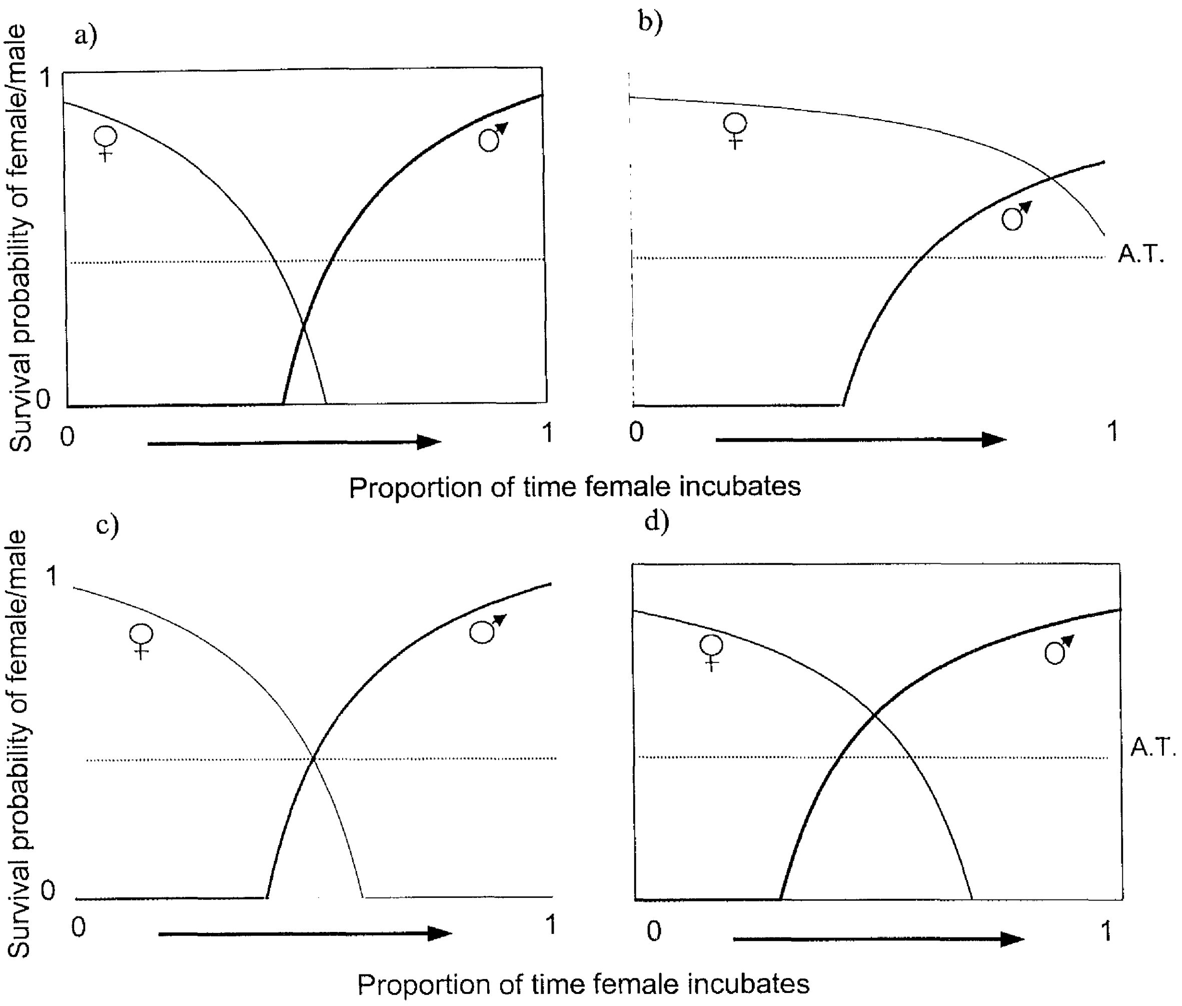


Figure 4. The female's survival curve is shown as a thin line, the male's as a thick line and the abandonment threshold (A.T.) as a dotted line. Each graph shows a different situation: a) where both parents are in poor condition and both will abandon the nest to preserve future reproductive success, b) where one parent is capable of completing all the incubation (in this case the female), c) where there is no conflict between the parents as the survival curves cross exactly on the abandonment threshold and d) where the parents are in conflict over the share of incubation.

APPLICATION OF THE MODEL

Reducing the condition of one or both parents narrows the possible strategies that they may follow (Fig. 6). This makes the pair less flexible in their choice of possible strategies while, at the same time, bringing their ideal strategies closer together, thereby lessening the conflict between them. This suggests that there should be less conflict over parental care under poor environmental conditions or when parents have been manipulated to have a lower condition. Several workers have noted that seabirds operating a more synchronised and equitable system of incubation are more successful (Burger 1987; Morris 1987; Bukacinska et al. 1996; Ratcliffe & Furness 1999) so less conflict between the birds may improve breeding success and compensate to some extent for poor conditions.

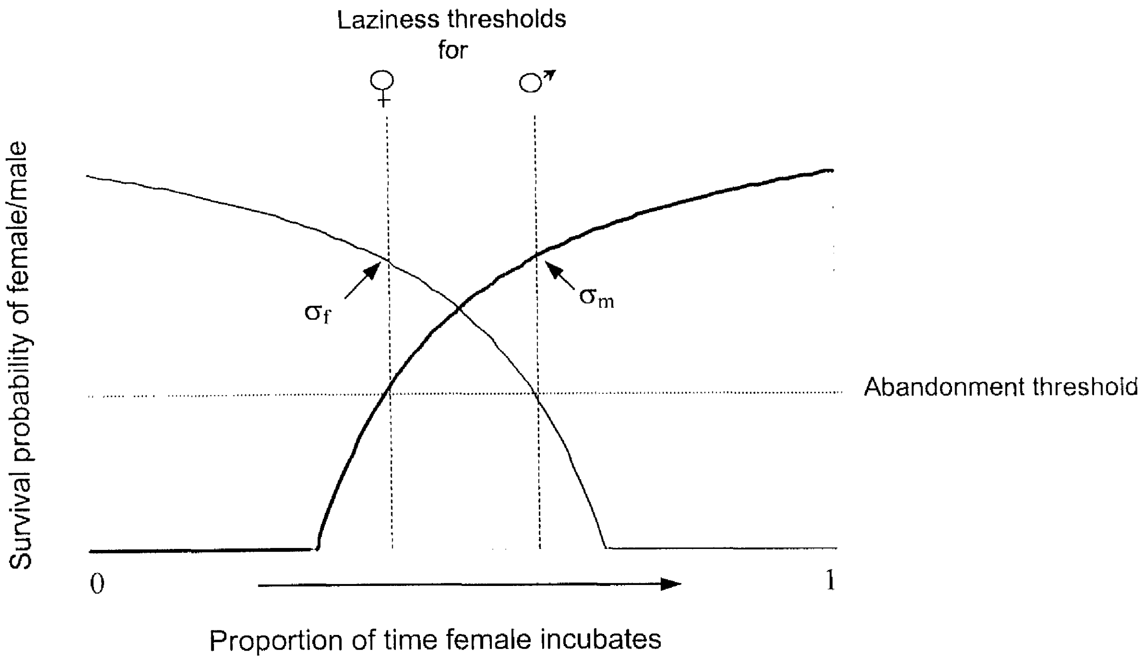


Figure 5. shows the model with a pair in similar body condition. The female's survival curve is denoted by the thinner curve, and the male's by the thicker curve. Dashed vertical lines denote the thresholds of laziness for the male and the female, the least amount of work that the individual can do without its partner abandoning. The arrows point to the preferred incubation proportion of the female (σ_f) and the male (σ_m) and the area of conflict between male and female is shaded.

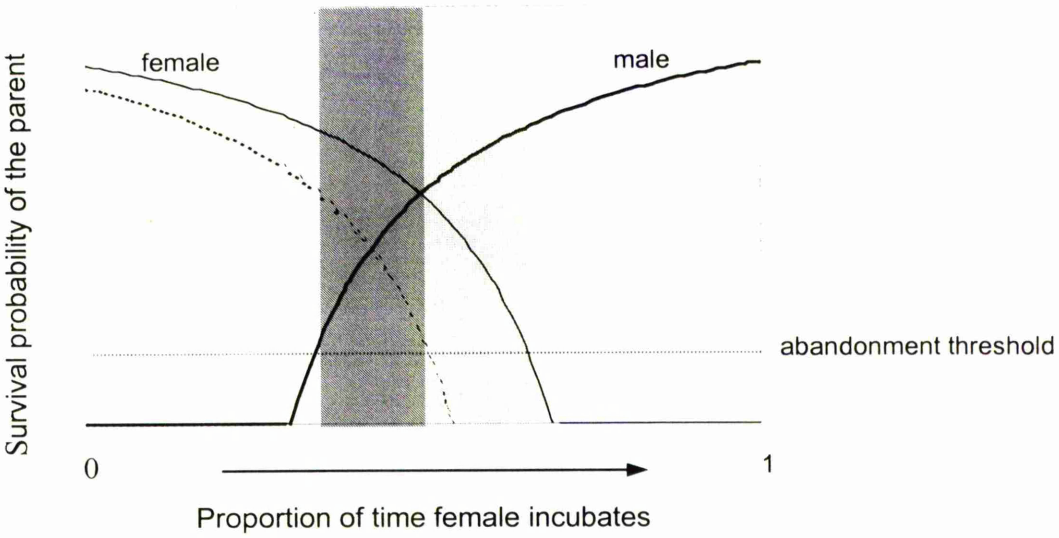


Figure 6. The effect of manipulating female condition on the area of sexual conflict over incubation. The females are denoted by the thinner curves and the males by the thick curve. In controls (solid line), where both parents are in good condition, the whole shaded area shows the region of conflict. In manipulated pairs, where the female is in poorer condition (dotted curve), the darkly shaded area denotes the region of conflict.

DISCUSSION

Many empirical studies have tested whether parents partially compensate for changes in parental care by their partner. Results have not been consistent between studies with some finding full-compensation (Mrowka 1982; Hunt et al. 1999; Sanz et al. 2000), which would be expected to make biparental care unstable. We have demonstrated, using a modification of Houston and Davies' (1985) model, that full compensation for decreased parental effort by one partner should occur under certain conditions, specifically, when a small decrease in parental effort results in a large decrease in breeding success. Ratneiks (1996) showed that biparental care becomes unstable when future fitness is a concave-down function of expenditure and Houston & Davies (1985) show that biparental care is an ESS only under a partial compensation strategy.

The second model described in this chapter shows that 'limits to the laziness' for each partner can maintain biparental care in a fully compensating system. Neither parent will want to decrease their effort so much that their partner will abandon the breeding attempt. This maintains biparental care in a system where neither parent can successfully bring up the offspring alone. It is likely, however, that the limits to laziness will be in different places for each partner (they will have different ideal levels of work). This will cause conflict between the parents over the distribution of the work. Since the pair will forfeit the breeding attempt if neither bird makes up for the shortfall of care between the preferred strategies of male and female, the conflict must be resolved.

There will be no ESS in this model. If, for example, the pair are sharing the work equally in the area of conflict and the female decides to do a little less work, then the male will have to compensate fully if they are not to lose the breeding attempt. She will be able to slacken off until he has nearly reached his abandonment threshold, at which point she will not be able to do any less work for fear of his abandoning. At this point the male can do less work and the female will have to compensate for his shortfall. Hence the combination of strategies played will bounce back and forth within the bounds of the laziness thresholds of male and female.

The flexibility of possible incubation strategies delineated by the laziness thresholds suggests that there can be a wide range of incubation behaviours observed in a group of similar partnerships. This flexibility will be reduced if one or both parents are in relatively poor condition, but the level of conflict between the parents will also decrease in such circumstances. We would, therefore, expect more co-operation between partners under poor environmental conditions or when one, or both, are in a poor condition.

The answer to the question of which bird is doing better out of the arrangement will depend on which parent in is control of the situation at that moment. For example, during incubation the foraging individual is in control because they make the decision of when to return. They will stay away from the nest until they think that their partner is going to leave. All solutions of the conflict, however, must lie within the bounds of the laziness thresholds. In reality there will be a buffer zone around each laziness threshold as neither bird can risk pushing their partner to abandon. Neither bird will have perfect information about his/her partner's condition and so they will have to err on the side of caution when making parental decisions. This will make the zone of conflict smaller.

Each parent needs to judge their partner's condition in order to estimate the time they can spend away from the nest, so that their partner does not desert. It will, therefore, be in the incubating partner's interests to be able to communicate their own state. Many seabirds, especially the pelecaniformes (Van Tets 1965) have evolved elaborate mutual displays that are performed during nest relief. The flexibility of nest-relief signals and responses in this group suggests that information is being exchanged (Johnsgard 1993). Van Tets (1965) suggests that some of the pre-takeoff displays convey information that the departing individual's intentions in order to encourage his/her partner to stay at the nest. Information may well pass in the other direction with the incubating partner displaying condition information. In some species, calls have been found to convey information about condition or body mass (e.g. Genevois & Bretagnolle 1994; Galeotti et al. 1997).

If partners are communicating information about state, it should be to an individual's advantage to deceive their partner into thinking that they are in a worse condition than they really are. This would mean that their partner would return from foraging sooner to relieve the incubation shift. However, just as there are limits to the laziness of each parent below which the partner will abandon, there will be a lower limit to how poor condition you can seem to your partner before they abandon. For example, if an individual makes their partner believe that they are in too poor a condition, then the partner will abandon, having assessed that they will not be able to complete the breeding attempt successfully. If, however, both partners are lying about their condition then the points at which they will abandon will come closer together and the breeding attempt may even be abandoned unnecessarily. Since the loss of a breeding attempt can be very costly, there will be a great advantage in being able to accurately interpret signals and also for honest signalling of condition.

For long-lived species that maintain the same partner from year to year, there will be an advantage for an individual in maintaining their partner's condition and ensuring their survival to the following year. This will reduce the amount of time and energy spent in finding a partner and courtship and increase the chance of a successful breeding attempt (reviewed in Mock and Fujioka, 1990; Fowler, 1995). Therefore, in species exhibiting long-term monogamy, we would expect partners to be less likely to exploit their partner. Species with long-term pair bonds may arrange the parental effort, within the zone of conflict, so that the partner who will benefit the most from contributing less parental effort does less work.

This graphical model has shown that full compensation for a decrease in a partner's parental effort can be maintained, albeit not as an ESS. This situation may occur commonly when there is a high probability of the loss of the breeding attempt with a small decrease in parental care; for example in dense bird colonies where predation rates on unattended eggs or young are very high, or in the Arctic or Antarctic where eggs are very vulnerable to cooling. It may be that there are different parental reactions during different phases of reproduction; e.g. partial compensation during chick rearing but full compensation during incubation. In situations of full compensation it would be possible to test some of the predictions of the model. We would predict that under poor conditions, or when one or both parents' condition has been negatively manipulated, there should be less conflict between the partners and that individuals should use information gathered about the condition of their partner when assessing how much time they can spend away from the offspring.

REFERENCES

Annett, C. A., Pierotti, R. & Baylis, J. R. 1999. Male and female parental roles in the monogamous cichlid, *Tilapia mariae*, introduced in Florida. *Environmental Biology of Fishes* **54**, 283-293.

Brouwer, A., Spaans, A. L. & Dewit, A. A. N. 1995. Survival of herring gull *Larus argentatus* chicks - an experimental-analysis of the need for early breeding. *Ibis*, **137**, 272-278.

Brown, J. L. 1967. Breeding success and population growth in a colony of herring and lesser black-backed gulls, *Larus argentatus* and *L. fuscus*. *Ibis*, **109**, 501-515.

Bukacinska, M., Bukacinski, D. & Spaans, A. L. 1996. Attendance and diet in relation to breeding success in herring gulls (*Larus argentatus*). *Auk* **113**, 300-309.

Bukacinski, D., Bukacinska, M. & Spaans, A. L. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the lesser black-backed gull *Larus fuscus*. *Ibis* **140**, 422-430.

Bukacinski, D. & Bukacinska, M. 2000. The impact of mass outbreaks of black flies (Simuliidae) on the parental behaviour and breeding output of colonial common gulls (*Larus canus*). *Annales Zoologici Fennici* **37**, 43-49.

Burger, J. 1977. Role of visibility in nesting Larus Gulls. *Journal of Comparative and Physiological Psychology* **91** p 1347-1358

Burger, J. 1987. Selection for equitability in some aspects of reproductive investment in herring-gulls *Larus argentatus*. *Ornis Scandinavica* **18**, 17-23.

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

Challet, E., Bost, C. A., Handrich, Y., Gendner, J. P. & Lemaho, Y. 1994. Behavioual budget of breeding king penguins (*Aptenodytes patagonica*). *Journal of Zoology* **233**, 669-681.

Davies, N. B. 1992. Dunnock Behaviour and Social Evolution. Oxford University Press, Oxford.

Davis, J. W. F. & Dunn, E. K. 1976. Intraspecific predation and colonial breeding in lesser black-backed gulls *Larus fuscus*. *Ibis,* **118**, 65-77

Dunn, P. O. & Robertson, R. J. 1992. Geographic variation in the importance of male parental care and mating systems in tree swallows. *Behavioral Ecology,* **3**, 291-299.

Fetherston, I. A., Scott, M. P. & Traniello, J. F. A. 1994. Behavioral compensation for mate loss in the burying beetle *Nicrophorus orbicollis*. *Animal Behaviour,* **47**, 777-785.

Fowler, G. S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist*, **35**, 318-328.

Galeotti, P., Saino, N., Sacchi, R. & Moller, A. P. 1997. Song correlates with social context, testosterone and body condition in male barn swallows. *Animal Behaviour,* **53**, 687-700.

Genevois, F. & Bretagnolle, V. 1994. Male blue petrels reveal their body-mass when calling. *Ethology Ecology and Evolution,* **6**, 377-383.

Hegner, R. E. & Wingfield, J. C. 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk*, **104**, 462-469.

Houston, A. I. & Davies, N. B. 1985. The evolution of cooperation and life history in the dunnock *Prunella modularis*. In: Behavioural Ecology (R.M.Sibly & R.H.Smith), pp. 471-487. Blackwell Scientific Publications, Oxford.

Hunt, K. E., Hahn, T. P. & Wingfield, J. C. 1999. Endocrine influences on parental care during a short breeding season: testosterone and male parental care in Lapland longspurs (*Calcarius lapponicus*). *Behavioral Ecology and Sociobiology*, **45**, 360-369.

Johnsgard, P. A. 1993. Cormorants, Darters and Pelicans of the World. Smithsonian Institution Press, Washington.

Lavery, R. J & Reebs, S. G. 1994. Effect of mate removal on current and subsequent parental care in the convict cichlid (*pisces, cichlidae*). *Ethology*, **97**, 265-277.

Lessells, C. M. 1991. The evolution of life histories. In: Behavioural Ecology: An Evolutionary Approach (J.Krebs & N.B.Davies), pp. 32-68. Blackwell Science Publications, Oxford.

Lorentsen, S. H. & Rov, N. 1995. Incubation and brooding performance of the antarctic petrel *Thalassoica antarctica* at Svarthamaren, Dronning-Maud land. *Ibis*, **137**, 345-351.

McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999. Incorporating rules for responding into evolutionary games. *Nature* **401**, 368-371.

Madsen, T. & Shine, R. 1999. The adjustment of reproductive threshold to prey abundance in a capital breeder. *Journal of Animal Ecology* **68**, 571-580.

Mand. R., Tilgar, V. & Leivits, A. 2000. Reproductive response of Great Tits, *Parus major*, in a naturally base-poor forest habitat to calcium supplementation. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **78**, 689-695.

Markman, S., YomTov, Y. & Wright, J. 1996. The effect of male removal on female parental care in the orange-tufted sunbird. *Animal Behaviour*, **52**, 437-444.

Markman, S., YomTov, Y. & Wright, J. 1995. Male parental care in the orange-tufted sunbird – behavioral adjustments in provisioning and nest guarding effort. *Animal Behaviour*, **50**, 655-669.

Mock D. W. & Fujioka, M. 1990. Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology and Evolution*, **5**, 39-43

Mock, D. W., Schwagmeyer, P. L. & Parker, G. A. 1996. The model family. In: Partnerships in Birds. (J.M.Black), pp. 53-71. Oxford University Press, Oxford.

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**, 70-81.

Moreno, J. & Hillstrom, L. 1992. Variation in time and energy budgets of breeding wheatears. *Behaviour*, **120**, 11-39.

Morris, R. D. 1987. Time-partitioning of clutch and brood care activities in Herring Gulls: A measure of parental quality? *Studies in Avian Biology*, **10**, 68-74.

Mrowka, W. 1982. Effect of removal on the parental care behaviour of the biparental cichlid *Aequidens paraguayensis*. *Animal Behaviour*, **30**, 295-297.

Naulleau, G. & Bonnet, X. 1996. Body condition threshold for breeding in a viviparous snake. *Oecologia*, **107**, 301-306.

Olsson, O. 1997. Clutch abandonment: a state dependent decision in king penguins. *Journal of Avian Biology*, **28**, 264-267.

Pinxten, R., Eens, M. & Verheyen, R. F. 1995. Response of male European starlings to experimental removal of their mate during different stages of the breeding cycle. *Behaviour*, **132**, 301-317.

Ratcliffe, N. & Furness, R. W. 1999. The effect of parental age and experimentally manipulated brood size on the foraging effort and breeding performance of great skuas (*Catharacta skua*). *Journal of Zoology*, **249**, 195-201.

Ratnieks, F. L. W. 1996. Evolution of unstable and stable biparental care. *Behavioral Ecology* **7**, 490-493.

Saino, N. & Moller, A. P. 1995. Testosterone induced depression of male parental behavior in the barn swallow - female compensation and effects on seasonal fitness. *Behavioral Ecology and Sociobiology*, **36**, 151-157.

Sanz, J. J., Kranenbarg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *Journal of Animal Ecology*, **69**, 74-84.

Sasvari, L. 1986. Reproductive effort of widowed birds. *Journal of Animal Ecology*, **55**, 553-564.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Stoehr, A. M., Hill, G. E. 2000. Testosterone and the allocation of reproductive effort in male house finches (*Carpodacus mexicanus*). *Behavioral Ecology and Sociobiology*, **48**, 407-411.

Thomson, D. L., Monaghan, P. & Furness, R. W. 1998. The demands of incubation and avian clutch size. *Biological Reviews of the Cambridge Philosophical Society*, **73**, 293-304.

Transue, G. J. & Burger, J. 1989. Responses to mate loss by herring gulls *Larus argentatus* and great black-backed gulls *Larus marinus*. *Ornis Scandinavica,* **20**, 53-58.

Van Tets, G. F. 1965. A comparative study of some social communication patterns in the pelecaniformes. *Ornithological Monographs* **2**, 1-88.

Williams, J. B. 1996. Energetics of avian incubation. In: Avian Energetics and Nutritional Ecology (C. Carey), pp 375-417. Chapman & Hall, New York.

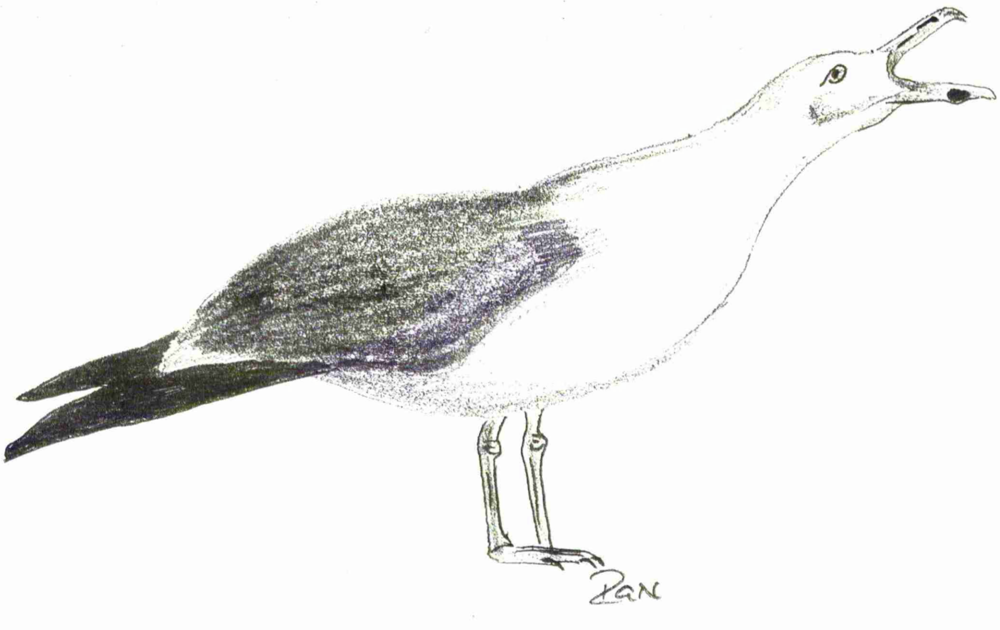
Whittingham, L. A., Dunn, P. O. & Robertson, R. J. 1994. Female response to reduced male parental care in birds - an experiment in tree swallows. *Ethology,* **96**, 260-269.

Winkler, D. W. 1987. A general-model for parental care. *American Naturalist,* **130**, 526-543.

Wright, J. & Cuthill, I. 1989. Manipulation of sex-differences in parental care. *Behavioral Ecology and Sociobiology,* **25**, 171-181.

Chapter 6

TERRITORY QUALITY AND INDIVIDUAL QUALITY



ABSTRACT

Birds nesting in high quality breeding sites generally have a higher breeding success. This could be due to the characteristics of the nesting site itself, or to the quality of the individuals choosing those sites. In this chapter I investigate this issue, using a field study on the lesser black-backed gull, *Larus fuscus*. Lesser black-backed gulls nest in small territories on sand dunes, preferring sites with patches of vegetation that protect eggs and young from predation. These territories contain no food resources for the adults or chicks and so clutch characteristics should reflect individual, rather than territory quality. I measured female quality in two diverse areas of a single colony, one with plenty of vegetation and one with very little vegetation. I found that birds in the plot with more vegetation laid eggs significantly earlier and showed a strong tendency towards laying larger eggs. There was no difference in clutch size between the two plots, although there was a significant decrease in clutch size with season, and no difference in the proportion of birds that laid a replacement egg. In general, gulls in more vegetated areas appear to be of higher quality and can therefore gain the advantage of reduced predation of eggs and chicks, which adds to the breeding advantages they already have as high quality individuals.

INTRODUCTION

There are many determinants of breeding success, most of which an individual cannot change directly, such as environmental conditions during the breeding season. An individual can, however, often influence the effect of environmental conditions on breeding success by making the right decisions when choosing a breeding location. (Newton 1991; Rees et al. 1991; Hatchwell et al. 1996; Côté 2000). The characteristics used by individuals to choose a breeding site differ between species with some choosing on the basis of food resources (Tye 1992) while, for colonial breeders where the sites do not hold any other resources, a protected position within the colony is preferred (Côté 2000). Individuals in good quality territories tend to have a higher breeding success (Vickery et al. 1992; Braden et al. 1997; Franklin et al. 2000) and be in better condition (Carlson 1998). However, the competition for good breeding sites means that individuals securing these sites may be higher quality, more dominant individuals from the outset. Accordingly, it is difficult to separate the effects of breeding site itself and individual quality on breeding success. Higher breeding success in particular sites or habitats could be due to the characteristics of the nest site, or to the quality of birds themselves (Goodburn 1991). We therefore need a measure of individual quality that is independent of territory or site quality. In the lesser black-backed gull, *Larus fuscus*, where breeding territories do not contain food resources, measures of clutch characteristics can give an independent measure of adult quality. Here I examine the extent to which territories with more cover (preferred by gulls - Davis & Dunn 1976) are occupied by birds of high quality.

Lesser black-backed gulls nest in colonies on sand dunes and defend small territories immediately surrounding the nest site. They generally nest in areas with 30-70% cover (Davis & Dunn 1976). Pairs that nest in territories with more cover are usually more successful (Brown 1967; Davis & Dunn 1976; Calladine 1997), as intra-specific predation is one of the greatest causes of mortality in eggs and young chicks (Brown 1967; Davis & Dunn 1976; Bukacinski et al. 1998). More vegetation cover also reduces levels of aggression between neighbouring pairs (Burger 1977). Although vegetation is generally sparse when gulls arrive on the breeding grounds in April, individuals lesser black-backed gulls have a high site-fidelity and so will be aware of the quality of each part of the colony.

Two contrasting and clearly differing habitats within a single large colony were chosen. These were close to each other in the central part of the colony, one with no vegetation and one with numerous patches of cover. In each plot I assessed the 'quality' of the females early in the breeding season using several factors thought to indicate individual quality: lay date (Reid 1988; Sydeman et al. 1991; De Forest & Gaston 1996; Hipfner et al. 1997), clutch size (Parsons 1975; Coulson & Porter 1984), egg size (Bolton 1991; Williams 1994), and the ability of females to lay an additional egg (reviewed in Hipfner et al. 1999).

METHODS

This study was undertaken in 1998 on Walney Island, Cumbria in a colony comprising c. 24 000 pairs of lesser-black backed gulls and c. 8 000 pairs of herring gulls. The birds nest on sand dunes covered with vegetation and clutches are laid over a two-month period; the earliest birds begin laying around 25th April and the bulk of the birds lay at the beginning to middle of May. There was a wide variation in laying date across the colony with nests in each area being well synchronised locally. For this study I chose two clearly contrasting plots, each containing about 100 nests. Plot 1 was well drained and contained numerous patches of cover in the form of nettles, thistles and grass (plate 1) and in this area nests were generally made near a patch of vegetation on flat ground. Plot 2, on the other hand, was in a poorly drained dune slack with short-cropped grass and no cover, even late in the year (plate 2). The two plots were adjacent to one another and towards the centre of the colony.

Laying date, clutch-size and egg-size

We checked nests twice a day to ascertain laying date. The first egg laid was measured with callipers and then nests were visited daily to record when the other eggs were produced and the final clutch size. If no egg had been laid for ten days (the minimum time that a gull takes to form a replacement clutch if the whole first clutch is lost, Brown 1967), the clutch was considered to be complete. In lesser black-backed gulls the modal clutch size is three. As the brood patch has space for only three eggs, it is extremely rare to get a four egg clutch and I found none in the year of study; however, two-egg (27 of 135 clutches–20%) or one-egg clutches (14 of 135 clutches–10.4%) were relatively common.

Egg size is a useful proxy for female quality (Birkhead & Nettleship 1982; Amundsen & Stokland 1990; Ried & Boersma 1990; Bolton 1991; Magrath 1992; Brouwer & Spaans 1994; Robertson et al. 1994; Verhulst 1995; Hipfner et al. 1997). To estimate volume of the eggs I used the following equation from Harris 1964,

$$\text{Volume} = 0.476 \times \text{length} \times \text{breadth}^2$$

Since manipulation of egg laying (see below) took place after females had laid the first egg, this egg was unaffected by the manipulation. The size of the first egg is therefore used as a comparative measure of female quality between manipulated and unmanipulated birds.

Ability to lay a replacement egg

About 80% of lesser black-backed gulls will lay a replacement egg if the first egg is removed within 12 hours of laying (Monaghan et al. 1995; 1998). As a further test of female quality I used the ability of the female to lay a replacement egg. Nests were allocated at random to the unmanipulated or manipulated groups. The unmanipulated nests were used to establish laying date, clutch size and egg size (see previous section). Manipulated nests had the first-laid egg removed within 12 hours of laying (under licence from English Nature). Eggs were measured and nests followed as described previously to determine whether the female replaced the removed egg.

Lesser black-backed gulls can only successfully incubate three eggs or less, therefore four-egg clutches are extremely rare under natural conditions. If four eggs are produced by females in the egg-removed group, I can therefore be almost certain that this includes a replacement egg. The same cannot, however, be said where less than four eggs are laid. When analysing the egg-removal data, I considered only those females that could be identified as having replaced the removed egg (i.e. they laid four eggs) and compared them with the equivalent unmanipulated females (ones that laid three eggs).

Breeding success

Nests were surrounded by a low fence of chicken wire to facilitate finding the chicks without causing undue disturbance, as in Bolton (1991) and the number of fledged chicks, defined as the number still alive after 35 days old, was recorded. Only nests unmanipulated throughout the breeding attempt were used in this analysis. Some of the nests in plot 1 had an egg removed after the clutch was complete (see chapter 3), and therefore these were excluded from analysis of breeding success. Up until the end of laying, all nests used in the analysis of clutch size, egg size and laying date had been treated identically and the measurements used in these analyses could not have been affected by the subsequent removal of an egg.

Means are presented plus and minus the standard error. In the analysis of female quality using laying date, egg size and clutch size I use only the unmanipulated clutches. This is because egg-removal can change the characteristics of the clutch (I found that first eggs of females that laid a fourth egg were larger than those of unmanipulated females - see results section). Manipulated clutches are used only in the analysis of the ability to lay a replacement egg.

Plate 1. Vegetation typical of plot 1, showing patches of vegetation offering cover to nesting gulls. This photograph was taken during the incubation period.

Plate 2. Vegetation typical of plot 2. This photograph was taken towards the end of the chick-rearing period showing very little vegetation, even at this late stage.

RESULTS

Laying date (unmanipulated nests)

Birds in the two plots had significantly different mean dates of laying the first egg. Birds in plot 1 (mean 7.6 May ± 0.75, $N = 66$) laid nearly 6 days earlier, on average, than those in plot 2 (mean 13.5 May ± 0.74, $N = 69$; t-test: $t_{133} = 5.67$ $P < 0.001$).

Clutch size (unmanipulated nests)

Clutch size decreased over the breeding season (Fig. 1) and this pattern did not differ between the two study plots. However, overall there was no significant difference in clutch size between the plots (Chi squared test on clutch-size and plot, Table 1: $\chi^2_2 = 1.581$, $P = 0.454$).

Table 1 number of clutches containing one, two and three eggs in each plot

Clutch size	1	2	3
Plot 1	5	12	49
Plot 2	9	15	45

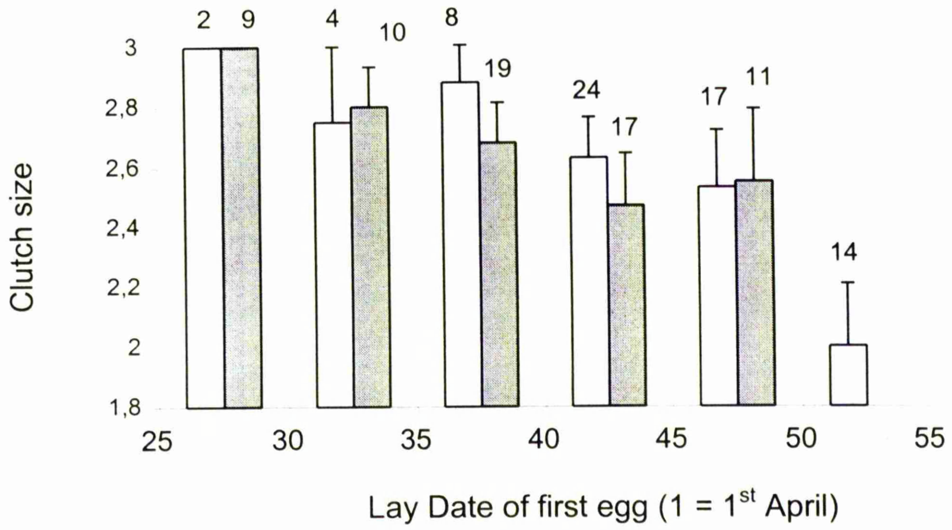


Figure 1. Clutch sizes of unmanipulated nests in plot 1 (grey bars) and plot 2 (white bars) according to their laying date. In both plots there is a significant but weak decrease in clutch size over the season (linear regression, plot 1: $R^2 = 0.06$, $F_{64} = 4.068$, $P = 0.048$; Plot 2: $R^2 = 0.144$, $F_{67} = 11.27$, $P = 0.001$) but no difference between the plots (ANCOVA: dependent variable - clutch-size; plot × lay late interaction, $F_{1,131} = 1.158$, $P = 0.284$, effect of plot, $F_{1,131} = 1.316$, $P = 0.253$). All females laying before 30th April laid a clutch of three eggs.

Egg size (unmanipulated nests)

The within clutch pattern of egg sizes in modal clutches (containing three eggs) was the same in each plot, and there was a strong tendency for eggs from plot 1 to be larger than those from plot 2 (Fig. 2).

There was a weak but significant trend for egg volume to decrease with laying date. The volume of first-laid eggs was not related to laying date ($R^2 = 0.032$, $F_{1,91} =$

3.05, $P = 0.084$) but that of second ($R^2 = 0.05$, $F_{1,87} = 4.572$, $P = 0.035$) and third eggs ($R^2 = 0.101$, $F_{1,90} = 10.131$, $P = 0.002$) declined with date and consequently so did total clutch volume ($R^2 = 0.092$, $F_{1,85} = 8.695$, $P = 0.004$). The low R^2 value, however, means that the effect of date on egg size may be biologically trivial. There was no effect of plot on egg volume after laying date had been controlled for (ANCOVA: dependent variable - clutch volume, fixed factor - plot and covariate - laying date; effect of plot, $F_{1,84} = 0.105$, $P = 0.747$; effect of laying date, $F_{1,84} = 06.253$, $P = 0.014$). There was no significant interaction between plot and laying date.

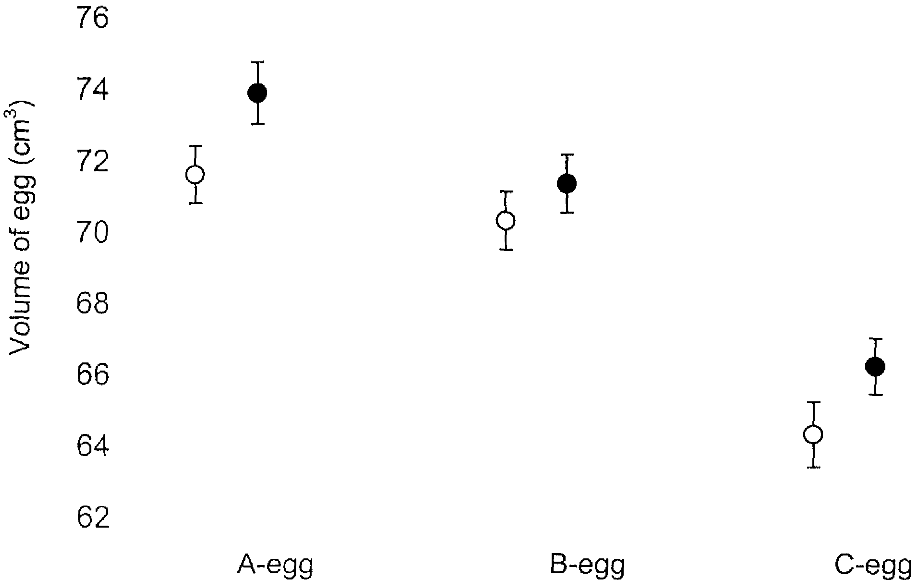


Figure 2. Volumes of eggs from unmanipulated females in plot 1 (filled circles) and plot 2 (empty circles). The pattern of egg sizes was the same between the plots (Repeated measured ANOVA: within subjects factor – egg, between subjects factor – plot. Egg × plot interaction; $F_{2,84} = 1.35$, $P =$

0.265). There was a nearly significant effect of plot on egg size ($F_{1,85}$ = 3.629, $P = 0.06$).

Table 2 Number of manipulated females that replaced and did not replace the removed egg, and the percentage of females that failed to replace.

	replaced removed egg	did not replace	% failing to replace
Plot 1	15	9	37.5
Plot 2	32	24	42.9

Laying a replacement egg (all nests)

Females that successfully replaced a removed egg had larger first eggs than unmanipulated females and there was no difference in this pattern between plots (Fig. 3). Nor was there any difference in the proportion of manipulated females that did not replace a removed egg between the two plots (Table 2: $\chi^2_1 = 0.04$, $P = 0.843$). The pattern of egg sizes laid by manipulated females was the same in each plot (Fig. 4). The replacement egg was 88.3% of the volume of the first-laid egg in plot 1, and 87.2% in plot 2. There was no difference between the size of the fourth egg relative to that of the first-laid egg between the two plots (t-test on arcsine transformed proportions: t_{39} = 0.740, $P = 0.464$).

Breeding success (unmanipulated nests)

There was no difference in the proportion of nests that failed in plot 1 (9 out of 15) and plot 2 (19 out of 43; $\chi^2_1 = 1.0$, $P = 0.318$). There was no difference between the average number of fledglings produced by nests in plot 1 (0.714 per nest ± 0.286, $N = 14$) and plot 2 (0.977 per nest ± 0.151, $N = 43$; Mann-Whitney U test: $Z = -0.975$, $P = 0.330$). Neither was there a difference in the mass of the brood produced in plot 1 (1160g ± 209.0, $N = 5$) and plot 2 (1188.5g ± 97.3, $N = 24$; t-test: $t_{27} = 0.122$, $P = 0.904$).

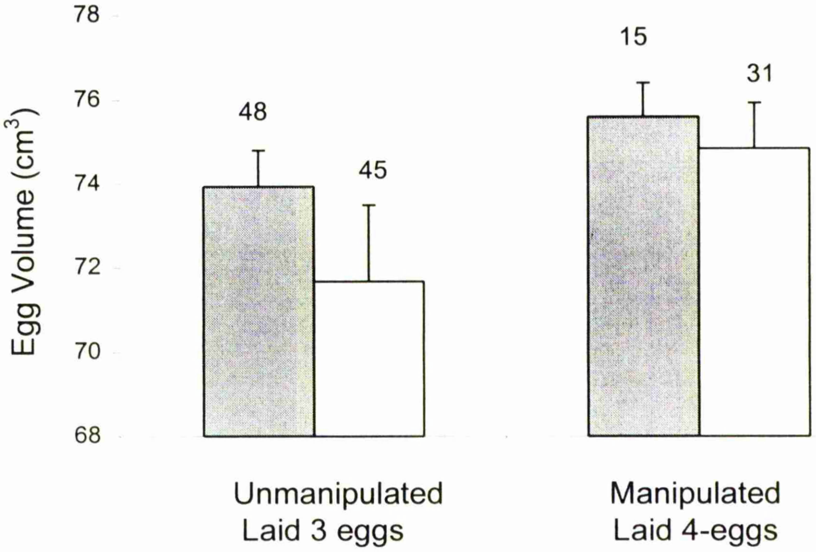


Figure 3. Volumes of first-laid eggs in plot 1 (grey bars) and plot 2 (white bars). Females that managed to lay a fourth egg laid a significantly larger first egg than unmanipulated females (ANOVA: $F_{1,136} = 5.663$, $P = 0.019$). There was no effect of plot (ANOVA: $F_{1,136} = 3.129$, $P = 0.079$) and no plot × treatment interaction.

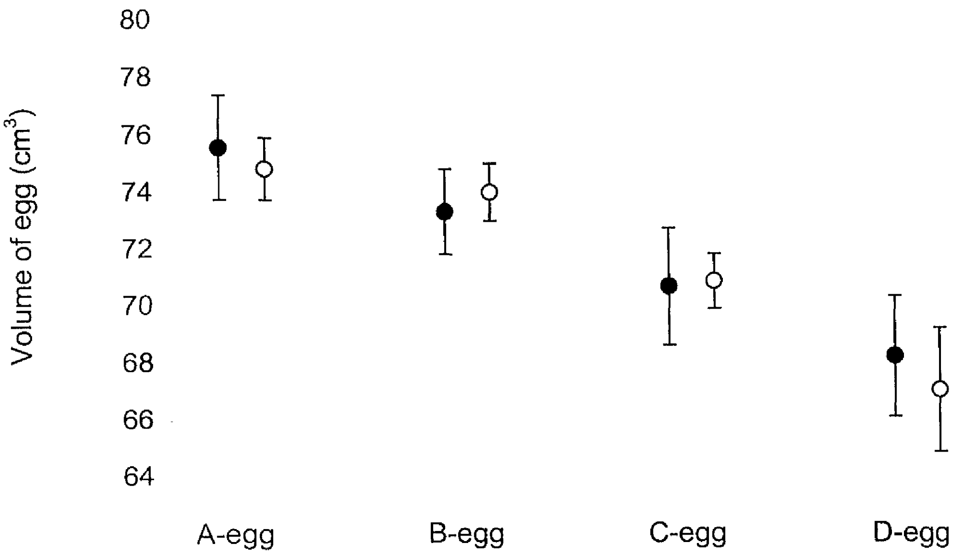


Figure 4. Volumes of eggs from manipulated females in plot 1 (filled circles) and plot 2 (empty circles). The pattern of egg sizes was the same between the plots (Repeated measures ANOVA: within subjects factor – egg, between subjects factor – plot. Egg × plot interaction; $F_{3,37} = 0.475$, $P = 0.147$). There was no significant effect of plot on egg size ($F_{1,39} = 0.286$, $P = 0.596$).

DISCUSSION

Females nesting in plot 1, the area with plenty of cover, had a significantly earlier laying date than those in plot 2. There was a strong tendency for eggs of unmanipulated clutches to be larger in plot 1 than in plot 2, although this was not quite significant. There was no significant difference in clutch size between the plots, although clutch size was strongly negatively correlated with laying date over both plots. Females from plot 1 were no more likely to lay a replacement egg than those from plot 2, however those that replaced a removed egg had laid a larger first egg than unmanipulated females, suggesting that they are a higher quality subset of the females that lay three eggs. Replacement eggs were the same size, relative to the first egg laid, in both plots and the pattern of egg sizes in manipulated clutches did not differ between the plots.

Some of the measures of quality used suggest that the two plots contain birds of differing quality. Birds in the vegetated plot nested, on average, six days earlier than those in the open plot. Date of clutch initiation has been shown to be related to individual quality, with better quality birds tending to lay earlier (Sydeman et al. 1991; Perdeck & Cavé 1992; Verhulst et al. 1995; De Forest & Gaston 1996; Hipfner 1997; Hipfner et al. 1997; Daunt et al. 1999, but see Barba et al. 1995). I also found that egg size and clutch size were correlated with laying date. This has also been found in many other studies (Mills 1973; Verhulst et al. 1995; Hipfner et al. 1997) and is attributed, either to 'parental quality' (Hipfner 1997), or declining environmental conditions over the season (Barba et al. 1995). Manipulation experiments have been carried out to separate the effects of individual quality and date (reviewed in Hipfner 1997 and

Moreno 1998). However, the results of such studies appear to vary between species, with some stressing the importance of 'seasonal deterioration' and some the importance of 'parental quality'.

Although laying date and egg size suggested that there were higher quality birds in plot 1, I found that females from plot 1 were no more likely to lay a replacement egg than those from the poorer plot 2. There was also no difference in the pattern of egg sizes laid by females that replaced a removed egg in each plot, in contrast to unmanipulated clutches. Females that do lay a fourth egg seem to be a higher quality subset of females since they lay a larger first egg, and this may explain why there were no differences in egg size between the plots. If females that lay a fourth egg are of a higher quality, as indicated by the size of their first egg, we may expect to find fewer females replacing the egg in the later-laying plot. This, however, was not the case. However, since the majority of females are able to lay a replacement egg, the additional costs of laying a replacement are, perhaps, not enough to differentiate between birds of differing quality.

Several studies have found that, especially where the territory provides food, birds with better territories breed earlier (Aebischer et al. 1996; Hinsley et al. 1999; Currie et al. 2000) however, fewer studies have looked at territory quality in species where it does not provide resources. Côté (2000) found that individuals with a territory peripheral to the colony bred later than those with a central position within the colony.

Breeding is also generally more successful in areas where nesting is synchronised (Parsons 1975; Westneat 1992).

Brown (1967) found that, independent of laying date, lesser black-backed gulls nesting in or near cover had a higher breeding success than those nesting in the open. This was mainly due to the high intra-specific predation rates in open areas rather than parenting ability. If intra-specific predation has such a marked effect on breeding success (Brown 1967; Davis & Dunn 1976; Burger 1977; Brouwer et al. 1995; Bukacinski et al. 1998) then there should be competition for protected nest sites. Brown (1967) found that earlier arrivals settle on territories with more cover. In other species, too, the early nesting individuals arrive earlier at the colony and so take the best available territories (Aebischer et al. 1996; Currie et al. 2000). In this study, however, I found no difference in breeding success between the plots, which may be due to the overall poor conditions during the study season (see chapter 4). The high chick mortality in general could have masked the differences due to habitat quality that would be expected between the plots.

It is also important to note that, since I studied only two 'plots', my effective sample size is only two. A much larger study, which takes in several plots of each type, would be needed in order to fully explore the link between territory quality and individual quality.

In conclusion, other studies have found that more vegetated territories are preferred by lesser black-backed gulls and that there is a higher breeding success in these areas (Brown 1967). This correlation of breeding success with habitat quality could be due to quality of the habitat, quality of the parents, or, a complex mixture of both (Bunin & Boates 1994). Using measurements of female quality independent of habitat quality, I found that higher quality females are, in fact, nesting in the more vegetated habitats. In a species where predation has such a large effect on breeding success (Brown 1967; Davis & Dunn 1976; Burger 1977; Brouwer et al. 1995; Bukacinski et al. 1998), the protection afforded to eggs and chicks by the territory will be an especially important factor in success of the breeding attempt. Early arriving birds, will benefit from having a good choice of territories on which to breed. These earlier arriving birds are generally higher in quality (Brown 1967), and will also get the added advantage of minimising the predation risk for chicks and eggs from a well protected nest site. Later arriving birds will be disadvantaged, not only by being generally poorer quality individuals, but also by a lack of territory choice.

REFERENCES

Aebischer, A., Perrin, N., Krieg, M., Studer, J. & Meyer, D. R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. *Journal of Avian Biology*, **27**, 143-152.

Amundsen, T. & Stokland, J. N. 1990. Egg size and parental quality influence nestling growth in the shag. *Auk*, **107**, 410-413.

Barba, E., Gildelgado, J. A. & Monros, J. S. 1995. The costs of being late – consequences of delaying great tit *Parus major* first clutches. *Journal of Animal Ecology*, **64**, 642-651.

Birkhead, T. R. & Nettleship, D. N. 1982. The adaptive significance of egg size and laying date in thick- billed murres *Uria lomvia*. *Ecology*, **63**, 300-306.

Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull - relative contributions of egg size and parental quality. *Journal of Animal Ecology*, **60**, 949-960.

Braden, G. T., McKernan, R. L. & Powell, S. M. 1997. Association of within-territory vegetation characteristics and fitness components of California Gnatcatchers. *Auk* **114**, 601-609.

Brouwer, A. & Spaans, A. L. 1994. Egg predation in the herring gull *Larus argentatus* - why does it vary so much between nests. *Ardea*, **82**, 223-231.

Brouwer, A., Spaans, A. L. & Dewit, A. A. N. 1995. Survival of herring gull *Larus argentatus* chicks - an experimental-analysis of the need for early breeding. *Ibis*, **137**, 272-278.

Brown, J. L. 1967. Breeding success and population growth in a colony of herring and lesser black-backed gulls, *Larus argentatus* and *L. fuscus*. *Ibis*, **109**, 501-515.

Bukacinski, D., Bukacinska, M. & Spaans, A. L. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the lesser black-backed gull *Larus fuscus*. *Ibis*, **140**, 422-430.

Bunin, J. S. & Boates, J. S. 1994. Effects of nesting location on breeding success of arctic terns on machias-seal-island. *Canadian Journal of Zoology-Revue Canadienne de Zoologie* **72**, 1841-1847.

Burger, J. 1977. Role of visibility in nesting Larus Gulls. *Journal of Comparative and Physiological Psychology* **91** p 1347-1358

Calladine, J. 1997. A comparison of Herring Gull *Larus argentatus* and Lesser Black-backed Gull *Larus fuscus* nest sites: their characteristics and relationships with breeding success. *Bird Stu*dy **44**: p 318-326

Carlson, A. 1998. Territory quality and feather growth in the White-backed Woodpecker *Dendrocopos leucotos*. *Journal of Avian Biology*, **29**, 205-207.

Coulson, J. C. & Porter, J. M. 1984. Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis*, **127**, 450-464

Côté, S. D. 2000. Aggressiveness in king penguins in relation to reproductive status and territory location. *Animal Behaviour*, **59**, 813-821.

Currie, D., Thompson, D. B. A. & Burke, T. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. *Ibis*, **142**, 389-398.

Daunt, F., Wanless, S., Harris, M. P. & Monaghan, P. 1999. Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1489-1493.

Davis, J. W. F. & Dunn, E. K. 1976. Intraspecific predation and colonial breeding in lesser black-backed gulls *Larus fuscus*. *Ibis*, **118**, 65-77

De Forest, L. N. & Gaston, A. J. 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology* **77**, 1501-1511.

Franklin, A. B., Anderson, D. R., Gutierrez, R. J. & Burnham, K. P. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in north-western California. *Ecological Monographs* **70**, 539-590.

Goodburn, S. F. 1991. Territory or habitat quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis*, **133**, 85-90.

Harris, M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus* and *L. marinus*. *Ibis*, **106**, 432-456.

Hatchwell, B. J., Chamberlain, D. E. & Perrins, C. M. 1996. The demography of blackbirds Turdus merula in rural habitats: Is farmland a sub-optimal habitat? *Journal of Applied Ecology*, **33** , 1114-1124.

Hinsley, S. A., Rothery, P. & Bellamy, P. E. 1999. Influence of woodland area on breeding success in Great Tits Parus major and Blue Tits *Parus caeruleus*. *Journal of Avian Biology* **30**, 271-281

Hipfner, J. M. 1997. The effects of parental quality and timing of breeding on the growth of nestling thick-billed murres. *Condor*, **99**, 353-360.

Hipfner, J. M., Gaston, A. J. & De Forest, L. N. 1997. The role of female age in determining egg size and laying date of thick-billed Murres. *Journal of Avian Biology*, **28**, 271-278.

Hipfner, J. M., Gaston, A. J., Martin, D. L. & Jones, I. L. 1999. Seasonal declines in replacement egg laying in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? *Journal of Animal Ecology*, **68**, 988-998.

Magrath, R. D. 1992. Seasonal changes in egg-mass within and among clutches of birds - general explanations and a field-study of the blackbird *Turdus merula*. *Ibis*, **134**, 171-179.

Mills, J.A. 1973. The influence of age and pair-bond on the breeding biology of the red-billed gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology*, **42**, 147-162.

Monaghan, P., Bolton, M. & Houston, D. C. 1995. Egg-production constraints and the evolution of avian clutch size. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **259**, 189-191.

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. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1731-1735.

Moreno, J. 1998. The determination of seasonal declines in breeding success in seabirds. *Etologia*, **6**, 17-31.

Newton, I. 1991. Habitat variation and population regulation in sparrowhawks. *Ibis* **133**, 76-88.

Parsons, J. 1975. Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging success. *Journal of Animal Ecology. 44*: 553-573.

Perdeck, A. C. & Cavé, A. J. 1992. Laying date in the coot - effects of age and mate choice. *Journal of Animal Ecology*, **61**, 13-19.

Rees, E. C., Black, J. M., Spray, C. J. & Thorisson, S. 1991. Comparative-study of the breeding success of whooper swans *Cygnus cygnus* nesting in upland and lowland regions of Iceland. *Ibis* **133**, 365-373.

Reid, W. V. 1988. Age specific patterns of reproduction in the glaucous-winged gull: increased effort with age?. *Ecology*, **69**, 1454-1465.

Reid, W. V. & Boersma, P. D. 1990. Parental quality and selection on egg size in the Magellanic penguin. *Evolution*, **44**, 1780-1786.

Robertson, G. J., Cooch, E. G., Lank, D. B., Rockwell, R. F. & Cooke, F. 1994. Female age and egg size in the lesser snow goose. *Journal of Avian Biology*, **25**, 149-155.

Sydeman, W. J., Penniman, J. F., Penniman, T. M., Pyle, P. & Ainley, D. G. 1991. Breeding performance in the western gull - effects of parental age, timing of breeding and year in relation to food availability. *Journal of Animal Ecology* **60**, 135-149.

Tye, A. 1992. Assessment of territory quality and its effects on breeding success in a migrant passerine, the wheatear *Oenanthe oenanthe. Ibis* **134**, 273-285.

Verhulst, S. 1995. Reproductive decisions in great tits: an optimality approach. PhD Thesis, University of Groningen.

Verhulst, S., Vanbalen, J. H. & Tinbergen, J. M. 1995. Seasonal decline in reproductive success of the great tit - variation in time or quality. *Ecology*, **76**, 2392-2403.

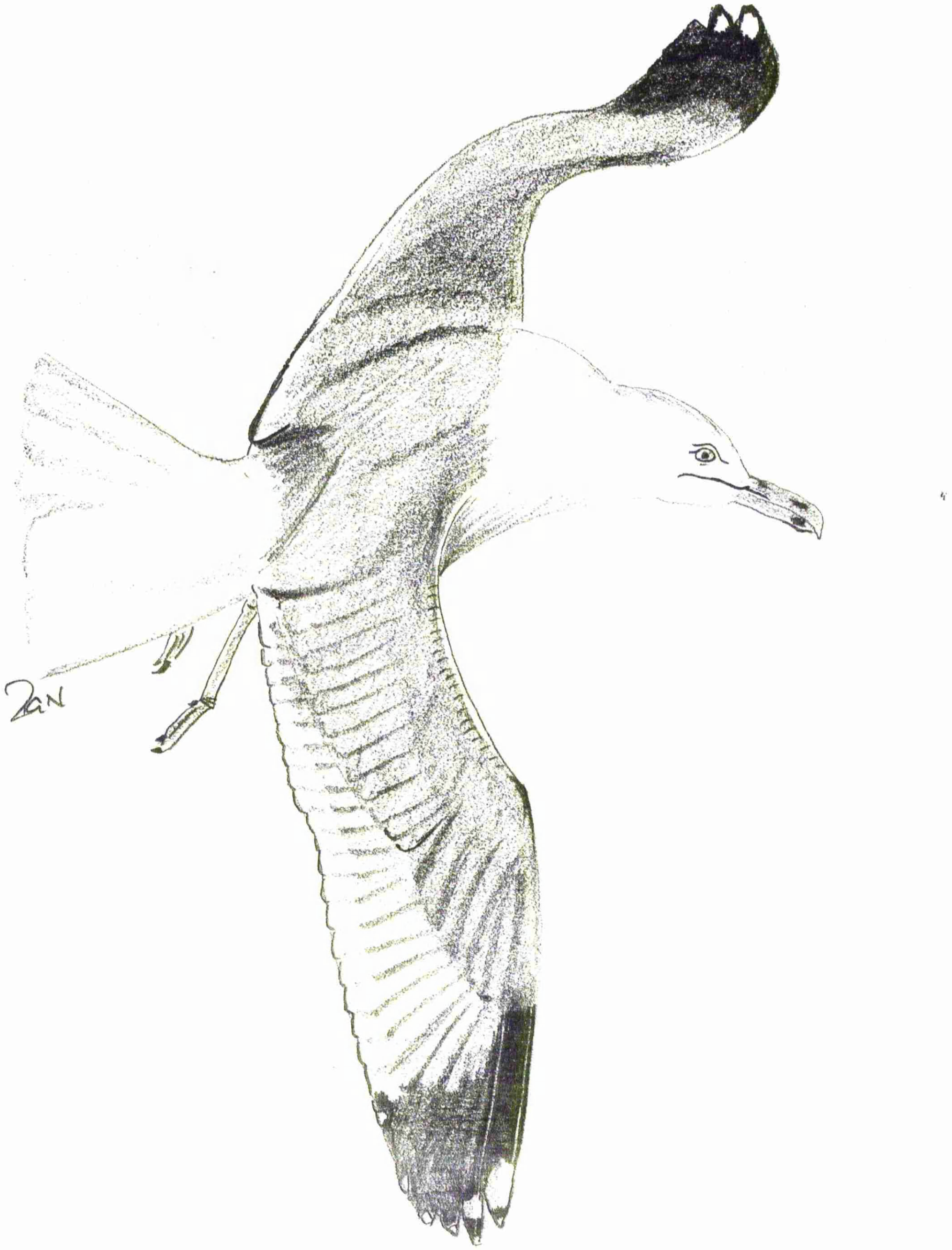
Vickery, P. D., Hunter, M. L. & Wells, J. V. 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. *Auk* **109**, 697-705.

Westneat, D. F. 1992. Nesting synchrony by female red-winged blackbirds - effects on predation and breeding success. *Ecology*, **73**, 2284-2294.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews*, **68**, 35-59

Chapter 7

THE IMPORTANCE OF BODY SIZE



ABSTRACT

State, of which body size is one component, is an important determinant of reproductive success and decision making. Body size is known to be an important factor in the fecundity of ectotherms, however, few studies have found a link between body size and fecundity in endotherms. In this chapter I investigate the relationship of body size with laying date and egg size in male and female lesser black-backed gulls, *Larus fuscus*. I found that larger gulls, both male and female, lay earlier, but that there is no trend in egg-size with laying date. The possible implications of this relationship are discussed.

INTRODUCTION

In many ectothermic animals, body size is an important determinant of fecundity (Côte & Hunte 1989; Honeka 1993; Merrett 1994; Kiorboe & Sabatini 1995; Clobert et al. 1998; Kraak & Bakker 1998; Garcia-Barros 2000). These species show considerable variation in body size, as most have indeterminate growth, and larger females potentially have the capacity for making and storing more, or larger, eggs.

The importance of body size for successful breeding is less obvious in endothermic animals such as birds and mammals, where there is less variation in body size than in other taxa (Schmidt-Nielsen 1984). Of course size can be an advantage when competing for mates and territories, especially for males in polygynous species, but there have been few studies that find a link between body size and fecundity itself. Most studies have focussed on 'condition', often taken as body mass corrected for size (Brown 1996) as a predictor of investment or breeding success. As body size is often included in calculations of 'condition', it is consequently difficult to separate the effects of body size from the effects of condition. Few studies have considered the influence of body size on fecundity in endotherms. However, large size must have an advantage for female raptors, at least, a group that exhibit reversed size dimorphism. Various explanations of this phenomenon have focussed on fecundity benefits to the female of large size (reviewed in Massemin 2000), though other factors may also be involved.

Two avian studies have found that egg size is related to body size of females (Bolton et al. 1993- lesser black-backed gull; Larsson et al. 1998- barnacle goose) and two found a relationship between clutch size and female body size (Larsson et al 1998; Boon & Ankney 1999- ruddy duck). However there is considerable variation between studies with some studies finding no effect of body size on egg size (Wiebe & Bortolotti 1995- American kestrel; Boon & Ankney 1999) or clutch size (Bolton et al. 1993). In a 12 year study of the Eurasian kestrel, Massemin et al. (2000) found that female size was not related to laying date or clutch size. Hakkarainen & Korpimakki (1993) found variation within their study of Tengmalm owls, with clutch volume being positively related to body size only in years of high food availability. Egg size and clutch size are often highly correlated with laying date, with earlier laying females having larger eggs or larger clutches (Barba et al. 1995 and Verhulst et al. 1995- great tit; Hipfner 1997 and Hipfner et al. 1997- thick-billed murres) and therefore trends in fecundity with body size may be due to a more general effect of laying date. In fact two studies have found that larger birds lay earlier (Larsson et al 1998; Boon & Ankney 1999) as well as having larger eggs/larger clutch. However Barbraud et al. (2000) found that larger snow petrels actually laid eggs later in the season.

Most of these studies have looked only at female body size and the relationship with clutch characteristics, as it is the female that lays the eggs. Larsson et al. (1998) looked at body size effects of both sexes and found that, although various breeding parameters were strongly related to body size in female barnacle geese, there were weak, or non-significant relationships between these factors and male body size.

In the lesser black backed gull, *Larus fuscus*, egg production involves a substantial investment (Monaghan et al. 1995) and a previous study found that egg size was positively related to female body size (Bolton et al. 1993). In this chapter I extend this work to examine whether the body size of male and female lesser black-backed gulls is linked to the date of egg laying and egg size.

METHODS

This study was carried out on Walney Island in 1998. The field site has been described in previous chapters. Nests were checked daily to record the date that the first egg was laid. The size of this first-laid egg was measured (length and breadth) using callipers. To estimate volume of the eggs I used the following equation (Harris 1964)

$$\text{Volume} = 0.476 \times \text{length} \times \text{breadth}^2$$

Clutch size was controlled for by studying only those gulls that had laid the modal clutch of three eggs. Gulls were captured during incubation, using a walk-in-trap. This was made of wire mesh and was placed over the nest and pegged to the ground. To prevent damage to the eggs while trapping, the clutch was replaced with wooden eggs and placed under another incubating female for the duration of the disturbance. The trap was set and when the adult returned to incubate the eggs, a foot treadle released the trap door. Once caught I measured total head and bill length, tarsus length, length of the 2nd primary (wing length), keel length and sternum diagonal (distance from the caudal end of keel to the proximal end of humerus, reflecting the effective length of the pectoral muscle). I also weighed the birds and collected a small blood sample from the tarsus of each bird (under home office licence) in order to identify sex using two CHD genes extracted from the blood (Griffiths et al. 1996). I caught 17 females and 13 males, for two of the females and one of the males I did not record the size of their egg.

Structural body size of the bird was calculated using principal component analysis of the body size measurements taken. Male lesser black backed gulls are, on average, significantly larger than females and the relationships between different body-parts may differ. I therefore calculated female and male principle components separately. In both sexes, the first principle component described a positive correlation between the five body size variables. For females; loadings were 0.88 for tarsus, 0.74 for wing, 0.65 for head-bill, 0.56 for keel length and 0.15 for keel diagonal and explained 41.5% of the variation in these five variables. For males; loadings were 0.81 for tarsus, 0.89 for wing, 0.68 for head-bill, 0.71 for keel length and 0.40 for keel diagonal and explained 51.3% of the variation in the variables

In three nests, both the male and the female were caught. In order to preserve the independence of the data, one individual of each pair was removed from the data set. This was done completely at random by tossing a coin.

RESULTS

Larger females lay earlier than small females (regression: $r^2 = 0.306$, $F_{1,16} = 7.061$, $P = 0.017$, Fig. 1); per unit increase in body size index, females lay 3.22 ± 1.212 days earlier. However, there was more variation in males and no significant relationship (regression: $r^2 = 0.042$, $F_{1,13} = 0.568$, $P = 0.465$, Fig. 2); though the slopes of the male and female regressions were not significantly different (comparison of slopes, $t_{27} = 1.00$, $P > 0.05$).

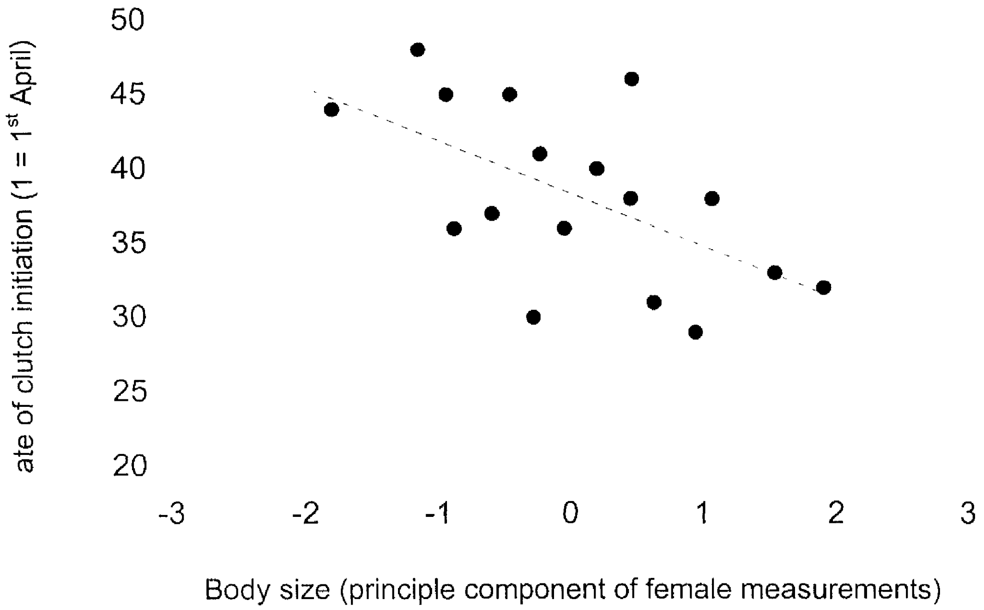


Figure 1. The relationship between body-size, as calculated from a PCA based on five measurements, and laying date in female lesser black-backed gulls. The relationship was significant (see text).

Egg size was analysed in relation to laying date and parental body size using a stepwise regression. For females, neither laying date ($F_{1,13}$ = 0.042, P = 0.841) nor body size ($F_{1,15}$ = 1.169, P = 0.297) affected egg size. A similar result was found in males with neither body size ($F_{1,10}$= 1.511, P = 0.247), nor laying date ($F_{1,11}$ = 4.458, P = 0.058) affecting egg size, although the relationship with laying date is approaching significance. Interactions between body size and lay date were non-significant in both cases.

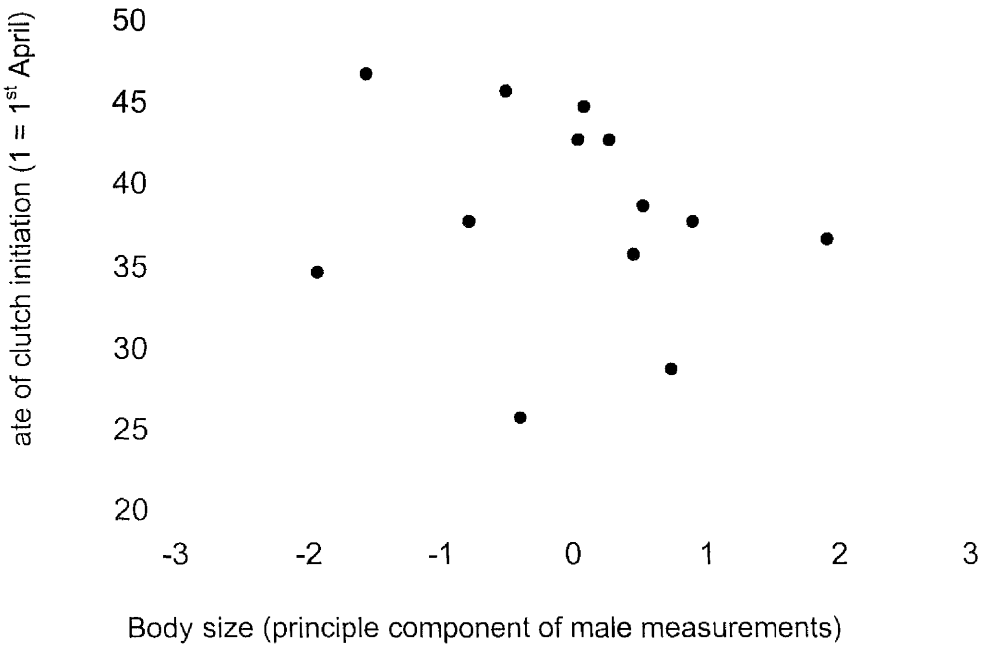


Figure 2. The relationship between male body size and laying date in lesser black-backed gulls. The relationship was not significant (see text).

Neither body mass nor mass corrected for size (condition) showed any trend with laying date (table 1).

Table 1 correlation coefficients of adult body mass and condition (mass corrected for size) in male and female gulls.

	Females (n = 17)		Males (n = 13)	
	Pearson correlation coefficient	Significance	Pearson correlation coefficient	Significance
Correlation with body mass	-0.387	0.125	-0.415	0.159
Correlation with mass corrected for size	0.093	0.721	-0.225	0.459

DISCUSSION

We found that larger body size, in females, was associated with an earlier laying date. Neither females of larger body size, nor females mated to large males produced larger eggs.

Earlier layers are normally more successful breeders (reviewed in Hipfner 1997 and Moreno 1998). This is due, both to seasonal declines in environmental conditions (Barba et al. 1995) and to earlier layers often being of better quality, e.g. older or more experienced (Reid 1988; Sydeman et al. 1991; De Forest & Gaston 1996; Hipfner et al. 1997). If conditions decline during the season, it will be advantageous for an individual to breed as early as possible.

Larger female lesser black-backed gulls may be able to lay eggs earlier because they can get into breeding condition earlier. Larger individuals have more pectoral muscle (Bolton et al. 1991), as measured from culled lesser black-backed gulls. This muscle is used as a protein reserve for egg formation (Houston et al. 1983; Jones 1991; Houston et al. 1995; Williams & Martyniuk 2000) and therefore larger females may have a greater capacity for storing the nutrients required for producing a clutch. Larger individuals generally win in disputes and therefore larger females may also be able to gain access to better food supplies and so come into laying condition earlier in the season.

One reason that larger females lay earlier may be that they arrive earlier on the breeding grounds. Studies in other species have found that earlier nesting individuals also arrive at their territories earlier in the season (Aebischer et al. 1996; Currie et al. 2000). I cannot, however, find any reports in the literature of larger individuals being faster flyers, rather the reverse (Norberg 1995) or reaching breeding grounds earlier.

Other studies have found that larger females lay earlier in the season (Larsson et al 1998; Boon & Ankney 1999). However in contrast to this Barbraud et al. (2000) found that larger snow petrel females laid later. They offer a couple of explanations for this unexpected trend. Firstly, that large females produce larger eggs relative to their size, and secondly that laying date may be inherited and the study colony is formed from the mixing of birds from colonies having small early-laying individuals with birds from colonies having large late-laying individuals. However they offer no evidence for either of these scenarios and the trend remains a mystery.

In this study, I found that the advancement in laying date due to body size was apparent in both males and females. This is in contrast to other studies, which have found no effect of male size on laying date of his partner (Larsson et al. 1998). We would not necessarily expect an effect of male body size as it is the females that are using their energy stores to produce the clutch and could therefore benefit from the larger storage capacity offered by a larger body size. The fact that, in this study, I found an effect of body size on lay date in both sexes suggests that large female gulls may be pairing assortatively with large males. Size assortative mating is well known among invertebrates where, in some cases it is due to male preference for large females which then reject small males (Hedge & Krishna 1997; Masumoto 1999), and in some cases due to the difficulties of mating for individuals of widely differing sizes (Brown 1993; Otronen 1993). This phenomenon has rarely been observed in higher taxa and, since I caught both partners in only three nests, I cannot find out whether the gulls in this study are exhibiting size assortative mating.

Size assortative mating could occur in gulls if larger females are better quality and males compete over them, the largest males winning. Lesser black backed gulls are monogamous, biparental species and would therefore be likely to exhibit mutual mate choice (Jones & Hunter 1993), if this is so then assortative mating could occur if both partners choose for size.

The decrease in body size with laying date in both sexes could also occur if large males offer their partners an advantage that allows them to lay earlier. For example, male gulls and terns courtship feed their partners in the pre-laying period (Cramp & Simmons 1983). Courtship feeding provides a significant proportion of a female's food demands during egg laying (Tasker & Mills 1981) and has been found to influence egg size (Nisbet 1973). If larger males can compete for better foraging areas, then they may be able to provide more courtship feeding, therefore allowing females with a larger partner to enter breeding condition earlier.

Laying date has been found to correlate with body size in some species, (Larsson et al 1998; Boon & Ankney 1999; Barbraud et al. 2000; this study), and it is also known to correlate with egg size and clutch size (Parsons 1975; Verhulst et al. 1995; Hipfner et al. 1997). There is considerable debate over whether the seasonal decline in egg size/clutch size is due to a seasonal decline in conditions (Barba et al. 1995) or in a decline in quality of laying birds (Hipfner 1997). This means that it is important to correct for laying date when looking at the effects of body size on fecundity as larger birds may be laying larger eggs simply because they are laying earlier in the season. In this study clutch size was standardised as I only caught birds that had laid the modal clutch of three eggs, and laying date did not have a significant effect on egg size.

As laying earlier in the season is usually an advantage, as discussed previously, and larger lesser black-backed gulls lay earlier, should there be selection for increased size in this species? We would not necessarily expect selection for increased body size as there may be costs to being large. Studies in raptors suggest that larger female body size can be a disadvantage in years of poor food availability (Hakkarainen & Korpimakki 1993; Massemin et al. 2000). Monaghan & Metcalfe (1986) found that larger female herring gulls had a higher mortality, especially towards the end of the breeding season, than smaller females. In males, however, smaller individuals had higher winter mortality than medium and large birds. Structurally larger birds may also have increased flight costs (Norberg 1995) as mass increases more rapidly with size than wing lengths and so larger birds will be heavier compared to their wing span. In birds, egg laying is only one aspect of breeding. There may also be opposing selection pressures on body size in other phases of breeding, such as incubation or chick rearing.

REFERENCES

Aebischer, A., Perrin, N., Krieg, M., Studer, J. & Meyer, D. R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides. Journal of Avian Biology*, **27**, 143-152.

Amundsen, T., Forsgren, E. & Hansen, L.T.T. 1997 On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London Series B-Biological Sciences* **264**, 1579-1586.

Barba, E., Gildelgado, J. A. & Monros, J. S. 1995. The costs of being late - consequences of delaying great tit *Parus major* first clutches. *Journal of Animal Ecology*, **64**, 642-651.

Barbraud, C., Lormee, H. & LeNeve, A. 2000. Body size and determinants of laying date variation in the Snow Petrel *Pagodroma nivea. Journal of Avian Biology* **31**, 295-302.

Bolton, M., Monaghan, P. & Houston, D. C. 1991. An improved technique for estimating pectoral muscle protein condition from body measurements of live gulls. *Ibis*, **133**, 264-270.

Bolton, M., Monaghan, P. & Houston, D. C. 1993. Proximate determination of clutch size in lesser black-backed gulls - the roles of food-supply and body condition. *Canadian Journal Of Zoology-Revue Canadienne De Zoologie*, **71**, 273-279.

Boon, L. A. & Ankney, C. D. 1999. Body size, nest initiation date and egg production in ruddy ducks. *Auk*, **116**, 228-231.

Brown, C.R. & Brown, M.B. 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution*, **52**, 1461-1475.

Brown, M. E. 1996. Assessing body condition in birds. In: Current Ornithology Vol. 13 (V. Nolan Jr & E. D. Ketterson eds.) 67-117.

Brown, W. D. 1993. The cause of size-assortative mating in the leaf beetle *Trirhabda canadensis* (Coleoptera, Chrysomelidae). *Behavioral Ecology and Sociobiology*, **33**, 151-157.

Clobert, J., Garland, T. & Barbault, R. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *Journal of Evolutionary Biology*, **11**, 329-364.

Côte, I. M. & Hunte, W. 1989. Male and female mate choice in the redlip blenny - why bigger is better. *Animal Behaviour*, **38**, 78-88.

Cramp, S. & Simmons, K. E. C. 1983. Birds of the Western Palearctic Vol III Waders to Gulls. Oxford University Press, Oxford.

Currie, D., Thompson, D. B. A. & Burke, T. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. *Ibis*, **142**, 389-398.

DeForest, L. N. & Gaston, A. J. 1996. The effect of age on timing of breeding and reproductive success in the thick-billed Murre. *Ecology*, **77**, 1501-1511.

Garcia-Barros, E. 2000. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society*, **70**, 251-284.

Griffiths, R., Daan, S. & Dijkstra, C. 1996. Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **263**, 1251-1256.

Hakkarainen, H. & Korpimaki, E. 1993. The effect of female body-size on clutch volume of Tengmalm owls *Aegolius funereus* in varying food conditions. *Ornis Fennica*, **70**, 189-195.

Harris, M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus, L. fuscus* and *L. marinus*. *Ibis*, **106**, 432-456.

Hegde, S. N. & Krishna, M. S. 1997. Size-assortative mating in *Drosophila malerkotliana*. *Animal Behaviour*, **54**, 419-426.

Hipfner, J. M. 1997. The effects of parental quality and timing of breeding on the growth of nestling thick-billed murres. *Condor*, **99**, 353-360.

Hipfner, J. M., Gaston, A. J. & De Forest, L. N. 1997. The role of female age in determining egg size and laying date of thick-billed Murres. *Journal of Avian Biology*, **28**, 271-278.

Honeka, A. 1993. Intraspecific variation in body size and fecundity in insects - a general relationship. *Oikos*, **66**, 483-492.

Houston, D. C., Jones, P. J. & Sibly, R. M. 1983. The effect of female body condition on egg laying in lesser black-backed gulls *Larus fuscus*. *Journal of Zoology*, **200**, 509-520.

Houston, D. C., Donnan, D., Jones, P., Hamilton, I. & Osborne, D. 1995. Changes in the muscle condition of female zebra finches *Taeniopygia guttata*: during egg-laying and the role of protein storage in bird skeletal-muscle. *Ibis*, **137**, 322-328.

Jones, I. L. & Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**, 238-239.

Jones, M. M. 1991. Muscle protein loss in laying house sparrows *Passer domesticus*. *Ibis*, **133**, 193-198.

Kiorboe, T. & Sabatini, M. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. *Marine Ecology-Progress Series*, **120**, 285-298.

Kraak, S. B. M. & Bakker, T. C. M. 1998. Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Animal Behaviour*, **56**, 859-866.

Larsson, K., van der Jeugd, H. P., van der, I. T. & Horslund, P. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. *Evolution*, **52**, 1169-1184.

Massemin, S., Korpimaki, E. & Wiehn, J. 2000. Reversed sexual size dimorphism in raptors: evaluation of the hypotheses in kestrels breeding in a temporally changing environment. *Oecologia*, **124**, 26-32.

Masumoto, T. 1999. Size assortative mating and reproductive success of the funnel- web spider, *Agelena limbata* (Araneae; Agelenidae). *Journal of Insect Behavior*, **12,** 353-361.

Merrett, N. R. 1994 Reproduction in the North Atlantic oceanic ichthyofauna and the relationship between fecundity and species sizes. *Environmental Biology of Fishes*, **41**, 207-245.

Monaghan, P. & Metcalfe, N. B. 1986. On being the right size: natural selection and body size in the herring gull. *Evolution*, **40**, 1096-1099.

Monaghan, P., Bolton, M. & Houston, D. C. 1995. Egg-production constraints and the evolution of avian clutch size. *Proceedings of the Royal Society of London Series B-Biological Sciences* **259**, 189-191.

Moreno, J. 1998. The determination of seasonal declines in breeding success in seabirds. *Etologia*, **6**, 17-31.

Nisbet, I. C. T. 1973, Courtship feeding, egg size and breeding success in common terns *Sterna hirundo*. *Nature*, **241**, 169-178.

Norberg, U. M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology*, **9**, 48-54.

Otronen,M. 1993. Size assortative mating in the yellow dung fly *Scatophaga stercoraria*. *Behaviour*, **126**, 63-76.

Parsons, J. 1975. Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging success. *Journal of Animal Ecology. 44*: 553-573.

Reid, W. V. 1988. Age-specific patterns of reproduction in the Glaucous-winged gull: Increased effort with age? *Ecology*, **65**, 1454-1465.

Schmidt-Nielsen, K. 1984. Scaling : why is animal size so important? Cambridge University Press, Cambridge.

Sydeman, W. J., Penniman, J. F., Penniman, T. M., Pyle, P. & Ainley, D. G. 1991. Breeding performance in the western gull - effects of parental age, timing of breeding and year in relation to food availability. *Journal of Animal Ecology*, **60**, 135-149.

Tasker, C. R. & Mills, J. A. 1981. A functional analysis of coutship feeding in the red-billed gull *Larus novaehollandiae scopulinus*. *Behaviour*, **77**, 222-241.

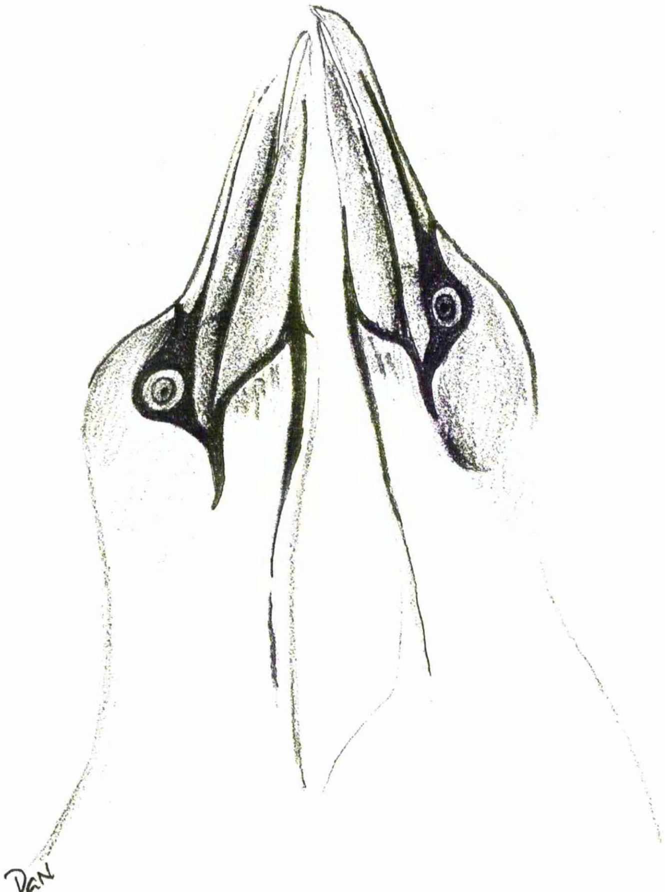
Verhulst, S., Vanbalen, J. H. & Tinbergen, J. M. 1995. Seasonal decline in reproductive success of the great tit - variation in time or quality. *Ecology*, **76**, 2392-2403.

Wiebe, K. L. & Bortolotti, G. R. 1995. Egg and clutch size in the reproductive investment of American kestrels. *Journal of Zoology*, **237**, 285-301.

Williams, T. D. & Martyniuk, C. J. 2000. Tissue mass dynamics during egg-production in female Zebra Finches *Taeniopygia guttata*: dietary and hormonal manipulations. *Journal of Avian Biology*, **31**, 87-95.

Chapter 8

GENERAL DISCUSSION



In this thesis I have investigated some of the decisions taken by biparental, monogamous birds during reproduction. I have used an experimental, correlational and mathematical modelling approach to investigate individual reproductive decisions. Each chapter has investigated a different aspect of reproductive decision making and includes discussion of the results and specific issues raised. In these chapters, individual 'quality' and 'condition' have proved to be especially important factors in the reproductive decisions that I have investigated. Both these factors are aspects of an organism's 'state' (*sensu* McNamara & Houston 1996). McNamara & Houston discuss the importance of recognising differences between individuals in studies of life-history strategies. Life-history models assume that fecundity and survival are functions of an organism's age, and that they are identical in all other ways (Stearns 1992; Roff 1992). This is obviously not true, and McNamara & Houston suggest that we look at the underlying physiological and environmental conditions that determine survival and reproductive success, which they refer to as 'state'. Many factors can constitute an organism's state, endogenous factors such as fat-reserves, immunocompetence, parasite load, and exogenous factors such as territory quality and foraging skills. In this final chapter, I will discuss how state affects reproductive decisions using examples from the preceding chapters, and the work of other authors, and then draw some general conclusions.

CONDITION AND QUALITY

'Condition' and 'quality' are often used to explain variation in reproductive success. However, they are rarely defined. Quality is more often used to refer to an intrinsic property of the individual, such as age or experience (Perdeck & Cavé 1992; de Forest &

Gaston 1996), whereas condition more often applies to short term changes in health or storage of resources. Avian condition indices are often calculated from mass corrected for skeletal size, amount of fat stored, the level of condition-dependent indicators in the blood (all reviewed in Brown 1996), or as the amount of pectoral muscle (Bolton et al. 1991).

When there is a trade-off, for example in allocating resources between and within reproductive events, the individual's strategy that maximises its fitness will depend on its state (McNamara & Houston 1996). This has been shown most extensively in the trade-off of allocating resources to producing females or males. Sex allocation decisions have been found to be dependent on a number of state variables (Simpson & Simpson 1982; Clutton-Brock et al. 1986; Kolliker et al. 1999; Côté & Festa-Bianchet 2001) including condition (Nager et al. 1999).

Trade-offs have also been found between number and size of offspring (Smith et al. 1989; Jakobsson & Eriksson 2000; Nager et al. 2000; Williams 2001) and, in birds, between an early laying date and a large egg (Hipfner et al. 1997). In order to maximise reproductive output, organisms must make individually optimised allocation decisions. For example, birds need to minimise the time taken to produce a clutch, in order to gain the advantage of early laying, while optimising the division of their resources between egg size and clutch size. In **chapter 6** I found that egg size, laying date and clutch size were all correlated, so females laying earlier had larger clutches and laid larger eggs. The correlative approach that I have used here cannot disentangle trade-offs, hence the apparent positive, rather than negative correlation between traits. In order to see the trade-off, individuals must be deflected from their chosen investment pattern with a manipulation experiment (Stearns 1992). Therefore, the correlation I found does not mean that there is no trade-off in partitioning resources between egg size, clutch size and laying date, but rather that individuals of different quality have differing amounts of resources to invest (Krebs & Davies 1987). Each individual is making a decision, dependent on its state, on how to balance the trade-off of egg size and egg number with the need for early laying. I used such an experimental approach to show that maternal condition affects time allocation to parental care in lesser black-backed gulls in **chapter 4**. When egg laying effort is increased and females, therefore, have a lower body condition at clutch completion (Monaghan et al. 1998), they reduced the time they spent incubating the eggs and brooding the chicks and decreased the amount of foraging that they did for their chicks.

The reason that females in a poorer condition have a lower offspring rearing effort is that a lowered investment in one breeding season will increase the probability of survival and successful breeding in subsequent breeding seasons (Roitberg 1989; Landwer 1994; Nager et al. in press). It is therefore important for individuals to balance current reproductive effort against residual reproductive value. Manipulated females are lowering their effort into incubation and chick rearing to compensate for increased egg-production costs but these females do not manage to completely regain their condition as they have been found to have a lower return rate than unmanipulated birds (Nager et al. in press).

There is some evidence that animals have a threshold of condition below which individuals will not initiate breeding (Naulleau & Bonnet 1996; Madsen & Shine 1999; Mand et al. 2000), or will abandon a breeding attempt (e.g. Monaghan et al. 1992; Lorentsen & Rov 1995; Olsson 1997). This acts to conserve residual reproductive value and is a key parameter in the second model in **chapter 5**, where I modelled its influence on reproductive decisions. Each partner must be aware of its own condition so that it can decide the maximum parental care it can allocate before it must abandon. This allows individuals to optimise their breeding success one season without compromising future reproductive potential, and reproductive decisions can be made within the framework of maintaining condition above that level. Birds of higher quality will be able to put in more effort, and therefore have a higher reproductive success before reaching the threshold of minimum condition. Under some conditions there may be an advantage to parents allocating care differently to different sexes in the nest if the advantages to their fitness through allocating effort to one sex exceeds that of the other sex (Lessells 1998).

The level of condition, below which a breeding attempt will be abandoned, may not be the same for all individuals. Individuals of a high quality, that are able to forage very efficiently, may allow their condition to dip lower than a poorer quality individual (Witter & Cutthill 1993); older individuals, with a poor residual reproductive value, may be expected to have a lower threshold due to terminal investment (Part et al. 1992; Clutton-Brock 1984). However, Bolton et al. (1993) found that all female lesser black-backed gulls, whether or not they received supplementary food, had a similar condition at clutch completion.

Since the model described in chapter 5 is for a biparental species, the behaviour and condition of an individual's partner will be of the utmost importance when making decisions about allocation of parental care. This issue will be tackled in more detail in a later section of this discussion.

BODY SIZE

In ectotherms, most of which have indeterminate growth, body size is a well studied aspect of state. Body size has been found to be highly correlated with fecundity in many species (Côte & Hunte 1989; Honeka 1993; Merrett 1994; Kiorboe & Sabatini 1995; Clobert et al. 1998; Kraak & Bakker 1998; Garcia-Barros 2000). In endotherms, however, which have a much lower variance in body size (Schmidt-Nielsen 1984), the effect of body size on life history parameters has been little studied.

In **chapter 7**, I found that larger lesser black-backed gulls had an earlier laying date. This gives them an advantage over smaller birds as early nesters are usually more successful (reviewed in Hipfner 1997 and Moreno 1998). Larger females did not, however, lay larger eggs, unlike other studies that have found a positive correlation between female size and egg size (e.g. Bolton et al. 1993; Larsson et al. 1998). Downhower (1976) suggests that smaller females should actually be able to lay earlier because they need less food to reach breeding condition and Barbraud (2000) found that larger female snow petrels lay later in the season. On the other hand, size may be advantageous in gaining a good territory or competing for good feeding sites, which may explain the correlation that I found.

BREEDING SITE QUALITY

McNamara & Houston (1996) include territory quality as one of their state variables. The quality of the breeding territory clearly influences an individual's survival and reproduction (Newton 1991; Rees et al. 1991; Hatchwell et al. 1996; Côté 2000). However, territory quality is not a simple state variable, such as size, or immunocompetence, as an individual's state (e.g. dominance-rank, age or quality) may determine which breeding site they obtain. The quality of their breeding site will then become one of a number of factors defining their state. Both individual quality and territory quality will interact. Using a correlative approach, I attempted to separate the effects of an individual's quality from the quality of its nest site in the lesser black-backed gull (**chapter 6**).

Gulls have been found to be more successful in nest sites with more vegetation (Brown 1967; Davis & Dunn 1976; Calladine 1997), as intra-specific predation is one of the greatest causes of mortality in eggs and young chicks (Brown 1967; Davis & Dunn 1976; Bukacinski et al. 1998). More vegetation cover also reduces levels of aggression between neighbouring pairs (Burger 1977). I found that the better quality territories, in terms of vegetation, were occupied by the earliest nesting gulls. Since territories in the lesser black-black gull hold no food resources, it is likely that the advanced laying date is due to the quality of the individuals, rather than the quality of the territory. I found that higher quality gulls were found in the plot with more vegetation, leaving the poorer quality, later nesting gulls with the additional problem of a high level of egg and chick predation (Brown 1967) from their unprotected nests. The better quality gulls are able to choose the best quality breeding territories and so increase the advantage they already have in terms of an earlier laying date. From this study it is not clear whether early laying is advantageous *per se*, or whether early laying birds obtain the best territories and therefore have a lower predation rate and therefore higher breeding success. Inevitably breeding success will result from a combination of both effects but, in order to separate them, a manipulation experiment would have to be carried out. For example, by increasing the cover of poorer quality areas and decreasing the cover of high quality territories.

STATE OF YOUR PARTNER

The state of an individual's partner can also be included as a factor of its own state, although it is not defined as such by McNamara & Houston (1996). This is because a partner's state can affect an individual's survival, breeding success and reproductive decisions directly (through their fecundity, or possession of a good territory), or indirectly (through influencing the behaviour and decision making of their mate). Since both of the pair contribute to the breeding success it is not only important what state you are in but also the state of your partner.

Mate-choice has long been recognised as a potentially important factor in the reproductive success of females in terms of finding good genes for the next generation, having 'sexy sons', or finding a good father to invest in the upbringing of the offspring (reviewed in Jennions & Petrie 2000). Less attention, however, has been given to the advantages for males being choosy in mate-choice (Amundsen 2000). If females vary substantially in fecundity and/or if males provide a substantial amount of breeding resources or parental care (Burley 1977; Jones & Hunter 1993; Andersson 1994; Amundsen 2000), then males should also be choosy about partners. For example, female zebra finches whose condition is experimentally increased lay more eggs (Selman & Houston 1996; Monaghan et al. 1996). Therefore males can increase their fitness when choosing to pair with these females. In the experiment reported in **chapter 2**, I found that male zebra finches choose to pair with females that had previously been fed on a high protein diet. In this experiment I ruled out the possibility that the higher quality female was dominating her rival and claiming the male as her mate by separating experimental females, visually and physically from each other.

Signals and communication are important in choosing the right partner. I found that male zebra finches are able to choose the better quality female, but found no difference in the female's behaviour between the treatment groups. Some authors have found evidence that females signal state (e.g. condition, quality, parenting ability) in plumage characteristics (Møller 1993; Johnsen et al. 1996; Potti & Merino 1996; Amundsen et al. 1997; Linville et al. 1998; Roulin et al. 2000) and carotenoid colourings (Burley et al. 1992; Cottam 1998, Negro et al. 1998; Saino et al. 2000). However there needs to be more study of physical indicators of quality and state and whether individuals use them in their mate choices. Signals can be hard to manipulate, especially under natural conditions (but see Jones & Hunter 1993), however, manipulation experiments are needed to study the effect that they have on mate-choice (Burley & Coopersmith 1987; Hunt et al. 1999).

Reproductive decisions in a biparental species, especially over the allocation of parental effort, will also depend on the behaviour of the partner. An individual will want to maximise the offspring it will obtain from the current reproductive event and those s/he may obtain from future reproductive events, but the decisions must take into account the effort that the partner is putting into the offspring. If one partner is in a reduced state and decreases investment into the breeding attempt, the other partner must make a decision of whether to alter its allocation of resources between self-maintenance and parental care. Houston & Davies (1985) showed that biparental care will only be an evolutionarily stable strategy (ESS) when each parent only partially compensates for a reduction in effort by the other. If this is not the case and partners fully compensate then they are open to cheating by the partner and the evolution of uni-parental care may result.

In **chapter 4** I found that males compensate fully for the reduced effort put in by the female whose condition has been manipulated. During incubation and brooding, when it is necessary that one parent is on the nest at all times to prevent predation, the male compensated fully for the female's absence. The male also compensated during chick rearing, although, due to the small sample size, the data cannot resolve whether he was compensating fully or only partially.

Current models (Houston & Davies 1985; Ratnieks 1996) would predict that this situation is evolutionarily unstable. However, some other studies of compensation have also found full compensation (Mrowka 1982; Hunt et al. 1999; Sanz et al. 2000). Using mathematical modelling (Model I, **chapter 5**), I found that when a small decrease in parental effort contributes to a large decrease in breeding success, for example in a situation of high predation, then there must be full compensation or the loss of the breeding attempt. An individual will only be able to fully compensate if it is in a state in which it can maintain this level of work. If it is not then it will abandon the breeding attempt.

The second model in chapter 5 then shows that full compensation will occur, albeit not as an ESS, when neither parent can undertake all the parental care alone. Just as communication of state to a partner is an advantage during courtship, and mate choice (chapter 2), so it is when negotiating the allocation of parental care between the pair in a situation of full compensation. Each adult must be aware of their partner's state so that they do not push him/her to do so much work that s/he abandons the breeding attempt. This means that there will be a benefit to individuals in communicating their own state to their partner in order to ensure that the breeding attempt does not have to be abandoned unnecessarily.

OTHER FACTORS INVOLVED IN REPRODUCTIVE DECISIONS

Duration of the Pair Bond

Reproductive decisions can be affected by the duration of the pair bond. In long lived species, such as seabirds, which generally pair for many breeding seasons (Cramp & Simmons 1983), breeding success increases with the time that the pair have bred together (reviewed in Mock & Fujioka 1990; Fowler 1995). This will have a number of effects on individual decision making. If pairs are more successful the longer they stay together, then future reproductive attempts may be worth more to the pair than current attempts. Therefore making it advantageous to choose to invest less in early attempts, with the hope of increasing their lifetime reproductive success. Also, if the success of next year's breeding effort relies on your partner's state, decisions of how to allocate parental care duties between the pair may involve more negotiation and result in an arrangement that benefits the weaker partner. This is what may have occurred in the experiment in chapter 4 on the lesser black-backed gull, a long-lived species that generally mates for life. Males may fully compensate for the decrease in effort of the female as it is in his interests to ensure her survival to the following year and maintain her in good condition. However, in contrast to this, species with short-term pair bonds may be expected to retaliate if partners try to do less parental care (Dearborn 2001).

Environmental Conditions

Reproductive decisions are likely to be dependent on environmental conditions as well as individual state. Individuals may tailor their effort to environmental conditions (e.g. Weimerskirch 2001) or choose not to breed at all in a year of poor condition in order to preserve their residual reproductive success for a time when the pay-off will be greater (Monaghan et al. 1992; Orell et al. 1994). In the year in which I undertook the study at Walney Island, there was a very poor breeding success over the whole gull colony. The poor environmental conditions, resulting in a very low fledging success, may have caused changes in the reproductive decisions of the gulls. This means that experiments such as that in **chapter 3**, where I investigated whether laying a replacement for an egg removed within 12 hours of laying was adaptive, should be carried out again in a year with good environmental conditions. This is because the relative costs and benefits of laying the replacement egg may differ under better conditions and individuals may make different decisions.

In the course of my PhD I also undertook another experiment with zebra finches that are not written up here due to the fact that they were breeding experiments and many of the birds did not breed under the experimental conditions. The idea was to repeat the gull experiment recounted in chapter 4 in the laboratory with zebra finches so that I could record their activities all of the time. In order to simulate a more realistic and harsh feeding situation and I diluted the seed that they were given with husks. Unfortunately this led to many of the pairs deciding not to breed at all.

CONCLUSION

Reproductive decisions are fundamental in determining how many genes are passed on to future generations. Organisms will therefore be selected to make appropriate decisions in order to maximise their lifetime reproductive success. In this thesis, I found that state is especially important in the decision making process. An individual's optimum behaviour may not only depend on their own state, but it may also depend on that of their partner. Hence breeding success will depend on choosing a good quality partner and reacting optimally to changes in their behaviour.

I found that poorer quality individuals, or those in a poorer condition do not always have the same choices available to them as the better individuals. It may pay to choose a higher quality territory, however, if there is competition for good breeding sites, then it is only the high quality birds that can actually choose a good territory. The same is true of choosing a mate because if all males wish to mate with high quality females then the competition will mean that the poorer quality males do not get to exercise choice.

It is important that an individual is in the best possible condition before breeding, as it increases the chance of a successful reproductive attempt: such an individual is more likely to gain a better partner; gain a better territory; breed earlier; and compensate more effectively for a reduction in care by their partner. If, however the individual is in a poor condition, it must still make decisions to maximise its reproductive success. A parent in poor condition may have a different optimum behaviour from that of an individual in good condition, for example when making decisions of when to lay and investment into the clutch, and how to divide resources between phases of reproduction. Having knowledge about the condition of other individuals will be important for all individuals when making decisions, for example when choosing a mate or predicting how long to stay away from the nest during incubation. Gaining reliable information about your own, and others', state, food availability, environmental conditions and behaviour of others will all be of the utmost importance in making the right decisions and thereby maximising lifetime reproductive success.

REFERENCES

Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution*, **15**, 149-155.

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **264**, 1579-1586.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton.

Barbraud, C., Lormee, H. & LeNeve, A. 2000. Body size and determinants of laying date variation in the Snow Petrel *Pagodroma nivea*. *Journal of Avian Biology* **31**, 295-302.

Bolton, M., Monaghan, P. & Houston, D. C. 1991. An improved technique for estimating pectoral muscle protein condition from body measurements of live gulls. *Ibis*, **133**, 264-270.

Bolton, M., Monaghan, P. & Houston, D. C. 1993. Proximate determination of clutch size in lesser black-backed gulls - the roles of food-supply and body condition. *Canadian Journal Of Zoology-Revue Canadienne De Zoologie*, **71**, 273-279.

Brown, J. L. 1967. Breeding success and population growth in a colony of herring and lesser black-backed gulls, *Larus argentatus* and *L. fuscus*. *Ibis*, **109**, 501-515.

Brown, M. E. 1996. Assessing body condition in birds. In: Current Ornithology Vol. 13 (V. Nolan Jr & E. D. Ketterson eds.) 67-117.

Bukacinski, D., Bukacinska, M. & Spaans, A. L. 1998. Experimental evidence for the relationship between food supply, parental effort and chick survival in the lesser black-backed gull *Larus fuscus*. *Ibis*, **140**, 422-430.

Burger, J. 1977. Role of visibility in nesting Larus Gulls. *Journal of Comparative and Physiological Psychology* **91** p 1347-1358

Burley, N. 1977. Parental investment, mate choice, and mate quality *Proceedings of the National Academy of Sciences U.S.A.*, **74,** 3476-3479.

Burley, N. T. & Coopersmith, C. B. 1987 Bill color preferences of zebra finches. *Ethology*, **76**, 133-151.

Burley, N. T., Price, D. K. & Zaan, R. A. 1992. Bill color, reproduction and condition effects in wild and domesticated zebra finches. *Auk*, **109**, 13-23.

Calladine, J. 1997. A comparison of Herring Gull *Larus argentatus* and Lesser Black-backed Gull *Larus fuscus* nest sites: their characteristics and relationships with breeding success. *Bird Stu*dy **44**: p 318-326

Clobert, J., Garland, T. & Barbault, R. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *Journal of Evolutionary Biology*, **11**, 329-364.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212-229.

Clutton-Brock, T. H., Albon, S. D. & Guiness, F. E. 1986. Great expectations:Maternal dominance, sex ratios and offspring reproductive success in red deer. *Animal Behaviour*, **34**, 460-471.

Côte, I. M. & Hunte, W. 1989. Male and female mate choice in the redlip blenny - why bigger is better. *Animal Behaviour*, **38**, 78-88.

Côté, S. D. 2000. Aggressiveness in king penguins in relation to reproductive status and territory location. *Animal Behaviour*, **59**, 813-821.

Côté, S. D. & Festa-Bianchet, M. 2001. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). *Behavioral Ecology & Sociobiology,* **49**, 260-265

Cottam, M. P. 1998. Selection, storage and utilization of protein in the zebra finch (*Taeniopygia guttata*). Ph.D. thesis, University of Glasgow.

Cramp, S. & Simmons, K. E. C. 1983. Birds of the Western Palearctic Vol III Waders to Gulls. Oxford University Press, Oxford.

Davis, J. W. F. & Dunn, E. K. 1976. Intraspecific predation and colonial breeding in lesser black-backed gulls *Larus fuscus. Ibis,* **118**, 65-77

De Forest, L. N. & Gaston, A. J. 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology* **77**, 1501-1511.

Dearborn, D. G. 2001. Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*). *Behavioral Ecology*, **12**, 200-206.

Downhower, J. F. (1976) Darwin's finches and the evolution of sexual dimorphism in body size. *Nature*, **263**, 558-563.

Fowler, G. S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist*, **35**, 318-328.

Garcia-Barros, E. 2000. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society*, **70**, 251-284.

Hatchwell, B. J., Chamberlain, D. E. & Perrins, C. M. 1996. The demography of blackbirds Turdus merula in rural habitats: Is farmland a sub-optimal habitat? *Journal of Applied Ecology*, **33** , 1114-1124.

Hipfner, J. M. 1997. The effects of parental quality and timing of breeding on the growth of nestling thick-billed murres. *Condor*, **99**, 353-360.

Hipfner, J. M., Gaston, A. J. & De Forest, L. N. 1997. The role of female age in determining egg size and laying date of thick-billed Murres. *Journal of Avian Biology*, **28**, 271-278.

Honeka, A. 1993. Intraspecific variation in body size and fecundity in insects - a general relationship. *Oikos*, **66**, 483-492.

Houston, A. I. & Davies, N. B. 1985. The evolution of co-operation and life history in the dunnock, *Prunella modularis*. In: Behavioural Ecology (Sibly, R.M. & Smith, R. H. eds). Blackwell Scientific Publications, Oxford, pp. 471-487.

Hunt, K. E., Hahn, T. P. & Wingfield, J. C. 1999. Endocrine influences on parental care during a short breeding season: testosterone and male parental care in Lapland longspurs (*Calcarius lapponicus*). *Behavioral Ecology and Sociobiology* **45**, 360-369.

Hunt, S., Cuthill, I. C., Bennett, A. T. D. & Griffiths, R. 1999. Preferences for ultraviolet partners in the blue tit. *Animal Behaviour,* **58**, 809-815.

Jakobsson, A. & Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**, 494-502.

Jennions, M. D. & Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society*, **75**, 21-64.

Johnsen, T. S., Hengeveld, J. D., Blank, J. L., Yasukawa, K. & Nolan, V. 1996. Epaulet brightness and condition in female red-winged blackbirds. *Auk*, **113**, 356-362.

Jones, I. L. & Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**, 238-239.

Kiorboe, T. & Sabatini, M. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. *Marine Ecology-Progress Series*, **120**, 285-298.

Kolliker, M., Heeb, P., Werner, I., Mateman, A. C., Lessells, C. M. & Richner, H. 1999. Offspring sex ratio is related to male body size in the great tit (*Parus major*). *Behavioral Ecology* **10**, 68-72.

Kraak, S. B. M. & Bakker, T. C. M. 1998. Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Animal Behaviour*, **56**, 859-866.

Krebs, J. R. & Davies, N. B. 1987. An Introduction to Behavioural Ecology (2nd edition). Blackwell Scientific Publications, Oxford.

Landwer, A. J. 1994. Manipulation of egg-production reveals costs of reproduction in the tree lizard (*Urosaurus ornatus*). *Oecologia*, **100**, 243-249.

Larsson, K., van der Jeugd, H. P., van der, I. T. & Horslund, P. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. *Evolution*, **52**, 1169-1184.

Lessells, C. M. 1998. A theoretical framework for sex-biased parental care. *Animal Behaviour* **56**, 395-407.

Linville, S. U., Breitwisch, R. & Schilling, A. J. 1998. Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour*, **55**, 119-127.

Lorentsen, S. H. & Rov, N. 1995. Incubation and brooding performance of the antarctic petrel *Thalassoica antarctica* at Svarthamaren, Dronning-Maud land. *Ibis*, **137**, 345-351.

Madsen, T. & Shine, R. 1999. The adjustment of reproductive threshold to prey abundance in a capital breeder. *Journal of Animal Ecology* **68**, 571-580.

Mand, R., Tilgar, V. & Leivits, A. 2000. Reproductive response of Great Tits, *Parus major*, in a naturally base-poor forest habitat to calcium supplementation. *Canadian Journal of Zoology-Revue Canadienne de Zoologie,* **78**, 689-695.

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

Merrett, N. R. 1994 Reproduction in the North Atlantic oceanic ichthyofauna and the relationship between fecundity and species sizes. *Environmental Biology of Fishes*, **41**, 207-245.

Mock D. W. & Fujioka, M. 1990. Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology and Evolution,* **5**, 39-43

Monaghan, P., Metcalfe, N. B. & Houston, D. C. 1996. Male finches selectively pair with fecund females. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **263**, 1183-1186.

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. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1731-1735.

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**, 70-81.

Moreno, J. 1998. The determination of seasonal declines in breeding success in seabirds. *Etología*, **6**, 17-31.

Mrowka, W. 1982. Effect of removal on the parental care behaviour of the biparental cichlid *Aequidens paraguayensis*. *Animal Behaviour*, **30**, 295-297.

Møller, A. P. 1993. Sexual selection in the barn swallow *Hirundo rustica*.3. female tail ornaments. *Evolution*, **47**, 417-431.

Nager, R. G., Monaghan, P. & Houston, D. C. 2000. 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. in press. The cost of egg production: increased egg production reduces future fitness in gulls. *Journal of Avian Biology*.

Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson, R. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 570-573.

Naulleau, G. & Bonnet, X. 1996. Body condition threshold for breeding in a viviparous snake. *Oecologia,* **107**, 301-306.

Negro, J. J., Bortolotti, G. R., Tella, J. L., Fernie, K. J. & Bird, D. M. 1998. Regulation of integumentary colour and plasma carotenoids in American Kestrels consistent with sexual selection theory. *Functional Ecology*, **12**, 307-312.

Newton, I. 1991. Habitat variation and population regulation in sparrowhawks. *Ibis* **133**, 76-88.

Olsson, O. 1997. Clutch abandonment: a state dependent decision in king penguins. *Journal of Avian Biology,* **28**, 264-267.

Orell, M., Koivula, K., Rytkonen, S. & Lahti, K. 1994. To breed or not to breed - causes and implications of non- breeding habit in the willow tit *Paras montanus*. *Oecologia* **100**, 339-346.

Part, T., Gustafsson, L. & Moreno, J. 1992. Terminal investment and a sexual conflict in the collared flycatcher (*Ficedula albicollis*). *American Naturalist*, **140**, 868-882.

Perdeck, A. C. & Cavé, A. J. 1992. Laying date in the coot - effects of age and mate choice. *Journal of Animal Ecology*, **61**, 13-19.

Potti, J. & Merino, S. 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: Implications for sexual selection. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **263**, 1199-1204.

Ratnieks, F. L. W. 1996. Evolution of unstable and stable biparental care. *Behavioral Ecology* **7**, 490-493.

Rees, E. C., Black, J. M., Spray, C. J. & Thorisson, S. 1991. Comparative-study of the breeding success of whooper swans *Cygnus cygnus* nesting in upland and lowland regions of Iceland. *Ibis* **133**, 365-373.

Roff, D. A. 1992. *The Evolution of Life Histories*. London: Chapman & Hall.

Roitberg, B. D. 1989. The cost of reproduction in rosehip flies, R*hagoletis basiola* - eggs are time. *Evolutionary Ecology*, **3**, 183-188.

Roulin, A., Jungi, T. W., Pfister, H. & Dijkstra, C. 2000. Female barn owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 937-941.

Saino, N., Ninni, P., Calza, S., Martinelli, R., De Bernardi, F. & Møller, A. P. 2000. Better red than dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 57-61.

Sanz, J. J., Kranenbarg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *Journal of Animal Ecology* **69**, 74-84.

Schmidt-Nielsen, K. 1984. Scaling : why is animal size so important? Cambridge University Press, Cambridge.

Selman, R. G. & Houston, D. C. 1996. The effect of pre-breeding diet on reproductive output in zebra finches. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **263**, 1585-1588.

Simpson, M. J. A. & Simpson, A. E. 1982. Birth sex ratio and social rank in rhesus monkey mothers. *Nature*, **290**, 49-51.

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

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Weimerskirch, H., Zimmermann, L. & Prince, P. A. 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology,* **12**, 22-30

Williams, T. D. 2001. Experimental manipulation of female reproduction reveals an intraspecific egg size-clutch size trade-off. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 423-428.

Witter, M. S. & Cuthill, I. C. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London Series Biological* **340**, 73-92.