The foraging behaviour and population dynamics of the northern gannet

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Sue Lewis

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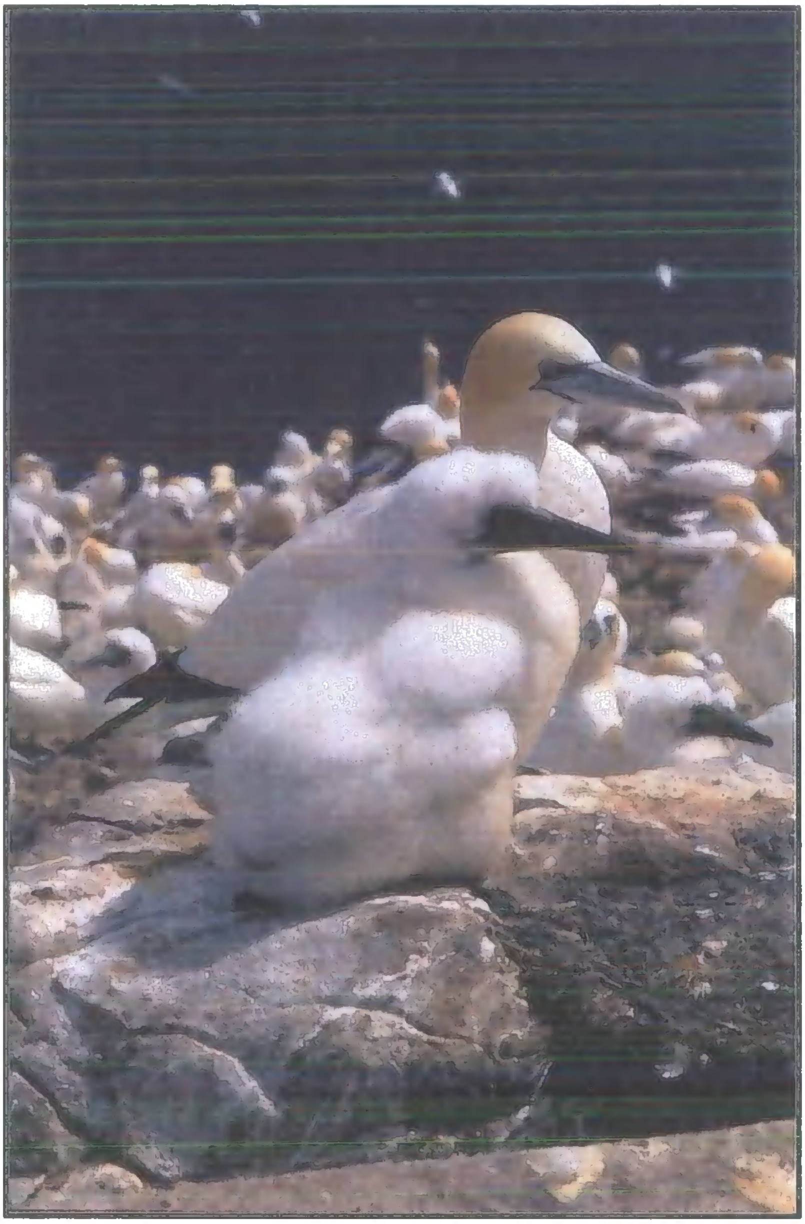

To Mum and Dad for always believing in me

Candidates declaration

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

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S. Lewis

Sue Lewis
December 2002

The foraging behaviour and population dynamics of the northern gannet
Ph.D. thesis submitted by Sue Lewis 2002

ABSTRACT

The northern gannet *Morus bassanus* population has been increasing in size over the last century. Larger gannet colonies in the British Isles are growing more slowly per capita than the smaller ones. For the first time, this study provides empirical evidence consistent with the hypothesis that seabird populations are regulated through density dependent competition for food (a theory proposed four decades ago). On average, gannets from larger colonies have to travel further to forage than birds from smaller colonies, leading to reduced provisioning rates at larger colonies.

Differences were found in the foraging behaviour of male and female gannets. Females dived deeper and spent more time resting on the sea surface than males. Females also tended to forage in a specific location whereas males were much more variable. This was the first demonstration of sex-specific foraging behaviour in a monomorphic seabird. Foraging location and depth may be driven by sex–specific dietary needs, differences in foraging efficiency or competitive ability.

State dependent foraging decisions were examined. Typically, gannets alternate foraging at sea with periods attending the chick at the nest. However, sometimes the attending parent will leave the chick alone. This decision is influenced by the prolonged absence of the partner and a low arrival mass of the adult, prior to its attendance shift. Unattended foraging trips were shorter in duration and therefore closer to the colony than attended trips. Since leaving the chick unattended is risky, there is a trade-off between offspring predation and short-term food requirements.

When aspects of the foraging behaviour of gannets were compared between a large and small colony, both striking contrasts and similarities were evident. At the larger colony there were no sex differences in trip duration or the propensity to leave the chick alone whilst at the smaller colony males made significantly shorter trips than females and left the chick alone much more than females. However at both colonies unattended trips were shorter than attended trips. These results suggest interactions between density dependent competition and sex-specific individual behaviour.

Identifying important areas for foraging is a major challenge for marine conservation. This study has demonstrated that colony size, sex and condition all affect the foraging decisions of the northern gannet.

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Chapter 1

General Introduction

General Introduction

Aims of the study

Trends in population size over time are of particular interest to nature conservation, and understanding the various factors that cause population change is a key question in ecology. Population size is driven by extrinsic effects such as food supply, competitors, predators, parasites, weather and anthropogenic activities, impacting on intrinsic changes in demography (Newton 1998). In most populations, numerous extrinsic effects operate on different demographic parameters simultaneously. These complex patterns fall into two broad categories: density dependent effects i.e. those that are dependent on the density of the population (e.g., many predation or competition situations), and density independent effects i.e. those which act in a similar way regardless of the density of the population (e.g., some extreme weather conditions). Density dependent effects maintain population size within certain limits that are much narrower than is generally feasible given minimal or maximal birth, death, immigration and/or emigration, and population change is generally gradual (Lack 1954). By contrast, density independent effects can be characterised by dramatic changes in population size. However, whilst these patterns are generally accepted, both the accurate measurement of intrinsic parameters and the demonstration of causality of extrinsic effects has been extremely challenging in ecology.

Populations are made up of individuals, each making daily life history decisions based on a range of factors. Effects of extrinsic factors on individuals, as with populations, are important, but equally difficult to measure. In addition, although much of life history strategy is fixed, a whole discipline has emerged in recent decades on the impact of the animal's internal state on its reproductive and foraging decisions (McNamara & Houston 1996). For example, both extrinsic and intrinsic effects are important in determining an animal's ability to find food (Milinski & Keller 1978; Milinski & Parker 1978).

Surprisingly, studies of population dynamics and animal behaviour have largely been carried out in isolation of each other (Sutherland 1996). There is a need to explore the relationship between population ecology and individual behaviour. The lack of empirical data on the drivers of population regulation, and the impact that state dependence has on population processes, forms the background to the thesis. It is imperative to collect comparable data on a species in different locations, so that it can be established whether the ecological patterns are general across environments, or whether there are interactions between the species' population ecology and density dependent and independent effects. This has been the approach taken in this thesis. The specific aim is to assess the impact of state dependent foraging decisions and intra-specific competition for food on population regulation. The study species, the northern gannet *Morus bassanus*, breeds in widely dispersed colonies varying in size by three orders of magnitude, at which state-dependent foraging strategies can be measured. As such, it provides an ideal model system to examine the interaction between individual and population processes.

This thesis also has applied relevance to the conservation of marine environments. Fish stocks have been widely exploited over recent decades, and there is considerable concern that the fisheries may be having an impact on top predators. Some authors have argued that by targeting the large predatory fish, North Atlantic fisheries have caused a severe decline in the chief competitors of seabirds (Furness & Tasker 1997; Furness 2002). However, more recently fisheries have turned their attentions to the smaller forage fish species preyed on by predatory fish, seabirds and mammals. Thus, whilst numbers of many seabird species have increased dramatically in the last century for a variety of reasons (Monaghan 1996), the interaction between fisheries and seabirds may now be shifting away from a favourable position. In this context, data on seabird foraging ecology and population regulation are vital for a proper understanding of the relationships among fish, fisheries and top predators.

Population regulation in seabirds

Seabird population regulation has long been the subject of considerable scientific debate. Most researchers have suggested that regulation operates in a density dependent manner, but a number of proximate causes of population regulation have been put forward. Lack (1966) suggested that populations were regulated by over-wintering mortality. However, the majority of other researchers have suggested that regulation is dictated by breeding success. At the forefront of this work, Ashmole (1963) put forward the hypothesis that breeding adults deplete fish stocks to such an extent around a colony that they generate a halo of prey ("Ashmole's halo"; Birt *et al.* 1987). He predicted that intense intra-specific competition for resources forces adults to forage further away as colony size increases (because increasing trip length should increase the probability of encountering prey), which in turn regulates colony size (through reduced provisioning rates to chicks because of the longer foraging trips at larger colonies). This theory was given an important boost when Furness & Birkhead (1984) analysed the distributions of several species of seabird in the British Isles and found that large colonies did not tend to be close together. However, Forbes *et al.* (2000) put forward the alternative suggestion that large colonies are isolated simply because large islands tend to be far apart. It has also been suggested that population regulation of seabirds is due to density-independent factors, keeping seabird numbers below the levels at which density dependent factors act (Croxall & Rothery 1991; Nur & Sydeman 2000).

Individual processes

Life history theory

Life history theory predicts that parents should balance their current investment in offspring against the probability of survival and future reproduction, so as to maximise lifetime reproductive success. A large expenditure in reproductive effort in one year may result in "costs of reproduction" in terms of reduced future reproductive potential through decreased adult survival or fecundity. (Williams 1966; Charnov & Krebs 1974; Stearns 1976; Ricklefs 1977; Calow 1979; Reznick 1985; Kacelnik & Cuthill 1990; Roff 1992; Stearns 1992).

Costs of reproduction are associated with the extra pressures breeders are under compared with non-breeders. Above all, the demand for resources is higher due to the increasing energy demands of the growing chicks (Clutton-Brock 1991). Manipulation experiments have demonstrated trade-offs between current and future breeding success by showing that parents can physically provision larger broods than they would do naturally (e.g. Nelson 1964). However, it is important to note that not all twinning experiments were as successful (see Jarvis 1974). Furthermore, such experiments generally do not account for the increased cost of laying an extra egg (see Heaney & Monaghan 1996). A second pressure common to many breeding individuals with dependent young is that they are central place foragers. This limits the area they can potentially use for food acquisition because of the regular need to return to the offspring (Orians & Pearson 1979).

In the context of food acquisition, the trade-off between current and future reproduction affects the decisions that parents must make, such as where and how often to forage. In addition, a balance between short-term food requirements of self and offspring is required. How to allocate the food between parents and their offspring, so as to maximise lifetime reproductive success, is central to life history theory (Trivers 1974; Parker & Macnair 1978; Ricklefs *et al.* 1985; Godfray & Parker 1992; Kilner & Johnstone 1997; Kolliker *et al.* 1998; Cotton *et al.* 1999).

State dependent foraging decisions

Among seabirds one of the most critical extrinsic factors governing breeding success is likely to be food supply (Furness & Monaghan 1987). The foraging ecology of seabirds is intricately linked not only to the external environment, but also to intrinsic state variation between individuals (McNamara & Houston 1996). The concept of 'state' encompasses all aspects of individual variation of this kind, for example sex, age and condition.

Sex effects on foraging behaviour have received considerable attention in seabird research. Many studies have found differences in the foraging behaviour and chick-provisioning rates between males and females. Virtually all studies have dealt with sexually size dimorphic species (Prince *et al.* 1992; Weimerskirch *et al.* 1993; Sagar & Weimerskirch 1996; Weimerskirch & Sagar 1996; Gonzalez-Solis *et al.* 2000) and the size difference has largely been implicated in the patterns observed, rather than sex. Size is likely to determine an individual's competitive ability, foraging efficiency and, ultimately, the costs associated with reproduction. Males and females in size dimorphic species may work at different rates but incur similar reproductive costs (Stearns 1992).

Equally, an individual's condition may dictate its foraging decisions with the aim of maximising short or long term gain in lifetime reproductive value. Empirical studies have shown that parents assess their own body condition, and use this information in behavioural decisions (Drent & Daan 1980; McNamara & Houston 1996; Tveraa *et al.* 1998a). Parents also use the state of the chick to adjust provisioning rate (Trivers 1974; Ricklefs *et al.* 1985; Betram *et al.* 1996; Erikstad *et al.* 1997; Kilner & Johnstone 1997; Kolliker *et al.* 1998; Tveraa *et al.* 1998b).

Measuring foraging behaviour in the field

To obtain empirical data on state dependent foraging decisions, quantification of foraging activity is necessary. With seabirds, unlike many animal groups, data collection by direct observation is problematic, because few species forage within view of land. Much can be learnt from observations from ships, but such work suffers from three main constraints. First, cruises are extremely costly. Second, observations can only be made of surface activities, when in reality many species of seabird forage below the surface during dives or plunges. Third, the breeding status and origin of the birds observed from ships is completely unknown. To overcome these constraints, colony based work is required.

The advent of instrumentation technology has revolutionized the study of seabird foraging ecology (Kooyman *et al.* 1971; Trivelpiece *et al.* 1984; Cairns *et al.* 1987; Croxall *et al.* 1988; Wanless *et al.* 1988; Wilson & Wilson 1988; Burger & Piatt 1990). Archival and transmitting loggers have provided a wide range of behavioural data in recent decades, including location, time-activity budgets, foraging depths and prey capture rates. Development of loggers is a continuous process and the data that can be obtained are ever expanding.

Outline of the thesis

Model species

The northern gannet is a very good model species for this study for several reasons. The species breeds in discrete colonies ranging in size from a few pairs to over 50,000. This range of colony size provides a good basis on which to construct a study of population regulation. Virtually all gannetries have increased over the last century, allowing the effect of population size on population growth to be investigated. In addition, good count data of most colonies are available dating back a century. Several studies have already contributed greatly to the knowledge of the life history of gannets, in particular to their breeding biology, notably Nelson's pioneering work and classic brood manipulation experiment (Nelson 1964, 1978).

The northern gannet is also an ideal species for the study of individual foraging behaviour. It is large, and therefore, capable of carrying instruments designed to provide information on the foraging behaviour of birds at sea. Second, it has a very long breeding season which provides a wide time window in which to collect data. Third, it is sexually monomorphic, so any sex differences in foraging behaviour will not be confounded by differences due to size. Finally, at one colony, the Bass Rock, the birds are easy to catch, and most importantly to re-catch, so that state-dependent foraging behaviour can be quantified.

Thesis structure

Chapter 2 describes the study species and introduces the main study colonies. General methods relevant to all chapters are also given. Chapter 3 describes an analysis of population growth in relation to colony size over the last century. These results are coupled with the measurement of foraging trip duration, a close surrogate of foraging range (Hamer *et al.* 2000; Hamer *et al.* 2001) at nine gannetries in one year, and historical trip duration data available for four of the nine gannetries. The work provides unique evidence that intra-specific competition for food is driving population regulation, by examining individual foraging behaviour and population growth rates. In Chapters 4 and 5, a detailed analysis is made of state dependent foraging dynamics of breeding northern gannets at one of the nine colonies examined previously, Bass Rock. Specifically, an account is given of the effects of sex (Chapter 4) and condition (Chapter 5) on foraging decisions of individual gannets. In Chapter 6, the approaches of the three previous chapters are brought together in a detailed comparison of state dependent foraging ecology of gannets at two gannetries, one very large and one twenty times smaller. The findings derived from the general approach and the specific patterns described in each chapter are then drawn together in a general discussion, Chapter 7.

References

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, **103b**, 458-473.

Barlow, K.E. & Croxall, J.P. (2002) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Marine Ecology Progress Series*, **232**, 291-304.

Betram, D.F., Welham, C.V.J., & Ydenberg, R.C. (1996) Flexible effort in breeding seabirds: adjustment of provisioning according to nestling age and mass. *Canadian Journal of Zoology*, **74**, 1876-1881.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., & Montevecchi, W.A. (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, **40**, 205-208.

Burger, A.E. & Piatt, J.F. (1990) Flexible time budgets in common murres: buffers against variable prey abundance. *Studies of Avian Biology*, **14**, 71-83.

Cairns, D.K., Bredin, K.A., & Montevecchi, W.A. (1987) Activity budgets and foraging ranges of breeding common murres. *The Auk*, **104**, 218-224.

Calow, P. (1979) The cost of reproduction. A physiological approach. *Biological Review*, **54**, 23-40.

Charnov, E.L. & Krebs, J.R. (1974) On clutch size and fitness. *Ibis*, **116**, 217-219.

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

Cotton, P.A., Wright, J., & Kacelnik, A. (1999) Chick-begging strategies in relation to brood hierarchies and hatching asynchrony. *American Naturalist*, **153**, 412-420.

Croxall, J.P., Davis, R.W., & O'Connell, M.J. (1988) Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. *Condor*, **90**, 157-167.

Croxall, J.P. & Rothery, P. (1991). Population regulation of seabirds: implications of their demography for conservation. In *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. LeBreton & G.J.M. Hirons), pp. 272-295. Oxford University Press, Oxford.

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

Erikstad, K.E., Asheim, M., Fauchald, P., Dahlhaug, L., & Tveraa, T. (1997) Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. *Behavioural Ecology and Sociobiology*, **40**, 95-100.

Forbes, L.S., Jajam, M., & Kaiser, G.W. (2000) Habitat constraints and spatial bias in seabird colony distributions. *Ecography*, **23**, 575-578.

Furness, R.W. (2002) Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *Ices Journal of Marine Science*, **59**, 261-269.

Furness, R.W. & Birkhead, T.R. (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature*, **311**, 655-656.

Furness, R.W. & Monaghan, P. (1987) *Seabird Ecology*. Blackie, Glasgow.

Furness, R.W. & Tasker, M.L. (1997). Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird population dynamics. University of Alaska, Fairbanks.

Godfray, H.C.J. & Parker, G.A. (1992) Sibling competition, parent offspring conflict and clutch size. *Animal Behaviour*, **43**, 473-490.

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

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., & Wood, A.G. (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies. *Marine Ecology Progress Series*, **224**, 283-290.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Heaney, V. & Monaghan, P. (1996) Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **263**, 1719-1724.

Jarvis, M.J.F. (1974) The ecological significance of clutch size in the South African gannet (*Sula capensis* (Lichtenstein)). *Journal of Animal Ecology*, **43**, 1-17.

Kacelnik, A. & Cuthill, I. (1990) Central place foraging in starlings (*Sturnus vulgaris*) II: food allocation to chicks. *Journal of Animal Ecology*, **59**, 655-674.

Kilner, R. & Johnstone, R.A. (1997) Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, **12**, 11-15.

Kolliker, M., Richner, H., Werner, I., & Heeb, P. (1998) Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour*, **55**, 215-222.

Kooyman, G.L., Drabek, C.M., Elsner, R., & Campbell, W.B. (1971) Diving behaviour of the emperor penguin *Aptenodytes forsteri*. *Auk*, **88**, 775-795.

Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Oxford University Press, Oxford.

Lack, D. (1966) *Population Studies of Birds*. Oxford University Press, Oxford.

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

Milinski, M. & Keller, R. (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus*). *Nature*, **275**, 642-644.

Milinski, M. & Parker, G.A. (1978). Competition for resources. In *Behavioural Ecology: An Evolutionary Approach* (eds J.R. Krebs & N.B. Davies), pp. 137-168. Blackwell scientific Publications, Oxford.

Monaghan, P. (1996) Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos*, **77**, 227-237.

Nelson, J.B. (1964) Factors influencing clutch size and growth in the northern gannet, *Sula bassana*. *Ibis*, **106**, 63-77.

Nelson, J.B. (1978) *The Gannet*. T. and A.D. Poyser.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, London.

Nur, N. & Sydeman, W.J. (2000) Survival, breeding probablity and reproductive success in relation to population dynamics of Brandt's cormorants *Phalacrocorax penicillatus*. *Bird Study*, **46**, S92-103.

Orians, G.H. & Pearson, N.E. (1979). On the theory of central place foraging. In *Analysis of Ecological Systems* (eds D. Horn, G. Stairs & R. Mitchell), pp. 155-177. Ohio State University Press, Columbus.

Parker, G.A. & Macnair, M. (1978) Models of parent-offspring conflict. *Animal Behaviour*, **26**, 97-111.

Prince, P.A., Wood, A.G., Barton, T., & Croxall, J.P. (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*, **4**, 31-36.

Reznick, D. (1985) Cost of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**, 257-267.

Ricklefs, R.E. (1977) On the evolution of reproductive strategies in birds: reproductive effort. *American Naturalist*, **111**, 453-478.

Ricklefs, R.E., Day, C.H., Huntington, C.E., & Williams, J.B. (1985) Variability in feeding rates and meal size of Leach's storm petrel at Kent Island, New Brunswick. *Journal of Animal Ecology*, **54**, 883-898.

Roff, D.A. (1992) *The Evolution of Life Histories*. Chapman & Hall, New York.

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

Stearns, S.C. (1976) Life history tactics: a review of the ideas. *Quarterly Review Biology*, **51**, 3-47.

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

Sutherland, W.J. (1996) *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford.

Trivelpiece, W.Z., Bengston, J.L., Trivelpiece, S.G., & Volkman, N.J. (1984) Foraging behaviour of gentoo and chinstrap penguin as determined by new radio telemetry techniques. *Auk*, **103**, 777-781.

Trivers, R.L. (1974) Parent-offspring conflict. *American Zoologist*, **14**, 249-264.

Tveraa, T., Saether, B.-E., Aanes, R., & Erikstad, K.E. (1998a) Body mass and parental decisions in the Antarctic petrel *Thalassoica antarctica*: how long should the parents guard the chick? *Behavioural Ecology and Sociobiology*, **43**, 73-79.

Tveraa, T., Saether, B.-E., Aanes, R., & Erikstad, K.E. (1998b) Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology*, **67**, 699-704.

Wanless, S., Morris, J.A., & Harris, M.P. (1988) Diving behaviour of guillemot *Uria aalge*, puffin *Fratercula arctica* and razorbill *Alca torda* as shown by radio telemetry. *Journal of Zoology*, **216**, 73-81.

Weimerskirch, H. & Sagar, P.M. (1996) Diving depths of sooty shearwaters *Puffinus griseus*. *Ibis*, **138**, 786-794.

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325-342.

Williams, G.C. (1966) Natural selection, the cost of reproduction, and a refinement of Lack,s principle. *American Naturalist*, **100**, 687-690.

Wilson, R.P. & Wilson, M.-P.T. (1988) Foraging behaviour in four sympatric cormorants. *Journal of Animal Ecology*, **57**, 943-955.

Chapter 2

General Methodology

General Methodology

Introduction

Detailed methods relevant to each results chapter are contained therein. However, a number of materials and methods are relevant to all chapters. These are set out below.

The study species

The northern gannet *Morus bassanus* is the largest seabird breeding in the North Atlantic, having a wing-span of 165-180 cm (Cramp & Simmonds 1977). Their dense gregarious colonies (which range from only a few hundred pairs to well over 50, 000) and plunge-diving behaviour make them one of the most familiar of the seabirds.

Gannets, like almost all other seabirds, are monogamous and commence breeding at age 4-7 years (Nelson 1978). Once recruited, they are very site faithful and on returning to the colony each year to breed, they take it in turns to defend their nest site and initiate nest building. However the male almost invariably collects all the nest material (Nelson 1978). The female lays a single egg, weighing on average 105 g (81-130 g; approximately 3.5% adult body mass) and both sexes incubate the egg in shifts, which lasts for six weeks (Nelson 1978). Chicks are altricial, and are brooded continuously during the first two weeks, until they reach homeothermy (Montevecchi & Porter 1980). Chick rearing lasts for 13 weeks, and parents alternate foraging and nest attendance duties (Nelson 1978). In line with work by Nelson (1978), Montevecchi & Porter (1980) observed that begging and feeding were more closely coupled with the arrival of the parents as the chick grew older, and probably learnt to associate parent arrival with food. It was suggested that early in the season, the delay in feeding after returning to the nest was to enable parents to transfer smaller, manageable amounts of partially digested food to the nestling, rather than the larger undigested meals that they can transfer to older chicks straight away.

The early studies by Nelson (1978) and Montevecchi & Porter (1980) provide a good basis for the development of modern studies, which can explore this area of biology in more detail, using novel techniques, such as those used by Garthe *et al.* (1999); Garthe *et al.* (2000); Hamer *et al.* (2000); Hamer *et al.* (2001). Hamer *et al.* (2000) equipped 17 chick rearing adults on the Bass Rock and 9 on Great Saltee (Hamer *et al.* 2001) with satellite transmitters. The mean foraging range (i.e., distance travelled on a foraging trip) on the Bass Rock was 223 km (s.d. ± 95, range: 39-540 km), while on Great Saltee the mean range was 89km (s.d. ± 49, range: 14-238 km), much shorter than that of the Bass Rock. He also showed that at both colonies, the maximum distance travelled on a foraging trip was strongly significantly positively correlated with the foraging trip duration (Bass Rock: $F_{1,67} = 988.7$, $p<0.001$, $r^2 = 0.94$; Great Saltee: $F_{1,58} = 305.4$, $p<0.001$, $r^2 = 0.84$), and the equation for this relationship was the same at both colonies ($t_{12} = 0.52$, $p = 0.6$; see Hamer *et al.* 2001 for more details). This finding provides a means of predicting the maximum distance travelled from the time spent at sea, and has been integral for much of the work in this thesis.

The study colony

The study was mainly carried out at two locations, the Bass Rock and Great Saltee, although gannets were observed at an additional seven gannetries within the British Isles in Chapter 3, where full details are given.

Bass Rock

The Bass Rock is a small island situated in the Firth of Forth, SE Scotland (56°6'N; 2°36'W), recently designated as a Special Protected Area (SPA), and is the site of the classic early work on gannet ecology and behaviour by Bryan Nelson. The island is an ideal place for studying gannets due to the substantial colony size, the ease of access to the birds nesting on the top of the island, and the relative tameness of birds compared to other UK gannetries.

Records of breeding pairs for the Bass Rock colony start in 1904, when the population was 3,000 breeding pairs (Gurney 1913). The population currently holds nearly 40,000 breeding pairs (last counted in 1994; see Murray & Wanless 1997), plus several thousand non-breeders, and is one of the largest populations of northern gannets in the world. The gannets now nest all over the island, except for a small area on the top.

Great Saltee

This is a small island designated as a SPA situated off the SE coast of Ireland (52°8'30''N; 6°41'W). Oscar Merne (Head of seabird studies for National Parks and Wildlife, Ireland) carries out annual census and ringing.

The Great Saltee colony was slow establishing from 1 pair in the 1920s to over 50 pairs in the 1960s. The population size in 2000 was nearly 2,000 breeding pairs. The gannets mainly nest at the southern most end of the island but have more recently colonised Makestone Rock, off the NE end, which has approximately 200 pairs.

Data collection and analyses

Catching, handling and attaching devices

Birds were captured at the nest using a 6 m telescopic pole and noose. Protective gloves and goggles were worn when the bird was held. The devices used to collect information on foraging behaviour were attached to the tail feathers of each bird with self-amalgamating tape and cable-ties. To minimise drag during flight and prevent tags being displaced during plunge-diving, tags were attached to the underside of the four central tail feathers, close to the base of the tail with the aerial (if present) pointing upwards through the feathers as described in Hamer *et al.* (2000) and Falk *et al.* (2000), respectively.

Blood sampling

Because the sexes are of similar size and cannot be reliably identified from plumage or soft-tissue colouration (Nelson 2002; Redman *et al.* 2002), a blood sample

(<0.1ml) was taken under licence from the tarsal vein of each bird, for subsequent sexing using two *CHD I* genes. The analyses were carried out by Glasgow university staff, as part of a collaborative link with Richard Griffiths (Glasgow University). The method involved initial digestion of the blood using 10mg/ml Proteinase K in a digestion solution containing: 20mM EDTA, 50mM Tris (base) 120mM NaCl,1.5%SDS. The sample was incubated overnight at 55°C, after which 4M Ammonium Acetate was used to precipitate out proteins, lipids etc. Absolute alcohol was then used to precipitate the DNA, which was subsequently used in a Polymerase Chain Reaction. The resulting PCR products were then separated using gel electrophoresis and visualised on an ethidium bromide stained gel using an ultraviolet light source see Griffiths *et al.* (1996) for further details.

Chick ageing

Chicks were aged using age-specific plumage characteristics adapted from Nelson (2002) and Wanless, pers. comm.; see Appendix 1.

Data analyses

Details of all statistical analyses are given in the relevant chapters. Genstat 5, release 4.2 and SPSS 10, release 10.0.5, were used throughout.

References

Cramp, S. & Simmonds, K.E.L. (1977) *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic.* Oxford University Press, Oxford.

Falk, K., Benvenuti, S., Dall'antonia, L., Kampp, K., & Ribolini, A. (2000) Time allocation and foraging behaviour of chick rearing Brunnich's guillemots *Uria lomvia* in high-arctic Greenland. *Ibis,* **142**, 82-92.

Garthe, S., Benvenuti, S., & Montevecchi, W.A. (2000) Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society of London Series B-Biological Sciences,* **267**, 1717-1722.

Garthe, S., Gremillet, D., & Furness, R.W. (1999) At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: a case study in Shetland. *Marine Ecology Progress Series,* **185**, 93-99.

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.

Gurney, J.H. (1913) *The Gannet. A Bird with a History.* Witherby, London.

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., & Wood, A.G. (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies. *Marine Ecology Progress Series,* **224**, 283-290.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series,* **200**, 257-264.

Montevecchi, W.A. & Porter, J.M. (1980). Parental investments by seabirds at the breeding area with emphasis on northern gannets, *Morus bassanus.* In *Behaviour of Marine Animals. Current Perspectives in Research.* (eds J. Burger, B.L. Olla & H.E. Winn), Vol. Vol 4. Marine Birds, pp. 323-365. Plenum Press, New York-London.

Murray, S. & Wanless, S. (1997) The status of the gannet in Scotland in 1994-95. *Scottish Birds,* **19**, 10-27.

Nelson, J.B. (1978) *The Gannet.* T. and A.D. Poyser.

Nelson, J.B. (2002) *The Atlantic Gannet.* Fenix Books Ltd., Norfolk.

Redman, K.K., Lewis, S., Griffiths, R., Wanless, S., & Hamer, K.C. (2002) Sexing northern gannets *Morus bassanus* from DNA, behaviour and morphology. *Waterbirds,* **25**, 230-234.

Chapter 3

Evidence of intra-specific competition for food in a pelagic seabird

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Evidence of intra-specific competition for food in a pelagic seabird

Abstract

The factors affecting the population dynamics of seabirds have long intrigued biologists. Current data suggest that density-dependent depletion of prey during the breeding season may regulate seabird population size. However, much of the evidence for this has been circumstantial, and the underlying mechanisms are unclear. Here, we show that the per capita population growth rates of northern gannet *Morus bassanus* at a number of colonies in the British Isles and Ireland have declined with increasing population size. Furthermore, direct observations of gannets at nine separate colonies, have revealed for the first time that the mean foraging trip duration of breeding gannets is positively correlated with colony size, both among colonies of different sizes in the same year, and within colonies as they change in size. To understand this phenomenon, a model was developed which demonstrates that disturbance of fish alone can readily generate conditions under which gannets at larger colonies have to travel further to obtain food. This study not only provides evidence for population regulation in a seabird species, but also highlights a demographically important correlate of colony size, and presents a simple explanation for this relationship.

Introduction

Almost all seabirds breed colonially, and the factors governing the sizes and locations of these colonies have long been debated (Ashmole 1963; Lack 1966; Birkhead & Furness 1985; Cairns 1989; Croxall & Rothery 1991). While some researchers have suggested that certain seabird populations are regulated by density-dependent mortality outside their breeding season (Lack 1966), the majority have argued that regulation is more likely to occur during the breeding season, through density-dependent reproductive success (Ashmole 1963; Gaston *et al.* 1983; Furness & Birkhead 1984; Hunt *et al.* 1986; Birt *et al.* 1987). Others have proposed that density-independent factors may keep some seabird populations below levels at which density-dependent factors act (Croxall & Rothery 1991; Nur & Sydeman 2000).

One of the most influential theories of seabird population regulation was proposed by Ashmole (1963). He argued that adults foraging close to the breeding colony are likely to cause local prey depletion, so that birds from larger colonies will have to travel further to find food for their chicks, than birds from smaller colonies. Therefore chicks from larger colonies will receive less food per unit time than chicks from smaller colonies, and it was these reduced provisioning rates at larger colonies that Ashmole suggested would affect breeding success and thus population growth, because fewer chicks would be surviving to recruit back into the population. While Ashmole emphasised that this phenomenon would be less likely to arise in temperate regions where marine productivity is generally higher, Furness & Birkhead (1984) found consistent negative correlations between colony size and numbers at neighbouring colonies in the UK and interpreted their results as providing evidence that even temperate species may compete for resources. However, the exact causes of this higher-order relationship are unclear (Croxall & Rothery 1991; Wooller *et al.* 1992). For instance, some authors have questioned whether seabirds could in general take sufficient fish to cause significant depletion (Croxall 1987) and whether negative correlations of this nature can at least in part be explained by a geographic tendency of large islands to be far apart (Forbes *et al.* 2000).

To evaluate the validity of Ashmole's population regulation hypothesis it is essential to first establish whether seabird populations actually exhibit density-dependent growth. Although smaller black-legged kittiwake *Rissa tridactyla* colonies tend to grow proportionately faster than larger ones (Coulson 1983), the evidence for density-dependent growth in seabird species is extremely limited. More specifically, despite nearly 40 years of research, Ashmole's principal regulatory mechanism, namely that birds from larger colonies need to travel further for food, remains untested. Even if this prediction were upheld in temperate waters, then a full explanation would need to justify why local depletion arises despite high marine productivity, and consider its likely demographic consequences. Finally an examination of breeding success at different colonies would be essential to test the mechanism affecting population regulation.

The northern gannet is a good model species to test Ashmole's theory for several reasons. First, many colonies in the British Isles and Ireland have been expanding in size over the past century (see Figures 3.1 a and b of the Bass Rock colony pre 1960 and in 2000). This expansion is believed to be in part due to a reduction of persecution (Lloyd *et al.* 1991), but perhaps also due to increased food availability (Furness *et al.* 1992), thereby providing an ideal opportunity to test whether per-capita population changes are indeed density-dependent. Second, satellite tracking of breeding birds has shown that foraging range is very closely correlated with trip duration in this species, so that the distances travelled by adults can be accurately estimated from observed trip durations (Hamer *et al.* 2000; Hamer *et al.* 2001). Finally, the gannet is the largest pelagic seabird breeding in the North Atlantic. It feeds mainly on pelagic shoaling fish (Hamer *et al.* 2000; Nelson 2002) by plunge diving for prey (Garthe *et al.* 1999; Garthe *et al.* 2000; Nelson 2002), and currently occurs in colonies which range in size from a few pairs to tens of thousands (Murray & Wanless 1997), providing high statistical power to detect evidence of intra-specific foraging competition, if indeed it occurs.

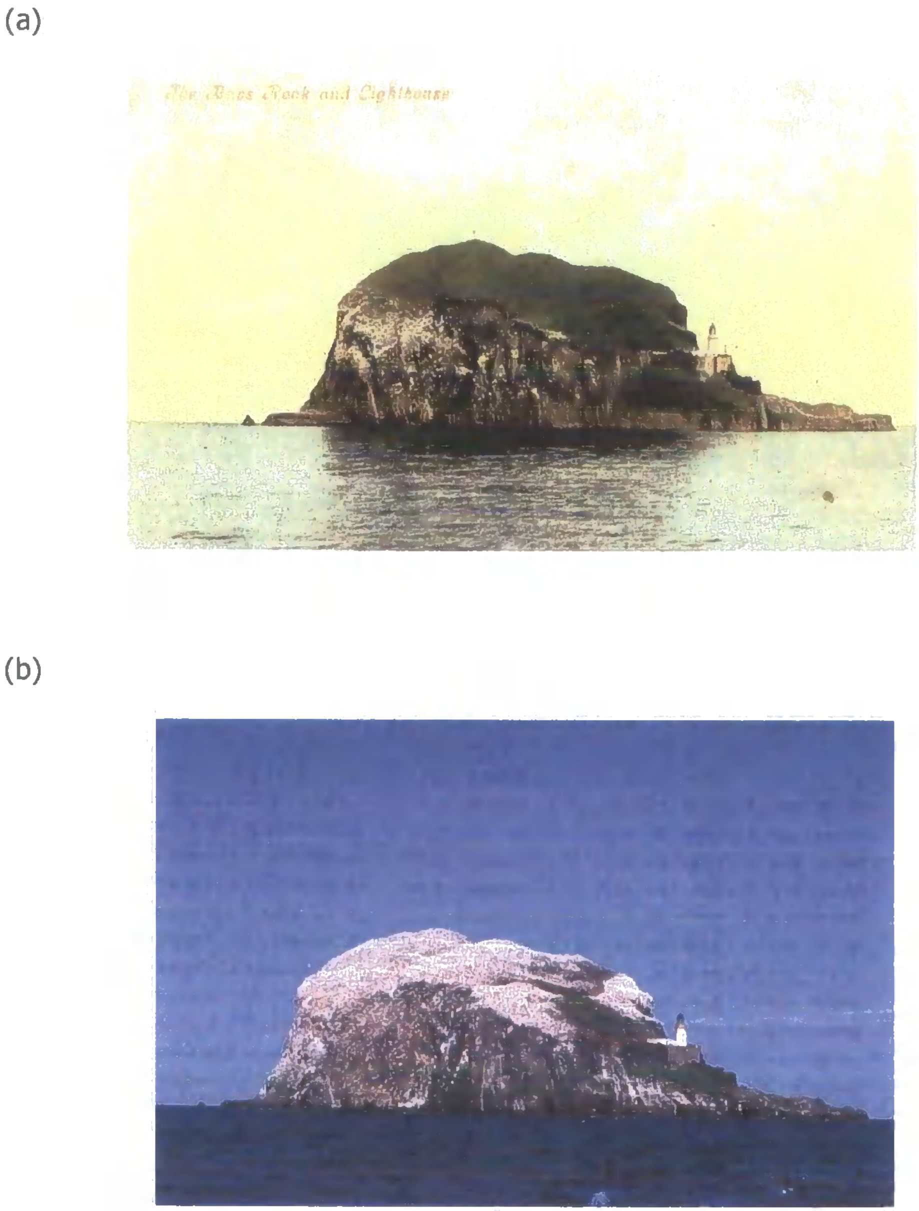

Figure 3.1: Photograph of the Bass Rock colony (a) from a postcard pre 1960 and (b) in 2000, illustrating the dramatic expanse in numbers of breeding pairs throughout this time interval.

Methods

Population censuses and detection of density dependence

The estimated population sizes of gannets at 17 of the 18 colonies in the British Isles and Ireland (A, BR, B, Bu, F, Fl, Fo, G, Gr, H, I, L, N, S, SR, SS, T; see Figure 3.2) were derived from published counts (Fisher & Vevers 1944; Cramp *et al.* 1974; Nelson 1978; Murray & Wanless 1986, 1997; Upton *et al.* 2000) of apparently occupied breeding sites and personal data. Data from Sula Sgeir were not examined because it is the only colony in the UK where chicks are still harvested. The minimum number of censuses per island was ten, spanning a maximum period of 1902-2000 (A: 51 censuses, from 1922-1995; BR: 13, 1904-1994; B: 34, 1924-2000; Bu: 12, 1902-1994; F: 27, 1973-2000; Fl: 10, 1968-1994; G: 51, 1929-2000; Gr: 21, 1903-1994; H: 21, 1920-1999; I: 10, 1988-2000; L: 13, 1913-1995; N: 18, 1913-1999; S: 10, 1902-1994; SR: 28, 1938-1995; SS: 10, 1904-1994; T: 12, 1988-2000).

To test for density-dependent population growth within colonies, the distribution-free randomisation test advocated by (Pollard *et al.* 1987) was used*, which involves calculating the slope *b* of $\log_e N[t+1]$ and $\log_e N[t]$ ($N[t]$ - population size at time t) and comparing this with gradients derived from 1000 randomly permutated time series. As this method relies on unbroken series of censuses at fixed intervals, it was possible to employ this method for the yearly censuses taken at only 7 colonies (A: 1947-1985; B: 1969-1984; F: 1974-1998; G: 1964-1980; H: 1974-1980; T: 1988-1998; SR: 1968-1976).

More gannet colonies were censused in the British Isles and Ireland in 1984/85 and 1994/95 than over any other period, so we also estimated the per capita growth rates of gannet populations at each of these colonies over this decade. To compare per capita population growth between colonies over the same period of time, the proportionate increase in gannet population size at 15 colonies between 1984/85-1994/95 was calculated (Irelands Eye and Troup Head were not considered since they were unoccupied in 1984/85).

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* *Analyses performed by T.N.Sherratt*

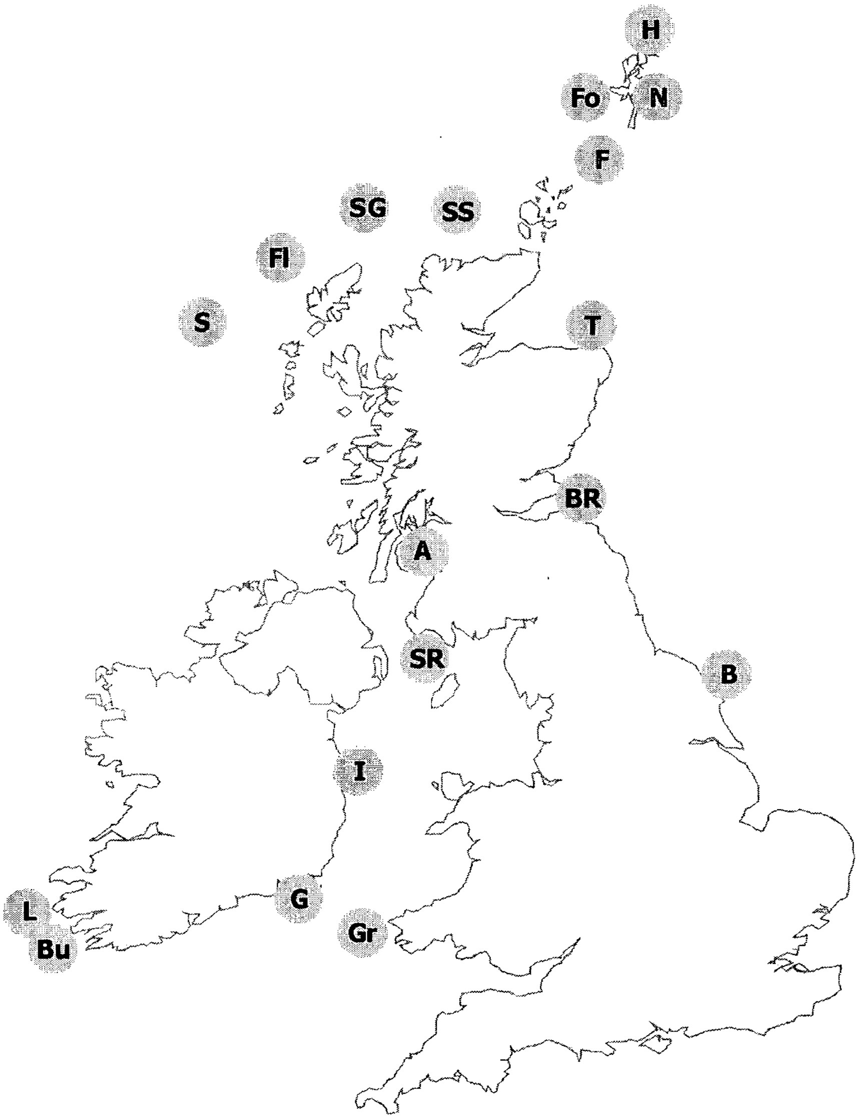

Figure 3.2: The distribution of the 18 gannetries in the UK and Ireland (A-Ailsa Craig , BR-Bass Rock, B-Bempton, Bu-Bull Rock, F-Fair Isle, Fl-Flannans, Fo-Foula, Gr-Grassholm, G-Great Saltee, H-Hermaness, I-Irelands Eye, L-Little Skellig, N-Noss, S-St Kilda, SR-Scar Rocks SG-Sula Sgeir, SS-Sule Stack and T-Troup Head).

Estimation of trip duration

Fieldwork took place during chick rearing (overall mean age of nestlings at each colony 7.4 weeks, range 5.0-9.9 weeks) at nine of the gannet colonies in the British Isles and Ireland (Ailsa Craig, Bass Rock, Bempton, Fair Isle, Great Saltee, Hermaness, Irelands Eye, Noss and Troup Head). Nestlings were always attended by at least one parent. At each colony, approximately 20 breeding pairs with chicks (range 18-24) were observed for a total time of 10-55 hours. By recording the arrival and departure times of adults at these nests it was possible to estimate the overall change-over rate of gannets per nest per day, from the number of arrivals per nest per day. The mean trip duration at each colony was calculated by dividing the mean time available per day for foraging (local daylight hours minus the mean time birds are together at the nest), by the estimated changeover rate. Time together at the nest was determined by calculating the number of minutes the pair remained together at the nest following the arrival of the foraging bird until the departure of its partner. Provisioning rate is equivalent to the change-over rate, i.e., the number of arrivals per nest per day.

The historical data on trip durations were collated from the following sources: Wanless 1973; Nelson 1978; Wanless 1978; 1981; Garthe *et al.* 1999, where data from the first four sources were based on observations of the mean time birds were away from the colony, whilst Garthe *et al.* (1999) used data loggers.

All of the nine study colonies were counted in 2000 with the exception of Bass Rock, Ailsa Craig, Hermaness and Noss, which were last counted in 1994, 1995, 1999 and 1999 respectively. The population sizes of these colonies in 2000 were estimated[†] using standard population growth trajectories (Murray & Wanless 1997).

Foraging range was related to trip duration by the following regression equation (Maximum distance (km) = 7.05 (1SE ± 0.22) trip duration (h); $r^2 = 0.94$; (Hamer *et al.* 2000; Hamer *et al.* 2001). Competition for food is proportional to the square root

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[†] *The estimates for population size for BR, A, H and N were only used for the analyses between population size and trip duration/daily feed rate calculated in 2000. These estimates were not used in the tests of density dependence.*

of the number of birds (Furness & Birkhead 1984). Therefore, we used square root transformations for our colony size estimates.

Determination of breeding performance

Data on the breeding success of gannets at six different colonies of varying size, between 1986 and 1999 were obtained from a Joint Nature Conservation Committee (JNCC) published report (Upton *et al.* 2000). For each colony, the mean number of chicks fledged per nest was correlated with the mean value of colony size, using Spearmans correlation, because data were not normally distributed.

Results

Density-dependence

Figure 3.3 shows changes in log transformed population sizes over time at several different colonies. The fact that a number of colonies (e.g., N, F, T and G) show a non-linear increase in population size indicates that their growth is not geometric, and reduces the higher the density. Time series analysis (Pollard *et al.* 1987) of the longest unbroken series of yearly censuses at 7 different gannetries identified significant density-dependent population growth at 3 of these colonies[‡] (Figure 3.3, Bempton $b = 0.9203$, $n = 16$, $p < 0.05$; Fair Isle $b = 0.8365$, $n = 25$, $p < 0.02$; Troup Head $b = 0.7708$, $n = 11$ $p < 0.005$; Ailsa Craig $b = 0.9079$, $n = 39$, $p > 0.05$; Hermaness $b = 0.2984$, $n = 7$, $p > 0.05$; Great Saltee (1964-1980) $b = 1.007$, $n = 17$, $p > 0.05$; Great Saltee (1987-2000) $b = 0.9361$, $n = 14$; Scar Rock $b = =0.0252$, $n = 9$, $p > 0.05$.).

The between-colony comparison also showed that the per capita growth rates of colonies declined significantly with population size (Figure 3.4, $r = -0.853$, d.f. = 13, $p < 0.001$), although we note that because N is in both axes, measurement error would lead to lack of independence.

Trip duration

A comparison of trip durations of chick rearing adults at different sized colonies showed that there was a highly significant positive correlation between trip duration, and hence foraging range, and square root colony size ($r = 0.898$, d.f. = 7, $p < 0.005$, Figure 3.5), with trip duration increasing three-fold between the smallest and largest population.

Historical data on foraging trip duration at four of these colonies (Figure 3.5) also fitted the same regression model extremely well (2000-only regression slope = 0.0492, SE 0.009; pooled within colony regression slope for the four colonies =

[‡] *Analyses performed by T.N. Sherratt.*

0.0622, SE 0.010, while a linear mixed model using combined data yielded a slope of 0.0548, SE 0.013), indicating that the relationship within colonies between years is similar to our relationship among colonies within the same year.

Although pairs at the smaller colonies spent significantly more time together at the nest (square root transformed data for colony size r = -0.725, d.f. = 7, $p < 0.05$), the rate of provisioning of chicks by the parents still tended to decrease with increasing population size (Figure 3.6; square root transformed data for colony size r = -0.662, d.f. = 7, $p = 0.052$; log transformed data for colony size r = -0.671, d.f. = 7, $p < 0.05$).

Breeding success

There was no significant relationship between the mean number of chicks fledged per nest and mean colony size (Figure 3.7; Spearman r = -0.086, d.f. = 4, $p = 0.87$).

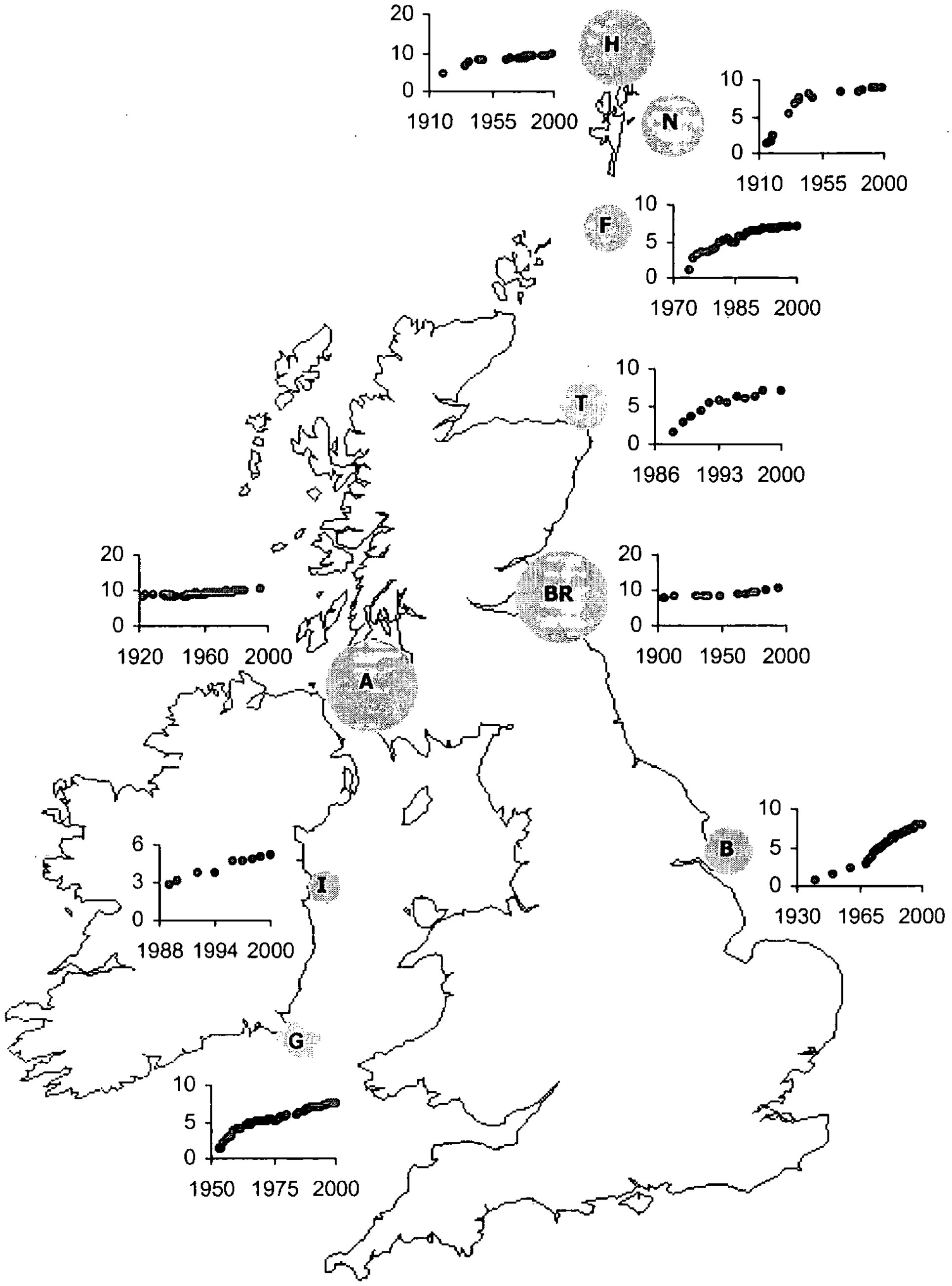

Figure 3.3: The current sizes, distribution and changes in $\log_e$ numbers of gannet pairs (breeding sites) over the last century at 9 of the 17 study colonies (labelled as Figure 3.2). Levelling off implies that per capita growth decreases with population size. Data on trip durations were collected at these 9 colonies.

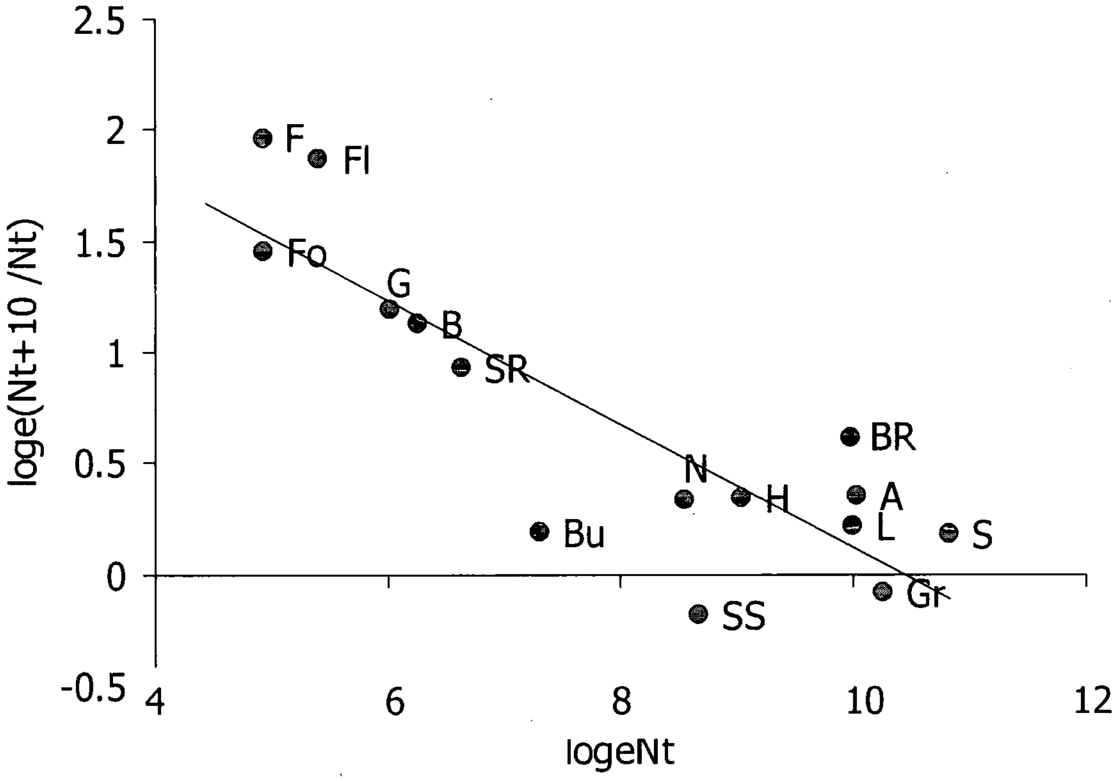

Figure 3.4: The relationship between $\log_e$ Nt (colony sizes in 1984/85) and $\log_e$(Nt+10 /Nt) (ratio of colony sizes in 1994/95 to 1984/85), at 15 gannetries throughout the British Isles and Ireland (labelled as in Figure 3.2).

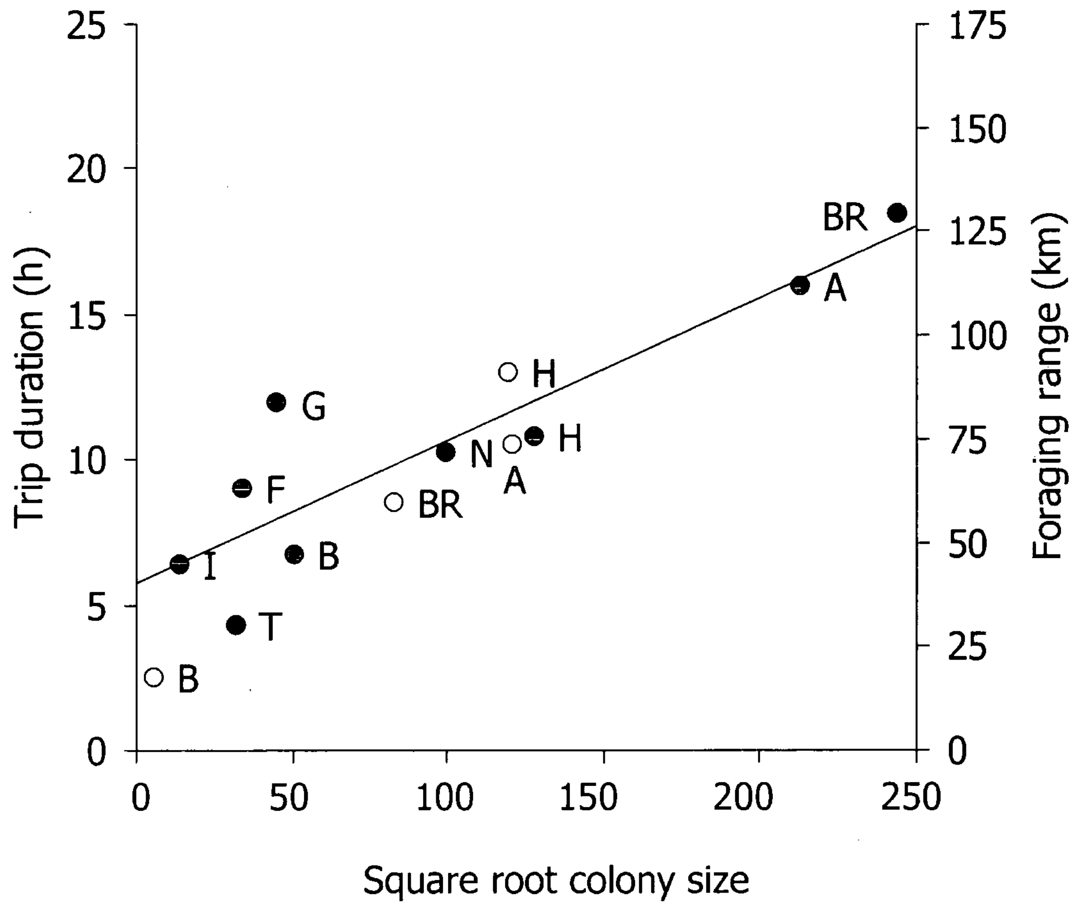

Figure 3.5: The relationship between foraging trip duration (h) and the square root of colony size for gannets at the nine study colonies in 2000 (labelled as in Figure 3.2). Earlier data collected at four colonies (BR in 1966, B in 1972, A in 1975 and H in 1997) are represented by open symbols. Line of best fit for 2000 data is shown.

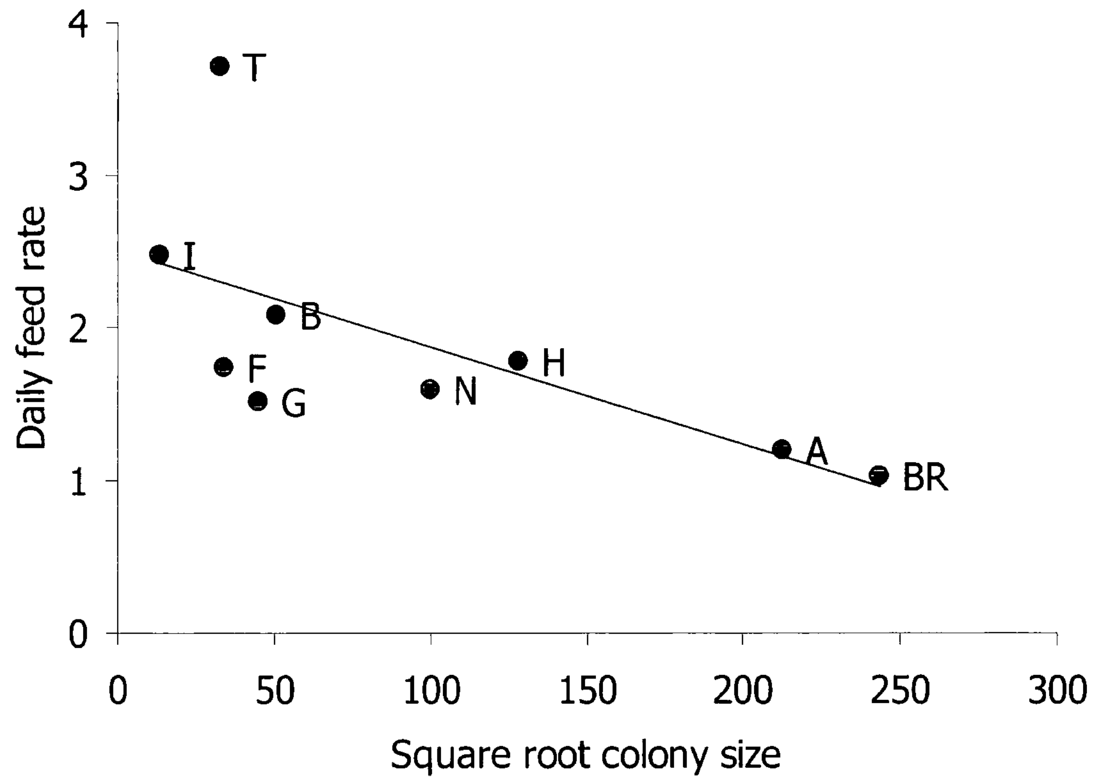

Figure 3.6: The relationship between daily feed rate and the square root of colony size for gannets at the nine study colonies (labelled as in Figure 3.2).

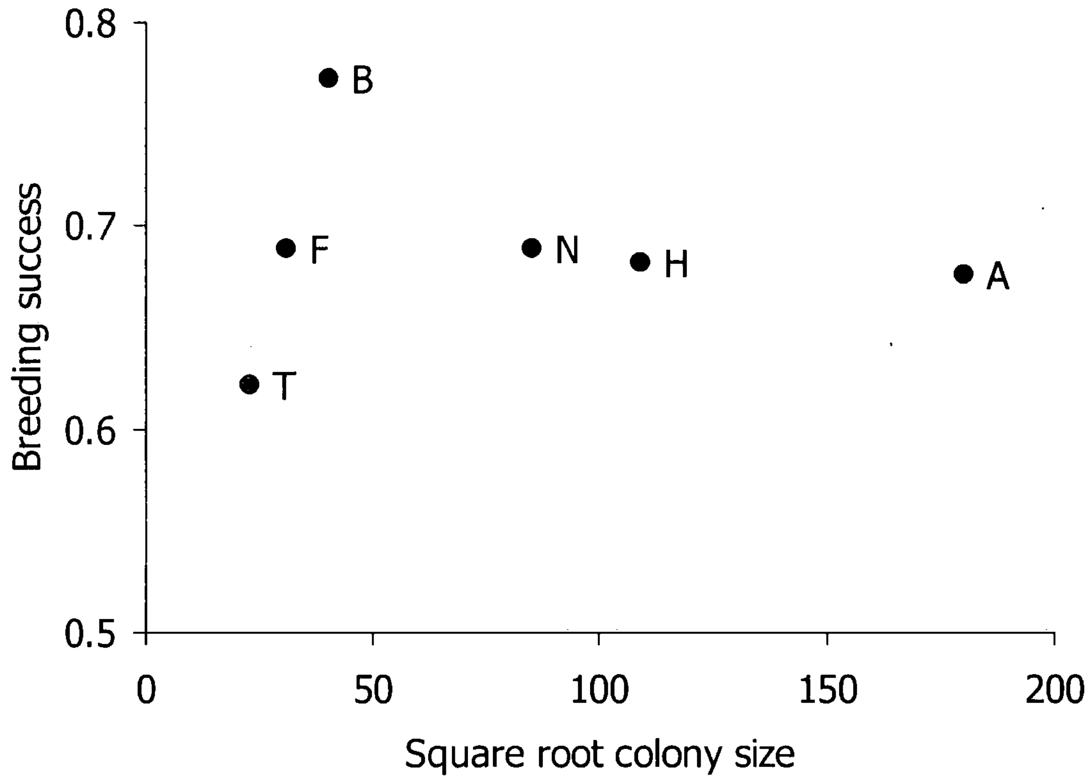

Figure 3.7: The relationship between the mean breeding success (number of chicks fledged per nest) and the mean square root colony size for six gannetries between 1986 and 1999 (labelled as Figure 3.2).

Discussion

These data provide the first empirical support for Ashmole's hypothesis of density-dependent population regulation in seabirds, first proposed in the 1960s. They not only support the contention that seabird populations are indeed growing in a density dependent way, but also test his prediction that adults from larger colonies have to travel further to find food for their chicks, than adults from smaller colonies.

Density dependent population growth

Larger populations of gannets grew more slowly on a per capita basis than smaller ones. This is consistent with previous observations by Nelson (Nelson 1978), a preliminary analysis of Scottish colonies (Murray & Wanless 1997) and an earlier analysis of the growth of 34 gannet colonies (Moss *et al.* 2002).

Trip duration

Gannets from larger colonies made longer trips and thus, on average, travelled further to collect food for their chicks than gannets from smaller colonies. The generality of this relationship was further confirmed using historical data for 4 of our study gannetries and for St Kilda (the largest colony in the North Atlantic), which was not observed in 2000. In 1980 St Kilda held 40,000 breeding sites (Murray 1981) and the average trip duration was around 21 hours (Wanless 1981), which fits in with our relationship well. There was also some evidence that foraging birds from neighbouring colonies may to some extent compete for food. Thus at two pairs of colonies that were very similar in size (Great Saltee (G) and Bempton (B); Fair Isle (F) and Troup Head (T)) one was above the regression line of trip duration against colony size (see Figure 3.5), and one was below. The colonies that were above the regression line (G and F) are both approximately 50 km from other large colonies, while the colonies below the regression line (B and T) are both over 100 km away from other large colonies.

What might the proximate causes for the differences in foraging range be? Birds may be depleting local fish populations as proposed by Ashmole. However, given the low estimates of biomass that seabirds actually consume in comparison to predatory fish, marine mammals and fisheries (Furness 2002), there is some debate as to whether seabirds can deplete fish stocks to such an extent that would generate this effect. An alternative hypothesis is that gannets are temporarily disturbing fish shoals. Empirical data have shown that pelagic fish exhibit a classic escape response when disturbed by predators (Logerwell & Hargreaves 1997), and so in order to examine the effects of disturbance by diving predators on the distribution of fish shoals, two complementary models were developed in which shoals of pelagic fish show escape responses, when they are attacked by diving gannets[§]. If gannets are the primary source of disturbance and the escape response of fish involves some lateral movement, then shoals close to a colony will inevitably be attacked more frequently than those further away, and the overall tendency will be for fish shoals to diffuse outwards. Such movements readily generate a slowly-growing "halo" (Figure 3.8, see Box 1) (Ashmole 1963). Under these conditions the mean foraging trip duration of gannets will increase with the square root of colony size (Figure 3.9, see Box 1). Alternatively some fish species may escape predation by swimming vertically downwards (Logerwell & Hargreaves 1997), while factors such as currents or disturbance by other predatory species may effectively mix shoals to such an extent that halo patterns do not clearly form. In such cases, the geometry of central place foraging may explain our observations, and so a second model was developed (Figure 3.10, see Box 2). By integrating foraging rewards over a given flight path, it becomes clear that if gannets compete for prey which is randomly distributed in discrete patches, then they should forage over approximately the same total area per bird to obtain the same amount of food, independent of colony size. Since the area covered increases with the square of the mean foraging radius, then this may explain why trip duration appears so closely correlated with the square root of population size.

What are the implications of adults taking longer to find food at larger colonies? One possibility is that adults have to work harder at larger colonies and therefore experience higher mortality. Perhaps more importantly, if the average food load

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[§] *Both models developed by T.N.Sherratt.*

brought back to feed the young is constant among colonies, then chicks from larger colonies will receive less food per unit time than those at smaller colonies. Many seabird species exhibit reduced breeding success during years when food is scarce (Croxall 1987; Monaghan *et al.* 1989), but gannets rear only a single chick and the analysis of available data on gannet breeding success did not indicate a significant relationship between the mean number of chicks fledged per nest and mean colony size. Like gannets, Brunnich's Guillemot *Uria lomvia*, have a single egg clutch, and while fledging success similarly did not appear to change with colony size, this species had significantly lower fledging weights in larger colonies (Gaston *et al.* 1983), which may affect the survival of chicks post fledging and thus recruitment of natal adults back into the breeding population, as proposed by Ashmole. Finally, it is important to note that there is evidence that gannets from large colonies recruit into smaller colonies (Nelson 2002), so it is possible that the provisioning rates within colonies could play some role in influencing where birds choose to breed for the first time. For example, several authors (Boulinier *et al.* 1996; Danchin *et al.* 1998; Suryan & Irons 2001) suggest that pre-breeding black-legged kittiwakes visit several colonies and use certain cues to assess breeding conditions at that colony. They suggest that such cues may aid them in selecting favourable breeding sites, which may give rise to differential rates of immigration depending on conditions at the colony.

By investigating how population sizes change over time these data have shown that gannet colonies do indeed exhibit a form of density-dependent growth. Moreover, this study provides empirical support for perhaps the best known, yet hitherto untested, candidate mechanism: seabirds take longer to find food at larger colonies. While significant density-dependent changes in provisioning rates are very likely to be demographically important, we do not know at this stage whether feeding rates have indeed played a major role in influencing the population growth patterns that we have observed, since adult survival is very likely to be important. Other density-dependent factors may also influence gannet dynamics, such as a gradual limitation of suitable breeding sites (Potts *et al.* 1980), or perimeter-restricted growth (Moss *et al.* 2002), and it is possible that these factors interact to some extent. Large colonies, such as the Bass Rock may soon reach their carrying capacity in terms of space. Therefore it will become increasingly difficult to separate whether density dependent population growth patterns are driven by food or space, because as the areas on the island used by non-breeders diminish, it seems very likely that recruitment will similarly decline. Density-independent factors (such as storm events) may also affect population size (Nur & Sydeman 2000), but evidently these factors were not sufficient to obscure the underlying density-dependence in this case.

Lower fish densities close to a breeding colony have already been observed for one species of seabird that forages inshore (Birt *et al.* 1987). However, it has long puzzled biologists how seabirds might show density-dependent competition for prey at sea when seabirds appear to contribute relatively little to total fish mortality (Furness & Tasker 1997). This work suggests that density-dependent fish disturbance is sufficient to significantly reduce the mean profitability of fish shoals close to colonies, and thereby generate suitable conditions for intra-specific competition. Since such competition can arise without significant prey mortality, these findings may have important implications for the interactions of seabirds with commercial fisheries.

Box 1: Fish disturbance simulation.

In this model, the sea surrounding a gannet colony of size N was partitioned into an m x m array of discrete cells. A fixed proportion p of these cells contained fish shoals, which were initially distributed at random within the matrix. Gannets flew out from the central colony to search for fish shoals either by: (i) a random walk (successive discrete steps between the eight neighbouring cells, each step taking one time unit) or (ii) directed movement (successive discrete steps along a given trajectory, with probability q of moving to a nearest neighbour other than that on the trajectory). At any one time, 50% of the birds in the colony searched for fish, and simulations were continued until each gannet had completed an average of T trips. Whenever a gannet flew over a shoal, it detected the shoal with probability d. If fish were not seen by a gannet within t_{max} time steps, then it returned to the colony without prey. However, once a gannet detected a shoal, then it dived into the shoal to forage and returned directly to the colony. Any fish shoals attacked by a diving bird moved immediately to a randomly chosen neighbouring area, so long as this cell was not occupied. Undisturbed fish shoals were assumed to move at an arbitrary average rate of either: (i) zero or (ii) one nearest neighbour per c units of time.

Box 2: Travel durations when central place foragers disturb prey

In this model, fish occur in discrete shoals of diameter s, which are randomly distributed with mean density d per unit distance. We assume that when foraging gannets disturb shoals they become temporarily unavailable through some avoidance response (e.g. sinking vertically and/or swimming away), but that they remain randomly distributed in space despite this disturbance. We consider a mainland colony of N pairs of gannets. Foraging gannets fly out to sea from the colony in straight lines with random directions, and each individual returns after they have gathered T units of fish biomass.

Let proportion p of the breeding adults leave the colony in search of food per unit time. Since gannets are in essence central place foragers, then the closer a shoal arises towards the colony the more birds are likely to encounter it. As a first approximation we have assumed that a mean proportion of $(s / \pi r)$ of gannets that leave the colony per unit time will encounter a shoal if it is at distance r from the colony (it is easy to show that the better approximation 2 atan(s/2r)/π yields very similar numerical results, but this function is less tractable analytically).

If g gannets encounter a given shoal (either simultaneously or in quick succession) per unit time, then let these individuals gain a mean reward of biomass $m(g)$. Here we have assumed that the immediately available prey are divided by the number of birds encountering the shoal, that is $m(g) = v / g$ where v is a constant. Nevertheless, functions with the highest foraging rewards per individual at non-zero gannet densities, such as $m(g) = 1 / \{(g-w)^2 + c\}$ (w and c constants) also generate similar conclusions so long as peak profitability arises for relatively few gannets. Under the above conditions, an individual gannet will gain the net biomass B from continuing to forage for distance j where:

$$B = \int_{r=0}^{r=j} d\,v / (s\,p\,N / \pi r)\,\mathrm{d}r$$

Furthermore if gannets cease foraging when $B = T$ then they should travel distance λ where:

$$\lambda = \sqrt{(2\,s\,p\,T\,N / d\,v\,\pi)}.$$

which implies that the mean total travel distance (hence travel time) will be proportional to $\sqrt{N}$.

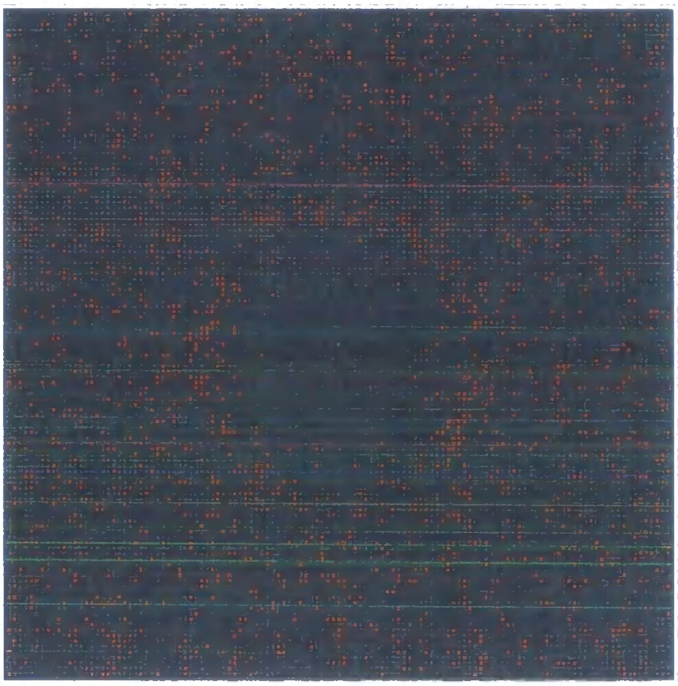

Figure 3.8**: The distribution of unoccupied cells (blue), and cells occupied by fish shoals (red), around a central colony (light blue) of 1000 gannets (500 pairs) after each individual had completed an average of 100 foraging trips. Gannets searched by random walk and undisturbed shoals did not move. Parameter values: m = 121, p = 0.1, d = 0.8, tmax = ∞.

** *Figure 3.8 by T.N. Sherratt.*

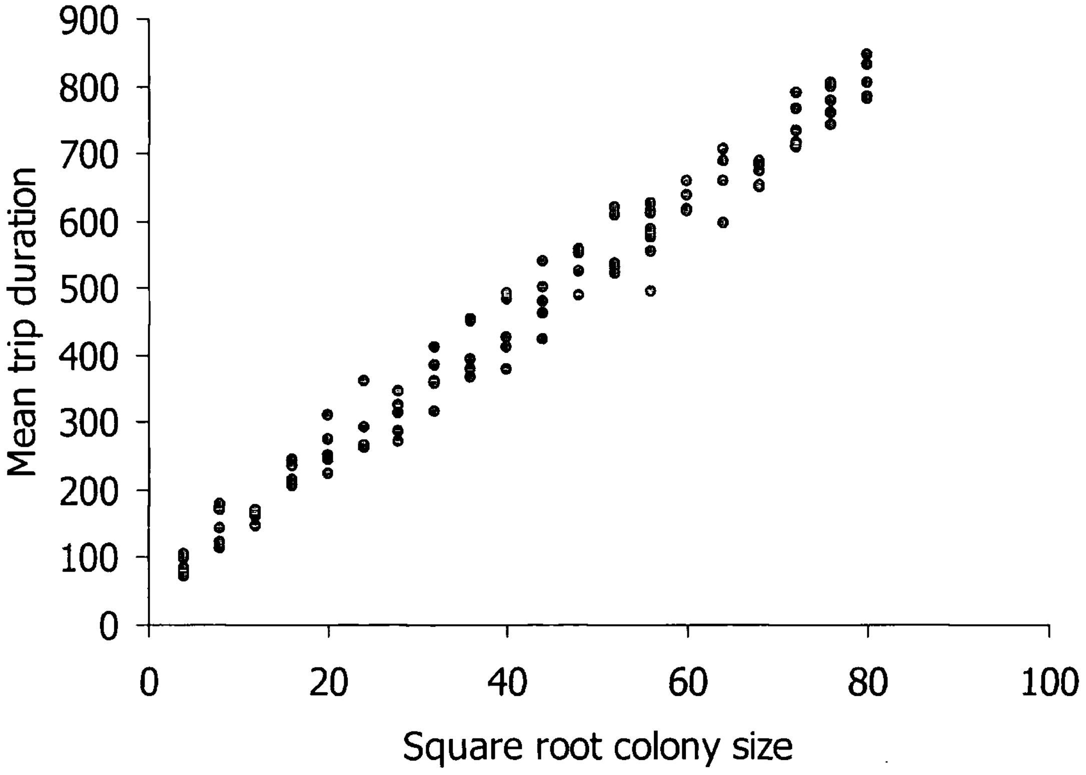

Figure 3.9[††]: Mean trip durations of gannets at different colony densities (five simulations per density). Gannets searched by random walk (each step taking 1 time unit) and undisturbed shoals did not move. Parameter values: $m = 121$, $p = 0.05$, $d = 0.8$, $T = 100$, $tmax = \infty$.

[††] *Figure 3.9 by T.N. Sherratt.*

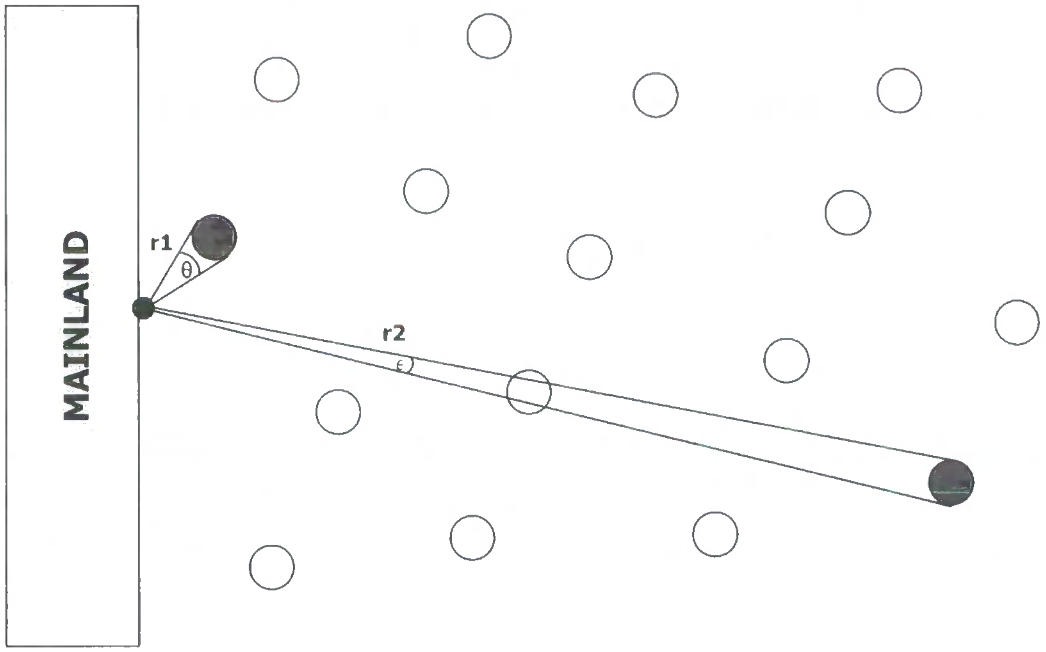

Figure 3.10: The geometry of central place foraging. As r1 < r2 then θ > ε, so a greater proportion of gannets leaving a colony (here depicted on the mainland) will encounter a shoal that is close, than a shoal that is more distant. If seabirds compete for available prey, then shoals that are encountered at greater distance from the colony will on average be more profitable to individual birds.

References

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, **103b**, 458-473.

Birkhead, T.R. & Furness, R.W. (1985). Regulation of seabird populations. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 145-167. Blackwell Scientific Publications, Oxford.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., & Montevecchi, W.A. (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, **40**, 205-208.

Boulinier, T., Danchin, E., Monnat, J., Doutrelant, C., & Cadiou, B. (1996) Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology*, **27**, 252-256.

Cairns, D.K. (1989) The regulation of seabird colony size: A hinterland model. *The American Naturaliist*, **134**, 141-146.

Coulson, J.C. (1983) The changing status of the Kittiwake *Rissa tridactyla* in the British Isles, 1969-1979. *Bird Study*, **30**, 9-16.

Cramp, S., Bourne, W.R.P., & Sanders, S. (1974) *The Seabirds of Britain and Ireland*. Collins, London.

Croxall, J.P. (1987) *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge.

Croxall, J.P. & Rothery, P. (1991). Population regulation of seabirds: implications of their demography for conservation. In *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. LeBreton & G.J.M. Hirons), pp. 272-295. Oxford University Press, Oxford.

Danchin, E., Wagner, R., & Boulinier, T. (1998) The evolution of coloniality: does commodity selection explain it all? Reply from E. Danchin, R. Wagner and T. Boulinier. *Trends in Ecology and Evolution*, **13**, 76-76.

Fisher, J. & Vevers, H.G. (1944) The breeding distribution, history and population of the North Atlantic Gannet (*Sula bassana*). *Journal of Animal Ecology*, **13, 14**, 49-62.

Forbes, L.S., Jajam, M., & Kaiser, G.W. (2000) Habitat constraints and spatial bias in seabird colony distributions. *Ecography*, **23**, 575-578.

Furness, R.W. (2002) Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *Ices Journal of Marine Science*, **59**, 261-269.

Furness, R.W. & Birkhead, T.R. (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature*, **311**, 655-656.

Furness, R.W., Ensor, K., & Hudson, A.V. (1992) The use of fishery waste by gull populations around the British Isles. *Ardea*, **80**, 105-113.

Furness, R.W. & Tasker, M.L. (1997). Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird population dynamics. University of Alaska, Fairbanks.

Garthe, S., Benvenuti, S., & Montevecchi, W.A. (2000) Pursuit plunging by Northern Gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society London B*, **267**, 1717-1722.

Garthe, S., Gremillet, D., & Furness, R.W. (1999) At-sea-activity and foraging efficiency in chick-rearing Northern Gannets *Sula bassana*: a case study in Shetland. *Marine Ecology Progress Series*, **185**, 93-99.

Gaston, A.J., Chapdelaine, G., & Noble, D.G. (1983) The growth of Thick-billed Murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. *Canadian Journal of Zoology*, **61**, 2465-2475.

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., & Wood, A.G. (2001) Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies. *Marine Ecology Progress Series*, **224**, 283-290.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of Gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Hunt, G.L., Eppley, Z.A., & Schneider, D.C. (1986) Reproductive performance of seabirds: the importance of population and colony size. *The Auk*, **103**, 306-317.

Lack, D. (1966) *Population Studies of Birds*. Oxford University Press, Oxford.

Lloyd, C., Tasker, M.L., & Partridge, K. (1991) *The Status of Seabirds in Britain and Ireland*. T & AD Poyser, London.

Logerwell, E.A. & Hargreaves, N.B. (1997). Seabird Impacts on Forage Fish: Population and Behavioral Interactions. University of Alaska, Fairbanks.

Monaghan, P., Uttley, J.D., & Okill, D. (1989) Terns and sandeels: seabirds as indicators of change in marine fish populations. *Journal of Fish Biology*, **35**, 339-340.

Moss, R., Wanless, S., & Harris, M. (2002) How small northern gannet colonies grow faster than big ones. *Colonial Waterbirds*, **25**, 442-448.

Murray, S. (1981) A count of Gannets on Boreray, St Kilda. *Scottish Birds*, **11**, 205-211.

Murray, S. & Wanless, S. (1986) The status of the Gannet in Scotland 1984-85. *Scottish Birds*, **14**, 74-85.

Murray, S. & Wanless, S. (1997) The status of the Gannet in Scotland in 1994-95. *Scottish Birds*, **19**, 10-27.

Nelson, J.B. (1978) *The Sulidae - Gannets and Boobies*. Oxford University Press, Oxford.

Nelson, J.B. (2002) *The Atlantic Gannet*. Fenix Books Ltd., Norfolk.

Nur, N. & Sydeman, W.J. (2000) Survival, breeding probablity and reproductive success in relation to population dynamics of Brandt's Cormorants *Phalacrocorax penicillatus*. *Bird Study*, **46**, S92-103.

Pollard, E., Lakhani, K.H., & Rothery, P. (1987) The detection of density-dependence from a series of annual censuses. *Ecology*, **68**, 2046-2055.

Potts, G.R., Coulson, J.C., & Deans, I.R. (1980) Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology*, **49**, 465-484.

Suryan, R.M. & Irons, D.B. (2001) Colony and population dynamics of black-legged kittiwakes in a heterogeneous environment. *Auk*, **118**, 636-649.

Upton, A.J., Pickerell, G., & Heubeck, M. (2000). Seabird numbers and breeding success in Britain and Ireland, 1999. JNCC, Peterborough.

Wanless, S. (1981). The gannets of Boreray. In *The Boreray 1980 expedition - a report on the ecology and natural history of St Kilda* (eds D.N. Bullock & D. Taylor), pp. 26-28. University of Durham (unpubl. expedition report), Durham.

Wooller, R.D., Bradley, J.S., & Croxall, J.P. (1992) Long-term population studies of seabirds. *TREE*, **7**, 111-114.

Chapter 4

Sex specific foraging behaviour in a monomorphic seabird

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Sex specific foraging behaviour in a monomorphic seabird

Abstract

Sexual differences in the foraging behaviour of parents have been observed in a number of sexually size dimorphic birds, particularly seabirds, and the usual inference has been that these sex-specific differences are mediated primarily by differences in body size. To test this explanation, a comparison was made between the foraging behaviour of parents in a monomorphic seabird species, the northern gannet *Morus bassanus*. Using specially designed instruments and radio telemetry it was found that individuals of both sexes were consistent in the directions and durations of their foraging trips. However female gannets were not only more selective than males in the areas where they foraged, but they also made longer, deeper dives and spent more time on the sea surface than males. As the sexes are morphologically similar in this species, then these differences are unlikely to have been mediated by body size. These results highlight the need to investigate sexual differences in the foraging behaviour of seabirds and other species more closely, in order to test alternative theories that do not rely on differences in body size.

Introduction

In many animal species, care by both parents is required for successful rearing of offspring (Lack 1968; Clutton-Brock 1991). In these situations a common question is whether or not there are differences between parents in their foraging behaviour. This question is particularly relevant among birds, where biparental monogamy occurs in over 90% of species (Lack 1968).

Previous research that has compared the foraging behaviour of the sexes during the breeding season has concentrated almost exclusively on sexually size dimorphic species, including species of passerine (e.g., Morse 1968; Aho *et al.* 1997) and raptor (e.g., Newton 1979; Marquiss & Newton 1982). These studies have reported some sexual differences in foraging behaviour, particularly the microhabitats and locations in which the two sexes tend to forage. More recently, the development of small, lightweight activity recorders and satellite tags has enabled researchers to investigate sex-specific foraging behaviour in seabirds. These studies have similarly reported sexual differences in foraging location, but also the times of day that birds forage, and the depths to which they dive (Table 4.1). As the majority of these investigations were based on sexually size dimorphic species, it is perhaps understandable that authors have generally argued that differences in foraging behaviour might be mediated by size-based mechanisms, such as asymmetrical competition or differences in foraging efficiency (e.g., Weimerskirch *et al.* 1997; Gonzalez-Solis *et al.* 2000).

If size were important in mediating feeding activities, then one would not expect to see sexual differences in foraging behaviour within monomorphic species. Indeed even within a monomorphic seabird species that exhibited distinct parental roles, one might expect them to forage for food in a similar way. Yet somewhat surprisingly, potential sexual differences in the foraging behaviour of monomorphic seabirds at sea have only rarely been investigated (Table 4.1). While Gray & Hamer (2001) found that females of the sexually monomorphic Manx shearwater *Puffinus puffinus* fed their chick less frequently than males, their study was unable to obtain any direct information on foraging at sea. Similarly, common terns *Sterna hirundo* are monomorphic and exhibit distinct parental roles (Wiggins & Morris 1987), but to our knowledge no study has examined whether the two sexes actually forage for prey in different ways.

Here data are presented to compare the foraging behaviour of the two sexes in a species with no size dimorphism. In so doing, the hypothesis that even phenotypically similar sexes can exhibit differences in foraging behaviour has been tested, thereby exploring the need to look beyond body size as an explanation for differences in the foraging behaviour of male and female parents. The study species was the northern gannet, a sexually monomorphic species (mean culmen length (mm): male: 100.1 (*n*=66), female: 99.2 (*n*=66); mean tarsus length (mm): male: 58.8 (*n*=7), female: 58.1 (*n*=5), see Nelson 2002; standard errors not available), where both parents help to rear the chick. Gannets have an expensive mode of flight (Birt-Friesen *et al.* 1989) and they capture prey by plunge and pursuit diving (Garthe *et al.* 2000). During chick-rearing parents generally alternate foraging trips with periods at the nest with the chick, such that when one parent arrives following a foraging trip and feeds the chick, its partner leaves almost immediately (Nelson 2002; this study). The foraging behaviours of males and females were investigated by simultaneously using a) radio transmitters that provided foraging trip durations and departure directions, which are a good indicator of bearings to foraging locations (Hamer *et al.* 2000; Hamer *et al.* 2001), and b) activity loggers that enabled the four main activities during chick rearing (flying, diving, sitting on the sea surface, attending the chick at the colony) to be investigated and also recorded dive depth.

Table 4.1: Studies that have investigated sexual differences in the foraging behaviour of seabird species at sea. Significant sex difference in foraging location (L), dive depth (D), time of day foraging (T); no sex difference in foraging location (No L).

Species	Size dimorphism	Behaviour	Study
Wandering albatross	male > female	L	Weimerskirch & Jouventin 1987
South Georgian shag	male > female	D	Croxall *et al.* 1991
European shag	male > female	No L	Wanless et al. 1991
South Georgian shag	male > female	D	Kato *et al.* 1992
Wandering albatross	male > female	L	Prince *et al.* 1992
Wandering albatross	male > female	L	Salamolard & Weimerskirch 1993
Wandering albatross	male > female	L	Weimerskirch *et al.* 1993
South Georgian shag	male > female	T	Wanless *et al.* 1995
Southern Buller's albatross	male > female	L	Sagar & Weimerskirch 1996
Japanese cormorant	male > female	D	Watanuki *et al.* 1996
Japanese cormorant	male > female	D	Kato *et al.* 1999
Subantarctic cormorant	male > female	D	Kato *et al.* 1999
Thick-billed murres	male = female	T+D	Woo *et al.* 1999
Northern giant petrel	male > female	L	Gonzalez-Solis *et al.* 2000
King cormorant	male > female	T+D	Kato *et al.* 2000
Grey-headed mollymawk	male > female	L	Nel *et al.* 2000
Southern Buller's albatross	male > female	L	Stahl & Sager 2000a
Southern Buller's albatross	male > female	L	Stahl & Sager 2000b
Antarctic shag	male > female	D	Casaux *et al.* 2001
Shy Albatross	male > female	No L	Hedd *et al.* 2001
Macaroni penguin	male > female	L	Barlow & Croxall 2002

Methods

The study was carried out between 19 June and 19 August 2001 at the Bass Rock. During the study, sunrise and sunset occurred at approximately 02:30 h and 21:30 h GMT respectively, and the hours of darkness were between 22:00 hand 02:00 h GMT.

Radio-transmitters

Twenty-eight adults (from 14 pairs) with 2-3 week old chicks were caught at the nest. A VHF radio transmitter (Biotrack Ltd) weighing 20g (< 1% of adult mass) was attached to each bird with self-amalgamating tape and cable-ties, and a blood sample was taken for sexing (see Chapter 2). To minimise drag during flight and prevent tags being displaced during plunge-diving, tags were attached to the underside of the four central tail feathers, close to the base of the tail with the aerial pointing upwards through the feathers. Attachment of tags and collection of blood samples took approximately 10 minutes and after release every bird returned to the nest almost immediately (usually within five minutes).

Birds were radio-tracked from a mainland station (ca. 1.5 km south of the Bass Rock) during four tracking sessions. Each session ran continuously from dawn to dusk for several days (gannets are not active during hours of darkness, (see Garthe *et al.* 2000; Hamer *et al.* 2000), throughout a period of 8 weeks (total tracking period 40.5 days). The age of chicks during the study period ranged between 3 and 11 weeks. The receiving system consisted of two parallel eight-element Yagi aerials joined by a 2m crosspiece, attached to a vertical 5m mast, which allowed the aerials to rotate freely through 360°. The aerials were connected to an ATS R4000 scanning receiver, operating in the 173 MHz band. The different frequencies of the tagged birds were checked every 15 minutes. Visual checks indicated that with this sampling interval there was no possibility of arrivals or departures being missed.

As a tagged bird approached the colony the signal strength gradually increased until it became very loud and erratic. Observations at the colony indicated that this erratic signal corresponded to the bird circling the Bass Rock prior to landing;

behaviour that typically lasted just a few minutes. Arrival time to the nest site was recorded as the moment the signal decreased in strength and became steady. Departure time of an attendant bird was when the signal suddenly became very loud and erratic, before fading as the bird flew out of range. Trip duration was calculated from the time that an individual departed the colony, to when it returned. In the same way, attendance duration was calculated from the arrival time at the colony until the departure time from the colony. The foraging trip departure direction was also obtained by recording the final bearing of departing birds, at the point of signal disappearance. This occurred on average between 15 and 30 minutes after departure from the colony, while the departure bearings ranged from 0° (N) to 130° (SE).

At the end of the study the birds were recaptured and the tags were removed. Previous work at the Bass Rock and Great Saltee using satellite telemetry has shown that departure direction, coupled with trip duration, provide a good indicator of the foraging locations of gannets because they have a linear outward flight to their foraging grounds, and because trip duration and maximum range are highly correlated (Hamer *et al.* 2000; Hamer *et al.* 2001).

Activity Loggers

Thirty different adults with chicks (age range 2-6 weeks) were caught from the same area of the colony and each was equipped with an activity logger using the same handling, attaching and sexing techniques as for birds with radio transmitters. These instruments were modified versions of the loggers designed at the Istituto di Elaborazione dell'Informazione (Dall'Antonia *et al.* 1993; Benvenuti *et al.* 1998; Benvenuti *et al.* 2001). Two types of loggers were used: type-1 was equipped with a depth meter (operative range 0-70 m, resolution 0.3 m), and a flight sensor (a small modified microphone). The time between successive recordings was set at 4 sec for the depth meter and 8 sec for the flight sensor, which allowed continuous recording for about 3.8 days. In type-2 activity loggers the depth meter was replaced with two short electric wires emerging from the housing. The water switch was activated if the wires were submerged in the sea. The time between successive recordings was set at 4 sec for the water switch and 6 sec for the flight sensor, which allowed continuous recording for about 3.5 days. Type 1 and 2 loggers weighed 28g and 19g respectively.

Each logger was deployed for 2-4 days on each bird, in order to record at least one foraging trip (mean trip duration at Bass Rock is ca. 24 hours, (Hamer *et al.* 2000; Lewis *et al.* 2001; see Chapter 3). After this time the bird was recaptured and the device removed. Recorded data were downloaded from the loggers to a portable computer and analysed using specially designed software* (A. Ribolini unpubl.). Of the 29 retrieved loggers, data were successfully downloaded in 20 cases (Type 1 logger: 9 males (of which 1 failed to give depth data) and 6 females; Type 2 logger: 4 males and 1 female). For type 1 loggers, four activities could be distinguished clearly from the distinct signals that the sensors produced: 1) nest attendance: weak, variable signal from flight sensor; 2) flight: strong, noisy signal from flight sensor; 3) sitting on sea surface: moderate signal from the flight sensor; 4) diving: strong, noisy signal from flight sensor and activation of the depth sensor (see Figures 4.1 and 4.2). Dives of less than 1 m were not taken into account because such shallow dives often occur during bathing or other movements not related to feeding. Furthermore, the sampling interval (4 s) may have prevented us from recording some of the 1-2 m dives. Garthe *et al.* (2000) provides further details of the methodology and accuracy of these instruments for northern gannets. For type 2 loggers, nest attendance and flight were distinguished in the same way as with type 1 loggers. Resting on the sea surface was characterised by a moderate signal from the flight sensor and activation of the water switch, and diving by a strong, noisy signal from the flight sensor and activation of the water switch. Unlike with the type 1 logger, when dive duration could be recorded accurately, the distinction between resting on the sea and diving recorded by type 2 loggers was not always clear-cut, and therefore not used for dive data. However, results from the type 1 loggers showed that diving only represented ca. 0.2% of total time for both males and females, so when comparing the time allocation to the different activities of male and female gannets, we combined time spent on the sea with time spent diving, enabling us to use the data from both types of loggers. Therefore the results on time allocation compare the three main activity types: nest attendance, flight and sitting on the sea.

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* Preliminary logger analyses performed by S. Benvenuti.

Statistical analysis

The bearings of foraging trips (treated as a linear variable because bearings were between 0 and 130 degrees), trip duration and dive depths were compared between males and females by fitting linear mixed models using residual maximum likelihood analyses (REML, type III: Patterson & Thompson 1971). The number of dives per trip and per hour between males and females were also compared by fitting a generalized linear mixed model (GLMM, type III) with a Poisson error distribution and logarithmic link function (Schall 1991). GLMMs are generalised linear models with additional random effects to enable the analysis of stratified data with more than one error term. In both GLMMs and REMLs, sex was included as a fixed factor, with bird identity as a random factor, to avoid problems of pseudo-replication. For bearings of foraging trips, the final best fitting model was also fitted without bird identity as a random factor in order to compare the deviance values between models, using the χ^2 distribution. This allowed the significance of individual variation in bearings from one bird to another to be assessed. There was a highly significant positive correlation between dive depth and dive duration (Spearman correlation: $r = 0.95$, $n = 720$, $p < 0.001$) so only dive depth was compared statistically between sexes. Previous studies have found evidence of diel patterns in dive depths of seabirds (Wilson *et al.* 1993; Wanless *et al.* 1999; Benvenuti *et al.* 2001; Dall'Antonia *et al.* 2001). To test for this effect in northern gannets, time of day (split into four six hour periods: 01:00-06:59, 07:00-12:59, 13:00-18:59, 19:00-00:59 h, GMT) was included as a fixed factor in the analysis of dive depth. The interaction between sex and time of day was also included in this analysis. In both the GLMM and REML analyses, the significance of terms were assessed by the Wald statistic at the final iteration of the algorithm, for each term when fitted last in the model with percentiles of chi-squared or F distributions (Elston *et al.* 2001). Non-significant terms were dropped sequentially from the model in reverse order of significance, commencing with the highest order interaction term, until the most parsimonious model was obtained. If an interaction term was significant, all lower order interaction terms and fixed effects were retained. Means ± 1SE are given (unless otherwise indicated), where means per individual are used.

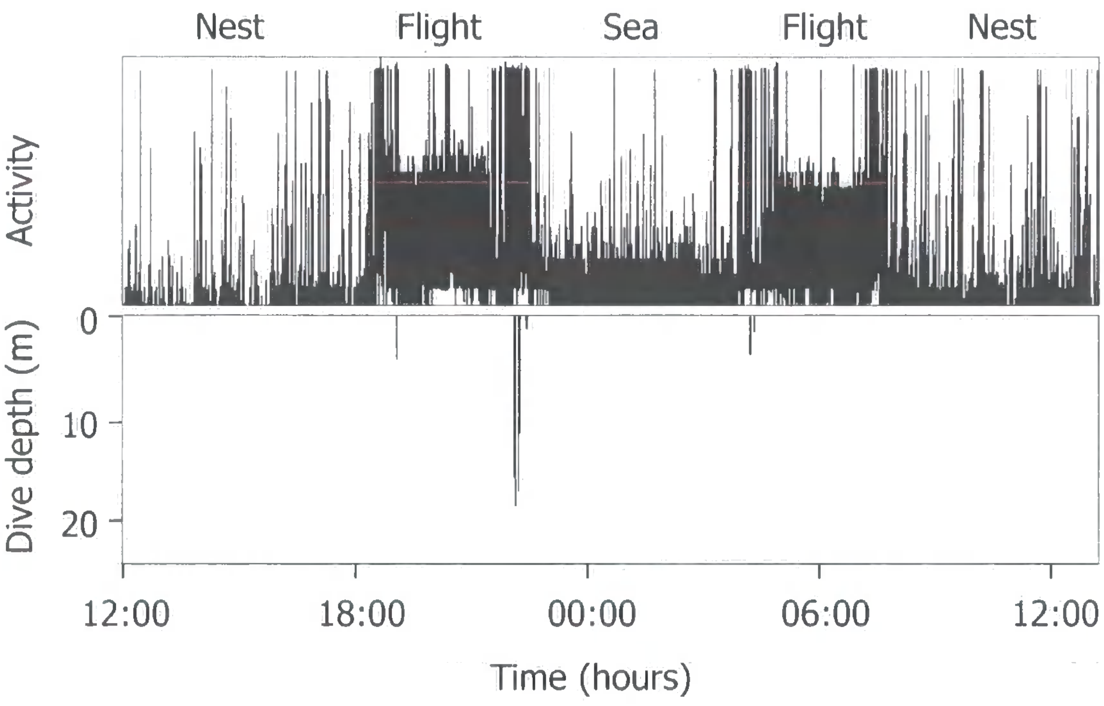

Figure 4.1: Data recorded from a flight activity logger/motion sensor (top) and depth meter (bottom) attached to a chick rearing northern gannet on the Bass Rock in 2001. The trace illustrates 24 hours of nest and foraging activity taken from a female gannet. The different activities were separated using specially designed software which could easily distinguish between the lower levels of activity associated to being on the nest and the higher levels when on the sea. The depth meter and salt switch also provided clarification. Furthermore nest checks were always compatible with interpretation of the activity data.

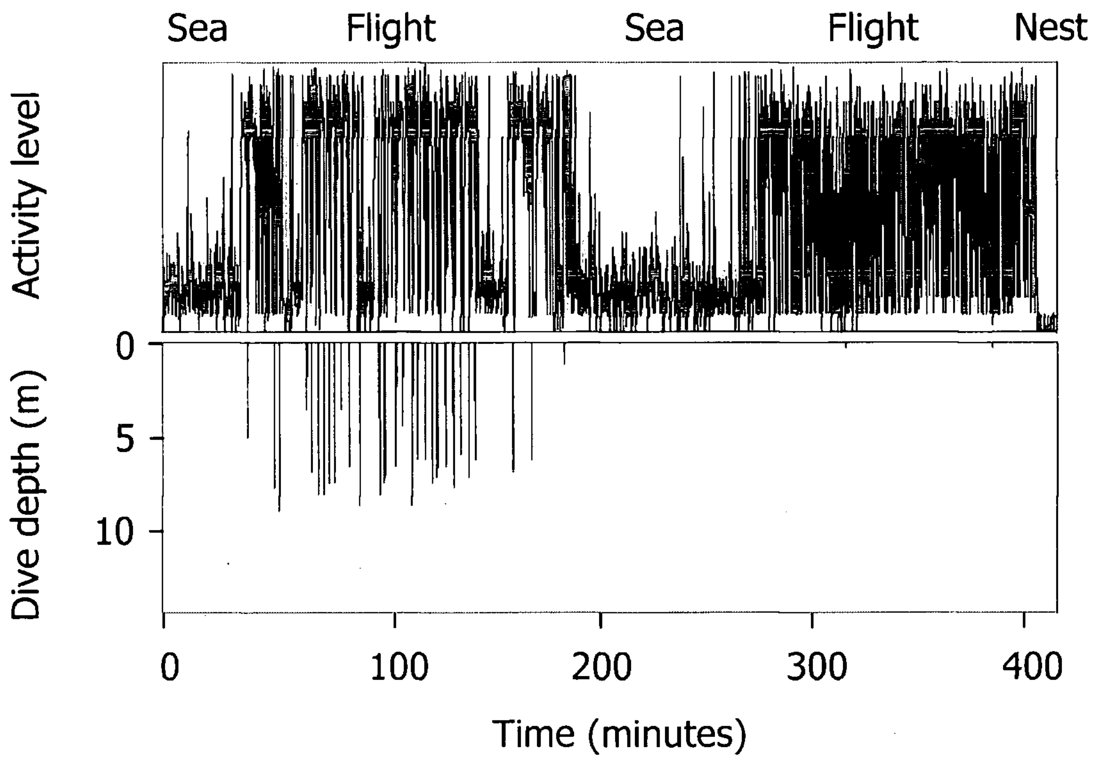

Figure 4.2: Data recorded from a flight activity logger/motion sensor (top) and depth meter (bottom) attached to a chick rearing northern gannet on the Bass Rock in 2001. The trace is a sample taken during a foraging trip and lasts for 412 minutes. The top section shows a series of foraging flights, during which the bird dived several times to a maximum depth of 10m. Between the two flights, the bird sat on the sea surface. The second flight includes two shallow dives ending with the bird back at the nest site.

Results

Directions of foraging trips

A total of 293 departure directions were recorded from 14 males and 14 females. The final flight directions that birds took when departing the colony differed significantly between sexes (REML: Wald statistic $\chi^2 = 5.83$, d.f. = 1, $p = 0.02$, $n = 293$). Females flew mainly at departure bearings greater than 65°, whereas males showed no directional preference (Figure 4.3). Comparison of the deviances between models with and without bird identity as a random factor showed that individual effects were highly significant, indicating that individual birds were consistent in departure bearings among trips ($\chi^2 = 62.93$, d.f. = 1, $p < 0.001$, $n = 293$).

Duration of foraging trips

A total of 348 foraging trip durations were recorded from 14 males and 14 females. There was no significant difference in the mean trip duration between the sexes, where means per bird were used (Table 4.2; REML, sqrt transformed data: Wald statistic $\chi^2 = 1.02$, d.f. = 1, $p = 0.32$, $n = 348$). Comparison of the deviances between models with and without bird identity as a random factor showed that individual effects were significant, indicating that individual birds tended to make foraging trips of similar durations ($\chi^2 = 4.09$, d.f. = 1, $p = 0.04$, $n = 348$).

Activity and time allocation

During a total of 1,429 hrs of recording, we obtained data on the time allocation of 13 males and 7 females over 29 complete foraging trips. Figure 4.4 illustrates the diurnal time allocation of the different activities of these birds. There was no difference in the mean time spent flying per trip for males and females, where means per individual were used when more than one trip was recorded (Figure 4.5; male: 10.9 h, $n = 13$, s.d. ± 4.7, female: 13.2 h, $n = 7$, s.d. ± 4.8; $t_{18} = 1.034$, $p = 0.32$). However, females spent significantly longer than males on the sea surface (Figure 4.5; male: 10.8 h, $n = 13$, s.d. ± 3.2, female 17.6 h, $n = 7$, s.d. ± 7.3; $t_{18} = 2.891$, $p = 0.01$). Birds did not fly at night (see Figure 4.4; see also Garthe *et al.* 1999; Garthe *et al.* 2000; Hamer *et al.* 2000; Hamer *et al.* 2001) and after removing hours of darkness from the data, females still spent a greater proportion of daylight hours than males on the sea surface (male: 0.18, female: 0.28; t-test with arcsine-transformed data; $t_{18} = 2.562, p = 0.02$).

Diving behaviour

A total of 720 dives was recorded from 14 birds (8 males and 6 females; one depth meter failed). Figure 4.6 illustrates the diurnal distribution of dives by both males and females. There were no significant differences between males and females in the mean number of dives made per trip or per hour on a trip (Table 4.2; GLMM, dives per trip: Wald statistic $\chi^2 = 2.68$, d.f. = 1, $p = 0.12$, $n = 22$ trips; dives per hour: Wald statistic $\chi^2 = 0.08$, d.f. = 1, $p = 0.78$, $n = 22$). However females consistently made deeper and thus longer dives than males (Table 4.2; REML (log transformed depth data): Wald statistic $F_{1,12} = 7.19$, $p < 0.03$, $n = 720$). The deepest and longest dives recorded were 11 m and 28 sec for males, compared with 18 m and 37 sec for females. From the same test, there was also a significant effect of time of day on dive depth (Figure 4.7; Wald statistic $F_{3,10} = 21.21$, $p < 0.001$, $n = 720$) and a significant interaction between sex and time of day (Wald statistic $F_{3,10} = 19.57$, $p < 0.001$, $n = 720$), indicating no difference between sexes in dive depth during the first and last periods of the day (Figure 4.7). Finally, there was a significant positive correlation between dive depth and the subsequent inter-dive duration (time spent between successive dives) in females, but not in males (Spearman correlation: females: $r = 0.197, p < 0.001, n = 374$; males: $r = 0.028, p = 0.62, n = 323$).

Table 4.2: Mean (± 1SE) trip duration, number of dives per trip and per hour, dive depth (m) and dive duration (sec) for male and female northern gannets during early chick rearing, on the Bass Rock in 2001.

	Males	Females
Trip duration (h)	22.64 (± 5.50)	23.79 (± 4.82)
Dives per trip	25.92 (± 6.06)	47.75 (± 13.45)
Dives per hours	1.35 (± 0.30)	1.50 (± 0.42)
Dive depth (m)	3.24 (± 0.11)	4.71 (± 0.16)
Dive duration (sec)	7.36 (± 0.28)	10.01 (± 0.35)

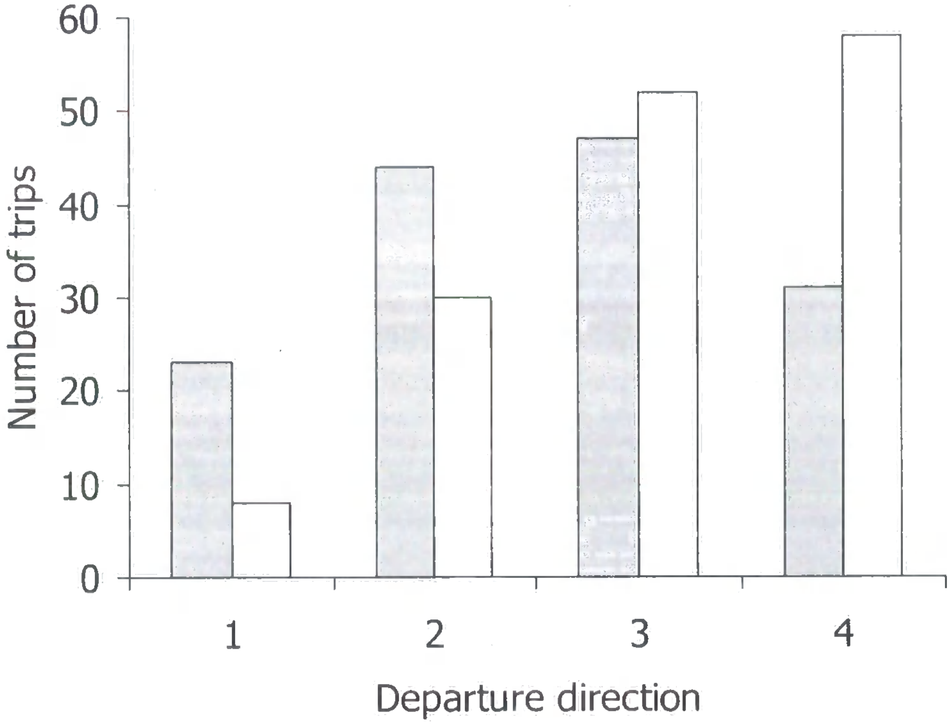

Figure 4.3: Frequency distribution of foraging trip departure directions (*n*=293) of 14 pairs of northern gannets during chick rearing on the Bass Rock in 2001 (Departure direction 1: 0-32 degrees, 2: 33-65 degrees, 3: 66-98 degrees, 4: 99-131 degrees; shaded bars are males; unshaded bars are females).

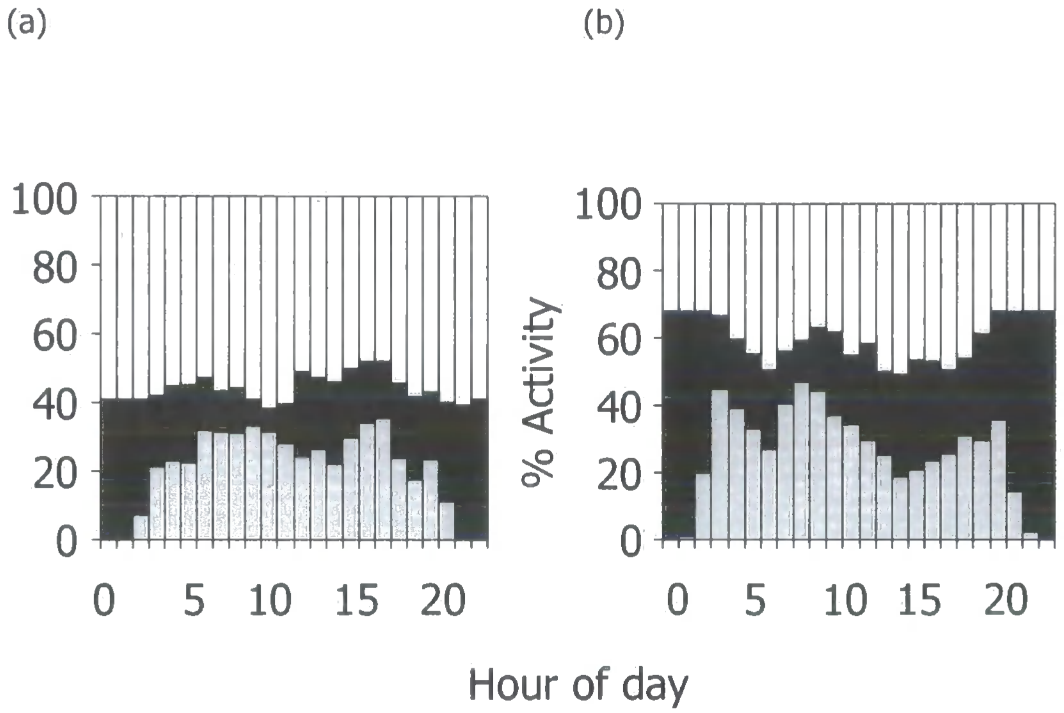

Figure 4.4: Diurnal time allocation of the different activities by a) male (*n*=13) and b) female (*n*=7) northern gannets during chick rearing on the Bass Rock in 2001; white bars represent time spent at the nest; black bars resting on the sea surface; grey bars time spent flying. Times are given as % proportion of total time. Hours of darkness were 22:00-02:00 h GMT.

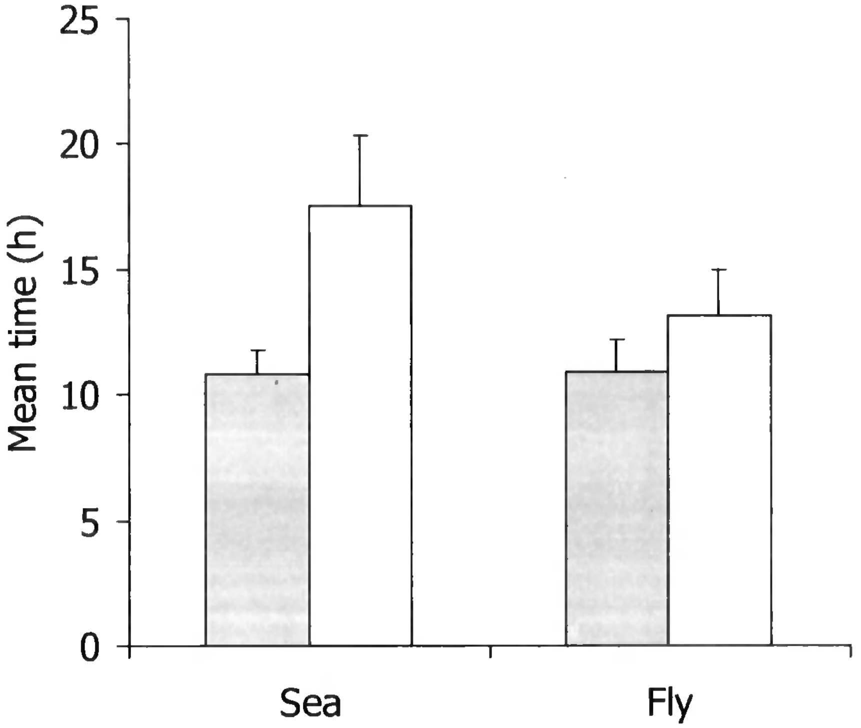

Figure 4.5: Mean (+1SE) time (h) spent on the sea and flying by male (shaded bars; *n*=13) and female (unshaded bars; *n*=7) northern gannets, during chick rearing on the Bass Rock in 2001.

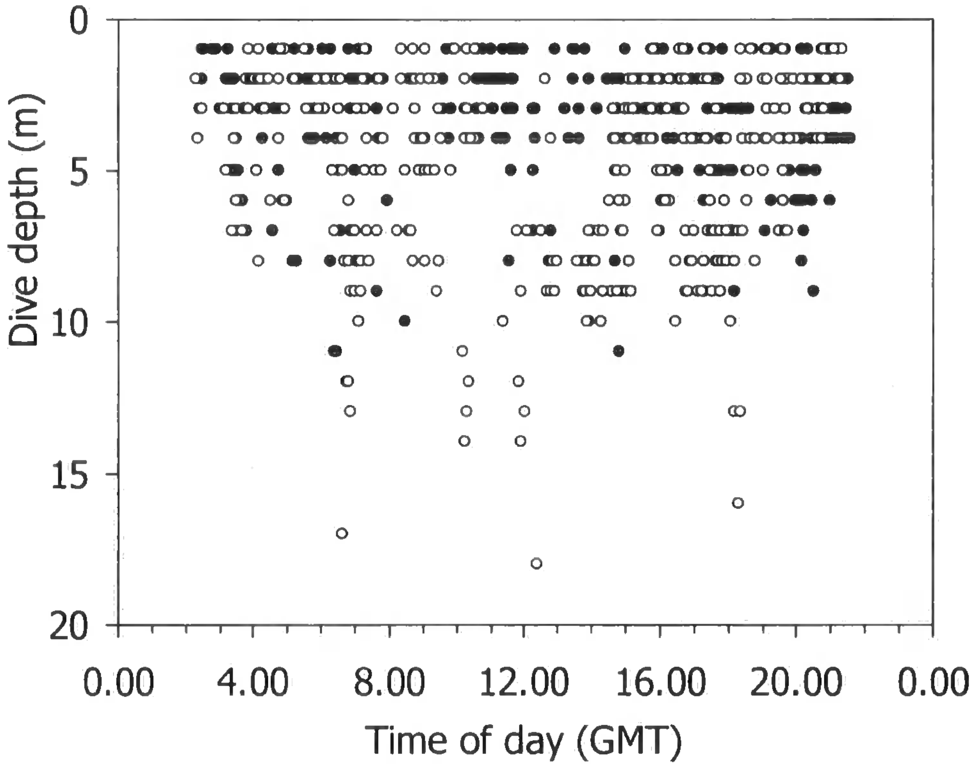

Figure 4.6: Diurnal distribution of dive depth by male (shaded circles; *n*=8) and female (white circles; *n*=6) northern gannets, during chick rearing on the Bass Rock in 2001.

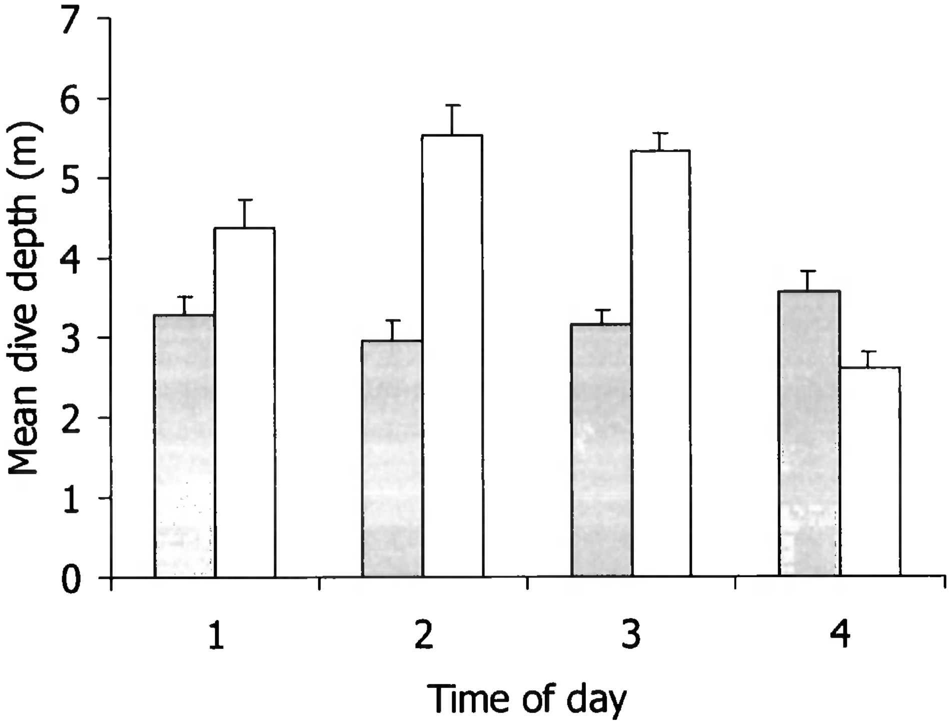

Figure 4.7: Mean (+1SE) dive depths (m) of male (shaded bars; *n*=8) and female (unshaded bars; *n*=6) northern gannets at different periods of the day (period 1: 01:00-06:59 h GMT; 2: 07:00-12:59 h GMT; 3: 13:00-18:59 h GMT; 4: 19:00-00:59 h GMT), during chick rearing on the Bass Rock in 2001.

Discussion

All study nests contained a chick at the end of the study period. It was not possible to compare trip durations of tagged birds with a control group of birds in this study because access to the island was limited to a few hours a day. However, the mean trip durations from radio tags and loggers (tags: 23 h ± 5.13 s.d.; loggers: 25 h ± 9.5 s.d.) were consistent with two recent studies that recorded trip durations at the Bass Rock from direct observations at the nest (27 h in 1998, Hamer *et al.* 2000; 19 h in 2000, Lewis *et al.* 2001).

Satellite telemetry of northern gannets at the Bass Rock in 1998 (Hamer *et al.* 2000) showed that 71% of birds foraged south east of the colony, although these authors did not consider sex in their analyses. The present study found that the majority of birds (64%) departed from the colony at bearings of greater than 65 degrees, but also showed that it was females that were largely responsible for this bias in directions of trips (Figure 4.3). Individuals tended to be consistent in their departure directions, as also found from satellite telemetry of northern gannets (Hamer *et al.* 2001) and radio tracking of black-legged kittiwakes *Rissa tridactyla* (Irons 1998), suggesting that bearings of foraging trips may have been influenced by birds' prior experience. Individuals were also consistent in the duration of their trips (and thus foraging range, see Hamer *et al.* 2000), providing further evidence that individual birds tended to return to familiar foraging locations. Although there were no significant differences between the sexes in trip duration, or the time spent flying on a trip, females spent more time on average on the sea surface in between foraging bouts, and this result is not explained by a difference in the number of dives made between the sexes. That females are not correspondingly spending less time flying per trip than males given the fact that there was no statistical difference in the trip duration of males and females is explained by the fact that the trip duration result comes from a much larger sample of birds than the time-activity data. Overall, these results highlight the issues associated with using different samples for related relationships. However, it was considered more appropriate to use the largest sample size available.

Females also dived significantly deeper than males during the middle of the day, but at dawn and dusk they dived at the same shallower depths as males. These temporal patterns in dive depth may be related to changes in light penetration into the water column through the diel cycle, influencing where birds can forage and/or the vertical migration of their prey (Wilson *et al.* 1993; Wanless *et al.* 1999). In particular, low light penetration during dawn and dusk may have forced females to forage at the same shallow depths as males did during these periods. Woo *et al.* (1999) similarly reported a difference in dive depths between male and female thick-billed murres *Uria lomvia*, also a monomorphic species. Females made deeper dives than males, yet in this species females are diurnal foragers whereas males are nocturnal. In our study, we found differences in dive depth between the sexes operating under the same light conditions, in the middle of the day.

The fact that sexual differences in the foraging behaviour of a monomorphic seabird have been observed, raises the possibility that differences reported in sexually dimorphic species (Table 4.1) are not mediated exclusively by differences in body size. Sexual differences in foraging behaviour could have arisen for a number of other reasons, which are not necessarily independent. Moreover, different components of foraging behaviour may be related. For instance, sexual differences in foraging location may have an impact on dive depth, if prey associated with different foraging locations have different vertical distributions. Similarly in this study, females that dived deeper also had greater inter-dive periods (probably because diving is energetically and physiologically demanding (Schmid *et al.* 1995), and this may have accounted to some extent for the longer total time that females spent on the sea surface. In the following sections, several potential proximate explanations for the observed sex-specific foraging patterns are discussed.

One possible explanation for the difference in foraging behaviour of males and females is that regardless of them being the same size, males are more effective than females at exploiting fish close to the sea surface, for instance by out-competing females within the same feeding group. Such interference competition would force females to dive deeper or forage elsewhere. Despite behavioural differences between the sexes at the colony (Nelson 2002), there are no obvious morphological asymmetries that might give one sex a competitive advantage over the other while feeding at sea. Furthermore, our radio tracking data show that females do not forage exclusively in areas that are not used by males, which might be expected if competition were driving these differences. Another possibility is that the two sexes differ in their abilities to capture prey at particular depths. If females are better able to exploit deeper-swimming fish which are found in particular areas of sea, then not only would the sexes tend to show different diving behaviour, but they might also tend to feed in different areas. Clearly to test this idea, one would need to examine the diving abilities of the two sexes in more detail.

These results suggest that females are more restricted than males in the areas where they forage, and one possibility is that this is driven by sexual differences in energy or nutrient requirements. These differential requirements could arise, for instance, from differences between sexes in the timing or extent of feather moult (Hemborg *et al.* 1998; Hemborg 1999b, a). Moulting is an energetically expensive process (Hull *et al.* 2001) which begins at the onset of hatching in northern gannets, and continues until late autumn (Nelson 2002). It is not known whether there are sex-specific differences in moult in gannets, but such differences do occur in other seabirds (Weimerskirch 1991) and could potentially create temporary sex differences in dietary needs and/or foraging abilities. Alternatively, the need for nutrients related to reproduction has been shown to influence females' dietary requirements (Carey 1996). For example, calcium deficiency greatly limits eggshell quality and even reproductive success in great tits *Parus major* (Graveland & Drent 1997), and prior to egg laying both female common terns and magellanic penguins *Spheniscus magellanicus* ingested more mollusc shells than males (Nisbet 1997; Boersma & Stokes 1999), presumably from the area around their nests, to improve their calcium nutrition. If female gannets do not have access to such a food source at their colonies then, despite the fact that they lay only one small egg (Nelson 2002), females may still need to restore their calcium levels post-laying by some means e.g., by selecting prey species with high calcium content. Thus, if nutritionally important prey species were found at specific areas and/or depths, then selection for these species by one sex in particular, might lead to the observed sex differences in foraging behaviour. Unfortunately there are currently no data available on the diets of northern gannets that would allow us to compare intakes of key nutrients between the sexes.

By using specially designed instruments to monitor the foraging behaviour of northern gannets at sea, these data have shown that even monomorphic seabirds can exhibit significant sexual differences in their foraging characteristics. In particular, females tended to forage in a more restricted location than males, made deeper dives and spent longer resting on the sea surface. As this is one of the first studies to look at the foraging behaviour monomorphic seabirds, it is not known how general these results are. However, because significant sexual differences in foraging behaviour in the absence of sexual size dimorphism have been demonstrated, this in itself raises some important questions, which may have implications for our understanding of the foraging ecology of seabirds and other species.

References

Aho, T., Kuitunen, M., Suhonen, J., Hakkari, T., & Jantti, A. (1997) Effects of male removal on female foraging behaviour in the Eurasian treecreeper. *Behavioural Ecology and Sociobiology*, **41**, 49-53.

Barlow, K.E. & Croxall, J.P. (2002a) Provisioning behaviour of macaroni penguins *Eudyptes chrysolophus*. *Ibis*, **144**, 248-258.

Barlow, K.E. & Croxall, J.P. (2002b) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Marine Ecology Progress Series*, **232**, 291-304.

Benvenuti, S., Bonadonna, F., Dall'antonia, L., & Gudmundsson, G.A. (1998) Foraging flights of breeding thick-billed murres (*Uria lomvia*) as revealed by bird-borne recorders. *Auk*, **115**, 57-66.

Benvenuti, S., Dall'Antonia, L., & Lyngs, P. (2001) Foraging behaviour and time allocation of chick-rearing razorbills *Alca torda* at Græsholmen, central Baltic Sea. *Ibis*, **143**, 402-412.

Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K., & Macko, S.A. (1989) Activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology*, **70**, 357-367.

Boersma, P.D. & Stokes, D.L. (1999) Calcium in penguins eggs: does diet matter? *Pacific Seabirds*, **26**, 32.

Carey, C. (1996). Female reproductive energetics. In *Avian Energetics and Nutritional Ecology* (ed C. Carey), pp. 324-374. Chapman & Hall, NY.

Casaux, R., Favero, M., Silva, P., & Baroni, A. (2001) Sex differences in diving depths and diet of Antarctic shags at the South Shetland Islands. *Journal of Field Ornithology*, **72**, 22-29.

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

Croxall, J.P., Reid, K., & Prince, P.A. (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, **177**, 115-131.

Dall'Antonia, L., Gudmundsson, G.A., & Benvenuti, A. (2001) Time allocation and foraging pattern of chick rearing razorbills in northwest Iceland. *Condor*, **103**, 469-480.

Dall'Antonia, P., Dall'Antonia, L., & Ribolini, A. (1993). Flight path reconstruction of birds by a route recorder. In *Biotelemetry XII, Proceedings of the XII International Symposium on Biotelemetry* (eds P. Mancini, S. Fioretti, C. Cristalli & B. Bedini), pp. 544-549. Litografia Felici, Pisa, Italy.

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

Garthe, S., Benvenuti, S., & Montevecchi, W.A. (2000) Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 1717-1722.

Garthe, S., Gremillet, D., & Furness, R.W. (1999) At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: a case study in Shetland. *Marine Ecology Progress Series*, **185**, 93-99.

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

Graveland, J. & Drent, R.H. (1997) Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology*, **66**, 279-288.

Gray, C.M. & Hamer, K.C. (2001) Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus*. *Animal Behaviour*, **62**, 117-121.

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., & Wood, A.G. (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies. *Marine Ecology Progress Series*, **224**, 283-290.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Hedd, A., Gales, R., & Brothers, N. (2001) Diving behaviour of the shy albatross *Thalassarche cauta* at Albatross Island, Tasmania, Australia. *Marine Ecology Progress Series*, **224**, 267-282.

Hemborg, C. (1999a) Annual variation in the timing of breeding and moulting in male and female pied flycatchers *Ficedula hypoleuca*. *Ibis*, **141**, 226-232.

Hemborg, C. (1999b) Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. *Journal of Animal Ecology*, **68**, 429-436.

Hemborg, C., Lundberg, A., & Siikamaki, P. (1998) Trade-off between reproduction and moult - a comparison of three Fennoscandian pied flycatcher populations. *Oecologia*, **117**, 374-380.

Hull, C.L., Wilson, J., & le Mar, K. (2001) Moult in adult royal penguins, *Eudyptes schlegeli*. *Emu*, **101**, 173-176.

Irons, D.B. (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology*, **79**, 647-655.

Kato, A., Croxall, J.P., Watanuki, Y., & Naito, Y. (1992) Diving patterns and performance in male and female blue-eyed cormorants *Phalacrocorax atriceps* at South Georgia. *Marine Ornithology*, **19**, 117-129.

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

Kato, A., Watanuki, Y., Shaughnessy, P., Le Maho, Y., & Naito, Y. (1999) Intersexual differences in the diving behaviour of foraging subantarctic cormorant (*Phalacrocorax albiventer*) and Japanese cormorant (*P. filamentosus*). *Comptes rendus de l'academie des sciences serie III-sciences de la vie-life sciences*, **322**, 557-562.

Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, London.

Lewis, S., Sherratt, T.N., Hamer, K.C., & Wanless, S. (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, **412**, 816-819.

Marquiss, M. & Newton, I. (1982) Habitat preference in male and female sparrowhawks *Accipiter nisus*. *Ibis*, **124**, 324-328.

Morse, D.H. (1968) A quantitative study of foraging of male and female spruce-woods warblers. *Ecology*, **49**, 779-784.

Nel, D.C., Nel, J.L., Ryan, P.G., Klages, T.W., Wilson, R.P., & Robertson, G. (2000) Foraging ecology of grey-headed mollymawks at Marion Island, southern Indian Ocean, in relation to longline fishing activity. *Biological Conservation*, **96**, 219-231.

Nelson, J.B. (2002) *The Atlantic Gannet*. Fenix Books Ltd., Norfolk.

Newton, I. (1979) *Population Ecology of Raptors*. Poyser, Berkhamsted.

Nisbet, I.C.T. (1997) Female common terns *Sterna hirundo* eating mollusc shells: evidence for calcium deficits during egg laying. *Ibis*, **139**, 400-401.

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

Prince, P.A., Wood, A.G., Barton, T., & Croxall, J.P. (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*, **4**, 31-36.

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

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.

Schall, R. (1991) Estimation in generalised linear models with random effects. *Biometrika*, **78**, 719-727.

Schmid, D., Gremillet, D.J.M., & Culik, B.M. (1995) Energetics of underwater swimming in the great cormorant. *Marine Biology*, **123**, 875-881.

Stahl, J.C. & Sagar, P.M. (2000a) Foraging strategies and migration of southern Buller's albatrosses *Diomedea b. bulleri* breeding on the Solander Is, New Zealand. *Journal of the Royal Society of New Zealand*, **30**, 319-334.

Stahl, J.C. & Sagar, P.M. (2000b) Foraging strategies of southern Buller's albatrosses *Diomedea b. bulleri* breeding on the Snares, New Zealand. *Journal of the Royal Society of New Zealand*, **30**, 299-318.

Wanless, S., Finney, S.K., Harris, M.P., & McCafferty, D.J. (1999) Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag *Phalacrocorax atriceps* and the European shag *P. aristotelis*. *Marine Ecology Progress Series*, **188**, 219-224.

Wanless, S., Harris, M.P., & Morris, J.A. (1991) Foraging range and feeding locations of shags *Phalacrocorax aristotelis* during chick rearing. *Ibis*, **133**, 30-36.

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

Watanuki, Y., Kato, A., & Naito, Y. (1996) Diving performance of male and female Japanese cormorants. *Canadian Journal of Zoology*, **74**, 1098-1109.

Weimerskirch, H. (1991) Sex-specific differences in molt strategy in relation to breeding in the wandering albatross. *Condor*, **93**, 731-737.

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

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

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325-342.

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

Wilson, R.P., Puetz, K., Bost, C.A., Culik, B.M., Bannasch, R., Reins, T., & Adelung, D. (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series*, **94**, 101-104.

Woo, K., Kober, K., & Gaston, A.J. (1999) Difference in timing of incubation shifts between male and female thick-billed murres are associated with variation in maximum diving depth. *Pacific Seabirds*, **26**, 55.

Chapter 5

Brood neglect and contingent choice of foraging location by a pelagic seabird

Brood neglect and contingent choice in foraging location

Abstract

In many species, parents take alternating shifts guarding offspring. This is particularly the case in cliff-nesting seabirds, where it is often risky to leave chicks unattended. However, even in these species, parents occasionally leave their offspring alone at the nest. Using the northern gannet *Morus bassanus*, the prediction that the foraging behaviour of adults that leave their offspring alone at the nest (unattended trips) would be different to their behaviour when leaving offspring with their partner (attended trips) was tested. To elucidate the motivation behind leaving offspring unattended, the arrival and departure masses of foraging adults were measured, and the length of time the attending parent stayed with the chick before it departed was recorded. Both the mean durations and the mean directions of foraging trips of individual northern gannets differed significantly between attended and unattended trips. Unattended trips were not only shorter (and therefore closer to the colony), but tended to be in a particular direction. Chicks were fed after attended and unattended trips, and there were no sexual differences in the propensity to leave chicks unattended. The number and the duration of unattended trips increased as chicks got older, which is consistent with a reduction in chick vulnerability with increasing age. Attended trips showed no such increase in duration. Therefore, parents may be making a trade off between risk of attack and food intake rate. The mean nest attendance duration prior to unattended trips (hence trip duration of partner) was significantly longer than that observed in attended trips, while the mean arrival mass prior to an unattended trip was lower than prior to an attended trip. Thus, brood neglect appears to arise as a consequence of two sets of circumstances acting together or independently: an individual arriving at low mass, and/or a partner foraging at sea for extensive period of time. These results were interpreted in the context of a simple state-dependent model. If there are energy requirements that need to be satisfied quickly and leaving a chick unattended is risky, then it may be better for a deserting parent to forage in a close location rather than in a more distant location that would maximise a parent's longer term foraging gain.

Introduction

It is widely acknowledged that the foraging decisions of individuals may be influenced by their current state (McNamara & Houston 1996; Clark & Mangel 2000). For instance, individuals may decide to include relatively unprofitable prey items in their diet if they are hungry (Houston & McNamara 1985) or choose to forage in areas of high predation risk if their energy reserves are low (Milinski & Keller 1978; Houston *et al.* 1988; Lima & Dill 1990; Pettersson & Bronmark 1993).

When both parents systematically alternate their activities between foraging and attending offspring, the time taken for one parent to return from a foraging trip can have important consequences for the behaviour of the attending parent (see Szekely *et al.* 1996 for review). For instance, many pelagic seabird species will leave their offspring alone if their fasting period is prolonged due to the continued absence of their partner (Nelson 1969; Davis 1982; Davis & McCaffrey 1986; Davis 1988; Olsson 1997; Tveraa *et al.* 1997; Tveraa *et al.* 1998; Numata *et al.* 2000), a phenomenon typically associated with low mass of the attending partner (Chaurand & Weimerskirch 1994; Yorio & Boersma 1994; Gauthier-Clerc *et al.* 2001). Such behaviour can have dramatic consequences for the offspring particularly when eggs and/or chicks suffer high predation risk or thermal stress if left alone (Croxall & Ricketts 1983; Hunter 1984; Nelson 2002).

There is now increasing evidence that foraging decisions of seabirds, such as their trip duration, are dependent not only on their own body condition (Weimerskirch *et al.* 1997a; Weimerskirch *et al.* 1997b; Weimerskirch 1998), but also on that of their partners (Tveraa *et al.* 1997; Tveraa *et al.* 1998) and in some cases, their chicks (Weimerskirch *et al.* 2000). However the prediction that the foraging behaviour of adults when leaving their offspring alone is different in character to trips where the offspring is not left alone has never been tested.

The northern gannet is an ideal model species to examine state-dependent foraging strategies associated with leaving chicks unattended, because breeding partners systematically alternate periods of attending their single chick at the nest with foraging at sea, only rarely leaving their chick unattended throughout the 13 weeks of chick rearing (Nelson 2002). There are good reasons for believing that leaving offspring unattended may have serious consequences for the chick (and therefore the reproductive success of the parent): gannets nest at high densities and adults are highly aggressive to their neighbours, including their neighbours' chicks. Furthermore, prospecting birds often attempt to usurp nests without an adult present, and can cause serious injury to chicks (Nelson 2002).

Working at the Bass Rock in two consecutive years, the durations and directions of foraging trips of individual northern gannets in which the chick was left guarded by its partner (attended trip) were compared with trips in which individuals left their offspring alone (unattended trip). To elucidate the motivation to leave the chick alone, the times that individuals spent attending the chick, and the arriving and departing masses of adults, were also compared between attended and unattended trips. Finally, to explore our results in more detail and show that there are indeed circumstances in which the optimal choice of parental foraging location might be state-dependent, an extension of the parental allocation model proposed by Mangel & Clark (Mangel & Clark 1986, 1988) is presented, which incorporates more than one patch[*].

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[*] Modelling carried out by T. N. Sherratt.

Methods

Study site and main methods

The study was carried out during chick rearing, from 19 June to 19 August 2001 and between 20 June and 20 August 2002 at the Bass Rock, SE Scotland (56° 6'N, 2° 36'W; ca. 40,000 breeding pairs). During 2001 fieldwork involved radio tracking individuals to record foraging trip duration, nest attendance duration and foraging trip departure direction. In 2002, electronic weighing platforms were used to record the mass of adults arriving to the nest (arrival mass) and prior to leaving on a foraging trip (departure mass), as well as foraging trip duration and nest attendance duration.

Foraging behaviour and nest attendance (2001)

Details of handling birds, attaching radio transmitters and the radio tracking set up are given in Chapter 4 (section Radio-transmitters). Blood was taken for sexing as described in Chapter 2.

Trips were classified as either attended, i.e. a trip commencing after the return of the partner to the nest resulting in the chick being attended by the partner, or unattended, i.e. a trip commencing prior to the partner's return, resulting in the chick being left alone at the nest. In the same way attendance periods were classified as attended i.e., following a normal change-over at the nest and ending when it leaves after its partner has returned from its trip, or unattended, i.e., when the attending adult leaves before its partner returns from its trip, thus leaving the chick unattended at the nest (see schematic in Figure 5.1). Attendance periods following the arrival of an individual to an unattended nest are clearly different from attendance periods following a normal changeover (see Figure 5.1b and c), and therefore they have not been analysed here.

Adult body mass, trip duration and nest attendance (2002)

Detailed measurements of adult body mass were obtained using an automatic weighing system consisting of weighing platforms, data loggers and software (Francis Scientific Instruments, Cambridge, UK). The weighing platform consisted of a single cantilever beam load cell (30 kg capacity) connected to a signal conditioning amplifier. This unit was mounted on a heavy plastic base plate beneath a non-slip/textured plastic nest cup, large enough to enable both parents and the chick to be weighed during a changeover. The amplifier generated a signal proportional to the load on the balance, and was transmitted to a separate data logger situated approximately 5-10 m away from the balances, where it was stored as digital data. Each balance was calibrated with zero and a 5 kg weight prior to installation in the field and these specific calibration constants enabled the binary data to be converted into metric units (accuracy ± 0.01 kg). Observations from the Bass Rock in 2001 (from 114 changeovers) indicated that changeovers typically took 8 minutes (7.6 min (s.d. ± 11.9)). Therefore, to maximise the likelihood of recording a changeover on the platform whilst conserving battery power and memory, the sampling interval was set at one minute.

Five study nests were selected with young chicks (age range 1-3 weeks). The adult on duty was caught using an extendible roach pole (see Chapter 2), and a sample of blood (<0.1ml) was taken for sexing (see Chapter 2). These birds were colour marked with plumage dye to enable members of each pair to be distinguished. The chick was removed from the nest and held whilst the weighing platform was positioned at the nest site. The whole procedure lasted approximately 5-10 minutes, after which the chick was placed on the platform and the adult released. All adults returned to the nest site immediately and brooded their chick normally on the weighing platform.

Nests were observed regularly throughout the season during seven daytime visits to the island and seven overnight visits, for a total of 222 hours. The bird attending the chick was identified at each nest during visits. Due to the aggressive territorial behaviour of gannets at their nest sites, and the high nest density at the Bass Rock, on no occasion was an attending adult observed adjacent to, but not on, the weighing platform. In addition, 15 changeovers were observed when the arrival time of the incoming bird and the departure time of its partner were recorded. Subsequent inspection of the mass data from the balances indicated that in every case changeovers were correctly identified.

During a changeover event, the mass of the incoming bird and outgoing bird could be unambiguously calculated from the difference in mass recorded by the balance, before and after the changeover (Figure 5.2a; see also Gremillet *et al.* 1996). Foraging trip duration and attendance duration could also be calculated from the times these mass changes were recorded. Unattended trips were also clearly recorded (Figure 5.2b), but concurrent observations were required to determine the identity of the returning bird, since the sexes were not readily distinguished by mass. As a result, we were not able to record the duration of some unattended trips because it was not always possible to observe which bird returned to the balance first, following a period of non-attendance.

Since the nest balance system recorded the mass of the adult and chick together, it was not possible to calculate the actual amount of food fed to the chick, or determine the rate of mass loss (due to digestion) of the adult and/or the chick on the nest with this balance system. Any effort to reduce this constraint would have led to excessive disturbance, and any modelling would have been too ambiguous.

Statistical procedures

The distribution of the two trip types, were compared between the sexes of the parents and among chick ages by fitting a generalized linear mixed model (GLMM, type III; see Chapter 4). The GLMM fitted a probability curve through the binomially distributed data on trip type (0 = unattended trip, 1 = attended trip) using logit link function, dispersion set at 1 and a binomial total of 1. Year and sex were fixed factors and chick age was a covariate, while bird identity was included as a random factor, to control for pseudo-replication.

Trip duration, attendance duration, departure bearings of foraging trips (treated as a linear variable because bearings were all between 0 and 130 degrees), arrival mass, departure mass, rate of mass loss and mass change after a foraging trip were compared between attended and unattended trips, by fitting linear mixed models using residual maximum likelihood analyses (REML, type III: Patterson & Thompson 1971). For analyses on trip duration and attendance duration the models included year, sex and trip type (or attendance type) as fixed factors, chick age as a covariate, and bird identity as a random factor, but attendance duration was also included as a covariate in the analysis of trip duration. Separate REML models were performed on trip duration and attendance duration using covariates that were only collected in 2002 (e.g., arrival mass and departure mass), to examine state dependent foraging decisions, but this time without year as a fixed factor. The departure bearings of foraging trips, and mass variables were compared between attended and unattended trips in the same way but again without year included as a fixed factor.

To increase the robustness of the GLMM and REML statistical models, chick age was grouped into three successive four-week age-classes (1 = 1-4 weeks old; 2 = 5-8 weeks and 3 = 9-12 weeks old respectively). In both the GLMM and REML analyses, the significance of terms were assessed by comparing Wald statistics with percentiles of chi-squared or *F* distribution (Elston *et al.* 2001). Non-significant terms were dropped from the model, but if an interaction term was significant, all lower order interaction terms and fixed effects remained in the model (see Chapter 4 for a more detailed explanation). Means ± 1SE are given (unless otherwise indicated), where means per individual are used.

Modelling procedures

A simple but instructive state-dependent model of parental allocation, based on the numerical optimisation technique of stochastic dynamic programming, has already been described in detail elsewhere (Mangel & Clark 1986, 1988). In Mangel & Clark's model (Mangel & Clark 1986, 1988) a single parent attempts to rear its chick(s) for a period of T time units, at which time it/they become independent. The parent and chicks have energy capacities of C_p and $C_n(t)$ respectively at any time t, while their metabolic costs per unit time at the nest are α_p and $\alpha_n(t)$ respectively. If the current energy reserves of the offspring or adult fall below 0 then the individual starves. Foraging trips by the parent incur a metabolic cost of α_f, and when the parent is away from the nest, the parent and offspring have probabilities β_p and β_n

respectively of being killed. In Mangel & Clark's model only one foraging patch was considered which gave a foraging reward of Y_1 with probability λ_1 and 0 with probability $(1-\lambda_1)$. In this model[†] however, parents have a choice of foraging patches, by assuming that there is an additional foraging location that gives a foraging return of Y_2 with probability λ_2 and 0 with probability $(1-\lambda_2)$. Like Mangel & Clark, the optimal foraging decisions were identified at any given time t for any given energy reserves of the parent and offspring that would maximise the probability of the offspring surviving to independence. Whereas Mangel & Clark only considered the decisions of whether or not to forage and what proportion of the foraging return should be allocated to the chick, this simple extension also allowed us to investigate the circumstances under which the choice of foraging location itself is likely to be state-dependent.

[†] *Modelling carried by T. N. Sherratt.*

a) typical systematic alternation of roles

b) neglect and return of partner 1 before return of partner 2

c) neglect by partner 2 but partner 1 returns before partner 2

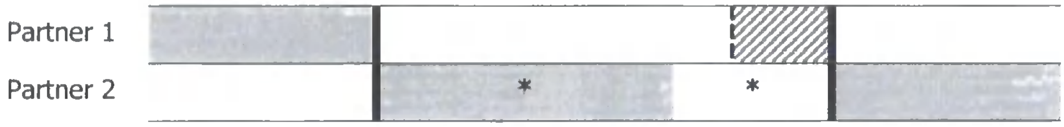

Figure 5.1: Schematic representation of attendance patterns in northern gannets during chick rearing. Shaded areas show periods of attendance. Time together at the nest by both parents is given as a solid heavy black vertical line, and arrival to an unguarded nest by a dashed black vertical line. Foraging trips where the chick is left alone and attendance periods prior to neglecting the chick are indicated by *. The diagonal shading depicts attendance periods not included in the data set (see methods).

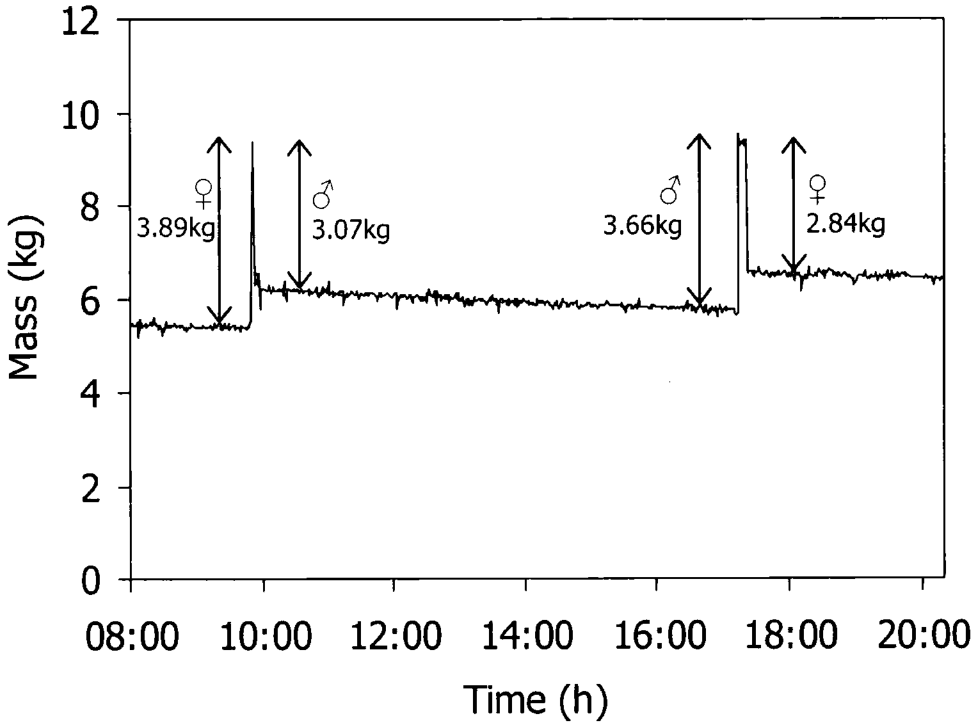

Figure 5.2a: Example of mass data changes during two changeovers at a gannet nest. In the first changeover, the female landed on the nest (arrival mass: 3.89 kg) and the male left to forage 2 minutes later (departure mass: 3.07 kg). The male returned 7.35 hours later 590 g heavier and the two remained at the nest for 9 minutes after which time the female departed on a foraging trip (departure mass: 2.84 kg) having attended the chick for 7.53 hours.

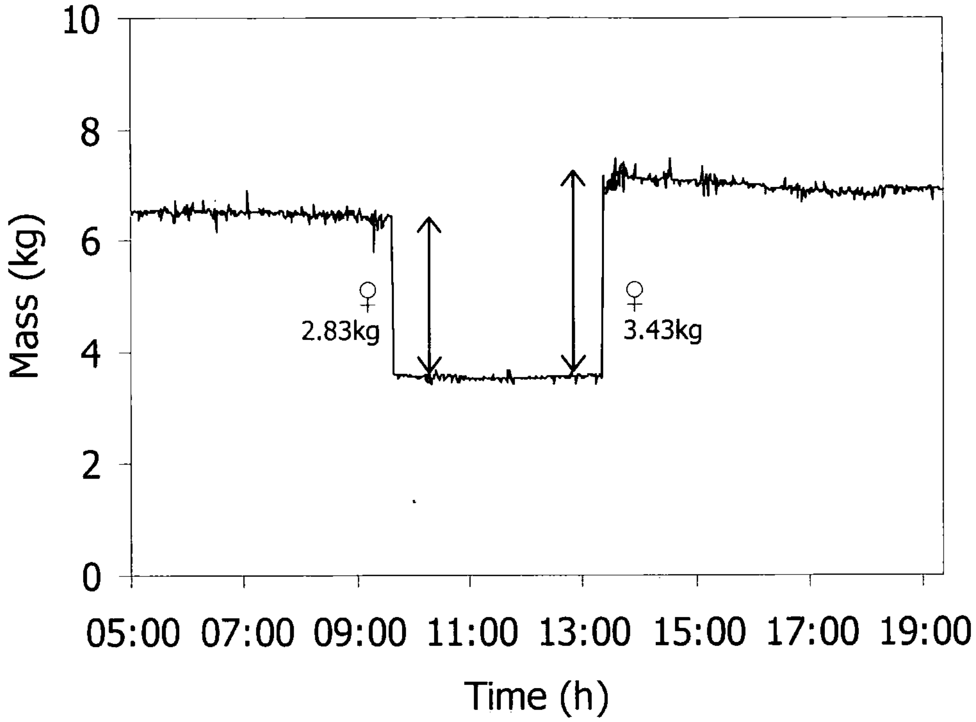

Figure 5.2b: Example of mass data changes when a female leaves the chick alone at the nest and goes on a foraging trip for 5 hours, returning 0.60 kg heavier.

Results

Trip type

A total of 348 trips was recorded from 28 birds (14 males and 14 females) in 2001 and 177 trips from 10 birds (5 males and 5 females) in 2002. The age at which a chick was first recorded being left alone was 4 weeks in 2001 and 6 weeks in 2002. In 2001, the overall proportion of trips where the chick was left alone was 0.22 (n = 175) and 0.17 (n = 173) for males and females respectively; in 2002 this value could not be recorded because of under-recording of unattended trips (see Methods). Using data from 2001 only, there was no significant difference in the number of unattended trips between the sexes (GLMM: Wald statistic $\chi^2 = 1.40$, d.f. = 1, $p = 0.24$), but there was a highly significant increase in the number of unattended trips with increasing chick age (Wald statistic $\chi^2 = 35.18$, d.f. = 1, $p < 0.001$). Although in most cases it was not possible to know if the chick was fed after a parent's return, opportunistic observations during colony visits confirmed that typically chicks were fed soon after adults returned from both attended and unattended trips.

Trip duration

The overall mean trip duration of gannets was 23.1 ± 1.0 h in 2001 and 24.9 ± 2.0 h in 2002. Foraging trips where the chick was left alone (13.1 ± 1.8 h) were significantly shorter than trips where the chick was left attended (24.5 ± 0.9 h) (Figure 5.3, REML: Wald statistic $\chi^2 = 36.23$, d.f. = 1, $p < 0.001$) and there was a tendency for birds leaving at a lower mass to go on a longer foraging trip, but this was of borderline statistical significance (Wald statistic $\chi^2 = 3.83$, d.f. = 1, $p = 0.05$). There was no difference in trip duration between years, sexes or among chick ages (year: Wald statistic $\chi^2 = 0.29$, d.f. = 1, $p = 0.59$; sex: Wald statistic $\chi^2 = 2.40$, d.f. = 1, $p = 0.12$; chick age: Wald statistic $\chi^2 = 0.34$, d.f. = 1, $p = 0.56$). There was however a highly significant interaction between trip type and chick age (Wald statistic $\chi^2 = 12.71$, d.f. = 1, $p < 0.001$): the length of unattended trips increased with chick age but there was no equivalent increase in attended trips. This implies that birds travelled to more distant sites as chicks got older when making unattended trips, but not when making attended trips. There was also no effect of arrival mass or nest attendance duration on trip duration (arrival mass: Wald statistic $\chi^2 = 0.20$, d.f. = 1, $p = 0.66$; attendance: Wald statistic $\chi^2 = 0.32$, d.f. = 1, $p = 0.57$), and no other interactions were significant.

Departure direction

A total of 293 departure directions was recorded from 28 birds (14 males and 14 females). Of these, 47 were trips where the chick was left alone (unattended trips). There was a significant difference between males and females in departure direction (Figure 5.4, REML Wald statistic $\chi^2 = 5.00$, d.f. = 1, $p = 0.02$), a significant effect of trip type (Wald statistic $\chi^2 = 15.50$, d.f. = 1, $p < 0.001$) and a weak interaction between sex and trip type. Males and females had different departure directions during attended trips, with females tending to head on average in a more easterly direction than males (Lewis *et al.* 2002; see Chapter 4). However during unattended trips, both males and females departed in a similar north-easterly direction (Figure 5.4; sex*trip type: Wald statistic $\chi^2 = 3.80$, d.f. = 1, $p = 0.05$). There was no effect of chick age (Wald statistic $\chi^2 = 0.01$, d.f. = 1, $p = 0.9$), but there was a significant interaction between trip type and chick age (Wald statistic $\chi^2 = 7.00$, d.f. = 1, $p = 0.01$) indicating that the departure direction of both male and females on unattended, but not attended trips, showed an easterly shift as chick age increased. No other interactions were significant.

Attendance duration

A total of 259 attendance periods was recorded from 28 birds (14 males and 14 females) in 2001 and 158 nest attendance periods were recorded from 10 birds (five males and five females) in 2002. The overall mean nest attendance duration of gannets was 24.9 ± 1.1 h in 2001 and 25.7 ± 2.0 h in 2002. The mean attendance period prior to leaving the chick alone on an unattended trip (28.3 ± 2.3 h) was significantly greater than prior to an attended trip (24.6 ± 1.0 h) (Figure 5.3, REML: Wald statistic $\chi^2 = 10.52$, d.f. = 1, $p < 0.001$) and attendance periods declined with increasing chick age (Wald statistic $\chi^2 = 16.78$, d.f. = 1, $p < 0.001$). As with trip duration, there was no effect of year or sex on attendance duration (year: Wald statistic $\chi^2 = 0.24$, d.f. = 1, $p = 0.62$; sex: Wald statistic $\chi^2 = 1.06$, d.f. = 1, $p = 0.30$).

There was evidence of a weak interaction between trip type and arrival mass on attendance duration (Wald statistic $\chi^2 = 3.91$, d.f. = 1, $p < 0.05$). Attendance duration was positively correlated to arrival mass prior to unattended trips but there was no relationship for attended trips, however this result was lost when non-significant terms were removed from the model. This may in part be due to a low sample size of unattended trips. No other interactions were significant.

Arrival mass

A total of 138 arrival masses was recorded from the five study nests. The mean arrival mass was 3.44 ± 0.05 kg. The arrival mass of birds prior to making an unattended trip and thus leaving before the partner returned, was significantly lower than the arrival mass prior to making an attended trip, i.e., leaving after the partner returned (Figure 5.5, REML: Wald statistic $\chi^2 = 6.64$, d.f. = 1, $p = 0.01$). There was no effect of sex or chick age on arrival mass (sex: Wald statistic $F_{1,8} = 4.81, p > 0.05$; chick age: Wald statistic $\chi^2 = 3.58$, d.f. = 1, $p = 0.60$). No interactions were significant.

Departure mass

A total of 156 departure masses was recorded from the five study nests in 2002. The mean departure mass was 2.80 ± 0.04 kg. There was no significant difference in departure mass prior to leaving the chick unattended or prior to making an attended trip (Figure 5.5), or between males and females (REML, trip type: Wald statistic $\chi^2 = 0.79$, d.f. = 1, $p = 0.37$; sex: $F_{1,8} = 3.32, p > 0.05$), although departure mass declined significantly with increasing nest attendance (Figure 5.6, Wald statistic $\chi^2 = 29.59$, d.f. = 1, $p < 0.001$). No interactions were significant. Chick age was not included as a covariate in this model because it is correlated with attendance duration and its inclusion led to an unstable model. Given that parents which eventually leave their chicks unattended stay longer than average on the nest (see above), one might expect their mean departure masses to be correspondingly lower. However, the predicted differences in the departure masses (from the regression in Figure 5.6) for periods corresponding to the mean length of nest attendances prior to attended (24.6 h) and unattended trips (28.3 h) is negligible ($\approx$0.02 kg), and would therefore be unlikely to be detected.

Mass change from foraging

The mean mass difference between departure and return was 0.67 ± 0.03 kg. Adults departing with a lower mass returned to the nest with a greater mass change than adults departing with a higher mass (Figure 5.7, REML: Wald statistic χ^2 = 40.56, d.f. = 1, $p < 0.001$). There was no effect of trip type, sex, trip duration or chick age on the mass change (trip type: Wald statistic $\chi^2 = 0.66$, $p = 0.42$; sex: Wald statistic $F_{1,8} = 2.33$, d.f. = 1, $p > 0.1$; trip duration: Wald statistic $\chi^2 = 0.05$, d.f. = 1, $p = 0.83$; chick age: Wald statistic $\chi^2 = 1.37$, d.f. = 1, $p = 0.24$). No interactions were significant.

Modelling[‡]

To facilitate comparison with the earlier results of Mangel & Clark (1986), the original parameter values and their temporal equations for chick metabolic costs and energy capacity, were adopted here with $N = 1$ chick. In the simplest case when only one suitable foraging patch was available ($\lambda_2 = 0$) identical results were obtained (see Table 4 in Mangel & Clark, 1986). When two alternative foraging patches were available however, then the optimal foraging location was often state-dependent. Not surprisingly, the precise set of optimal strategies was dependent on the parameter values assumed, such as the rate at which parents and offspring consumed energy. As might be expected, when one patch was consistently more reliable ($\lambda_1 > \lambda_2$) and provided greater reward than the other ($Y_1 > Y_2$) then this patch, was always the optimal foraging location. By contrast when the patch that gave the least reward was at the same time more reliable, then the optimal foraging location of the parent was in general dependent on both its state and that of its offspring (Figure 5.8a). For instance, when the chick is close to starvation but the parent is well fed then the parent should typically forage at the poor quality but guaranteed patch of food. Similarly, the optimal proportion of food given by the parent to its offspring varied

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[‡] *Modelling carried out by T.N.Sherratt.*

with both the parent's and offspring's state: if the parent had high energy levels, then the majority of its food was typically predicted to be given to its offspring (Figure 5.8b). Analysis of a rather more complicated version of the above model in which patches had similar reliability but had different rewards and took different times to travel to (effectively a different "handling time" Mangel & Clark, 1988, p64) produced analogous results: once again, the optimal patch choice was predicted to be state-dependent.

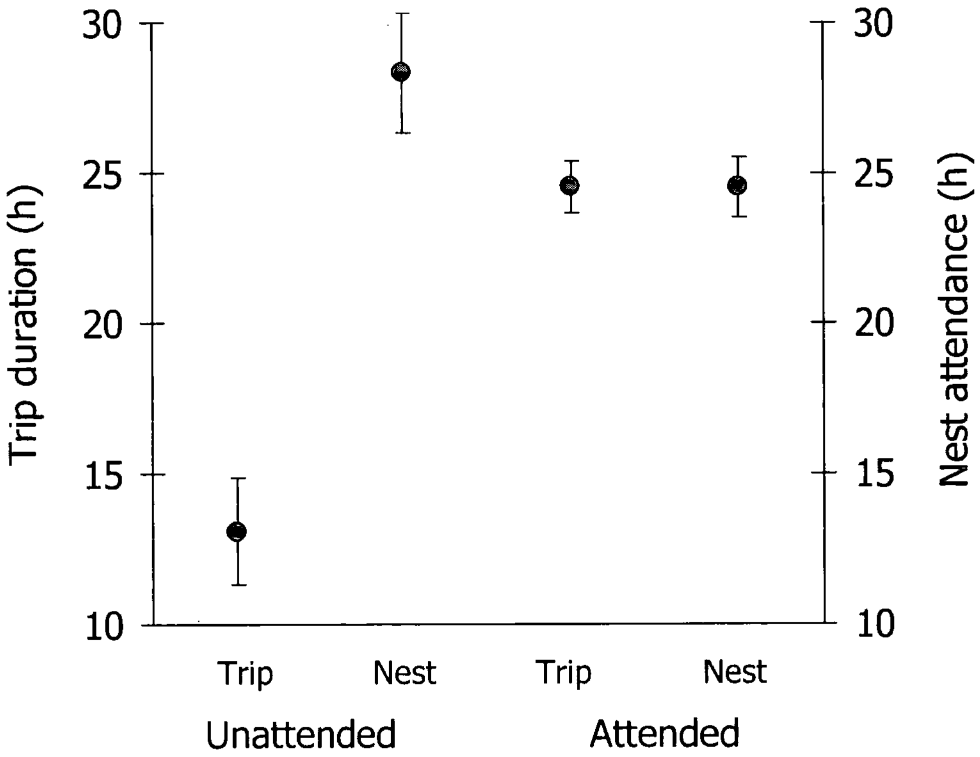

Figure 5.3: Mean trip duration and nest attendance duration (hours ±1SE) of northern gannets (*n*=38) on the Bass Rock in 2001 and 2002, for trips where the chick is left unattended and attended.

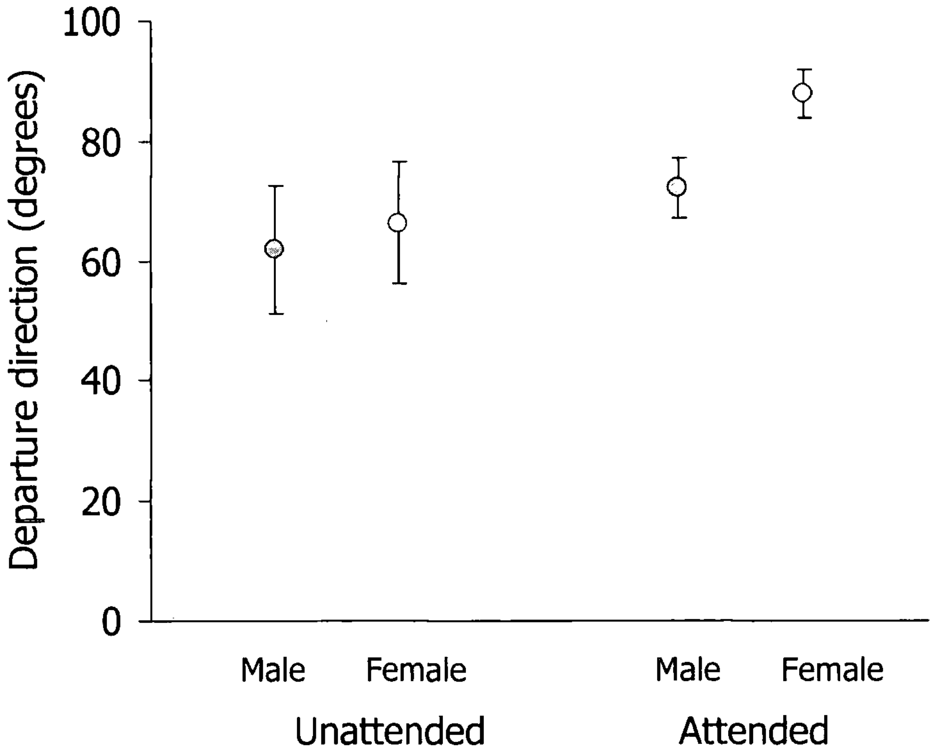

Figure 5.4: Mean foraging trip departure direction (degrees ±1SE) of male (grey circles; *n*=14) and female (white circles; *n*=14) northern gannets for trips where the chick is left alone and typical trips, on the Bass Rock in 2001.

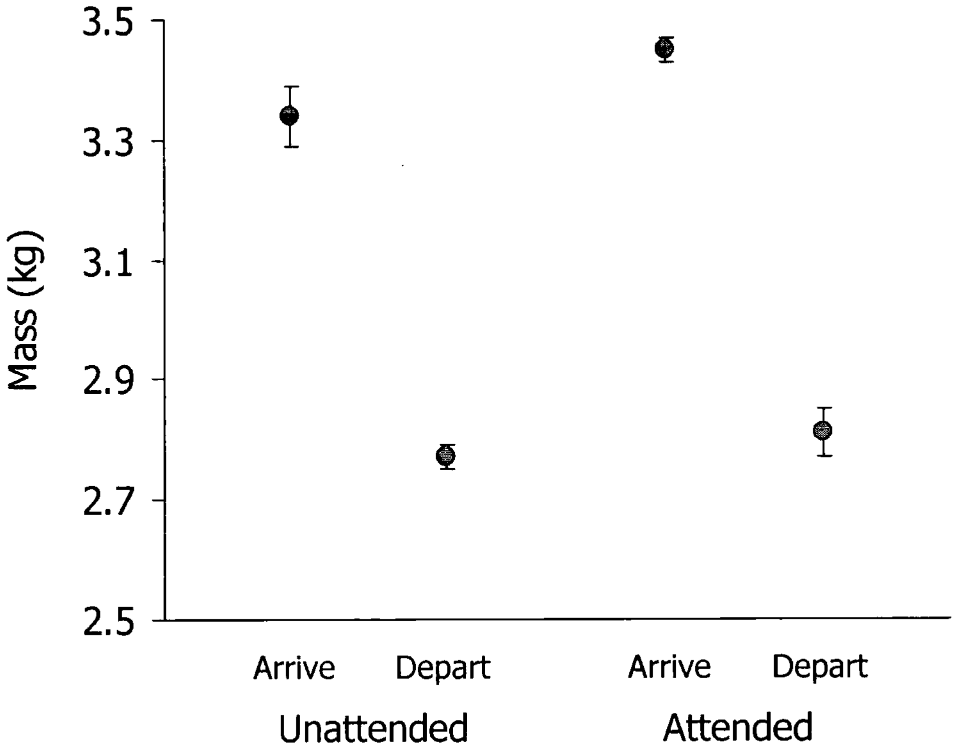

Figure 5.5: Mean arrival and departure mass (kg ± 1SE) prior to leaving the chick unattended and attended from 5 pairs of northern gannets during chick rearing on the Bass Rock in 2002.

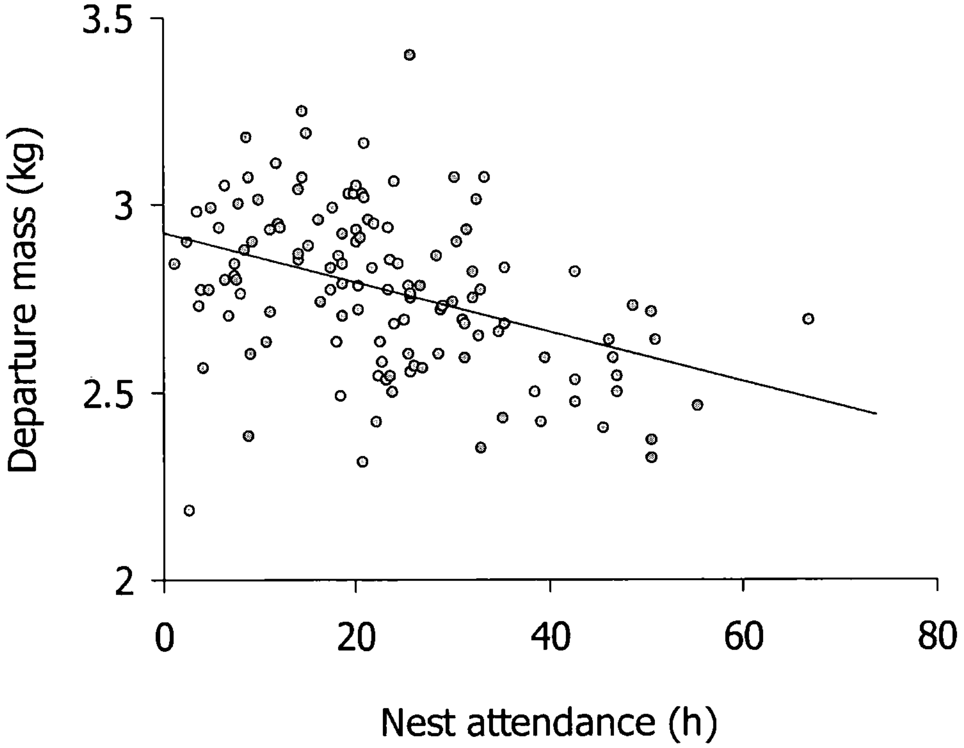

Figure 5.6: Relationship between departure mass (kg) and nest attendance duration (h) from 5 pairs of northern gannets during chick rearing on the Bass Rock in 2002.

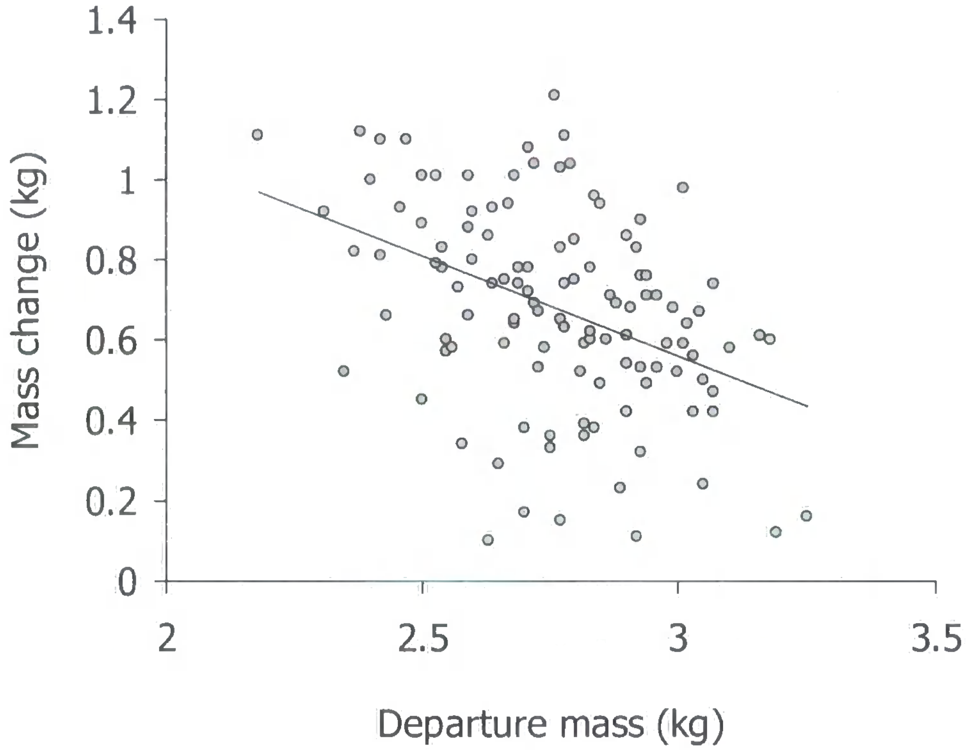

Figure 5.7: Relationship between mass change (kg) and departure mass (kg) from 5 pairs of northern gannets during chick rearing on the Bass Rock in 2002.

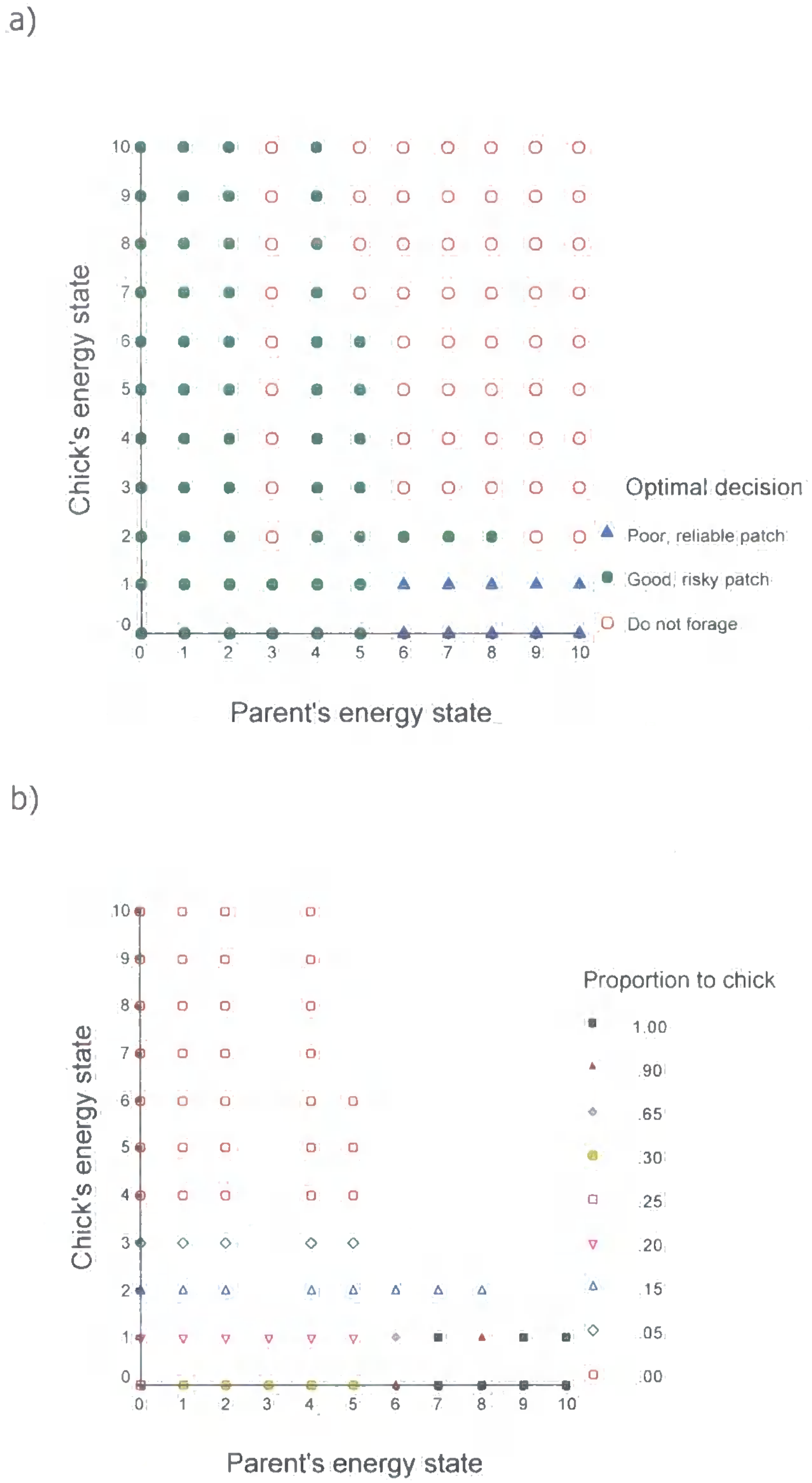

Figure 5.8[§]: Optimal decisions of a parent (whether to forage, where to forage and how much to allocate to offspring) at $t = 1$ as predicted by the dynamic allocation model with two foraging locations. Parameters: $C_p = 10$, $\alpha_p = 2$, $\alpha_f = 3$, $\beta_n = 0.05$, $\beta_p = 0.025$, $Y_1 =$

[§] *Figure 5.8 by T.N. Sherratt.*

12, $\lambda_1 = 0.85$, $Y_2 = 2$, $\lambda_2 = 1$, $\alpha_n(t) = 0.1 + \alpha_p\,[1\text{-}\exp(-0.3\ t)]$, $C_n(t) = 0.1 + C_p\,[1\text{-}\exp(-0.3\ t)]$, $T = 10$. Under these conditions: (a) when the chick is close to starvation and the parent is well fed it then it should chose to feed at the poor but reliable patch (patch 2), (b) similarly, when the chick is close to starvation and the parent is well fed then the parent should give the majority of the food it collects to its offspring. Combinations of state under which one particular decision was optimal did not always conform to a simple pattern, particularly when different decisions had approximately equal fitness consequences.

Discussion

Radio tags had no noticeable adverse effects on the study birds or their chicks and the mean trip duration of tagged birds (23 h (s.d. ± 5.1)) was consistent with two recent studies of untagged birds that recorded trip durations at the Bass Rock (27 h in 1998, Hamer *et al.* 2000; 19 h in 2000, Lewis *et al.* 2001).

Effects of chick age on propensity to leave the chick unattended

Chicks were not left alone at the nest until they were at least 4 weeks old, by which age they are homeothermic (Montevecchi *et al.* 1984). From then on, the frequency of desertion trips increased with chick age, as was also found in black-legged kittiwakes *Rissa tridactyla* (Cadiou & Monnat 1996). This was probably because older chicks were less vulnerable to attack by conspecifics and thermal stress. The duration of unattended trips also increased with chick age, which further suggests lower costs of leaving older chicks unattended. The easterly shift in departure direction and trip duration of unattended trips with chick age (a phenomenon not observed in attended trips) provide evidence of a systematic change in the location of foraging areas of adults making this type of trip. This shift in foraging location may in part be related to seasonal changes in prey distribution in the vicinity of the colony, because chick age and date were highly positively correlated ($r = 0.869$, $n = 384$, $p < 0.001$).

Foraging behaviour during attended and unattended trips

To my knowledge, the characteristics of attended and unattended trips have never previously been compared. When gannets left their chick alone at the nest, their foraging trips were, on average, only half as long as attended trips, highlighting the fact that birds were foraging much closer to the colony when making unattended trips. Examination of the departure directions of adults also showed that unattended trips of both males and females tended to a particular direction (north east of the colony). Attended trips showed no such directional bias overall, but in this instance there were differences in the foraging location between males and females (Lewis *et al.* 2002; see Chapter 4). Therefore if parents and/or their chicks face an acute/short-term nutritional need then it may be more beneficial to visit a nearer foraging site, even if more distant sites are more beneficial under other circumstances.

The mass change after foraging was the same when males and females used the same feeding area during unattended trips and when males and females used different areas during attended trips. Therefore there is no direct evidence that unattended trips were less profitable than attended ones. However this seems likely, because a longer trip will enable the adult to consume and digest more food for itself (Weimerskirch *et al.* 1994). Finally, given that chicks are also always fed following unattended trips, we have no reason to believe that unattended trips were exclusively for self feeding, or that the chick was fed any less under these circumstances.

Motivation to leave offspring alone: general circumstances and specific triggers

The mean attendance period of gannets (and consequently the mean trip durations of their partners) prior to leaving the chick unattended was >10% longer than when the chick was left attended (Figure 5.3). Adults which temporarily left their offspring unattended were lighter on arrival (after the previous foraging trip), while the interaction term between attendance type and arrival mass on attendance duration suggested that individuals which eventually left their offspring alone tended to stay longer if they arrived heavier. Tveraa *et al.* (1998) similarly found that among Antarctic petrels *Thalassoica antarctica*, the number of days that adults guarded their chicks prior to leaving them unattended for the first time, was positively related to their own body mass on arrival. Overall therefore, leaving offspring unattended appears to arise as a consequence of two sets of circumstances acting together or independently: a partner foraging at sea for an extensive period of time, and/or an individual arriving at low weight.

Given that the mass of both the attending parent, and presumably its chick, diminishes the longer they go without food, and that attendance duration prior to leaving a chick unattended appears dependent on arrival mass, it seems likely that the proximate motivation to leave offspring unattended is state-dependent. One key question is whether the motivation to leave offspring is triggered by adult and/or chick state. Birds in good condition have been shown to sustain longer periods of nest attendance than those in poorer condition (Chaurand & Weimerskirch 1994; Yorio & Boersma 1994; Tveraa *et al.* 1998), which might indicate that adult condition is more important than chick condition in the decision when to leave. However, in some cases adult and chick condition are correlated (Tveraa *et al.* 1998). Furthermore, the data on departure mass suggest that adults depart their nest at similar masses in all circumstances. This could be interpreted as a threshold trigger to leave to forage, but equally this mass could reflect empty body mass, which may have been reached some time prior to departure (Jackson 1992). Indeed, as the mean adult mass loss (and rate) is lower during nest attendances prior to unattended trips (because arrival mass of the adult is lower yet departure mass is the same), it is likely that chicks receive less food in these circumstances. Finally, the observation that parents that temporarily leave their offspring return much more quickly, and always feed their chicks on return, further suggests that the state of the chick has an important motivational role.

The parental allocation model

The state-dependent parental allocation model is simplistic for several reasons. For instance, decisions are identified that maximise the probability of a chick surviving to independence, yet in iteroparus species such as gannets, decisions that maximise current and lifetime reproductive success are not necessarily the same. Like Mangel & Clark (1986) this model considers the activities of only a single parent when in reality two parents often tend their chick. In these cases the optimal strategy of one parent may well be dependent on the strategy adopted by its partner, so to understand adult foraging behaviour in full would most likely require a state-dependent game theoretical model (see Jones *et al.* 2002). Nevertheless, even this simplistic model serves a role in highlighting the fact that state-dependent patch choice can arise not only from the need to trade predation risk against foraging gain, but also from something as fundamental as satisfying immediate needs versus anticipated longer-term needs.

Overview

This work shows that when gannets leave their chick alone then they spend a much shorter time at sea and forage closer to the colony, than when they leave their chick with their partner. Unattended trips were more frequent and became longer with increasing chick age, reflecting a reduced risk associated to leaving the chick alone. Since unattended trips were also associated with longer than average periods of prior attendance, and lower adult prior arrival mass, it is likely that the motivation to leave the chick alone is dependent on the energetic states of the parent and/or chick. Given the contingent nature of temporary desertion, such behaviour may necessitate different forms of foraging than are typically optimal. Thus if there are energetic requirements that need to be satisfied quickly and leaving a chick unattended is risky, then it may be better for a parent leaving its chick alone to forage in a close location rather than in more distant areas that would maximise a parent's longer term foraging gain.

References

Cadiou, B. & Monnat, J.Y. (1996) Parental attendance and squatting in the kittiwake *Rissa tridactyla* during the rearing period. *Bird Study*, **43**, 164-171.

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

Clark, C.W. & Mangel, M. (2000) *Dynamic State Variable Models in Ecology; Methods and Applications.* Oxford University Press.

Croxall, J.P. & Ricketts, C. (1983) Energy costs of incubation in wandering albatross *Diomedea exulans. Ibis*, **125**, 33-39.

Davis, L.S. (1982) Timing of nest relief and its effect on breeding success in Adelie penguins (*Pygoscelis adeliae*). *Condor*, **84**, 178-183.

Davis, L.S. (1988) Coordination of incubation routines and mate choice in Adelie pengunins (*Pygoscelis adeliae*). *Auk*, **105**, 428-432.

Davis, L.S. & McCaffrey, F.T. (1986) Survival analysis of eggs and chicks of Adelie penguins (*Pygoscelis adeliae*). *Auk*, **103**, 379-388.

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

Gauthier-Clerc, M., Le Maho, Y., Gendner, J.P., Durant, J., & Handrich, Y. (2001) State-dependent decisions in long-term fasting king pengins, *Aptenodytes patagonicus*, during courtship and incubation. *Animal Behaviour*, **62**, 661-669.

Gremillet, D., Dey, R., Wanless, S., Harris, M.P., & Regel, J. (1996) Determining food intake by great cormorants and European shags with electronic balances. *Journal of Field Ornithology*, **67**, 637-648.

Houston, A.I., Clark, C.W., McNamara, J.M., & Mangel, M. (1988) Dynamic models in behavioural and evolutionary ecology. *Nature*, **332**, 29-34.

Houston, A.I. & McNamara, J.M. (1985) The choice of two prey types that minimises the possibility of starvation. *Behavioural Ecology and Sociobiology*, **17**, 135-141.

Hunter, S. (1984) Breeding biology and population dynamic of giant petrels *Macronectes* at South Georgia (Aves: Procellariiformes). *Journal of Zoology*, **203**, 441-460.

Jackson, S. (1992) Do seabird gut sizes and mean retention times reflect adaptaion to diet and foraging method? *Physiological Zoology*, **65**, 674-697.

Jones, K.M., Ruxton, G.D., & Monaghan, P. (2002) Model parents: is full compensation for reduced partner nest attendance compatible with stable biparental care? *Behavioral Ecology*, **13**, 838-843.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., & Hamer, K.C. (2002) Sex specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 1687-1693.

Lewis, S., Sherratt, T.N., Hamer, K.C., & Wanless, S. (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, **412**, 816-819.

Lima, S.L. & Dill, L. (1990) Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.

Mangel, M. & Clark, C.W. (1986) Towards a unified foraging theory. *Ecology*, **67**, 1127-1138.

Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, New Jersey.

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

Milinski, M. & Keller, R. (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus*). *Nature*, **275**, 642-644.

Montevecchi, W.A., Ricklefs, R.E., Kirkham, I.R., & Gabaldon, D. (1984) Growth energetics of nestling northern gannets (*Sula bassanus*). *Auk*, **101**, 334-341.

Nelson, J.B. (1969) The breeding ecology of the red-footed booby in the Galapagos. *Journal of Animal Ecology*, **38**, 181-198.

Nelson, J.B. (2002) *The Atlantic Gannet*. Fenix Books Ltd., Norfolk.

Numata, M., Davis, L.S., & Renner, M. (2000) Prolonged foraging trips and egg desertion in little penguins (*Eudyptula minor*). *New Zealand Journal of Zoology*, **27**, 277-289.

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

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

Pettersson, L.B. & Bronmark, C. (1993) Trading off safety against food - state-dependent habitat choice and foraging in crucian carp. *Oecologia*, **95**, 353-357.

Szekely, T., Webb, J.N., Houston, A.I., & McNamara, J.M. (1996). An evolutionary approach to offspring desertion in birds. In *Current Ornithology* (eds V. Nolan, Jr. & E.D. Ketterson), Vol. 13, pp. 271-330. Plenum Press, New York.

Tveraa, T., Lorentsen, S.H., & Saether, B.-E. (1997) Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). *Behavioural Ecology*, **8**, 465-469.

Tveraa, T., Saether, B.-E., Aanes, R., & Erikstad, K.E. (1998) Body mass and parental decisions in the Antarctic petrel *Thalassoica antarctica*: how long should the parents guard the chick? *Behavioural Ecology and Sociobiology*, **43**, 73-79.

Weimerskirch, H. (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *Journal of Animal Ecology*, **67**, 99-109.

Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeyer, X., & Judas, J. (1994) Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour*, **47**, 472-476.

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

Weimerskirch, H., Mougey, T., & Hindermeyer, X. (1997b) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioural Ecology*, **8**, 635-643.

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

Yorio, P. & Boersma, P.D. (1994) Causes of nest desertion during incubation in the magellanic penguin (*Spheniscus magellanicus*). *Condor*, **96**, 1076-1083.

Chapter 6

Contrasting patterns of foraging behaviour of northern gannets at two different colonies

Contrasting patterns of foraging behaviour of northern gannets

Abstract

A common limitation of field studies is that they have only been carried out in one location. Collecting data in more than one location is helpful if we are to understand intrinsic and extrinsic factors that may affect the dynamics of populations and individual foraging decisions. In this chapter, a detailed comparison of the foraging behaviour of male and female northern gannets *Morus bassanus* at two colonies, Great Saltee and Bass Rock, is presented. Significant differences were recorded between the two populations.

Sex differences in the foraging trip duration of northern gannets were only observed at Great Saltee, but together with results from Chapter 4 highlight that sex differences in the location of foraging trips were evident at both colonies. Not only did males at Great Saltee make shorter foraging trips than females but also left their offspring alone much more frequently than females. This contrasts with the observation on the Bass Rock where no sex differences in these aspects of their foraging behaviour were recorded.

At both colonies unattended trips were significantly shorter than attended trips, and thus in a different location to attended trips, because trip duration and distance travelled are very highly correlated. Unattended trips also increased in number and duration with increasing chick age at both colonies. However, the time spent attending the chick prior to leaving it alone at the nest was significantly greater than prior to leaving the chick with the partner on the Bass Rock, but not on Great Saltee.

These findings are discussed in the context of colony size. Since the colony at Bass Rock is over 20 times larger than Great Saltee, it is possible that density dependent factors may have a role in shaping these colony specific interactions.

Introduction

The foraging behaviour of seabirds has been widely studied over the last two decades, particularly more recently with the advent of new technologies, such as locational loggers (satellite telemetry, GPS; see Wilson *et al.* 2002 for review) and archival data loggers that record aspects of foraging behaviour such as dive depth and time activity budgets (Croxall *et al.* 1991; Weimerskirch & Sagar 1996; Benvenuti *et al.* 1998; Wanless *et al.* 1999; Benvenuti *et al.* 2001; Dall'Antonia *et al.* 2001; Daunt *et al.* 2002; Lewis *et al.* 2002). Most field studies are carried out at a single location and, as such, the results obtained may be unique to the study site in question. Intrinsic and/or extrinsic effects may create an interaction between foraging behaviour and location. For example, we have shown that the trip duration of gannets differs between locations due to density dependent effects (Lewis *et al.* 2001; see Chapter 3).

Sex differences in foraging behaviour have been observed in many sexually size dimorphic species (e.g., Creelman & Storey 1991; Kato *et al.* 1992; Prince *et al.* 1992; Salamolard & Weimerskirch 1993; Weimerskirch *et al.* 1993; Watanuki *et al.* 1996; Kato *et al.* 1999; Wanless *et al.* 1999; Gonzalez-Solis *et al.* 2000; Stahl & Sagar 2000; Casaux *et al.* 2001) and more recently in monomorphic species (Gray & Hamer 2001; Lewis *et al.* 2002; see Chapter 4). However, these studies were carried out at individual colonies. It is therefore instructive to collect comparable data on a species in different locations, to establish whether the ecological patterns are consistent across environments, or whether there are interactions between the species' ecology and density dependent and independent effects.

Chapter 4 has shown that female northern gannets from the Bass Rock dive deeper, spend more time resting on the sea surface during foraging trips, and forage in a different location to males (Lewis *et al.* 2002). Chapter 5 has shown that both male and female gannets at this colony occasionally leave their chick alone at the nest when their partner's return is delayed. Such trips were defined as unattended trips, whilst the more typical trips where the chick was left with its partner, were defined as attended trips. Unattended trips were more than 50% shorter than attended trips, highlighting the fact that birds were foraging much closer to the colony when making unattended trips. Radio tracking data also showed that birds departed from the colony at different bearings when making these unattended trips. Furthermore unattended trips occurred more often and became longer as chicks got older. However, these findings were derived from work carried out at a single colony, the Bass Rock. In this chapter, a comparison is made between these data for the Bass Rock and Great Saltee, which differed markedly in size and mean trip duration (Lewis *et al.* 2001; see Chapter 3). They also differ in terms of the likely distribution and variability of marine food resources (see Hamer *et al.* 2001). The foraging behaviour of male and female northern gannets is compared throughout chick rearing to examine the interaction between sex and chick age effects, and colony size on trip and attendance duration of attended and unattended trips.

Methods

Study sites

The study was carried out during chick rearing, from 3 May to 14 August 2000 on Great Saltee and from 19 June to 19 August 2001 at the Bass Rock. Trip duration and nest attendances were recorded from observations on Great Saltee, and by radio tracking on the Bass Rock.

Great Saltee

Adults at 12 nests with young chicks were caught at the nest and ringed with a unique lettered code on a colour ring, and a sample of blood was taken (under license) from each bird, for sexing. Details of the methodology are as described in Chapter 2. Adults at a further 11 nests where one member of the pair was ringed with a British Trust for Ornithology metal ring, were sexed from behavioural observations (principally nape-biting behaviour, which is completely reliable; Redman et al., 2002). This provided a total sample of twenty-three pairs of gannets with chicks, which were observed over seven observation periods, from a hide situated 30m from the colony. Each watch ran continuously from dawn to dusk (since no change-overs occur during the hours of darkness, see Garthe *et al.* 1999; Garthe *et al.* 2000; Hamer *et al.* 2000) for two to six days (total observation period 22.3 days), in order to record at least one complete trip per nest. The ages of chicks during the study period ranged from 1 to 12 weeks. The arrival and departure times of study birds were recorded to the nearest minute at each nest.

Bass Rock

Details of handling birds, attaching radio transmitters and the radio tracking system are given in Chapter 4 (section Radio-transmitters) and Lewis *et al.* (2002). Blood was taken for sexing in the same way as on Great Saltee, as described in Chapter 2.

Trip durations and attendance durations were calculated in the same way as described in Chapter 4, and attended and unattended trips were classified as described in Chapter 5.

Statistical procedures

The distribution of the two trip types were compared between colonies, the sex of the parents and among chick ages by fitting a generalized linear mixed model (GLMM, type III, see Chapter 4) with a binomial error distribution, logit link function and a binomial total of 1; unattended trips = 0, attended trips= 1 (Schall 1991). Colony and sex were fixed factors and chick age was a covariate, while bird identity was included as a random factor, to control for pseudo-replication.

Trip duration and attendance durations were compared between colony, sex, trip type (or attendance type) and among chick ages by fitting linear mixed models using residual maximum likelihood analyses (REML, type III: Patterson & Thompson 1971). In each case the model included colony, sex and trip type as fixed factors, chick age as a covariate and bird identity as a random factor. As in previous models, chick age was grouped into three successive four-week age-classes (1 = 1-4 weeks old; 2 = 5-8 weeks; 3 = 9-12 weeks old respectively), to increase the robustness of the statistical models.

In both the GLMM and REML analyses, the significance of each term was determined by comparing Wald statistics (which show the effect of removing that term from the full fixed model) with percentiles of chi-squared (Elston *et al.* 2001). Non-significant terms were dropped sequentially from the model in reverse order of significance, commencing with the highest order interaction term, until the most parsimonious model was obtained. If an interaction term was significant, all lower order interaction terms and fixed effects were retained. Means ± 1 SE are given (unless otherwise indicated), where means per individual are used.

Results

Trip type

A total of 246 trips was recorded from 45 birds (22 males and 23 females) from Great Saltee, and 348 trips were recorded from 28 birds (14 males and 14 females) from the Bass Rock. The age when a chick was first recorded being left alone was 3 weeks on Great Saltee and 4 weeks on the Bass Rock. There was no overall significant difference in the relative frequencies of unattended trips between colonies (GLMM: Wald statistic $\chi^2 = 0.18$, d.f. = 1, $p = 0.67$), but there was a significant effect of sex (Wald statistic $\chi^2 = 4.66$, d.f. = 1, $p = 0.03$) and a significant interaction between sex and colony (Wald statistic $\chi^2 = 4.63$, d.f. = 1, $p = 0.03$). Females made significantly fewer unattended trips than males on Great Saltee, but there was no significant difference between the sexes on the Bass Rock (Figure 6.1). There was also a highly significant increase in the number of unattended trips with increasing chick age (Wald statistic $\chi^2 = 49.32$, d.f. = 1, $p < 0.001$). At both colonies, chicks were fed soon after the arrival of its parent from both types of trips (Lewis, pers. obs.). The daily feed rate for chicks increased by 7.3% to 1.62 feeds per day on Great Saltee and by 4.8% to 1.09 feeds per day on the Bass Rock as a result of adults making unattended trips.

Trip duration

Gannets from Great Saltee made, on average, significantly shorter trips than those on the Bass Rock (Figure 6.2, REML (using sqrt transformed data): Wald statistic $\chi^2 = 18.07$, d.f. = 1, $p < 0.001$; overall mean trip duration, Great Saltee: 17.91 ± 1.07 h; Bass Rock: 23.03 ± 0.97). Females made significantly longer trips than males, but the sex differences on Great Saltee, were significantly greater than those on the Bass Rock (Figure 6.3, sex: Wald statistic $\chi^2 = 17.83$, d.f. = 1, $p < 0.001$; sex*colony: Wald statistic $\chi^2 = 5.26$, d.f. = 1, $p = 0.02$). Unattended trips were significantly shorter than attended trips at both colonies (Figure 6.3: Wald statistic $\chi^2 = 68.85$, d.f. = 1, $p < 0.001$). There was also a highly significant interaction between trip type and chick age (Wald statistic $\chi^2 = 22.74$, d.f. = 1, $p < 0.001$). The length of unattended trips increased with chick age at both colonies, but there was no equivalent increase in attended trips. Overall, males made significantly shorter trips than females as chicks got older (sex*chick age: Wald statistic $\chi^2 = 4.14$, d.f. = 1, $p = 0.04$), but this was most marked on Great Saltee (Figure 6.4a). On the Bass rock, males only made shorter trips than females when chicks were aged 5-8 weeks old (Figure 6.4b). There was no direct effect of chick age on trip duration (Wald statistic $\chi^2 = 0.50$, d.f. = 1, $p = 0.48$), and no other interactions were significant.

Nest attendance duration

A total of 191 attendance periods was recorded from 45 birds (23 males and 22 females) on Great Saltee, and 259 attendance periods were recorded from 28 birds (14 males and 14 females) on the Bass Rock. Gannets from Great Saltee had significantly shorter attendance periods than those on the Bass Rock (Figure 6.5, REML (using sqrt transformed data): Wald statistic $\chi^2 = 16.30$, d.f. = 1, $p < 0.001$; overall mean attendance duration, Bass Rock: 24.84 ± 1.08 h; Great Saltee: 18.13 h ± 0.99 h). Whilst there was no significant difference in attendance duration between males and females, or attendance type overall (sex: Wald statistic $\chi^2 = 2.32$, d.f. = 1, $p = 0.13$; attendance type: Wald statistic $\chi^2 = 2.95$, d.f. = 1, $p = 0.09$), there was a significant interaction between sex and attendance type (Wald statistic $\chi^2 = 6.61$, d.f. = 1, $p = 0.01$), although this relationship was different at each colony (see Figure 6.6). On Great Saltee, males had significantly longer attendance periods than females prior to making attended trips, but not prior to making an unattended trip, whereas on the Bass Rock, a different pattern was evident: the mean attendance period prior to making an unattended trip was greater than prior to leaving the chick alone (see Chapter 5), but was most marked for females (Figure 6.6). Attendance periods decreased significantly with increasing chick age (Wald statistic $\chi^2 = 36.85$, d.f. = 1, $p < 0.001$). Despite this overall decline with chick age, males had significantly longer attendance periods than females as chicks got older (sex*chick age: Wald statistic $\chi^2 = 6.45$, d.f. = 1, $p = 0.01$), but this was more marked on Great Saltee (Figure 6.7a) than on the Bass Rock (Figure 6.7b). No other interactions were significant.

Table 6.1: Colony size and foraging characteristics of males and females at the Bass Rock and Great Saltee (means ±SE are shown).

Parameters	sex	Bass Rock	Great Saltee
Colony size (breeding pairs)		> 40,000	2,000
Age (weeks) chick first left unattended	M	4	3
	F	7	6
Frequency of unattended trips	M	0.22	0.28
	F	0.17	0.06
Mean trip duration (h)	M	22.26 ± 1.47	14.34 ± 0.97
	F	23.79 ± 1.29	21.33 ± 1.60
Duration of attended trips (h)	M	23.33 ± 1.33	16.31 ± 1.07
	F	24.74 ± 1.41	21.49 ± 1.60
Duration of unattended trips (h)	M	14.29 ± 3.17	6.69 ± 1.31
	F	14.14 ± 2.99	16.61 ± 5.21
Mean attendance duration (h)	M	25.23 ± 1.60	19.90 ± 1.62
	F	24.45 ± 1.51	16.28 ± 1.02
Duration of attendance prior to attended trip (h)	M	24.84 ± 1.73	20.50 ± 1.65
	F	23.59+/1.50	15.86 ± 1.10
Duration of attendance prior to unattended trip (h)	M	28.16 ± 4.18	17.69 ± 3.13
	F	30.64 ± 4.02	18.74 ± 3.75

Table 6.2: Significance values of statistical tests performed on the frequency of unattended trips, trip duration and attendance duration data at the Bass Rock and Great Saltee, where *p* <0.001: ***; *p* <0.01: **; *p* <0.05: *; ns: non significant.

Statistical tests	Frequency of unattended trips	Mean trip duration (h)	Mean attendance duration (h)
colony *p*	ns	***	***
sex *p*	*	***	ns
trip type *p*		***	ns
chick age *p*	***	ns	***
colony*sex *p*	*	*	ns
sex*trip type *p*		ns	*
sex*chick age *p*	ns	*	*
trip type*chick age *p*		***	ns

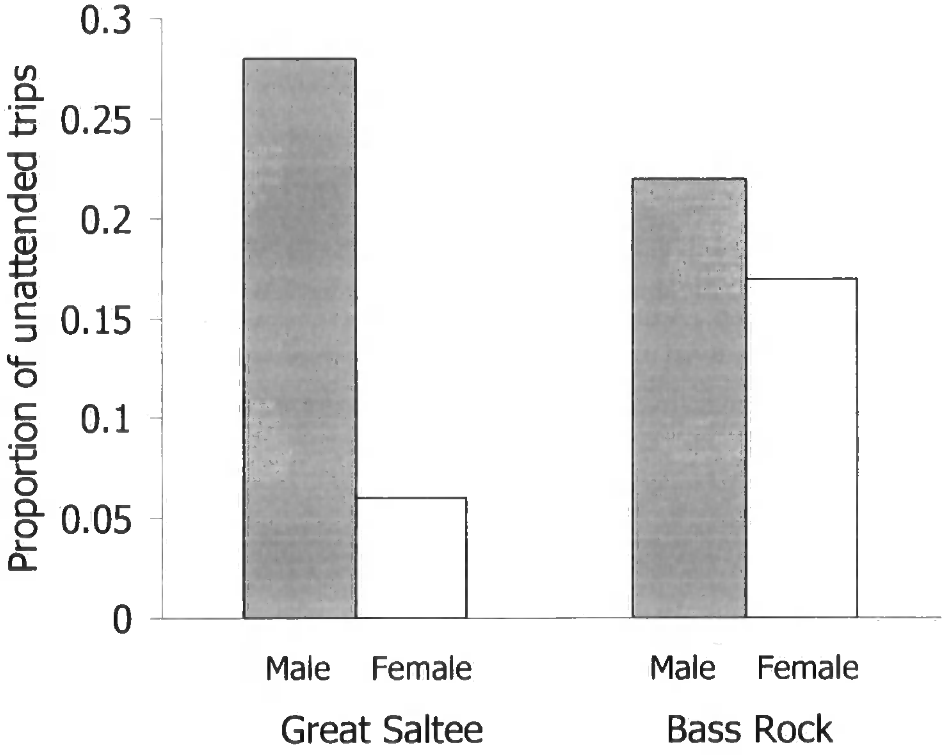

Figure 6.1: Proportion of trips by the northern gannet where the chick is left unattended for males (grey bars) and females (white bars) at Great Saltee in 2000 (n=45) and the Bass Rock in 2001 (n=28) during chick rearing.

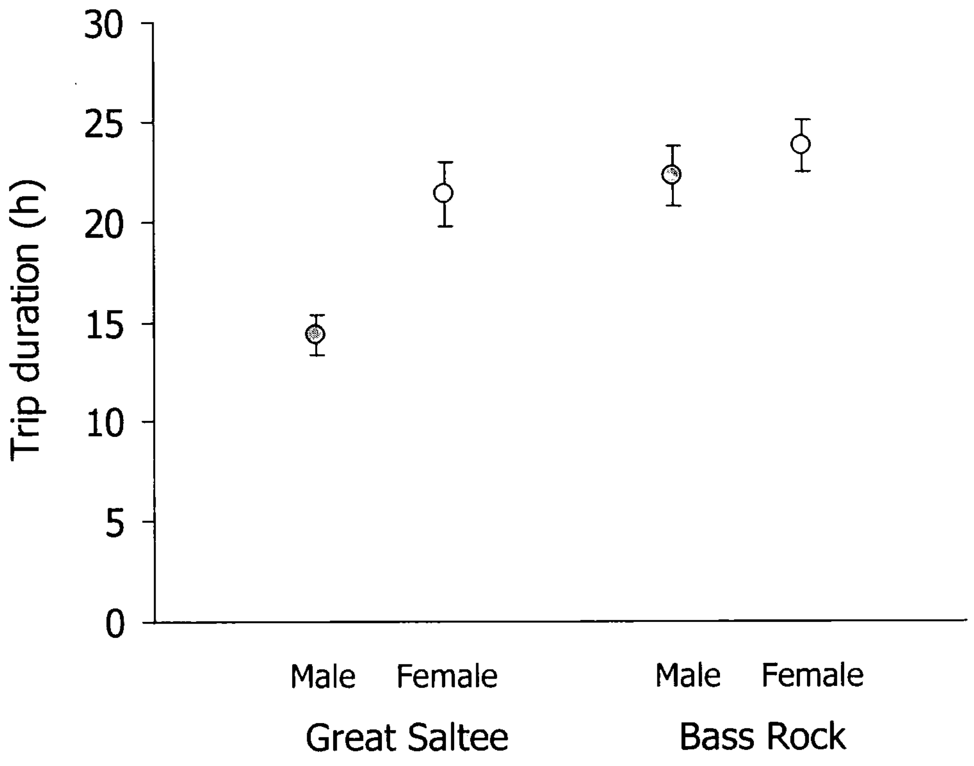

Figure 6.2: Mean trip duration (hours ±SE) of male (grey circles) and female (white circles) northern gannets on Great Saltee in 2000 (*n*=45) and the Bass Rock in 2001 (*n*=28).

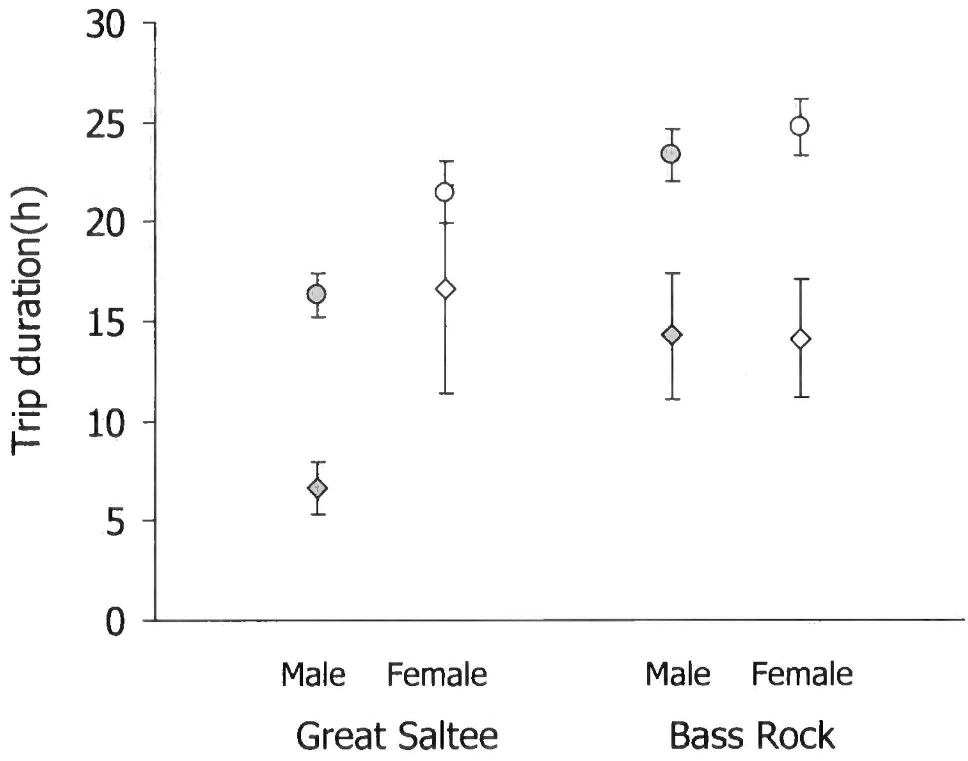

Figure 6.3: Mean trip duration (±SE) of male (grey) and female (white) northern gannets on Great Saltee in 2000 (*n*=45) and the Bass Rock in 2001 (*n*=28), for attended (circles) and unattended (diamonds) trips.

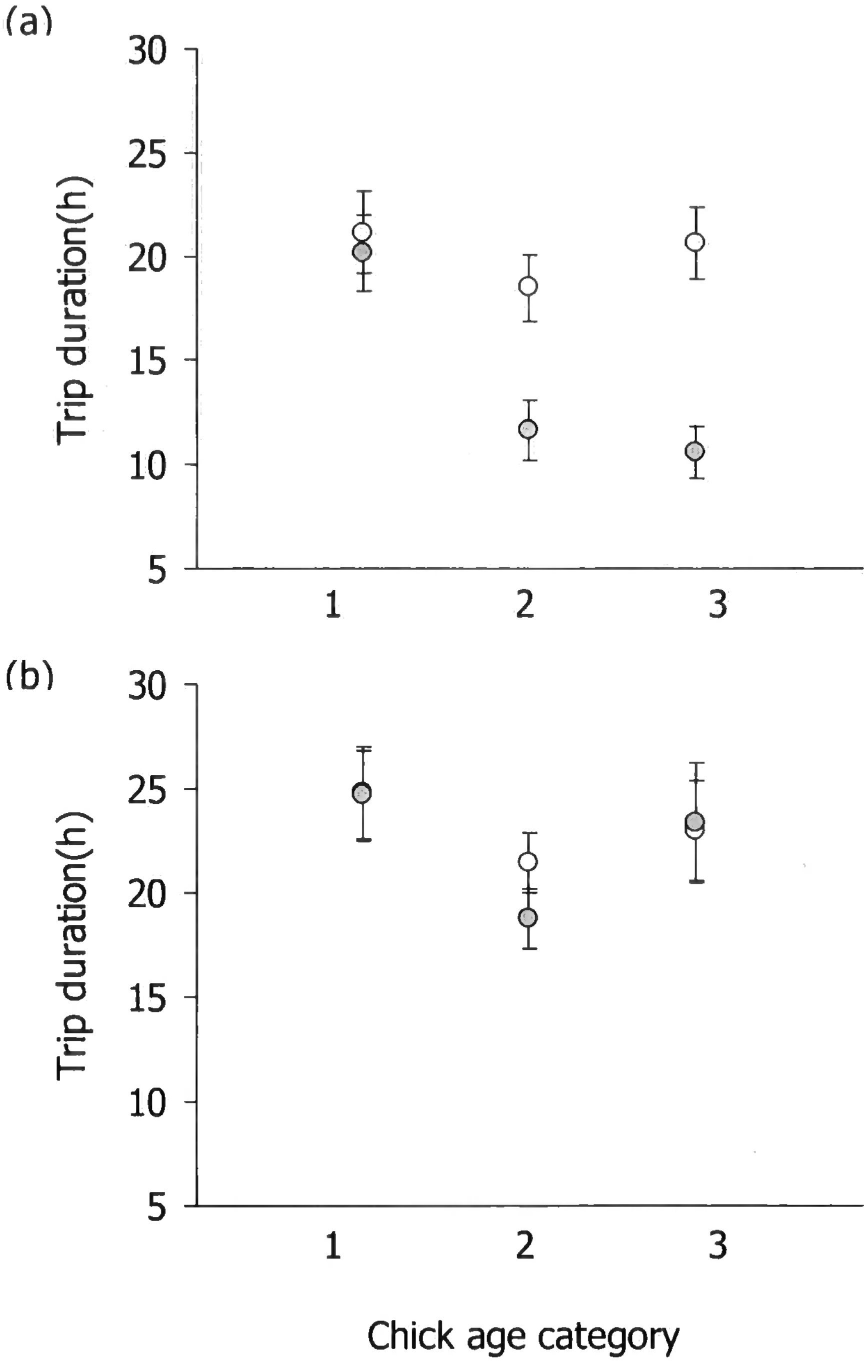

Figure 6.4: Overall mean trip duration (±SE) of male (grey circles) and female (white circles) northern gannets on (a) Great Saltee in 2000 (*n*=45) and (b) the Bass Rock in 2001 (*n*=28), for chicks aged 1-4 weeks (1); 5-8 weeks (2) and 9-12 weeks old (3).

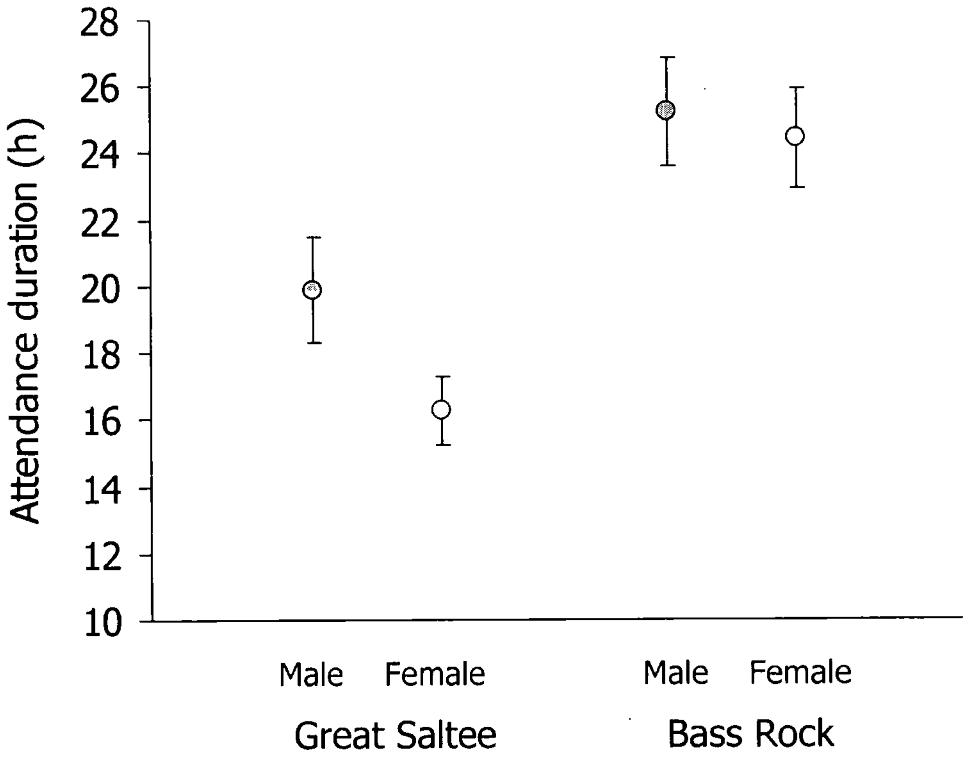

Figure 6.5: Mean nest attendance duration (hours ±SE) of male (grey circles) and female (white circles) northern gannets on Great Saltee in 2000 (*n*=45) and the Bass Rock in 2001 (*n*=28).

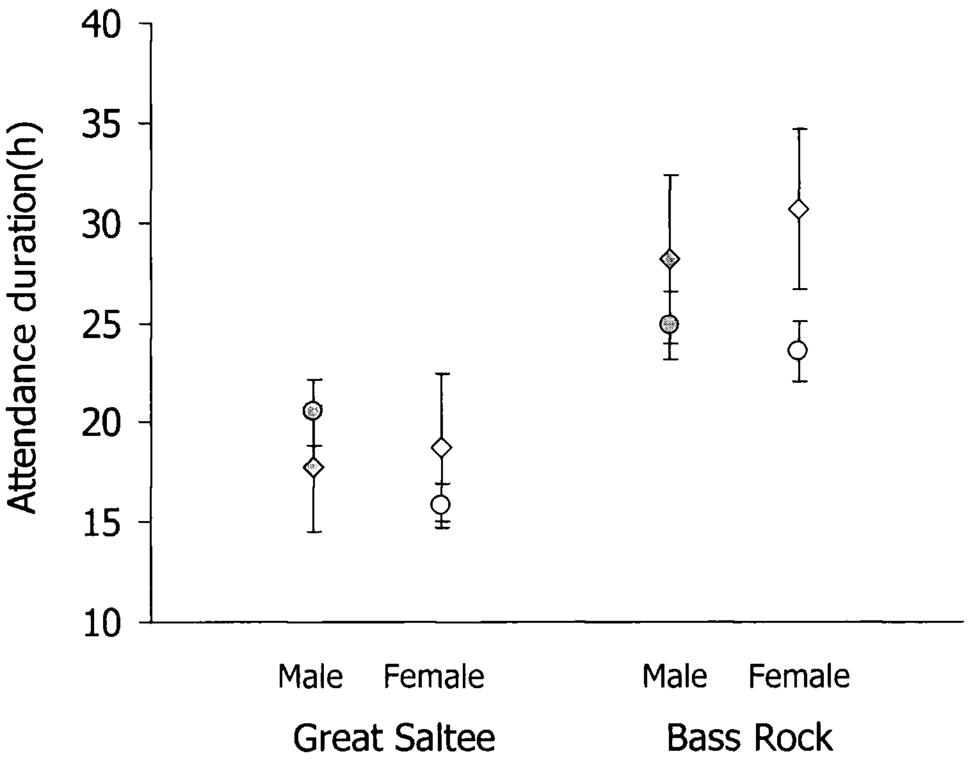

Figure 6.6: Mean nest attendance duration (±SE) of male (grey) and female (white) northern gannets on Great Saltee in 2000 (*n*=45) and the Bass Rock in 2001 (*n*=28), for attendance periods prior to leaving the chick attended (circles) and attendance periods prior to leaving the chick alone (diamonds).

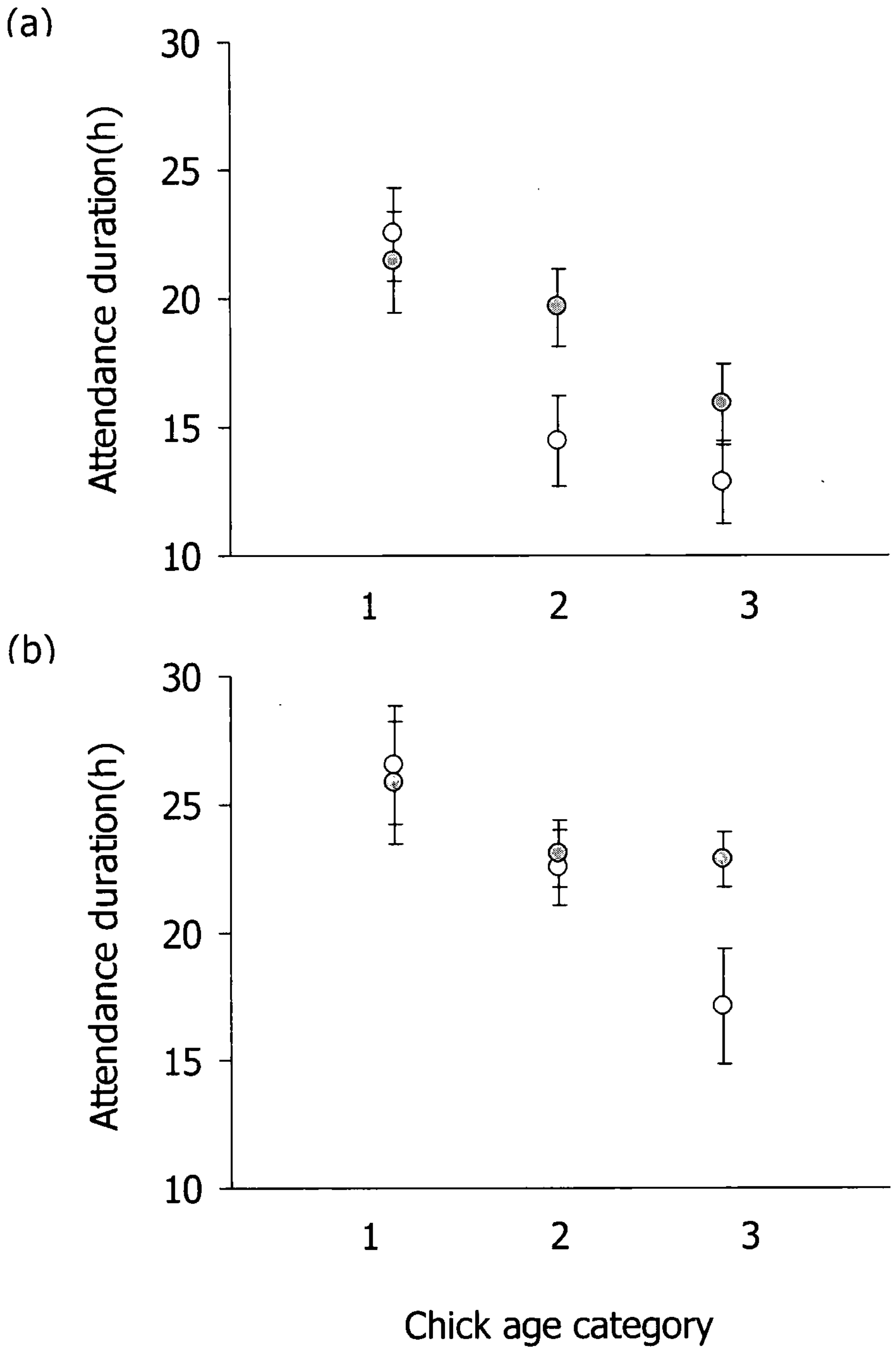

Figure 6.7: Overall mean nest attendance duration (±SE) of male (grey circles) and female (white circles) northern gannets on (a) Great Saltee in 2000 (*n*=45) and (b) the Bass Rock in 2001 (*n*=28), for chicks aged 1-4 weeks (1); 5-8 weeks (2) and 9-12 weeks old (3).

Discussion

When the foraging behaviour of gannets on the Bass Rock and Great Saltee were compared, both striking contrasts and similarities to the Bass Rock emerged. Firstly the overall mean trip duration of gannets on the Bass Rock was approximately 24 hours, while on Great Saltee this was significantly shorter (≈18 hours). The shorter trip duration at Great Saltee compared to the Bass Rock was the same as that reported by Lewis *et al.* (2001; see Chapter 3) when the mean trip duration at both colonies were compared within the same season, reducing the possibility that any differences in foraging behaviour between the colonies reported in this study were confounded by inter-annual variation in environmental conditions.

The differences in trip duration between the two colonies was largely due to sex effects. Whilst there were no sex differences in trip duration on the Bass Rock, males on Great Saltee made significantly shorter trips than females and therefore had correspondingly longer attendance periods. Indeed females on Great Saltee had a very similar trip duration to both males and females on the Bass Rock. The average daily feed rate of chicks on the Bass Rock was 1.1 feeds per day, compared to 1.6 feeds per day on Great Saltee, nearly 50% more than on the Bass Rock. If food loads are of similar size and quality at the two colonies, this represents a large difference in offspring provisioning rate. On the Bass Rock, the overall mean trip duration was lowest when chicks were between 5 and 8 weeks old, although this was most marked in males, and so the feeding rate was maximised over this age range. On Great Saltee, the overall mean trip duration declined with chick age for males, though not for females.

The patterns of trip duration with the chick age were explained by changing strategies of the length and frequency of unattended trips with increasing chick age. There was a striking similarity between the Bass Rock and Great Saltee with unattended trips at both colonies significantly shorter than attended trips and therefore closer to the colony, because trip duration and foraging range are highly correlated (see Hamer *et al.* 2000; Hamer *et al.* 2001). At both colonies, the number and duration of unattended trips increased as chicks got older, but the duration of attended trips remained constant throughout chick rearing. Therefore attended trips were not used to adjust the provisioning rate; this was achieved by increasing the frequency of the shorter unattended trips at certain ages, since chicks were also fed after unattended trips at both colonies.

Chapter 3 addresses how population processes such as density dependent competition for food can affect factors such as population regulation, mediated through foraging behaviour and provisioning rates. Chapter 4 highlights the effects of individual-based factors, notably sex, on foraging behaviour. Our comparison between the Bass Rock and Great Saltee suggests that population and individual processes may interact. The Bass Rock has a much larger population of gannets than Great Saltee, and as competition for food is likely to be more intense in larger colonies, then this may explain why the mean foraging trip duration of adults at the Bass Rock was longer (Lewis *et al.* 2001; see Chapter 3). The intensity of density-dependent competition in the two colonies may also explain the observed sex-colony interactions in trip duration and nest attendance, which will affect sex specific provisioning rates. Males may prefer to make shorter trips to increase the rate of food delivered to the chick, but this may only be possible when intra-specific competition is depressed. Females may not show a similar pattern because they may need to replace energy lost during egg production, and this may only be possible during chick-rearing when overall provisioning rates are fairly high. Through these two processes, males increase the provisioning rate but females do not at smaller colonies . At larger colonies such as Bass Rock, females may only be able to replenish lost energy after the breeding season, when the intensity of competition will be greatly reduced as adults disperse.

There is some evidence that the observed sex-colony interactions between the two colonies are not due to differences in population size. At both colonies, the sexes foraged in different locations: on Bass Rock females tended to forage south east of the colony, while males foraged in all locations (Lewis *et al.* 2002; see Chapter 4), and on Great Saltee, males had shorter trips and therefore foraged closer to the colony than females. Satellite telemetry data on the foraging locations of three adults from Great Saltee in 2000 show that the birds tended to use different foraging areas (see Appendix 2) but the sample size and ratio of males to females were too small to consider any formal analyses related to sex. If sexes have different dietary needs e.g., if females need to replace specific nutrients lost during egg production (Lewis *et al.* 2002; see Chapter 4), then the different foraging locations used by males and females at both colonies may simply be a reflection of differences in prey distribution around the colonies (see Appendix 3).

Chapter 5 suggested that unattended trips enabled the short-term nutritional need of the adult and/or its offspring to be satisfied. Since chicks are fed following unattended trips at both colonies, it seems likely that the function of unattended trips was the same at the both colonies. However, there was a marked sex-colony interaction with regards to the frequency of unattended trips. Both sexes on the Bass Rock made unattended trips at similar rates, while on Great Saltee males made approximately five times more unattended trips than females, the latter only rarely making an unattended trip (six recorded throughout 535 hours of observations). It is very likely that this phenomenon is related to the colony specific sex differences in trip duration, and therefore that the motivation to leave on an unattended trip is different between colonies. On the Bass Rock the motivation to leave a chick unattended was due to an extended time at the nest and/or reduced state of adult and/or chick independent of sex (see Chapter 5). However, on Great Saltee, while females tended not to leave their chicks unattended, males left their chick unattended sooner than expected, which suggests that time was not the cue driving this decision to leave. Similarly it seems unlikely that this was a state-dependent decision because of the higher provisioning rates and lower intra-specific competition for food associated with being at a smaller colony, which may lead to higher chick and adult condition, respectively. Therefore, the risk associated to leaving the chick unattended may be lower at Great Saltee because the *actual* number of conspecifics and prospectors will be smaller at a small colony. Such a reduced risk may shift the trade off away from chick protection to foraging at a smaller colony. One possibility why females on Great Saltee make very few unattended trips may be because males make much shorter trips, maintaining a high provisioning rate and so the trade off between chick protection and provisioning may be less intense. Conversely, the males on Great Saltee may leave their chicks unattended more often because of the lower provisioning rate of the females, and their willingness to do this may be because of the reduced risk of leaving the chick unattended at a smaller colony.

However, there were no data available to establish whether the number of attacks at Great Saltee were any less than on the Bass Rock, in order to test this mechanism.

The approach taken in this chapter has been to make a detailed comparison between two colonies in a range of foraging behaviours. This has revealed some striking inter-colony differences, and interactions between colony and sex, in the foraging behaviour of northern gannets and highlights the danger of inferring general patterns from studies at a single location. It is very likely that there are both density-dependent and density-independent effects occurring that explain the different patterns observed at the two colonies. These findings highlight the need to investigate these processes in much more detail.

References

Benvenuti, S., Bonadonna, F., Dall'antonia, L., & Gudmundsson, G.A. (1998) Foraging flights of breeding thick-billed murres (*Uria lomvia*) as revealed by bird-borne recorders. *Auk*, **115**, 57-66.

Benvenuti, S., Dall'Antonia, L., & Lyngs, P. (2001) Foraging behaviour and time allocation of chick-rearing razorbills *Alca torda* at Græsholmen, central Baltic Sea. *Ibis*, **143**, 402-412.

Casaux, R., Favero, M., Silva, P., & Baroni, A. (2001) Sex differences in diving depths and diet of Antarctic shags at the South Shetland Islands. *Journal of Field Ornithology*, **72**, 22-29.

Creelman, E. & Storey, A.E. (1991) Sex differences in reproductive behaviour of Atlantic puffins. *Condor*, **93**, 390-398.

Croxall, J.P., Naito, Y., Kato, A., & Rothery, P. (1991) Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of Zoology (London)*, **225**, 177-199.

Dall'Antonia, L., Gudmundsson, G.A., & Benvenuti, A. (2001) Time allocation and foraging pattern of chick rearing razorbills in northwest Iceland. *Condor*, **103**, 469-480.

Daunt, F., Benvenuti, S., Dall'Antonia, L., Harris, M.P., Elston, D., & Wanless, S. (2002) Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Marine Ecology Progress Series*, **245**, 239-247.

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

Garthe, S., Benvenuti, S., & Montevecchi, W.A. (2000) Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 1717-1722.

Garthe, S., Gremillet, D., & Furness, R.W. (1999) At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: a case study in Shetland. *Marine Ecology Progress Series*, **185**, 93-99.

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

Gray, C.M. & Hamer, K.C. (2001) Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus*. *Animal Behaviour*, **62**, 117-121.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Kato, A., Croxall, J.P., Watanuki, Y., & Naito, Y. (1992) Diving patterns and performance in male and female blue-eyed cormorants *Phalacrocorax atriceps* at South Georgia. *Marine Ornithology*, **19**, 117-129.

Kato, A., Watanuki, Y., Shaughnessy, P., Le Maho, Y., & Naito, Y. (1999) Intersexual differences in the diving behaviour of foraging subantarctic cormorant (*Phalacrocorax albiventer*) and Japanese cormorant (*P. filamentosus*). *Comptes rendus de l'academie des sciences serie III-sciences de la vie-life sciences*, **322**, 557-562.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., & Hamer, K.C. (2002) Sex specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 1687-1693.

Lewis, S., Sherratt, T.N., Hamer, K.C., & Wanless, S. (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, **412**, 816-819.

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

Prince, P.A., Wood, A.G., Barton, T., & Croxall, J.P. (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*, **4**, 31-36.

Redman, K.K., Lewis, S., Griffiths, R., Wanless, S., & Hamer, K.C. (2002) Sexing northern gannets *Morus bassanus* from DNA, behaviour and morphology. *Waterbirds*, **25**, 230-234.

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.

Schall, R. (1991) Estimation in generalised linear models with random effects. *Biometrika*, **78**, 719-727.

Stahl, J.C. & Sagar, P.M. (2000) Foraging strategies of southern Buller's albatrosses *Diomedea b. bulleri* breeding on the Snares, New Zealand. *Journal of the Royal Society of New Zealand*, **30**, 299-318.

Wanless, S., Finney, S.K., Harris, M.P., & McCafferty, D.J. (1999) Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag *Phalacrocorax atriceps* and the European shag *P. aristotelis*. *Marine Ecology Progress Series*, **188**, 219-224.

Watanuki, Y., Kato, A., & Naito, Y. (1996) Diving performance of male and female Japanese cormorants. *Canadian Journal of Zoology*, **74**, 1098-1109.

Weimerskirch, H. & Sagar, P.M. (1996) Diving depths of sooty shearwaters *Puffinus griseus*. *Ibis*, **138**, 786-794.

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325-342.

Wilson, R.P., Gremillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schafer-Neth, C., Scolaro, J.A., Bost, C.A., Plotz, J., & Nel, D. (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series*, **228**, 241-261.

Chapter 7

General Discussion

General Discussion

Introduction

There is currently widespread concern about the state of world fisheries. Research on the foraging ecology of seabirds and other marine top predators is a focus for fishery management, because in many cases, these top predators are dependent on the same fish as the fishery. The aim of this thesis was to advance our understanding of the foraging ecology of an important predator in the North Atlantic, the northern gannet *Morus bassanus*. The findings also have wider implications in the field of population biology and behavioural ecology because novel tests of hypotheses and predictions have been carried out for the first time within both areas. In this chapter, the aim is to draw together the wider implications of the work, and to set priorities for future research.

Implications of thesis findings

Nearly four decades ago, Ashmole (1963) proposed that seabird populations were regulated during the breeding season, through density-dependent competition for food. He argued that adults foraging close to the breeding colony are likely to cause local prey depletion, so that birds from larger colonies will have to travel further to find food for their chicks than birds from smaller ones. Therefore, chicks from larger colonies will receive less food per unit time than chicks from smaller colonies. Ashmole suggested that the reduced provisioning rates at larger colonies would affect breeding success and in turn population growth, because fewer chicks would survive to recruit back into the population.

The first empirical data to support Ashmole's hypothesis is described in Chapter 3, although Furness & Birkhead's analysis of interactions between the size and distribution of seabird colonies provided compelling indirect evidence (Furness & Birkhead 1984). The very close relationship between foraging trip duration and the square root of colony size is revealing. The data are consistent with the view that intra-specific competition for food can regulate population size, and follows for both cross-sectional and longitudinal data. Although few have contested Ashmole's hypothesis in principal, the evidence has remained elusive until now, although Croxall & Rothery (1991) and Nur & Sydeman (2000) have proposed that density-independent factors may keep certain seabird populations below the levels that density-dependent factors act.

The findings of Chapter 3 differ from Ashmole's original hypothesis in one important respect. Ashmole proposes that intra-specific competition causes local prey depletion. By contrast, Chapter 3 demonstrates that population regulation can be achieved through patterns of prey disturbance rather than depletion. This is significant if we are to understand the short and long term consequences of this predator-prey interaction. In our model, the disturbance response of the prey is predicted to expand and retract in a yearly cycle between the breeding season, when the majority of adults will be constrained to regularly return to the colony, and the non-breeding season, when adults disperse.

The apparent role of intraspecific competition begs the question of why coloniality has evolved in this species. One might expect selection to favour individuals that breed in isolation of conspecific competitors. Other factors must be driving selection for colonial behaviour. The lack of suitable nesting habitat or food is a possible cause for the focussing of populations, but seems unlikely because of the wide range of habitats used for breeding and the diverse food taken (Hamer *et al.* 2000; Appendix 3). There may also be social reasons driving the evolution of coloniality in seabirds. For instance seabirds may learn about good foraging grounds by following successful feeders on a foraging trip (Clode 1993). Large colonies may provide protection from predators, through safety in numbers, although larger colonies will surely be more noticeable (Tinbergen *et al.* 1967).

Chapter 4 describes differences between the foraging behaviour of male and female northern gannets on the Bass Rock. Females tended to depart on a foraging trip in a particular direction, which suggests that the sexes were using different foraging grounds. Females also dived deeper than males and spent more time than males sitting on the sea surface whilst on a foraging trip. These findings provide a new perspective on the field of sex-specific foraging performance following considerable work on size-dimorphic species (Table 4.1). In the latter studies, size differences probably explain much of the variation in competitive ability and/or foraging efficiency between males and females. The observation of sex-specific foraging behaviour of northern gannets suggests that general statements about parental behaviour in monomorphic species cannot be made.

Most studies use structural size to demonstrate dimorphism or monomorphism (but see Croxall 1995 for review). However, an important consideration is body composition. One sex may dominate the other or forage more efficiently than the other due to differing physiologies, such as the ratio of muscle mass to total mass. Thus, the two sexes of northern gannets may vary in a great number of respects that can not be seen by measuring size. Equally, size may not be the true cause of sex differences in foraging performance in size dimorphic species.

For both sexes, the state of the individual and its offspring are critical variables if we are to understand the foraging decisions of breeding adults, as illustrated in Chapter 5. Intriguing foraging patterns are evident with respect to trips when an individual leaves its chick with its partner compared to when the bird leaves its chick unattended. Whilst it was not possible to measure the amount of food fed to chicks directly, it would appear that parents were departing on unattended foraging trips because their partner had been away for an extended period and/or because they themselves returned from their previous trip with a low arrival mass (which might infer insufficient food for the chick). The cue is likely then to be the state of the chick rather than the parent, but further work is required to establish this conclusively. The characteristics of these unattended trips are also of prime interest with respect to short-term and long-term implications of state dependent behaviour. Unattended trips were shorter, and by implication closer to the colony, where the bird would find food quickly to satisfy a short-term need. Nothing is known about the profitability of near and distant foraging grounds, but it seems likely that those closest to the colony are not the most profitable because attended trips, which are much more common than unattended trips at all times, would use these grounds as well. Unattended trips occurred more often, and increased in duration, as chicks got older for both males and females. There was no equivalent difference with attended trips. This highlights the complex interaction between chick protection, the more prominent behaviour, and unattended foraging.

Clearly, this work illustrates the need to take account of state and density dependence when drawing conclusions at the population level. Indeed, this was one of the main conclusions to emerge from the detailed comparison between the foraging behaviour of gannets at the Bass Rock and Great Saltee (Chapter 6). Trip durations on Great Saltee were significantly shorter than on Bass Rock, as expected from the findings in Chapter 3. On Great Saltee, males made significantly shorter attended trips than females, and many more unattended trips. There was also evidence that the sexes were foraging in different locations at both colonies (Great Saltee: different distances from the colony; Bass Rock: similar distances but different directions away from the colony). The approach taken offers evidence for an interaction between individual based foraging decisions and density dependent competition for food, a prominent theme throughout this thesis.

The findings from this thesis are very relevant to conservation biology: both temporal and spatial scales are clearly important when predicting marine area usage, a key factor in the designation of protected areas, and that birds from larger colonies have greater foraging ranges must now be considered. Furthermore, that males and females use different areas and forage closer to the colony under certain circumstances, has added another level of complexity to determining where birds forage and has been an incredibly important finding. Overall this highlights that our colonies may need different forms of protection at certain times of the year.

Future work

The findings of this thesis have highlighted a number of important priorities for further work. Identifying the ultimate causes of population regulation remains at the forefront of demographic and conservation biology. The evidence described in this thesis of the role of intraspecific competition is compelling, but causality was not confirmed. Two lines of research are now required. First, the link between competition and regulation must be tightened. In this thesis, a strong relationship between foraging range and population growth rate was established. However, very little is known about the interaction between predators and prey in the marine environment, because of the formidable logistical problems. Prey disturbance, in which the magnitude of the effect is dependent on the size of the predator colony, is a compelling idea, but ultimately the prey response must be demonstrated directly. If possible, one could quantify how long different sized groups of foraging seabirds persist at sea, before moving on to another shoal of fish, whilst using ultra sound to determine the size of the shoal, but without knowing the status of the individuals foraging, this may be less instructive. One of the prime concerns is the question of scale. The patterns of disturbance driving the expanding foraging ranges with increasing colony size are operating on scales that would be very difficult to measure in the field. It is hard to envisage a field protocol that would work with current technology. Even general patterns of prey distribution are only available at too crude a scale, both temporally and spatially. Optimistically, cameras carried by predators, might be able to sample prey distribution and behaviour at a finer scale.

There is more opportunity for further work linking foraging range with breeding success more tightly than was possible here. Whilst feeding rates were shown to be lower at larger colonies, due to the longer trip durations, food load size was not quantified, nor was offspring condition, parental condition or breeding success measured directly. Some data from monitoring work were available on breeding success at some of the gannetries, but found no evidence for a difference in this attribute between colonies. However, the sample size for these data is small and moreover, population regulation may occur not because of a reduced breeding success, rather it may be due to reduced condition of fledglings, emigration to a better site or lower adult survival at larger colonies. Thus, comparative data on provisioning rate, offspring condition, adult condition and breeding success are required across a range of colony sizes. Another priority for the future lies in the impact of immigration and emigration on population growth rate. Moss *et al.* (2002) suggest that new gannetries have higher immigration rates than older, larger colonies, which tend to be the providers of new recruits to the former. An intercolony programme of ringing, or the use of molecular techniques which could distinguish birds from different colonies (Parker *et al.* 1998), would be required to factor these important processes in.

Whilst extensive observational data would be very instructive, an experimental approach is ultimately required to establish a causal link between intraspecific competition for food and population regulation. A number of approaches are available in theory. One option would be to manipulate colony size and monitor the foraging range of individuals at these experimental colonies. If, for example, birds at an experimentally decreased colony had a shorter foraging trip duration, a causal link between range and colony size would be established. Food supply could be reduced around small colonies to the levels at which large colonies are predicted to be taking prey, to see whether the growth rate of that colony drops to the level of the larger colony, thereby demonstrating a link between food supply and population regulation. In such a case, the findings would support Ashmole's depletion model, as Birt *et al.* (1987) have done with observational data, rather than models of prey disturbance.

Manipulation of colony size is of course morally completely unthinkable. It is mentioned here for academic reasons only (a "thought experiment"), and might be appropriate in other contexts where colonies can be manipulated simply and without harm to the animals. Manipulation of the marine food supply, through disturbance or removal, also raises ethical concerns for the fish, and there would be issues to contend with, with respect to local fishermen. Researchers in the past may have felt able to solve or at least come to terms with the moral issues of this kind of experiment, but logistical hurdles have largely precluded them from taking place. Where this approach has generally been more successful is when the manipulation is already taking place for other reasons, and scientists have been able to influence the design of the manipulation, such as current studies harvesting kelp beds and monitoring impacts on fish and great cormorants (David Grémillet, pers. comm.).

In general, the experimental approach employed by seabird scientists has been to manipulate food requirements at the nest as a surrogate for artificial changes in food supply (Cook & Hamer 1997; Tveraa *et al.* 1998; Nager *et al.* 2000; Weimerskirch *et al.* 2000). In the context of this work, experiments of this kind would improve our understanding of the relationship between the breeding birds and energy requirements. However, it is not clear how experiments such as brood manipulation or supplementary feeding would tell us whether intra-specific competition around colonies regulates population size.

The demonstration of sex-specific foraging decisions in a monomorphic bird raises a number of unanswered questions. Ultimately the goal must be to find mechanisms underlying these patterns. Measuring competitive ability and foraging efficiency would be a first priority, as they are the two processes that are thought to be most important in size dimorphic species, but they would be extremely challenging to measure in the field. To establish whether the two sexes have different nutrient requirements is considerably more tangible, and demands a physiological approach. For example, much progress is currently being made on the nutrient contents of eggs (Carey 1996), the sole responsibility of the female in species without courtship feeding like the northern gannet.

Priorities for future work on state dependent foraging decisions lie primarily in the ability to distinguish chick from adult state, in order to fully understand state-dependent foraging dynamics. As with aspects of the sex-dependent work described above, a physiological approach is required to more completely examine the effect of state (Brown 1996).

The experimental approach should play a large role in sex and state-dependent foraging dynamics. Both at the whole animal and molecular level, the manipulative approach would certainly aid in establishing causality between sex and/or state and foraging behaviour. For example, a supplementary feeding experiment of nutrients that the female dedicates to the egg (Blount *et al.* 2002), followed by measurement of foraging location of known prey availability, would establish whether the foraging decisions of females are based on the search for specific nutrients.

The overall priority for future work that arises from the final results chapter in this thesis is to expand the approach to include a much larger sample of colonies of different size, such as the number studied in Chapter 3, and to collect all the data that was achieved at the two colonies set out in Chapters 4, 5 and 6, plus the priorities set out in the paragraphs above. This is a massive task, but it is that level of detail on individual and population based processes that, combining observational work with carefully designed experiments, will reveal the closest picture of the interaction between the two.

Model systems

The northern gannet has provided a highly suitable species for many aspects of this study. It would also be appropriate as a model system for a number of the future priorities set out above. For example, an examination of the nutritional requirements of the two sexes would be tractable in the field, although the physiological processes are not currently well understood. However, the northern gannet is not the best species to develop other aspects of this work for a number of reasons. In the aim to tighten the link between intra-specific competition and population regulation, the measurement of provisioning rates and adult and chick condition at a number of gannetries would not be possible because most, whilst suitable for observing trip durations, are not easily accessible. Even for accessible colonies, it is not easy to quantify chick provisioning. A nest balance design that would distinguish parent from offspring mass, as well as factor in progressive mass gain from guano, is hard to envisage in a busy gannetry. Establishing the mechanisms of sex-specific foraging patterns is also extremely difficult, because of the species' pelagic foraging strategy.

A seabird species is the appropriate choice for further work if a tight link is to be maintained with both interests of this thesis, namely the interaction between individual behaviour and population dynamics, and the relevance of these findings to applied ecology. A number of candidate species would be appropriate model systems for the future observational work proposed. However, as with the northern gannet, other seabird species would be associated with the same limitations for experimental work. If the applied perspective is put to one side, other model systems could be considered. For example, invertebrates would open a host of opportunities for further work, because of the ease of manipulation both logistically and morally.

Conclusions

Northern gannet populations in Britain and Ireland are reaching a fascinating point in their recent history. Based on the colony size specific population growth rate figures shown in Chapter 3, the largest colonies are approaching the critical size (c 40,000 pairs) above which no further increase in size is predicted using the relationship shown in Figure 3.4. Whether they will stabilise or even decline with time remains to be seen. This is a fascinating crossroads both from the point of view of population dynamics, but also for the conservation of a species of which the UK and Ireland holds a greater proportion of the world's population (71%; Lloyd *et al.* 1991) than any other seabird. How the large gannetries' population sizes change in the coming years may depend not only on intra-specific competition for food, but on many other factors. Two very notable ones are worth mentioning. First, a number of other seabird species and marine mammals compete for the same food as gannets, and they may play a large role in gannet population regulation. Second, the impact of human activities, in particular the fish that we remove from the oceans, and in the direct effect we are having on climate change, may have a crucial role to play. Thus a multi species approach to population regulation, which considers anthropogenic effects, should be the next challenge.

It is hoped that this thesis has highlighted a number of important features of the life history and population biology of the northern gannet, a key top predator in the North Atlantic. It is also acknowledged that the complex interactions between different species and trophic levels, with humans playing an important role, demands ever more complex approaches to species and ecosystem ecology.

References

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, **103b**, 458-473.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., & Montevecchi, W.A. (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, **40**, 205-208.

Blount, J.D., Surai, P.F., Nager, R.G., Houston, D.C., Moller, A.P., Trewby, M.L., & Kennedy, M.W. (2002) Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 29-36.

Brown, M.E. (1996) Assessing body condition in birds. *Current Ornithology*, **13**, 67-135.

Carey, C. (1996) *Avian Energetics*. Academic Press, New York.

Clode, D. (1993) Colonially breeding seabirds: predators or prey. *Trends in Ecology and Evolution*, **8**, 336-338.

Cook, M.I. & Hamer, K.C. (1997) Effects of supplementary feeding on provisioning and growth rates of nestling puffins *Fratercula arctica*: evidence for regulation of growth. *Journal of Avian Biology*, **28**, 56-62.

Croxall, J.P. (1995) Sexual size dimorphism in seabirds. *Oikos*, **73**, 399-403.

Croxall, J.P. & Rothery, P. (1991). Population regulation of seabirds: implications of their demography for conservation. In *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. LeBreton & G.J.M. Hirons), pp. 272-295. Oxford University Press, Oxford.

Furness, R.W. & Birkhead, T.R. (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature*, **311**, 655-656.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Lloyd, C., Tasker, M.L., & Partridge, K. (1991) *The Status of Seabirds in Britain and Ireland*. T & AD Poyser, London.

Moss, R., Wanless, S., & Harris, M. (2002) How small northern gannet colonies grow faster than big ones. *Colonial Waterbirds*, **25**, 442-448.

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

Nur, N. & Sydeman, W.J. (2000) Survival, breeding probablity and reproductive success in relation to population dynamics of Brandt's cormorants *Phalacrocorax penicillatus*. *Bird Study*, **46**, S92-103.

Parker, P.G., Snow, A.A., Schug, M.D., Booton, G.C., & Fuerst, P.A. (1998) What molecules can tell us about populations: choosing and using a molecular marker. *Ecology*, **79**, 361-382.

Tinbergen, N., Impekoven, M., & Franck, D. (1967) An experiment in spacing-out as a defence against predation. *Behaviour*, **28**, 307-321.

Tveraa, T., Saether, B.-E., Aanes, R., & Erikstad, K.E. (1998) Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology*, **67**, 699-704.

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

Appendix 1

Chick age plumage characteristics

Chicks were aged from observations in the field using age-specific plumage characteristics given in Table A.1.1 (adapted from Nelson (2002) and Wanless, pers. comm.).

Table A.1.1: Chick age from specific plumage characteristics.

Chick age (weeks)	Description
1	Fairly black, with sparse, hair-like down; very wobbly (normally brooded constantly by adult)
2	Partly covered with down; larger than parents' feet; head and neck bare; movements well coordinated
3	Body and wings covered in white down, but lacks luxuriantly fluffy look of 4 week old; cannot be covered by parent
4	Down long and fluffy; two-thirds adult size, taking up most of the nest
5	Still fluffy, approaches adult size; pin primary and tail feathers show black through the down.
6	Fluffy, but scapulars, wings, and tail-feathers clear of down; looks bigger than parent
7	Mantle and back a mixture of white down and black feathers breast upperparts, head and neck covered in long white down
8	Mainly black above; down disappearing from forehead, mantle/back, and tail
9	Down starts to go from ventral surface, but still thick on flanks, belly, and parts of neck; looks scruffy
10	Some down on nape, flanks, and back
11	Only wisps of down remain, on nape and flanks
12	Completely juvenile plumage

References

Nelson, J.B. (2002) *The Atlantic Gannet* Fenix Books Ltd., Norfolk.

Appendix 2

Foraging locations from satellite telemetry on Great Saltee in 2000

The foraging locations of northern gannets from Great Saltee during chick rearing were investigated using satellite telemetry. Tags were attached on 10 July and locational data were collected until the last tag fell off on 9 August 2000. Satellite tags (Platform Terminal Transmitters; Microwave Telemetry Inc., USA) weighing 30g were attached in the same way as radio tags (see Chapter 4) and a small sample of blood was taken for sexing (see Chapter 2). Data from the satellite tags were processed using the ARGOS facility (CNES, France). Only location classes above 0 were used (see Hamer *et al.* 2000 for further details) to increase the accuracy of these data. The locations obtained from each bird were distinguished by different symbols and overlaid on a projection of the UK and Ireland using ArcGis (see Figure A.2.1).

Figure A.2.1 illustrates that although there is a lot of variation in location between and within birds, there appears to be a tendency for individuals to use particular areas.

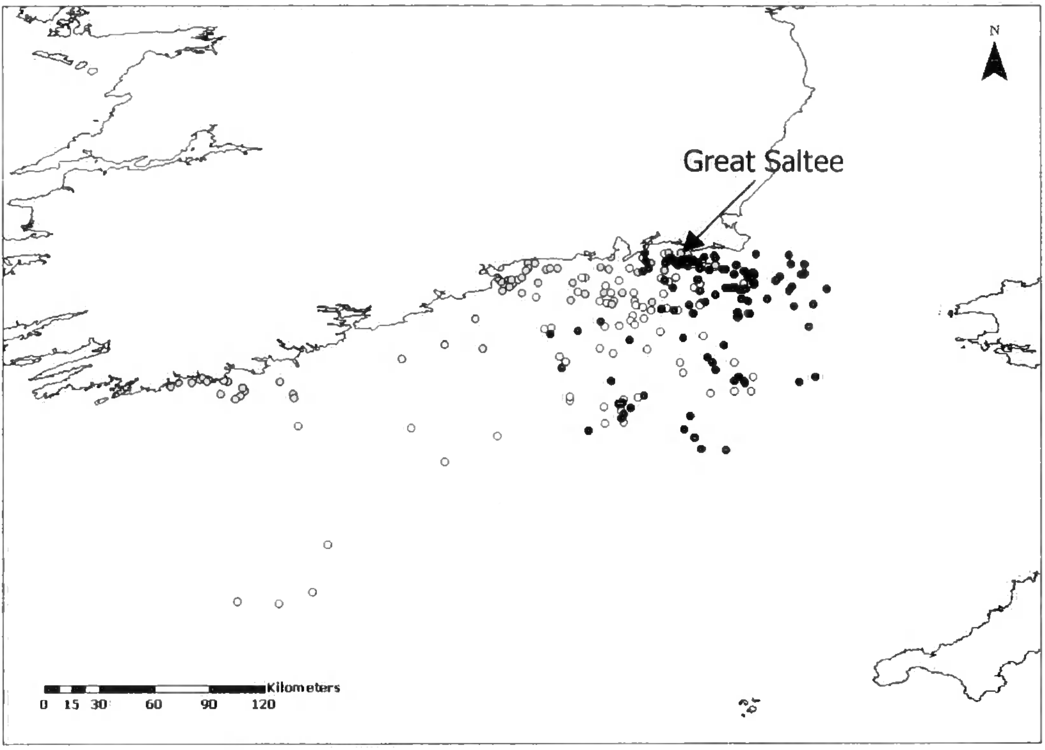

Figure A.2.1: Foraging locations of northern gannets (*n*=3) on Great Saltee, SE Ireland, in 2000, during chick rearing. The location of the two different males, are shown separately as white and black circles, and the locations from the single female are shown as grey circles (see Figure 3.2 for locations of other gannetries).

References

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of Gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Appendix 3

Diet of northern gannets on Great Saltee and the Bass Rock

The diet of northern gannets was investigated on Great Saltee in 2000 and the Bass Rock in 2001 by obtaining food samples from voluntary regurgitations from adults and chicks. On Great Saltee, a total of 40 food samples were obtained from chicks that regurgitated during the routine handing associated with ringing on the 19 June and 17 July 2000 (carried out by Oscar Merne of Duchas, Ireland), whilst on the Bass Rock, 48 food samples were collected between 19 June and 15 August 2001 from adult birds that voluntarily regurgitated when moving away from researchers walking on the footpath.

An immediate qualitative assessment was made of the species composition and approximate size of individual items. Most prey items were too digested to allow accurate measurements of body length and estimates of prey size were derived indirectly from sagittal otoliths or vertebrae length (Härkönen 1986; Watt *et al.* 1997). Each regurgitate was placed in a saturated solution of biological washing powder (Biotex) and kept in an oven at 40-50 °C for at least 5 hours until flesh and soft material had been digested. All the remaining otoliths and fish bones were identified using a binocular microscope (25x magnification) and keys in Härkönen (1986) and Watt *et al.* (1997).

The presence ('1') or absence ('0') of the four main prey types (sandeels, mackerel, clupeids and gadoids) and a final category containing all other prey species was recorded for each diet sample. For each colony, the number of samples of each possible combination of presence/absence of the five prey types (n = 32) was counted. A table of diet distribution was formulated containing 64 rows (32 x 2 colonies) and seven columns (five prey types, colony id, number of samples).

A type III generalised linear model (GLM) with a poisson error distribution and a logarithm link function was fitted and the inter-colony diet differences were assessed from the interactions between colony and prey type. The model was instructed to remove the rows with forced zeros prior to analysis, i.e., the combination where all prey types were absent, because this was not a valid combination due to our method of sampling diet. The deviance values show the effect of removing each term from the model and are distributed by χ^2.

Great Saltee: The main prey types were sandeels (lesser sandeel *Ammodytes marinus* and greater sandeel *Hyperoplus lanceolatus*), gadoids (whiting *Merlangius merlangius*, Norway pout *Trisopterus esmarcki* and unidentified gadids), mackerel *Scombrus scombrus*, garfish *Belone belone*, clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*), plaice *Pleuronectes platesa*, hake *Merluccius merluccius*, red gurnard *Aspitrigla cuculus*, dragonet *Callionymus lyra*, bull-rout *Myoxocephalus scorpius*, salmon *Salmo salar* and scad *Trachurus trachurus*, in decreasing order of importance (see Table A.3.1a). The size of prey varied widely from 55 mm (0-group sandeels) to 650 mm (garfish) (see Table A.3.2a).

Bass Rock: The main prey types were lesser sandeels, mackerel, clupeids (herring and sprat), gadoids (cod *Gadus morhua,* haddock *Melanogrammus aeglefinus,* whiting, Norway pout), flatfish (halibut *Hippoglossus hippoglossus* and long rough dab *Hippoglossoides platessoides*), hake, red gurnard and dragonet, in decreasing order of importance (see Table A.3.1b). The size of prey varied widely from 60 mm (0-group sandeels) to 407 mm (mackerel) (see Table A.3.2b).

There were no differences in the occurrence of sandeels, clupeids, mackerel or gadoids between colonies but there was a significant interaction between "other" prey items and location due to Great Saltee having a greater number of food samples containing these other prey types than the Bass Rock (GLMM, sandeel*location: deviance = 0.32, p = 0.573; GLMM, mackerel*location: deviance = 0.093, p = 0.093; clupeid*location: deviance = 0.01 p = 0.932; gadoid*location: deviance = 1.60, p = 0.206; other*location: deviance = 15.21, p < 0.001).

Diet data of gannets from the Bass Rock in 1998 from Hamer *et al.* (2000) show similarities in the prey taken, but differences in the frequency of occurrence seem apparent (although not tested statistically). Sandeels and mackerel were more important in the diet in 2001 than in 1998 (frequency of occurrence of sandeels and mackerel in 1998 were 31.6 % and 29.3 % respectively), while clupeids were much less important (herring: 21.5 %; sprat: 23.0 % in 1998). Whether the increase in occurrence of sandeels in the diet is related to the closure of the sandeel fishery in the Wee Bankie since 2000 is not known.

Table A.3.1: Diet of adult gannets *Morus bassanus* at (a) Great Saltee in 2000 (*n*=40) regurgitates and (b) the Bass Rock in 2001 (*n*=48; from chicks).

(a)

Species	Frequency of occurrence (%)			
	All (n=40)	Jun (n=15)	Jul (n=25)	Aug (n=0)
Ammodytidae	35	33	36	
0-group	15	13	12	
Older	28	20	28	
Gadidae	23	33	16	
Scombridae	20	33	24	
Belonidae	15	7	20	
Clupeidae	13	27	4	
Pleuronectidae	13	7	16	
Merlucidae	8	7	8	
Triglidae	8	13	4	
Callionymidae	8	13	4	
Cotidae	3	0	4	
Salmonidae	3	7	0	
Carandidae	3	7	0	

(b)

Species	Frequency of occurrence (%)			
	All (n=48)	Jun (n=8)	Jul (n=29)	Aug (n=11)
Ammodytidae	48	38	55	36
0-group	48	50	55	36
Older	4	0	7	0
Scombridae	46	50	41	55
Clupeidae	15	0	10	36
Gadidae	6	25	14	0
Pleuronectidae	4	0	3	9
Merlucidae	2	0	3	0
Triglidae	2	13	0	0
Callionymidae	2	0	3	0

Table A.3.2a: Lengths (mm) of fish eaten by gannets *Morus bassanus* at Great Saltee in 2000.

Family	Species	n sampled	n measured	Mean	SD	Min.	Max.
Ammodytes	Lesser sandeel						
	0-group	5	5	82.5	26.32	55	113
	Older	4	4	180.1	36.95	149	232
Ammodytes	Greater sandeel						
	0-group	6	6	161.8	19.16	127	184
	Older	3	3	276.4	32.82	257	314
Scombridae	Mackerel	8	8	315.1	85.17	119	400
Clupeidae	Sprat/Herring	9	9	158.3	103.66	78	410
Belonidae	Garfish	1	1	650.0		650	650
Pleuronectidae	Plaice	4	4	210.8	26.30	187	248
Gadidae	Whiting	1	1	299.0		299	299
Gadidae	Norway pout	1	1	217.0		217	217
Merlucidae	Hake	4	4	283.0	33.09	236	312
Triglidae	Red gurnard	3	3	340.3	40.05	297	376
Callionymidae	Dragonet	3	3	256.3	21.94	239	281
Cotidae	Bull-rout	1	1	119.0		119	119
Salmonidae	Salmon	1	1	241.0		241	241
Carandidae	Scad	1	1	279.0		279	279

Table A.3.2b: Lengths (mm) of fish eaten by gannets *Morus bassanus* at the Bass Rock in 2001*.

Family	Species	n sampled	n measured	Mean	SD	Min.	Max.
Ammodytes	Lesser sandeel						
	0-group	2321*	539**	84.8	9.18	60	110
	Older	6	6	109.1	17.90	91	135
Scombridae	Mackerel	17	17	312.4	35.06	260	407
Clupeidae	Sprat/Herring	87*	45**	81.6	13.39	64	117
Gadidae	Cod	1	1	230.0		230	230
Gadidae	Haddock	7	7	240.6	68.94	155	343
Gadidae	Whiting	3	3	246.7	55.00	192	302
Gadidae	Norway pout	1	1	99.0		99	99
Pleuronectidae	Halibut	1	1	339.0		339	339
Pleuronectidae	Long rough dab	2	2	315.0	41.01	286	344
Merlucidae	Hake	1	1	220.0		220	220
Callionymidae	Dragonet	1	1	219.0		219	219
Triglidae	Red gurnard	1	1	150.0		150	150

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* total number of otoliths extracted from food samples; ** = number of fish measured (from intact fish, otoliths or vertebrate obtained from sample). Where paired otoliths present in sample, the mean was used in the calculation of the overall mean, except for 0 group sandeel and clupeids, where it was impossible to identify pairs).

References

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P., & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of Gannets in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, **200**, 257-264.

Härkönen, T. (1986) *Otoliths* Danbiu ApS, Hellerup, Denmark.

Watt, J., Pierce, G.J., & Boyle, P.R. (1997) Guide to the identification of North Sea fish using premaxillae and vertebrae. *ICES Cooperative Research Report*, **No. 220**.