Foraging and food provisioning strategies of Northern Fulmars and Manx Shearwaters

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Foraging and Food Provisioning Strategies of Northern Fulmars and Manx Shearwaters

Catherine Mairi Gray

Presented in candidature for the degree of Doctor of Philosophy

University of Durham
Department of Biological Sciences
2001

Candidate's Declaration

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Foraging and Food Provisioning Strategies of Northern Fulmars and Manx Shearwaters
Ph.D. thesis submitted by Catherine Mairi Gray, 2001

Abstract

Northern fulmars and Manx shearwaters are pelagic seabirds of the Order Procellariiformes, a group that is characterised by extreme life-history traits. Many of these traits have been associated with the unpredictability of marine food sources. However, fulmars and Manx shearwaters feed their chicks at relatively frequent intervals compared with other procellariiforms, and the life-history implications of this strategy are poorly understood. In this thesis I examined food provisioning and chick growth strategies in fulmars and Manx shearwaters, and discussed these strategies in the context of life history – environment interactions. I tested the efficacy of a periodic weighing method for assessing food provisioning, and found that this gave a very similar estimate of the frequency and size of feeds compared to periodic weighing combined with data on parental attendance, determined by radio tracking. However, periodic weighing was much less effective at distinguishing meals from one or two parents. In Manx shearwaters, chick growth was highly correlated with food provisioning rate, and both variables showed significant annual variation. Both individual and environmental effects contributed to this variation, and in particular, peak mass showed highly significant repeatability coefficients. Fulmars showed significant variation in breeding success, diet and chick growth between two years, but chicks were apparently heavier in a very poor year. This was caused by differential mortality of chicks in poor condition. In Manx shearwaters, male parents visited the nest more frequently and made a greater contribution to food provisioning than females, a strategy that has seldom been reported in sexually monomorphic seabirds. I used a cross-fostering experiment to examine the parent-chick interactions responsible for the mass recession period prior to fledging in Manx shearwaters. Both parents and chicks had an active role in controlling food intake, and the results indicated that mass recession was not caused by parental desertion as previously thought.

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Chapter 1

General Introduction

Life-history traits encompass patterns of growth, reproduction and longevity in an organism. Many of these traits are adaptations of organisms to the environment in which they are found, and they also interact with other life-history traits. Such interactions may produce constraints so that allocation decisions must be made between conflicting life-history traits (Begon *et al.* 1986). Life-history theory predicts a number of trade-offs faced by an organism during its lifetime (Roff 1992; Stearns 1992). For most iteroparous animals, reproduction is envisaged as a costly process in which finite resources must be partitioned between current and future reproductive events (Drent & Daan 1980; Boggs 1992). Reproduction imposes two major energetic demands on birds; egg production and, except in species with precocial young, providing food for the offspring. The input of parents to egg production (Bolton *et al.* 1992; Monaghan *et al.* 1995; Heaney & Monaghan 1995) and food provisioning (Nur 1984; Ydenberg & Bertram 1989; Kacelnik & Cuthill 1990; Sæther *et al.* 1993; Weimerskirch *et al.* 1995; Tveraa *et al.* 1998) have been well studied in recent years. This thesis focuses only on the latter, which for many birds is the most energetically demanding component of reproduction

(Ricklefs 1983). However, any costs incurred prior to hatching, such as egg production or fasting during incubation, may create an energy deficit in addition to the energetic requirement of feeding a brood (Monaghan *et al.* 1998).

1.1. Relationship between marine food availability and seabird life-histories

Lack (1968) hypothesised that brood size and nestling development rates in birds were constrained by the abundance and proximity of food supplies. Compared with most avian groups, seabirds tend to have small clutch sizes and slow rates of embryonic and postnatal development, although they exhibit a variety of modes of development. Within seabirds, the general trend is for inshore feeders to have larger and faster developing broods than offshore feeders. Pelagic seabirds also tend to have lower adult mortality and a greater age of first breeding than inshore feeders (Lack 1968; Hamer *et al.* 2001).

During the breeding season, pelagic seabirds are central place foragers, and many species travel hundreds or even thousands of kilometres from the nest (Pennycuick *et al.* 1984) to exploit prey with a patchy and unpredictable distribution, both spatially and temporally (Ashmole 1971). The energetic demand of providing food for the offspring is thought to be particularly high in pelagic seabirds, due to the constraint of transporting food between distant feeding grounds and the nest site (Houston 1995). Pelagic feeding also imposes the problem of maintaining a regular pattern of food provisioning to meet the energy requirements of the developing chick (Weimerskirch & Cherel 1998).

Pelagic seabirds of the Order Procellariiformes (e.g. albatrosses, petrels and shearwaters) represent one extreme of the life-history spectrum in birds. Procellariiforms are characterised by deferred breeding (for up to 12 years; Warham 1990) and low annual fecundity, with a slow-growing, single-chick brood raised annually (Ricklefs 1990) or even biennially (Tickell 1968; Prince & Ricketts 1981; Tickell 2000). The age of first breeding may be partly related to body size (Croxall & Gaston 1988; but see Hamer *et al.* 2001) and is correlated with annual adult survival (Hamer *et al.* 2001). However, foraging ability probably acts as a proximate constraint on age at first breeding, since pelagic seabirds are thought to defer breeding until their foraging efficiency allows them to meet the chick's energy demands as well as their own (Weimerskirch 1992; Berrow *et al.* 2000).

Slow growth rates and low annual fecundity have been attributed to constraints of large foraging ranges and the unpredictable distribution of marine prey (Lack 1968; Ashmole 1971). However, the relationship between reproductive output and the availability of marine food resources is much more complex than previously thought. For instance, experimental brood enlargements have shown that seabirds are capable of increasing provisioning rates (see Ydenberg & Bertram (1989) for a review), and many studies reported no negative effect of brood enlargements on adult body mass or adult survival (Stearns 1992). These findings have questioned the view that average clutch size corresponds to the number of offspring that can be raised in a given season.

An alternative to Lack's (1968) hypothesis is that clutch size corresponds to the number of offspring that can be raised under unfavourable environmental conditions, rather than the maximum number that can be raised when conditions are optimal (Ricklefs 1990; Hamer *et al.* 2001), thus reducing the risk of adult mortality in bad years. Procellariiform seabirds produce a single chick brood, and in keeping with Ricklefs' (1990) hypothesis, some species breed successfully in all but the poorest conditions; however, others are limited to breeding only in the most favourable years (Chastel *et al.* 1995). Since procellariiforms have no capacity to increase the number of offspring they produce in a single breeding season, even in favourable conditions, offspring quality is a particularly important fitness component. Interactions between food availability and parental foraging ability may therefore affect the ability of parents to produce a high quality chick with high reproductive potential.

Procellariiform seabirds exhibit physiological and behavioural adaptations to exploiting highly variable marine food resources. For example, nestlings accumulate large lipid deposits, which may function as a buffer against unpredictable food provisioning (Hamer & Hill 1993; Ricklefs & Schew 1994; 1997; Bolton 1995; Hamer & Thompson 1997; Hamer *et al.* 2000), and parents adopt foraging strategies, either individually or as pairs, which combine distant foraging trips with more frequent visits to feed the chick (Weimerskirch *et al.* 1997; Weimerskirch & Cherel 1998; Booth *et al.* 2000). For many procellariiforms, however, the roles of individual parents in foraging and food provisioning are only poorly understood.

1.2. Natural and human influences on seabird breeding ecology

Breeding success in many seabird populations is affected by natural or fisheries-induced depletion of fish stocks (see Furness (1996) for a review). The sensitivity of seabirds to changes in food supply is influenced by their mode of foraging, with specialised, surface feeding species being most affected (Furness & Ainley 1984; Burger & Piatt 1990). The flexible feeding behaviour, large foraging ranges and inexpensive mode of flight in procellariiforms make them less susceptible to localised food shortages (Furness & Ainley 1984), and nestling lipid reserves may reduce the impact of variable food provisioning. However, occasional food shortages affecting procellariiform chick growth or survival have been recorded (Harris 1969; Granadeiro *et al.* 1998; Huin *et al.* 2000). Commercial fisheries may also have a positive effect on food availability through discarded fisheries waste (Hudson & Furness 1989; Furness 1996), because discards form part of the diet of many pelagic seabirds (Croxall *et al.* 1995; Camphuysen & Garthe 1997; Freeman 1998).

The large foraging ranges of procellariiforms mean that threats to their populations may originate far from the breeding site, and so may not be immediately apparent from colony-based studies. For example, declines of many petrel and albatross populations are a direct result of adult mortality from long-line fisheries by-catch, which is a threat across foraging ranges of more than 3000 km from the sub-Antarctic breeding grounds of some species (e.g. Weimerskirch *et al.* 1999). Understanding the foraging ecology of pelagic seabirds is therefore important for the implementation of conservation requirements. Recently, the use of satellite telemetry and data loggers have provided new insights in to the foraging distribution and strategies of larger species during the breeding season, but data for smaller species are very limited.

Abiotic factors such as weather have also been found to influence seabird breeding success. High rainfall, low temperature and high windspeed can cause chick mortality, either independently or through interactions with food availability (Thompson & Furness 1991; Robinson *et al.* in press), and stormy conditions affect foraging success of both surface feeding and diving seabirds (Dunn, 1975; Becker & Specht 1991; Finney *et al.* 1999). However, energetic costs of foraging may be significantly reduced by strong winds, particularly in procellariiforms, many of which are highly specialised for gliding flight (Arnould *et al.* 1996; Furness & Bryant 1996; Weimerskirch *et al.* 2000). Predation, nest site quality, and inter- and intraspecific competition for food are among other external influences on seabird breeding success (Furness & Birkhead 1984; Moors & Atkinson 1984; Coulson & Thomas 1985), and many of these factors may interact with intrinsic factors associated with parental quality.

1.3. Individual variation in parental quality

Variation in a phenotypic trait has environmental and genetic components (Lessells & Boag 1987), and variation in breeding performance is influenced by interactions between extrinsic (environmental) and intrinsic effects, e.g. heritable patterns of chick development, or characteristics of parental care (Ricklefs & Peters 1981; Phillips &

Furness 1998). Parental quality is a major influence on breeding success in seabirds, e.g. 23-33% of the variance in breeding parameters of kittiwakes *Rissa tridactyla* was explained by individual variation (Coulson & Thomas 1985). These effects are often due to variation in foraging ability, and may interact with factors such as age or breeding experience (Ollason & Dunnet 1978; Weimerskirch 1990; Bradley *et al.* 1991). However, other studies have failed to find changes in breeding success with age or experience (Berrow *et al.* 2000), which may be due to deferred breeding until birds are competent at finding food (Croxall 1991). Behavioural traits such as co-ordination of incubation shifts also influence breeding success (Hatch 1990), and the importance of these traits may vary according to their interaction with environmental conditions, e.g. the amount of time available for different activities will be constrained by food supply and foraging ability.

Interactions between individual and environmental effects highlight the need for information on annual variation, particularly since long-lived seabirds encounter variation in the marine environment on temporal scales of days to years or even decades. Many studies of seabird breeding biology have focused on a small number of years, representing a small proportion of a seabird's reproductive life, whereas longer-term research has produced valuable insights into life-history strategies (Wooller *et al.* 1992).

1.4. Study species

Northern fulmars *Fulmarus glacialis* and Manx shearwaters *Puffinus puffinus* are two procellariiform species that breed in the United Kingdom. In common with other procellariiforms, both species are socially monogamous with high site- and mate-fidelity (Dunnet & Ollason 1978; Brooke 1986). They lay a single-egg clutch and after hatching, the chick is brooded by either parent, in short shifts, until it has attained homeothermy (1-2 weeks after hatching), then both parents forage simultaneously and return to the nest only to feed the chick (Harris 1966; Ollason & Dunnet 1978). Patterns of nestling development in both species are typical of procellariiforms, with chicks reaching a peak mass greatly in excess of adult mass, followed by a period of mass recession prior to fledging (Brooke 1990; Hamer & Thompson 1997). Although they share common characteristics with other procellariiforms, fulmars and (to a lesser extent) Manx shearwaters are somewhat atypical of the group in their relatively high rates of food provisioning (Hamer & Thompson 1997; Hamer & Hill 1997). This makes them interesting model species for exploring the ways in which pelagic seabirds provision their chicks, and for making comparisons with the better-studied pattern of infrequent food provisioning that occurs in most procellariiforms.

1.4.1. Northern fulmar

The northern fulmar is one of the fulmarine petrels, a small, variable procellariiform group of five genera and seven species (Warham 1990). The two species in the genus *Fulmarus* have a high latitude distribution, with the northern fulmar *F. glacialis* breeding in Arctic and boreal regions, and the southern or Antarctic fulmar *F. glacialoides* restricted to Antarctic and sub-Antarctic regions. The northern fulmar (hereafter referred to as fulmar) is a stocky, surface nesting petrel with a body mass of around 800g (Phillips & Hamer 2000). With an estimated world population of 15-20 million breeding pairs (Lloyd *et al.* 1991), it is one of the most abundant seabirds in the northern hemisphere. Its circumpolar breeding distribution covers the north-western Pacific (Hatch 1990), the Atlantic coast of Canada (Brown 1968) and the north-eastern Atlantic, with an estimated 2-4 million pairs breeding in the Western Palearctic (Snow & Perrins 1998). The last 200 years have seen a dramatic population increase and expansion of the fulmar's range from the Arctic to numerous breeding sites in the north Atlantic (Fisher 1952; Williamson 1996). This rapid colonisation may have been facilitated by an increase in the availability of discards from commercial fisheries (Fisher 1952; Thompson *et al.* 1995). This is supported to some extent by correlations between the fulmar's spread and an increase in fishing activity in the north eastern Atlantic, but the spatial overlap between fulmars and commercial fisheries is insufficient to suggest that they rely completely on fisheries waste as a food source (Camphuysen & Garthe 1997; Phillips *et al.* 1999). Fulmars have a broad dietary range with considerable spatial and temporal variation in prey composition (Furness & Todd 1984; Hamer *et al.* 1997; Phillips *et al.* 1999). Their chicks are fed nocturnally or diurnally, and feeding rates are among the highest recorded in the Procellariiformes (Hamer & Thompson 1997; Phillips & Hamer 2000). For their size, fulmarine petrels have relatively short incubation and nestling periods compared to other procellariiforms, and this may be an adaptation for breeding at high latitudes with a relatively short period of high food abundance (Lack 1968; Croxall 1984). Indeed, northern fulmars have the most northerly distribution of any procellariiform (Fisher 1952). Studying food provisioning in northern fulmars links together two interesting features of their ecology; the variability in diet and feeding strategies, and the relatively rapid chick growth for a procellariiform seabird. The adaptive value of the fulmar's flexible foraging behaviour, e.g. as a response to changes in prey distribution or to enable opportunistic exploitation of new food sources, requires further investigation.

1.4.2. Manx shearwater

Shearwaters of the genus *Puffinus* are structurally lighter and longer-winged than fulmars. Most are highly pelagic, and take fish, squid and crustacea by surface-seizing or pursuit-diving (Warham 1990). Manx shearwaters, in common with other *Puffinus* species, nest in burrows in dense colonies and are active at the colony at night, to avoid predation (Thompson 1987; Brooke 1990). The world population of Manx shearwaters is c.330, 000 pairs. With the exception of a few small colonies in North America, their breeding range is restricted to the north-eastern Atlantic, with colonies in Iceland, the Faeroes, Britain and Ireland, France, the Azores, Madeira and the Canary Islands. Britain and Ireland hold more than 90% of the world population, with an estimated 300,000 pairs (Brooke 1990), of which 102,000 pairs breed on Skomer Island, Wales (Smith *et al.* in press).

Despite extensive studies of Manx shearwater breeding biology (Thompson 1987; Brooke 1990), its pelagic feeding distribution and nocturnal visits to the colony mean that knowledge of its foraging and food provisioning behaviour is still limited. For instance, average provisioning rates have been inferred from detailed measurements of chick mass (e.g. Hamer & Hill 1997), but have not been examined in individual parents. In this context, it would be interesting to test whether foraging strategies similar to those found in other shearwaters (Granadeiro *et al.* 1998; Weimerskirch 1998; Weimerskirch

& Cherel 1998) would occur in species such as Manx shearwaters that feed their chicks at relatively frequent intervals.

1.5. Study sites

1.5.1. Fair Isle

Fair Isle (59°32' N, 1°38'W) lies c. 25 km south of Shetland (Fig. 1.1), and is 5 km long by 3 km wide. The northern part of the island consists of rough sheep grazing and moorland with a maximum elevation of 217 m. The southern part is lower, fertile land, used for small-scale farming. Most of the coastline consists of steep cliffs 50-200 m high, providing breeding habitat for large populations of cliff-nesting seabirds. In addition, the heavily grazed moorland is used by ground nesting seabirds, e.g. skuas, gulls and terns. The sea surrounding Fair Isle is an important spawning and recruitment ground for sandeels *Ammodytes marinus*, on which many seabirds are dependent. This area is heavily exploited by industrial fisheries, and over-harvesting of sandeels is a potential threat to seabird populations, although recent changes in sandeel abundance around Shetland may be mainly attributable to variation in natural mortality and migration affecting recruitment (Wright 1996). Shetland holds a large proportion of the UK fulmar population, with c. 43, 000 pairs breeding at Fair Isle each year (Riddington *et al.* 1997). Fair Isle is an important breeding site for great skuas *Catharacta skua*, Arctic skuas *Stercorarius parasiticus*, kittiwakes, puffins *Fratercula arctica,* guillemots *Uria aalge*, razorbills *Alca torda* and shags *Phalacrocorax aristotelis*, and also has breeding populations of black guillemots *Cepphus grylle,* common terns *Sterna hirundo*, herring gulls *Larus argentatus*, lesser black backed gull *L. fuscus*, greater black backed gulls *L. marinus*, and Gannets *Morus bassanus* (Lloyd *et al.* 1991).

1.5.2. Skomer

Manx shearwater data were collected at Skomer Island, Wales (51°44' N, 5°17'W; Fig. 1.1). Most of this 219-hectare island is a flat plateau c. 60 m above sea level. The vegetation and soil are heavily influenced by rabbit *Oryctolagus cunniculus* grazing and burrowing, as well as burrowing from Manx shearwaters and puffins. The coastal vegetation consists of dry grassland (*Agrostis*, *Festuca* and *Holcus*), with small areas of *Calluna* heath. This short coastal turf is the favoured habitat for Manx shearwater burrows, although erosion and collapse of burrows is a problem at the cliff edges. Inland areas are dominated by bracken *Pteridum aquilinum*, in which Manx shearwater burrows are found at lower densities, and nesting by puffins is largely inhibited. The focal area for this study was a narrow isthmus c. 30 m above sea level, with a high density of shearwater burrows.

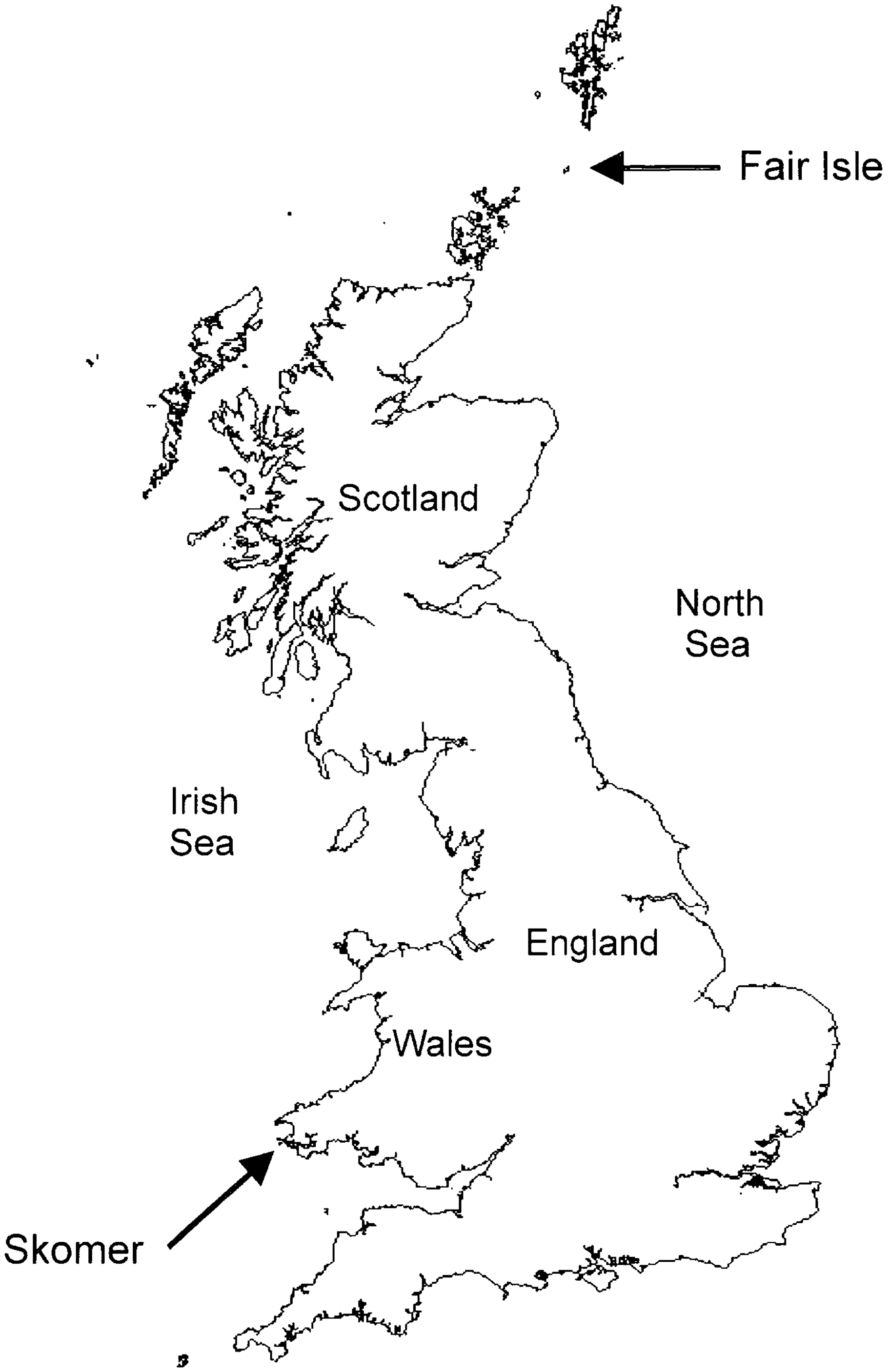
As well as Manx shearwaters and puffins, Skomer is an important breeding site for lesser black-backed gulls, guillemots and razorbills. Fulmars, British storm petrels *Hydrobates pelagicus*, kittiwakes, herring gulls and greater black-backed gulls also breed in smaller numbers (Lloyd *et al.* 1991). Manx shearwater research on the Welsh Islands of Skomer and Skokholm spans more than 70 years, from pioneering studies by Lockley (e.g. Lockley 1930), to more recent research (e.g. Harris 1966; Perrins *et al.* 1973; James 1985; Brooke 1986; 1990; Hamer & Hill 1997; Hamer *et al.* 1999), providing a wealth of published and unpublished data. This has allowed me to make detailed comparisons of past and current patterns of chick growth and provisioning.

1.6. Aims of this study

In this thesis I aim to examine the strategies used by northern fulmars and Manx shearwaters to provision their chicks, within the conceptual framework of life-history theory. In particular, I will focus on interactions between environmental variability and individual effects, and how these influence food provisioning, chick growth and breeding success in these two long-lived seabirds. I also aim to clarify some areas of the species' breeding biology that are poorly understood. For example, the roles of individual parents in food provisioning have never been studied in Manx shearwaters, and the behavioural mechanisms responsible for the period of mass recession prior to fledging have not been rigorously examined in any procellariiform.

Quantifying food provisioning is fundamental to understanding the relationships among marine food resources, foraging and chick growth. In *Chapter 2*, conventional methods of assessing food provisioning from periodic weighing (e.g. Ricklefs 1984) are evaluated using concurrent data on parental attendance. The remaining data chapters deal with patterns of food provisioning and their relationship with other breeding parameters. In *Chapter 3,* long-term databases are used to examine variation in the breeding performance of Manx shearwaters at a colony and individual level, and to examine sources of variation in breeding success. In *Chapter 4*, breeding success, diet and foraging behaviour of fulmars are compared in two years of contrasting environmental conditions, and relationships between breeding parameters and food abundance are discussed. *Chapter 5* focuses on the roles of individual Manx shearwater parents in food provisioning, using radio tracking to monitor nest attendance, combined with periodic weighing of chicks to quantify food provisioning. I describe differences between male and female parents in attendance and food provisioning, and discuss the implications of these results for potential foraging ranges and prey exploitation strategies. *Chapter 6* examines the pre-fledging mass recession period in Manx shearwaters. A cross-fostering experiment is used to test whether the reduction in feeding prior to fledging is controlled by parents, chicks or by parent-offspring interactions. In the General Discussion *(Chapter 7)*, I draw together conclusions from previous chapters to discuss patterns of food provisioning and chick growth, and the ways in which these reflect adaptations to environmental variability. The strategies observed in fulmars and Manx shearwaters are placed in the wider context of studies of other seabirds, with respect to their common life-history traits and the relationships of these traits to characteristics of the marine environment.

Figure 1.1. Location of Fair Isle and Skomer



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Chapter 2

Assessing food provisioning to nestling Manx shearwaters: an evaluation of methods

2.1. Summary

One of the central aims of this thesis is to use patterns of food provisioning to test hypotheses concerning chick growth, the variability of marine food availability and the evolution of life history traits. Many studies, including this one, use periodic weighing methods to measure food provisioning. The efficacy of these methods has been tested with independent data on parental attendance in fulmars, but has not been tested in Manx shearwaters due to the difficulty of monitoring attendance in nocturnal, burrow-nesting birds. The aim of this chapter is to validate the methods used in this thesis to measure food provisioning, using radio-tracking to monitor adult attendance. Periodic weighing alone gave very similar estimates of the timing and mass of meals, compared with combined weighing and radio-tracking data. However, periodic weighing was less effective at distinguishing between feeds from one or two parents, and had a tendency to over-estimate the mass of double meals. Some of the potential problems and mis-uses of periodic weighing methods are discussed.

2.2. Introduction

Measuring rates of food provisioning in seabirds can give valuable insights into variation in food supply and foraging success at a colony and individual level (Monaghan *et al.* 1989, Huin *et al.* 2000), and into the evolution of life-history traits (Drent & Daan 1980, Ricklefs 1990). Recent research has examined many of the factors that influence food delivery to nestling seabirds, for example, the effects of parental age and experience (Weimerskirch 1990) and the roles of adult and chick body condition (Tveraa *et al.* 1998).

Many researchers use periodic weighing of chicks to measure food provisioning (e.g. Ricklefs *et al.* 1985, Bolton 1995, Hamer & Hill 1997). However, few studies have tested this method with independent monitoring of adult attendance. Phillips & Hamer (2000) tested periodic weighing data in northern fulmars against direct observations of adult attendance. However, parental visits and feeds are more difficult to observe in seabirds that nest in burrows and are nocturnal at the colony. Granadeiro *et al.* (1999) used an attendance logging system to record Cory's shearwater *Calonectris diomedea* adults entering and leaving the nest, and found considerable discrepancies in feeding frequencies of chicks inferred from this system and from periodic weighing. However, these could have been due to characteristics of food provisioning in this species, or to problems associated with the methods, e.g. the assumption that all visits resulted in food delivery to the chick, which is not always the case (Hamer *et al.* 1999). Reid *et al.*

(1999) found a tendency for periodic weighing to under-estimate the size of feeds delivered to Antarctic prions *Pachyptila desolata*, compared with data from an automatic weighing system, although their periodic weighing methods may not have been consistent with methods used here. Extrapolating methods and assumptions between species may present problems in itself (Reid *et al.* 1999), and data from other species are therefore required. In this chapter I compare attendance monitoring and periodic weighing methods of measuring food provisioning in Manx shearwaters, and I discuss potential problems associated with each method.

2.3. Methods

Fieldwork took place in July and August 1999 Skomer Island, Wales (Chapter 1). I recorded numbers of visits and numbers of feeds to Manx shearwater chicks during the linear phase of mass growth (20-50 days post-hatching) using three methods; (i) periodic weighing only; (ii) monitoring attendance only; (iii) using both methods combined. I compared estimates of the mass of single and double meals (i.e. feeds from one or both parents), determined from periodic weighing and using both methods combined. In addition, I used daily mass increments to estimate the mass of food delivered per night (Hamer & Hill 1997), and compared this with masses calculated from periodic weighing. Throughout this paper, I refer to the total amount of food received by a chick in a night as a feed, and the amount of food delivered by each parent on a visit as a meal.

2.3.1. Periodic weighing

Feed sizes were calculated by weighing chicks at four-hour intervals overnight (2100h, 0100h and 0500h) and correcting mass increments between successive weighings for weight loss due to respiration and excretion, following Hamer & Hill (1997), with the following changes in methods. Hamer & Hill (1997) calculated age- and mass-specific rates of mass loss. However, mass loss in 1999 was not significantly related to chick age or mass (stepwise multiple regression; $P > 0.05$), possibly due to the lower range of ages and masses in this study. I therefore corrected each mass increment according to mean mass loss rates of 1.87 ± 1.51 ($n = 85$) g/hour in the absence of feeding, and 3.17 ± 2.68 ($n = 56$) g/hour following a feed. Proportions of single and double meals were then calculated from a binomial distribution, following Ricklefs (1984), Bolton (1995) and Hamer & Hill (1997). If p is the probability of a parent feeding its chick on any night, then the proportion of double meals (p^2) can be calculated from the observed proportion of non-feeds $(1-p)^2$. This allows each feed to be classified as a meal from either one or two parents, based on the assumption that the largest feeds represent meals from both parents.

2.3.2. Parental attendance

Parental attendance at the colony was monitored using a radio tagging system. The system is described in detail in Chapter 5, and summarised briefly here. Both parents at ten nests were fitted with a small (2 g) VHF radio transmitter attached to two central tail feathers. The presence of tagged birds in the colony was detected using a scanning receiver with a three-element Yagi antenna located 100 m from the colony. Trials at the colony indicated that tags had a maximum range of 1 km, and the location of the antenna meant that birds outside the colony (e.g. at sea) would have been beyond the range of the system. Visits of tagged birds to the colony were monitored for 20 consecutive nights, from 2230h (before the first adults returned) until 0430h (after the last adults had left the colony). Five radio tags failed before the end of the tracking period, so these were excluded from further analysis, leaving data for 133 chick-nights. Mass increments of chicks indicated that there were no instances of a chick being fed without us recording an adult at the nest, so I was confident that no visits were missed. Chicks at study nests grew similarly to those at a sample of 24 nests, where adults were not tagged and chicks were weighed once daily (study chicks: 8.8 ± 1.8. g/day (n = 10); control chicks: 9.2 ± 3.5 g/day (n = 24); $t_{32} = 0.7$, $P = 0.5$).

2.3.3. Periodic weighing and attendance combined

By combining adult attendance with periodic weighing data, I was able to assign meals to individual parents. If one parent and one feed were detected in the same four-hour period, this was classified as a single meal. If both parents were present and two feeds were detected in different four-hour periods, this was classified as a double meal. On a small number of occasions (n = 6), both parents were present in the same period and it was not possible to determine the number of meals. These were classified as three single and three double meals from the proportions of known meals on double visits, with the three larger feeds classified as double meals.

2.3.4. Food provisioning estimated from daily mass increments

Hamer & Hill (1997) calculated overnight food delivery using daily mass increments, and found that this correctly identified 98.7% of known feeds and 90.2% of known non-feeds as determined by periodic weighing. However, the mass of feeds estimated by the two methods also needs to be compared. I used a regression equation of overnight food delivery on daily mass increment, initial chick mass and age (Hamer & Hill 1997) to identify feeding events and estimate feed size. The equation was:

$$\text{daily mass increment} = 0.62 \times \text{feed size} - 0.061 \times \text{mass} + 0.28 \times \text{age} - 9.13$$

I then compared this estimate with feed size determined by periodic weighing data for the same chicks.

In this chapter and throughout the thesis, means are presented ± standard deviation unless otherwise stated.

2.4. Results

Using the periodic weighing method alone, I recorded 104 feeds from one or both parents over 133 chick-nights. The proportion of zero feeds $(1-p)^2$ was 0.22 (29/133), giving an estimated 37 double meals. The 37 largest masses were then classified as double meals and the remaining 67 as single meals. By monitoring attendance, I recorded 145 visits, of which 75 visits were by one parent and 35 visits were by both parents, giving a total of 110 chick nights in which one or both parents visited the nest. Assuming that each visit resulted in a feed, this would give a total of 110 feeds, consisting of 75 single meals and 35 double meals. Using periodic weighing combined with attendance data, I recorded a total of 145 visits by individual parents resulting in 122 feeds on 133 chick-nights. 23 visits resulted in no food being delivered; chicks were either visited by one parent without being fed (six chick-nights) or visited by both parents and fed by only one (17 chick-nights). Of the 122 feeds, 86 were single meals and 18 were double meals.

2.4.1. Comparison of methods

Compared with combined periodic weighing and parental attendance combined, either method alone estimated a higher proportion of double meals, and parental attendance alone over-estimated the total number of feeds (Table 2.1). This was due to the mis-classification of meals by the periodic weighing method, and the assumption that all visits result in the chick being fed (see Discussion).

Proportions of zero, single and double meals calculated from periodic weighing were significantly different from the proportions calculated using both methods combined (Table 2.1; $\chi^2_2 = 24.3$ $P < 0.001$). Parental attendance data also produced significantly different proportions from combined methods (Table 2.1; $\chi^2_2 = 17.5$, $P < 0.001$). In both cases, using a single method over-estimated the proportion of double feeds, and attendance alone under-estimated the proportion of zero feeds. The mean masses of single and double meals differed significantly between periodic weighing and combined methods of calculation (Table 2.2; single meals: $t_{153} = -2.96$, $P < 0.01$; double meals: $t_{53} = 2.04$, $P = 0.05$). The periodic weighing method suggested that double meals were significantly heavier than, and more than twice the mass of single meals (Table 2.2; t_{102}

$= 7.14$, $P < 0.001$). Where meals were matched to known visits by one or both parents, the difference was less pronounced with some overlap in size, but double meals were still significantly heavier than single ($t_{102} = 2.05$, $P = 0.04$).

2.4.2. Estimating feeding from daily mass increments

I estimated overnight food delivery using daily chick weights only, following Hamer & Hill (1997). This method correctly identified 98.0% of known feeds as determined by periodic weighing ($n = 104$) and 93.1% of known non-feeds ($n = 29$). Where feeds were correctly identified, these had a very similar mass to feeds determined by periodic weighing of the same chicks (periodic weighing: 59.5 ± 29.6 g; daily weighing: 57.1 ± 29.7 g; paired t-test: $t_{99} = 0.90$, $P = 0.4$).

Table 2.1. Numbers of zero, single and double meals estimated from periodic weighing, adult attendance and the two methods combined. n = 133 chick-nights at ten nests.

	not fed	single meals	double meals
periodic weighing only	29	67	37
adult attendance only	23	75	35
both methods	29	86	18

Table 2.2. Mass of single and double meals estimated from periodic weighing alone and combined with adult attendance data.

	mass of single meals (g)			mass of double meals (g)		
	n	mean	SD	*n*	mean	SD
periodic weighing	67	43.0	28.8	37	88.3	32.1
both methods	86	56.3	25.8	18	71.0	28.1

2.5. Discussion

Using periodic weighing combined with monitoring adult attendance, I identified 23 occasions on which parents returned without feeding the chick (17% of chick-nights, and 16% of visits by parents). Similar patterns of non-feeding visits were found in other studies (Ricklefs 1992, Granadeiro *et al.* 1999, Phillips & Hamer 2000), and may have been due to poor foraging success, or to the chick refusing food. These visits would not have been detected using periodic weighing alone, and this has implications for inferring parental attendance from patterns of feeding (Phillips & Hamer 2000).

Periodic weighing data had a tendency to overestimate the proportion of double meals compared to both methods combined. The periodic weighing method assumes that the largest feeds represent meals from both parents, but classifying feeds using attendance data indicated that there was considerable overlap in the sizes of single and double meals. The mean mass of single meals was therefore underestimated and the mean mass of double feeds overestimated by periodic weighing alone, as found in other studies (Granadeiro *et al.* 1999, Reid *et al.* 1999; Phillips & Hamer 2000). This may be partly due to constraints of chick gut capacity, which may prevent chicks from accepting two large meals in a short period of time (Bolton 1995, Granadeiro *et al.* 1999, Phillips & Hamer 2000). There may also be some overlap in the mass of single and double meals due to natural variability in food delivery. This method of estimating single and double meals assumes that a parent feeds the chick independently of its partner (Ricklefs *et al.* 1985; Reid *et al.* 1999), and will be more effective if this assumption is upheld.

Reid *et al.* (1999) found that periodic weighing underestimated feed size when compared with instantaneous weights from an automated chick weighing system. However, no mention was made of correcting mass increments for rates of mass loss, so the exact methods used are unclear. Hamer & Hill (1997) corrected individual mass increments using equations relating mass loss before and after a feed to chick age and initial mass, and I adopted a similar approach here. Failure to correct mass increments on an individual basis may have led to Reid *et al.* (1999) underestimating feed sizes. Another possible source of error with periodic weighing is the assumption that chicks are fed exactly in the middle of an interval between successive weighings. Since Manx shearwater chicks may be fed at any time between weighings, feed size will be slightly under- or over-estimated from earlier or later feeds respectively. However, it is difficult to see how this could produce consistent errors in one direction only.

This chapter has shown that accurate information on attendance or food delivery by individual parents cannot be obtained by periodic weighing alone. However, the data presented here and elsewhere (Granadeiro *et al.* 1999, Phillips & Hamer 2000) show that periodic weighing is a useful method for assessing both the intervals between feeds and the mass of food delivered when chicks are fed. I am therefore confident that the methods used in this thesis are effective at measuring patterns of food provisioning from the chick's perspective. I have also confirmed that daily weighing gives a very similar estimate of feed size to periodic weighing, and Chapter 3 uses daily chick weights to quantify food provisioning. Where data were required on the roles of individual parents, I combined periodic weighing with the radio-tracking system, to assign meals to each parent (Chapter 5).

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Chapter 3

Annual variation in food provisioning and chick growth in Manx shearwaters

3.1. Summary

Many long-lived seabirds exhibit high annual variability in some breeding parameters, e.g. fledging mass, but lower variability in others, e.g. clutch size, timing of breeding. Certain reproductive traits are known to be highly consistent in individual birds or pairs in successive breeding attempts, but the repeatability of other traits, for example, chick growth, has received little attention, particularly in seabirds. This chapter tests for annual variation in the breeding performance of Manx shearwaters, using data from ten years (spanning 28 years) at the same colony. Hatching date, chick growth and food provisioning showed significant annual variation, but there was no significant variation in hatching or fledging success. Hatching date and peak mass showed significant repeatabilities. Growth rate was repeatable in a sample of nests in the 1970s but not in another sample in the 1990s, and patterns of food provisioning showed no individual consistency. Food provisioning rate explained the greatest proportion of variance in peak mass and growth rate, and there was a weak but significant relationship between variability of food provisioning and peak mass. These results are discussed in the context of nestling obesity and stochastic variation in food provisioning.

3.2. Introduction

Different components of avian breeding performance have different levels of variability within a population. For example, many long-lived seabirds are highly consistent in breeding phenology (Brooke 1978b; Wanless & Harris 1988), whereas annual productivity tends to be more variable (Hatch 1987; Murphy *et al.* 1991), and traits such as food provisioning rate, nestling growth rate and fledging mass are often sensitive to short-term environmental conditions and therefore show considerable annual and seasonal variation (Barrett *et al.* 1987; Cairns 1987).

As well as being affected by annual environmental fluctuations, seabirds may also experience infrequent or cyclical changes in environmental conditions (Wooller *et al.* 1992; Ratcliffe *et al.* 1998; Thomas *et al.* in press). Such events would go undetected by many studies, which only examine a small proportion of a seabird's reproductive lifespan. Long-term studies of long-lived seabirds are relatively rare (Nisbet 1989; Croxall *et al.* 1990; Bradley *et al.* 1991), and tend to examine broad-scale parameters such as adult survival and breeding success (Bradley *et al.* 1991; Ratcliffe *et al.* in press; but see Coulson & Porter 1985.). There is a need for long-term data on variables such as chick growth and food provisioning in many seabirds, particularly since poor conditions need arise only occasionally to have a strong influence on the evolution of traits such as nestling growth (Hamer *et al.* 2001).

In addition to long-term studies, another method for examining the importance of environmental conditions for different aspects of breeding performance is repeatability analysis. Variability in reproductive performance has both individual and environmental components (Hatch 1990; Goodburn 1991). The proportion of genetic and environmental variance contributing to phenotypic variance among individuals can be described by the repeatability coefficient (r_i), according to the equation $r_i = (V_G + V_{Eg})/V_P$, where V_G is the genotypic variance, V_{Eg} is general environmental variance, and V_P is the phenotypic variance (Falconer 1981; Lessells & Boag 1987). Despite extensive testing of repeatabilities of breeding phenology and clutch size (Sydeman & Eddy 1995; Catry *et al.* 1999; Banbura & Zielinski 2000), relatively few studies have focused on the repeatability of factors that contribute to chick survival or fledging mass (which may be an important determinant of post-fledging survival; Perrins *et al.* 1973). Chick growth indices in established pairs of Arctic skuas *Stercorarius parasiticus* had low repeatability values (0.26), indicating a strong influence of environmental variation (Phillips & Furness 1998), but to date, no study has examined repeatability of food provisioning, which forms an important link between food availability, individual parental effects and chick growth.

Although a strong, positive relationship generally exists between food intake and chick growth, considerable intra-specific variation exits in patterns of food provisioning (e.g. meal mass and feeding frequency may be highly variable whilst contributing to very similar overall rates of food provisioning; Weimerskirch 1990; Berrow *et al.* 2000). Differences in patterns of feeding have been shown to affect chick mass growth (Schaffner 1990), and may therefore have fitness consequences for the parents and chick (Perrins 1965; Haywood & Perrins 1992; Gebhardt-Henrich & Richner 1998).

Variability of food provisioning has attracted considerable recent attention as a possible explanation for nestling obesity (see *Chapter 1*). Numerous hypotheses have been offered for lipid storage in nestling pelagic seabirds (Lack 1968; Ricklefs *et al.* 1980; Taylor & Konarzewski 1989; Ricklefs & Schew 1994; Phillips & Hamer 1999; Reid *et al.* 2000). The hypothesis that lipid stores act as a buffer against stochastic variation in food provisioning (Ricklefs & Schew 1994) is consistent with patterns of food provisioning in a number of species (Ricklefs *et al.* 1985; Hamer & Hill 1997; Hamer *et al.* 1997b; Granadeiro *et al.* 1998) but has only been tested in a small number of inter-colony or inter-specific studies (Hamer *et al.* 1997a; Hamer *et al.* 2000). Although these studies found that chicks fed more variably were heavier (either in terms of age-specific mass or as a proportion of adult body mass), further comparative data are required to examine annual variation in provisioning and growth at individual colonies. Using data from the same species at the same location in a number of years has the advantage of fewer confounding factors, and may therefore provide a more effective test of the relationship between the variability of food provisioning and patterns of mass growth.

Manx shearwaters *Puffinus puffinus* have high nest- and mate-fidelity (Perrins *et al.* 1973), and established pairs have consistently high breeding success (Brooke 1990). The mass of the single chick at fledging varies among years and among pairs, with lower variation within than among pairs (Brooke 1986). However, variation in different components of growth (e.g. rates of mass gain, peak mass and the duration of the mass recession period before fledging) has not been examined. Patterns of mass growth have been studied in a number of other pelagic seabird species, and have been particularly well described in albatrosses *Diomedea spp.* (Ricketts & Prince 1981; Huin & Prince

2000; Huin *et al.* 2000). However, despite extensive studies of food provisioning and growth of Manx shearwaters (Hamer & Hill 1997; Hamer *et al.* 1998; 1999), few studies have examined patterns of growth in more than one breeding season (but see Thompson 1987).

The aims of this chapter are to describe patterns of breeding success, chick growth and food provisioning in Manx shearwaters, and to examine the annual variability and repeatability in these different components of breeding performance. I also discuss the relationships between feeding patterns and chick growth in the context of nestling obesity.

3.3. Methods

3.3.1. Study site

The islands of Skomer, Skokholm and Middleholm, SW Wales, hold the world's largest population of Manx shearwaters (Smith *et al.* in press), with an estimated 151, 000 breeding pairs. Because of the short distance between the islands (4 km between Skokholm and Skomer; < 1 km between Skomer and Middleholm), and the fact that shearwaters fledged at one island in the group have been recorded breeding at a different one (Brooke 1978a), I consider the three islands as one colony, and examine data from both Skokholm and Skomer.

3.3.2. Chick growth

Chick growth data were collected on Skokholm from 1973-1976 (M. Brooke) and on Skomer from 1995-2000 (K.C. Hamer, C.M. Gray). Chick age was estimated from wing length, measured with a stopped wing ruler and calibrated against measurements for chicks of known age (Brooke 1990). In 1973-1976, hatching dates were determined by checking nests daily (Brooke 1986), and these dates were in agreement with chick ages determined from wing lengths. Chick ages estimated from wing lengths in 1995-1998 were also in close agreement with those determined by direct observation (K.C. Hamer, unpublished data). Wing length was measured at ten-day intervals during the growth period in 1995 and 1998-2000, and when chicks were 60 days old in all years except 1996 (see Results). Chicks were weighed daily from the age of c.20 days to peak mass at 50-60 days in all years except 1996, when data collection ceased when chicks were c.55 days. Growth curves were fitted to data for individual chicks up to peak mass using weighted non-linear regression. The weighting factor 1/mass was used to counteract the increasing variance in mass with chick age (Ricketts & Prince 1981), and this resulted in a uniform distribution of the residuals with respect to age. It was not possible to fit growth curves for 1996, since it was unclear whether or not chicks had reached their peak mass when data collection ceased.

3.3.3. Food provisioning

Meal mass, feeding frequency and rates of food provisioning were calculated from daily mass increments following Hamer & Hill (1997). This method determines with a high degree of accuracy whether or not a chick has been fed overnight (Hamer & Hill 1997) and produces very similar values for meal mass and provisioning rates compared with periodic weighing methods (Chapter 2). I calculated a coefficient of variation (CV) for meal mass and provisioning rate between 30 and 50 days in each chick, as S.D./mean x 100. This represented the period of growth prior to peak mass and the onset of mass recession, and data were available for this entire period in all years. The mean number of days between successive feeds was calculated for individual chicks aged 30 – 50 days, and this was also used as a measure of variability of food provisioning.

3.3.4. Repeatability

Individual parents were identified from numbered leg rings, and repeatabilities of breeding parameters were examined in pairs that remained unchanged over two or more years. The repeatability coefficient r_i can range from –1 to 1, with values close zero representing a strong environmental influence and values close to 1 representing strong individual effects. Negative values indicate an inverse relationship between individual and environmental effects. Repeatability coefficients were calculated from the mean squares of an analysis of variance, according to the formula:

$$r_i = \text{groups MS} - \text{error MS} / \text{groups MS} + (\text{n}-1) \times \text{error MS}$$

This was calculated for chick growth rate, peak mass, fledging mass, provisioning rate and meal mass. The number of observations (years) for each nest was not equal, so I calculated a mean value for n using the equation $n = (\Sigma\, n_i - (\Sigma n_i^2 / \Sigma\, n_i)) / k\text{-}1$, where n_i is the number of observations for nest i and k is the number of nests (Zar 1996).

3.4. Results

3.4.1. Breeding success

Table 3.1 shows hatching and fledging success at Skokholm (1963-1964; Harris 1966; 1973-1976; Brooke 1990) and Skomer (1993-2000; C.M. Perrins, unpublished data). Breeding success ranged from 52% in 1993 to 77% in 1998, with most breeding failures occurring during incubation. There was no significant difference among years in hatching success ($\chi^2_{12} = 2.85$, $P = 0.9$) or fledging success ($\chi^2_{13} = 13.1$, $P = 0.4$). Statistical tests were not performed on overall breeding success, because additional nests were included after hatching in 1973-1975 (Table 3.1), and so proportions of fledglings to eggs were not known in these years.

Table 3.1. Breeding success of Manx shearwaters on Skokholm and Skomer. Hatching success is the percentage of eggs that hatched, fledging success is the percentage of chicks hatched that survived to fledging and breeding success was calculated as hatching success x fledging success. See text for sources of data.

year	hatching success			fledging success			breeding success
	egg	hatched	%	hatched	fledged	%	%
1963			-	27	24	88.9 %	-
1964	56	44	78.6 %	44	39	88.6 %	69.6 %
1973	67	55	82.1 %	66	61	92.4 %	75.9 %
1974	79	54	68.4 %	56	56	100 %	68.4 %
1975	69	44	63.8 %	45	44	97.8 %	62.4 %
1976	72	57	79.2 %	57	54	94.7 %	75.0 %
1993	49	29	59.2 %	26	23	88.5 %	52.4 %
1994	45	34	75.6 %	34	31	91.2 %	68.9 %
1995	58	45	77.6 %	45	39	86.7 %	67.2 %
1996	61	45	73.8 %	45	44	97.8 %	72.1 %
1997	62	46	74.2 %	46	39	84.8 %	62.9 %
1998	57	48	84.2 %	48	44	91.7 %	77.2 %
1999	61	46	75.4 %	46	42	91.3 %	68.9 %
2000	82	64	78.5 %	64	55	81.3 %	63.4 %

Table 3.2. Hatching dates of Manx shearwater chicks in 1973-1976 and 1995-2000. Letters indicate values that were significantly different from each other (non-parametric multiple comparisons, $P < 0.05$).

year	*n*	hatching date	
		median	range
1973	107	28 June ^{ab}	14 June - 16 July
1974	80	28 June ^{ab}	14 June - 11 Aug
1975	69	29 June ^{ab}	10 June - 7 Aug
1976	20	26 June ^{a}	4 June - 25 July
1995	53	25 June ^{a}	10 June - 25 July
1996	22	3 July ^{b}	18 June - 14 July
1997	37	1 July ^{ab}	13 June - 25 July
1998	50	28 June ^{ab}	15 June - 30 July
1999	45	26 June ^{ab}	3 June - 13 July
2000	38	25 June ^{ab}	13 June - 13 July

3.4.2. Timing of breeding

Median hatching dates ranged from 25th June in 1976 and 2000 to 3rd July in 1997 (Table 3.2). Hatching date varied significantly among years (Kruskal-Wallis $\chi^2_9 = 33.0$, $P < 0.001$) and was later in 1996 than in 1976 or 1995 (non-parametric multiple comparisons (Zar 1996), $P < 0.05$). Repeatability of hatching date was examined in 29 nests in 1995 and 1998-2000, with an average of 2.55 observations per nest. 1996 and 1997 not included since only a small number of nests were the same individuals used in other years. Hatching date showed significant repeatability in 1995 and 1998-2000 ($r_i = 0.38$, $F_{28,45} = 2.59$, $P < 0.01$). Data for 1973-1976 could not be normalised and so were not tested for repeatability of hatching date.

3.4.3. Annual variation in mass growth

Mass growth of Manx shearwater chicks in 1973-76 and 1995-2000 is shown in Figures 3.1 and 3.2 respectively. Points represent mean masses for each age in each year, and error bars have been omitted for clarity. Growth curves were fitted for all years except 1996, when data collection finished before all the chicks had reached peak mass. The best fitting equation was the Gompertz curve $W(t) = A \times e^{-e^{-k(t - t_i)}}$ where A is the asymptotic (or peak) mass, k is the growth rate constant and t_i is the point of inflection (the age at which the maximum growth rate occurs). Table 3.3 shows mean growth parameters A, k and t_i for each year. All the regressions were highly significant and r^2 values for individual chicks ranged from 0.88 to 0.99 in all years.

I examined annual variation in growth parameters using analysis of covariance (ANCOVA) with hatching date as a covariate, to control for possible seasonal effects on growth (Thompson 1987). All three mass growth parameters showed significant variation among years (asymptote: effect of hatching date: $F_{1,405} = 0.002$, $P = 0.9$; effect of year: $F_{8,405} = 10.39$, $P < 0.001$. Maximum growth rate: effect of hatching date: $F_{1,405} = 19.18$, $P < 0.001$; effect of year: $F_{8,405} = 2.67$, $P < 0.01$. Age at maximum growth: effect of hatching date: $F_{1,405} = 3.45$, $P = 0.06$; effect of year: $F_{8,405} = 5.17$, $P < 0.001$). Asymptotes were significantly higher in 1974 and 1976 and than in 1995 and 1998. Growth rates were significantly higher in 1999 than in 1995 and 1998, and age at maximum growth was significantly higher in 1975, 1995 and 2000 than in 1998 (Tukey's H.S.D. tests, $P < 0.05$).

3.4.4. Repeatability of mass growth

Repeatability statistics were calculated for mass growth parameters of Manx shearwater chicks raised by the same parents from 1973-1975. (Table 3.4) and in 1995 and 1998-2000 (Table 3.5). Growth parameters were not available for 1996, and were only available for a small sample of nests ($n = 13$) in 1997, of which only nine were the same individual nests used in other years, so 1996 and 1997 were not included in this analysis. Data in the two tables were analysed separately, as they were taken from different samples of nests. Mass growth data for 1973-1975 showed significant repeatability, with coefficients ranging from 0.24 to 0.27. In 1995 and 1998-2000, repeatabilities were lower (0.04 to 0.22) and only peak mass showed marginally significant repeatability ($P = 0.05$).

3.4.5. Wing growth

Figure 3.3 shows the relationship between chick age and wing length in 1995 and from 1998-2000. The best-fitting equation for wing growth in these years was the sigmoidal curve: wing length (mm) = 246.6 / (1 + $e^{-(\text{age} - 34.5) / 13.4}$). ($r^2 = 0.98$). However, wing growth data were not collected throughout the growth period in all years (e.g. in 1973-1976, wing length was only measured in chicks older than 60 days). To test for annual variation in wing growth, I compared wing length at 60 days, since this was the most complete data set (all years except 1996). There was no significant variation among years (Table 3.6; Kruskal-Wallis ANOVA, $\chi^2_{9,324} = 15.8$, $P = 0.07$). Wing length at 60 days was not significantly related to asymptotic mass (linear regression; $F_{1,328} = 0.003$, $P = 0.9$).

Figure 3.1. Mean age-specific mass of Manx shearwater chicks in 1973-1976. A reference line at 550g has been added for comparison with Figure 3.2.

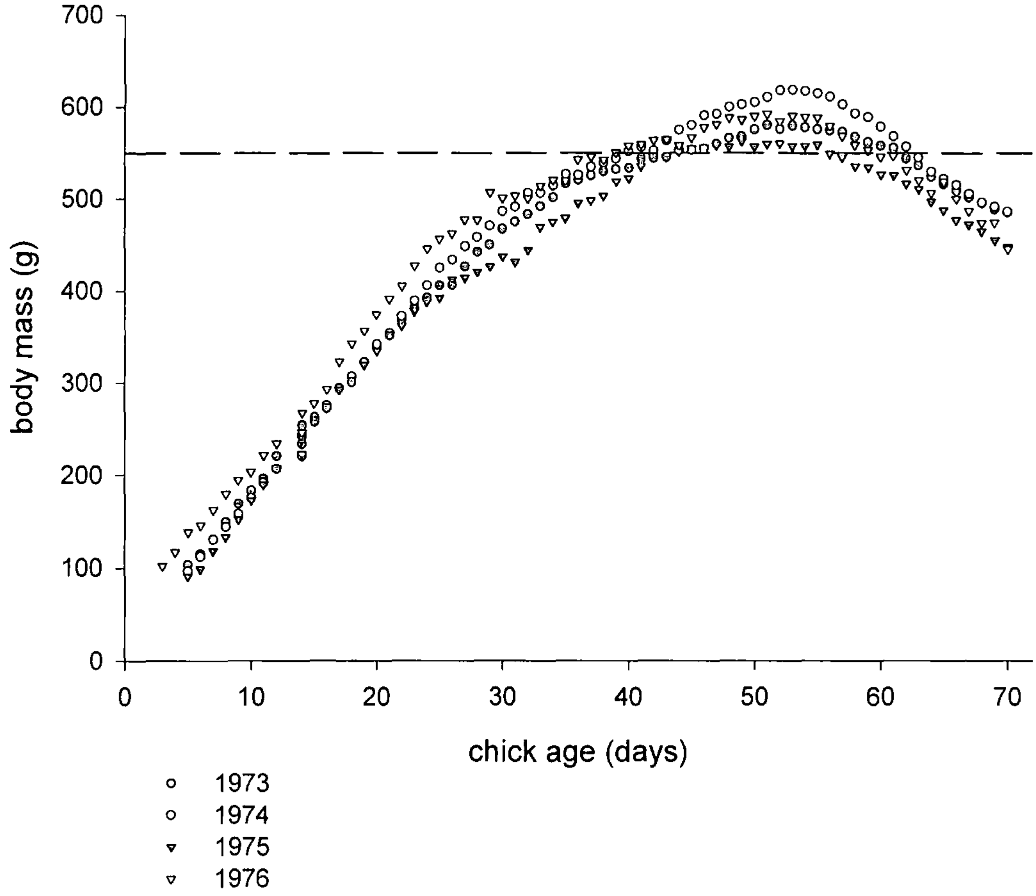

Figure 3.2. Mean age-specific mass of Manx shearwater chicks in 1995-2000. A reference line at 550g has been added for comparison with Figure 3.1.

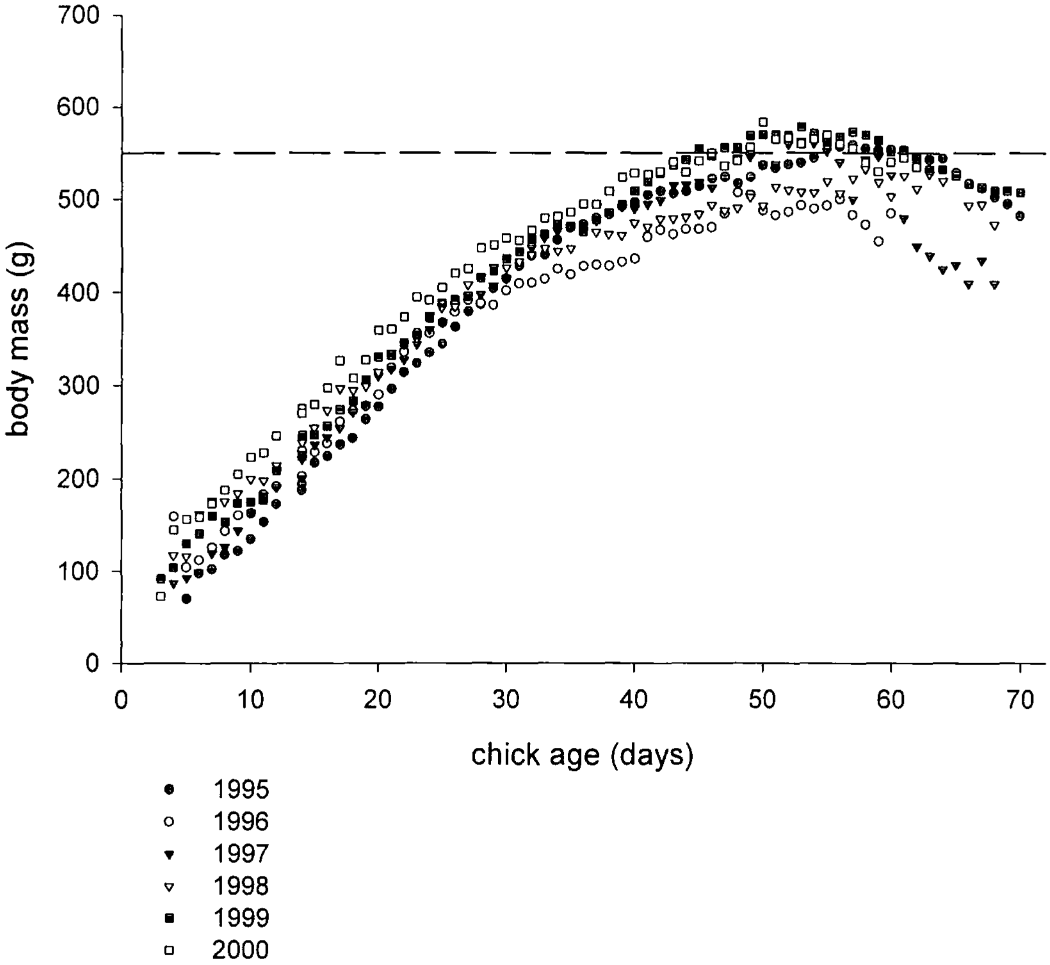

Table 3.3. Mass growth parameters of Manx shearwater chicks on Skokholm and Skomer. *A* is the asymptote, *k* is the growth rate and *ti* is the point of inflection.

year	*n*	*A*		*k*		*ti*	
		mean	SE	mean	SE	mean	SE
1973	107	617.8	5.30	13.55	0.18	13.04	0.20
1974	80	654.1	7.56	13.78	0.22	14.00	0.24
1975	69	602.6	7.27	13.38	0.25	13.69	0.31
1976	19	630.7	10.78	13.70	0.51	13.47	0.44
1995	42	590.0	8.25	13.26	0.28	14.44	0.34
1997	13	593.5	15.39	13.06	0.62	13.61	0.87
1998	28	557.6	7.53	12.73	0.49	11.94	0.60
1999	32	610.6	8.83	14.94	0.37	13.84	0.55
2000	25	600.0	7.41	13.42	0.72	15.42	0.60

Table 3.4. Repeatability of mass growth in Manx shearwater chicks raised by the same parents in 1973-1975. $n = 60$ nests and 2.28 observations per nest.

Parameter	F	d.f.	r_i	P
A	1.75	59,77	0.24	0.01
k	1.81	59,77	0.26	< 0.01
ti	1.89	59,77	0.27	< 0.01

Table 3.5. Repeatability of mass growth in Manx shearwater chicks raised by the same parents in 1995 and 1997-2000. $n = 29$ nests and 2.55 observations per nest. (Growth parameters were not calculated for 1996, were only available for a small sample of nests in 1997 so these years were not included in this analysis).

Parameter	F	d.f.	r_i	P
A	1.76	28,45	0.23	0.05
k	1.36	28,45	0.12	0.2
ti	1.12	28,45	0.04	0.4

Figure 3.3. Wing growth of Manx shearwater chicks in 1995 and 1998-2000.

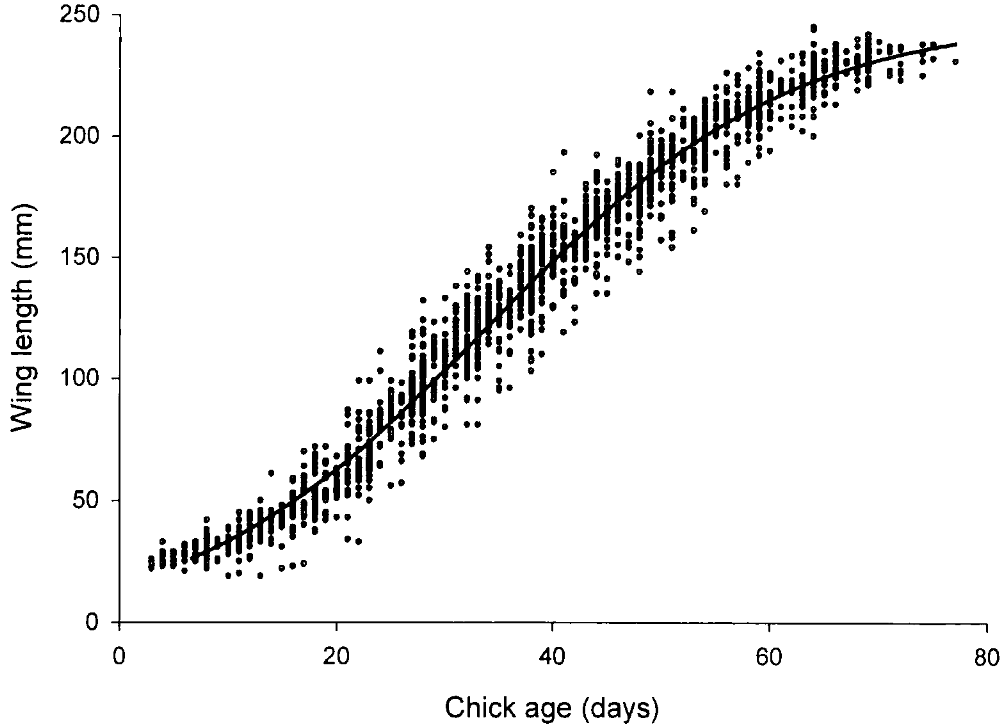

Table 3.6. Mean (± SD) wing length of Manx shearwater chicks aged 60 (± 1) days.

year	*n*	wing length (mm)	
		mean	S.D.
1973	98	215.9	7.41
1974	53	215.1	8.45
1975	40	215.9	7.53
1976	18	218.6	5.22
1995	48	214.3	7.83
1997	4	224.3	6.45
1998	6	220.2	4.54
1999	9	219.4	6.21
2000	9	216.8	7.30

3.4.6. Food provisioning

Mean meal mass showed significant variation among years (Table 3.7; $F_{9,475} = 3.91$, $P < 0.001$) and was significantly higher in 1974 and 1976 than in 1995 and 1998 (Tukey's H.S.D. tests, $P < 0.05$). The two years with the highest meal masses also had the highest values of peak mass, and the years with the lowest meal masses had the lowest peak masses. Food provisioning rates showed significant annual variation (Table 3.7; $F_{9,475} = 8.28$, $P < 0.001$) and were significantly lower in 1996 and 1998 compared with 1973-1976, 1999 and 2000, and lower in 1995 than in 1974 and 1999 (Tukey's H.S.D. tests, $P < 0.05$). The low food provisioning rates in 1998 and 1995 were reflected in low peak masses in these years, but growth parameters were not calculated for 1996 which also had low provisioning rates.

There was no significant variation among years in coefficients of variation (CV) for meal mass (Table 3.7; $F_{9,475} = 1.75$, $P = 0.08$), but the CV for provisioning rate showed significant annual variation (Table 3.7; $F_{9,475} = 3.22$, $P = 0.001$), and was highest in 1996. This may be partly due to the small sample size ($n = 20$), but may also be a result of the longer average intervals between feeds. The mean number of days between feeds differed significantly among years (Table 3.8; Kruskal-Wallis ANOVA; $\chi^2_{9,475} = 29.7$, $P < 0.001$) with longer intervals in 1996 than in 1973, 1975, 1999 and 2000 (nonparametric multiple comparisons, $P < 0.05$). Repeatability coefficients for meal mass, feeding frequency and provisioning rate were low (ranging from –0.02 to 0.14) and non-significant (Tables 3.9 and 3.10).

3.4.7. Relationship between food provisioning and chick growth

To examine the effect of rate and variability of food provisioning on peak mass, I used stepwise multiple regressions with asymptotic mass as the dependent variable, and mean food provisioning rate, CV for provisioning rate, mean interval between feeds, hatching date (to control for timing of breeding) and wing length at 60 days (to control for chick body size) as independent variables. Peak mass (A) was significantly related to mean provisioning rate and CV for provisioning rate according to the equation: $A = 6.29$ (SE ± 0.32) x provisioning rate (g/day) + 0.32 (SE ± 0.15) x CV + 232.7 (SE ± 23.2). ($r^2 = 0.54$, $F_{2,326} = 195.4$, $P < 0.001$).

Maximum growth rate (k) showed a significant positive relationship to mean provisioning rate and hatching date, and a significant negative relationship to wing length, according to the equation: $k = 0.05$ (SE ± 0.01) x provisioning rate (g/day) + 0.05 (SE ± 0.01) x hatching date (julian day) – 0.05 (SE ± 0.01) x wing (mm) + 14.4 (SE ± 3.8). ($r^2 = 0.12$, $F_{3,325} = 13.1$, $P < 0.001$).

Table 3.7. Mean meal mass and provisioning rates with their coefficients of variation. *n* = number of nests; CV = mean of coefficients of variation for individual chicks; SD = standard deviation of each coefficient of variation.

year	*n*	meal mass (g)			provisioning rate (g/day)		
		mean	CV (%)	SD	mean	CV (%)	SD
1973	106	68.1	53.4	11.8	56.4	74.5	15.9
1974	80	72.2	56.9	11.5	59.4	78.3	13.9
1975	69	67.6	54.9	12.1	56.5	75.3	15.2
1976	20	75.9	55.3	14.0	58.8	83.3	16.0
1995	53	65.6	55.4	9.8	53.7	77.7	13.1
1996	20	65.8	58.1	10.6	48.5	90.9	16.2
1997	23	70.1	52.0	10.3	55.2	79.8	18.1
1998	47	64.9	53.5	13.1	51.4	80.0	19.2
1999	32	70.1	55.6	11.6	59.6	74.1	14.3
2000	35	69.4	49.0	13.8	57.2	72.2	20.2

Table 3.8. Mean (± SD) intervals between successive feeds for individual chicks. *n* = number of nests.

year	*n*	interval between feeds (days)	
		mean	SD
1973	106	1.20	0.11
1974	80	1.21	0.12
1975	69	1.19	0.15
1976	20	1.29	0.14
1995	53	1.21	0.14
1996	20	1.33	0.16
1997	23	1.24	0.17
1998	47	1.21	0.13
1999	32	1.18	0.10
2000	25	1.19	0.14

Table 3.9. Repeatability of food provisioning of Manx shearwater chicks raised by the same parents in 1973-1975. n = 65 nests and 2.4 observations per nest. Feeding frequency data were log-transformed prior to analysis.

Parameter	F	d.f.	r_i	P
meal mass	1.04	64,90	0.02	0.4
feeding frequency	1.36	64,90	0.13	0.1
provisioning rate	1.05	64,90	0.02	0.4

Table 3.10. Repeatability of food provisioning of Manx shearwater chicks raised by the same parents in 1995 and 1997-2000. n = 19 nests and 3.26 observations per nest. Feeding frequency data were log-transformed prior to analysis.

Parameter	F	d.f.	r_i	P
meal mass	1.11	18,43	0.03	0.4
feeding frequency	1.54	18,43	0.14	0.5
provisioning rate	0.93	18,43	-0.02	0.5

3.5. Discussion

3.5.1. Breeding success

In the 14 years for which data were available, there was no significant variation in either hatching or fledging success. Thompson (1987) found significant annual variation in hatching success of Manx shearwaters on Rhum, Scotland, but found no annual variation in fledging success. Failures during incubation were attributed to flooding of burrows, due to the high rainfall on Rhum (Thompson & Furness 1991), but such events on Skomer and Skokholm are rare. This may be one factor explaining the difference in breeding success between the two colonies (70% on Skokholm and 52% on Rhum; Brooke 1990).

3.5.2. Hatching date

Hatching date differed significantly among years and showed moderate and significant repeatability ($r_i = 0.38$, $P < 0.01$). Other studies found similar repeatabilities for timing of breeding (e.g. 0.2 for laying date in female barn swallows *Hirundo rustica* (Banbura & Zeilinski 2000), 0.2 for relative laying date in female guillemots *Uria aalge* (Sydenham & Eddy 1995), 0.5 for relative laying date and 0.45 for absolute laying date in pairs of Arctic skuas *Stercorarius parasiticus* (Phillips & Furness 1998). However, Catry *et al.* (1999) found that repeatability of laying date in great skuas *Catharacta skua* was high over a small number of years but disappeared over a longer timescale, suggesting that timing of breeding was not a fixed trait. Manx shearwaters, like great skuas, are long-lived birds and established pairs have high mate-fidelity. It would therefore be interesting to test repeatabilities over a greater number of years to determine whether repeatable traits in Manx shearwaters are consistent over a longer period of time.

3.5.3. Chick growth

Mass growth followed a Gompertz curve which differed among years in both shape and scale, indicating differences in growth rate and asymptotic (peak) mass. Peak masses were highest in 1974 and 1976 and lowest in 1995 and 1998, and growth rates were also low in 1995 and 1998. Annual variation in the point of inflection indicated differences in the age at which maximum growth rates occurred. Chicks attained maximum growth rates at an older age in 1995 and 2000 and at a younger age in 1998. 1995 and 1998 were similar in their low growth rates and low peak masses, but differed in the timing of maximum growth, perhaps indicating better feeding conditions during early chick-rearing in 1995 and later in 1998 and 2000.

Peak mass and growth rates of chicks raised by the same parents in successive years showed significant repeatabilities in 1973-1975. Repeatabilities in 1995-2000 were marginally significant for peak mass, and non-significant for other growth parameters. This may suggest that extrinsic factors had a greater influence on growth in 1995-2000, although it could also be a result of the smaller sample size in these years.

There are currently few published data for repeatabilities of chick growth in seabirds. However, repeatabilities in this study were similar to those for chick growth indices in Arctic skuas (r_i = 0.43 for a growth index based on residuals; Phillips & Furness 1998), and fledging mass in Manx shearwaters (an approximate r_i of 0.28 for (Phillips & Furness 1998, based on data from Brooke 1986).

Of the different components of chick growth, mass growth is the most variable and shows the greatest response to food limitation (Bryant 1975), whereas feather and skeletal growth are largely genetically determined and show little variation (Schew & Ricklefs 1998; Wienecke *et al.* 2000). For example, skeletal growth in fork-tailed storm petrels *Oceanodroma furcata* was only retarded during extreme food shortages (Boersma 1986). Although I only present data for wing length in chicks aged 60 days, there were no significant differences among years, indicating that rates of feather growth in Manx shearwater chicks are relatively fixed compared with mass growth.

3.5.3. Food provisioning

Most previous studies of food provisioning in Manx shearwaters have focused on a single year, and examined short-term variability in meal mass and feeding frequency (Hamer & Hill 1997; Hamer *et al.* 1999). Thompson (1987) compared food provisioning in two years, and found a significant difference in feeding frequency but not in meal mass. The current study found significant annual variation in meal mass, feeding frequency and rate of food provisioning. Annual variation in food provisioning rate was reflected by variation in chick growth, and suggested that food availability was higher in 1974 and 1976, and lower in 1995 and 1998. Rates of food provisioning were also low in 1996, with longer intervals between feeds but similar meal sizes to other years, but unfortunately mass growth parameters could not be calculated for this year. The non-significant repeatabilities of food provisioning parameters suggest strong environmental effects on provisioning, in keeping with the idea that food provisioning in pelagic seabirds is affected by stochastic variation in foraging success (Ricklefs & Schew 1994; Hamer & Hill 1997).

I found a positive relationship between peak mass and mean food provisioning rate, and between peak mass and coefficients of variation for provisioning rates in individual chicks. Growth rate showed a similar, but weaker relationship with provisioning rate. Peak mass was not related to wing length at 60 days, which suggests that body mass mainly represented body condition rather than structural size. This gives some support to the hypothesis that chicks experiencing more variable food provisioning will store greater amounts of fat, as found in a comparison of growth and feeding variability in three shearwater species (Hamer *et al.* 2000).

High variability of food provisioning may make annual and individual differences difficult to detect. Using chick growth data integrates short-term food provisioning over a longer period of time, thus smoothing out the day to day fluctuations. Mass growth is more sensitive than wing growth to changes in food provisioning, and may therefore be the best indicator of parental foraging success. I discuss this further in Chapter 7. The extent to which chick growth reflects food availability is not known, and requires investigation. However, this study has identified appropriate indices for monitoring breeding performance in Manx shearwaters, and provided baseline data describing the variability of different breeding parameters over a number of years.

3.6. References

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Chapter 4

Annual variation in chick growth, food provisioning and diet of northern fulmars, and implications for monitoring marine environments

4.1. Summary

Chick growth and food provisioning of northern fulmars *Fulmarus glacialis* were studied at Fair Isle, Shetland, in two years of contrasting environmental conditions. Low sandeel availability resulted in very low breeding success in many seabirds in Shetland in 1998, whereas breeding success in 1997 indicated a normal season. Fulmars at Fair Isle made fewer breeding attempts in 1998 and those that did breed experienced lower success than in 1997. There were also significant differences in diet and food provisioning in the two years; sandeels *Ammodytes marinus* were the most abundant prey items in 1997, but were completely absent from the diet in 1998. A prolonged period of bad weather ocurred shortly after hatching in 1998, resulting in high nestling mortality. Those chicks that survived this episode had been heavier for their age

immediately prior to its onset, and remained heavy throughout development in comparison to chicks in 1997, despite a continued absence of sandeels from the diet. Surviving chicks in 1998 were subsequently fed comparatively small meals at frequent intervals, but with no overall difference in the amount of food delivered. I discuss the implications of differential mortality and resulting growth patterns for the use of seabird breeding parameters to monitor marine environments.

4.2. Introduction

Seabird breeding performance is increasingly being used as an indicator of changes in marine environments (Cairns 1987; Cairns 1992; Montevecchi 1993). Different parameters are predicted to be sensitive to different ranges of marine food supplies; e.g. changes from good to moderate food supply are likely to affect diet and adult time-activity budgets, whereas changes from moderate to poor food availability additionally impact on chick growth and survival (Cairns 1987). However, chick mortality is unlikely to occur randomly, and may be affected by factors such as body condition or characteristics of parental care. Higher mortality of chicks in poor condition could, paradoxically, lead to apparently better growth in poor environments. This problem was recognised by Williams & Croxall (1990) and discussed by Cairns (1992), but has seldom been addressed in other studies (but see Bost & Jouventin 1991).

Northern fulmars *Fulmarus glacialis* (hereafter referred to as fulmars) are among the most abundant seabirds in the North Atlantic Ocean, with an estimated 235, 000 pairs breeding in Shetland, UK (Lloyd *et al.* 1991; Snow & Perrins 1998). Sandeels

Ammodytes marinus normally make up a large part of the diet of fulmars in Shetland (Furness & Todd 1984; Harris & Riddiford 1989; Hamer *et al.* 1997; Phillips *et al.* 1999). Breeding success of other seabirds (Kittiwakes *Rissa tridactyla*, Arctic terns *Sterna paradisaea*, Arctic skuas *Stercorarius parasiticus*, black guillemots *Cepphus grylle* and puffins *Fratercula arctica*) in Shetland was greatly reduced in 1998 in comparison to previous years, indicating a major reduction in the availability of sandeels around Shetland (Thompson *et al.* 1999). In this chapter I test the prediction that non-random mortality of chicks may confound the relationship between food availability and chick growth. I compare the diet, food provisioning, chick growth and survival of fulmars in a normal breeding season (1997) and a poor breeding season (1998).

4.3. Methods

4.3.1. Study site

Fair Isle, Shetland (59°32' N 1°38'W) has one of the largest UK fulmar colonies, with an estimated breeding population of 43,000 pairs (Riddington *et al.* 1997). Fulmars nest on cliffs and offshore stacks as well as inland sites (e.g. in old buildings or in the shelter of stone walls). Fieldwork took place in July - September 1997 and 1998. Data in 1997 were collected by R.A. Phillips.

4.3.2. Diet

Regurgitated food samples were collected from 118 breeding adults or chicks in 1997 and 62 in 1998, with no bird being sampled more than once. Samples were frozen prior to identification. In the laboratory, prey items were identified to the lowest possible taxonomic level from external appearance or morphology of squid beaks, fish vertebrae and sagittal otoliths using reference material and published guides (Härkönen 1986, Watt *et al.* 1997). Prey abundance was measured by frequency of occurrence based on presence or absence (Duffy & Jackson 1986; Thompson *et al.* 1995).

4.3.3. Chick growth

Adult fulmars brood their chick for up to ten days post-hatching, so to avoid disturbance work at nest sites began when chicks were no longer attended continuously. Chick age was estimated from wing length (maximum flattened chord, excluding down feathers, measured with a stopped wing rule to the nearest 1 mm), calibrated against data for chicks of known age (Phillips & Hamer 2000a). A sample of accessible chicks (1997: $n = 26$; 1998: $n = 18$) was weighed daily at 1600h to the nearest 5 g, using a Salter spring balance. Wing length (see above), head plus bill length and tarsus length (both measured with vernier callipers to the nearest 0.1 mm) were recorded at 5-day intervals. An index of body size was calculated as the sum of head plus bill and tarsus length, both transformed to z-scores (mean = 0, SD = 1).

4.3.4. Food provisioning

To determine the sizes of meals, chicks at the study nests (1997: $n = 26$; 1998: $n = 18$) were weighed at 6-hour intervals (at 1600h, 2200h, 0400h and 1000h) for periods of 48 hours every ten days. In addition, adult attendance and chick feeding frequency were monitored directly by visual observation at a sub-sample of these nests (1997: $n = 14$; 1998: $n = 18$), with three 6-hour observations (covering all daylight hours) made within

48 hours within every 10 day period. In both years, three sets of observations were carried out during the linear phase of mass growth, and a fourth took place when chicks were in mass recession.

Separate equations describing mass loss in relation to age, body size and initial mass were calculated for chicks that had, or had not been fed in the previous six hour period (Phillips & Hamer 2000a). All mass increments were then corrected using these equations. Following Phillips & Hamer (2000b), a 20 g margin of error was adopted so that any corrected mass increments of less than 20 g were excluded. Fulmar chicks rapidly become accustomed to handling (Hamer & Thompson 1997; Phillips & Hamer 2000a), but to test for possible adverse effects of repeated weighings I compared age-specific body mass, mass growth rate and survival of frequently weighed chicks and a sample of control chicks (1997: n = 23; 1998: n = 15) at a different part of the colony, weighed at ten day intervals. Repeatability of meal mass and daily food delivery in fulmar chicks is low and not statistically significant (Phillips & Hamer 2000a), so these data were considered to be independent in the following analyses.

4.4. Results

4.4.1. Diet

Table 4.1 lists the species identified in food samples in 1997 and 1998 (n = 118 and 62 respectively). Proportions of different categories of prey (sandeel, other fish, crustacea and squid) in food samples are shown in Table 4.2. Sandeels were found in 37% of samples in 1997, but were entirely absent in 1998. Other fish (excluding sandeel) were present in 89% and 94% of samples in 1997 and 1998 respectively, with Gadidae the predominant family in both years. There were significant differences between the two years in the proportion of samples containing sandeels ($\chi^2_1 = 28.6$, $P < 0.001$), but not any other prey category ($P > 0.05$ for all three categories).

4.4.2. Breeding success

There were no differences in survival of chicks in the frequently-weighed group compared with the control group (Table 4.3; $\chi^2_3 = 2.28$, $P = 0.5$) but survival was much poorer in 1998 than 1997 (Table 4.3; $\chi^2_3 = 14.5$, $P = 0.002$). Overall, the proportion of chicks hatched that survived to fledging decreased markedly, from 87% in 1997 to 55% in 1998.

A prolonged period of bad weather (heavy rainfall, low temperatures and high windspeed) occurred during early chick-rearing in 1998, between 12th and 21st July. Chicks were not handled during this period, and 13 of the 47 study chicks had died when the nests were re-visited on 23 July. Prior to this period, on 11th July, 28 of these 47 chicks were weighed (of which nine died and 19 survived). Controlling for age, chicks that subsequently died had a lower initial body mass than those that survived (Fig 4.1: ANCOVA with age as a covariate: effect of group (died or survived): $F_{1,25} = 8.57$, $P < 0.01$; covariate (age): $F_{1,24} = 14.0$, $P = 0.001$; interaction: $F_{1,24} = 4.15$, $P = 0.053$). A further eight of the remaining 34 chicks died (from 28th July to 26th August, all on different days; chick age range = 22 - 45 days), due to predation ($n = 2$), desertion by parents ($n = 1$), being swept off the nest by waves ($n = 1$) and unknown causes ($n = 4$).

4.4.3. Chick growth

There were no differences in age-specific masses of frequently weighed and control chicks, either in 1997 (Phillips & Hamer 2000b), or 1998 (repeated measures ANCOVA of chick mass on 1st, 11th and 21st August, with chick age as a covariate: effect of age: $F_{1,22} = 0.45$, $P = 0.5$; effect of treatment: $F_{1,22} = 0.1$, $P = 0.9$; effect of date: $F_{2,46} = 47.9$, $P < 0.001$; interaction between treatment and date $F_{2,46} = 1.62$, $P = 0.2$).

During the linear phase of wing growth (20-50 days; Phillips & Hamer 2000a) there were no significant differences between years in the relationship between age and wing length (ANCOVA: year: $F_{1,267} = 3.26$, $P = 0.1$; age: $F_{1,266} = 10464.9$, $P < 0.001$; interaction: $F_{1,266} = 0.09$, $P = 0.8$), or age and body size index (year: $F_{1,267} = 0.01$, $P = 0.9$; age: $F_{1,266} = 552.1$, $P < 0.001$; interaction: $F_{1,266} = 0.02$, $P = 0.9$). The effects of structural size on age-specific mass were therefore considered to be negligible, and mass growth data were not adjusted for size. Figure 4.2 shows mass growth of chicks that survived to fledging. Chicks were significantly heavier in 1998 than in 1997 (repeated measures ANOVA of mean mass in 10-day age-classes (11-20 to >50 days); age-class: $F_{4,168} = 246.0$ $P < 0.001$; year: $F_{1,42} = 4.37$, $P = 0.04$; interaction: $F_{4,168} = 0.61$, $P = 0.7$).

4.4.4. Feeding frequency and meal mass

Following Phillips and Hamer (2000b), intervals in which chicks were fed were identified from nest observations. Rates of mass loss in the absence of feeding were significantly and independently related to initial mass and age in both years, and to body size index in 1997, according to the following equations:

1997: $\log_{10}$ mass loss (g/hour) = [2.21 (S.E. ± 0.23) x $\log_{10}$ initial mass] - [1.47 (S.E. ± 0.20) x $\log_{10}$ age] - [0.77 (S.E. ± 0.26) x $\log_{10}$ body size index] - 2.73 (S.E. ± 0.35). ($F_{3,217} = 36.8, P < 0.001, r^2 = 0.34$).

1998: $\log_{10}$ mass loss (g/hour) = [2.43 (S.E. ± 0.34) x $\log_{10}$ initial mass] - [1.92 (S.E. ± 0.36) x $\log_{10}$ age] - 3.32 (S.E. ± 0.56). ($F_{2,86} = 27.00, P < 0.0001, r^2 = 0.39$).

Rates of mass loss in the interval following a feed were significantly and independently related to initial mass and age in both years, according to the equations:

1997: $\log_{10}$ mass loss (g.hour^{-1}) = [2.02 (S.E. ± 0.20) x $\log_{10}$ initial mass - [1.00 (S.E. ± 0.17) x $\log_{10}$ age] - [0.87 (S.E. ± 0.19) x body size index] - 2.64 (S.E. ± 0.30). ($F_{3,320}$ = 68.7, $P < 0.0001, r^2 = 0.48$)

1998: $\log_{10}$ mass loss (g. hour^{-1}) = [1.28 (S.E. ± 0.34) x $\log_{10}$ initial mass] - [0.66 (S.E. ± 0.32) x $\log_{10}$ age] - 1.91 (S.E. ± 0.58). ($F_{2,141} = 12.09, P < 0.0001, r^2 = 0.15$)

The mass of food delivered to a chick by one or both parents in a 6-hour interval (referred to here as meal mass) was calculated using the above equations, assuming that chicks were fed half way through each interval. Meal mass increased with age in chicks up to 50 days, then decreased slightly towards fledging (Fig. 4.3). There was significant variation in meal mass among ten-day age-classes (two-way ANOVA: $F_{5,575} = 6.93$, $P < 0.001$), and chicks received heavier meals in 1997 than 1998 ($F_{1,575} = 9.04$, $P < 0.01$) with no significant interaction between year and age-class ($F_{5,575} = 1.96$, $P = 0.08$).

To examine variation in feeding frequency (the number of meals delivered to chicks per day) and total daily food delivery between years and among age-classes I used non-parametric two-way ANOVAs (Scheirer-Ray-Hare tests; Sokal & Rohlf 1995). Feeding frequency differed significantly between years and among age-classes (Table 4.4; for effect of year: $H_1 = 7.77$, $P < 0.01$; for effect of chick age: $H_4 = 31.27$, $P < 0.001$; for interaction between year and chick age: $H_4 = 4.02$, $P = 0.4$), and was consistently higher in 1998. The total mass of food delivered in 24 hours increased with chick age, and was greatest in chicks aged 31-40 days (Fig. 4.4). There were no significant differences in total daily food delivery between the two years (for effect of year: $H_1 = 0.27$, $P = 0.6$; for effect of chick age: $H_4 = 23.25$, $P < 0.001$; for interaction between year and chick age: $H_4 = 3.27$, $P = 0.5$)

Table 4.1. Prey species in fulmar diets at Fair Isle in 1997 and 1998.

Species	1997 (118 samples)		1998 (62 samples)	
	n	%	*n*	%
Crustacea				
Hyperia galba	5	4	1	2
Eurydice pulchra	4	3	1	2
Pandalus borealis	9	8	0	0
Nephrops sp.	5	4	0	0
Euphausiacea	1	1	2	3
Mysidacea	1	1	0	0
Caligus elongatus	39	33	21	34
Unidentified crustacea	21	18	11	18
Cephalopods				
Gonatus steenstrupii	1	1	0	0
Todarodes sagittatus	1	1	0	0
Unidentified squid	7	6	9	15
Fish				
Trisopterus esmarkii	0	0	2	3
Trisopterus minutus	16	14	1	2
Trisopterus sp.	16	14	17	27
Micromesitius poutassou	3	3	0	0
Melanogrammus aeglefinus	7	6	5	8
Merlangius merlangus	3	3	11	18
Pollachius spp.	3	3	0	0
Unidentified gadids	17	14	28	45
Clupea harengus	0	0	6	10
Unidentified clupeids	3	3	1	2
Argentinia sphyraena	0	0	1	2
Scomber scombrus	0	0	2	3
Ammodytidae	44	37	0	0
Hippoglossoides platessoides	1	1	0	0
Unidentified fish	20	17	14	23
Fish offal	1	1	1	2

Table 4.2. Categories of prey in food samples in 1997 and 1998.

Prey type	1997 (n = 118)		1998 (n = 62)	
	n	%	*n*	%
sandeel	44	37	0	0
other fish	103	87	58	94
crustacea	38	32	12	19
squid	9	8	9	15

Table 4.3. Fledging success of fulmars at study sites in 1997 and 1998.

year	treatment	hatched	fledged	% fledged
1997	weighed	31	26	83.8%
	control	24	22	91.6%
1998	weighed	32	18	56.2%
	control	15	8	53.3%

Table 4.4. Feeding frequency (number of meals per day) of fulmar chicks on Fair Isle in 1997 and 1998.

	1997		1998	
age-class (days)	n (chick-days)	Mean number of meals per day	n (chick-days)	Mean number of meals per day
11-20	41	1.52 ± 0.89	11	1.73 ± 0.65
21-30	63	1.29 ± 0.73	29	1.45 ± 0.74
31-40	65	1.34 ± 0.89	25	1.96 ± 0.89
41-50	54	1.28 ± 0.66	33	1.36 ± 1.03
>50	26	0.38 ± 0.57	17	0.94 ± 0.75

Figure 4.1. Age-specific mass of fulmar chicks on 11th July 1998, in relation to subsequent survival. Open circles are chicks that died between 12th and 23rd July; closed circles are chicks that survived beyond 23rd July.

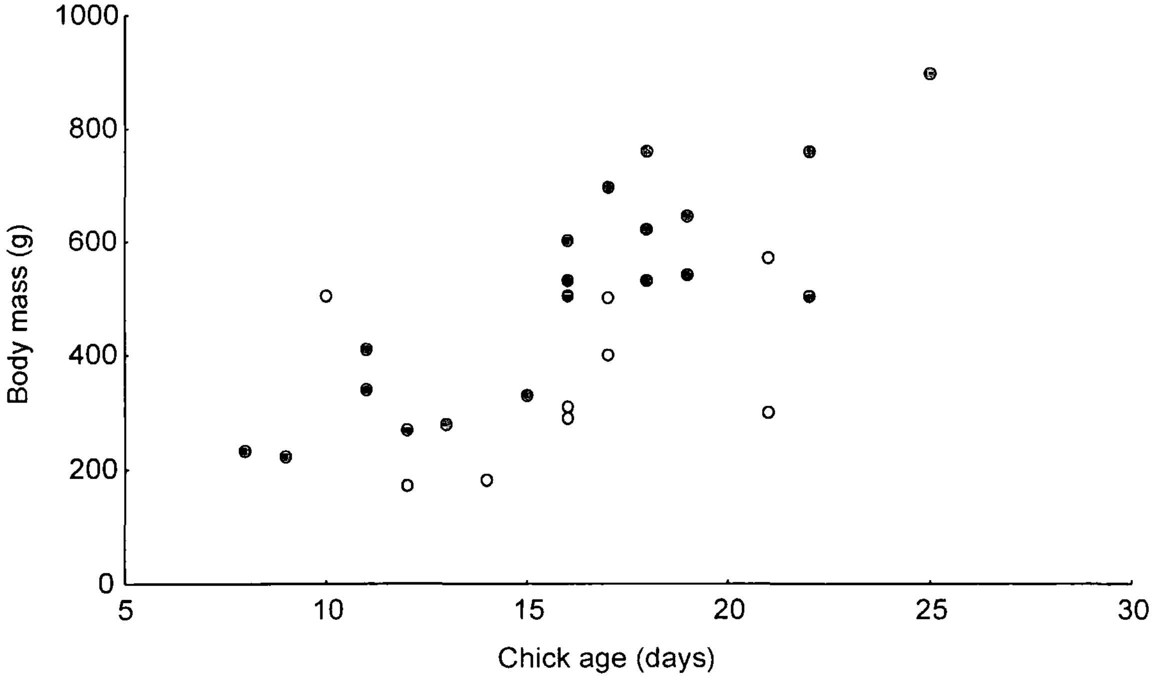


Figure 4.2. Mass growth of fulmar chicks (that survived to fledging) in 1997 (□; *n*=26 chicks) and 1998 (▲; *n*=18 chicks). Error bars are ± 1 S.E.

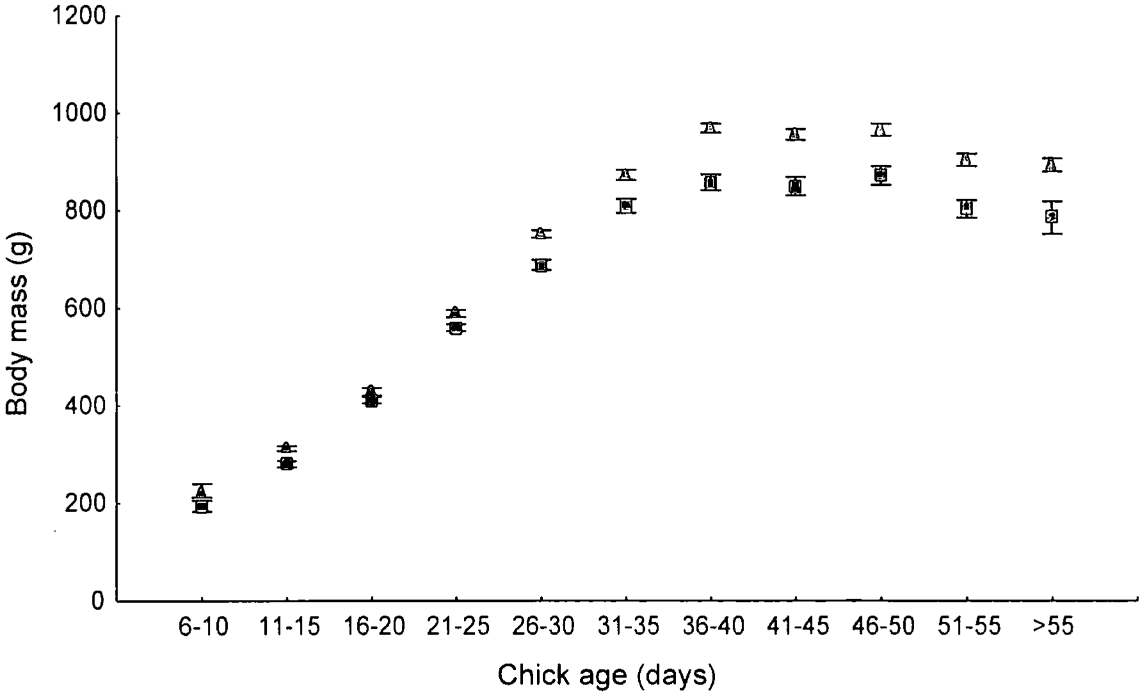


Figure 4.3. Meal mass (mass of food delivered in a 6-hour period) in fulmar chicks in 1997 (■; *n*=26 chicks) and 1998 (▲; *n*=18 chicks). Error bars are ± 1 S.E.

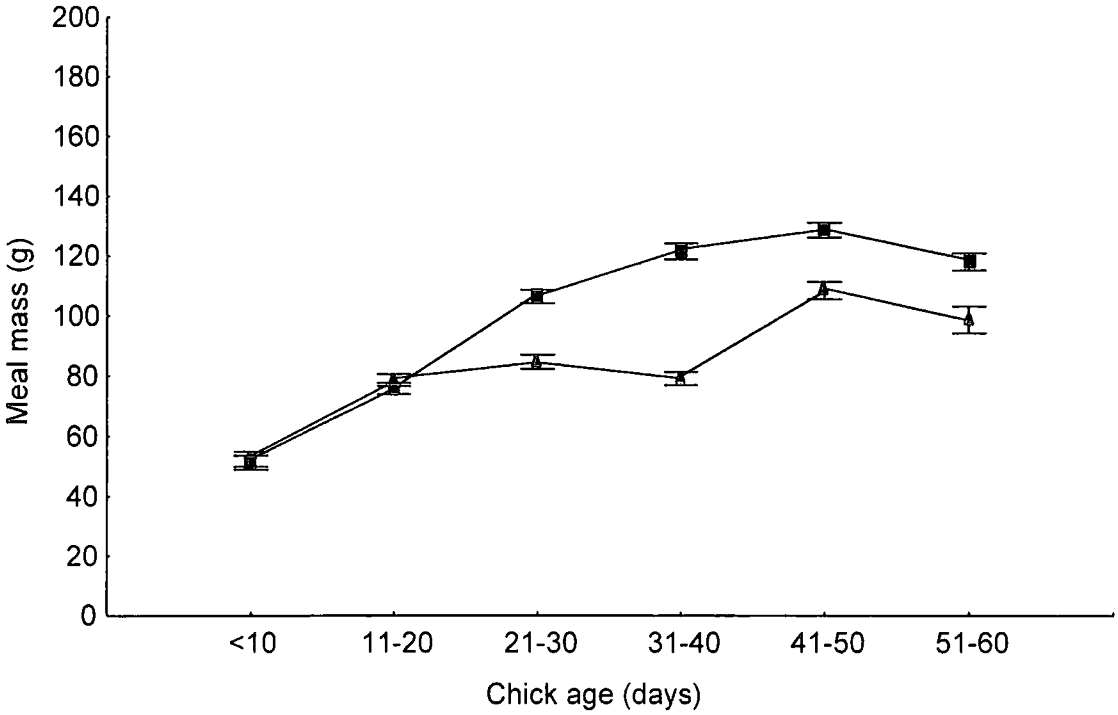
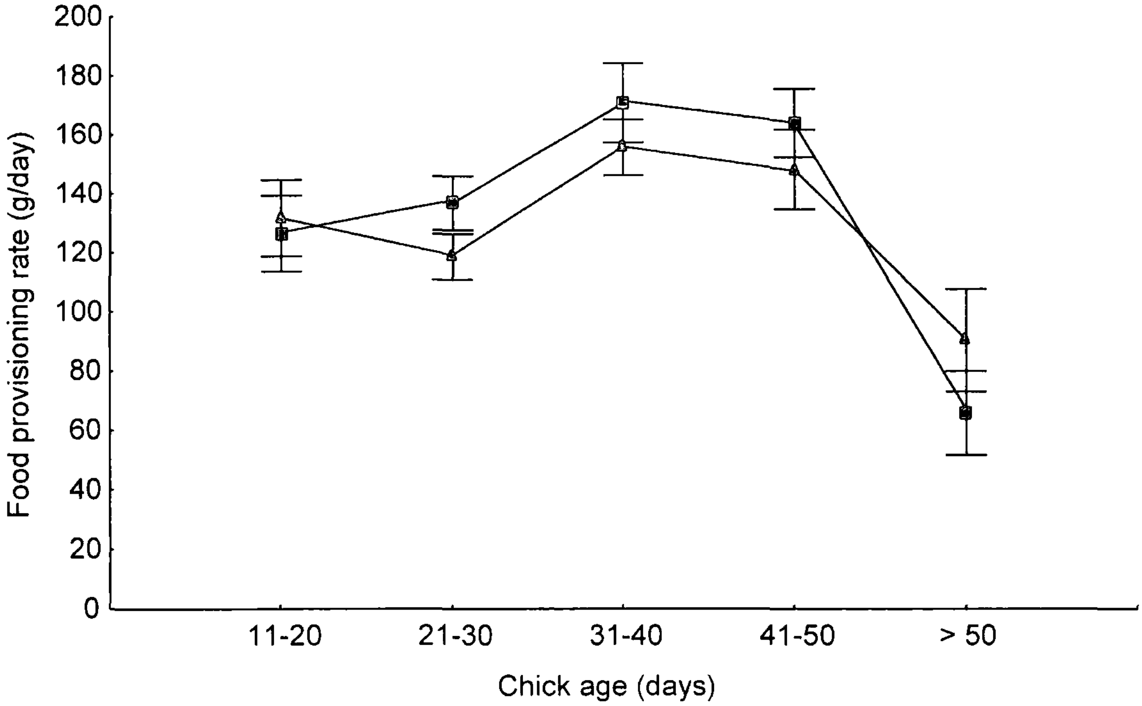


Figure 4.4. Rate of food provisioning (g/day) to fulmar chicks in 1997 (▣; *n*=26 chicks) and 1998 (▲; *n*=18 chicks). Error bars are ± 1 S.E.



4.4.5. Parental attendance and duration of foraging trips

Nest observations prior to mass recession indicated that individual parents made an average of 1.40 and 1.49 visits per nest per 18 hours of daylight in 1997 and 1998 respectively (1997: n = 756 nest-hours; 1998: n = 972 nest-hours). Periodic weighing data indicated that the proportion of chicks fed overnight was lower than during daylight hours (1997: 0.13 visits; 1998: 0.22 visits per nest per 6 hours of darkness). Assuming that all parents visiting at night feed their chick (Phillips & Hamer 2000a), the mean number of visits in 24 hours would be 1.50 in 1997 and 1.71 in 1998. This is equivalent to an interval of 32 hours between visits in 1997, and 28 hours in 1998. The median time spent on nests was 1h in 1997 and 0.3 hours in 1998, which gives a mean foraging trip duration of 31 hours in 1997 and 27.7 hours in 1998.

4.5. Discussion

Dietary samples indicated that fulmar chicks were fed on a broad range of prey in both years (Table 4.1). In 1998 when sandeels were absent from the diet, fulmars fed predominantly on other fish (Table 4.2), particularly gadids. Fulmars in the North Sea make extensive use of discarded fish and offal at whitefish trawlers (Hudson & Furness 1989; Camphuysen & Garthe 1997). In this study, erosion of otoliths in the proventriculus and probable overlap in size between discarded and small live fish meant that the size and source of gadids in the diet could not be quantified. However, the size of otoliths and vertebrae suggested that fulmars captured small, live gadids as well as taking larger discarded fish in both years.

Fulmar breeding success in 1998 was low compared to 1997, with 55% fledging success (see Results) However, Arctic terns and kittiwakes experienced total breeding failures on Fair Isle and throughout Shetland in 1998 (Thompson *et al.* 1999). That some fulmars were still able to raise chicks in 1998 may be partly explained by their mode of foraging. Fulmars are generalist feeders with a broad dietary range (Phillips *et al.* 1999), so should be less affected by shortages of sandeels than specialised, surface-feeding species such as terns and kittiwakes (Furness & Ainley 1984).

In addition to reduced fledging success, numbers of breeding fulmars at monitored sites on Fair Isle decreased by 32.5% from 400 apparently occupied sites (AOS) in 1997 to 270 AOS in 1998 (Baker *et al.* 1999). Non-breeding has often been associated with poor environmental conditions prior to or early in the breeding season, suggesting that seabirds are most likely to defer breeding when costs of reproduction are too high (Murphy *et al.* 1991; Crawford & Dyer 1995; Catry *et al.* 1998).

Patterns of chick growth in 1997 and 1998 (Figure 4.2) suggested an inverse relationship between body mass and presumed sandeel abundance, in contrast to the prediction by Cairns (1987). However, differential mortality of lighter chicks in 1998 was primarily associated with heavy rainfall (see Results). Mortality was therefore unlikely to have been associated with food availability *per se*, but probably resulted from an interaction between abiotic effects and variation in chick body condition, arising from individual variation in food provisioning ability. This also explains why chick survival in 1998 was poorer despite no evidence of decreased food provisioning compared with 1997.

Williams & Croxall (1990; 1991) recorded differential chick mortality in poor years, with only the larger chick of two-chick broods surviving. In this study, survival of single chicks was strongly influenced by body mass, suggesting that the food provisioning ability of parents may be an important determinant of breeding success. Fledging mass may be important for post-fledging survival in seabirds (Perrins *et al.* 1973), as fledglings may need to rely on body reserves until they become competent at foraging for themselves (Phillips & Hamer 1999). This selection for heavier birds probably occurs mainly after fledging under normal conditions, but in the extreme conditions in 1998 it occurred during the nestling stage.

Although the overall rate of food provisioning was very similar in both years, parents made shorter, more frequent foraging trips and delivered smaller meals in 1998 (see Results). Patterns of food delivery may have be influenced by food availability or foraging conditions (Granadeiro *et al.* 1998; Weimerskirch *et al.* 1999; Huin *et al.* 2000), or could have reflected inter-year differences in average foraging ability of birds sampled. The pattern of small, frequent feeds has been associated with experienced parents in Antarctic fulmars *Fulmarus glacialoides* and wandering albatrosses *Diomedea exulans* (Lequette & Weimerskirch 1990; Weimerskirch 1990) and with high rates of chick growth in comparison to chicks fed larger, less frequent meals (Schaffner 1990; Weimerskirch 1990; Berrow *et al.* 2000). Breeding histories of fulmars in this study were not known, but the poor environmental conditions in 1998 may have biased the sample towards more capable or more experienced parents that fed their chicks using a strategy that maintained a relatively high body mass throughout the nestling period.

Age-specific and fledging masses of seabird chicks are among the parameters used as indicators of marine food supplies (e.g. Gaston 1985; Shea & Ricklefs 1996), since these are more sensitive than breeding success to short-term changes in food availability (Cairns 1987). However, if chick mass is only measured after differential mortality has occurred (here at a median chick age of 18 days), it may be a misleading indicator of food supply (Williams & Croxall 1990). Although differential mortality in this study was primarily due to abiotic factors, periods of food shortage could have a similar effect, resulting in higher fledging mass when feeding conditions are poor. Croxall *et al.* (1988) suggested that the use of several breeding parameters for several species would produce a much more robust evaluation of marine food availability than just one parameter, and this study supports the view that data based on a single parameter (e.g. chick mass) should be interpreted with caution.

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Chapter 5

Food provisioning behaviour of male and female Manx shearwaters

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5.1. Summary

Recent attention has focused on the foraging and food provisioning strategies that allow procellariiform seabirds (e.g. albatrosses and shearwaters) to exploit pelagic food resources whilst providing food for dependent offspring at the nest. Several studies have found sexual differences in foraging and provisioning strategies in sexually dimorphic procellariiforms. However there are few such data for species such as Manx shearwaters *Puffinus puffinus* that have negligible sexual size dimorphism. We used radio-tracking coupled with periodic weighing of chicks to examine foraging trip durations and overall contributions to food provisioning by individual male and female Manx shearwaters at Skomer Island, UK. Both sexes made trips of 1-4 days but females also made longer trips of up to seven days. As a result, mean trip duration was significantly longer in females (2.1 days) than in males (1.5 days). Males fed their chick on a greater proportion of nights, delivered food to chicks at a higher rate and made a greater contribution to overall food provisioning than females. Meal size increased with foraging trip duration but the yield to the chick in g/day was greater after short trips. Trips of 5-7 days would give females access to the highly productive nursery grounds for sardines *Sardina pilchardus* in the SE Bay of Biscay. This area was previously thought to be exploited by birds from Skomer but was more recently considered to be beyond the foraging range of chick-rearing adults, based on a mean trip duration of two days.

5.2. Introduction

Procellariiform seabirds such as shearwaters and albatrosses are noted for their extreme life-history traits, which include delayed reproduction, single-egg clutches and slow chick growth (Lack 1968; Ricklefs 1990). These traits are thought to reflect the sparse, patchy and unpredictable distribution of marine food resources, coupled with constraints on the transport of food to the nest from distant foraging sites (Ashmole 1971). In this context, much attention has focused on food provisioning of procellariiform chicks under both natural and experimental conditions (Prince & Ricketts 1981; Ricklefs *et al.* 1985; Hamer *et al.* 1998). However, many of these studies have focused only on the chick and have inferred the food provisioning behaviour of parents from changes in chick mass over short time intervals (Hamer 1994; Bolton 1995; Hamer & Hill 1997). A number of recent studies have shown that considerable additional understanding of the foraging patterns and food provisioning behaviour of procellariiforms can be obtained by studying individual parents. Several species have been shown to use a dual foraging strategy in which individual parents intersperse short foraging trips to obtain food for the chick with one or more long trips to feed themselves (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994, 1997; Booth *et al.* 2000). A less frequently recorded phenomenon is for the durations of foraging trips and contributions to food provisioning at the nest to differ between male and female parents. This pattern has been recorded in giant petrels *Macronectes halli* (Hunter 1983) and wandering albatrosses *Diomedea exulans* (Weimerskirch *et al.* 1997), both of which have considerable sexual size dimorphism, but to our knowledge it has not been recorded in a species in which males and females are similar in body size.

A dual foraging strategy, which involves making both short and long trips, and sex-specific food provisioning, which involves one sex making longer trips, are both associated with a low average feeding frequency. In northern Europe, several studies of procellariiforms have reported relatively high rates of food provisioning, from 1 - 2 meals per chick per day in British storm petrels *Hydrobates pelagicus* (Bolton 1995) and Manx shearwaters *Puffinus puffinus* (Hamer & Hill 1997) to an average of 2.3 meals per chick per day in northern fulmars (Hamer *et al.* 1997). This implies abundant food and raises the question of whether these foraging strategies would occur in species breeding in northern European waters.

Manx shearwaters are widely distributed in the North Atlantic Ocean. Adults weigh about 400g with little sexual dimorphism in body size (<1mm in wing length and bill length, 1mm in tarsus length; Brooke 1990). They show the typical procellariiform pattern of a single-egg clutch and slow nestling development, with an average fledging period of 72 days (Harris 1966; Brooke 1986). Hamer & Hill (1997) recorded that chicks were fed at short average intervals (1.2 nights), with little temporal variation in meal size or feeding frequency, and a maximum interval of four nights between feeding events for any chick. However food provisioning by individual parents was not investigated. Here we use radio tracking combined with periodic weighing of chicks to examine the food provisioning behaviour and the overall contribution to food provisioning by individual male and female Manx shearwater parents.

5.3. Methods

Fieldwork took place from May to August 1999 at a colony of c.100,000 breeding pairs of Manx shearwaters (Smith *et al.* in press) on the island of Skomer, SW Wales, UK (51° 44’N, 5° 17’W). Manx shearwaters nest in burrows, and nest chambers were reached via short access tunnels dug into the roof of each burrow, with removable earth lids. Parents at ten nests with laying dates within 10 days from the mode (of 52 nests) were sexed from cloacal inspection shortly after egg laying in May (females’ cloacae were bluish and swollen after egg laying). Both birds were ringed to allow individual identification. The sexes of all these birds were subsequently confirmed from vocalisations at the nest during incubation and early chick rearing (Brooke 1978; James 1985).

All 20 ringed adults were caught at the nest at night during the middle of chick rearing (mean chick age = 23 days) from 14th to 18th July. Each adult was weighed to the nearest 5 g using a Salter spring balance and fitted with a VHF radio transmitter (Biotrack, Dorset, UK). Transmitters weighed 2 g (< 1 % of body mass), and measured 19 mm x 10 mm x 8 mm, with an external aerial measuring 135 x 0.6 mm. Transmitters were attached to two central tail feathers with self-amalgamating tape (RS Components, Newcastle, UK) which formed a seal over the feathers and transmitter, and was covered by the surrounding feathers. The aerial was thin and flexible, and extended c.60 mm beyond the tail. The process from capture to returning a bird to its burrow took no longer than ten minutes.

Visits of tagged birds to the colony were monitored for 20 consecutive nights, using a scanning receiver (MVT-7100, Yupiteru Industries, Tokyo) with a three-element Yagi antenna, located on a hillside at a distance of 100 m and elevation of 20 m from the study nests. Trials at the colony indicated that the range of this system was < 1 km, so we were confident that signals received were from birds in the colony and not at sea. Signals were detected for 2-3 minutes before birds entered their nest. Attendance was monitored overnight from 2230h (before the first adults returned) until 0430h (after the last adults had left the colony). Following Hamer & Hill (1997), chicks at study nests were weighed at 2100, 0100 and 0500h each night, to determine the sizes of meals delivered by each adult. Chicks were occasionally visited without being fed, but on no occasion was a chick fed without our recording an adult at the nest. To control for possible adverse effects of radio tagging and overnight weighing on chick growth, chicks at a sample of 24 nests with untagged adults, in a separate part of the colony, were weighed daily at 2100h.

Tagged birds were recaptured over a period of six nights after the end of the tracking period. Each bird was reweighed and the tag removed. Two radio tags lost their aerial, and a further three emitted weak or intermittent signals towards the end of the tracking period. These birds were excluded from further analysis after the tags were known to be unreliable, giving attendance and feeding data for 133 chick-nights at 10 nests (136 nest-nights for female parents and 130 nest-nights for males).

Overnight food delivery to chicks was calculated from mass increments between consecutive weighings. These were corrected for mass loss due to digestion, respiration and excretion, using equations in Hamer & Hill (1997). Throughout this paper, feeds refer to food delivery to the chick, whether by one or both parents, and meals distinguish food delivery by individual parents. If one parent and one feed were detected in the same four-hour period, this was classified as a single meal. If both parents were present and two feeds were detected in different four-hour periods, this was classified as a double meal. On a small number of occasions (n = 6), both parents were present in the same period and it was not possible to determine the number of meals. These were classified as three single and three double meals from the proportions of known meals on double visits (see Results), with the three larger feeds classified as double meals.

To avoid pseudoreplication of data, mean values of variables were calculated for each parent, and paired t-tests were used in comparisons of male and female parents at each nest. Proportions were arcsine transformed prior to analysis. All tests are two-tailed and means are expressed ± 1 standard deviation.

5.4. Results

There was no significant difference in body mass of adults weighed before and after the radio-tracking period (442 ± 30 g and 434 ± 29 g respectively, n = 20 birds; paired t-test: $t_{19} = 1.6$, $P = 0.1$). Chicks of tagged parents grew at a mean rate of 8.8 ± 1.8 g/day, which was no different to the growth rate of control chicks (9.2 ± 3.5 g/day; t-test: $t_{32} = 0.7$, $P = 0.5$). To confirm that overnight weighing did not disrupt feeding, we compared the mass of single meals from parents that arrived between 0030h and 0100h (and therefore may have been feeding the chick shortly before weighing at 0100h) with single meals from parents that arrived at other times. We found no significant effect on meal mass (adult present between 0030h and 0100h: 60.0 ± 28.4g, $n = 25$ meals from 16 parents; adult not present during this period: 54.7 ± 30.4g, $n = 61$ meals from 20 parents, $t_{34} = 0.7$, $P = 0.5$).

5.4.1. Nest attendance

We recorded 145 visits by parents over 133 chick-nights (Table 5.1; 1.1 parents/nest/ night on average). Chicks were visited on 110 chick-nights (83%), with one or other parent returning on 75 nights (56%), both parents returning together on 35 nights (26%) and neither parent returning on 23 nights (17%). Of the 75 visits by one parent, 45 (60%) were by males and 30 (40%) were by females. Mean foraging trip duration was 1.8 ± 0.5 days, with males making significantly shorter trips (Fig. 5.1; mean = 1.5 ± 0.2 days, $n = 91$, range = 1-4 days) than females (mean = 2.1 ± 0.2 days, $n = 75$, range = 1-7 days; paired *t*-test comparing mean trip durations by males and females at each nest; $t_9 = 3.8$, $P < 0.01$). However there was no significant difference in arrival times of males and females at the nest, in terms of minutes elapsed since nightfall, taken as 2200h (males: 0109h ± 35 minutes; females: 0125h ± 55 minutes; paired t-test: $t_9 = 0.9$, $P = 0.4$).

As a result of shorter trip durations, males visited the nest on a significantly greater proportion of nights than females (Table 5.2; $P < 0.01$). To examine whether or not each parent returned independently of its partner, we compared the observed proportions of chicks visited by nought, one or two parents overnight (0.17, 0.56, 0.26) with those expected from independent returns. On 266 parent-nights, the probability of a male returning (p_m) was 0.62 and the probability of a female returning (p_f) was 0.48 (Table 5.2). If males and females returned independently of each other, then the proportion of nests not visited by either parent would be ($[1 - p_m] \times [1 - p_f]$), the proportion visited by one or other parent would be ($p_m \times [1 - p_f]$) + ($p_f \times [1 - p_m]$) and the proportion visited by both parents would be ($p_f \times p_m$). The expected proportions (0.20, 0.50, 0.30) were no different to those observed ($\chi^2_2 = 1.2$, $P = 0.5$), indicating that parents returned independently of their partners.

5.4.2. Food provisioning rate

Food provisioning can be viewed from the chick's and the parents' perspective. From the chick's perspective, chicks received 122 feeds on 133 chick-nights (Table 5.1; 0.9 meals/night on average). Chicks were fed on 104 nights (78%), receiving a feed from one parent only on 86 nights (65%), from both parents together (i.e. two meals) on 18 nights (14%) and no feed on 29 nights (22%). Chicks were visited overnight without being fed on two single visits by males and four by females (5% of chick-nights), all at different nests. Visits by both parents overnight always resulted in at least one meal, but 17 of 35 double visits (49%) resulted in only a single meal.

From the parents' perspective, parents fed their chick on 122 of 266 parent-nights (46%) and returned without feeding the chick on 23 nights (9%). Adults had a much higher probability of returning without feeding the chick if they were one of two parents to return to a nest overnight (0.24) than if they were the only parent to return overnight (0.08; $\chi^2_1 = 7.2$, $P < 0.01$). Males had a significantly higher probability of feeding their chick overnight than did females (Table 5.2). There was no significant difference between sexes in the proportion of visits resulting in a feed (Table 5.2).

To examine whether or not the two parents fed their chick independently of each other, we compared the observed proportions of chicks fed by nought, one or two parents overnight (0.22, 0.65, 0.14) with those expected from independence of feeding. On 133 chick-nights, the probabilities of males and females feeding their chick were 0.53 and 0.39 respectively (Table 5.2). The expected proportions of chicks fed by nought, one or both parents (0.29, 0.51, 0.21) were significantly different from those observed ($\chi^2_2 = 10.9$, $P < 0.01$), indicating that more chicks were fed by one parent overnight than expected by chance, and that fewer chicks were fed by neither parent or both.

5.4.3. Meal sizes

The mean mass of food delivered to chicks when fed overnight was 59.3 ± 29.6 g ($n = 104$). Single meals ($n = 86$) weighed 56.3 ± 25.8 g and double meals ($n = 18$) weighed 71.0 ± 28.1 g. There was no difference in the masses of single meals delivered by males and females (58.0 ± 11.7 g and 54.1 ± 5.8 g respectively; paired $t_9 = 0.95$, $P = 0.4$) or in the masses of all meals, including contributions to double meals, delivered by males and females (Table 5.2). However as a result of a higher feeding frequency, males delivered more food/nest/night than did females (Table 5.2). Meals delivered by females after trips of 1-4 nights were significantly smaller (mean = 47.3 ± 11.8 g) than meals delivered after trips of 5-7 nights (mean = 60.0 ± 10.5 g; $t_{23} = 2.2$, $P = 0.04$).

Table 5.1. Proportions of Manx shearwater chicks visited and fed overnight by male and female parents (based on 133 chick-nights at 10 nests).

	visited		fed		not fed	
	number of chicks	%	number of chicks	%	number of chicks	%
neither parent	23	17.3	-	-	-	-
male only	45	33.8	43	32.3	2	1.5
female only	30	22.6	26	19.5	4	3.0
both parents	35	26.3	18	13.5	17 *	12.7

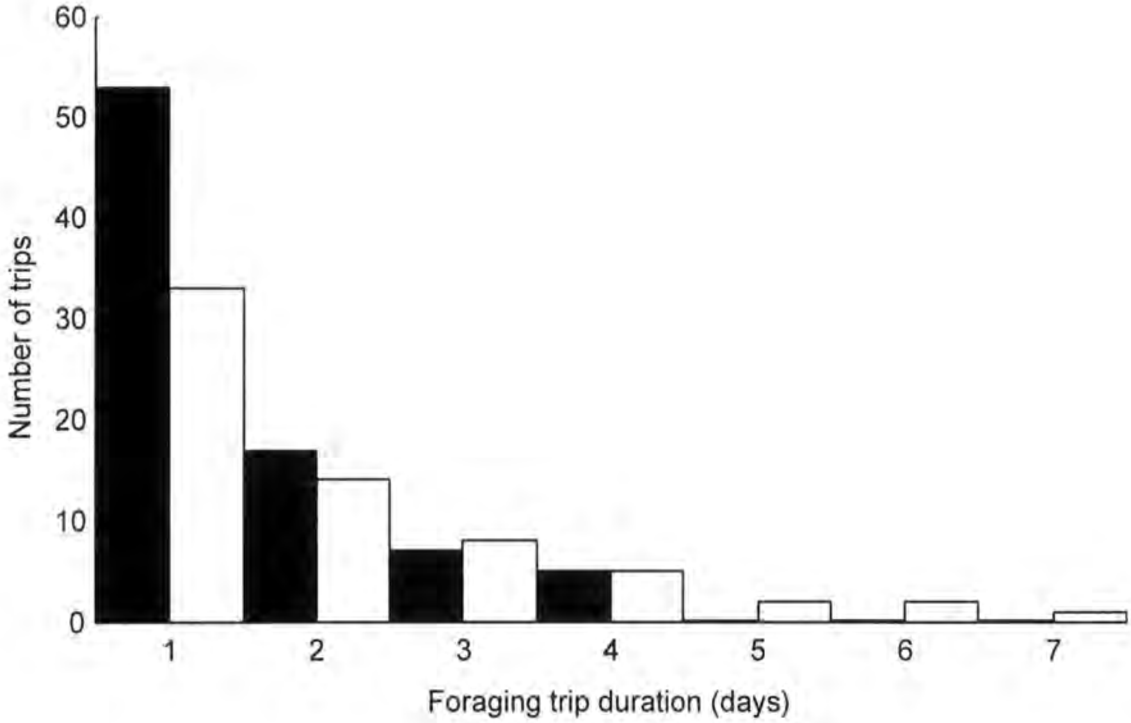
* Chicks were fed by one parent only (8 feeds were from males and 9 were from females).

Table 5.2. Nest attendance and food provisioning by male and female Manx shearwaters (based on 133 chick-nights at 10 nests).

	males		females		
	mean	SD	mean	SD	paired t-test
visits/night	0.62	0.07	0.48	0.07	$t_9 = 3.4, P < 0.01$
meals/night	0.53	0.07	0.39	0.11	$t_9 = 2.6, P = 0.02$
meals/visit	0.86	0.07	0.82	0.12	$t_9 = 1.0, P = 0.4$
meal mass (g)	53.3	12.3	49.9	12.4	$t_9 = 0.52, P = 0.6$
food provisioning rate (g/night)	28.9	9.0	20.1	7.8	$t_9 = 3.93, P < 0.01$

Figure 5.1. Durations of foraging trips by male and female Manx shearwaters.

■ = trips by male parents; □= trips by female parents.



5.5. Discussion

The food provisioning rate of chicks in this study was 53.4 g/night (0.9 feeds/night x 59.3 g/feed) which was very similar to the rate of 55 g/night recorded by Hamer & Hill (1997). The sizes of individual meals delivered by adults (mean = 56 g) were also similar to those recorded previously (mean = 49 g; Hamer & Hill 1997). Mass growth rates of chicks weighed repeatedly overnight were similar to those of control chicks weighed only once daily, and adults wearing radio transmitters maintained constant body mass throughout the study. We were therefore confident that collection of data had no adverse effects on adult food provisioning behaviour or chick growth.

5.5.1. Nest attendance and food provisioning

The distribution of visits by adults indicated that the two members of each pair visited the nest independently of each other (Table 5.1). However, the greater proportion of single feeds than predicted indicated that parents did not feed the chick independently. Almost half of all double visits resulted in a single feed, and the mass of double meals (71 g) was much smaller than twice the mass of single meals (2 x 56 = 112 g). These data strongly suggest that ingestion of food by chicks was limited by gut capacity constraints, as also found in other species that feed their chicks relatively frequently (Phillips & Hamer 2000).

In total, 9% of visits by parents did not result in delivery of food to the chick. Such non-feeding visits have also been recorded in several other procellariiforms including Christmas shearwater *Puffinus nativitatis* and phoenix petrel *Pterodroma alba* (Ricklefs 1984), Leach's storm petrel *Oceanodroma leucorhoa* (Ricklefs 1992), Cory's shearwater *Calonectris diomedea* (Hamer *et al.* 1999) and northern fulmar (Phillips & Hamer 2000). This behaviour probably also occurs in other species but would be under-recorded in studies that do not monitor adult attendance independently of food provisioning.

5.5.2. Food provisioning by males and females

The longer foraging trips (Fig. 5.1), lower feeding frequency and smaller contribution to food provisioning by female parents (Table 5.2) could result from females allocating more time to foraging for themselves in order to regain body reserves used in egg production (Hatch 1990). However, female Manx shearwaters regain body mass during incubation (Harris 1966) and so egg production would not explain the longer trips by females during chick-rearing. Another possibility is that high nest attendance of males has a territorial function (Brooke 1978; James 1985). However this hypothesis would predict a higher proportion of non-feeding visits by males than by females, which was not found in this study, and would not explain the greater contribution that males made to food provisioning.

Meals delivered by females after trips of 5-7 days were substantially larger than those delivered (by females, and by both sexes combined), after trips of 1-4 days. However, despite this difference in meal size, the average yield to each chick from trips of 1-4 days (48.0/2.5 = 19.2 g per day) was almost twice that from trips of 5-7 days (60.0/6 = 10.0 g per day). The caloric density of food delivered to the chick may have been higher after longer trips due to concentration of stomach oils (Roby et al. 1989), but it was unlikely to have been twice as high, since in Manx shearwaters the prey captured by adults are not greatly modified before delivery to the chick (Brooke

1990). Thus chicks probably benefited much more from short trips made by both sexes (1-4 days) than from long trips made by females (5-7 days).

Long trips may have reduced competition with males for food resources close to the colony (Hunter 1983). Another possibility is that females used long trips to recuperate body mass lost in short trips, at the expense of a lower yield to the chick. This strategy has been recorded in two closely related species, short-tailed shearwaters *Puffinus tenuirostris* and sooty shearwaters *P. griseus* (Weimerskirch 1998; Weimerskirch & Cherel 1998). However, we present no information on changes in body mass over foraging trips, and it is not immediately apparent why in Manx shearwaters, only females should adopt such a strategy.

Lockley (1953) suggested from recoveries of ringed birds that Manx shearwaters breeding in Wales might travel up to 850 km from the colony on foraging trips (a round-trip of up to 1700 km) in order to exploit nursery grounds for sardines *Sardina pilchardus* in the SE Bay of Biscay (44°N). In contrast Brooke (1990) suggested that an average trip duration of two days would result in a foraging range no greater than about 360 km, so that birds rearing chicks on Skomer would be unlikely to forage south of Brittany (48°N). However, trips of 5-7 days would allow more than sufficient time for females to reach the SE Bay of Biscay. Although this requires further investigation, it is possible that the long trips made by females could allow them to exploit highly productive foraging areas at long distances from the colony at the expense of a reduction in yield to the chick.

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Chapter 6

Pre-fledging mass recession in Manx shearwaters: parental desertion or nestling anorexia?

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6.1. Summary

In many species of bird, nestlings undergo a period of mass recession, associated with a large reduction in food provisioning, before they fledge. This has been ascribed to parental desertion, although it could equally result from voluntary limitation of feeding (i.e. anorexia) among chicks. We examined the interactions between Manx shearwater *Puffinus puffinus* parents and chicks, to test whether the pre-fledging reduction in feeding was controlled by parents, chicks or both. In a cross-fostering experiment, chicks of different ages were switched between nests. We predicted that under a parental control model, switching would have no effect on food provisioning by the parents, but under chick control, the level of provisioning would be adjusted according to the age-specific requirements of the foster chick. Older chicks switched to the nests of younger chicks entered mass recession at an older age and had a higher peak mass and fledging mass than unmanipulated chicks, supporting the parental control model. Younger chicks switched to the nests of older chicks entered mass recession at a younger age and had a lower peak mass and fledging mass than unmanipulated chicks, which also supports this model. However, parents continued to feed younger chicks beyond the date at which their own chick would have fledged. This suggests that chicks also influenced provisioning, and that mass recession resulted from interactions between a fixed provisioning pattern in parents, and age-specific food requirements of chicks.

6.2. Introduction

Growth patterns of many birds (e.g. Procellariidae, Sulidae, Apodidae, Hirundinidae) include a period of mass recession before fledging. This is caused partly by loss of water from maturing tissues (Ricklefs 1968; Phillips & Hamer 1999), but in many species mass recession is associated with a reduction in food provisioning by parents. This reduction is most pronounced among pelagic seabirds of the Order Procellariiformes (e.g. petrels, shearwaters and albatrosses). These species accumulate large lipid reserves during nestling development, attaining peak masses of up to 170% of adult mass (Ricklefs *et al.* 1980). They then lose mass at the end of development, before fledging close to adult mass (Warham 1990). This mass recession has been ascribed to parental desertion, allowing parents to recover body reserves or depart earlier on migration than would otherwise be possible (Harris 1966; Brooke 1990; but see Warham 1990). This notion is supported to some extent by the fact that mass recession is more prevalent in chicks of migratory than non-migratory species (Table 7.9 in Brooke 1990). In this context, nestling obesity has been viewed as providing an energy source to sustain chicks during the period between desertion by their parents and fledging. However, there is surprisingly little evidence that parental desertion actually occurs, and some evidence to the contrary. For instance, several pelagic seabird species continue to feed their chicks during mass recession (e.g. up to one day before fledging in northern fulmars *Fulmarus glacialis*; Phillips & Hamer 2000). Moreover, where food consumption by the chick does decline or even cease altogether, this could be due to chicks refusing to accept food offered by their parents rather than parental desertion.

In this paper we adopt an experimental approach to determine whether changes in food provisioning prior to fledging are controlled by adults, chicks or both in Manx shearwaters *Puffinus puffinus*. In common with other procellariiforms, Manx shearwaters have a single-chick brood and slow nestling development (average fledging period = 72 days; Harris 1966; Brooke 1986). Chicks attain a peak mass of c.134% of adult mass at around 55 days post-hatching, followed by a sharp decline in feeding and a mean mass recession period of ten days before fledging (Perrins *et al.* 1973; Hamer & Hill 1997). We switched chicks between nests so that parents were given a foster chick ten (±1) days older or ten (±1) days younger than their own chick. If mass recession was controlled by parents, then older chicks switched to the nests of younger chicks should have entered mass recession at an older age and had higher peak masses and fledging masses than unswitched control chicks, whilst younger chicks switched to the nests of older chicks should have entered mass recession at a younger age and had lower peak masses and fledging masses than controls. If, on the other hand, mass recession was controlled by chicks, then switching should have had no effect on the age at which chicks entered mass recession. Peak mass and fledging mass of chicks in both groups should have been similar to controls, and parents should have continued to visit and feed a younger foster chick beyond the date at which their own chick would have fledged. If both parents and chicks influenced mass recession, the extent of their influence should have been reflected in an intermediate effect.

6.3. Methods

Fieldwork took place from 14 July to 30 August 1999 at a colony of c.100,000 breeding pairs of Manx shearwaters (Smith *et al.* in press), on Skomer Island, Wales, UK (51° 44'N, 5° 17'W). Manx shearwaters are burrow nesters, and we reached chicks in their nest chambers via short access tunnels dug into the roof of each burrow and capped with removable earth lids. We determined hatching dates (to the nearest day) of chicks at 60 nests by calibrating wing length (maximum flattened chord measured to the nearest mm with a stopped wing rule) against wing growth in chicks of known age (Brooke 1990).

We selected 13 pairs of chicks which differed in age by 10 (± 1) days, and switched them between nests at 1600 hours on 22 July. At switching, chicks in the younger group were 29 days old on average (range = 22-35 days), and chicks in the older group were 38 days old on average (range = 31-44 days). The minimum distance between each pair of nests was 100 metres, and none of the switched chicks left their new nests. Manx shearwater parents locate their nests using a combination of visual cues and proprioception, not by recognition of chick calls (James 1986), and so parents were unlikely to switch nests along with their chick (Hamer *et al.* 1999). In a cross-fostering experiment with chicks of similar ages, both switched and unswitched chicks had very similar growth rates, indicating that foster chicks were fed normally (Hamer *et al.* 1999), so individual recognition by parents or chicks does not appear to affect feeding. Chicks were weighed (to the nearest 5 g, using a Salter spring balance) at 2100h for the next three days to confirm that they were being fed normally. Daily weighing was resumed when chicks were 40 days old, prior to attainment of peak mass (Hamer & Hill 1997), and continued until fledging. Peak mass was calculated as the mean of the three largest weights, since large feeds may result in an over-estimate of peak mass based on a single weight. Similarly, age at peak mass was calculated as the mean of the chick ages corresponding to the three highest masses. Overnight food delivery (including occasions when chicks were not fed) was calculated for chicks aged 50 days to fledging. This was achieved by weighing chicks at 2100h and 0500h each night, and correcting mass increments between weighings for mass loss by digestion, respiration and excretion, following methods and equations in Hamer & Hill (1997). A sample of 23 control chicks (mean age on 22 July = 33 days; range = 24-46 days) in their natal nests was weighed daily throughout the study. Throughout this paper, "younger chicks" refers to young chicks switched to the nests of older chicks, "older chicks" are older chicks switched to the nests of younger chicks, and "controls" are chicks in their natal nests.

6.3.1. Data analysis

Where repeated measurements were taken from the same chicks, statistical tests were performed on mean values, to avoid pseudoreplication. We examined changes in body mass and rate of food provisioning at the end of the nestling period by comparing mean values for chicks in the older, younger and control groups in two age-classes; 51-60 and 61-70 days, using a repeated measures ANOVA. All tests are two tailed, and means are presented ± S.D. unless otherwise stated.

6.4. Results

6.4.1. Mass growth of control and switched chicks

Chicks in their natal nests (n = 23) grew at a mean rate of 13.1 g/day from 10 to 30 days of age, then at a slower rate of 6.8 g/day from 30 to 50 days. They attained a peak mass of 623.0 ± 46.5g between 50 and 55 days, then lost weight at a mean rate of 5.6 g/day from 55 to 70 days (Fig. 6.1). There was no significant difference in daily mass increments between switched and control chicks on the first three days after switching (mean mass increment: 8.33 ± 4.52 g (older chicks); 8.81 ± 3.71 g (younger chicks); 8.91 ± 3.25 (control chicks); Analysis of covariance (ANCOVA) with chick age as a covariate: effect of chick age: $F_{1,45} = 1.84$, $P = 0.2$; variation among groups: $F_{2,45} = 2.14$, $P = 0.1$).

6.4.2. Peak mass

The age at which chicks attained peak mass differed significantly among treatments (Figure 6.2; Table 6.1; ANOVA: $F_{2,46} = 3.88$, $P = 0.03$). In particular, older chicks switched into the nests of younger chicks attained peak mass at a greater age than controls, indicating that food provisioning was influenced by the length of time the parents had been providing food (Tukey's H.S.D. test, $P < 0.05$). However, the difference between treatments (4 days) was much less than the difference in the ages of chicks (10 days) indicating that food provisioning was also strongly influenced by the chick. Younger chicks switched into the nests of older chicks attained peak mass at a similar age to controls (Table 6.1; Tukey's H.S.D. test, $P < 0.05$).

6.4.3. Fledging

Chick mass at fledging varied significantly among groups (Table 6.1; $F_{2,46} = 7.35$, $P < 0.01$), with younger chicks fledging at a lower mass than chicks in other groups (Tukey's H.S.D. test, $P < 0.05$). However, there was no significant variation among groups in age at fledging (Table 6.1; $F_{2,46} = 0.26$, $P = 0.8$).

6.4.4. Food provisioning

We examined daily food delivery (g/day, including instances when chicks were not fed) to chicks in two age-classes, 51-60 days and 61-70 days, in the three treatment groups (Table 6.2). The rate of food provisioning differed significantly among groups (Table 6.2; repeated measures ANOVA: $F_{2,46} = 6.73$, $P < 0.01$) and between age-classes ($F_{1,46} = 65.6$, $P < 0.001$), with no significant interaction between the effects of group and age-class ($F_{2,46} = 0.84$, $P = 0.4$). Provisioning rate was highest in the older group and lowest in the younger group (Tukey's H.S.D. test, $P < 0.05$).

There was no significant difference among treatment groups in the age at which chicks received their last meal (older chicks: 65.0 ± 4.8 days; younger chicks: 64.9 ± 3.0 days; control chicks: 64.6 ± 4.0 days; $F_{2,46} = 0.04$, $P = 0.9$), or in the number of days between the last meal and fledging (older chicks: 3.92 ± 2.33 days; younger chicks: 5.00 ± 2.45 days; control chicks 4.36 ± 1.62 days; $F_{2,46} = 0.91$, $P = 0.4$).

Figure 6.1. Mean (± S.D.) mass growth of Manx shearwater chicks (*n* = 23) in their natal nests.

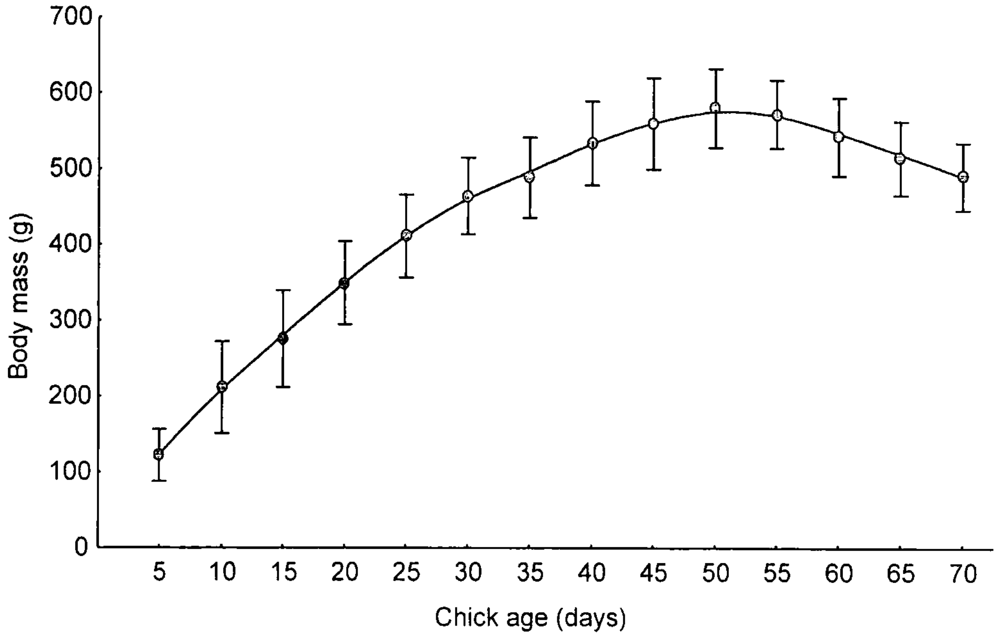

Figure 6.2. Mean (± S.E.) body mass of switched and control Manx shearwater chicks at peak mass and during mass recession. ▲ = older chicks switched to the nests of younger chicks (*n* = 13); ■ = younger chicks switched to the nests of older chicks (*n* = 13); ● = control chicks in their natal nests (*n* = 23).

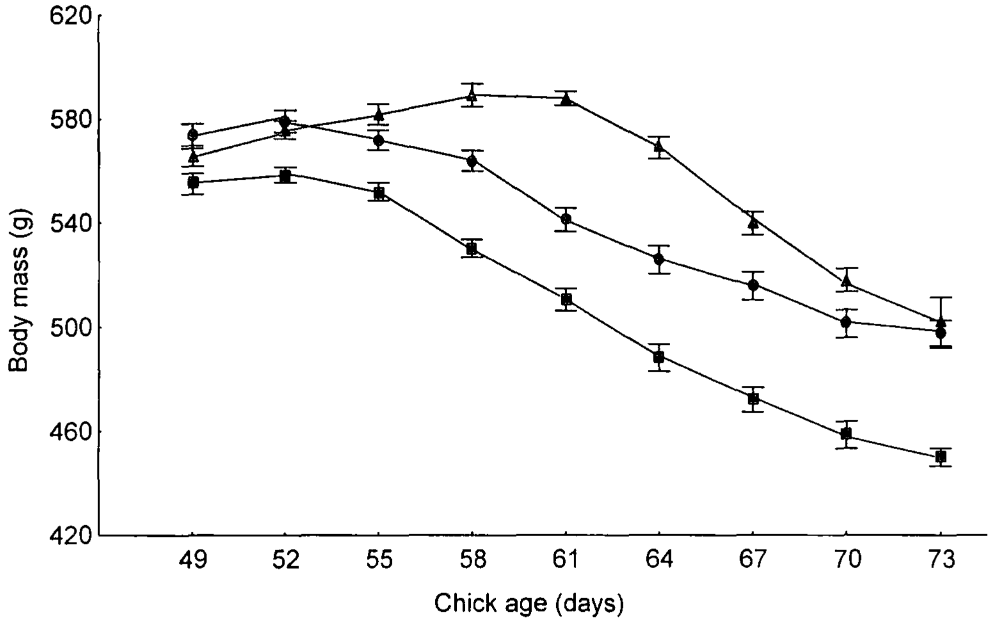

Table 6.1. Peak mass, fledging mass, and mass recession in switched and control Manx shearwater chicks.

	treatment group					
	older (n = 13 chicks)		younger (n = 13 chicks)		control (n = 23 chicks)	
	mean	S.D.	mean	S.D.	mean	S.D.
peak mass (g)	627.3	40.2	600	27.2	621.7	45.0
age at peak mass (days)	56.6	5.0	51.8	5.1	53.0	4.1
fledging mass (g)	494.2	56.6	433.1	38.1	486.6	44.1
fledging age (days)	70.2	6.1	70.0	3.5	69.1	4.4
mass loss (g)	133.1	56.7	166.9	41.0	132.1	46.7
rate of mass loss (g/day)	9.8	2.8	9.7	3.4	8.5	3.2

Table 6.2. Rate of food provisioning (g/day) to switched and control chicks.

			treatment group			
chick age	older (n = 13 chicks)		younger (n = 13 chicks)		control (n = 23 chicks)	
	mean	S.D.	mean	S.D.	mean	S.D.
51-60 days	43.5	14.2	35.6	15.7	37.5	7.1
61-70 days	30.4	14.4	15.6	8.8	21.0	6.3

6.5. Discussion

The results of this experiment indicate that mass recession in Manx shearwaters is not caused by parental desertion, but represents a decline in feeding influenced by parents and chicks. Younger chicks switched into the nests of older chicks received less food than chicks in the other two treatment groups during the last ten days of nestling development (Table 6.2), indicating a strong parental influence on mass recession. Chicks in the older group reached peak mass at an older age than controls, and chicks in the younger group reached peak mass at a younger age, which further suggests a parental influence. However, the difference between treatment groups and controls was less than the predicted ten days, indicating that chicks also have a strong influence on rates of food provisioning. This is in keeping with other studies which found that food provisioning rates in shearwaters were influenced, to some extent, by the chick (Hamer *et al.* 1999), for example through begging intensity (Granadeiro *et al.* 2000).

All chicks in all three treatment groups were fed from 61-70 days post-hatching, the age at which chicks were previously assumed to be deserted (Harris 1966; Brooke 1990). The interval between the last feed and fledging (c. 4 days, see Results) may represent a short desertion period. However, it could also correspond to intervals between successive feeds (2.07 ± 0.91 days in the older treatment group; 4.03 ± 2.04 days in the younger group; 2.29 ± 0.83 days in controls, for chicks aged 61-70 days). The intervals between the last feed and fledging were slightly longer than the average intervals between feeds, but this difference was insufficient to suggest that one or both parents had deserted the chick. Furthermore, the similarities among treatment groups in the age of chicks receiving their last feed, and in the period between the last feed and fledging (see Results) do not suggest that parents desert their chick at a fixed period of time after hatching.

The lower fledging mass of chicks in the younger group suggests that Manx shearwater parents are limited in their capacity to increase their rate of food provisioning. Similarly, Manx shearwater parents that were given an extra chick increased the frequency of food provisioning, but twinned chicks received less food than single chicks (Harris 1966). However, the data presented here indicate that parents were able to prolong the period of food provisioning to chicks in the younger treatment group. This suggests that nest desertion is not an innate behaviour, but that it may be stimulated by a decline in chick demand or even the absence of a chick. The latter is supported by observations of Wilson's storm petrel *Oceanites oceanicus* parents visiting the nest after the chick had fledged (Obst & Nagy 1993).

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Chapter 7

General Discussion

Ever since Lack's (1968) hypothesis that avian reproductive rates are constrained by food availability, an enormous amount of research has been directed at the relationships between food availability and different aspects of reproductive performance. The breeding ecology of pelagic seabirds poses particularly interesting questions, due to the large distances parents must travel to obtain food for their offspring, and the unpredictable distribution of marine prey (Ashmole 1971).

In this thesis I have examined food provisioning and chick growth in two species that are unusual among procellariiforms in that they provision their chick relatively frequently (Hamer & Hill 1997; Hamer & Thompson 1997). High rates of food provisioning may reflect abundant food relatively close to the colony (Furness & Todd 1984; Hamer *et al.* 1997), but could also be caused by parental strategies to increase the frequency and reduce the variability of provisioning (Weimerskirch 1998; Booth *et al.* 2000). Although I do not intend to make direct comparisons of provisioning and growth in the two species, I will discuss their similarities and differences in the context of their breeding ecology and life histories. However, my main aim in this thesis has been to use fulmars and Manx shearwaters as model species to add to current understanding of food provisioning and chick growth in pelagic seabirds that that feed their chicks at relatively high frequencies, and to examine how these strategies may reflect interactions between life-history traits and the marine environment.

7.1. Individual and environmental effects on breeding performance

While severe changes in environmental conditions may affect reproductive success across entire seabird colonies (Wooller *et al.* 1992; Prince *et al.* 1994), it is more common for changes to reduce breeding success or chick growth in certain individuals or pairs (Hatch 1990; Ratcliffe *et al.* 1998). Chick growth in grey-headed albatrosses *Diomedea chrysostoma* is highly consistent in individual pairs, and this is thought to be associated with patterns of food provisioning in individual parents (Cobley *et al.* 1998), but few studies have examined individual effects, or interactions between environmental and individual effects on chick growth in other seabirds. In Chapter 3, I found that Manx shearwater breeding success showed no significant annual variation, but chick growth and peak mass differed significantly among years. The relative importance of genetic and environmental effects on chick growth was unclear. Repeatability analysis of a sample of nests in the 1970s suggested that some pairs consistently produced chicks with higher growth rates and a heavier peak mass compared to other pairs. However, the significant annual variation and lower repeatabilities in a sample of pairs in the 1990s suggested a strong environmental influence, and the strength of environmental effects probably varies among years.

7.2. Annual variation in breeding parameters

Certain parameters in seabirds may be useful indices of marine food availability within an appropriate range of conditions or within a certain time scale (Cairns 1987; Burger & Piatt 1990; Murphy *et al.* 1991), but it is difficult to identify parameters that are generally useful for environmental monitoring, since the location, spatial scale, duration and severity of environmental changes are variable and difficult to predict. My aim here is to discuss levels of variation in different breeding parameters in fulmars and Manx shearwaters, the relevance of these parameters to the species' ecology and their potential for detecting environmental effects on breeding performance.

7.2.1. Breeding success

Of the different components of chick-rearing in Manx shearwaters discussed in Chapter 3, hatching and fledging success showed very low annual variation. This is in contrast to the results of a study by Thompson (1987), who found that a majority of breeding failures at the Manx shearwater colony on Rhum occurred during incubation, due to effects of weather. Sources of variation in breeding success are often site-specific (e.g. predation; Moors & Atkinson 1984), so important factors at one colony may have less relevance in a different area. Breeding success in fulmars differed markedly between two years (Chapter 4), although this may have been largely due to unusually bad environmental conditions in one year, and data from a greater number of years are required to determine the extent of annual variation in breeding success at Fair Isle. Studies of fulmars at other colonies have shown variation in breeding success within and among breeding seasons (Hatch 1990; Thompson *et al.* 1999; Upton *et al.* 2000), and that older, more experienced birds have higher breeding success (Ollason & Dunnet 1978; Hatch 1990).

7.2.2. Mass growth

Compared to breeding success, mass growth in Manx shearwater chicks was more variable (Chapter 3). Several studies have shown fitness implications of mass growth in seabirds. For example, mass growth affected chick survival in lesser black-backed gulls *Larus fuscus* (Bolton 1991), postfledging survival in great skuas *Catharacta skua* (Hamer *et al.* 1991) and recruitment in kittiwakes *Rissa tridactyla* (Coulson & Porter 1985). Mass growth is therefore both responsive to environmental variation and important for fledging success and post-fledging survival. I did not examine fledging mass in this study, but Brooke (1986) found that it varied among years and among pairs. Fledging mass is important for post-fledging survival in Manx shearwaters (Perrins *et al.* 1973), so is a relevant indicator of breeding performance. Further investigation of peak mass and fledging mass over several years may clarify their relationship to each other and to food provisioning.

I have not presented data on the abundance or distribution of marine prey, and relating seabird breeding parameters to measures of marine productivity is beyond the scope of this thesis. However, the data in Chapter 4 strongly indicate two years of contrasting conditions both in terms of food availability and weather. In Chapter 4, I provided evidence to support the little-explored hypothesis that differential mortality of chicks can create an inverse relationship between food availability and chick growth (Williams & Croxall 1990). Mass growth data should be interpreted with caution in light of this confounding effect. An ideal approach would incorporate data on different components of overall breeding success throughout the season (in addition to chick growth data), preferably sampling the same individual pairs each year to avoid biases towards successful, high quality pairs in poor years.

7.2.3. Wing growth

No annual variation was found in wing growth of either Manx shearwaters (Chapter 3) or fulmars (Chapter 4). Studies of chick growth under nutritional stress have shown that non-structural (i.e. mass) growth may be retarded, whereas structural components of growth are largely unaffected, indicating that developmental priority is given to the skeleton and feathers (Bryant 1975; Schew & Ricklefs 1998; Robinson 1999). Retardation of structural growth has only been recorded during severe food stress (Boersma 1986). Although fulmars experienced a poor breeding season in 1998, the high mortality may explain why retardation of mass and wing growth was not observed in the study chicks. Mass growth of Manx shearwater chicks (Chapter 3) did not suggest severe food limitation in any year, so the low variation in wing length is not particularly surprising. Preferential allocation of resources to wing growth is particularly important to birds with post-fledging migration or long-distance dispersal (Reid *et al.* 2000), but also occurs in Atlantic puffins *Fratercula arctica* which need functional wings for pursuit-diving (Gaston 1985; Øyan & Anker-Nilssen 1996).

*7.2.4. **Food provisioning and diet***

Food provisioning rates are thought to be a good reflection of the availability of food to parents (Croxall *et al.* 1988), although flexible time budgets and changes in parental effort may confound this relationship (Burger & Piatt 1990; Hamer *et al.* 1991; Erikstad *et al.* 1997). The rate of food provisioning had a strong influence on growth rate and peak mass in Manx shearwaters, both on an individual basis and based on mean values for each year (Chapter 3). Similar relationships have been found in black-browed *Diomedea melanophris* and grey-headed albatrosses (Huin *et al.* 2000). In fulmars, I found no significant variation in provisioning rates between two years, despite differences in age-specific body mass throughout the nestling period (Chapter 4). The lack of association between provisioning rates and chick growth in fulmars may have been due to differences in the caloric density of prey (Hislop *et al.* 1991), or to individual differences in foraging ability (see below). Fulmars adjusted their strategy to exploit prey in two very different breeding seasons (Chapter 4), in keeping with the prediction that polyphagous birds are more able adjust to food shortages than specialised, monophagous species (Furness & Ainley 1984). Diets of generalist or opportunistic foragers are thought to be a poor indicator of prey abundance due to prey-switching behaviour, but may be useful for monitoring prey stocks that are at low levels (Montevecchi 1993).

The inter-year comparison of fulmar breeding ecology (Chapter 4) did not use the same individual pairs, so the possibility of interactions between environmental and individual effects cannot be discounted. The non-random mortality of chicks in 1998 meant that surviving chicks were heavier for their age compared with 1997, and the tendency for these chicks to receive small, frequent meals may have reflected parental foraging abilities. This pattern of food provisioning has been associated with high rates of chick growth in other species (Berrow *et al.* 2000) and with parental breeding experience (Weimerskirch 1990; Lequette & Weimerskirch 1990). Individual differences in experience or quality could therefore have confounded the relationship between food provisioning and chick growth in fulmars.

Of the parameters discussed above, mass growth indices appear to be the most appropriate indicators of feeding conditions in Manx shearwaters, with peak mass showing the strongest relationship to provisioning rate. Peak mass also has the advantage of being easy to measure, but since feeding events cause considerable fluctuations in body mass I would recommend fitting growth curves and using the calculated asymptote (Chapter 3), or using an average peak mass (e.g. the three highest values; see Chapter 6). Further data are required before any conclusions can be drawn about annual variation in different breeding parameters in fulmars, although breeding success may reflect variation in food availability (Chapter 4; Hatch 1990). Chapter 4 also suggested that numbers of breeding attempts were lower when conditions were poor, and data from a greater number of years may confirm this.

7.3. Roles of individual parents in food provisioning

So far in this chapter I have discussed food provisioning from the perspective of the chick, without examining the roles of individual parents. In common with most other seabirds, Manx shearwaters are socially monogamous with bi-parental care, and both parents contribute to incubation and chick-provisioning (Brooke 1990). Although bi-parental care in common in birds, the amount of care is not always divided equally between the sexes (Lack 1968; Clutton-Brock 1991), and differences in parental roles in procellariiforms have been attributed to sexual dimorphism (Gonzáles-Solis *et al.* 2000). Chapter 5 examined for the first time the roles of male and female Manx shearwater parents in chick provisioning, and found that males made shorter foraging trips and made a greater contribution to food provisioning than females. This raises a number of interesting points. It questions the role of sexual dimorphism in producing and maintaining sexual differences in foraging and food provisioning (see Chapter 5 for alternative hypotheses). These results also add to growing evidence that mean foraging trip durations (or feeding frequencies) may imply little about individual behaviour, or potential foraging ranges (Table 7.1). Booth *et al.* (2000) found that in little shearwaters *Puffinus assimilis* the two parents co-ordinated long and short foraging trips to reduce the variability of food provisioning. However, I found that Manx shearwater parents visited the nest independently of each other (Chapter 5), which does not suggest a co-ordinated foraging strategy. Such a strategy may confer little benefit to Manx shearwaters, since only females made long trips and males visited the nest on most nights. The high frequency of short (1-2 day) foraging trips in Manx shearwaters implies abundant food relatively close to the colony. In southern-hemisphere breeders such as short-tailed and sooty shearwaters *Puffinus tenuirostris* and *P. griseus*, short trips have a greater energetic cost to parents, and both males and females regularly make long, pelagic trips to replenish their own body reserves (Weimerskirch 1998; Weimerskirch & Cherel 1998). Male Manx shearwaters have little apparent difficulty in making short foraging trips during chick-rearing, although this may not have been the case for females. The results presented in Chapter 5 suggest that optimum levels of food provisioning may be lower in females than in males, and further data are now required to assess reproductive effort and resource allocation processes in Manx shearwaters.

Table 7.1. comparison of mean and maximum foraging trip durations in Manx shearwaters and other procellariiforms.

species	mean trip (days)	max trip (days)	reference
Puffinus puffinus	1.8	7	Chapter 5
Puffinus griseus	2.7	17	Weimerskirch 1998
Puffinus tenuirostris	7.5	17	Weimerskirch & Cherel 1998
Calonectris diomedea	1.9	6	Granadeiro *et al.* 1998
Diomedea exulans	3.4	21	Weimerskirch *et al.* 2000

7.4. Mass recession

Nestling growth in procellariiforms is characterised by the attainment of a peak mass in excess of adult mass, followed by a period of mass recession prior to fledging (Warham 1990). Pre-fledging mass loss in many birds is partly due to water loss from maturing tissues (Ricklefs 1968; Phillips & Hamer 1999). However, the mass recession period is also characterised by a marked decrease in food provisioning (Thompson 1987; Phillips & Hamer 2000) or parental desertion and cessation of feeding (Richdale 1963; Warham

1990). There is little evidence that northern fulmar or Manx shearwater nestlings are deserted. In both species, the interval between the last feed and fledging is no longer than the mean age-specific interval between feeds (Phillips & Hamer 2000; *Chapter 6*).

Parental desertion is thought to occur in a number of procellariiforms, many of which embark on long-distance migrations at the end of the breeding season. Species that do not desert their chicks are generally non-migratory (Warham 1990). There are exceptions to this general rule, notably the southern giant petrel *Macronectes giganteus* which is non-migratory and has a desertion period of 6-14 days (Conroy 1972). However, the finding that migratory Manx shearwaters do not desert their chicks is unusual, and contrasts with most *Puffinus* shearwaters, or at least those breeding in temperate regions (see Harris 1969).

7.5.General conclusions

The consistently high breeding success of Manx shearwaters supports the idea that long-lived seabirds produce a clutch size that is optimal for poor years (Ricklefs 1990; Hamer *et al.* 2001). Annual variation in Manx shearwater chick growth probably reflected environmental variation, suggesting that parents were unable or unwilling to increase their reproductive effort in poor years (Weimerskirch *et al.* 1999). The incidence of non-breeding in fulmars and other seabirds in poor breeding seasons (see Chapter 4) is also consistent with the view that parents will reduce breeding effort when costs become too high (Chastel *et al.* 1995). Flexible patterns of chick growth may be viewed as adaptations that allow parents to raise chicks in poor conditions without compromising their own survival (Drent & Daan 1980; Monaghan *et al.* 1989; Lorentsen 1996).

Lack's (1968) hypothesis that pelagic seabirds have more extreme life-history traits than in inshore feeders holds true in a number species (Nelson 1983; Furness & Monaghan 1987; Ricklefs 1990; Robinson 1999). Two studies that have examined the relationship between feeding strategy and life-histories within the procellariiforms found more extreme life-histories in the more pelagic procellariiforms (Weimerskirch *et al.* 1987; Chastel *et al.* 1995). The frequency of food provisioning in fulmars is much higher than in many pelagic seabirds (Chapter 4; Hamer & Thompson 1997; Phillips & Hamer 2000), and is more consistent with species that are regarded as intermediate or inshore feeders. However, annual survival and longevity and age at first breeding in fulmars is more consistent with life-histories of pelagic seabirds than inshore feeders (Dunnet *et al.* 1979). Corrected for body size, fulmars have high rates of chick growth and short breeding seasons compared with most procellariiforms, and this is also true of the other fulmarine petrels (Warham 1990). The evolution of high growth rates may have been facilitated by abundant food close to the colony, or short incubation and fledging periods may be important in fulmarines, which are surface-nesters and may therefore be more vulnerable to predation than burrow nesters. Manx shearwaters provision their chick less frequently than fulmars, but more frequently and less variably than sooty or short-tailed shearwaters (Weimerskirch 1998; Hamer *et al.* 2000). The life-histories of Manx and short-tailed shearwaters appear to be very similar with respect to annual adult survival and age at first breeding (Serventy & Curry 1984; Brooke 1990), although short-tailed shearwaters occasionally defer breeding for a year, which may represent a decision to reduce risks or adult mortality. Such "sabbatical" years have not been recorded in Manx shearwaters (Brooke 1990), possibly due to abundant food supplies, or to inter-specific differences in life-history strategies.

Many life-history traits of fulmars and Manx shearwaters remain poorly understood. For example, this study did not measure parental body condition, which may be an important determinant of parental responses to natural or induced variation in reproductive costs. In both species there is considerable scope for future research, which may determine whether the relatively unusual foraging patterns in fulmars and Manx shearwaters are associated with life-history traits that are also atypical of the procellariiforms.

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