Early warnings of environmental change on ecosystems: hormonally-mediated life-history decisions in seabirds

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Abstract

Biological indicator species can reveal consequences of changes in physical processes within the environment, through effects on their physiology, behaviour and population dynamics. Long-lived species tend to be positioned at the top of the food chain where they can act as indicators of environmental change occurring at lower trophic levels. During poor conditions, these long-lived top predators have been selected to prioritise their own survival above the current breeding attempt, in order to maximise lifetime reproductive success. Endocrine mechanisms involving corticosterone, the 'stress hormone', and possibly prolactin, the 'parental hormone', are involved in mediating the abandonment of breeding in response to environmental perturbations. This thesis aimed to assess what the breeding success of a top marine predator indicates about changes in the marine ecosystem and what mechanisms control changes in breeding success, using the black-legged kittiwake *Rissa tridactyla* as the model species. I combined population-level analyses of long-term datasets (1997–2010) of diet composition, adult body mass, breeding success and foraging behaviour from the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11' N, 02° 33' W) with an individual-level field experiment to simulate chronic stress.

Kittiwakes breeding in the north-western North Sea depend primarily on adult (1+ group) lesser sandeels *Ammodytes marinus* at the start of the breeding season and subsequently switch to depend primarily on young of the year (0 group) sandeels. Analysis of the long-term data showed that the timing of the kittiwake breeding season has become later in recent years, whilst the timing of the switch from 1+ group to 0 group sandeels in the kittiwake diet has become earlier, which may suggest mismatches in the timing of prey availability and predator demand. Increasing proportions of clupeids (mainly sprat *Sprattus sprattus*) were seen in the diet and further years of study may reveal whether clupeids could be a beneficial alternative prey type for kittiwakes. Foraging trip duration was unrelated to diet composition, suggesting that the main prey types of kittiwakes do not differ in their distance from the colony. Whilst foraging trip duration during incubation was related to changes in adult body mass and hatching success, diet composition was unrelated. There was a weak effect of diet composition during chick-rearing on fledging success, mediated via changes in adult body mass. However, this effect was masked by a stronger, independent, negative effect of foraging trip duration during chick-rearing.

To simulate chronic stress in kittiwakes, individuals were implanted with corticosterone, using Alzet® osmotic pumps, for a week at the end of incubation. The methodology applied to kittiwakes was based on a preliminary experiment carried out in Japanese quail *Coturnix coturnix japonica*. The body mass and prolactin concentrations of kittiwakes were unchanged after this treatment. Corticosterone concentrations had returned to pre-treatment values by the end of the treatment week, which may have been due to down-regulation or suppression of the stress response as a result of the treatment. Corticosterone-implanted males showed lower nest attendance than sham-implanted males but the opposite was true for females. Breeding success at the end of the season was lower in corticosterone-implanted birds, suggesting a prolonged effect of chronic stress. In order to investigate the effects of disturbance to a group or colony of birds prior to the capture of an individual, a preliminary experiment was also carried out to test the stress responsiveness of a captive bird, the Japanese quail. No increase in corticosterone concentrations was seen after a capture-restraint protocol and with increasing time since the group of birds was first disturbed. A suppressed stress response in this bird may be explained by long-term captivity or domestication.

These results show that the breeding success of a top marine predator can indicate changes in the timing of prey availability and prey location, mediated through changes in adult body mass. I also found that changes occurring during the chick-rearing period contributed most to the outcome of the breeding season. Chronically elevated concentrations of corticosterone are important in the control of breeding success, whereas prolactin may only play a role close to the timing of breeding failure or after failure has occurred. This thesis demonstrates the need for continued long-term monitoring of wild populations and refining of experimental methodology to better understand the impacts of environmental change on top predators.

List of Contents

List of Tables

List of Figures

List of Accompanying Material

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Declaration

I declare that the work in this thesis is entirely my own unless otherwise cited or acknowledged. No part of this thesis has been submitted for any other degree or qualification.

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Chapter One

General introduction

1.1 Indicators of environmental change

Environmental change is having profound impacts on both human populations and the environment, through losses in biodiversity and habitat suitability. Detecting early warnings of these often detrimental, and at times devastating, impacts can help us understand, buffer against and prepare for change. Climate change is one example of anthropogenic-induced change in our environment, resulting in increasing temperatures and higher frequencies of extreme weather events. Measures of climate change include carbon dioxide concentration, global surface temperature, Arctic sea ice area, land ice (Antarctica and Greenland) area and sea level (National Aeronautics and Space Administration (NASA); http://climate.nasa.gov/keyIndicators/). As long-term, wide-ranging and large-scale environmental processes can be complicated to relate to the consequences they have on the ecosystems associated with them, indicators of change can be useful measures. Such indicators may be related to processes happening on multiple levels and therefore can provide insights into the direction, magnitude and consequences of environmental change.

1.1.1 Indicator species

Indicator species define characteristics or traits of the environment. The concept of using plants and animals as indicators of the wider environment was first used by Hall and Grinnell (1919). Since then indicator species have been used widely in conservation planning, habitat assessment and policy (reviewed in Carignan and Villard, 2002). Environmental change can be manifested in the behaviour, for example breeding activity, and physiology, for example increased corticosterone secretion, of organisms. Physiological changes, whilst not being visible like behavioural traits can be, are often measureable, allowing an organism's physiology to act as an indicator of processes occurring outside its body. Particular species or groups of species can act as useful indicators, often due to the ways that they interact with their environments or their specific roles within ecosystems.

There are several possible definitions of an indicator species (reviewed in Lindenmayer et al., 2000): 1) a species whose presence indicates that a range of other

species within the ecosystem is present and whose absence indicates that those other species are absent; 2) a keystone species, which is a species that causes major changes in the abundance or presence of other species as a result of its presence or absence in the ecosystem; 3) a species whose presence indicates anthropogenic-induced abiotic conditions such as pollution; 4) a dominant species that provides a large proportion of the biomass or number of individuals in an ecosystem or habitat; 5) a species that indicates particular environmental conditions such as certain soil or sediment types; 6) a species that is highly sensitive to changes in its environment, allowing it to act as an early warning of changes such as climate change; 7) a management indicator species, which is a species that reflects the effects of a disturbance regime or the degree of success resulting from disturbance mitigation.

Rhopalocera (butterflies and skippers) have been suggested as being particularly valuable as ecological indicators due to their sensitivity to micro-climates and interaction with plant hosts during both the larval and adult stages (e.g. Brown, 1982, Kremen, 1992). Within many aquatic ecosystems, algae such as diatoms (Bacillariophyceae) can be useful early warnings of environmental deterioration and indicators of water quality, due to their rapid response to a range of pollutants (McCormick and Cairns, 1994). Fish can be useful indicators of both extreme weather events and pollution such as wastewater effluent (e.g. three-spined sticklebacks *Gasterosteus aculeatus*; Pottinger et al., 2011). Birds respond to environmental changes over many spatial scales, often linking terrestrial, freshwater and marine ecosystems, and thus can act as useful multi-ecosystem indicators (Temple and Wiens, 1989). Birds can be relatively easily detected in their environments and can be monitored visually and audibly, making them a practical choice for monitoring.

1.2 Life-history strategies

Species or groups of species are often valuable as indicators of environmental change due to the ways in which they respond to their environments during both predictable and unpredictable variation. Opportunistic breeders such as the zebra finch *Taeniopygia guttata*, crossbill *Loxia curvirostra* and musk shrew *Suncus murinus* have life-history strategies designed to cope with unpredictability, whilst many fish and other bird species, for example Atlantic salmon *Salmo salar* and great tits *Parus major*, have life-history strategies designed to cope with predictability and seasonality. The life-history strategy of an organism describes the characteristics by which it maximises its lifetime reproductive success. Such strategies depend largely on the fecundity and lifespan of the organism (Drent and Daan, 1980).

1.2.1 The life cycle

Environmental variation is to some extent predictable and thus organisms can adapt to maximise their fitness in response to cues relating to future conditions (e.g. Baker, 1938, Perrins, 1970). Seasonality within environments means that stages of the life cycle of animals tend to be timed according to energetic demands and resource availability, and tend to follow a specific sequence through the year. This sequence will match the predictable order of changing seasons in the environment, assuming stable environmental conditions (reviewed in Jacobs and Wingfield, 2000, Wingfield, 2008). Each life-cycle stage has characteristic morphologies, physiologies and behaviours associated with it, and over-lap between stages is limited due to differing sets of these often mutually exclusive suites of characteristics. The transition between stages can be stimulated by predictable environmental cues, such as photoperiod, and mediated by less predictable or unpredictable cues (e.g. weather, food availability) or by individual state (e.g. body condition). More life-history stages tend to occur if environmental variation is large, whereas fewer stages occur if environmental variation is low (Wingfield, 2008). Breeding is a key stage in the life-cycle of all vertebrates. Species with short, restricted breeding seasons are likely to use a single predictable cue to time the onset of their breeding, whereas those with longer, more flexibly timed breeding seasons are likely to use a range of cues to time the optimum onset of breeding (Jacobs and Wingfield, 2000).

1.2.2 Timing of seasonal events

Environmental change often results in changes in the timing of seasonal events as conditions suitable for certain behaviours, activities or development start occurring earlier or later (Visser et al., 1998). The timing of these seasonally recurring biological events is known as phenology and, due to the interconnected nature of the trophic levels within an ecosystem, changes in phenology can result in trophic groups becoming mismatched with each other (e.g. Perrins, 1970, Cushing, 1990, Visser et al., 1998, reviewed in Visser and Both, 2005, Burthe et al., 2012). Peaks in food demand, for example when foraging for young during the breeding season, are often timed to coincide with peak abundance in prey. However, when phenologies shift and become desynchronised, trophic mismatch occurs, which means that food resources may no longer meet the peak demands of the predator.

1.2.3 Life-history variation

The resources available to an organism are often limiting, which results in a trade-off in the allocation of energy to competing demands such as current reproduction and self-

maintenance for survival (Drent and Daan, 1980, Wingfield et al., 1998). The fitness consequences of this trade-off determine the resulting optimal resource allocation pattern. The number of potential reproductive opportunities within the lifetime of an organism is an important consideration when assessing the value of a single reproductive attempt. Life-history variation occurs along a slow–fast gradient resulting in constraints on the combinations of traits possible (reviewed in Ricklefs and Wikelski, 2002). Long-lived (k-selected) species tend to have slow rates of development, a long lifespan, low fecundity, iteroparous reproduction and low dispersal whilst short-lived (r-selected) species tend to develop faster, have shorter life-spans, higher fecundity and fewer breeding opportunities. Thus, when facing harsh environmental conditions, it may be adaptive for short-lived species to prioritise investment in their current reproductive attempt, and for long-lived species to prioritise their own survival above that of their current brood.

1.2.4 Seabirds as indicators of marine ecosystems

Long-lived species can be useful indicators of problems occurring throughout an ecosystem due to their slow development and long lifespan. Having a long lifespan, and hence multiple breeding opportunities, means that individuals can be sensitive to environmental conditions when deciding whether or not to breed in a given year (Drent and Daan, 1980). Long-lived species tend to be positioned near the top of the food chain, which makes them good indicators of changes occurring at lower trophic levels, within the geographical areas where they occupy the top predator position (Sergio et al., 2008).

Seabirds are a group of long-lived indicator species that are often used to better understand the health and status of marine ecosystems (Croxall and Prince, 1979, Furness and Camphuysen, 1997, Piatt et al., 2007a, Parsons et al., 2008). Seabirds breed on land where they are visible and accessible for study, nest in colonies where large numbers can be monitored and studied simultaneously and forage in important marine hotspots for productivity (Piatt et al., 2007b). Seabirds are positioned at, or near, the top of the food chain, have long-lived life-history characteristics and some species are highly sensitive to environmental change through their dependency on specific prey (e.g. Monaghan et al., 1989, Harris and Wanless, 1990, Croxall et al., 1999, Furness and Tasker, 2000). Seabird species with limited foraging ranges, limited diving depths, limited resting time during foraging trips and limited access to suitable prey species tend to be the most sensitive to environmental change (Furness and Tasker, 2000, reviewed in Einoder, 2009). For example, North Sea breeding terns (Arctic tern *Sterna paradisaea*; roseate tern *S. dougallii*; little tern *S. albifrons*; common tern *S. hirundo*; sandwich tern *S. sandvicensis*)

and black-legged kittiwakes *Rissa tridactyla* have been scored as most vulnerable in terms of their breeding success to changes in prey availability, whilst the northern fulmar *Fulmarus glacialis* and northern gannet *Morus bassanus* were scored the least vulnerable (Furness and Tasker, 2000).

The life-history characteristics of a seabird species can determine in part its sensitivity to changes in food availability; longer-lived species are more likely to abandon breeding during unfavourable conditions compared to shorter-lived species (Montevecchi, 1993, reviewed in Einoder, 2009). Cairns (1987) identified five population and behavioural parameters that can act as useful indicators of prey availability over differing time scales: survivorship, which acts over an annual time scale, breeding success, which acts over a monthly time scale, chick growth and colony attendance, which act over a weekly time scale and activity budget, which acts over an hourly or daily time scale. These parameters tend to be correlated non-linearly with prey density (Piatt et al., 2007a). When food is scarce adult survivorship may be the most useful indicator; if food availability is poor breeding success, chick growth and colony attendance may be the best indicators; if food availability is good activity budgets may be useful indicators (Cairns, 1987). However, different species respond differently depending on how close they are to their maximum performance limit under normal foraging conditions, and thus how much they can buffer against variation in foraging conditions (Piatt et al., 2007a). Additionally, breeding stage can affect the sensitivity of a seabird to changes in food density, with chick-rearing birds showing higher sensitivity and incubating birds not always proving as useful indicators of changes in the marine environment (Harding et al., 2007). Body size is another useful measure of the sensitivity of a seabird species, with smaller species tending to be less flexible in energy and time budget and tending to require more frequent feeds to their young even during poor foraging conditions (Furness and Camphuysen, 1997). Seabirds with limited access to suitable prey species reveal changes in fish stocks or suitable oceanographic conditions for their prey, because they are less likely to switch to an alternative prey species, which would buffer these changes (Furness and Tasker, 2000). Surface-feeders are more likely to respond to changes in food availability because they are unable to obtain prey that occur at greater depths (e.g. Monaghan et al., 1992). Similarly seabird species with restricted foraging ranges are less able to access prey in more distant locations, making them more susceptible to localised changes in prey availability (e.g. Furness and Tasker, 2000).

Abundance data are useful when used to indicate seabird population status, because the long-lived nature of seabirds means that they can buffer against a degree of environmental change, resulting in only gradual changes in population numbers (reviewed in Parsons et al., 2008). However, variation between seabird species means that it is vital to assess the trends in a specific species rather than making generalisations between species. For example, whilst a multi-species approach does show an overall decline in abundance of a range of Scottish seabirds between 1986 and 2004, some species such as the Arctic skua *Stercorarius parasiticus* have seen a slight decline since 1986, whilst others such as the Arctic tern have seen a dramatic decline (Parsons et al., 2008). Productivity data are useful to indicate the marine environment; for example, there is a positive relationship between the productivity of a range of seabird species and food supply (Parsons et al., 2008). Separating species into groups of similar food resources, or other aspects of the marine environment, can be a useful way of indicating the ability of the marine environment to support those species (Parsons et al., 2008). For example, all species depending on similar food resources may show similar trends; however, it is possible that these trends could be driven by a confounding factor such as weather conditions.

High quality long-term datasets and support from policy makers and the public can enable an indicator species to be practical for monitoring purposes. UK breeding seabirds have the backing of long-term population and demographic datasets, international status with regards to their protection and are charismatic species that attract popular public interest (Parsons et al., 2008). Seabirds are, therefore, useful indicator species of marine ecosystems and are particularly useful means of monitoring the marine environment surrounding the UK. 76 % of the UK populations of breeding seabirds are found in Scotland (Mitchell et al., 2004), making this region of the UK an important centre for seabird research and monitoring.

1.3 Using seabirds as indicators of marine environmental change

Changes in the marine ecosystem are having impacts on the breeding success and survival of seabirds. For example, changes in sea surface temperature (SST) can have knock-on effects on the timing of prey availability (e.g. Becker et al., 2007, Durant et al., 2007) or the distribution of prey (e.g. Montevecchi and Myers, 1997, Perry et al., 2005); fisheries may compete directly with top predators for food resources (e.g. Furness, 1982, Tasker et al., 2000) and may contribute to habitat degradation through dredging or trawling the seafloor (e.g. Dayton et al., 1995, Pikitch et al., 2004); pollutants, often originating from

land-based human activities, can affect seabirds directly or indirectly through the food chain (Jenssen, 2006, Camphuysen et al., 2010).

Seabirds can be used in a variety of ways to reveal information about the marine environment. Their physiology can provide indications of prey availability and investment of energy into self-maintenance, whilst their foraging and breeding behaviour can display methods of coping with environmental conditions and the extent of their behavioural plasticity. There is a range of parameters that can be measured in order to indicate changes in the marine environment through changes in the prey availability of seabirds. The body condition or body mass of a seabird can indicate long-term changes in prey availability, whilst composition of the seabird's diet and its energy acquisition rate may indicate short-term changes (Montevecchi, 1993, reviewed in Einoder, 2009).

1.3.1 Diet composition as an indicator of food availability

The diet of seabirds can act as an indicator of food availability, with more available or higher quality prey predominating in the diet. Changes in diet composition during a breeding season may also indicate the timing of prey availability and whether the timing of peak prey availability matches the timing of peak predator demand, or has become desynchronised in line with the mismatch hypothesis (Cushing, 1990, Visser and Both, 2005). However, diet composition will also be influenced by the quality, location, distance from the colony and ease of capture of different prey types. If prey is low in availability adults may have less successful foraging trips, with implications for their own body mass, the provisioning of their chicks and ultimately their breeding success (Monaghan et al., 1989, Chastel et al., 1995, Sydeman et al., 2001, Suryan et al., 2002). Prey types that are low in calorific value can further reduce the body mass and breeding success of predators (Rosen and Trites, 2000, Litzow and Piatt, 2003, Osterblom et al., 2008), as stated by the junk food hypothesis (Alverson, 1992). Therefore, when interpreting the diet composition of a seabird, it is important to consider both prey quantity and prey quality (Kadin et al., 2012).

Seabirds may select certain prey types to feed themselves and other prey types to feed their chicks (reviewed in Barrett et al., 2007). For example, single-prey loaders should bring back to the nest larger and more calorific fish for their chicks compared to the fish that they feed themselves during foraging trips at sea (reviewed in Barrett et al., 2007, e.g. common guillemot *Uria aalge*; Barrett and Erikstad 2013).

1.3.2 Body mass as an indicator of food availability

Adult body mass is a useful indicator of food availability with lower body mass often associated with poorer foraging conditions (e.g. Jodice et al., 2002, Golet et al., 2004, Jacobs et al., 2011). However, Piatt et al. (2007a) suggested that adult body condition was unrelated to prey density, or that it may only show a response under severely low prey densities. Body mass is not straightforward to measure as it either requires catching birds or having an automated system of recording weight, for example a weighbridge (e.g. Gauthier-Clerc et al., 2001, Ballard et al., 2010) or a concealed balance (e.g. Monaghan et al., 1989).

Birds tend to lose mass during the breeding season and two main hypotheses have suggested why this might occur. The 'reproductive stress hypothesis' states that mass loss is a result of the energetic costs of breeding (e.g. Wendeln and Becker, 1999, Moe et al., 2002, Santos et al., 2010). The 'programmed anorexia hypothesis' (Mrosovsky and Sherry, 1980) states that mass loss is an adaptive strategy to increase mobility, and hence efficiency, during intensive foraging (e.g. Moreno, 1989, Coulson, 2010). It is possible that there is an upper limit ('lean and fit hypothesis'; Schultner et al., 2013), as well as a lower limit ('fat and fit hypothesis'; Schultner et al., 2013), on optimum body mass; birds in favourable environments may refrain from increasing their body mass above this limit whilst birds in poor food environments may undergo mass loss due to reproductive stress.

There have been few long-term studies to date that have attempted to assess how mass change during the breeding season might vary between years of varying environmental conditions. Coulson (2010) concluded that abrupt mass loss seen at the time of hatching in both male and female black-legged kittiwakes between 1954 and 1995 was due to programmed anorexia. However, during this study period, mean adult body mass showed only small changes between years and breeding success was high, suggesting consistent and favourable foraging conditions in the area. Coleman et al. (2011) monitored kittiwakes in Scotland between 1990 and 2007 and found that adult body mass was variable between years but did not correlate with mean number of nestlings, which was used as a proxy for breeding success. Weimerskirch et al. (2000) concluded that in both good and poor food years between 1991 and 1997 yellow-nosed albatrosses *Diomedea chlororhynchos* lost mass due to programmed anorexia; however, in poor food years additional body mass was lost due to reproductive stress.

1.3.3 Foraging behaviour in the marine environment

The timing of the stages in the avian annual cycle is largely associated with foraging behaviour (Humphreys et al., 2006). The duration, distance and direction of foraging trips can be critical for successful foraging. When foraging further or for longer durations to exploit better food sources, there is a trade-off between the costs of travelling and searching for prey and the quality or quantity of food obtained. The optimal foraging theory states that natural selection will favour organisms that forage in the most economical way within a patchy environment, such that the energetic gain in time spent per unit food exceeds the loss (MacArthur and Pianka, 1966, e.g. Krebs et al., 1974, Krebs et al., 1977). In order to provide sufficient food to their young, adult birds must forage at a sufficient rate and collect sufficient quantity and quality of food. In addition adults must feed themselves to maintain their own body condition. Life-history theory suggests that long-lived species would allow their provisioning effort to decrease if foraging conditions were poor, in order to favour their own survival above that of their brood (Drent and Daan, 1980, Linden and Møller, 1989). However, an experimental study showed that male black-legged kittiwakes breeding in good environmental conditions, but that had been handicapped to increase flight costs when foraging, decreased their body condition in order to maintain their provisioning rate (Leclaire et al., 2011).

Foraging behaviour could be a mechanism linking food availability to adult body condition and breeding success or could act additively with diet composition to explain variation in adult body condition and breeding success. Density-dependent effects such as colony size may be important by causing local depletion or disturbance of prey, particularly during poor conditions, resulting in greater average foraging range (Ashmole, 1963, Lewis et al., 2001a, Moseley et al., 2012). On the other hand, Paredes et al. (2012) suggested that the proximity of a seabird colony to alternative foraging habitats may be of greater importance than density-dependent effects in determining reproductive and population processes. The variation in feeding strategies of seabird species means that climate change driven alterations in the trophic structure of marine communities can have contrasting implications on seabird survival and success (Kitaysky and Golubova, 2000). Kitaysky and Golubova (2000) showed that the breeding success of planktivorous auklets *Aethia cristatella* and *Cyclorhinchus psittacula* was negatively correlated with SST, because cooler waters favoured macro-zooplankton; whereas the breeding success of pisciverous puffins *Lunda cirrhata* and *Fratercula corniculata* was positively correlated with SST, because warmer waters favoured meso-zooplankton, which is the main prey for juvenile pelagic fish.

As central place foragers, breeding seabirds provide a useful study system and many studies have investigated foraging behaviour in a range of species through observational techniques and using radio telemetry and global positioning system (GPS) loggers (e.g. Galbraith, 1983, Monaghan et al., 1994, Chivers et al., 2012). Foraging trip duration has been shown to be a useful indicator of prey density, and has been highlighted as a parameter worthy of more attention in seabird studies (Piatt et al., 2007a). Some studies to date have compared two years of poor and good food availability, finding markedly longer foraging trips during the poor food year (Costa et al., 1989, Hamer et al., 1993, Monaghan et al., 1994, Chivers et al., 2012). Welcker et al. (2009) showed that, across five different breeding sites, little auks *Alle alle* increased the length of their foraging trips during unfavourable conditions.

Weimerskirch et al. (2001) studied yellow-nosed albatrosses in the southern Indian Ocean over seven successive seasons and found that adults were able to regulate their provisioning behaviour and foraging trip duration according to the nutritional status of their chicks; however, this was only possible when environmental conditions were favourable. Hamer et al. (2006) showed that annual variation (1998, 2001–2003) in the availability of the prey of Northern gannets breeding on the Bass Rock reflected to some extent variation in trip duration. However, in 2002 food availability was much higher than predicted from foraging trip duration, which was explained by the long foraging range of birds in this year, suggesting that prey was unavailable close to the colony but was readily available further away. Few other studies to date have investigated whether patterns of longer foraging trips in poorer food years hold up across long-term datasets. Whether estimating through observations, or measuring using loggers, foraging trip duration provides a useful indication of the amount of effort a bird has had to undertake in order to gain food for their chicks and the time spent obtaining it.

1.3.4 Breeding success as an indicator of environmental conditions

The breeding success of long-lived species can reveal more about local recent environmental conditions than the breeding success of short-lived species; short-lived species may breed regardless of current conditions (Drent and Daan, 1980). Experimental manipulations of breeding success have been used to study the survival costs and fitness implications of raising a brood in a seabird, the black-legged kittiwake (Golet et al., 2004). Clutches of manipulated birds were removed to simulate reproductive failure and their body condition and nest attendance behaviour was compared to those of chick-rearing controls. It was found that in the latter period of the breeding season, chick-rearing parents

spent longer undertaking foraging trips and had reduced body condition (Golet et al., 1998). This also resulted in a 55 % reduction in life expectancy when the costs of the current brood were projected across the expected breeding lifespan of an average kittiwake. Further investigation into the body condition of chick-rearing birds revealed that the reserves available to these birds were allocated differently, with a greater contribution to lean mass and a 28 % reduction in body fat (Golet and Irons, 1999). Altered reserve allocation may be an adaptive response to the need for efficient flight muscles during more intense foraging activity. The mechanisms that determine the reproductive costs of chick-rearing are still under investigation. However, it is clear that both reproductive state, and the factors determining that state, influence the survival of parent kittiwakes (Golet et al., 2004). Whilst chick-rearing control birds had lower survival rates than manipulated failures, natural non-breeders showed the lowest survival rates. This implies that body condition, resulting from overwintering foraging conditions, may act along with energy turnover rate and reserve allocation to determine the breeding capability of a bird and its subsequent survival.

1.3.5 Methods of studying indicator species

When monitoring responses to changes in the environment, long-term datasets are vital (Weimerskirch et al., 2001) and in order to understand climate change vast amounts of historical data must be presented before any projections into the future can be considered. There have been few long-term studies to date that have linked phenology, diet, foraging behaviour, adult body condition and breeding activity in seabirds. Long-term datasets are particularly valuable in providing a backdrop to experimental studies on wild organisms. In concert, long-term datasets and results from experimental manipulations can inform how organisms respond to normal fluctuating conditions across many years and how they respond to simulated variation within the limits of a specific study.

One limitation of long-term population-level studies is that they are often restricted to non-causal correlations, which can be spurious, if confounding variables are in fact driving the relationships. However, whilst experimental studies allow causal questions to be answered, these can involve complicated logistics when carried out in the wild. Experimental studies often involve capturing, handling and manipulating individuals, which lead to ethical considerations and practical considerations such as whether sufficient sample sizes are obtainable, particularly when individuals must be recaptured. Methods of data collection often vary between long-term datasets, which can restrict comparability. For example breeding success can be defined in different ways (e.g. number of chicks

fledged per nest that laid; number of chicks fledged per completely built nest; number of chicks fledged per egg laid; proportion of nests that fledged at least one chick) and proxy measures taken earlier in the season can also be used (e.g. clutch size; brood size by mid chick-rearing). In light of these limitations, studies that combine long-term datasets and experimental manipulations can be highly valuable.

1.4 Stress as an indicator

The described mechanisms and methods of studying environmental change using indicator species can help provide a better understanding of how ecosystems operate under normal conditions and are resilient to unpredictable changes or events. Such perturbations may result in responses throughout the ecosystem; these responses can occur at differing times depending on when impacts are felt at different trophic levels, to differing extents depending on the level of disturbance and in differing directions depending on the life-history strategy of each organism. Species with long-lived life-history characteristics may respond to stress by averting reproduction and favouring their own survival, in an attempt to maximise life-time reproductive success at the expense of the disrupted breeding attempt (Wingfield et al., 1998).

1.4.1 Definition of stress

Stress has been defined in a variety of ways during the history of its study within physiological and biomedical research (reviewed in Koolhaas et al., 2011). Stress was first defined as the non-specific response of the body to any noxious stimulus, this response having the potential to be adaptive or maladaptive (Selye, 1950). This definition was expanded to describe the physiological responses that attempt to restore optimality within an animal, based on the concept of homeostasis (Cannon, 1932), with stress occurring as a deflection from the homeostatic state. However, this encompasses a wide range of stimuli and responses, many of which are not related to stressors. Instead, physiological responses can be activated by a suite of positive (e.g. sexual behaviour; winning a social conflict) and negative (e.g. starvation; losing a social conflict) stimuli or situations (reviewed in Koolhaas et al., 2011). Therefore, the magnitude of such responses may reflect the metabolic demands of a situation rather than whether a situation is a favourable or an unfavourable perturbation.

Koolhaas et al. (2011) proposed that the term stress ‘should be restricted to conditions where an environmental demand exceeds the natural regulatory capacity of an organism, in particular situations that include unpredictability and uncontrollability’. The

natural regulatory capacity of an organism relates to its adaptive capacity, i.e. the physiological mechanisms optimised for a range of environmental conditions, which make up the organism's regulatory range. Under this definition, stressors are stimuli that cause a mismatch between response demands and the adaptive capacity of the organism (reviewed in Koolhaas et al., 2011). Allostasis refers to the concept of maintaining stability through change, with the activation of the mechanisms that facilitate the return to homeostasis in response to a stressor causing allostatic load on the individual (McEwen and Wingfield, 2003). Within this thesis, a stressor is defined as a stimulus or set of stimuli that shift an organism away from homeostasis, whilst stress responses facilitate the return to homeostasis.

1.4.2 The emergency life-history stage

During stress the life cycle may be disrupted through hormonal control mechanisms. Experimental evidence supports the idea of an emergency life-history stage that can be triggered by elevated glucocorticoid concentrations (reviewed in Wingfield et al., 1998). The emergency life-history stage may be adopted in which energy is redirected away from non vital activities (e.g. breeding) and towards survival. Following perception of a stressor, corticotrophin-releasing hormone (CRH) is secreted from neurosecretory neurones within the hypothalamus. CRH passes from the median eminence to the anterior pituitary, where it causes the release of adrenocorticotropic hormone (ACTH). This targets the adrenal gland stimulating the release of a glucocorticosteroid—corticosterone in the case of birds. This pathway is known as the hypothalamic-pituitary-adrenal (HPA) axis and it is this adrenocortical response that is adaptive as a mechanism of stress-avoidance and survival promotion (Wingfield et al., 1998).

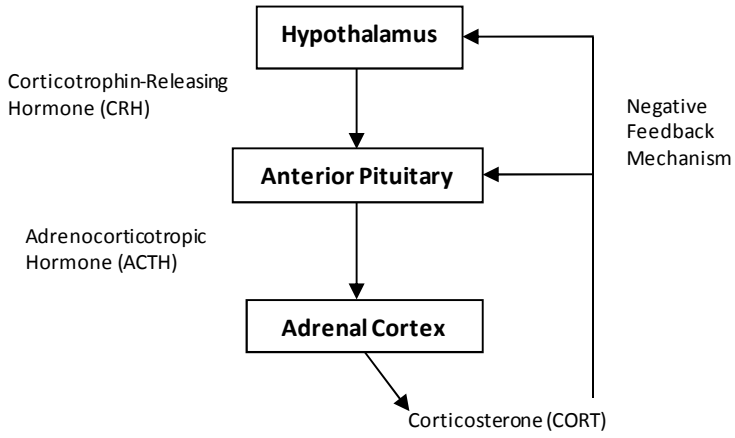


Fig. 1-1 Schematic of the hypothalamic-pituitary-adrenal (HPA) axis.

1.4.3 Consequences of raised corticosterone

Corticosterone, the main 'stress' hormone in birds, has a range of physiological and behavioural effects, including both short-term (e.g. increased gluconeogenesis) and long-term (e.g. suppressed immune system; suppressed growth) effects (reviewed in Wingfield et al., 1998). The short-term effects of stress avoidance and survival promotion are adaptive (Wingfield et al., 1998), whereas the long-term implications of prolonged elevations of glucocorticosteroids on survival and fitness tend to have negative fitness consequences, though they may still be adaptive with long-term survival traded off against the short-term benefits (reviewed in Breuner et al., 2008, Crespi et al., 2013). When glucocorticosteroids are elevated, the rate of passive clearance increases and an active negative feedback mechanism results in the suppression of the HPA axis, which means that the detrimental effects of long-term stress and prolonged high levels of glucocorticosteroids can be reduced (Sapolsky et al., 2000, Romero, 2002, Romero et al., 2005).

Natural variation in corticosterone concentrations have been explained by differences between years, breeding stages and the experience of breeding birds, with higher baseline concentrations during early breeding stages and in inexperienced birds (Lanctot et al., 2003). Lanctot et al. (2003) suggested that the differences in corticosterone concentrations with breeding stage may be due to poor feeding conditions early in the breeding season, or due to large numbers of inexperienced birds prospecting early in the season. Indeed, poor food availability and low body condition have been found to correlate with higher baseline concentrations of corticosterone in a range of studies (e.g. Buck et al., 2007, Williams et al., 2008, Bokony et al., 2009), with corticosterone acting as a reliable measure of food stress and indicator of food availability in seabirds (Kitaysky et al., 2007). However, experimental manipulation of feeding conditions has shown that, whilst food availability is reflected in the body condition and breeding success of birds, corticosterone concentrations may be similar between birds that are food limited and those with abundant food (Lanctot et al., 2003).

Raised baseline concentrations of corticosterone have also been related to enhanced locomotory and foraging activity, which may have positive implications for chick provisioning (Breuner et al., 1998). Raised concentrations of corticosterone can occur in response to acute stressors, causing a rapid peak in corticosterone followed by a return to baseline concentrations, or in response to chronic stressors, causing a gradual but sustained elevation of corticosterone. When corticosterone concentrations are elevated by acute

stress, body condition has been found to decrease (e.g. Angelier et al., 2009b, Angelier et al., 2013; snow petrel *Pagodroma nivea* and Cape petrel *Daption capense*, respectively), increase (e.g. Angelier et al., 2007; male black-legged kittiwakes) or remain unchanged (e.g. Criscuolo et al., 2006; common eider *Somateria mollissima*).

1.4.4 Corticosterone and lifetime fitness

The role of corticosterone during the breeding season is of particular interest when considering the modulation of life-history decisions in response to environmental perturbation. Depending on the life-history characteristics of a species, it may be adaptive to suppress the stress response during breeding (reviewed in Wingfield and Sapolsky, 2003). In the case of long-lived birds with multiple breeding opportunities, corticosterone may be adaptive in its role in the redirection of energy away from reproduction and towards self-maintenance. Birds breeding in predictable environments may have increased responses to stress (e.g. Wingfield et al., 1992, Boonstra, 2004) whilst those breeding in harsh or unpredictable environments, such as in the Arctic or at high altitude, may have suppressed stress responses (e.g. Silverin and Wingfield, 1998, Wilson and Holberton, 2004, but see Li et al., 2011). Closely related species, on the other hand, may have similar adrenocortical responses despite breeding in varying environments due to a high stability of the physiological functions of corticosterone through evolutionary adaptation (Li et al., 2012).

Many studies have focussed on the consequences of corticosterone release in the survival and fitness of organisms (reviewed in Breuner et al., 2008, Crespi et al., 2013). However, Crespi et al. (2013) said ‘if there is a general relationship between GCs [glucocorticoids] and reproduction, it is a pattern with many exceptions’. Large scale phylogenetic comparative analyses, across 64 avian species, have been used to evaluate the inter-specific variation in corticosterone concentrations during parental care (Bokony et al., 2009). Longer-lived species, for which the value of a single reproductive event (brood value) was lower, had lower baseline corticosterone concentrations but higher stress induced corticosterone concentrations. These results support the prediction that long-lived species, whose lifetime fitness depends on the overall number of breeding attempts, invest less energy and resources into a single reproductive event and tolerate lower amounts of stress.

1.4.5 Prolactin: the parental hormone

Hormones involved in the control of reproduction may shed light on how the trade-off between current and future reproduction is controlled. Prolactin, the ‘parental hormone’ is

a large single poly-peptide hormone present in a range of species that displays a variety of functions associated with reproduction, growth and osmoregulation (Norris, 1980). Prolactin originally obtained its name from its role in stimulating the secretion of crop milk by the pigeon crop sac during chick feeding (Riddle, 1931). Prolactin secretion is predominantly controlled by vasoactive intestinal peptide (VIP), which acts as the prolactin-releasing factor and has been found in the median eminence of the hypothalamus (Macnamee et al., 1986, reviewed in Scanes, 2000). Thyrotropin releasing hormone is another, less active, hypothalamic prolactin-releasing factor, whilst arginine vasotocin can stimulate prolactin release from the pituitary with negative feedback control (El Halawani et al., 1992, Scanes, 2000). Dopamine acts as an inhibitor of prolactin secretion (Hall et al., 1986, Scanes, 2000). Many of the behaviours associated with avian reproduction, such as incubation and the development of an incubation patch, are controlled by prolactin secretion (Norris, 1980).

The photo-induced secretion of prolactin results in seasonal cycles of its concentration in the blood. Both breeding and non-breeding birds show seasonal changes in prolactin concentrations. However, during breeding, parental care stimulation modulates prolactin secretion (Dawson and Goldsmith, 1985). Tactile and visual stimuli from the nest, eggs and chicks of a breeding bird enhance prolactin secretion, resulting in a positive feedback mechanism controlling incubation behaviour (Hall and Goldsmith, 1983). However, the stimulatory effects of the egg and brood on prolactin secretion do not necessarily have a direct or rapid enough influence on prolactin concentrations for changes to occur within individuals between incubating and foraging shifts; incoming and outgoing birds, to and from the nest, had similar prolactin concentrations in three species of albatross, which undertake long incubation shifts alternately with their partners (Hector and Goldsmith, 1985).

During its secretion, prolactin plays a key role in the expression of parental behaviours through initiating and maintaining parental care (reviewed in Angelier and Chastel, 2009). Prolactin concentrations are elevated during incubation and chick-rearing compared to the non-breeding and pre-laying nest building stage (starling *Stunus vulgaris*; Dawson and Goldsmith, 1985). Prolactin concentrations peak in incubation with a similar pattern occurring in male as well as female starlings (Dawson and Goldsmith, 1982). Species with precocial young have elevated prolactin during incubation, which declines when young can accompany their parents (e.g. mallard *Anas platyrhynchos*; Goldsmith and Williams, 1980), whereas species with altricial young have elevated prolactin throughout

the chick-rearing period (e.g. canary *Serinus canarius*; Goldsmith, 1982). Prolactin concentrations in capital breeding eiders are positively correlated with body mass and modulated by clutch size (Criscuolo et al., 2006). Sex differences in prolactin concentrations are largely dependent on the level of bi-parental care present within a species. In cases where males and females display equal roles in parental care investment, sex-differences may be absent. In the Wilson's phalarope *Phalaropus tricolor* sex roles are reversed with males alone incubating eggs and rearing young and having higher prolactin concentrations than females (Buntin et al., 1998). In the case of the mute swan *Cygnus olor,* females alone incubate but both sexes guard young. The high concentrations of prolactin in females during incubation start to decline at the end of this stage, whilst prolactin in males declines later in the season (Dawson et al., 2009). This temporal sex difference in behaviour and physiology ensures that parental care is maintained by at least one pair member throughout the breeding season.

Prolactin is important in the control of the timing of moult, which tends to occur in birds after breeding. Dawson et al. (2009) showed that decreasing plasma prolactin concentrations were related to moult in the mute swan, and that moult was inhibited whilst plasma prolactin remained high or increasing. This mechanism may ensure that the important life-cycle stages of breeding and moulting do not overlap, which may result in chick-rearing birds having missing or growing feathers, but instead that moulting occurs soon after breeding, in order to use all the time available for high quality feather replacement (Dawson et al., 2000, Dawson, 2004, Dawson et al., 2009).

1.4.6 Prolactin and the stress response

Prolactin may have a role in the trade-off between breeding effort and self-maintenance for survival (Chastel et al., 2005, reviewed in Angelier and Chastel, 2009). This means that the relationship between prolactin and corticosterone is of importance when investigating the physiological control mechanisms of life-history decisions and responses to environmental perturbation. Baseline concentrations of corticosterone and stress-induced concentrations, generated by capture-restraint protocols or subcutaneous implants of corticosterone, have been measured in a variety of correlational and experimental studies. These have been analysed in conjunction with variables relating to diet (e.g. food availability, foraging effort; Kitaysky et al., 1999, Buck et al., 2007, Kitaysky et al., 2007), adult body condition (e.g. Criscuolo et al., 2006, O'Dwyer et al., 2006, Angelier et al., 2009a) and breeding success (e.g. timing of breeding, parental effort, nest attendance, number of chicks fledged; Buck et al., 2007, Angelier et al., 2009a, Goutte et al., 2010b) in a range of seabirds.

Some studies have also looked for relationships between corticosterone and prolactin (e.g. Groscolas et al., 2008, reviewed in Angelier and Chastel, 2009, Miller et al., 2009, Mochiduki et al., 2010, Riou et al., 2010, Crossin et al., 2012) with a range of often conflicting or inconclusive results (Table 1-1). The role of prolactin in the life-history decisions of long-lived species remains unclear; however, it is possible that this hormone could provide a target through which the adreno-cortical response to stress induces abandonment of reproduction (Angelier et al., 2009a).

There is a disproportionate number of studies of ecophysiology that have used seabirds as study species. This may be due to their characteristic long-lived life-history traits, dependence on highly seasonal productivity peaks in the marine environment coinciding with their breeding seasons, and role as indicators of marine ecosystem change (Monaghan et al., 1989, Cushing, 1990, Harris and Wanless, 1990). In a Web of Science literature search for 'corticosterone and prolactin' 25 hits were studies of seabirds and only 16 were studies in other birds. The lack of evidence of a link between corticosterone and prolactin in poultry may suggest that any relationship found predominantly in seabirds is not necessarily a widespread physiological relationship.

Table 1-1 A review of the major avian endocrine studies to date that look for a relationship between corticosterone and prolactin directly or indirectly by comparing factors modulating the secretion of these hormones. BL CORT = Baseline corticosterone concentration; SI CORT = Stress induced corticosterone concentration.

Study	Species	Results
Koch et al. (2004)	Ring dove	Prolactin is positively related to CORT in non breeders
		SI CORT is not related to hyperphagia induced by prolactin
Chastel et al. (2005)	Kittiwake (Atlantic)	SI CORT is not related to parental effort
		Prolactin increases with increased parental effort
Criscuolo et al. (2006)	Common eider	SI CORT increases with clutch size but is not related to body mass
		Prolactin is not related to clutch size but increases with body mass during incubation
Angelier et al. (2007d)	Black-browed albatross	BL CORT is not related to age or breeding experience
		Prolactin is positively related to age and breeding experience and decreases with time spent attending the nest
		BL CORT increases with time spent attending nest and decreases the probability of fledging a chick
Angelier et al. (2007b)	Snow petrel	SI CORT is not related to age
		Prolactin is negatively related to age and egg neglect
Angelier et al. (2007c)	Wandering albatross	BL CORT is reduced after a foraging trip and is negatively related to foraging success
Groscolas et al. (2008)	King penguin	BL CORT is positively correlated with nest abandonment
		Prolactin is negatively correlated with nest abandonment
Angelier et al. (2009c)	Snow petrel	Prolactin is not related to body condition
		BL CORT is lower in birds of better condition but is no different between birds of differing breeding status
Miller et al. (2009)	Mourning dove	BL CORT and prolactin are higher in birds with heavier chicks
		SI CORT is negatively correlated with parental effort
Angelier et al. (2009a)	Kittiwake (Atlantic)	SI CORT is negatively related to breeding success and nest attendance
		Prolactin decreases with SI CORT
Riou et al. (2010)	Manx shearwater	Prolactin is negatively related to brood value
		SI CORT is positively related to brood value
Schmid et al. (2011)	Eurasian hoopoe	Prolactin is positively related to parental investment and body condition, and is negatively related to date since hatching
		Prolactin is reduced after a stress protocol
Leclaire et al. (2011)	Kittiwake (Pacific)	Prolactin, BL CORT and SI CORT were unaffected by handicapping males during chick-rearing
Crossin et al. (2012)	Macaroni penguin	Prolactin is reduced after a foraging trip and is unaffected by low dose implants of CORT
		BL CORT is positively related to chick mass and is raised a after foraging trip
Riechert et al. (2012)	Common tern	Prolactin is positively related to early breeding experience
		BL CORT is positively related to senescence in males
Angelier et al (2013)	Cape petrel	SI CORT modulated by body condition; Prolactin response to stress modulated by breeding status

1.4.7 Methods of studying chronic stress

Manipulating corticosterone experimentally is an important way to assess whether there are effects on concentrations of prolactin or on reproductive success. Whilst some studies

have attempted to do this, there are various methodological limitations that can be identified. Previous studies have elevated corticosterone in a way similar to that observed in acutely stressful situations (Fig. 1-2), using open-ended silastic tubes to administer corticosterone. These tubes are designed to be sealed so that the hormone is released in a controlled way through the walls of the tubing. However, because steroid hormones such as corticosterone are hydrophobic, the ends of the tubes must be cut off or the tubing must be punctured with holes, in order for the hormone to be released. This results in a large acute dose of corticosterone and consequently an increased clearance rate of exogenous corticosterone, massive negative feedback, down-regulation of endogenous secretion of corticosterone (Newman et al., 2010) and the contents of the pumps being rapidly used up. Alzet® osmotic pumps (Fig. 1-3), which release their contents at a constant rate over a number of days (> 13,500 publications in the Alzet® bibliography; e.g. corticosterone delivery to white throated sparrows *Zonotrichia albicollis*; Horton et al., 2007), may better mimic chronic stress, such as poor food availability and adverse environmental conditions. In chronic stress, the stressor remains for a prolonged period of time, and therefore there may be a balance between negative feedback and the stimulatory effects of the continued stress (Fig. 1-2).

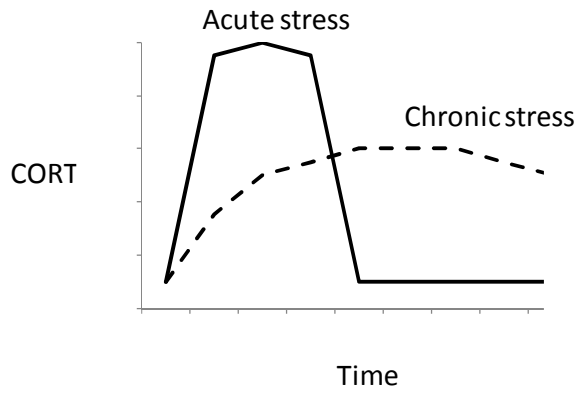


Fig. 1-2 Profiles of corticosterone concentrations (CORT) in response to an acute (solid line) and a chronic (hatched line) stressor.

Fig. 1-3 Alzet® osmotic pumps in three sizes (length, diameter, reservoir volume, weight): small 1.5 cm, 0.6 cm, 100 µl, 0.4 g; medium 3.0 cm, 0.7 cm, 200 µl, 1.1 g; large 5.1 cm, 1.4 cm, 2 ml, 5.1 g (www.alzet.com).

When collecting blood samples in order to measure corticosterone concentrations the effect of the acute stress response associated with capturing an individual must be considered. Romero and Reed (2005) tested five avian and one reptilian species (n = 945) in an attempt to find a more generalised time limit for blood sample collection. They concluded that samples collected in less than two minutes could be reliably used to measure baseline corticosterone. Corticosterone measured in samples collected within three minutes was consistently baseline or at least near baseline. It has therefore since been accepted that blood sampling should occur within two to three minutes of capture.

When recommending baseline blood sampling time limits, Romero and Reed (2005) did not consider the possibility of a stress response being induced before capture, when the colony or group of individuals was first disturbed by the presence of an investigator in their vicinity. When carrying out studies looking at the stress response in free-living birds, it is important to consider disturbance effects (e.g. Harris and Wanless, 1984, Sandvik and Barrett, 2001, Carlini et al., 2007, Brewer et al., 2008). Beale and Monaghan (2004) have shown that tourism can cause disturbance to seabird colonies (black-legged kittiwakes and common guillemots), due to the perceived predation risk associated with the presence of humans. Whilst many colonial species are often inaccessible and therefore unaffected by visitors, disturbance at a single accessible nest may have widespread impacts across the whole colony, due to the close proximity of one nest to the next. Models show that disturbance is enhanced with increasing visitor numbers and proximity of these visitors to the nests, and that capping daily visitor numbers may have some conservation benefits (Beale and Monaghan, 2004, Beale and Monaghan, 2005, Beale, 2007). These findings also have implications for researchers working at a colony, due to the impacts of disturbance whilst observing or, in particular, capturing individual birds. Such impacts may include reducing the likelihood of recapturing individuals in the colony, as well as having impacts on the birds' behaviour and physiology in response to disturbance-induced stress. These impacts therefore have implications for the results collected by a researcher, as well as the welfare of the birds being studied.

1.5 Study species and area

The black-legged kittiwake (hereafter 'kittiwake') is the most widely monitored seabird species in terms of population size and productivity (Frederiksen et al., 2005a, Hatch, 2013), and is commonly used as an indicator of marine environmental change due to the sensitivity of its breeding success to environmental variation (Frederiksen et al., 2007b, Wanless et al., 2007, Parsons et al., 2008). Kittiwakes are small marine gulls that breed

colonially, typically out of reach of mammalian predators on vertical sea cliffs, often on offshore islands (Baird, 1994, Parsons et al., 2008). Kittiwakes have a wide breeding distribution ranging across the Atlantic and Pacific Oceans. Phenotypic variation arises between populations in response to differences in environmental conditions. For example, the demography of kittiwakes varies between North Pacific and North Atlantic colonies (Hatch et al., 1994). Higher survival rates and lower fecundity characterise the North Pacific populations and the opposite traits characterise North Atlantic populations (Hatch et al., 1993, Gill and Hatch, 2002, Frederiksen et al., 2005a, Suryan et al., 2009). Such demographic variation between geographically separated colonies results in population-dependent implications for the optimal life-histories of individuals. Comparative studies suggest that environmental factors such as food availability, as opposed to adaptive genetic traits, primarily control this life-history variation (Gill and Hatch, 2002). However, larger-scale studies are required to test the prediction that this life-history variation occurs primarily between, and not within, oceans (Kitaysky et al., 2010, Vincenzi et al., 2013). It is important that generalisations are not made between ocean basins or geographically distinct populations of the same species, due to these potential differences in life-history strategy and environmental conditions.

The aim of my research was to investigate what mechanisms cause changes in breeding success of a top marine predator in response to marine environmental change. I used the kittiwake as the model species. This thesis focussed on kittiwakes breeding on the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11‘ N, 02° 33’ W), which is an important breeding site for many seabird species within the North Sea. Long-term datasets available for Isle of May breeding kittiwakes made this a good choice of study species and study area to base my research on.

1.5.1 Isle of May

Breeding populations of seabirds have been studied continuously since the breeding season of 1972 on the Isle of May (Figs. 1-4 and 1-7). The island is approximately eight kilometres from the mainland and covers around 57 hectares. Kittiwakes nest all around the island, both on the high cliffs of the western side and the lower rocky eastern side. The island supports breeding populations of Atlantic puffins *Fratercula arctica*, common guillemots, razorbills *Alca torda*, European shags *Phalacrocorax aristotelis*, northern fulmars, common and Arctic terns, herring gulls *Larus argentatus*, lesser *L. fuscus* and great black-backed gulls *L. marinus*, and kittiwakes, with most of these populations being of international importance (Mitchell et al., 2004).

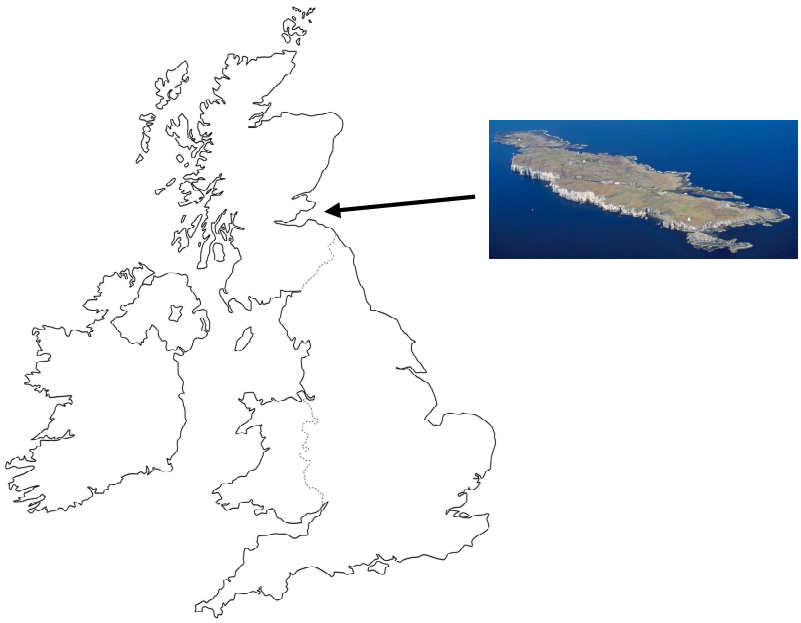


Fig. 1-4 Map of the British Isles showing the location of the Isle of May.

A multi-colony analysis of north-western (NW) North Sea breeding kittiwakes showed that the Isle of May breeding colony had the highest correlation with the regional mean for productivity and therefore was regarded as the most appropriate colony for monitoring purposes within this region (Frederiksen et al., 2007b). Long-term monitoring of these populations has led to the accumulation of large datasets concerning reproductive activity and population dynamics since the late 1980s. The number of breeding pairs of kittiwakes on the Isle of May has fallen from 8129 pairs in 1990 to 2316 pairs in 2009 (Alampo and Ash, 2010; Fig. 1-5a). Breeding success has fluctuated during this period with no linear trend (Fig. 1-5b). The Isle of May is one of the Joint Nature Conservation Committee (JNCC) key monitoring sites as it is a designated Special Area of Conservation (SAC). Many of the kittiwake nest sites on the Isle of May can be accessed when catching with a noose pole and therefore it is possible to collect information on body mass, collect diet samples and deploy loggers to record foraging location and activity (e.g. Daunt et al., 2002, Bogdanova et al., 2011). However, because most of the kittiwakes breeding on the Isle of May are no longer naive birds with respect to capture methods, capturing them can prove difficult, especially when attempting to recapture individuals multiple times during the season (pers. obs.).

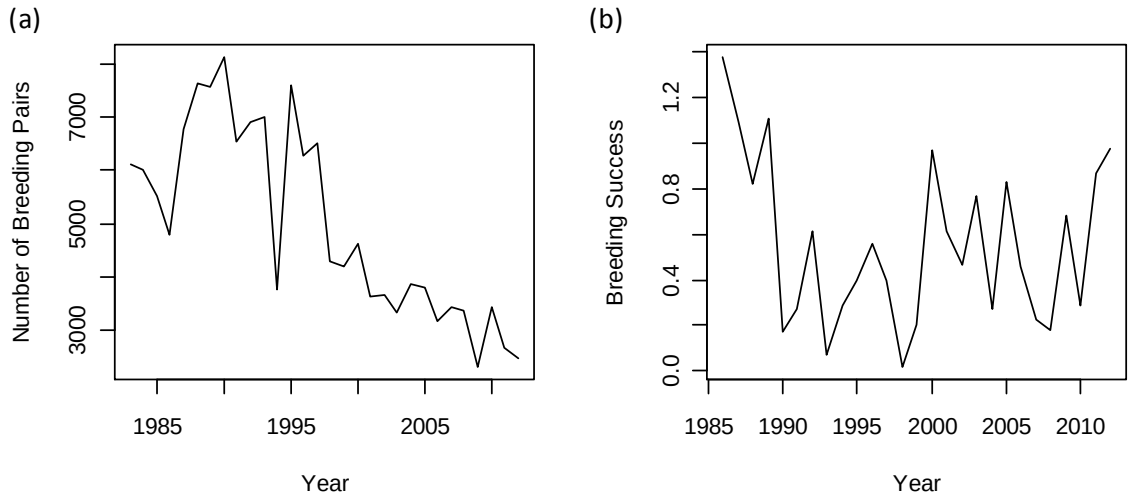


Fig. 1-5 (a) Number of breeding pairs and (b) mean breeding success of kittiwakes breeding on the Isle of May (1983–2012 and 1986–2012, respectively).

1.5.2 Kittiwake biology

The kittiwake is a specialist surface-feeder with often low availability of suitable prey species in their foraging range around the colony, which explains its sensitivity to changes in the marine trophic web (Furness and Tasker, 2000). Feeding on small surface-dwelling pelagic fish, kittiwakes forage in mixed species flocks near to their breeding sites (Camphuysen and Webb, 1999, Camphuysen et al., 2006). Kittiwakes feed by plunge diving from above the water surface or surface seizing while sitting on the water (Baird, 1994). Food availability is an important factor affecting the population dynamics and reproductive success of kittiwakes (Oro and Furness, 2002, Barrett, 2007).

As with some other species of long-lived colonial seabirds, kittiwakes display high nest-site and mate fidelity. Breeding individuals start the season by building nests or bringing in new nesting material (Fig. 1-6a) to repair existing nest sites. Kittiwakes lay between one and three eggs during late spring and incubate their eggs (Fig. 1-6b) for approximately 25 days (25–27.4 d; Baird, 1994, 25–29 d; Coulson, 2011). Chick-rearing (Fig. 1-6c) lasts for longer than incubation, with chicks typically ready to fledge (Fig. 1-6d) between the ages of 34 and 58 days (Baird, 1994, Coulson, 2011). Males and females share equal roles in parental care at the incubation and chick-rearing stages. Females reach sexual maturity at three or four years of age. The low fecundity and long lifespan of kittiwakes means that the total number of breeding years within an individual's life is an important factor influencing its overall reproductive success (Coulson and Thomas, 1985); however, compared to many other seabirds, kittiwakes have relatively high fecundity, early sexual maturity and low adult survival. Kittiwakes breeding in the Pacific tend to be

characterised by lower breeding success and higher survival compared to Atlantic breeding kittiwakes (Hatch et al., 1993, Frederiksen et al., 2005a, Suryan et al., 2009). However, estimates of survival rate may have varied over time with advances in modelling techniques that reduce the under-estimation of survival due to missing birds at a colony being recorded as dead. Adult survival rate for kittiwakes breeding at South Middleton Island, Alaska has been estimated at 93 % (Hatch et al., 1993) Adult survival rate has been estimated from UK ringing return data at 81% for males and 86% for females (Coulson and Wooller, 1976) and more recently using mark-recapture (White and Burnham, 1999) at 94 % (Frederiksen et al., 2004).Other recent estimates of Atlantic kittiwake survival are reviewed in Coulson, 2011 (e.g. 88 % for kittiwakes breeding on Hornøya, Norway; Sandvik et al., 2005).

Fig. 1-6 (a) Adult kittiwake in flight carrying nesting material; (b) three kittiwakes incubating; (c) kittiwake adult standing by nest with two chicks; (d) kittiwake chick ready for fledging. Photos: David Hawkins (a, b) and Afra Skene (c, d).

1.5.3 Diet of kittiwakes

Diet data are less available than population count or breeding success data because, whilst observing cliff-nesting kittiwakes is relatively easy, collecting diet samples involves capturing individuals from their nest sites and not all individuals captured will regurgitate (Hatch, 2013). Regurgitations may reflect adult and/or chick diet; however, distinguishing between the species composition of these two aspects of the kittiwake diet is impossible from regurgitations alone. Adult kittiwakes feeding for chick provisioning should optimize their energy load for each foraging trip by selecting larger or more fatty fish that have a

higher calorific value. Adult feeding for self-maintenance alone may be able to meet their requirements by choosing readily available fish that are smaller or of lower calorific value (reviewed in Barrett et al., 2007). Diet can also be estimated from stable isotope analysis (Hobson and Welch, 1992, e.g. Newfoundland and Labrador cod *Gadus morhua*; Sherwood et al., 2007, reviewed in Inger and Bearhop, 2008) and fatty acid analysis (Cordain, 2002, Iverson et al., 2004, Iverson et al., 2007, Käkelä et al., 2007) using tissue samples including blood, muscle, adipose, hair or feathers collected from captured individuals. Stable isotope analysis only allows estimates of the trophic level at which individuals have fed, and how far off-shore they have fed, whereas fatty acid analysis allows species composition to be identified (Iverson et al., 2007). Fatty acid analysis, on the other hand, requires the profiles of potential prey items for comparison. Kittiwakes are mainly piscivorous during the breeding season. However, geographical location and habitat type determine to some extent what specific prey types kittiwakes utilise (e.g. Suryan et al., 2000, Bull et al., 2004, Frederiksen et al., 2005b, Markones et al., 2009). Environmental variability is having increasing impacts on kittiwake diets, for example through changing the suitability of the environment for the copepod *Calanus finmarchicus* on which certain mid-trophic level fish feed (Edwards et al., 2002, Frederiksen et al., 2013). Baseline concentrations of corticosterone have been shown to be negatively correlated with availability of suitable prey species in the kittiwake (e.g. Kitaysky et al., 1999, Buck et al., 2007, Kitaysky et al., 2010), suggesting detrimental impacts on the kittiwake's physiology.

The North Sea is a highly productive region of the Atlantic, with strong seasonality featuring a spring phytoplankton bloom (Edwards et al., 2002). Kittiwakes breeding in the Wee Bankie NW North Sea region (Fig. 1-7), and in much of their North Sea range, feed on, and subsequently regurgitate for their chicks (Fig. 1-8a), the lesser sandeel *Ammodytes marinus* (hereafter 'sandeel'; Fig 1-8b) during the breeding season (e.g. Galbraith, 1983, Lewis et al., 2001b) and occasionally on clupeids (mainly sprat *Sprattus sprattus*; Fig 1-8c). The Wee Bankie region is within the foraging range of Isle of May breeding kittiwakes and thus is an important area for them during the breeding season (Wanless et al., 2007). Winter SST has bottom-up ecosystem impacts that affect the availability of sandeels in this region of the North Sea and hence the reproductive success and survival of kittiwakes breeding off the east coast of the UK (Wanless and Harris, 1992, Wanless et al., 2007). Frederiksen et al. (2004) showed a lagged effect of winter SST (i.e. occurring one and a half years later) on breeding success and an effect on the current year's adult survival. A sandeel-specific fishery was active on the Wee Bankie (Fig. 1-7) between 1991 and 1998, which compromised kittiwake breeding success further through reduced sandeel

availability (Rindorf et al., 2000, Frederiksen et al., 2004). This additive effect of fishery activity and increasing SST was also apparent at other kittiwake colonies within the NW North Sea (Frederiksen et al., 2007b). Kittiwakes were found to benefit from the closure of the Wee Bankie fishery, an effect that was not widespread across all seabird species (Daunt et al., 2008).

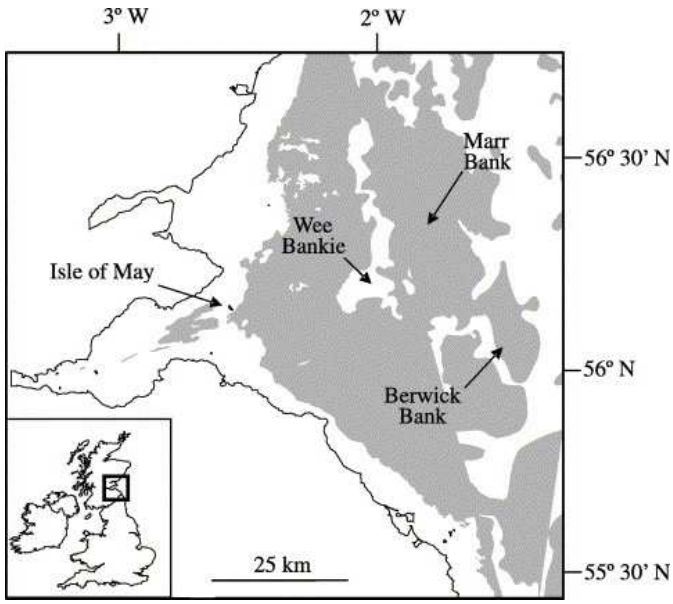


Fig. 1-7 Map of the British Isles showing the location of the Wee Bankie region of the NW North Sea, surrounding regions and the Isle of May (Wanless et al., 2007).

Fig. 1-8 (a) Kittiwake feeding chick; (b) puffin with sandeels; (c) puffin with sprat. Photos: Afra Skene.

The changes in a sandeel-specialised kittiwake's diet during the breeding season, in terms of prey size and prey composition, mirrors the seasonal changes in sandeel life-history. Adult (1+ group) sandeels are available in the Wee Bankie region (Fig. 1-7) during early spring, after which they retreat to the sandy sea floor and are unavailable to surface-feeders. Young of the year (0 group) sandeels subsequently form dense shoals at the sea surface, after metamorphosing from larvae to juveniles, and predominate in the kittiwake diet (Lewis et al., 2001b). Breeding success is increased in years when 0 group sandeels appear in the water column early (Rindorf et al., 2000). This may be due to a reduction in

the likelihood of a gap in prey availability after the 1+ group sandeels have disappeared into the benthic zone (Rindorf et al., 2000, Lewis et al., 2001b). Whilst kittiwakes breeding in Shetland, northern North Sea depend primarily on 1+ group sandeels for productivity and 0 group sandeels for adult survival (Oro and Furness, 2002), the productivity of kittiwakes breeding in the Wee Bankie region has been linked to both 0 group and 1+ group sandeels (Lewis et al., 2001b). The reproductive output of many different seabird species is affected by the timing of peak sandeel abundance (Rindorf et al., 2000). However, species vary in their capacity to compensate for changes in sandeel availability, depending on the availability and accessibility of suitable alternative prey species.

1.5.4 Nest attendance

Initially members of a kittiwake pair alternate roles of nest guarding and foraging. However, during the mid to late chick-rearing period it is increasingly common to see the nests of Isle of May breeding kittiwakes left unattended (Fig. 1-9), with both members of a pair foraging simultaneously (pers. obs.). This tends to occur when one parent alone cannot provide the brood with sufficient food, and therefore may act as an indicator of poor food supply. Galbraith (1983) showed that whilst kittiwakes were able to increase their rate of chick provisioning, there was a threshold above which chick provisioning rate would be limited. It may be assumed that unattended broods are at greater risk of predation as chicks are vulnerable when unguarded; however evidence from kittiwakes breeding in the NW North Sea suggests that predation risk remains low even in unattended chicks (Wanless and Harris, 1992, Harris and Wanless, 1997, pers. obs.).

The size of a brood may influence the likelihood of unattendance at a nest, with larger broods requiring more feeds and therefore increasing the probability of the parents foraging simultaneously (Wanless and Harris, 1989, Wanless and Harris, 1992). Some avian studies have suggested that larger broods have higher rates of siblicide (e.g. Cattle egret *Bubulcus ibis*; Mock et al., 1987, Mock and Lamey, 1991, Drummond, 2001). However, this apparent effect is inconclusive and may be due to lower provisioning rates in larger broods rather than brood size per se (Drummond and Rodriguez, 2009). Siblicide does indeed occur at a higher rate when food availability is lower (Alaskan kittiwakes; White et al., 2010a) and is relatively common in kittiwakes compared to other seabird species (Vallarino, 2008). Siblicide, resulting from size asymmetry as a result of variation in egg size and hatching asynchrony, may be an adaptive mechanism during unpredictable environmental conditions, as shown by higher fledging success in natural broods compared

to those in which experimental egg manipulation had removed size asymmetry from the brood (Vallarino, 2008).

Fig. 1-9 (a) Adults attending chicks; (b) two unattended chicks. Photos: Afra Skene.

1.6 Behaviour and physiology of breeding kittiwakes in 2010

1.6.1 Introduction

To date, no studies have examined the physiology of kittiwakes breeding on the Isle of May and how this links to their behaviour. Therefore, baseline data were collected in 2010 with the aim of measuring seasonal changes in the behaviour and physiology of Isle of May kittiwakes as preliminary work for this thesis. This was achieved by catching a sample of individuals through the breeding season and recording adult body mass, corticosterone concentration, prolactin concentration and breeding success. Because 2010 was the first season in which corticosterone and prolactin was measured in kittiwakes at this colony, these data provided useful baseline values prior to my field experiment during 2011 (chapter four).

1.6.2 Methods

The breeding behaviour of 240 kittiwake pairs was observed throughout the breeding season (May–July) of 2010 on the Isle of May. Blood sampling was carried out four times during the breeding season (for full details see chapter four). Initially all nest sites were targeted intensively for one week (May 23–May 29) during which 30 incubating birds were captured, blood sampled, ringed with a British Trust for Ornithology (BTO) metal ring, weighed, marked using picric acid and released. Subsequently attempts were made to recapture birds that had been previously captured and, when this was not possible, to catch new birds from the same colonies. The second catching attempt was carried out at the end of incubation (June 2–June 4) and during this period 22 birds were captured of which 15 were recaptures. The third catching attempt was carried out during early chick-rearing (June 15–June 18) and during this period 24 birds were captured of which 15 were recaptures (eight had been captured once already and seven had been captured twice

already). The fourth catching attempt was carried out during late chick-rearing (June 28–June 29). Only 9 birds were captured of which 6 were recaptures. One bird was captured four times in total. The final catching period was restricted by the failure of birds, which resulted in their absence at the nest sites and the disturbed nature of the colony. Catching was limited to four periods in order to minimise the level of disturbance at the colonies and to maximise the chance of recapture. This is because kittiwakes tend to become harder to catch with repeated disturbance rather than habituating to the presence of an investigator (pers. obs.).

A maximum of 1 ml of blood was taken from the alar vein using non-heparinised 1 ml syringes. Only 54 samples—taken from a total of 36 individuals—had sufficient quantities of blood for both corticosterone and prolactin concentrations to be determined. Samples were centrifuged and the serum aspirated. The serum and blood cell pellets were frozen separately until analysis in the laboratory. A dictaphone was used to record the time taken to capture and blood sample each bird. Blood sampling was aimed to be carried out within two minutes of capture, so that baseline levels of corticosterone would be obtained. Capturing birds took 3.5 ± 0.2 (mean ± SE) min with the longest time spent capturing being 9.8 min. Blood samples were collected 2.7 ± 0.1 min after capture with the longest blood sampling taking 5.5 min. There was no relationship between corticosterone concentration and time taken for capture (linear model: $t = 0.93$, $df = 52$, $P = 0.35$, $R^2 = 0.02$) or taken for blood sampling (linear model: $t = 1.17$, $df = 52$, $P = 0.25$, $R^2 = 0.03$) and therefore all values were included as baseline concentrations.

All statistical analyses were performed using R (version: 3.0.1, R Development Core Team, 2013). Values are presented as means ± standard error unless specified otherwise. We used a linear mixed effects model fit by restricted maximum likelihood (REML) to analyse the effect of date of sample relative to lay date, adult body mass, prolactin concentration and sex on corticosterone concentration. We used a similar model to analyse the effect of date of sample relative to lay date, adult body mass, corticosterone concentration and sex on prolactin concentration. We included ring number as a random factor to account for repeated measures. We used backward stepwise elimination to select the best model and chose the model with the lowest Akaike Information Criterion AIC (> 2 units lower) (Hurvich and Tsai, 1989, Burnham and Anderson, 2002). As corticosterone concentrations were constrained by being positive and the residuals were not normally distributed, we transformed this response variable by taking the logarithm to base ten. To assess whether prolactin concentrations differed between individuals that

ultimately failed and those that were successful, we used a linear mixed effects model to analyse the effect of breeding success, sex and the interaction between these variables on prolactin concentrations, including ring number as a random factor.

1.6.3 Results and discussion

The first recorded lay date in 2010 was May 7 and the median lay date was May 15, which was early compared to the long-term average (1997–2009: May 27 ± 6). Mean clutch size was 2.3, which was larger than the long-term average (1997–2009: 1.7 ± 0.2), and 78 (33 %) apparently occupied nests (AON i.e. a breeding site where a pair has built a complete nest and therefore equivalent to the number of breeding pairs; Walsh et al., 1995) laid clutches of three. Hatching success (the proportion of AONs that laid at least one egg, that went on to hatch at least one chick) was 0.87, which was higher than the long-term average (1997–2009: 0.75 ± 0.12) and mean brood size was 2.1. On average 0.3 chicks were fledged per AON, which was low compared to the long-term average (1997–2009: 0.4 ± 0.2). 215 nests reached the chick-rearing stage and 117 nests successfully fledged chicks. 52 % of AONs successfully fledged at least one chick (103 AONs fledged one chick; 14 AONs fledged two chicks). There was no linear trend over time of log corticosterone concentrations (linear mixed effects model: $t = 1.02$, $df = 17$, $P = 0.32$; Fig. 1-10a) or prolactin concentrations (linear mixed effects model: $t = 1.73$, $df = 17$, $P = 0.10$; Fig. 1-10b). Mean body mass across the season was 373 g, which was similar to the long-term average (1997–2009: 369 ± 11 g). However, mass declined during the season by 1.3 g per day (linear mixed effects model: $t = 4.09$, $df = 17$, $P < 0.001$; Fig. 1-10c), with mass at fledging lower than the long-term average (1997–2009: 346 ± 21 g; 2010: 332 g).

There was a significant effect of mass (linear mixed effects model: $t = 3.23$, $df = 17$, $P < 0.005$; Fig. 1-10d) and sex (linear mixed effects model: $t = 2.06$, $df = 34$, $P = 0.05$) on log corticosterone, with a decrease in corticosterone concentrations of 0.98 ± 1.01 ng/ml per gram and with males having 2.67 ± 1.61 ng/ml higher corticosterone than females. There was no effect of date of sampling relative to lay date (linear mixed effects model: $t = 1.786$, $df = 16$, $P = 0.09$), corticosterone (linear mixed effects model: $t = 1.76$, $df = 16$, $P = 0.10$) or sex (linear mixed effects model: $t = 1.54$, $df = 34$, $P = 0.13$) on prolactin concentrations. All other variables were removed from these two models during model selection. There was a significant interaction between breeding success and sex on prolactin concentrations (linear mixed effects model: $t = 2.08$, $df = 32$, $P = 0.045$; Fig. 1-11). However, as prolactin measurements were taken prior to failure, it was not possible to tell how prolactin concentrations changed at, or just before, failure.

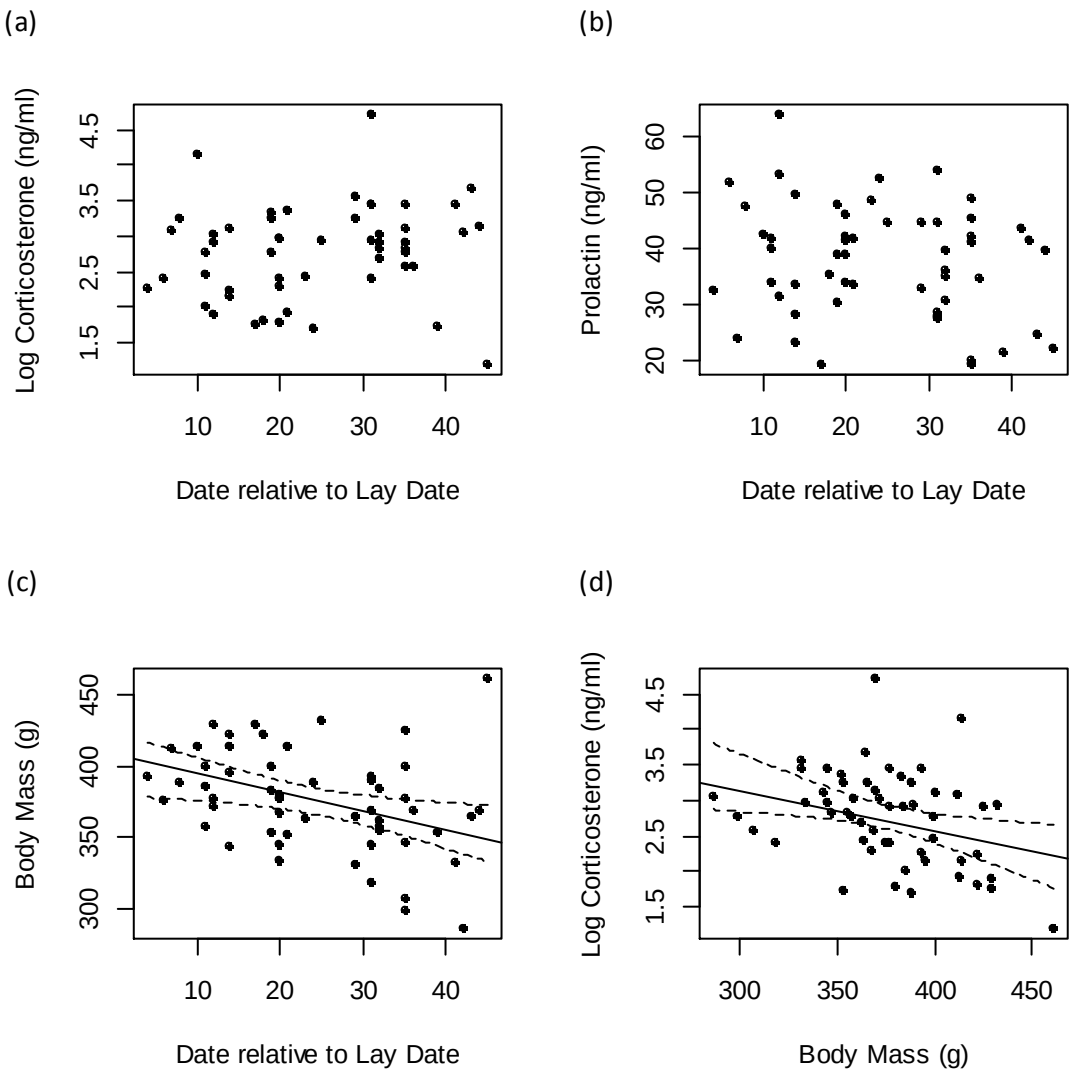


Fig. 1-10 (a) No change in log corticosterone concentrations over time, (b) no change in prolactin concentrations over time, (c) loss of body mass over time and (d) negative correlation between body mass and log corticosterone. Hatched lines show 95 % confidence intervals.

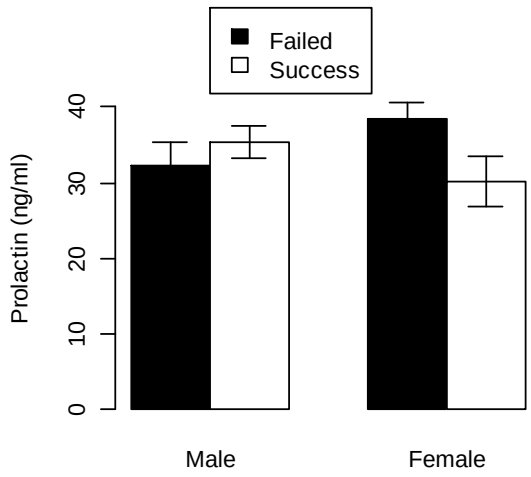


Fig. 1-11 Prolactin concentrations of males and females that failed at their breeding attempt (filled bars) and that successfully raised at least one chick (open bars).

These results show that 2010 started off as a successful season in terms of early breeding and large clutch size relative to the long-term average on the Isle of May. Hatching success was also high compared to recent years but body mass declined during the season, resulting in lower mass at hatching than recent years. There was a period during chick-rearing when conditions appeared to be unfavourable and many nests failed completely or lost chicks (pers. obs.). This resulted in most failures occurring during chick-rearing and low overall breeding success relative to the long-term average. There was no evidence for an increase in corticosterone concentrations during the season, nor a decrease in prolactin concentrations. This may be explained by a lack of data at the end of the chick-rearing period, close to when failures occurred. Whilst there was no correlation between corticosterone concentrations and prolactin concentrations, males had higher corticosterone concentrations than females, and females that ultimately failed had significantly higher prolactin concentrations during incubation and early chick-rearing than those that were successful breeders. Whilst these data cannot be compared with previous years of data from Isle of May breeding kittiwakes, they do provide baseline data with which the experimental data in chapter four can be compared.

1.7 Outline of the thesis

The data described in section 1.6, along with chapters two and three, together provide a general background for my field experiment (chapter four), the methods for which were trialled in the laboratory and are described in Appendix A. In chapter two I analyse long-term datasets that have been collected on the Isle of May since 1997 to assess how changes in the timing of availability of 1+ group and 0 group sandeels have impacted the diet composition, adult body mass and breeding success of the kittiwake. In chapter three I analyse long-term data on the foraging trip duration of breeding kittiwakes on the Isle of May to assess whether trip duration explains some of the variation in adult body mass and breeding success and whether this is mediated by diet composition. In chapter four I describe a field experiment to manipulate corticosterone concentrations in wild kittiwakes to mimic chronic environmental stress. This experiment was carried out in order to assess whether the mechanism linking chronic stress and breeding failure is mediated by adult body mass, prolactin concentrations and nest attendance behaviour. Chapter five describes the stress responsiveness of a captive bird, the Japanese quail *Coturnix coturnix japonica*, in response to a standardised capture-restraint protocol and with increasing time since the group of birds was first disturbed. Chapter six is a broader discussion of my main findings and highlights areas for future work.

Chapter Two

The diet composition of chick-rearing black-legged kittiwakes is associated with their body mass and subsequent breeding success

2.1 Abstract

The timing of biological events is modified in response to environmental change. Within the North Sea ecosystem, evidence suggests that trophic mismatch has been occurring, with resource demands of consumers no longer coinciding with peak prey availability. When the timing of availability of certain prey types changes this has implications on the diet composition of predators, with certain prey types no longer available and others replacing them in the diet. Trophic mismatch can affect the condition and breeding performance of top predators, such as seabirds, via changes in the availability or quality of prey. Using a long-term dataset (1997–2010), we assessed the effects of changes in diet composition on adult body mass and breeding success in a population of black-legged kittiwakes *Rissa tridactyla* breeding on the Isle of May, south-east Scotland. The diet of this breeding population switches from being predominantly composed of adult (1+ group) lesser sandeels *Ammodytes marinus* to young of the year (0 group) sandeels and, in some years, clupeids (mostly sprat *Sprattus sprattus*). We found that the timing of this switch has become earlier, coinciding with late incubation at the start of the dataset but occurring at laying in more recent years. In years when birds were heavier at the start of the season, laying was earlier and clutch size larger. Furthermore, years of higher adult body mass at laying were associated with greater mass loss during incubation and lower hatching success. However, diet composition during incubation was unrelated to these changes. During chick-rearing, years of higher adult body mass at hatching were associated with greater mass loss and lower fledging success. The proportion of clupeids relative to sandeels was not related to these changes; however, years of higher proportions of 1+ group relative to 0 group sandeels were associated with years of greater body mass loss, and lower fledging success. We speculate that the changes in diet composition that are

affecting the body mass and breeding success of the kittiwake may be occurring as a result of trophic mismatch within the North Sea ecosystem.

2.2 Introduction

The timing of seasonally recurring biological events (phenology) is strongly influenced by climatic conditions and, as such timings shift, species interdependence can be disrupted (e.g. Perrins, 1970, Visser et al., 1998, Visser et al., 2006, Chamberlain and Pearce-Higgins, 2013, Fletcher et al., 2013). Specifically, mismatches can occur between the timing of peak food demand and the timing of peak food availability. The mismatch hypothesis was first used by Cushing (1990) in the context of the availability of plankton prey for fish and subsequent effects on fish stocks, but has since been applied to numerous cases of predators and prey and more generally to consumers and food resources (reviewed in Visser and Both, 2005). Mismatch has been identified as an important route through which climate change can negatively affect the reproductive success of a predator via changes in the timing of prey availability (reviewed in Durant et al., 2007). However, the mechanisms underpinning relationships between trophic mismatch and predator fitness are poorly understood.

Marine ecosystems have highly seasonal primary production, which means that mismatches in the timing of breeding of predators and their prey can have particularly important implications for predator breeding success (Cushing, 1990). Studies of the relationship between trophic mismatch and the fitness of marine top predators are rare because data are lacking (reviewed in Burthe et al., 2012). However, the available evidence suggests that there are negative implications of mismatch on top predator fitness (Atlantic puffin *Fratercula arctica*; Durant et al., 2006, Cassin's auklet *Ptychoramphus aleuticus*; Hipfner, 2008, rhinoceros auklet *Cerorhinca monocerata*; Watanuki et al., 2009, Burthe et al., 2012). The diet composition of top predators is likely to be affected when the timing of availability of certain prey types changes, as certain prey types become unavailable and other prey types replace them in the diet. Therefore, the consequences of trophic mismatch on predator breeding success may be mediated through effects of prey availability, abundance and quality on adult body condition (Sydeman et al., 2001, Suryan et al., 2002). Low prey availability or abundance may result in adults undertaking longer and less successful foraging trips with consequences on their body mass (e.g. Monaghan et al., 1989, Chastel et al., 1995), which affect the likelihood of abandoning young to safeguard their long-term survival (Drent and Daan, 1980). In seabirds and other marine predators, adult body mass typically declines during the breeding season because of the high

energetic costs at this time (e.g. Monaghan et al., 1989, Wendeln and Becker, 1999, Moe et al., 2002, Santos et al., 2010). The ‘fat and fit hypothesis’ (reviewed in Schultner et al., 2013) states that energy stores are maximised under optimum foraging conditions and that mass loss increases as environmental conditions deteriorate. However, reductions in adult mass during breeding may also occur as an adaptive mechanism to reduce flight costs ('lean and fit hypothesis'; reviewed in Schultner et al., 2013). The lean and fit hypothesis states that during optimum conditions energy stores are accumulated below the maximum possible level and that mass loss is an adaptive strategy to increase the efficiency of mobility during foraging, in particular in preparation for the chick-rearing period (e.g. Moreno, 1989, Coulson, 2010, Neto and Gosler, 2010). Previous studies have considered that if the body mass of individuals prior to the most energetically demanding period of the breeding season is positively related to breeding success, the fat and fit hypothesis is supported, and if it is negatively related, the lean and fit hypothesis is supported (Wendeln and Becker, 1999, Moe et al., 2002). Schultner et al. (2013) suggested that under optimum foraging conditions there is an upper limit on body mass, above which the costs of reduced mobility outweigh the benefits of increased body reserves. However, under unfavourable conditions, Schultner et al. (2013) suggested that there is a lower limit on body mass, below which the costs of low body reserves outweigh the benefits of improved mobility. Thus, it is possible that these two hypotheses may apply under different foraging conditions, with mass loss occurring adaptively when food is plentiful and maladaptively when food is scarce.

The lesser sandeel *Ammodytes marinus* (hereafter ‘sandeel’) dominates the mid-trophic level in many regions of the North Sea food web and its availability and quality is vital for the breeding success of marine top predators in those regions (e.g. Monaghan et al., 1992, Rindorf et al., 2000, Wanless et al., 2005). Data from the Wee Bankie region in the Firth of Forth, north-western (NW) North Sea have shown that young of the year (0 group) sandeels have been changing in two ways in recent years: firstly, they have been hatching earlier since the early 1990s (Frederiksen et al., 2011); secondly, their growth rate has been declining (Wanless et al., 2004, Frederiksen et al., 2011). The date at which these 0 group sandeels reach a given threshold length (55 mm) has become later over the last 25 years (Burthe et al., 2012), suggesting that the effect of the reduction in their growth rate is greater than the effect of their earlier hatching. Timing of breeding of sandeel-dependent seabird predators has not tracked this phenological change in their prey, resulting in reductions in sandeel energy content at peak periods of seabird energy demand (Burthe et al., 2012).

The black-legged kittiwake (hereafter 'kittiwake') is highly dependent on sandeels during the breeding season in many parts of the North Sea (Pearson, 1968, Harris and Wanless, 1990, Hamer et al., 1993, Lewis et al., 2001b, Wanless et al., 2007, but see Bull et al., 2004, Markones et al., 2009). Kittiwakes from the population breeding in the Wee Bankie shift their diet in response to the changing availability of different age classes of sandeels during the season (Lewis et al., 2001b, Bull et al., 2004). Early in the breeding season, adult (1+ group) sandeels are available in the water column as they feed on the abundant zooplankton, which are available due to the spring bloom, during the day and bury in the sea floor at night (Jensen et al., 2003). These 1+ group sandeels therefore form an important part of the diet of kittiwakes at this time. However, these 1+ group sandeels then retreat into the sandy sea floor (Rindorf et al., 2000) and are replaced in the kittiwake diet by 0 group sandeels, which have metamorphosed from larvae and recruited as young of the year, forming dense shoals at the sea surface during the day and burying in the sea floor at night. Thus these two prey types dominate the kittiwake diet in a reciprocal manner, with the timing of the switch from 1+ group dominance to 0 group dominance reflecting in part sandeel phenology and determining the predominant composition of the kittiwake diet during the breeding season. The kittiwake is one of the species that has seen a decline in prey quality during peak energy demand due to the reduced growth rate of 0 group sandeels, which dominate the diet during chick-rearing (Burthe et al., 2012). Clupeids (mostly sprat *Sprattus sprattus*) also form a small component of the diet of North Sea kittiwake populations in some years (Lewis et al., 2001b). Studies in both the Atlantic and the Pacific have shown that poor food availability can be detrimental to kittiwake breeding success. For example, Gill et al. (2002) showed that hatching, fledging and overall breeding success of kittiwakes at a Pacific colony were reliable indicators of food availability and Coleman et al. (2011) showed that reduced food availability resulted in lower kittiwake chick survival in an Atlantic population. Studies in the North Sea have shown that both 1+ group (Rindorf et al., 2000, Frederiksen et al., 2004, Daunt et al., 2008) and 0 group (Harris and Wanless, 1997, Lewis et al., 2001b, Daunt et al., 2008) sandeels are linked to breeding success, and that food availability during chick-rearing determines the rate at which kittiwakes provision their chicks (Galbraith, 1983). We aimed to address whether temporal change in diet composition has affected the breeding success of kittiwakes via adult body mass at a North Sea colony, the Isle of May. To our knowledge, no studies have explored the possible implications of diet composition on the body mass and breeding success of a top predator using long-term data across a range of environmental conditions. Specifically, we investigated how changes in the proportions of

sandeels and clupeids relate to the timing of breeding, adult body mass trajectory during incubation and chick-rearing, and hatching, fledging and overall breeding success, using a dataset spanning 14 years. We tested the following hypotheses: 1) the timing of the diet switch from 1+ group sandeels to 0 group sandeels has shown a trend over recent years; 2) diet composition relates to body mass change during incubation and chick-rearing; 3) body mass change in incubation and chick-rearing relates to hatching and fledging success, respectively.

2.3 Methods

2.3.1 Breeding phenology and success

The study was carried out on the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11‘ N, 02° 33’ W) from 1997–2010. To estimate hatching success, fledging success and overall breeding success, plots distributed around the island were monitored every five days throughout each breeding season (mean ± SD number of plots per year: 5 ± 1; number of nests monitored each year: 219 ± 70; range: 126–330). The monitoring plots were chosen so that birds could be observed with minimal disturbance; the nests at these plots were generally not accessible. Nests were coded according to breeding status: nest building (bringing in of new nesting material); incubating (presence of an egg in nest or adult sitting and assumed to be incubating); chick-rearing (presence of a chick in nest). An apparently occupied nest (AON) was a site where a complete nest had been built, whether or not an egg was laid (Walsh et al. 1995). These monitoring data were used to calculate annual values for median lay date (median across all nests within a year). Hatching success (the proportion of AONs that laid at least one egg, that went on to hatch at least one chick), fledging success (the proportion of AONs that hatched at least one chick, that went on to fledge at least one chick) and breeding success (the number of chicks fledged per AON) were also calculated. Although kittiwakes lay up to three eggs, calculations were made at the level of the nest, because clutch size and brood size were unavailable for these monitoring plots. A nest was recorded as failed once all eggs or chicks were dead or had disappeared from the nest, unless chicks had been recorded as ready for fledging, in which case they were assumed to have fledged. Readiness for fledging is recognised by the loss of all down feathers and the lengthening of the flight feathers beyond the tail feathers, with chicks likely to fledge 35 ± 4 days after hatching (pers. obs.). Clutch size was monitored once laying was complete using a different sample of nests where nest contents could be easily seen and disturbance to other species breeding nearby minimised (mean ± SD number of nests monitored: 258 ± 149; range: 25–509).

2.3.2 Adult body mass data

To obtain data on adult body mass at different breeding stages, breeding birds were captured from accessible nest sites on the island using a nylon noose attached to an 8 m pole. For individuals already carrying a British Trust for Ornithology (BTO) metal ring, the unique ring number was recorded, and remaining birds were ringed. Birds were weighed to the nearest gram using a Pesola spring balance (mean ± SD number of samples: 336 ± 129; range: 196–652; n = 4706 across all years; total number of individuals captured across all years = 2375; individuals captured between once and 18 times).

2.3.3 Dietary data

Upon capture some birds regurgitated a food sample (mean ± SD number of samples: 148 ± 59; range: 62–264; n = 2076 across all years). The regurgitates were collected to estimate inter-annual and within-season changes in biomass proportion of each prey type (Barrett et al., 2007). The samples were examined visually to identify the species or species group composition, weighed using a digital balance to the nearest 0.1 g and frozen for further analysis. Typically, the regurgitates were partially digested and therefore visual examination was not sufficient to determine prey composition. Therefore, samples had to be analysed in the laboratory as follows. Samples were frozen after collection in the field and were thawed at the time of analysis. Samples were placed in a saturated solution of biological washing powder (biotex) and heated at 40–50 °C for a minimum of 5 hours in order for any soft material to be digested. The otoliths and vertebrae that remained following this digestion process were identified using keys in Härkönen (1986) and Watt et al. (1997) and measured to ± 27 µm using a binocular microscope (25 x magnification). In the case of clupeids, fish lengths were back-calculated from otolith widths using regression equations in the literature (Härkönen, 1986); sprat equations were used because, whilst we could not identify to species level, clupeids in puffin and guillemot diets are almost exclusively sprats (Wilson et al., 2004, Harris and Wanless, 2011). In the case of sandeels, 0 group and 1+ group sandeels were distinguished from otolith macrostructure using counts of annuli (Lewis et al., 2001b). Age-specific (0 group and 1+ group) sandeel otolith length to fish length regression equations were calculated each year from intact fish obtained from flight-netting Atlantic puffins *Fratercula arctica* (see Lewis et al., 2001b for details). Fish lengths were converted into weights using regression equations in the literature in order to work out the proportion of the total mass of the regurgitation that each prey type contributed (Harris and Hislop, 1978, Hislop et al., 1991, Lewis et al., 2003).

From these estimates, the proportions of total biomass that comprised 1+ group sandeel, 0 group sandeel and clupeid were estimated for each food sample. During the study period, sandeels and clupeids together accounted for over 85 % of the incubation and chick-rearing diet in all years except the incubation period of 2007 and the chick-rearing period of 2008 (75 % and 73 % respectively; Fig. 2-1). All other diet types were excluded from our analyses as these were in negligible proportions.

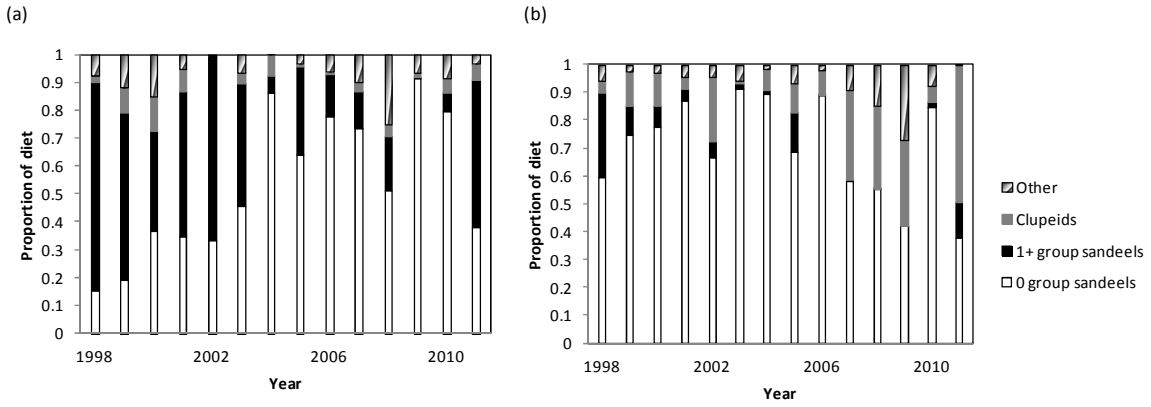


Fig. 2-1 Bars represent proportions of major prey types—0 group sandeels (white), 1+ group sandeels (black), clupeids (grey) and other (hatched)—found in the diet in each year of the study (1997–2010) in (a) incubation and (b) chick-rearing.

2.3.4 Statistical Methods

All statistical analyses were performed using R (version: 3.0.1, R Development Core Team, 2013). Values are presented as means ± standard error unless specified otherwise. All dates presented in the analyses were first recalculated relative to kittiwake median lay date; thus, annual median lay date represented day zero in each year. Hatching was estimated to take place on day 25, based on a 25-day incubation period (Baird, 1994, Coulson, 2011). Sufficient body mass and diet sample sizes were available in all years up to day 50 (i.e. 25 days into the chick-rearing period). Therefore, to standardise the time period across years, we analysed data up to that point. We considered mass at day 50 to represent fledging mass, although kittiwake chicks do not fledge until 35 ± 4 days old (pers. obs.). In the absence of data, we were not able to test how representative the estimates at day 50 were of true fledging mass. Furthermore, since the data on breeding phenology and success were collected on different individuals from the data on body mass and diet we assumed that both groups followed the same breeding schedule; for example, mass at laying refers to birds weighed when the plots used for recording phenology and breeding success indicated median laying date. However, this will have introduced some assignment errors in our analysis since in some cases diet samples and mass measurements

will have come from birds that had chicks during the period we defined as incubation (day 0–day 25) and, similarly, from birds that were still incubating during the period we defined as chick-rearing (day 25–day 50). Such assignment errors would tend to result in a reduction in the strength of the relationships between diet composition, body mass and hatching and fledging success. However, it was not possible for us to test this as details of the breeding stage of captured birds were not recorded in the dataset.

We used a quasi-binomial model to estimate when the switch from > 50 % 1+ group sandeels to > 50 % 0 group sandeels occurred in the kittiwake diet; this model accounted for proportional data and overdispersion in the data. To calculate the timing of the switch, we used the proportion of total sandeel biomass that was 0 group sandeel biomass (0 group biomass / (1+ group + 0 group biomass) in each sample as the response variable and the date on which the sample was collected, relative to the median kittiwake lay date for the corresponding year, as the explanatory variable. In 2008 the switch occurred before the annual diet sampling had begun, and therefore we disregarded the extrapolated model estimate for a switch date in this year. For the remaining years we used the switch date relative to kittiwake lay date estimated from the model (supplementary material S1) and from these we back-calculated the actual calendar date of each switch.

When calculating the overall proportion of each diet type during incubation and chick-rearing for each year, i.e. the average proportions across all diet samples between days zero and 25 and between days 25 and 50, log ratios were used to achieve normality in the data and to prevent values being constrained between zero and one. The use of log ratios also enabled us to include both the proportion of 1+ relative to 0 group sandeels and the proportion of clupeids relative to sandeels during chick-rearing in the same regression model. We did not examine the proportion of clupeids during incubation since they do not occur in notable proportions during this breeding stage (Fig. 2-1a). The following log ratios were used: proportion of 1+ relative to 0 group sandeels during incubation = log (proportion of 1+ group sandeel biomass during incubation / proportion of 0 group sandeel biomass during incubation); proportion of clupeids relative to sandeels during chick-rearing = log (proportion of clupeid biomass during chick-rearing / (proportion of 0 group sandeel biomass + proportion of 1+ group sandeel biomass during chick-rearing)); proportion of 1+ relative to 0 group sandeels during chick-rearing = log (proportion of 1+ group sandeel biomass during chick-rearing / proportion of 0 group sandeel biomass during chick-rearing).

To examine differences in adult body condition, we used mass rather than size-corrected mass because the high sample sizes meant that variation in mass due to size would not mask inter-annual variation in mean mass measurements. Furthermore, there is a lack of agreement in the literature about which, if any, methods for calculating body condition are recommended. Green (2001) showed that the use of residuals from a least squares linear regression of body mass against a linear measure of size can easily lead to Type I and Type II statistical errors. On the other hand, Schulte-Hostedde et al. (2005) argued that the use of residuals from least squares regression did satisfy critical assumptions, whilst Schamber et al. (2009) discouraged the use of any unverified indices of body condition, instead endorsing the use of raw body mass data.

In order to estimate values for mass at day zero (laying), day 25 (hatching) and day 50 (fledging), we used random effects models for each year of the study with body mass as the response variable, date as the explanatory variable and ring number as a random effect in order to account for repeated measures. We checked for autocorrelation by looking at residual plots but found no such evidence so we did not fit an autocorrelation term into the model (supplementary material S2 and S3). We compared constant, linear and broken stick models in order to assess the most appropriate model for each year (White et al., 2010b). We initially considered broken stick models with fixed break-points specified at day 25 as this marks the end of incubation and start of chick-rearing. We then compared these broken stick models with those where the break-point was allowed to vary between a value of day 4 and day 44. These lower and upper limits were set to reduce the likelihood of the model estimating the break-point at the very edge of the data where single or few data points can have unreasonable weighting; only 6 ± 3 % (mean ± SD; range: 0.4–12 %) of mass measurements in each year were collected prior to day 4 and after day 44. We selected models using a backward stepwise regression procedure and chose the model with the lowest Akaike Information Criterion (AIC) for each year (Burnham and Anderson, 2002; supplementary material S4, S5 and S6); however, in cases where there was more than one model within two units of each other, the models were considered equally valid (Hurvich and Tsai, 1989) and the model with the least number of explanatory variables was selected. In order to further reduce the chances of the variable broken stick model pushing the break-point to the edges of the data, we checked that, in cases where this model was favoured, there was sufficient spread of data for that specific year on both sides of the break-point. As a result of this, in 2002 (variable break-point = day 4; 10 % of data collected prior to day 4 in 2002) and 2005 (variable break-point = day 38; 11 % of data collected after day 38 in 2005) the model with the lowest AIC value (variable broken stick

model) was rejected. We therefore chose broken stick models with a fixed break-point for 2002 and 2005, because these had the next lowest AIC values.

To examine how diet has changed over the study period, we plotted trends over time (1997–2010) in sandeel switch date, kittiwake median lay date and switch date relative to median lay date. We also plotted further temporal trends as exploratory analyses, including composition of the kittiwake diet (including the proportions of 1+ group sandeels, 0 group sandeels and clupeids) in incubation and chick-rearing, adult body mass at laying, hatching and fledging, and hatching, fledging and breeding success. We used simple linear regression to analyse all temporal trends except those relating to measures of clutch size and success, where we used quasi-binomial generalized linear models to account for constrained data (maximum of three eggs per nest) and proportional data, respectively.

Before assessing the relationships between diet composition, adult body mass and breeding success, we explored how adult body mass relates to breeding activity at the start of the season. To examine the relationships between adult body mass at laying and timing of laying we used a linear regression. To examine the relationships between clutch size and timing of laying, and between adult body mass at laying and clutch size, we used quasi-binomial generalized linear models. Visual examination of the mass data suggested that there was a correlation between mass at laying and mass change between laying and hatching (Fig. 2-2a) and between mass at hatching and mass change between hatching and laying (Fig. 2-2c), with those years where mass was higher at the start of each stage (incubation and chick-rearing, respectively) showing greater mass loss during that stage. Therefore, when examining the relationship between change in adult body mass from laying to hatching and the proportion of 1+ relative to 0 group sandeels in incubation, we included mass at laying in a multiple linear regression. We also examined the relationship between adult body mass at hatching and the change in adult body mass during incubation to further assess how mass change related to mass at the start and end of this breeding stage. To assess whether hatching success was related to mass at hatching and clutch size, we used a quasi-binomial generalized linear model.

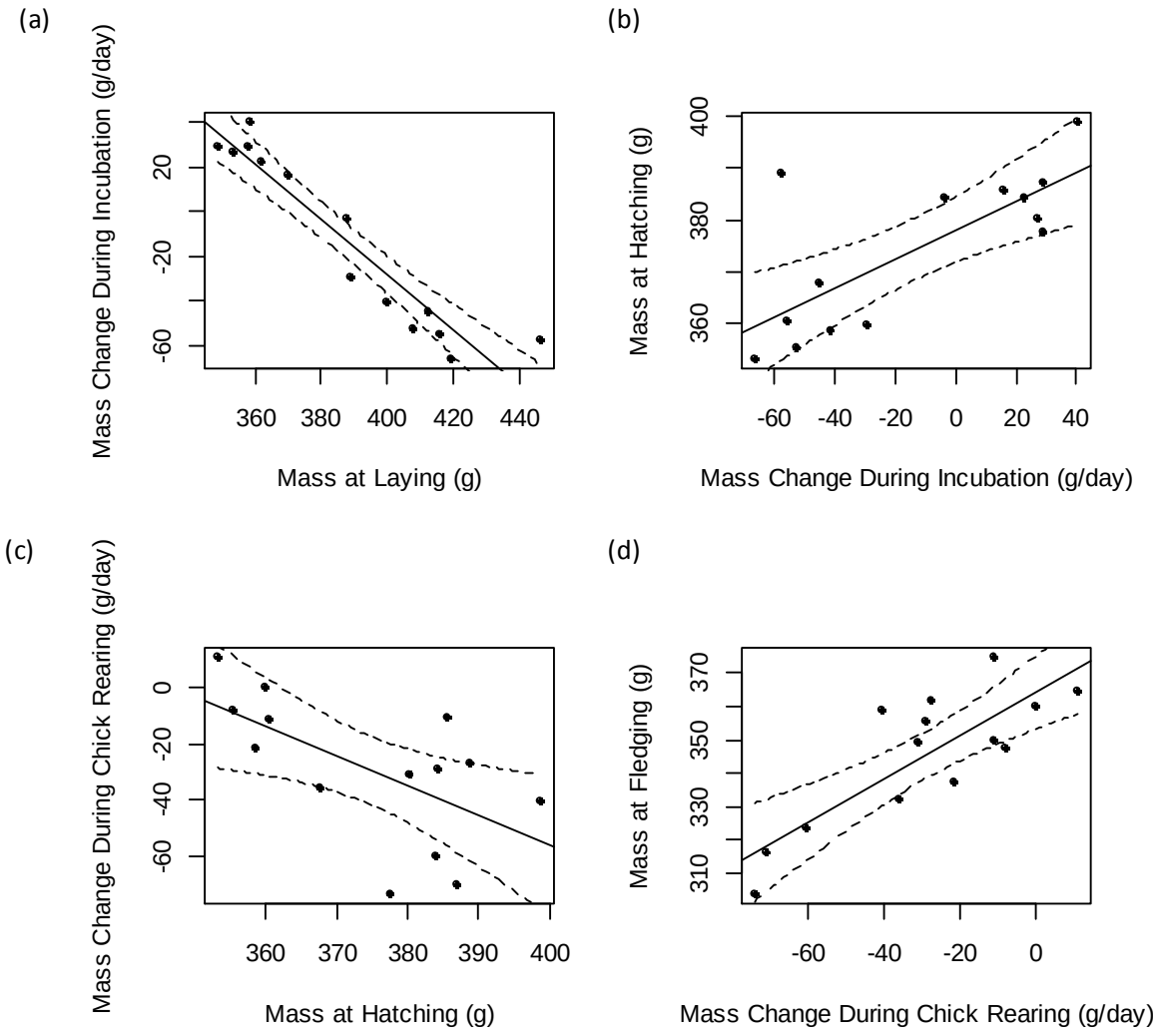


Fig. 2-2 Linear regression between (a) change in adult body mass during incubation and adult body mass at laying; (b) adult body mass at hatching and change in adult body mass during incubation; (c) change in adult body mass during chick-rearing and adult body mass at hatching; (d) adult body mass at fledging and change in adult body mass during chick-rearing. Each data point represents the mean for that year from the study period (1997–2010). Hatched lines represent 95 % confidence intervals.

To examine whether there was a relationship between the proportion of clupeids relative to sandeels during chick-rearing and the sandeel switch date, we used linear regression. To examine whether the change in adult body mass from hatching to fledging was related to the proportion of 1+ relative to 0 group sandeels during chick-rearing, the proportions of clupeids relative to sandeels and adult body mass at hatching, we used a multiple linear regression. We also examined the relationship between adult body mass at fledging and the change in adult body mass during chick-rearing to further assess how mass change related to mass at the start and end of this breeding stage. To examine whether fledging success was related to adult body mass at fledging and hatching success, we used a quasi-binomial generalized linear model. We examined whether overall breeding

success was related to adult body mass at hatching (i.e. prior to the energetically demanding chick-rearing period) and the change in mass between laying and hatching, using a quasi-binomial generalized linear model. Finally, we examined whether overall breeding success was associated with the timing of the diet switch relative to kittiwake laying. We report the models with the lowest Akaike Information Criterion (AIC) for each year (Burnham and Anderson, 2002); however, in cases where there was more than one model within two units of each other, the models were considered equally valid (Hurvich and Tsai, 1989) and the model with the least number of explanatory variables was chosen.

2.4 Results

2.4.1 Annual trends and trophic mismatch

Over the study period (1997–2010) the date of the switch from 1+ to 0 group sandeels has become earlier by an average of 1.1 ± 0.5 days per year (linear model: $t = 2.32$, $P = 0.04$, $R^2 = 0.33$; Fig. 2-3a). The timing of kittiwake laying has varied with no significant trend (linear model: $t = 1.51$, $P = 0.16$, $R^2 = 0.16$; Fig. 2-3b). The timing of the switch in sandeels relative to kittiwake laying has become earlier by 1.7 ± 0.6 days per year (linear model: $t = 2.59$, $P = 0.03$, $R^2 = 0.38$; Fig. 2-3c). This shift in switch date means that the kittiwake diet has comprised increasing proportions of 0 group relative to 1+ group sandeels during incubation (linear model: $t = 2.80$, $P = 0.02$, $R^2 = 0.40$; Fig. 2-1a), but this relationship does not hold up during chick-rearing (linear model: $t = 1.55$, $P = 0.15$, $R^2 = 0.18$; Fig. 2-1b). During chick-rearing, the proportion of clupeids relative to sandeels has shown a marginal increase over the study period (linear model: $t = 1.95$, $P = 0.07$, $R^2 = 0.24$; Fig. 2-1b).

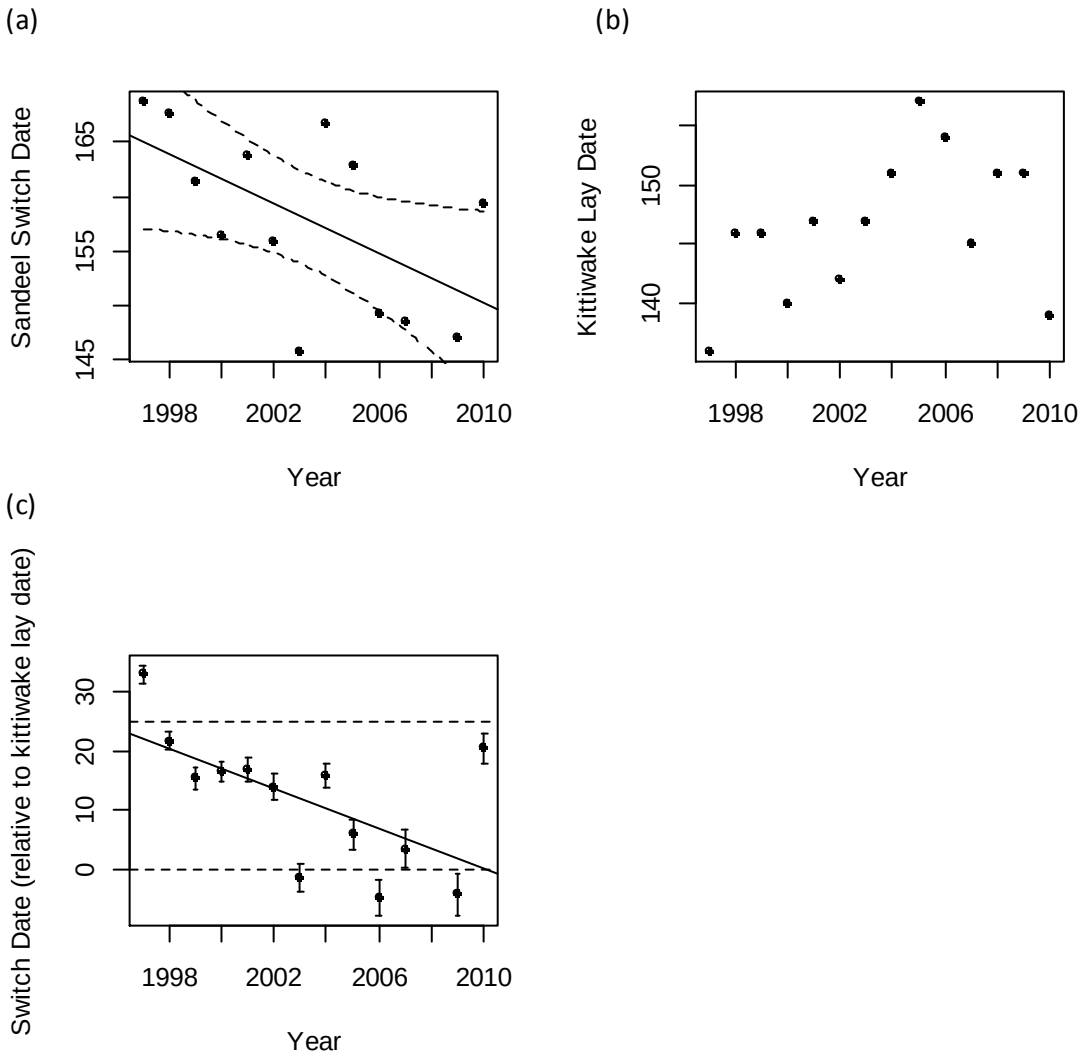


Fig. 2-3 (a) Change in sandeel switch date (Julian date), estimated from quasi-binomial model, over time (1997–2010; excluding 2008 as the switch occurred before diet monitoring had begun; hatched lines represent 95 % confidence intervals), (b) change in median kittiwake lay date (Julian date) over time and (c) model output of change in sandeel switch date relative to kittiwake lay date over time (mean ± SE). The horizontal hatched lines mark the timing of laying and the timing of hatching. The proportion of 1+ group and 0 group sandeels are reciprocals of one another.

On average across the study period, adult body mass declined during the breeding season (mean ± SD: laying 388 ± 30 g; range: 348–447 g, hatching 374 ± 15 g; 353–399 g; fledging 345 ± 20 g; 304–375 g); however, there were no temporal trends in body mass at laying, hatching and fledging, or body mass change during incubation and chick-rearing (Table 2-1 and Fig. 2-4a). Clutch size (linear model: t = t = 0.72, P = 0.49), hatching success (quasi-binomial generalized linear model: t = 1.51, P = 0.16; Fig. 2-4b), fledging success (quasi-binomial generalized linear model: t = 0.77, P = 0.45; Fig. 2-4b) and breeding success (quasi-binomial generalized linear model: t = 0.60, P = 0.56; Fig. 2-4b) have also shown no temporal trends during the study period.

Table 2-1 Correlation matrix for diet, body mass and breeding parameters (YR = year; SS = sandeel switch; SI = proportion of 1+ group sandeels relative to 0 group during incubation; CC = proportion of clupeids relative to sandeels during chick-rearing; SC = proportion of 1+ group sandeels relative to 0 group during chick-rearing; ML = mass at laying; MH = mass at hatching; MF = mass at fledging; LD = lay date; CS = clutch size; HS = hatching success; FS = fledging success) showing r values. Values in bold are significant.

	YR	SS	SI	CC	SC	ML	MH	MF	LD	CS	HS
SS	**-0.62**										
SI	**-0.63**	**0.94**									
CC	0.49	-0.07	0.01								
SC	-0.42	**0.80**	**0.68**	-0.03							
ML	-0.39	0.49	**0.67**	-0.10	0.24						
MH	0.31	-0.33	-0.36	-0.14	-0.14	-0.49					
MF	-0.16	-0.48	0.26	-0.20	**-0.55**	0.31	-0.05				
LD	0.40	**-0.70**	**-0.61**	0.18	**-0.60**	**-0.65**	0.29	0.24			
CS	-0.20	**0.60**	0.41	-0.01	0.39	**0.54**	-0.28	-0.07	**-0.61**		
HS	0.42	-0.18	-0.13	-0.04	-0.18	-0.15	**0.75**	-0.09	-0.10	-0.02	
FS	-0.22	-0.18	0.06	-0.33	-0.11	0.06	0.32	**0.54**	-0.02	0.27	0.25

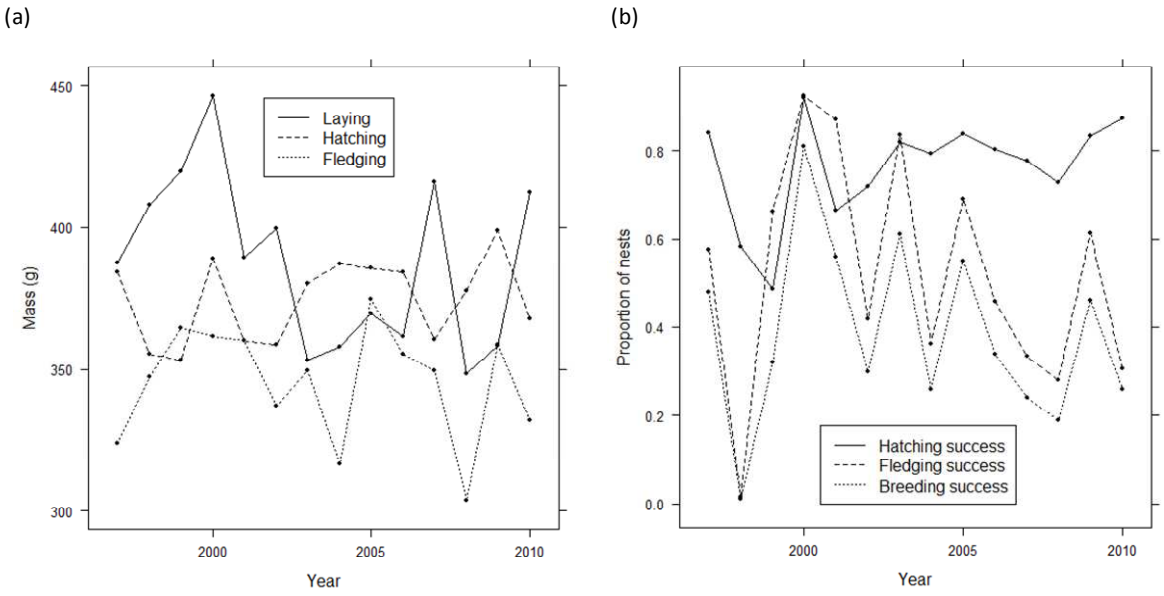


Fig. 2-4 (a) Change in adult body mass at laying (continuous line), hatching (hatched line) and fledging (dotted line) over time (1997–2010); (b) trends in breeding success over time: hatching success (continuous line), fledging success (hatched line) and breeding success (dotted line).

2.4.2 Effects of diet on body mass in incubation and hatching success

Mean annual clutch size, starting mass and timing of laying were all correlated (Table 2-1). Adult body mass at laying was lower in years of later laying dates (linear model: t = 2.99, P = 0.01, R^2 = 0.43), smaller clutches were laid in years of later laying dates (linear model: t = 2.66, P = 0.02; Fig. 2-5a) and, accordingly, smaller clutches were laid in years of lower adult body mass at laying (linear model: t = 2.20, P = 0.05; Fig. 2-5b). The change in adult

body mass from laying to hatching was not related to the proportion of 1+ group relative to 0 group sandeels during incubation (linear model: t = 0.17, P = 0.87; Fig. 2-5c), once laying mass had been accounted for (t = 7.04, P < 0.0001; full model: $F_{2,11} = 46.97$, $R^2 = 0.90$; Fig. 2-1a). In years when birds had high mass at hatching they had lost less mass during incubation (linear model: t = 3.89, P = 0.002, $R^2 = 0.56$; Fig. 2-1b). Years of lower hatching success were associated with years of lower adult body mass at hatching (quasi-binomial generalized linear model: t = 3.80, P = 0.003; Fig. 2-5d), with 0.06 ± 0.002 fewer chicks hatched for every 10 g decrease in adult body mass at hatching; however, years of lower hatching success were not associated with years of smaller clutches (t = 0.95, P = 0.36).

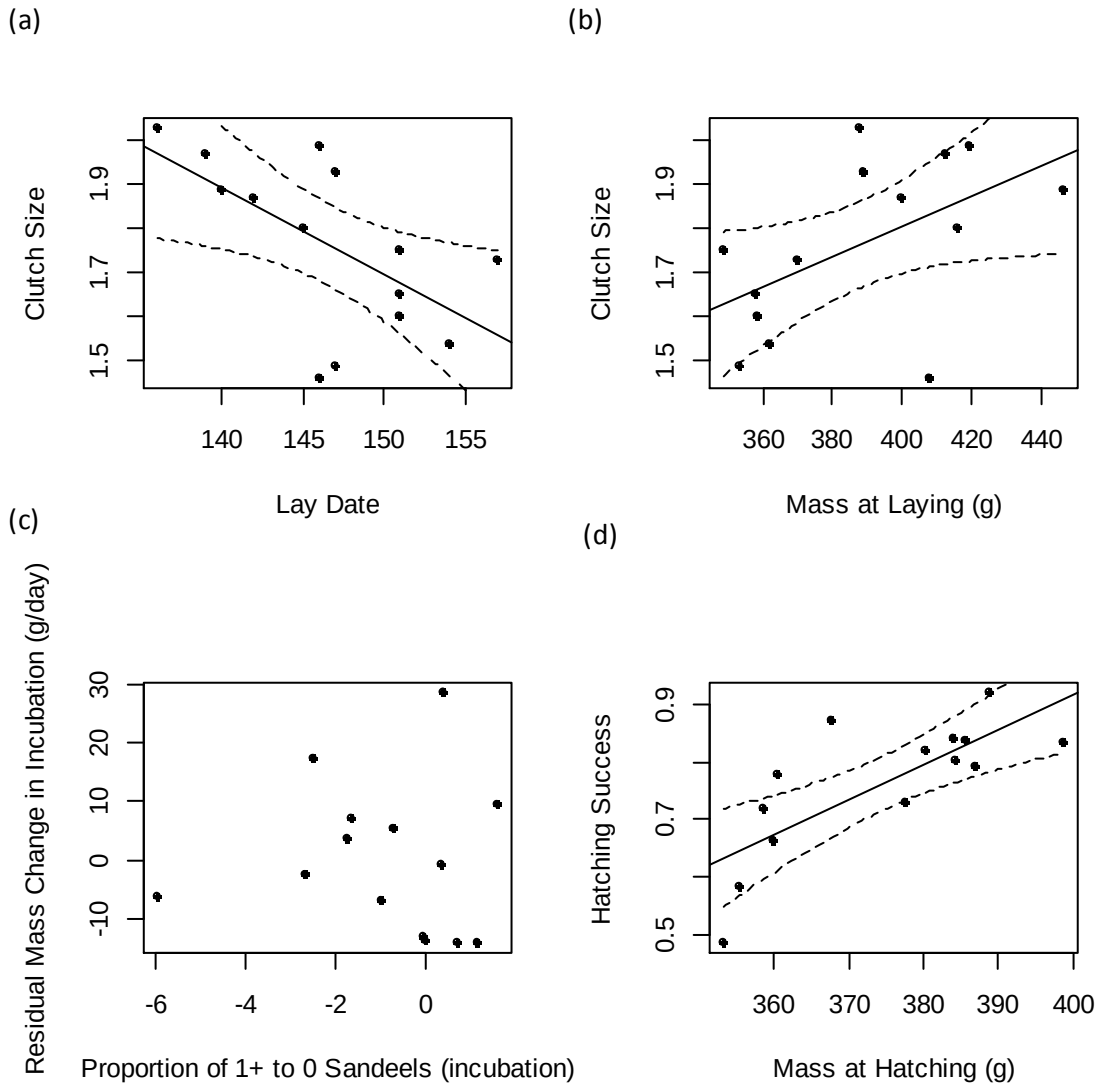


Fig. 2-5 Linear regression between (a) clutch size and lay date; (b) clutch size and adult body mass at laying; (c) residual change in adult body mass during incubation and the proportion of 1+ group relative to 0 group sandeels during incubation (lower numbers indicate higher proportions of 1+ group and lower proportions of 0 group sandeels; zero indicates equal proportions of each age group), having corrected for laying mass; (d)

hatching success and adult body mass at hatching. Each data point represents the mean for that year from the study period (1997–2010). Hatched lines represent 95 % confidence intervals.

2.4.3 Effects of diet on body mass in chick-rearing and fledging success

The proportion of clupeids relative to sandeels during chick-rearing was not related to the timing of the sandeel switch (linear model: $t = 0.25$, $P = 0.81$, $R^2 < 0.01$). Years of greater adult body mass loss during chick-rearing were marginally associated with years of higher proportions of 1+ group relative to 0 group sandeels ($t = 2.15$, $P = 0.06$; Fig. 2-6a), once hatching mass had been accounted for ($t = 3.78$, $P = 0.004$; full model: $F_{2,10} = 8.48$, $R^2 = 0.63$; Fig. 2-1c). The proportion of clupeids relative to sandeels was removed from the model during model selection (Fig. 2-6b). In years when birds had higher mass at fledging they had lost less mass during chick-rearing (linear model: $t = 4.91$, $P < 0.001$, $R^2 = 0.67$; Fig. 2-1d). Years of lower fledging success were associated with years of lower adult body mass at fledging (quasi-binomial generalized linear model: $t = 2.17$, $P = 0.05$; Fig. 2-6c), but years of lower fledging success were not associated with years of lower hatching success ($t = 1.14$, $P = 0.28$). Overall breeding success was positively related to adult body mass at hatching (quasi-binomial generalized linear model: $t = 2.35$, $P = 0.04$; Fig. 2-6d), but was unrelated to the change in mass between laying and hatching ($t = 1.44$, $P = 0.18$). Breeding success was not correlated with the timing of the sandeel switch relative to kittiwake laying (quasi-binomial generalized linear model: $t = 0.48$, $P = 0.64$). Most failures occurred during chick-rearing and therefore breeding success was largely driven by survival rates of young during that period (Fig. 2-4b).

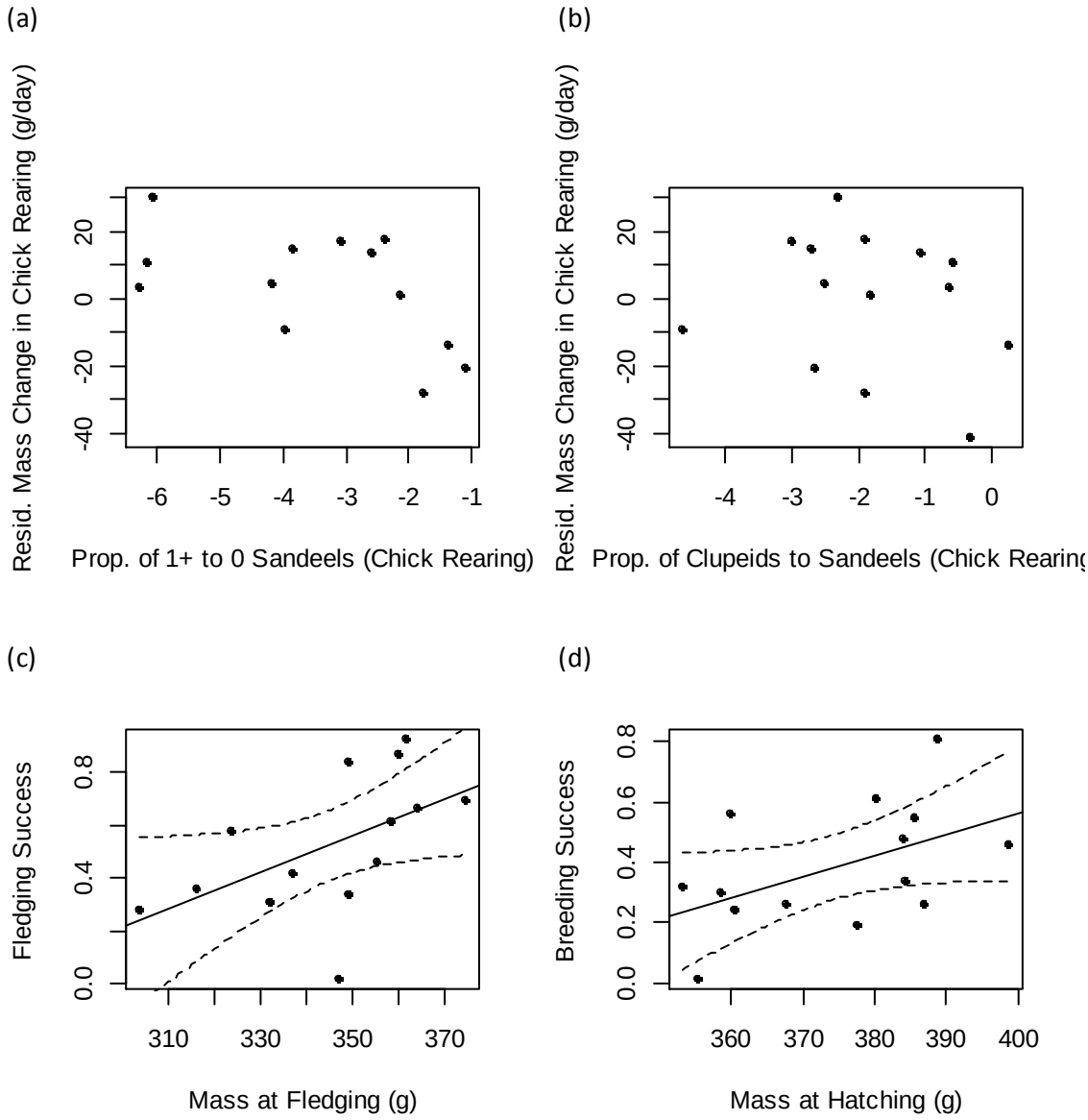


Fig. 2-6 Linear regression between (a) residual change in adult body mass during chick-rearing and the proportion of 1+ group relative to 0 group sandeels during chick-rearing (lower numbers indicate higher proportions of 1+ group and lower proportions of 0 group sandeels; zero indicates equal proportions of each age group), having corrected for hatching mass; (b) residual change in adult body mass during chick-rearing and the proportion of clupeids relative to sandeels during chick-rearing, having corrected for hatching mass; (c) fledging success and adult body mass at fledging; (d) breeding success and adult body mass at hatching. Each data point represents the mean for that year from the study period (1997–2010). Hatched lines represent 95 % confidence intervals.

2.5 Discussion

Our findings suggest for the first time in a long-term dataset that diet composition during chick-rearing is related to changes in adult body mass, which in turn positively relate to breeding success. Whilst variation in diet composition during incubation was unrelated to change in adult body mass during this stage, diet composition during chick-rearing was

marginally related to change in adult body mass. Adult body mass at the time of hatching and fledging was positively related to hatching and fledging success, respectively, suggesting that changes in diet composition may have implications for the fledging success of top predators, mediated via changes in adult body mass. Our dataset is limited by the lack of individual-level data which means that average values for each year of the study were used, resulting in a relatively small sample size of 14 years. Therefore, we must be conservative in the conclusions drawn from the results of this study.

Previous studies of phenological change in the North Sea have focussed on timing of breeding of seabirds relative to the phenology of 0 group sandeels (Frederiksen et al., 2011, Burthe et al., 2012). Growth rates of 0 group sandeels have declined since the mid-1990s such that the date at which they reach a threshold length has become later. Whilst there has been a long-term trend towards later kittiwake breeding (Wanless et al., 2009), this has not been sufficient to match the changes in 0 group sandeel length (Burthe et al., 2012). We used an integrated measure of the timing of appearance of both age classes of sandeel in the kittiwake diet. We found that the switch from 1+ to 0 group sandeels in the kittiwake diet has been occurring earlier in the kittiwake breeding season since the mid-1990s. It is perhaps surprising that 0 group sandeels are appearing in the kittiwake diet earlier, given that their growth rate is declining, since this suggests that the size of 0 group sandeels when they first appear in the diet is considerably smaller than it was at the start of the study. It is therefore possible that the timing of the switch is determined by the phenology of 1+ group sandeels such that they are becoming unavailable in the water column earlier. This would mean that whilst later breeding might benefit kittiwakes by increasing the size and quality of 0 group sandeels available to them during chick-rearing, later breeding might also result in lower proportions of 1+ group sandeels in the diet earlier in the season. Changes in the timing of appearance of 1+ group and 0 group sandeels in the kittiwake diet may be indicative of changes in the phenology of sandeels or changes in the relative profitability of the two age classes of sandeel to breeding kittiwakes. Specifically, the increasing divergence in the timing of laying in Isle of May breeding kittiwakes and the timing of the shift from 1+ group sandeels to 0 group sandeels in the kittiwake diet, may suggest trophic mismatch between kittiwakes and their primary prey source. However, further data on the phenology of sandeels and the timing of their availability in the NW North Sea is necessary.

Both et al. (2009) predicted that species occupying higher trophic levels show less phenological change than their prey. Seabirds time laying in accordance with a number of

constraints and optimisations: firstly, birds are constrained photoperiodically as to the timing of the onset of breeding (Dawson, 2008); secondly, chicks that fledge early have higher survival rates (Harris et al., 2007); thirdly, the timing of laying determines whether peak food demands later in the breeding season will coincide with peak food availability (Visser et al., 1998). Therefore, kittiwakes may be facing fitness trade-offs or physiological constraints that are further limiting their ability to track changes in sandeel phenology (Burthe et al., 2012).

1+ group sandeels are important for the diet of adult kittiwakes before laying and during incubation (Lewis et al., 2001b). This may be due to their predominant availability during this part of the season and their higher energy content compared to 0 group sandeels (Hislop et al., 1991). During our study period, in years when there were more 1+ group sandeels in the diet of breeding kittiwakes during incubation, body mass was higher at laying and laying occurred earlier. It is possible that in years when there were higher proportions of 1+ group sandeels in the diet during incubation, there were also greater proportions available prior to laying, allowing adults to build up greater reserves and lay earlier (e.g. Barrett, 2004). Alternatively, if the period of availability of 1+ group sandeels is constant, higher proportions during incubation may mean lower availability pre-laying, with adults relying on alternative prey sources. Our results suggest that the timing of availability of the different age classes of sandeels may be important for adult body mass at the start of breeding. However, in order to better understand the inter-annual variation in lay date and mass at laying, pre-laying diet and mass data would be required. Pre-laying mass data would also be useful to reduce the potential limitations and inaccuracies of estimating mass at laying (day 0) from the edges of the data ranges available for each year of the study.

We showed that years of higher adult body mass at hatching also had higher hatching success; however, this was not determined by diet composition. Previous studies have shown that as 1+ group sandeels start to disappear out of the water column, 0 group sandeels become increasingly important in the kittiwake diet, with an earlier appearance of 0 group sandeels reducing the likelihood of a gap in prey availability (Rindorf et al., 2000, Lewis et al., 2001b). However, we found no significant effect of diet composition during incubation on change in adult body mass during this stage. Instead, we can speculate that the abundance of prey, its proximity to the colony or its size and quality may determine adult body mass and hatching success. Reductions in the calorific value of prey can compromise adult body mass and breeding success ('junk food hypothesis'; Alverson,

1992, see also Rosen and Trites, 2000, Litzow and Piatt, 2003, Osterblom et al., 2008). Therefore, detailed data on the availability and quality of the different age classes of sandeels during incubation would be required to better understand the importance of each prey type to incubating kittiwakes.

Whilst we were unable to distinguish between the composition of adult kittiwake diet and chick diet during the chick-rearing period, we made the assumption that the species composition reflected in adult regurgitations would likely be indicative of both adult and chick diets. In addition, we assumed that any difficulties in finding food of sufficient quality for chicks and of sufficient quantity for self-maintenance would have fitness consequences reflected in adult body mass and subsequent breeding success. The use of regurgitations for assessing diet composition is also limited by the partial or full digestion of certain prey types and not others, which can result in a biased indication of total diet composition (Barrett et al., 2007). Despite these limitations, our results support the findings of previous studies indicating an importance of 0 group sandeels during the chick-rearing stage for breeding kittiwakes (e.g. Harris and Wanless, 1997, Lewis et al., 2001b, Daunt et al., 2008). We showed that the importance of 0 group sandeels for fledging success may be mediated by adult body mass during the chick-rearing period. This is likely to be partly due to the abundance of 0 group sandeels in the water column during this period, despite the lower calorific value of 0 group sandeels compared to 1+ group sandeels (Hislop et al., 1991). 0 group sandeels may also be closer to the colony, more easily captured by surface-feeding kittiwakes, or more easily facilitated through being driven to the sea surface by plunge-diving birds such as auks (e.g. Camphuysen and Webb, 1999, Camphuysen et al., 2006).

Whilst 1+ group sandeels are more calorific than 0 group sandeels, clupeids are more calorific than either age group of sandeel (Hislop et al., 1991). Therefore, if clupeids are sufficiently abundant and attainable, they may be a beneficial prey source. As well as energy differences among prey species, inter-annual variation in prey quality is apparent within species, supporting the junk food hypothesis. Wanless et al. (2005) found that in a year of poor breeding success, the calorific value of sandeels and sprat was less than 25 % of that recorded in the region in previous years (Hislop et al., 1991). This suggests that both the timing of availability and the quality of the various prey types utilised by kittiwakes are important for their breeding success. However, the highly calorific clupeid (Hislop et al., 1991) is not abundant in the diet of Isle of May breeding kittiwakes. Whilst we show that clupeids have been appearing in higher proportions in the diet during chick-

rearing in recent years, we found no relationship between the proportion of clupeids relative to sandeels and changes in kittiwake body mass during chick-rearing. Our results may suggest a lack of support for the junk food hypothesis; however, detailed data on prey quality and availability would be necessary to confirm this. The low proportions of clupeids in the kittiwake diet may be explained by their unavailability in the kittiwake foraging grounds, further distance from the colony or lower accessibility for surface-feeding birds. It is possible that the recent reduction in the availability and quality of 0 group sandeels is forcing kittiwakes to utilise clupeids as an alternative prey type (Frederiksen et al., 2013). Alternatively, clupeids may become more available to kittiwakes in some years independent of changes in sandeel availability. However, regardless of the mechanism, the proportion of clupeids was not an important determinant of adult body mass or breeding success, which may suggest that they are an adequate alternative prey source. The success of seabirds breeding in changing and unpredictable environments is determined largely by the degree of dependence on specific prey types and the feasibility of utilising alternative prey types (Croxall et al., 1999). Further years of study may shed light on whether clupeids are becoming consistently more common in the kittiwake diet and, if so, how this alternative diet type might impact breeding success in the future.

The extent to which adult body condition can be maintained is a key contributor to the resilience of seabirds in the face of adverse environmental conditions, with reductions in body condition mediating the effect of low prey availability on the breeding success of top predators (e.g. Monaghan et al., 1989, Hamer et al., 1993, Harding et al., 2011). The body mass of breeders must be maintained above a certain limit, otherwise breeding will be abandoned (e.g. incubating blue petrels *Halobaena caerulea*; Chaurand and Weimerskirch, 1994, Numata et al., 2000, Gauthier-Clerc et al., 2001, chick-rearing Adélie penguins *Pygoscelis adeliae*; Ballard et al., 2010). Variation in the body mass of seabirds has rarely been studied over multiple years (herring gull *Larus argentatus*; Coulson et al., 1982, Arctic tern *Sterna paradisaea*; Monaghan et al., 1989, Monaghan et al., 1992, petrels; Chastel et al., 1995). We consistently found across a long-term dataset that adult body mass at the end of each stage of the breeding season was positively related to the success of that stage, suggesting that low body mass was maladaptive. In addition, years of higher body mass at hatching, i.e. prior to the energetically demanding chick-rearing period, were associated with years of higher breeding success. These results may be in line with the fat and fit hypothesis; however, individual-level data would be necessary to test this fully. It is possible that in years of poor conditions birds lose mass due to the energetic costs of breeding, whilst in good conditions birds lose mass in order to reduce flight costs

(Schultner et al., 2013). However, we did not find any evidence to support this on a population-level across 14 years of varying environmental conditions. Some seabirds, for example the yellow-nosed albatross *Diomedea chlororhynchos*, are able to continue provisioning their chicks at low rates during poor foraging conditions, due to their wide safety margin in terms of body reserves (Weimerskirch et al., 2000). Kittiwakes, on the other hand, have a smaller safety margin, compared to larger and longer-lived seabirds, which makes them more likely to desert when conditions are unfavourable and body mass declines (e.g. Furness and Tasker, 2000).

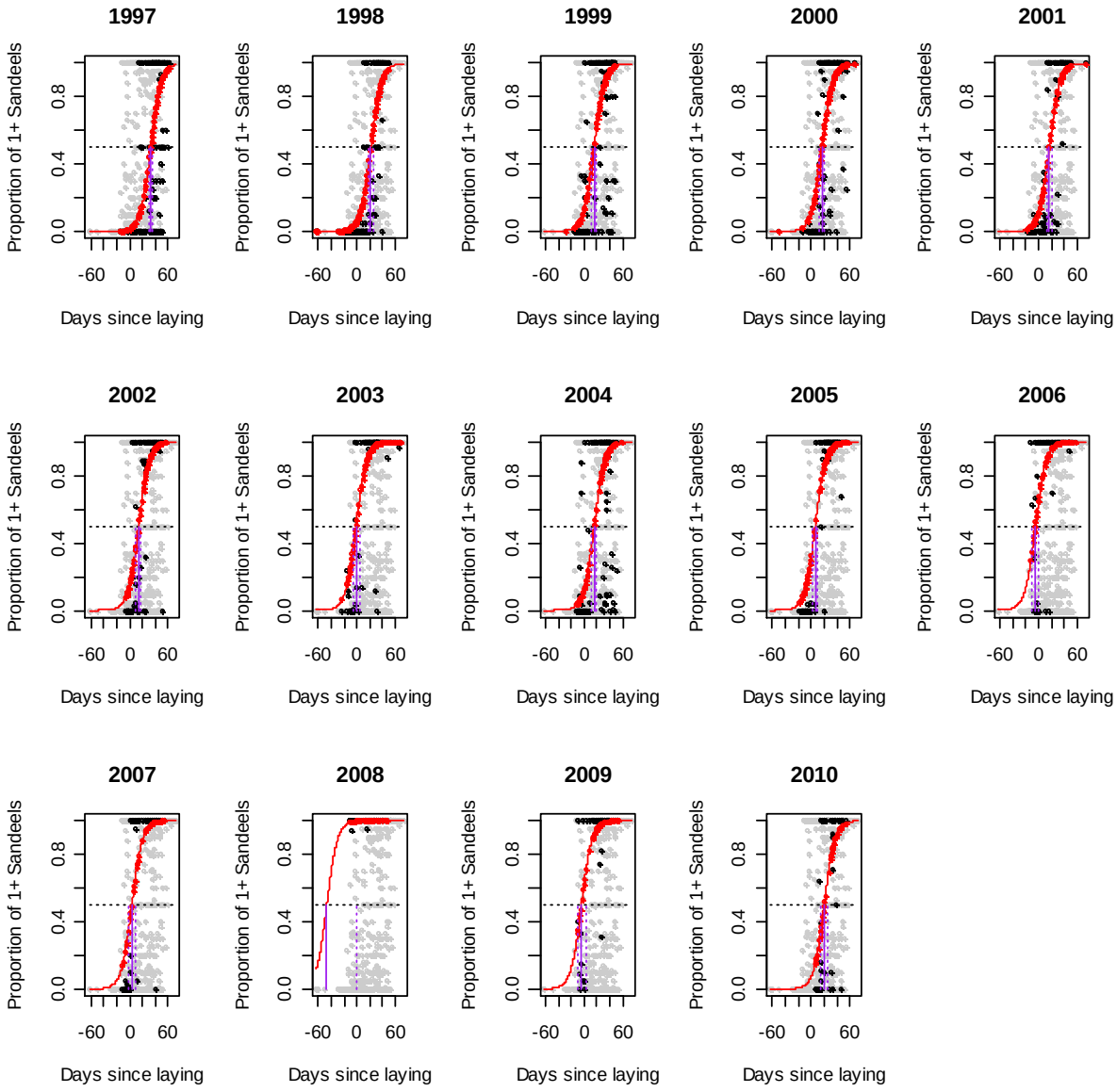
Our results showed a negative correlation between change in adult body mass during each stage of breeding and mass at the start of each stage. The strong negative correlation between the change in body mass during the incubation period and mass at laying could be explained by the fact that years of high mass at laying were correlated with years of larger clutches; therefore in those years females may have invested more energy into the start of the breeding season, resulting in a decline in mass during incubation. However, this is unlikely to explain the pattern seen in a sample of both males and females. Ballard et al. (2010) showed across 10 breeding seasons that individual Adélie penguins starting the season heavy, lost more mass and provisioned more food to their chicks, whilst those starting off light, recovered their body condition and provisioned less food to their chicks. We showed a similar pattern of mass change but on a population-level. Our results may show on a population-level the condition-dependent life-history decisions of adults that have previously been demonstrated in the literature (e.g. Chastel et al., 1995, Weimerskirch et al., 2001, Ballard et al., 2010), which allow individuals in poor condition to gain body mass at the expense of their breeding effort and those in good condition to lose body mass and benefit their breeding attempt.

An early study of Isle of May kittiwakes showed that, when chick-rearing was constrained by food availability, adults were limited in the rate at which they could provision their chicks (Galbraith, 1983). In our study breeding failure tended to occur during chick-rearing, resulting in a close correlation between fledging success and breeding success, which suggests that food availability may have been a limiting factor during this period of high energetic demands. However, there was no correlation between clutch size, hatching success and fledging success. The lack of any correlation between these breeding stages suggests that the outcome of a breeding season may not always be accurately predicted from measures such as clutch size that are taken early in the season. Instead, changes in prey availability and quality during the chick-rearing period may be of

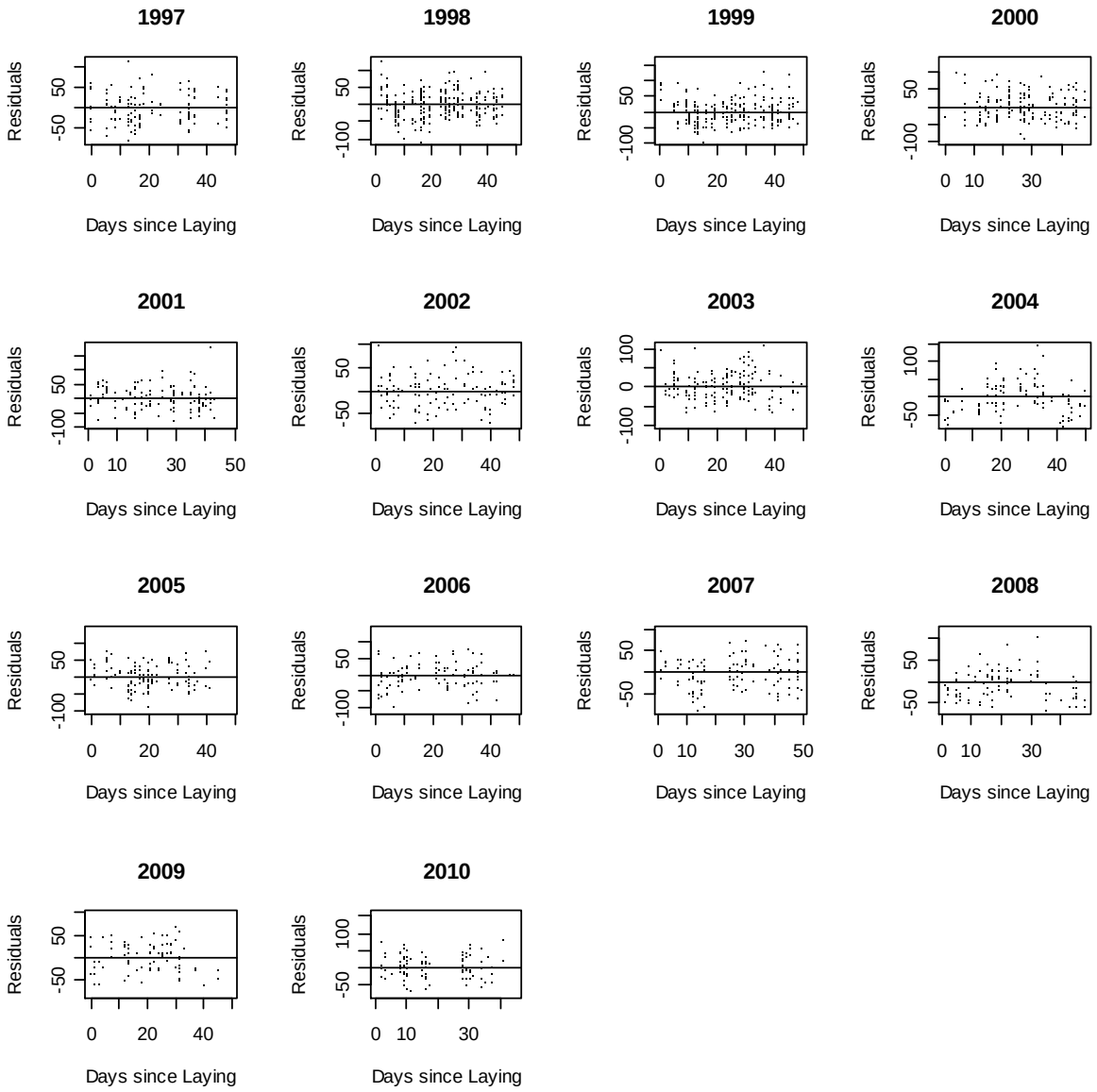
primary importance in contributing to inter-annual variation in breeding success. One limitation of long-term population-level studies is that they are often restricted to non-causal correlations. Non-causal correlations are in danger of being spurious, if confounding variables are in fact driving the relationships. However, what we can conclude from this study is that, across a range of environmental conditions, changes in diet composition during chick-rearing are associated with changes in the body mass of a marine top predator, with higher body mass at the end of the season being subsequently associated with higher breeding success.

2.6 Supplementary material

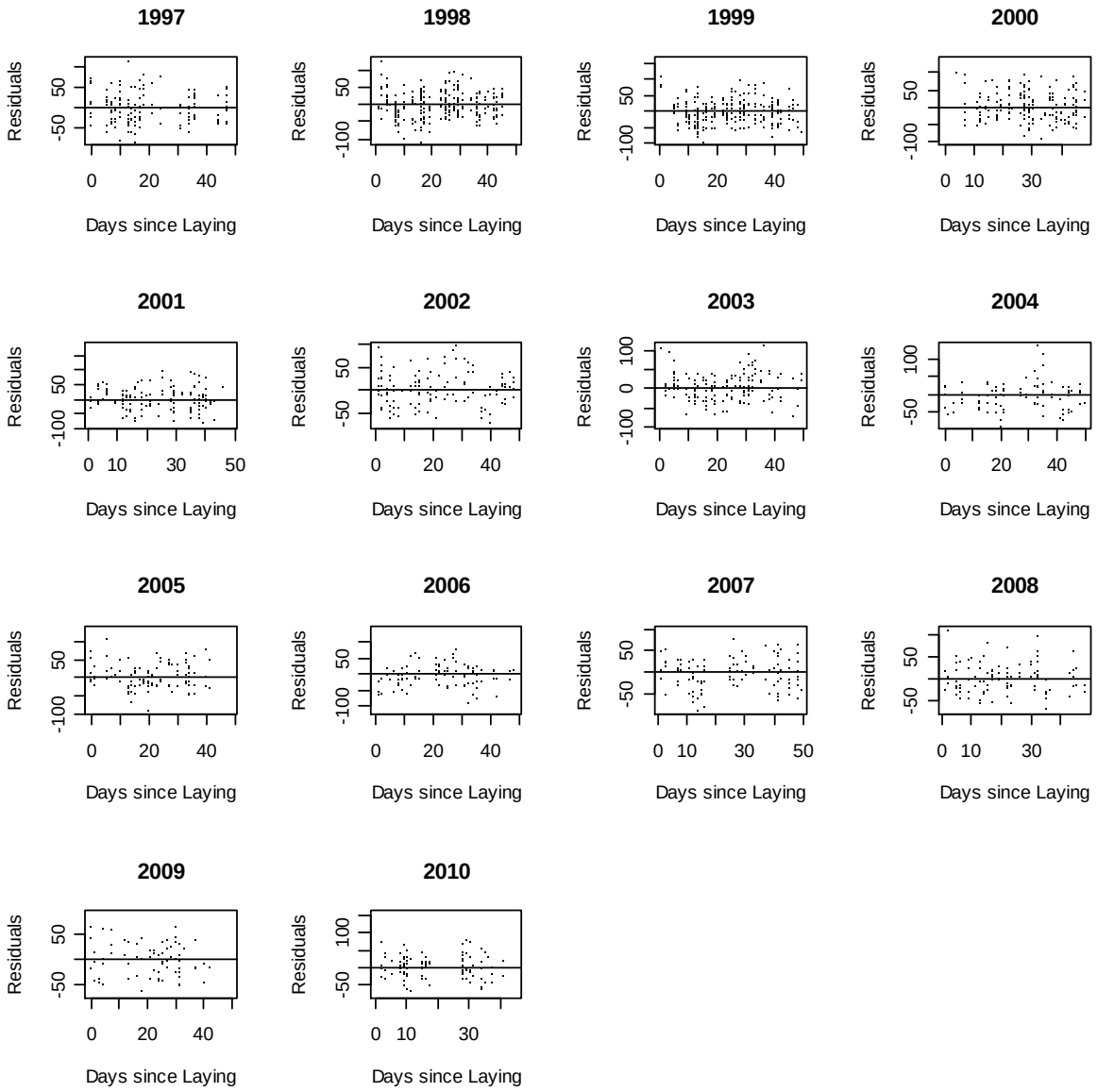
S-1 Proportional diet data for all years (grey) and for individual years (black) with fitted values (red) against time relative to median lay date. Fitted values estimated from quasi-binomial model.



S-2 Residual plots of body mass data: linear models.



S-3 Residual plots for body mass data: Broken stick models.

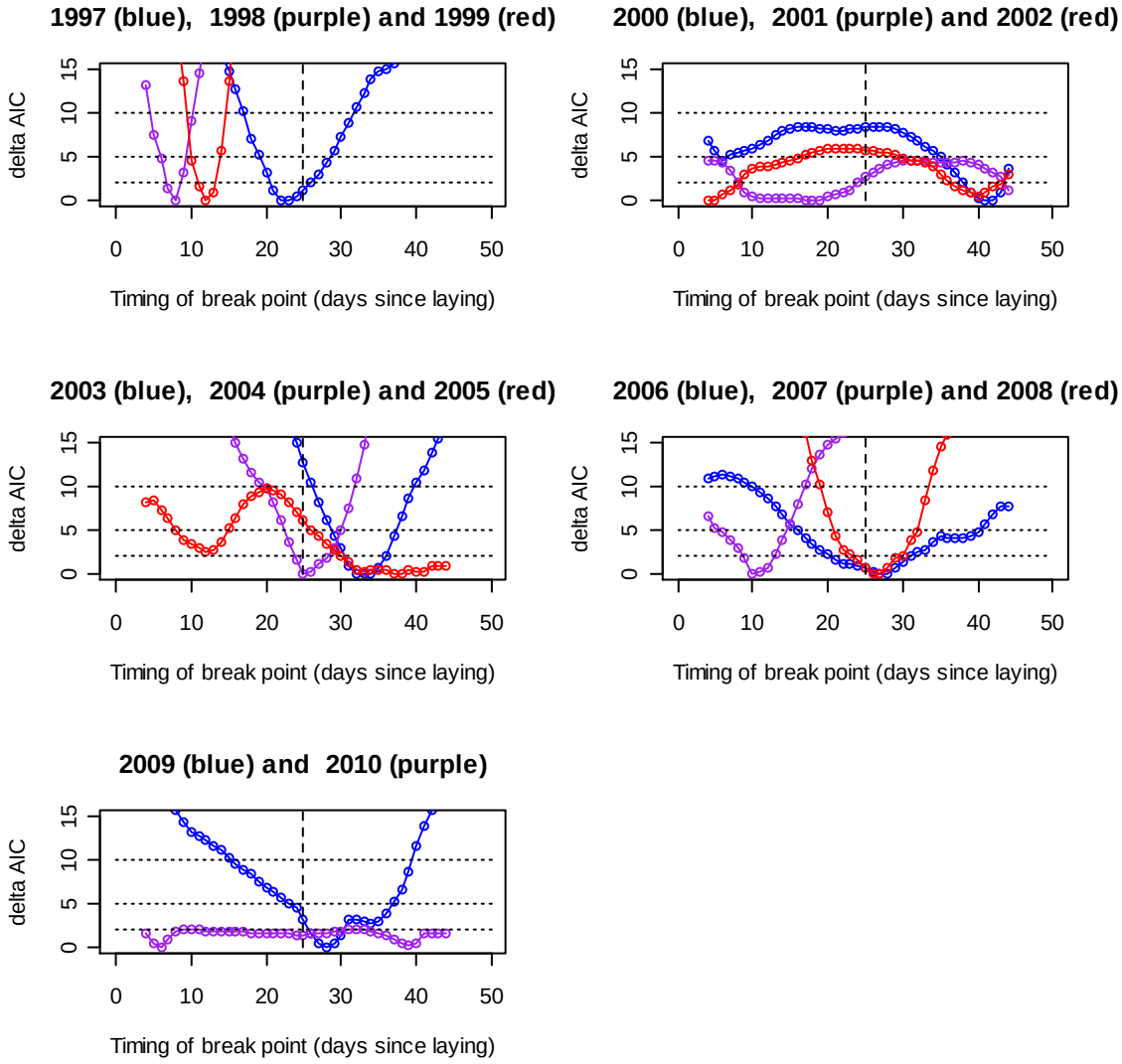


S-4 Break-points, intercepts, gradients and AIC values for each of the four body mass models tested (constant, linear, broken stick with fixed break-point and broken stick with variable break-point) for each year of the study (1997–2010). Models with the lowest AIC values (and those < 2 units from the lowest AIC value) are shown in bold. The models chosen, based on lowest AIC values after checking for sufficient data distribution on both sides of a variable break-point, are underlined.

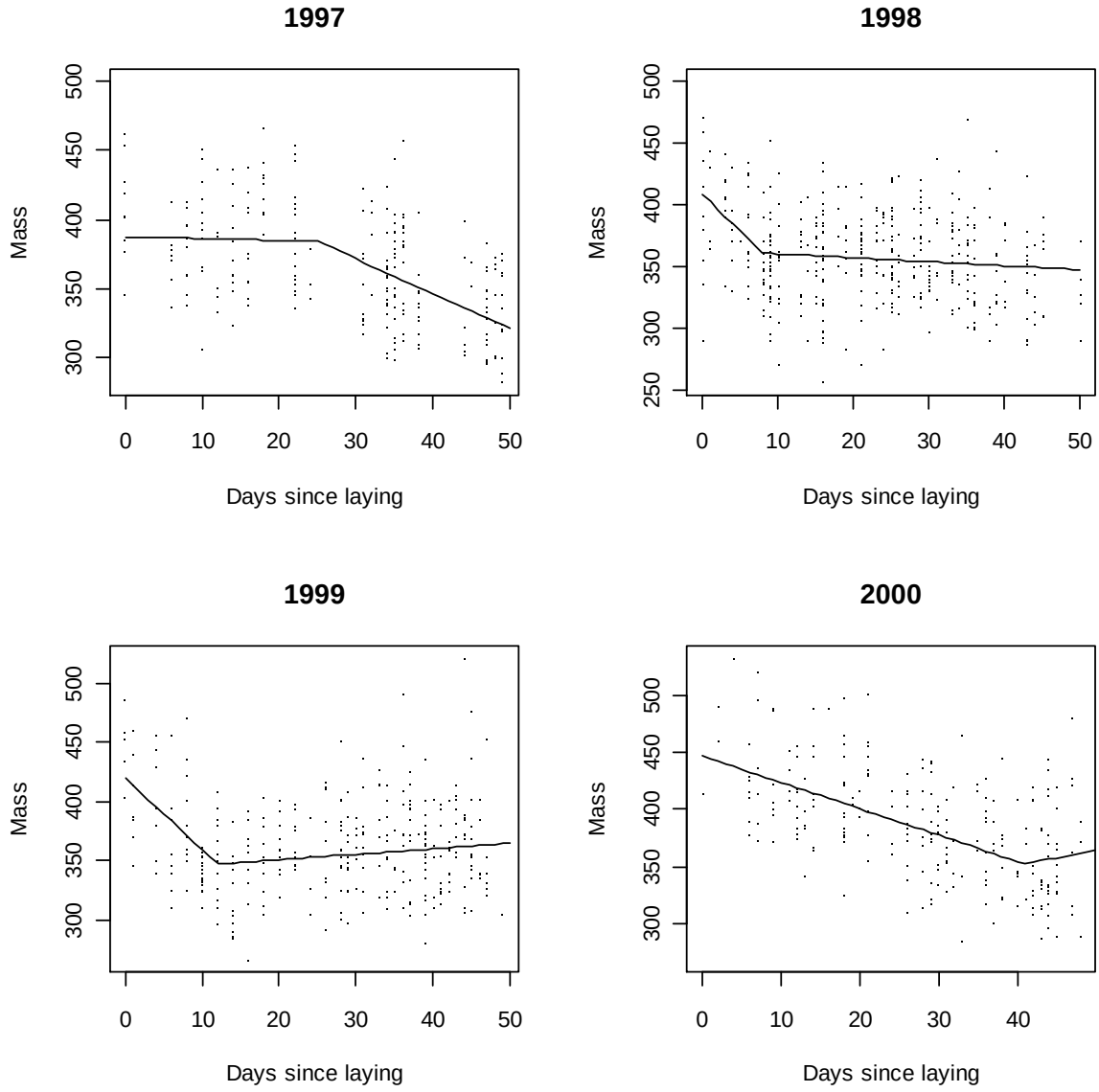
Year	Model	Break-point	Intercept	Gradient 1	Gradient 2	Delta AIC
1997	Constant	NA	370.97	0.00	NA	126.45
	Linear	NA	403.15	-1.37	NA	21.26
	Fixed BP	**25**	**387.51**	**-0.14**	**-2.38**	**0.00**
	Variable BP	**22**	**407.95**	**-2.28**	**0.94**	**0.79**
1998	Constant	NA	360.24	0.00	NA	83.42
	Linear	NA	376.37	-0.75	NA	37.50
	Fixed BP	25	375.18	-0.65	-0.25	39.11
	Variable BP	**8**	**409.89**	**-7.68**	**7.19**	**0.00**
1999	Constant	NA	359.69	0.00	NA	69.24
	Linear	NA	365.75	-0.26	NA	67.13
	Fixed BP	25	435.85	-13.28	13.32	56.57
	Variable BP	**12**	**435.85**	**-13.28**	**13.32**	**0.00**
2000	Constant	NA	387.90	0.00	NA	165.24
	Linear	NA	440.59	-1.99	NA	4.44
	Fixed BP	25	439.77	-1.94	-0.10	6.41
	Variable BP	**41**	**470.52**	**-7.41**	**5.51**	**0.00**
2001	Constant	NA	364.10	0.00	NA	5.56
	Linear	**NA**	**377.20**	**-0.50**	**NA**	**0.68**
	Fixed BP	**25**	**383.58**	**-0.97**	**0.97**	**0.84**
	Variable BP	**18**	**383.88**	**-1.80**	**1.34**	**0.00**
2002	Constant	NA	366.81	0.00	NA	82.15
	Linear	NA	396.29	-1.32	NA	3.99
	Fixed BP	25	399.72	-1.64	0.75	3.77
	Variable BP	**4**	**415.14**	**-5.42**	**4.31**	**0.00**
2003	Constant	NA	373.07	0.00	NA	25.71
	Linear	NA	361.42	0.55	NA	16.95
	Fixed BP	25	353.05	1.20	-1.71	10.71
	Variable BP	**34**	**374.87**	**-2.20**	**2.88**	**0.00**
2004	Constant	NA	363.72	0.00	NA	70.67
	Linear	NA	380.79	-0.71	NA	51.34
	Fixed BP	**25**	**357.88**	**1.17**	**-3.99**	**0.00**
	Variable BP	**25**	**349.15**	**5.95**	**-6.966**	**2.00**
2005	Constant	NA	379.78	0.00	NA	5.31
	Linear	NA	375.58	0.19	NA	5.72
	Fixed BP	25	369.75	0.64	-1.10	4.16
	Variable BP	**38**	**386.34**	**-2.15**	**2.48**	**0.00**
2006	Constant	NA	371.84	0.00	NA	6.55
	Linear	NA	370.851	0.05	NA	8.47
	Fixed BP	**25**	**361.696**	**0.90**	**-2.12**	**0.00**
	Variable BP	**27**	**370.914**	**0.03**	**0.01**	**1.18**
2007	Constant	NA	363.362	0.00	NA	41.98

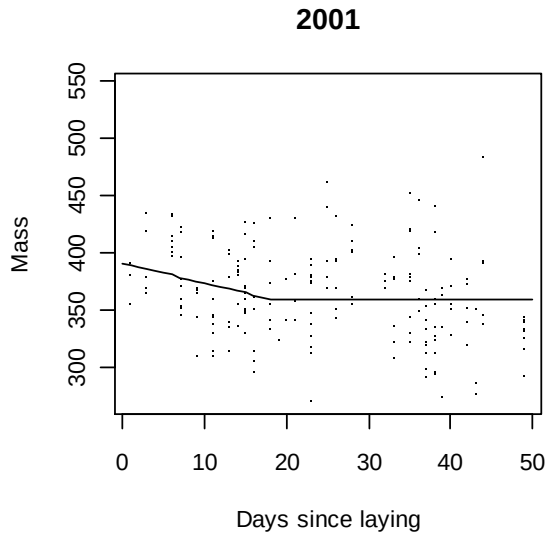
	Linear	NA	385.754	-0.85	NA	13.31
	Fixed BP	25	386.822	-0.94	0.16	15.23
	Variable BP	**10**	**427.274**	**-8.84**	**8.21**	**0.00**
2008	Constant	NA	356.264	0.00	NA	50.30
	Linear	NA	373.589	-0.77	NA	37.66
	Fixed BP	**25**	**347.224**	**1.22**	**-4.43**	**0.00**
	Variable BP	**26**	**351.300**	**3.38**	**-4.26**	**1.21**
2009	Constant	NA	385.835	0.00	NA	30.06
	Linear	NA	371.133	0.66	NA	21.17
	Fixed BP	**25**	**356.935**	**1.81**	**-3.23**	**1.21**
	Variable BP	**28**	**351.971**	**5.15**	**-4.83**	**0.00**
2010	Constant	NA	378.133	0.00	NA	102.84
	Linear	**NA**	**412.395**	**-1.79**	**NA**	**0.00**
	Fixed BP	**25**	**410.644**	**-1.62**	**-0.55**	**1.40**
	Variable BP	**6**	**426.181**	**-4.49**	**2.81**	**1.89**

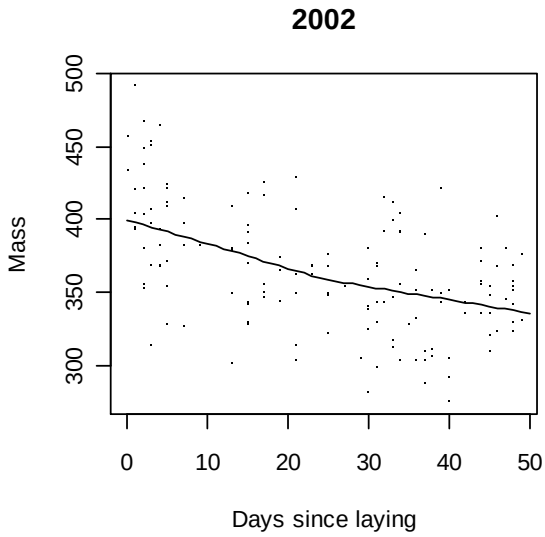
S-5 Model fit (delta AIC) for broken stick models with variable break-points for each year. Vertical lines (dashed) mark day 25 when a break-point might be expected due to the end of incubation and the start of chick-rearing.

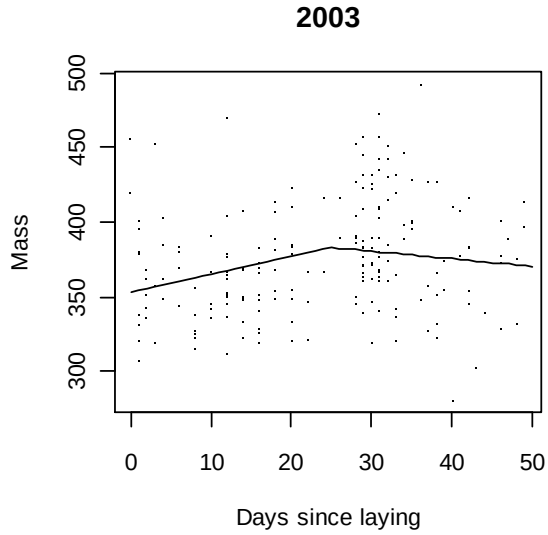


S-6 Body mass data with best-fit lines of the favoured model for each year of the study (1997–2010).




2001
Mass
300
350
400
450
500
550
0
10
20
30
40
50
Days since laying


2002
Mass
300
350
400
450
500
0
10
20
30
40
50
Days since laying


2003
Mass
300
350
400
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500
0
10
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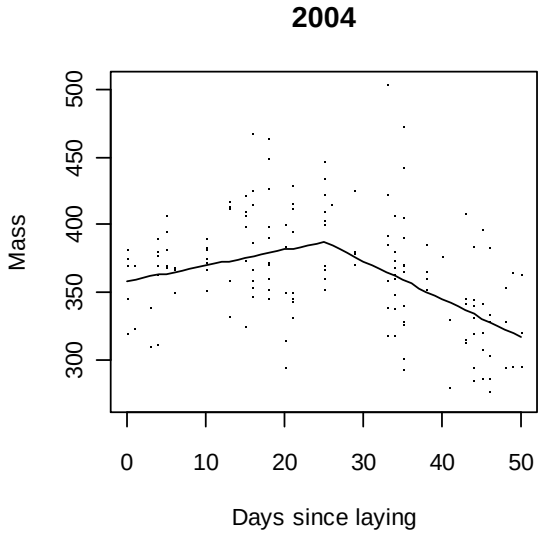
30
40
50
Days since laying


2004
Mass
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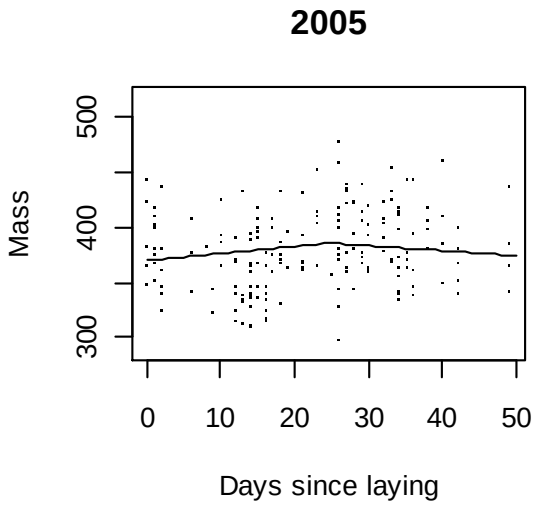
Days since laying


2005
Mass
300
400
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0
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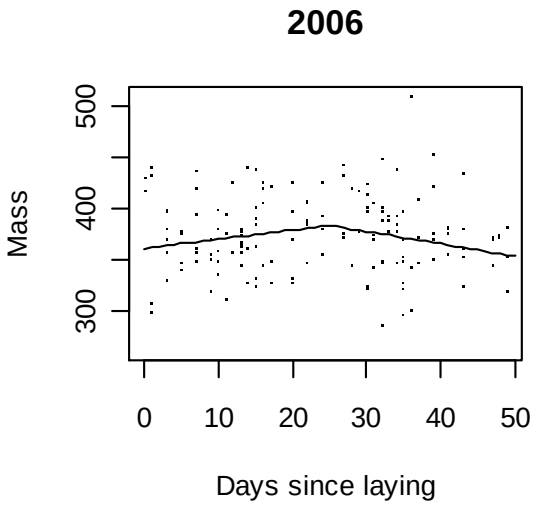
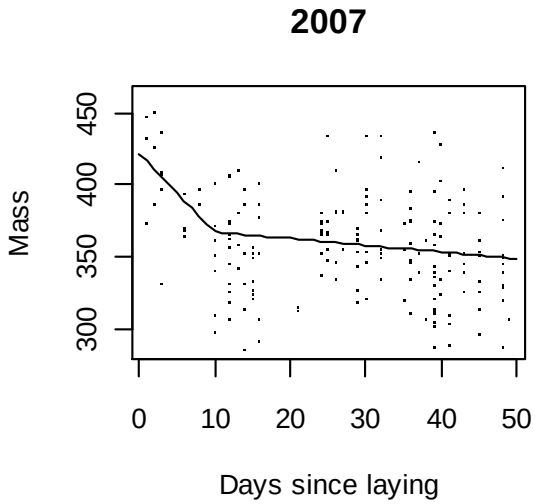
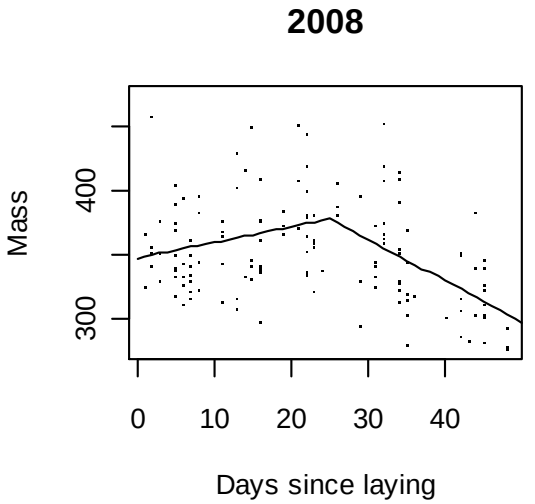
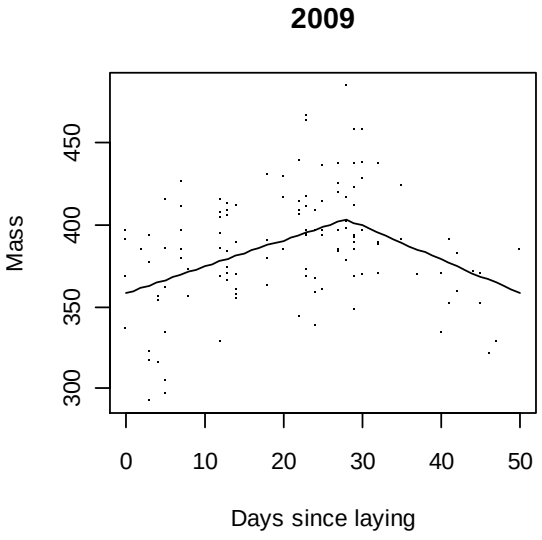
40
50
Days since laying


2006
Mass
300
400
500
0
10
20
30
40
50
Days since laying


2007
Mass
300
350
400
450
0
10
20
30
40
50
Days since laying


2008
Mass
300
400
0
10
20
30
40
Days since laying


2009
Mass
300
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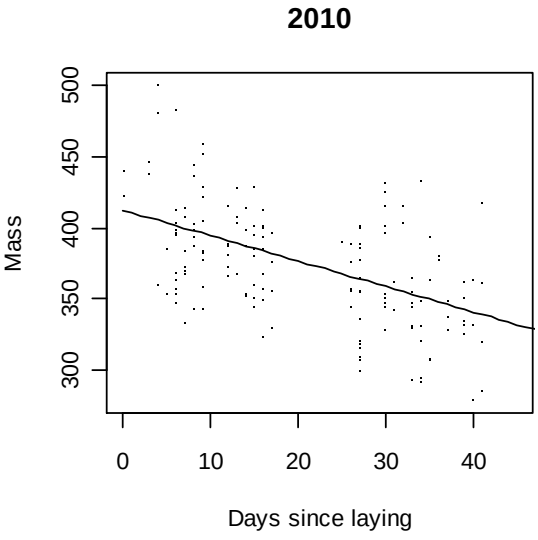
50
Days since laying


2010
Mass
300
350
400
450
500
0
10
20
30
40
Days since laying

Chapter Three

Longer foraging trips are associated with lower adult body mass and breeding success in the black-legged kittiwake

3.1 Abstract

For long-lived income breeders, foraging during the breeding season is of paramount importance due to the need to provision young as well as to obtain resources for self-maintenance. The distribution and availability of prey will determine the foraging range and, therefore, the length of foraging trips undertaken by central place foragers such as breeding seabirds. Foraging trip duration affects the cost of foraging for adults and delivery rates to offspring, which may have important implications for adult body mass and breeding success. Long-term datasets from the Isle of May breeding population of black-legged kittiwakes *Rissa tridactyla* (1997–2010) have shown that years of higher body mass loss during incubation and chick-rearing result in lower hatching and fledging success, respectively. In addition, higher proportions of young of the year lesser sandeels *Ammodytes marinus* are marginally associated with years of less mass loss during chick-rearing. In this study we recorded trip duration from observations of changeover rates of mates at nests, and proportion of captured adults that regurgitated their stomach contents as a proxy for trip duration, annually over the same time period. We tested whether duration of foraging trips during incubation and chick-rearing is linked to adult body mass and breeding success, and whether this is mediated via diet composition or acts on these effects independently of diet. Foraging trips undertaken during incubation were longer than foraging trips undertaken during chick-rearing. Years of longer trips during incubation and chick-rearing were associated with years of greater adult body mass loss during these respective periods. Furthermore, trip duration during chick-rearing was negatively correlated with breeding success. However, we found no relationship between trip duration and diet composition. Our results suggest that diet composition and foraging trip duration have independent effects on the body mass and breeding success of kittiwakes.

3.2 Introduction

Income breeding predators require sufficient prey in order for them to forage successfully to rear their young and maintain their own condition (e.g. Croxall et al., 1999, Madsen and Shine, 2000, Santos et al., 2010, Jacobs et al., 2011). Central place foragers are constrained to return to a common site to provision their young, and therefore require food in sufficient quantity and proximity to the central place in order to forage profitably. There is a lack of understanding in how the foraging dynamics of such species may mediate the link between prey availability and predator breeding success. The marine environment supports a suite of higher predators, including breeding seabirds, which as central place foragers (Orians and Pearson, 1979) provide a useful study system to investigate the impacts of changing prey availability on predator foraging dynamics.

Foraging range of central place foraging seabirds is influenced by inter- and intra-seasonal variation in environmental conditions and intrinsic factors. As such, it has been highlighted as a parameter worthy of more attention in seabird studies (Piatt et al., 2007a). Foraging range of breeding seabirds varies with prey availability (Furness and Camphuysen, 1997), with a number of studies demonstrating that seabirds, and other marine predators, have larger foraging ranges in years of poorer food availability (e.g. Antarctic fur seal *Arctocephalus gazella*; Costa et al., 1989, black-legged kittiwake *Rissa tridactyla*; Hamer et al., 1993, common guillemot *Uria aalge*; Monaghan et al., 1994, black-legged kittiwake; Chivers et al., 2012). Increasing foraging range during food shortages may enable adults to select higher quality prey that will better meet the demands of chick-rearing (Burke and Montevecchi, 2009). Alternatively, density dependent effects causing local depletion or disturbance of prey may be particularly strong in poor conditions, resulting in greater average foraging range than when conditions are good (Ashmole, 1963, Lewis et al., 2001a, Moseley et al., 2012). Foraging range may also differ due to intrinsic factors. For example, energy and time allocation often differ between incubation and chick-rearing (Salamolard and Weimerskirch, 1993, Weimerskirch et al., 1994a, Obst et al., 1995, Houston et al., 1996, Shaffer et al., 2003), with incubating birds tending to spend longer away on foraging trips than chick-rearing birds (e.g. black-legged kittiwakes; Humphreys et al., 2006, chinstrap penguin *Pygoscelis antarctica*; Ichii et al., 2007, thick-billed murres *Uria lomvia*; Ito et al., 2010). This is thought to result from the differing demands on parents during these two periods, with the need to return less regularly to relieve the mate from incubating duties than during chick provisioning. However, longer time spend away from the nest during incubation may arise as a result of

greater time spent resting on the sea surface, greater time spent actively foraging close to the colony, or greater distances travelled to foraging grounds.

Seabirds can also adjust their foraging effort in response to extrinsic conditions. For example, individuals may increase dive frequency during shorter trips compared to longer trips to compensate for the shorter time available (e.g. red-footed booby *Sula sula* and brown booby *Sula leucogaster*; Lewis et al., 2004b). Alternatively, they may increase the time spent foraging as conditions deteriorate (e.g. Arctic tern *Sterna paradisaea*; Monaghan et al., 1989, black-legged kittiwake *Rissa tridactyla*; Wanless and Harris, 1992, Hamer et al., 1993, common guillemot (murre); Uttley et al., 1994, Wanless et al., 2005, Kadin et al., 2012). Welcker et al. (2010), on the other hand, showed evidence for a threshold level of daily energy expenditure in black-legged kittiwakes, below which extrinsic factors had little effect. Whilst increasing foraging range or time spent foraging may reduce the negative effects of poor prey availability these strategies may not always be sufficient to ensure that breeding is successful (e.g. little penguin *Eudyptula minor*; Numata et al., 2000, black-legged kittiwake; Suryan et al., 2002, Magellanic penguin *Spheniscus magellanicus*; Boersma and Rebstock, 2009, thin-billed prion *Pachyptila belcheri*; Quillfeldt et al., 2010). However, differences in energy expenditure during foraging do not necessarily have consequences for adult survival (e.g. Welcker et al., 2010).

Increased foraging range is typically associated with longer foraging trip durations, which may affect breeding success directly, for example through the increased risk of starvation of chicks from reduced provisioning rates (e.g. Ballance et al., 2009, Watanuki et al., 2010, Chivers et al., 2012) or of an individual's mate abandoning incubation or brooding duties resulting in death from exposure (reviewed in Durant et al., 2004), predation (e.g. Mullers and Tinbergen, 2009) or conspecific attack (Lewis et al., 2004a, Ashbrook et al., 2008). Increased foraging trip duration may also affect breeding success indirectly through adult body condition falling below a threshold at which breeding is abandoned (Ballard et al., 2010). Adult birds have to expend more energy when undertaking longer foraging trips, which can compromise their body mass if the energetic gain from successful foraging does not outweigh the costs of travelling (Ballance et al., 2009). Adult body mass is especially likely to be compromised during chick-rearing when a bird's energetic expenditure increases (Golet and Irons, 1999, Weimerskirch and Lys, 2000). The effects of trip duration may be mediated not only by changes in the costs of foraging, but by the prey encountered. Whilst the relationship between diet composition

and trip duration is poorly understood (e.g. Rayner et al., 2010), it is possible that prey types differ in distribution relative to the colony (Casaux et al., 2008), resulting in variation with distance in energy gained as well as energy expended.

To date, the majority of studies exploring the links between foraging behaviour, adult body mass and breeding success have been limited to one or a few years of data (e.g. Lescroël and Bost, 2005; see examples above). There is, therefore, a need to utilise long-term datasets in order to explore these relationships across a range of environmental conditions (Weimerskirch et al., 2000). However, long-term datasets on metrics such as foraging range, foraging effort or trip duration are rare. In this chapter, we explored long-term data on changes in foraging trip duration of a top predator breeding in the North Sea. The black-legged kittiwake (hereafter 'kittiwake') is a surface-feeding species (Baird, 1994, Furness and Tasker, 2000, Suryan et al., 2000) and, as in many species, foraging range and trip duration are positively correlated (e.g. Daunt et al., 2002, Kotzerka et al., 2010, Chivers et al., 2012). The Isle of May is an important colony in the north-western (NW) North Sea (Frederiksen et al., 2007b) and kittiwakes from this colony depend predominantly on two age classes (adult 1+ group and young of the year 0 group) of the lesser sandeel *Ammodytes marinus* (hereafter 'sandeel') during the breeding season (Lewis et al., 2001b) and increasingly in recent years on clupeids (mostly sprat *Sprattus sprattus*; chapter two).

Chapter two showed that years of lower adult body mass at hatching and fledging were associated with years of lower hatching and fledging success, respectively. Furthermore, whilst no link was found between diet composition during incubation and change in body mass between laying and hatching, years of higher proportions of 1+ group sandeels relative to 0 group sandeels in chick-rearing were marginally associated with years of greater adult body mass loss between hatching and fledging. In light of these findings, we aimed to assess whether inter-annual variation in trip duration during incubation and chick-rearing is related to changes in adult body mass and hatching, fledging and breeding success, and whether these relationships are mediated by diet composition. Specifically, we tested whether foraging trip duration during incubation was longer in years with greater adult body mass loss between laying and hatching and lower hatching success and, similarly, whether trip duration in chick-rearing was longer in years with greater mass loss between hatching and fledging and lower fledging success. We explored whether any relationship between trip duration, adult body mass and breeding success was mediated by diet composition in chick-rearing by first testing whether

foraging trip duration was negatively correlated with the proportion of 1+ group relative to 0 group sandeels. Where this was not the case, we tested both variables simultaneously in models of body mass and fledging and breeding success. A significant effect of both trip duration and diet composition during chick-rearing would suggest that they have independent effects on body mass and breeding performance. We made the assumption that foraging trip duration was an indicator of the length of time birds spent searching for prey, including both travelling to suitable foraging grounds and actively diving for prey at these foraging grounds. Thus foraging trip duration was used as a proxy for the effort undertaken to obtain food.

3.3 Methods

We defined foraging trip duration as the time in minutes between a bird leaving the nest on a foraging trip and its return to the nest (Hamer et al., 1993). We estimated trip duration in two ways.

3.3.1 Observations of changeovers

Trip duration was recorded from observations of changeovers between mates at the nest—corresponding to the end of one foraging trip and the commencement of another by the mate (Hamer et al., 1993)—at a sample of kittiwake nests distributed across seven plots on the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11‘ N, 02° 33’ W) from 1998–2010. The distribution of watches among plots varied between years. In 2001, four different plots were used, whereas in all other years a single plot was used. Watches took place at the same plot between 2002 and 2010. It is possible therefore that plot effects could in part explain the differences recorded between years; however, we were unable to test this because there was only one year where multiple plots were observed. Observers were concealed within hides approximately four to 10 metres from the nests. Watches were either undertaken continuously from dawn to dusk (typically 03:30-22:00) on a single day by multiple observers (each undertaking a watch of 2–3 hours duration), or as a series of watches 2–3 hours in duration carried out on different days by the same or by multiple observers, designed so that all hours from dawn-to-dusk were observed once during each series (Tables 3-1 and 3-2). Such watches that covered the hours from dawn-to-dusk, either on a single day or on different days, are described hereafter as covering one ‘watch period’. Kittiwakes do not commence or end foraging trips in darkness so we did not miss changeovers by not observing at night (Galbraith, 1983, Coulson and Wooller, 1984). Calculations of trip durations from changeover rates were therefore on the basis that 24 hours had been observed. Most years of our study

period involved at least one watch period during each of the stages of early- to mid-incubation, mid- to late-incubation, early- to mid-chick-rearing and mid- to late-chick-rearing (Tables 3-1 and 3-2; no incubation watches occurred in 1998).

Table 3-1 Format of watches during incubation in each year of the study (1999–2010). No incubation watches occurred in 1998. In cases where the number of nests in each watch of a given year was the same, standard deviations are equal to zero.

Year	Number of Watches	Duration of Watches (hours)	Number of Watch Periods	Date of Watches	Number of Nests (mean ± SD)
1999	12	3	2	06/06/99; 16/06/99	95 ± 0
2000	12	3	2	29/05/00; 09/06/00	11 ± 0
2001	8	19	8	03/06/01–16/06/01	15 ± 0.4
2002	12	3	2	08/06/02–14/06/02	28 ± 4.6
2003	12	3	2	09/06/03–14/06/03	24 ± 0
2004	12	3	2	08/06/04–16/06/04	19 ± 0.5
2005	18	2	2	20/06/05–23/06/05	27 ± 0
2006	18	2–3	2	23/06/06–28/06/06	23 ± 1.5
2007	2	19	2	07/06/07; 13/06/07	27 ± 2.1
2008	2	19	2	02/06/08; 13/06/08	18 ± 3.5
2009	2	19	2	08/06/09; 21/06/09	18 ± 0.7
2010	2	19	2	28/05/10; 06/06/10	29 ± 1.4

Table 3-2 Format of watches during chick-rearing in each year of the study (1998–2010). In cases where the number of nests in each watch of a given year was the same, standard deviations are equal to zero.

Year	Number of Watches	Duration of Watches (hours)	Number of Watch Periods	Dates of Watches	Number of Nests (mean ± SD)
1998	5	19	5	17/06/98–05/07/98	8 ± 2.1
1999	14	3	2	19/06/99–03/07/99	54 ± 9.9
2000	25	3	4	17/06/00–01/07/00	10 ± 0
2001	4	19	4	23/06/01–27/06/01	12 ± 1.0
2002	12	3	2	16/06/02–27/06/02	19 ± 2.2
2003	12	3	2	26/06/03–05/07/03	17 ± 2.9
2004	18	3	3	29/06/04–10/07/04	15 ± 1.1
2005	18	2–3	2	02/07/05–08/07/05	18 ± 2.9
2006	18	2–3	2	06/07/06–14/07/06	22 ± 1.5
2007	2	19	2	28/06/07; 05/07/07	19 ± 1.4
2008	2	19	2	28/06/08; 10/07/08	19 ± 2.1
2009	2	19	2	01/07/09; 12/07/09	13 ± 2.1
2010	2	19	2	23/06/10; 05/07/10	16 ± 0

At each changeover, the nest number, the time of the incoming bird's arrival, the time the two mates spent together (hereafter 'time together'), and the time of departure of the outgoing bird were recorded. Kittiwakes tend to alternate incubation and foraging shifts; however, birds returning from a foraging trip may arrive at a nest and depart again several times before a changeover occurs. Therefore, only true changeovers in which one bird was seen to arrive at the nest and its mate was seen to leave the nest, and thus the pair swapped incubation or brood duties, were recorded. The number of changeovers that occurred during a watch period was used to back-calculate average trip duration, across the nests in a watch period, using the following equation (Hamer et al., 1993):

Trip Duration = ((Watch Period Duration / Number of Changeovers) * Number of Active Nests) – (Sum of Time Together / Number of Changeovers)

Watch Period Duration = 24 hours; Number of Changeovers = Total number of changeovers in a watch period; Number of Active Nests = Total number of nests with eggs (for incubation watch period) or chicks (for chick-rearing watch period) during watch period; Sum of Time Together = Sum of time (in hours) across all nests that mates spent at the nest together during changeovers in a watch period.

This equation provides a single estimate of mean trip duration across nests in each watch period. We then calculated mean trip duration across watch periods in incubation and chick-rearing in each year to give annual estimates of trip duration in incubation and chick-rearing. The advantage of this method over recording the duration of completed trips directly by carrying out watches that capture both the departure and arrival of individual birds is that the latter tends to be biased against long trips (Hamer et al., 1993). For all incubation watches we excluded any birds that had already hatched a chick and for chick-rearing watches we excluded any birds that were incubating. Nests that were left unattended by both adults of a pair at any point during a watch were also excluded (on average 1 % of nests overall were unattended during incubation and 13 % of nests were unattended during chick-rearing). Time together was not recorded in 1999, so we took averages over the study period for incubation and chick-rearing and used these as estimates for this year.

3.3.2 Frequency of regurgitations

Our second approach was to use the proportion of birds that regurgitated upon capture as a proxy of trip duration. Breeding birds were captured from their nest sites using a nylon noose attached to an eight metre pole during the breeding seasons of 1997–2010 (see Table 3-3 for sample sizes). We assumed that the probability of an individual regurgitating was linked to the duration since arrival at the nest, with a bird that had arrived more recently being more likely to regurgitate. This is based on the supposition that the longer birds have been on the nest, the more likely it is that they will have digested their food or fed it to their chicks. If a large proportion of birds regurgitate, this indicates that changeover rates between pair members are high and thus foraging trips short. Whilst these assumptions have not been formally validated, we know that kittiwakes breeding on the Isle of May always regurgitate when captured on their immediate return to the nest, which supports the suggestion that there is a link between regurgitation likelihood and proximity to arrival time (Reid, 2001, Humphreys, 2002). High regurgitation frequency was also found in

kittiwakes breeding at Fowlsheugh and St Abbs when birds were captured just after their return to the nest (Bogdanova, pers. comm.).

Table 3-3 Number of birds captured to calculate frequency of regurgitations in incubation and chick-rearing in each year of the study (1998–2010).

Year	Sample Size (n)	
	Incubation	Chick-rearing
1997	227	143
1998	426	246
1999	312	247
2000	195	264
2001	230	198
2002	167	107
2003	209	142
2004	152	118
2005	188	108
2006	141	97
2007	122	150
2008	147	84
2009	115	97
2010	157	127

3.3.3 Dietary data, body mass and breeding success

Full details of dietary data, body mass and breeding success methods can be found in chapter two. Briefly, a sample of breeding birds was captured each year. For individuals already carrying a British Trust for Ornithology (BTO) metal ring, the unique ring number was recorded, and remaining birds were ringed. Captured birds were weighed to the nearest gram using a Pesola and regurgitated food samples were collected. Each food sample was assessed visually and biomass proportions of each prey type quantified from otoliths and vertebrae (Lewis et al., 2001b, Barrett et al., 2007; chapter two). The average biomass proportions of the three major prey types (1+ group sandeels, 0 group sandeels and clupeids) in incubation and chick-rearing was then estimated. Body mass data was collected throughout each breeding season so that mass at laying, hatching and fledging could be estimated, and the change in mass during incubation and chick-rearing could be determined (see chapter two).

All apparently occupied nests (AON i.e. a breeding site where a pair has built a complete nest and therefore equivalent to the number of breeding pairs; Walsh et al., 1995) were monitored every five days throughout each breeding season at five plots distributed around the island (mean ± SD number of nests monitored: 219 ± 70.31; range: 126–330;

see chapter two). This monitoring allowed us to estimate hatching success (the proportion of AON that laid at least one egg, that went on to hatch at least one chick), fledging success (of those AON that hatched young, the proportion that fledged young) and breeding success (the number of chicks fledged per AON) for each year of the study period. Timing of laying and hatching recorded in these monitoring plots were used to apportion diet and body mass data to incubation and chick-rearing (see chapter two for full details). This was based on the assumption that the birds captured for diet sampling and body mass had the same timing of breeding as those monitored for breeding success. The annual median lay date represented day zero of the breeding season and a 25-day incubation period (Baird, 1994, Coulson, 2011) was used to estimate the timing of hatching (day 25). In order to standardise the mass data we had available for each year in our study, we took day 50 as a proxy of fledging mass. However, it must be noted that the fledging period of a kittiwake lasts for longer than 25 days; chicks are likely to fledge until 35 ± 4 days after hatching (pers. obs.). In some cases diet samples or mass data will have been collected from birds that had chicks during the defined incubation time period (day 0 to day 25) and from birds that had eggs during the defined chick-rearing time period (day 25 to day 50). Log ratios were used to calculate the proportion of 1+ group sandeels relative to 0 group sandeels during incubation and chick-rearing, and the proportion of clupeids relative to sandeels during chick-rearing (see chapter two for details). Constant, linear and broken stick models were used to model mass data and the best fitting model was selected in each year (subject to post-hoc examination of the spread of data in broken stick models, since these models are susceptible to error if the number of data points either side of the break-point is low; see chapter 2 for full details). These models provided estimates of adult body mass at day 0 (laying), day 25 (hatching) and day 50 (fledging) for each year (see chapter two for details).

3.3.4 Statistical methods

All statistical analyses were performed using R (version: 3.0.1, R Development Core Team, 2013). Values presented are means ± standard error unless specified otherwise. To test whether years of longer foraging trips during incubation would be associated with years of greater adult body mass loss, we used a linear model to test the effect of foraging trip duration on change in adult body mass between laying and hatching, accounting for the effect of mass at laying (which we have previously shown to be important in chapter two). To test whether years of longer foraging trips during incubation would be associated with years of lower hatching success, we used a quasi-binomial generalized linear model to analyse the relationships between hatching success and foraging trip duration.

To explore whether the relationship between foraging trip duration and body mass may be mediated by diet composition during chick-rearing, with birds travelling further to obtain certain prey types, we used a multiple linear regression to analyse the relationship between trip duration during chick-rearing and both the proportion of 1+ group relative to 0 group sandeels and the proportion of clupeids relative to sandeels during this stage. Since there were no significant relationships (see results), there was no evidence that trip duration and diet composition were correlated so we could fit them simultaneously to models of body mass and breeding success. To test whether foraging trip duration and diet composition affected change in body mass during chick-rearing, we used a multiple linear regression to model simultaneously the effects of foraging trip duration and proportion of 1+ relative to 0 group sandeels during chick-rearing on the change in adult body mass between hatching and fledging, whilst also accounting for the effect of mass at hatching (which we have previously shown to be important in chapter two). To test whether trip duration and diet composition during chick-rearing were associated with fledging success, we used a quasi-binomial generalized linear model to analyse the relationships between fledging success and foraging trip duration and the proportion of 1+ relative to 0 group sandeels during chick-rearing. Finally, we tested the effect on trip duration during incubation and trip duration and proportion of 1+ relative to 0 group sandeels during chick-rearing on breeding success, using a quasi-binomial generalized linear model.

All the above linear regressions were repeated using regurgitation frequency. We selected models using a backward stepwise regression procedure and report the models with the lowest Akaike Information Criterion (AIC) for each year (Burnham and Anderson, 2002); however, in cases where there was more than one model within two units of each other, the models were considered equally valid (Hurvich and Tsai, 1989).

3.4 Results

3.4.1 Observations of changeovers

During incubation, foraging trips were on average 2.69 times longer than in chick-rearing (incubation: 19.27 ± 1.78, range 7.69–27.72 hours; chick-rearing: 7.15 ± 0.62, range 3.46–10.81 hours). There was no correlation between trip duration during incubation and trip duration during chick-rearing in the same year (correlation coefficient (r) = 0.11; Fig. 3-1).

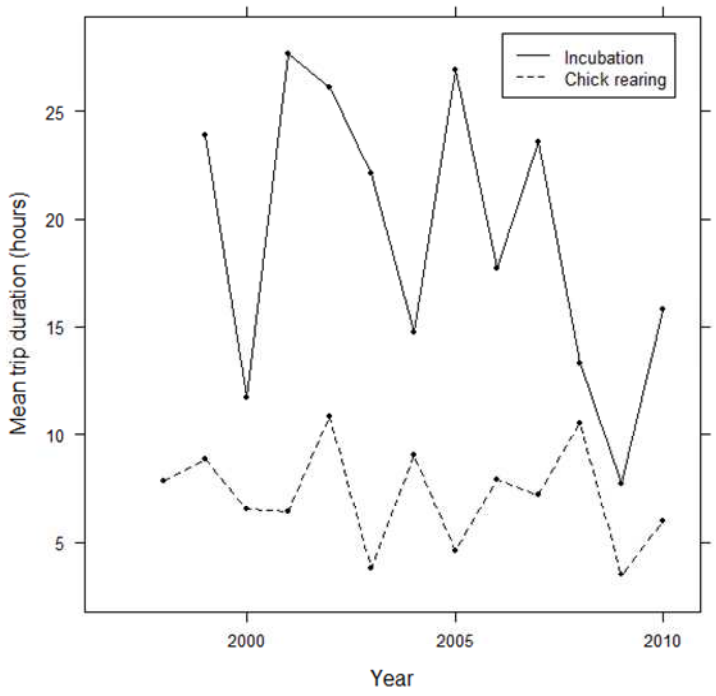


Fig. 3-1 Mean trip duration for foraging kittiwakes in incubation and chick-rearing (1998–2010), estimated from observations of changeovers.

Years of greater adult body mass loss between laying and hatching were associated with years of longer foraging trips during incubation (linear model: t = 3.06, P = 0.01; Fig. 3-2a), with a decrease of 1.41 g per day for every additional hour foraging, once mass at laying had been accounted for (t = 12.36; P < 0.0001; Fig. 2-5a; full model: $F_{2,9}$ = 88.66, R^2 = 0.95). However, hatching success was not significantly related to trip duration during incubation (quasi-binomial generalized linear model: t = 1.76, P = 0.11; Fig. 3-2c).

We found no significant relationships between trip duration and the proportion of clupeids relative to sandeels during chick-rearing (linear model: t = 0.59, P = 0.57) or the proportion of 1+ relative to 0 group sandeels during chick-rearing (t = 0.60, P = 0.56; full model: $F_{2,9}$ = 0.35, R^2 = 0.07). Years of greater adult body mass loss between hatching and fledging were associated with years of longer foraging trips during chick-rearing (linear model: t = 2.68, P = 0.02; Fig. 3-2b), with a decrease of 6.25 g per day for every additional hour foraging, once mass at hatching had been accounted for (t = 3.96, P = 0.003; Fig. 2-5c; full model: $F_{2,10}$ = 8.33, R^2 = 0.63). When trip duration was included in this model it masked the marginal effect of the proportion of 1+ group relative to 0 group sandeels during chick-rearing on change in body mass between hatching and fledging (t = 1.61, P = 0.15), and this variable was removed from this model during model selection. There was a tendency for years of lower fledging success to be associated with years of

longer foraging trips during chick-rearing; however this relationship was not significant (quasi-binomial generalized linear model: t = 1.80, P = 0.10; Fig. 3-2d). Years of poorer overall breeding success were associated with years of longer foraging trips during chick-rearing (quasi-binomial generalized linear model: t = 2.16, P = 0.05; Fig. 3-3) but were not associated with trip duration during incubation (t = 0.267, P = 0.80). Diet composition during chick-rearing was unrelated to fledging success and breeding success, and was removed from these models during model selection.

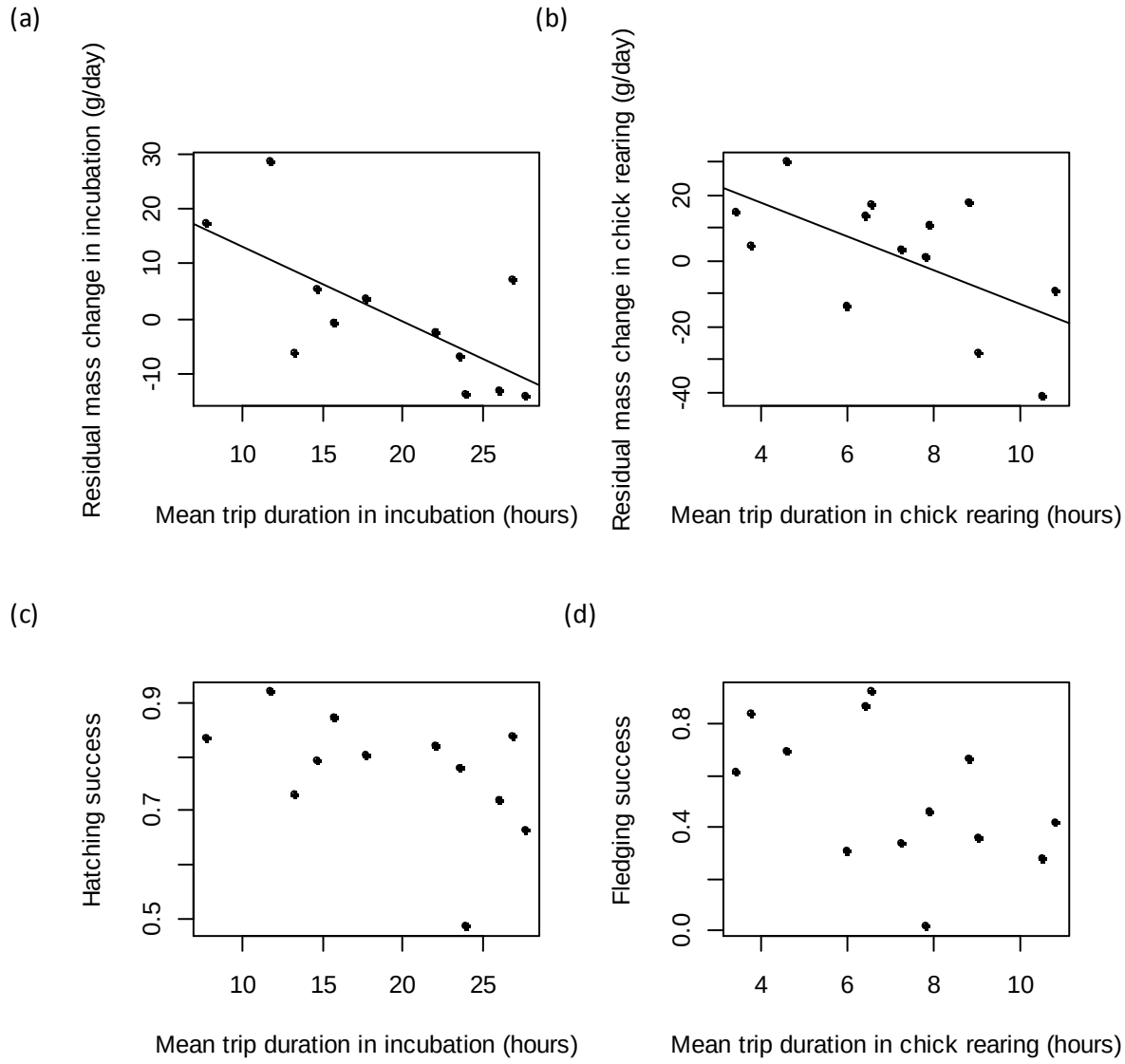


Fig. 3-2 Linear regression between (a) mean trip duration during incubation and residual adult body mass change during incubation, adjusted for mass at laying; (b) mean trip duration during chick-rearing and residual adult body mass change during chick-rearing, adjusted for mass during incubation; (c) mean trip duration during incubation and hatching success; (d) mean trip duration during chick-rearing and fledging success.

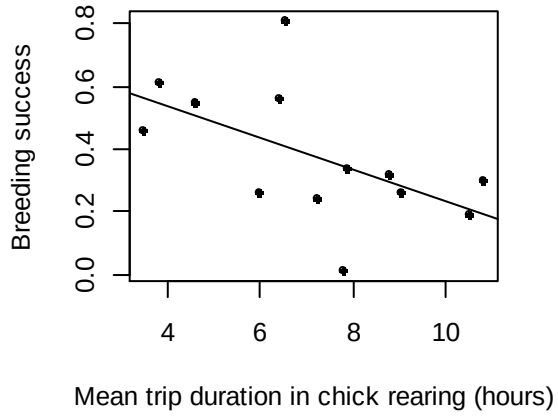


Fig. 3-3 Linear regression between mean trip duration during chick-rearing and breeding success (number of chicks fledged per AON). Breeding success incorporates both hatching and fledging success.

3.4.2 Frequency of regurgitations

Regurgitation frequency was correlated with mean trip duration, calculated from the observations of changeovers, during chick-rearing (linear model: $t = 2.96$, $P = 0.01$, $R^2 = 0.44$; Fig. 3-4b) but not during incubation (linear model: $t = 1.07$, $P = 0.31$, $R^2 = 0.10$; Fig. 3-4a).

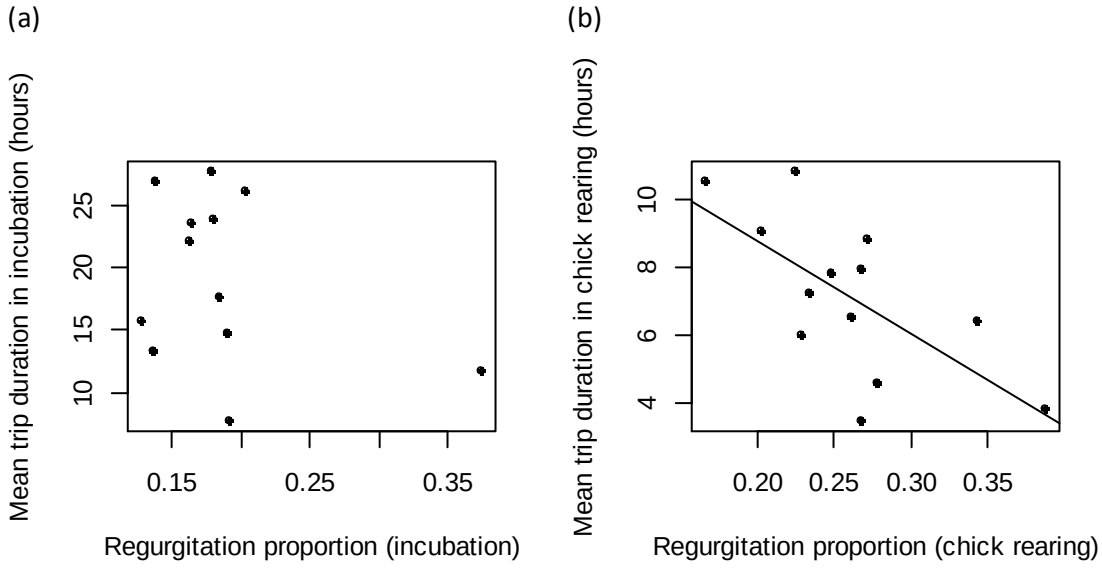


Fig. 3-4 Linear regression between (a) mean trip duration, calculated from observations of changeovers, during incubation and the regurgitation frequency during incubation and (b) mean trip duration, calculated from observations of changeovers, during chick-rearing and the regurgitation frequency during chick-rearing.

Across all years of the study period, 18.89 ± 1.59 % of birds regurgitated upon capture during incubation. This figure rose to 25.75 ± 1.48 % during chick-rearing. There was no correlation between regurgitation frequency during incubation and regurgitation frequency during chick-rearing in the same year (correlation coefficient (r) = 0.02; Fig. 3-4). There was a marginally significant decrease in the frequency of regurgitations in incubation during the study period (linear model: t = 1.98, P = 0.07, R^2 = 0.25; Fig. 3-5) but no such trend occurred in chick-rearing (t = 0.74, P = 0.48, R^2 = 0.04; Fig. 3-5).

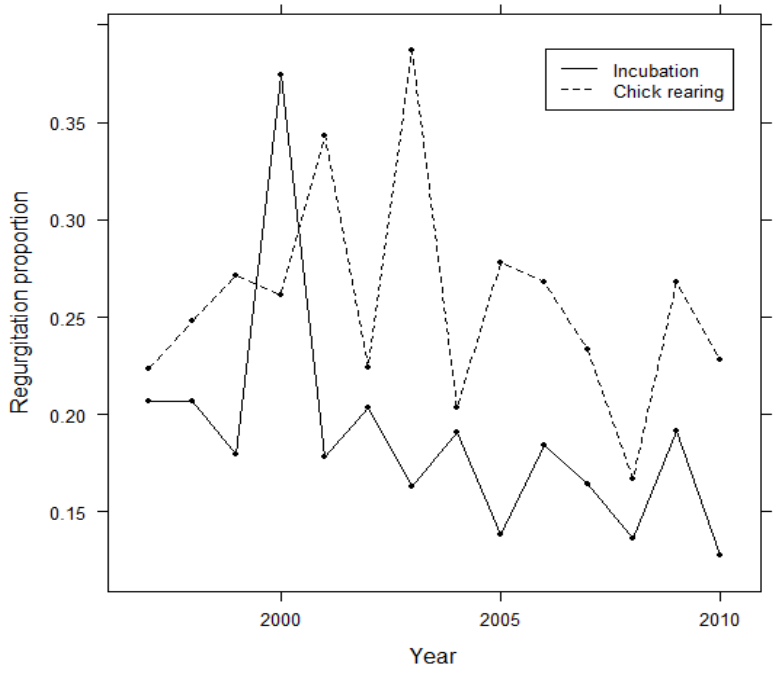


Fig. 3-5 Mean regurgitation frequency of captured kittiwakes for incubation and chick-rearing over the study period (1997–2010).

Years of greater adult body mass loss between laying and hatching were associated with years of lower regurgitation frequency during incubation, with a decrease of 17.4 ± 5.8 g per 10 % decrease in regurgitation frequency (linear model: t = 3.03, P = 0.01; Fig. 3-6a), once mass at laying had been accounted for (t = 12.64, P < 0.0001, Fig. 2-5a; full model: $F_{2,11}$ = 90.52, R^2 = 0.94). However, upon visual examination of the data, a single influential data point (year 2000) was observed. Once this data point had been excluded from the analysis the relationship between mass change and regurgitation frequency was no longer significant (t = 0.16, P = 0.88). Regurgitation frequency during incubation was not related to hatching success (quasi-binomial generalized linear model: t = 0.76, P = 0.46; Fig. 3-6c).

We found no significant relationship between regurgitation frequency and the proportion of clupeids relative to sandeels during chick-rearing (linear model: $t = 0.12$, $P = 0.90$) or the proportion of 1+ relative to 0 group sandeels during chick-rearing ($t = 0.76$, $P = 0.46$; full model: $F_{2,10} = 0.31$, $R^2 = 0.06$). Years of greater adult body mass loss between hatching and fledging were marginally associated with years of higher proportions of 1+ relative to 0 group sandeels during chick-rearing ($t = 2.24$, $P = 0.05$; Fig. 2-6c), once mass at hatching had been accounted for ($t = 3.83$, $P = 0.003$, Fig. 2-5c; full model: $F_{2,10} = 8.84$, $R^2 = 0.64$). When regurgitation frequency was included in this model it was non-significant ($t = 1.71$, $P = 0.12$; Fig. 3-6b) and was removed from the model during model selection. However, upon visual examination of the data, a single influential data point (year 2003) was identified. When this data point was excluded from the analysis a significant relationship between mass change and regurgitation frequency during chick-rearing was observed ($t = 3.60$, $P = 0.01$). Years of higher fledging success were associated with years of higher regurgitation frequency during chick-rearing (quasi-binomial generalized linear model: $t = 2.89$, $P = 0.01$; Fig. 3-6d). In addition, years of higher overall breeding success were associated with years of greater regurgitation frequency during both incubation (quasi-binomial generalized linear model: $t = 2.34$, $P = 0.04$; Fig. 3-7a) and chick-rearing ($t = 2.74$, $P = 0.02$; Fig. 3-7b). However, once a single influential data point (year 2000) had been excluded from the analysis the relationship between breeding success and regurgitation frequency during incubation was no longer significant ($t = 0.51$, $P = 0.62$). Diet composition during chick-rearing was unrelated to fledging success and breeding success and was removed from these models during model selection.

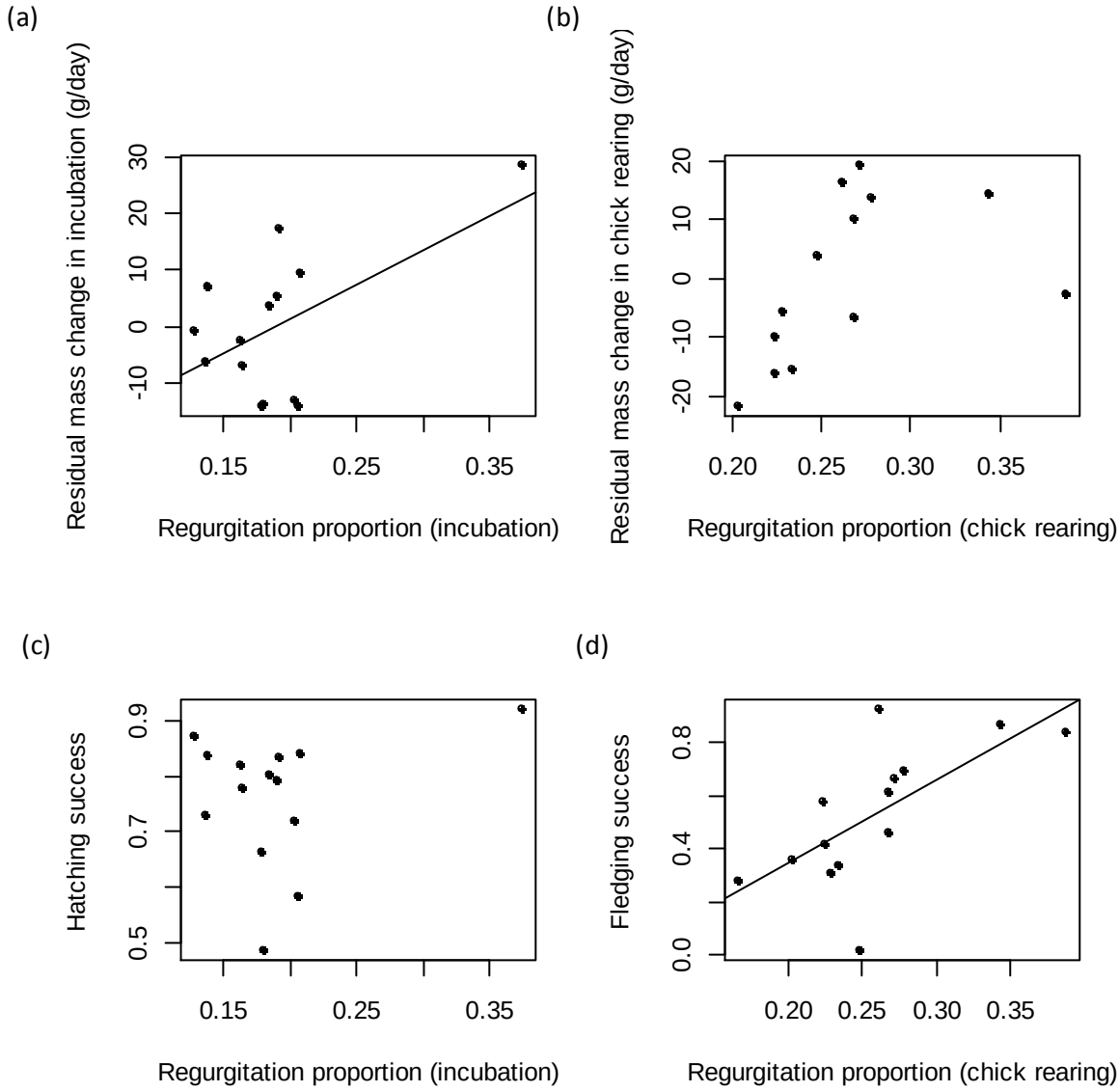


Fig. 3-6 Linear regression between (a) regurgitation frequency during incubation and residual adult body mass change during incubation, adjusted for mass at laying; (b) regurgitation frequency during chick-rearing and residual adult body mass change during chick-rearing, adjusted for mass at hatching; (c) regurgitation frequency during incubation and hatching success; (d) regurgitation frequency during chick-rearing and fledging success.

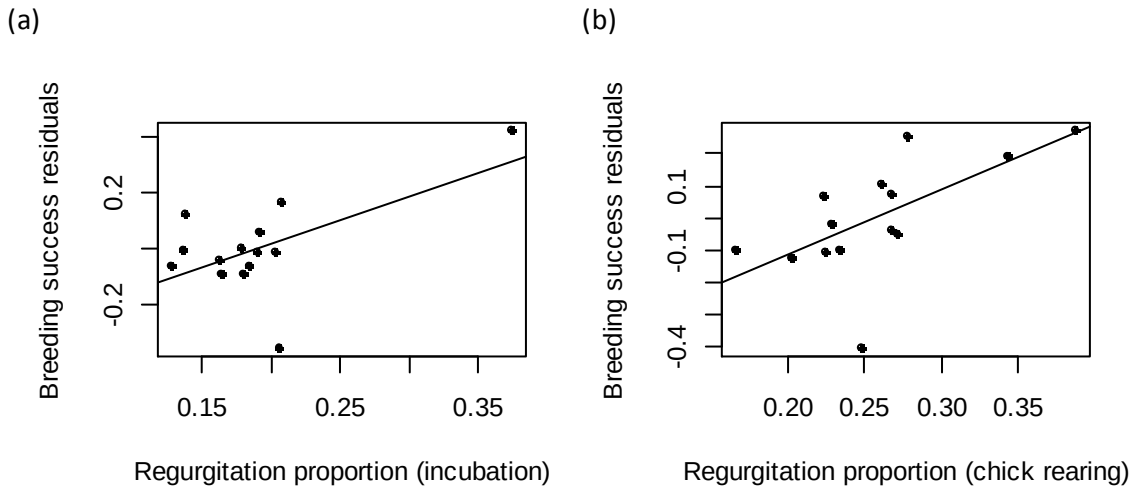


Fig. 3-7 Linear regression between (a) regurgitation frequency during incubation and breeding success, adjusted for regurgitation frequency during chick-rearing and (b) regurgitation frequency during chick-rearing and breeding success, adjusted for the regurgitation frequency during incubation.

3.5 Discussion

In this study we demonstrated that in years when foraging trip duration was greater during incubation and chick-rearing, body mass loss was greater, culminating in a negative impact on breeding success. In addition, proportion of adults that regurgitated was positively related to fledging and breeding success. Unlike most previous studies that have explored the fitness consequences of foraging range, foraging effort and trip duration, which have been based on one or a few years, our results are based on a dataset of 14 years, providing evidence that these effects are robust across a broad range of environmental conditions. Furthermore, we showed that the effect of foraging trip duration was not mediated via diet composition.

Foraging trips were longer during incubation than during chick-rearing, in line with previous studies of seabirds (e.g. black-legged kittiwakes; Humphreys et al., 2006, chinstrap penguin; Ichii et al., 2007, thick-billed murres; Ito et al., 2010). Whilst some studies suggest this may be due to a shift in prey distribution between breeding stages (e.g. Olrog's gull *Larus atlanticus*; Suárez et al., 2012), stage-dependent differences in energetic requirements are also likely to be important (e.g. Salamolard and Weimerskirch, 1993). It is also possible that during incubation, birds spend more time resting on the sea surface whilst away from the nest rather than spending longer actively foraging or travelling to more distant foraging grounds.

3.5.1 Trip duration, body mass and breeding success

Few studies have looked at how foraging trip duration is linked to changes in adult body mass during the breeding season (Chaurand and Weimerskirch, 1994, Weimerskirch, 1998). Some breeding seabirds have shown flexibility in trip duration that has reduced the negative effect of variation in food availability on their body mass (e.g. Cape gannets *Morus capensis*; Moseley et al., 2012). However, our results instead support the findings of Hamer et al. (1993), who compared two years of Shetland breeding kittiwakes and found reduced body condition and breeding success in the year of poorer food availability, which was characterised by longer foraging trips. We extend these findings to a long-term dataset and show that the body mass of breeding kittiwakes in our study was related to trip duration over a broad range of conditions.

Furthermore, our results suggest that trip duration is related to hatching and fledging success via changes in adult body mass during incubation and chick-rearing, respectively. Foraging for chicks is a costly activity for adult kittiwakes particularly during the second half of chick-rearing when demands are high (Salamolard and Weimerskirch, 1993, Weimerskirch et al., 1994a, Obst et al., 1995, Houston et al., 1996, Shaffer et al., 2003). Our results show that longer foraging trips and lower regurgitation frequencies were associated with lower breeding success. Our results accord with Lewis et al. (2001b) who found that regurgitation frequency was highest in the year with highest breeding success. As kittiwakes are long-lived birds, they favour their own condition and survival over their current breeding attempt (reviewed in Stearns, 1977, Linden and Møller, 1989), which means that when food is scarce and their body condition is reduced to a threshold level, they are likely to abandon breeding and forage in order to replenish their own energy reserves (Wingfield et al., 1998). Thus, it is possible that in years of poor breeding success, increased foraging trip durations during chick-rearing may have reduced body mass sufficiently to result in increased incidence of nest abandonment. Alternatively, the link between trip duration and fledging success may have been due to effects on chick provisioning rate or mate abandonment rate. However, we do not have data available to distinguish these two mechanisms.

Variation in trip duration may be caused by a number of factors including changes in the foraging effort of individuals (e.g. Lewis et al., 2004b), the distribution of prey (e.g. Weimerskirch et al., 1994b) and the abundance of prey (e.g. Boyd et al., 1994). Whilst foraging trip duration does equate to foraging range in some studies (Hamer et al., 2000, Hamer et al., 2001), this is not always the case due to variation in foraging effort across a

patchy environment. We were unable to test the link between foraging range and trip duration and this has not been fully tested in Isle of May breeding kittiwakes to date (Daunt et al., 2002); however studies of other systems have shown these variables to be related (Kotzerka et al., 2010, Chivers et al., 2012). Therefore, we cannot assume that kittiwakes in our study are foraging over greater distances in years when they lose more body mass and have lower breeding success. It is possible that in poor conditions when prey is less abundant or available and, therefore, birds encounter prey items at a lower rate, they may need to spend longer foraging in order to obtain their daily energy requirements and the requirements of their young. Alternatively, longer foraging trip duration could be due to a lower foraging rate, with birds spending more time resting on the sea surface and less time actively foraging; however, this is unlikely to explain why birds in our study lost more body mass and had lower breeding success in years when foraging trips were longer.

3.5.2 Trip duration and diet composition

We did not find any evidence that the relationship between foraging trip duration and body mass was mediated by diet composition. Whilst chapter two showed a marginal relationship between change in adult body mass and diet composition during chick-rearing, this relationship did not hold up once foraging trip duration was considered. This cannot be explained by trip duration and diet composition being correlated, but may suggest that the effect of trip duration on adult body mass change masked a weak but independent effect of diet composition. The lack of correlation between trip duration and diet composition suggests that different prey types may not have differed in distribution relative to the breeding colony or in the foraging effort required to obtain them. Our results contrast with Suryan et al. (2000, 2002), who found that changes in the prey selection of kittiwakes breeding in Alaska resulted in changes in the duration of foraging trips, which may be due to different spatial distributions of prey or differing foraging time required to exploit alternative prey. Lewis et al. (2001b) found that regurgitation frequency was highest in the year where 0 group sandeel proportion was also greatest. However, we found no link between diet composition and regurgitation frequency to support this.

Prey often aggregates in patches, which may be predictable (e.g. northern gannet *Morus bassanus*; Hamer et al., 2001) or unpredictable (e.g. masked booby *Sula dactylatra*; Weimerskirch et al., 2008), rather than being distributed evenly throughout the marine environment. Within the North Sea, aggregations of sandeels are largely determined by physical characteristics such as stratification of the water column (Scott et al., 2010) and the movement of tidal currents (Embling et al., 2012). Our results may support those of

Benoit-Bird et al. (2013), who found that prey biomass, density and abundance could not predict the spatial foraging patterns of three marine predators, including kittiwakes. Instead predator–prey relationships were regulated by characteristics of prey patches, for example patch depth (Benoit-Bird et al., 2013). A better understanding of prey patch locations within the foraging range of Isle of May breeding kittiwakes and the characteristics of these patches may help to explain why foraging trip duration was not related to diet composition.

3.5.3 Methods of measuring foraging trip duration

The results from our study and other short-term studies suggest that foraging trip duration acts as a reliable indicator of food availability. This suggests that whilst many short-term studies now use accurate data loggers to monitor foraging behaviour, there is still an important place for continuing the collection of observational data as part of established long-term studies, which use traditional, low-technology methods. Such observational studies allow greater sample sizes through simultaneous observation of multiple nests and the inclusion of birds that are inaccessible for capture. Furthermore, observing individuals prevents the disturbance caused by capture and handling.

To our knowledge, few studies to date have used regurgitation frequency as a proxy for foraging trip duration. Regurgitation frequency may reflect the amount of food in the stomachs of birds, the speed of digestion, or the stress response of birds captured and thus their likelihood to involuntarily regurgitate. However, regurgitation frequency is also likely to reflect, to some extent, the length of time an individual has spent on the nest and, therefore, the duration of foraging trips and nest attendance shifts. This assumption is supported by the finding that birds that are captured from the nest immediately after their return from a foraging trip invariably regurgitate (Bogdanova, pers. comm.). There is usually a diurnal variation in feeding frequency of kittiwakes with peak feeding occurring at dawn. In our dataset birds were captured each year throughout the day between the hours of 04:30 and 22:30 with a peak in captures between 10:00 and 12:00. This will have reduced any bias in the data due to capture at popular feeding times in certain years.

We found that years of lower regurgitation frequency during chick-rearing were associated with years of longer foraging trips during chick-rearing; however, there was no such correlation during incubation. This effect may have been reduced during incubation by the fact that incubating birds forage to feed themselves and therefore may have started to digest food prior to arrival at the nest, resulting in them having less food in their stomachs on average. It is also possible that incubating birds spend longer time resting on

the sea surface during foraging trips, which may result in time for digestion and lower stomach contents upon return to the nest. Incubating birds may also have a reduced regurgitation response upon capture compared to those that are rearing chicks and therefore regurgitating regularly when provisioning young. However, we did find that regurgitation frequency during incubation has shown a marginal negative trend across the study period, which may suggest that in more recent years birds have had to undertake longer foraging trips and therefore have been less likely to regurgitate upon capture. We conclude that our results, together with findings in Lewis et al. (2001b) that regurgitation frequency was linked to breeding success, suggest that regurgitation frequency offers a useful proxy of feeding conditions, but that it is likely to integrate a range of factors, including trip duration. A priority for future work would be to formally test the relationship between regurgitation frequency and trip duration.

Chapter Four

Corticosterone manipulation to mimic chronic stress reduces breeding success in a long-lived bird

This chapter appears as the following publication: NELSON, B. F., DAUNT, F., MONAGHAN, P., WANLESS, S., BUTLER, A., HEIDINGER, B. J., NEWELL, M., DAWSON, A., Corticosterone manipulation to mimic chronic stress reduces breeding success in a long-lived bird (*in review*).

4.1 Abstract

Determining the physiological mechanisms underpinning life-history decisions is essential for understanding the constraints under which life-history strategies can evolve. In long-lived species where the residual reproductive value of breeders is high, adult survival is a key contributor to lifetime reproductive success. We therefore expect that when adult survival is compromised during reproduction mechanisms will evolve to redirect resources away from reproduction, with implications for reproductive hormones, adult body mass, nest attendance behaviour and breeding success. We examined the hormonal factors underpinning resource allocation to parental behaviour in a long-lived bird, the black-legged kittiwake *Rissa tridactyla*. We investigated whether manipulating corticosterone, to simulate chronic environmental stress, affected the secretion of prolactin—a pituitary hormone that largely controls parental care in birds—and breeding success. To simulate chronic stress we used Alzet® osmotic pumps to administer corticosterone at a constant rate over eight days to incubating kittiwakes and measured prolactin concentration at the time of implantation and implant removal. Prolactin concentrations and body mass were unaffected after eight days of implantation. Corticosterone-implanted males showed lower nest attendance compared to sham-implanted males; however, the opposite pattern was found in females. Corticosterone treatment significantly reduced breeding success compared to sham-implanted birds. Prolactin may decrease prior to failure, or as a consequence of failure due to the absence of the stimulatory effect of young. However, our results suggest a longer-term effect of chronic stress on breeding success rather than an immediate suppression of prolactin concentrations causing premature failure.

4.2 Introduction

Life-history theory predicts that, when resources are limiting, trade-offs occur between reproductive investment in the current breeding opportunity and self-maintenance to preserve future breeding opportunities (Stearns, 1977). In long-lived species, in which the success of any one breeding event is a relatively small component of lifetime reproductive success, allocation decisions that favour parent rather than offspring survival are expected (reviewed in Linden and Møller, 1989). Whilst breeding can be timed to coincide with predictable seasonality in the environment, unpredictable environmental events require facultative responses in organisms. The emergency life-history stage modulates the physiology and behaviour of organisms, through redirecting energy away from non-essential physiology and behaviours, such as reproduction or immune response, towards those needed for survival (reviewed in Wingfield et al., 1998).

The emergency life-history stage involves the elevation of corticosterone—the main glucocorticoid in birds—in response to the activation of the hypothalamic-pituitary-adrenal axis (Wingfield et al., 1998). Chronic stress involves long-term exposure to a stressor, often resulting in negative fitness consequences such as low productivity, suppressed immunity and inhibited growth, rather than the short-term adaptive benefits of the emergency life-history stage, associated with acute stress. However, Boonstra (2013) has suggested that chronic stress, specifically related to predation pressure, may only arise in wild populations if such a response is adaptive. During chronic stress the duration of both the stressor and the consequences on an animal's physiology are long-lasting (Boonstra, 2013), resulting in sustained elevations of corticosterone. However, when corticosterone concentrations increase above baseline, the rate of passive clearance increases and active negative feedback reduces endogenous production (Sapolsky et al., 2000, Rich and Romero, 2005, Romero et al., 2005). This means that corticosterone is not maintained at stress-induced concentrations for long periods of time and therefore reduces the negative fitness consequences of long-lasting elevated corticosterone (Sapolsky et al., 2000, Romero, 2002).

Changes in corticosterone concentrations have a variety of implications for parental behaviour (reviewed in Crossin et al., 2012, Crespi et al., 2013). Baseline concentrations of corticosterone can be positively correlated with parental behaviour ('corticosterone-adaptation hypothesis') through stimulatory effects on foraging behaviour, which enhance provisioning to chicks (Kitaysky et al., 2001, Angelier and Chastel, 2009). On the other hand, chronic stress-induced elevations of corticosterone suppress parental behaviour

('corticosterone-induced reproductive conflict'), causing the redirection of resources away from breeding and towards self-maintenance (Love et al., 2004). The corticosterone-induced reproductive conflict can be managed by the up-regulation of corticosterone to increase baseline concentrations, which will enhance foraging activity and also minimise the chances of reproductive failure (Love et al., 2004).

Changes in corticosterone also have implications on the body mass of breeders. However, there is no clear prediction as to how chronic stress affects body mass. Correlational studies often show that increases in baseline corticosterone concentrations are correlated with declines in body mass or body condition (i.e. size-corrected body mass) (e.g. king penguin *Aptenodytes patagonicus*; Cherel et al., 1988, Cherel et al., 1994, black-legged kittiwake *Rissa tridactyla*; Kitaysky et al., 1999). However, Schultner et al. (2013) showed that initial increases in baseline corticosterone concentrations were associated with an increase in fat reserves. Corticosterone secretion has also been found to be independent of changes in body condition in some species (e.g. pied flycatcher *Ficedula hypoleuca*; Silverin and Wingfield, 1982, blue-footed booby *Sula nebouxii*; Wingfield et al., 1999, red-footed booby *Sula sula*; Lormée et al., 2003). If breeding is terminated as a result of chronic stress, failed breeders are likely to gain mass again as they favour self-maintenance (Wingfield et al., 1998).

Evidence regarding the mechanistic process that modulates the stress response during breeding is currently inconclusive. One potential mediator of the stress response is via changes in prolactin concentrations (Chastel et al., 2005, reviewed in Angelier and Chastel, 2009). Prolactin has a wide variety of roles throughout the vertebrates (Norris, 1980). In birds it promotes incubation and parental care, and is secreted in response to long photoperiods and further by the presence of eggs and young in the nest (Dawson and Goldsmith, 1985, El Halawani et al., 1986). Chronic stress is expected to cause declines in reproductive hormones (Sapolsky, 2000) and, therefore, it is possible that corticosterone may disrupt prolactin secretion and reduce breeding behaviour such as nest attendance (Angelier et al., 2009a).

Studies to date that have looked for relationships between corticosterone and prolactin in long-lived seabirds have reached a range of often conflicting conclusions: some studies have found a negative correlation between the two hormones whilst others have found no relationship (reviewed in Angelier and Chastel, 2009, Riou et al., 2010). It has been suggested that, whilst the responses of corticosterone and prolactin to acute stress are not mechanistically linked, their responses to chronic stress are, with prolactin

mediating the effect of corticosterone on breeding behaviour (reviewed in Angelier and Chastel, 2009, Angelier et al., 2013). Implantation of corticosterone in black-legged kittiwakes breeding in Svalbard, Norway caused a reduction in prolactin concentrations, breeding success and nest attendance (Angelier et al., 2009a). However, corticosterone was not successfully manipulated to mimic chronic stress but rather increased to a peak on day one and had returned to baseline concentrations by day three (Angelier et al., 2009a).

The kittiwake is a long-lived seabird with a typical bi-parental care system, which has been studied in both the Atlantic and the Pacific with regards to its breeding biology and physiology (e.g. Golet et al., 2004, Angelier et al., 2009a, Goutte et al., 2010a, Kitaysky et al., 2010). Whilst Pacific kittiwakes may live on average for 20 years, Atlantic birds tend to survive for eight years after first breeding (reviewed in Coulson, 2011). We used Alzet® osmotic pumps, which release substances at a constant rate over a number of days, in an attempt to simulate chronic stress in a North Sea population of black-legged kittiwakes (hereafter 'kittiwake'). We hypothesised that protracted elevation of corticosterone via Alzet® osmotic pumps would have a disruptive effect on breeding, specifically causing a reduction in prolactin concentration and body mass after a week, a reduction in nest attendance during the chick-rearing period, and lower breeding success by the end of the season.

4.3 Methods

4.3.1 Nest activity

270 kittiwake nests from 15 different plots on the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11' N, 02° 33' W) were observed daily from laying to fledging in 2011 and for each nest we recorded the lay date, clutch size and either timing of failure or number of chicks fledged (breeding success), as relevant (Fig. 4-1).

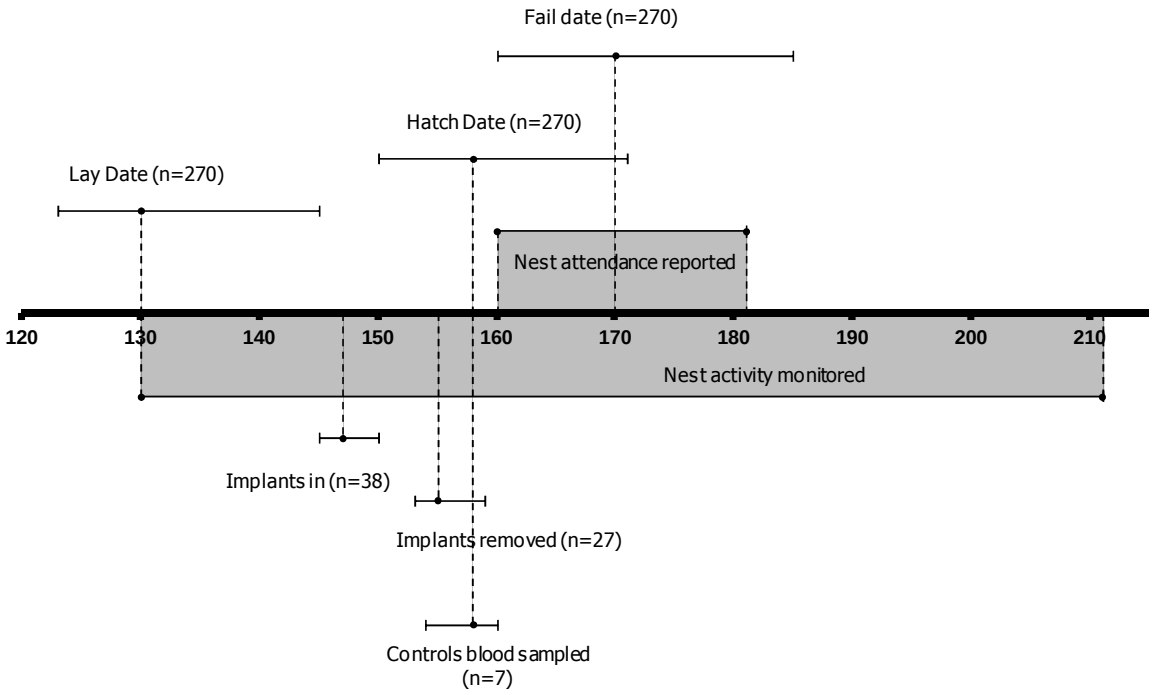


Fig. 4-1 Timing of experimental procedures and how these correspond to key events within the breeding season are indicated along a timeline of day of year. For events signified by a single point with a vertical hatched line (mean), horizontal lines show the range of the data. For events signified by a grey rectangle between two single points each with vertical hatched lines, the horizontal line joining the two points indicates the duration of time which these events lasted.

4.3.2 Blood sampling of kittiwakes

38 kittiwakes (27 females and 11 males) were captured, each from different nests, during late incubation (May 25–May 30; 18 ± 5.4 (mean ± SD) days after laying; all birds were incubating at the time of initial capture; Fig. 4-1) using an eight metre long noose pole. A maximum of 1 ml of blood was taken from the wing vein using sterile 1 ml non-heparinised syringes. Samples were centrifuged, once the blood had been allowed to clot, and frozen as separate red blood cells and serum for analysis in the laboratory. A dictaphone was used to precisely record the elapsed time between capture (i.e. when the noose was placed over a bird's head) and the end of blood sampling (individual sampling time), which we aimed to complete within three minutes of capture so that baseline concentrations of corticosterone would be obtained (Romero and Reed, 2005).

Individual sampling time was on average 2.7 ± 0.6 (mean ± SD) min, with 15 % of samples being obtained within two minutes, 75 % within three minutes and 25 % of samples taking longer than three minutes. All samples were collected within 5.7 min. We also recorded the elapsed time between the extension of the noose pole towards the target

bird and the lifting of the captured bird off its nest (capture time). Capture time was on average 1.2 ± 0.8 (mean ± SD) min with 56 % of captures occurring within one minute, 88 % within two minutes and 98 % within three minutes. In order to assess any impact of disturbance to birds during the catching of other individuals at the same colony, birds were ranked in the order that they were captured at a given site, on a given catching attempt. If a site was returned to later that day (> 6 hours later) or on the subsequent day, this was assumed to be a new catching attempt. There was a maximum of eight birds captured per site on a given catching attempt.

4.3.3 Corticosterone manipulation in kittiwakes

For individuals already carrying a British Trust for Ornithology (BTO) metal ring the unique ring number was recorded and remaining birds were ringed. Birds were weighed to the nearest gram using a Pesola. Alzet® osmotic pumps (length: 3.0 cm; diameter: 0.7 cm; mass: 1.1 g; nominal volume: 200 µl; delivery period: 14 days; rate of delivery: 0.5 $\mu l.h^{-1}$) were inserted subcutaneously on the flank immediately anterior to the thigh, under local anaesthesia. These osmotic pumps are used widely in a range of studies including pharmacology, biotechnology and immunology (> 13,500 publications in the Alzet® bibliography) and have been successfully used to administer corticosterone in white throated sparrows *Zonotrichia albicollis* (Horton et al., 2007). A small incision was made using a sterile scalpel blade and this was closed with suture. The pumps contained either corticosterone dissolved in polyethylene glycol 400 (PEG) at a concentration of 28 $mg.ml^{-1}$ (corticosterone-implanted birds; n = 17) or PEG only (sham-implanted birds; n = 21). Kittiwakes weigh approximately 380 g and therefore two pumps were necessary to deliver the required dose of corticosterone, which we estimated using data from Horton et al. (2007). We scaled up the amount of corticosterone administered according to the greater body mass of kittiwakes compared to the passerines used in Horton et al. (2007). We matched experimental groups for location to account for potential plot effects. Birds were marked with picric acid on the head or tail feathers to aid identification during attempted recapture. There were no significant differences in the clutch size (linear model: $t = 1.71$, $df = 36$, $P = 0.10$, $R^2 = 0.07$), lay date (linear model: $t = 0.89$, $df = 36$, $P = 0.38$, $R^2 = 0.02$) or sex ratio (Binomial generalized linear model: $z = 1.23$, $P = 0.22$) between the treatment groups when the treatment was implemented.

Implanted birds were recaptured 8 ± 1 (mean ± SD) days later (26 ± 1 days after laying; 40% of nests had hatched at least one egg by the time of recapture), which was timed to occur sufficiently after first capture to maximise recapture probability and before

all the corticosterone had been delivered (see Appendix; contents of pumps had been used up 11 days after implantation in a captive bird). Birds were blood sampled, as described above, weighed and the implants were removed. The removed implants were empty. 71 % of implanted birds were successfully recaptured (n = 27; 14 sham-implanted birds; 13 corticosterone-implanted birds). At the time of implant removal an additional seven birds (controls) that had not been implanted, and whose partners had not been implanted, were captured and blood sampled in order to test for any adverse effects of the initial capture and implantation of the osmotic pumps. In order to reduce disturbance at the colonies and maximise the chances of recapture, birds were only captured twice and we did not undertake any monitoring visits in between initial catching and attempted recapture. The birds used in this study were not part of any other study and therefore remained relatively undisturbed outside of our experimental protocols, minimising their exposure to acute stress.

All work was carried out under Home Office personal (Bethany Nelson: PIL 60/12426 and Alistair Dawson: PIL 70/1697) and associated project licences (Alistair Dawson: PPL 60/4176 and Francis Daunt: PPL 60/4001) and Scottish Natural Heritage (MON/RP/131) permit.

4.3.4 Nest attendance

We recorded nest attendance by identifying which members of the pair were present at the nest using the unique pattern of white and black markings on the tips of the wing feathers (Chardine, 2002) and the picric acid markings that were issued upon capture. Data were collected from 37 out of the 38 nests included in the corticosterone manipulation experiment, during early to mid chick-rearing (9 June to 30 June; Fig. 4-1). One nest was excluded because it was in a colony that was easily disturbed and therefore was hard to access for individual identification purposes. Nest attendance was checked up to three times daily (total: 824 checks; time of day: 8:00–20:40). We treated each nest check as an independent event as no autocorrelation was detected in our model (Phi = 0).

4.3.5 Molecular sexing

DNA was extracted from the red blood cells of all samples using a Qiagen DNeasy® Blood and Tissue Kit (QUIAGEN Ltd., West Sussex, UK), following the manufacturer's instructions. Birds were sexed as described by Griffiths et al. (1998) using the primers described by Albores-Barajas et al. (2010). Samples from birds of known sex were included as controls in all PCR amplifications and agarose gels. A negative control was

also included containing no DNA. 50 % of the samples were repeated to check for consistency and no contradictory results were found.

4.3.6 Hormone assays

Prolactin concentrations were determined in November 2011 by a heterologous RIA using a primary antibody raised in rabbit against recombinant starling prolactin and a donkey anti rabbit secondary antibody, as described in Bentley et al. (1997). Duplicate 20 µl samples were assayed. All samples were run in one assay and the intra-assay variation was 4.5 %. Serial dilutions of serum samples were parallel to the serial dilutions of the standard.

Corticosterone concentrations were determined in March 2012 by a quantitative competitive enzyme-immuno assay (EIA). Serum samples were equilibrated with 2000 cpm ¬3 H-CORT to measure recovery and extracted using diethyl ether. Extracted samples were analysed in duplicate using an EIA kit as described in Wada et al. (2007). A dose response curve of kittiwake serum ran parallel to the standard curve. Values were corrected for sample dilution and recovery. The average extraction efficiency was 80 ± 0.9 %. The inter-assay variation was 6.4 % and the intra-assay variation ranged from 5.6 to 6.8 %.

4.3.7 Statistical methods

All statistical analyses were performed in the R computing environment (version: 2.10.1, R Development Core Team, 2009). Values are presented as means ± standard error unless specified otherwise. To examine differences between treatment groups in adult body condition, we used mass rather than size-corrected mass because previous studies disagree about which, if any, methods for calculating body condition are validated. Specifically, Green (2001) showed that the use of residuals from a least squares linear regression of body mass against a linear measure of size can easily lead to Type I and Type II statistical errors. On the other hand, Schulte-Hostedde et al. (2005) argued that the use of residuals from least squares regression did satisfy critical assumptions and therefore could be validated, whilst Schamber et al. (2009) discouraged the use of any unverified indices of body condition, instead endorsing the use of raw body mass data.

When analysing the effect of treatment on corticosterone concentrations, prolactin concentrations and body mass, we used linear mixed models fitted by restricted maximum likelihood and calculated P values using the Markov chain Monte Carlo method. We only included birds that had been successfully recaptured and therefore had both pre- and post-implant data: including birds that were only captured once would bias the pre-implant data

because these birds tended to be more easily disturbed, and therefore less prudent parents, than those captured twice. We included individual as a random factor to account for repeated measures. The interaction between treatment (i.e. sham-implanted or corticosterone-implanted) and pre/post-implant (i.e. 0 = pre-implant sample; 1 = post-implant sample) was fitted to the model and was the key variable of interest. We also included date relative to lay date as a fixed effect in order to control for temporal environmental variation, because prolactin cycles seasonally, rising during incubation (Dawson, 2006, Dawson, 2008) and mass tends to decline during the season, (e.g. Mrosovsky and Sherry, 1980, Wendeln and Becker, 1999, Moe et al., 2002). We included sex as a fixed effect, the interaction between treatment and pre/post-implant, the interaction between treatment and sex, the interaction between pre/post-implant and sex and the three-way interaction between treatment, pre/post-implant and sex, because of sex-specific patterns in corticosterone and body mass change (Lormée et al., 2003), and sex-specific responses of prolactin to stress (Angelier et al., 2009b). As corticosterone and prolactin concentrations were constrained by being positive and the residuals were not normally distributed, we transformed these two response variables by taking the logarithm to base ten. We selected models using a backward stepwise regression procedure and report models with the lowest Akaike Information Criterion (AIC) for each year (Burnham and Anderson, 2002); however, in cases where there was more than one model within two units of each other, the models were considered equally valid (Hurvich and Tsai, 1989).

We also ran three additional models with corticosterone, prolactin and body mass as response variables to compare the post-implant measurements of sham-implanted birds with control birds, which were measured at the time of implant removal (Fig. 4-1). We did not need to include individual as a random factor, because only one sample was being analysed per bird, and therefore used linear models. Treatment (i.e. sham-implanted or control) was fitted to the models and was the key variable of interest. We also included date relative to lay date, sex and the interaction between treatment and sex.

We used a generalized linear mixed model fit by maximum likelihood with a binomial distribution to test for any effect of treatment on the presence of birds at the nest during the chick-rearing period (i.e. after implant removal; Fig. 4-1): we used an explanatory variable with birds coded as present (1) or absent (0). Nest was included as a random effect. Treatment was the main fixed effect of interest and we also included the interaction between day since implant and treatment to assess whether any differences became more or less apparent over time. We included brood size as a fixed effect due to

previous studies suggesting that larger broods are more likely to be left unattended (Wanless and Harris, 1989). Sex and the interaction between sex and treatment were both also included due to evidence that daily energy expenditures may be higher in female kittiwakes (Fyhn et al., 2001) or higher in male kittiwakes (Thomson et al., 1998).

To compare breeding success across groups, we used a generalized linear model with a binomial distribution with treatment (i.e. control, sham-implanted or corticosterone-implanted) as the fixed effect and breeding success (number of chicks fledged) as the response variable. We assumed that the maximum number of chicks that could have fledged was equal to three. This enabled us to detect whether there was an effect of corticosterone implantation on reproductive success, by comparing sham and corticosterone-implanted birds, and whether there was any adverse effects of the implants, by comparing sham-implanted birds with controls.

4.4 Results

There were no signs of any adverse effects of the implants at the time of recapture: there was a 100 % survival rate during the experiment; by the time of implant removal—eight days after insertion—the incision area had completely healed; there was no significant difference in breeding success between sham-implanted birds and controls (Fig. 4-3b).

4.4.1 Hormone concentrations

We found no effect of individual sampling time (linear model: $t = 0.87$, $P = 0.39$), capture time ($t = 0.67$, $P = 0.51$), rank order of capture ($t = 0.31$, $P = 0.76$), an interaction between individual sampling time and capture time ($t = 0.85$, $P = 0.40$) or an interaction between individual sampling time and rank order of capture ($t = 0.24$, $P = 0.81$) on corticosterone concentrations (full model: $F_{5,66} = 0.67$, $R^2 = 0.05$). There was also no effect of total time (total = individual sampling time + capture time; linear model: $t = 1.01$, $P = 0.32$), rank order of capture ($t = 0.79$, $P = 0.43$) or the interaction between total time and rank ($t = 0.76$, $P = 0.45$) on corticosterone concentrations (full model: $F_{3,68} = 0.38$, $R^2 = 0.02$). Therefore, we included all samples in our analyses as representative of baseline concentrations.

There was a marginally significant effect of sex on corticosterone concentrations (linear mixed effects model: $t = 1.90$, $P = 0.06$). All other fixed effects were removed from the model during model selection, including the interaction between treatment and pre/post-implant. The corticosterone data were largely sensitive to one value (corticosterone-implanted male; pre-implant: 7.7 ng/ml; post-implant: 169.9 ng/ml;

Mahalanobis distance: MD = 45.9, degrees of freedom (df) = 9; critical value = 27.9), which resulted in a large standard error associated with the post-implant mean for corticosterone-implanted individuals (23.6 ± 12.3; Fig. 4-2a). However, there was no significant change in the model if this value was excluded.

There was no significant effect of sex on prolactin concentrations (linear mixed effects model: t = 1.76, P = 0.08), but there was a significant effect of pre/post-implant on prolactin concentrations (linear mixed effects model: t = 2.39, P = 0.02). Prolactin concentrations were 12.8 ± 5.1 ng/ml lower at the time of the post-implant blood sample compared to the pre-implant sample. All other fixed effects were removed from the model during model selection, including the interaction between treatment and pre/post-implant (Fig. 4-2b).

There was no significant effect of days since laying on the corticosterone concentrations of post-implant sham birds and control birds (linear model: t = 0.62, P = 0.54, R^2 = 0.02). All other fixed effects were removed from the model during model selection, including the effect of treatment (Fig. 4-2a). There was a significant effect of sex (linear model: t = 2.53, P = 0.02), treatment (linear model: t = 2.45, P = 0.03) and the interaction between sex and treatment (linear model: t = 2.56, P = 0.02) on the prolactin concentrations of post-implant sham birds and control birds (control females: 50.1 ± 3.3; control males: 35.5 ± 4.4; sham females: 38.9 ± 2.1; sham males: 43.4 ± 3.6; full model: $F_{3,17}$ = 2.78, R^2 = 0.33). All other fixed effects were removed from the model during model selection, including the effect of treatment (Fig. 4-2b).

4.4.2 Body mass

There was a significant effect of sex on body mass (linear mixed effects model: t = 3.94, P < 0.001), with males having an average body mass across the two sampling periods of 415 ± 9 g and females a body mass of 368 ± 7 g. All other fixed effects were removed from the model during model selection, including the interaction between treatment and pre/post-implant (Fig. 4-2c). There was no significant effect of sex on the body mass of post-implant sham birds and control birds (linear model: t = 1.75, P = 0.10, R^2 = 0.14). All other fixed effects were removed from the model during model selection, including the effect of treatment (Fig. 4-2c).

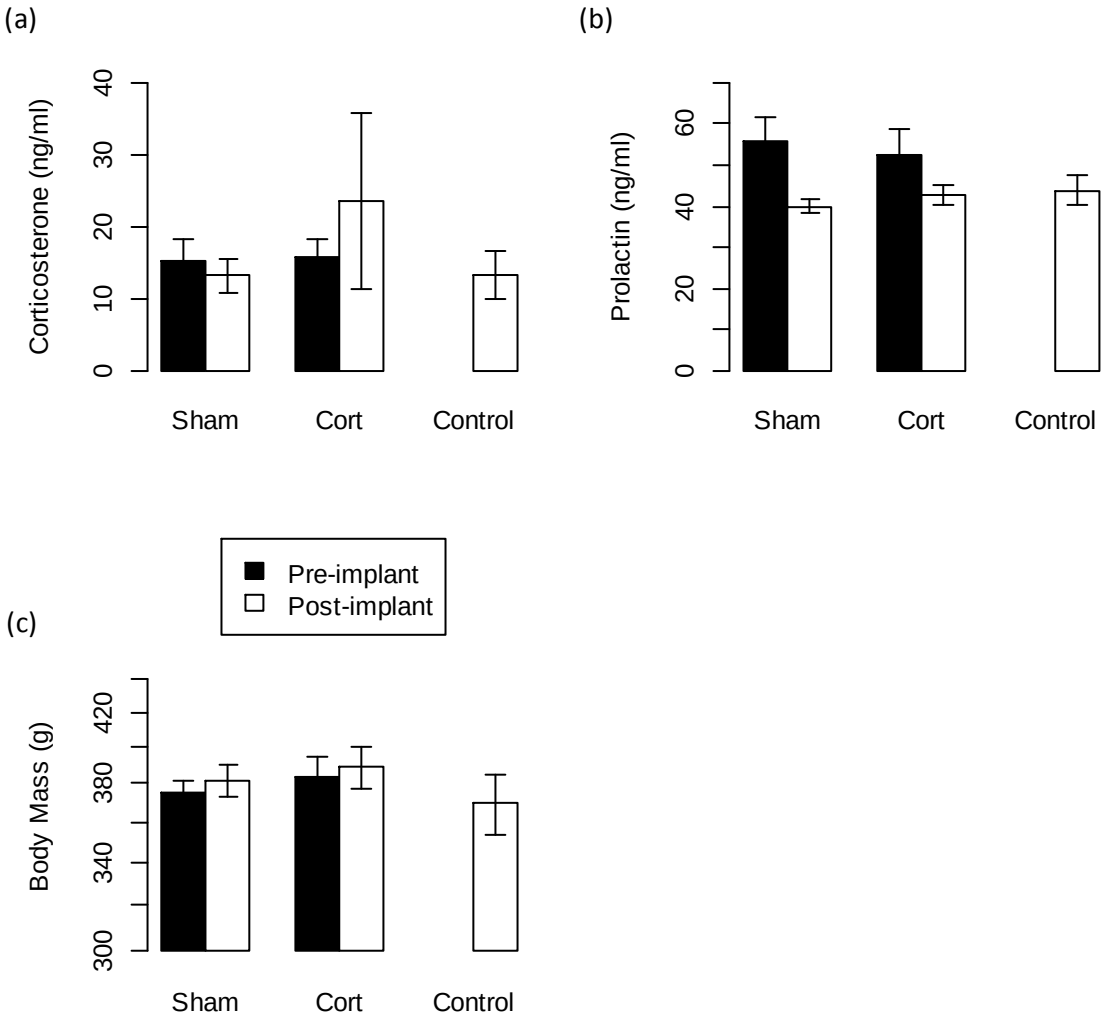


Fig. 4-2 (a) Corticosterone concentration, (b) prolactin concentration and (c) body mass (mean ± standard error) for kittiwakes given sham implants (Sham: n = 14), corticosterone implants (Cort: n = 12) and no implants (Control: n = 7). Only implanted birds that were successfully recaptured are included and only samples taken at the time of post-implant are available for control birds.

4.4.3 Nest attendance

There was no treatment effect on the presence of a previously implanted bird at the nest (linear mixed effects model: t = 0.38, df = 33, P = 0.71). However there was a significant effect of sex (t = 2.95, df = 33, P = 0.01) and the interaction between treatment and sex (linear mixed effects model: t = 2.42, df = 33, P = 0.02; Fig. 4-3a), with treated females attending more than untreated females and treated males attending less than untreated males. There was a significant effect of time since implant (linear mixed effects model: t = 2.19, df = 784, P = 0.03) with a 4.1 ± 1.3 % reduction in nest attendance per day. There was no significant effect of brood size (linear mixed effects model: t = 1.04, df = 784, P = 0.30) or the interaction between treatment and time since implant on nest attendance during chick-rearing (linear mixed effects model: t = 0.21, df = 784, P = 0.83).

4.4.4 Breeding success

Corticosterone-treated birds fledged fewer chicks than sham treated birds (binomial generalized linear model: z = 2.50, P = 0.01; Fig. 4-3b) and there was no significant difference in the number of chicks fledged at sham and control nests (z = 0.89, P = 0.38; Fig. 4-3b). However, when breeding success was calculated as the number of chicks fledged per egg laid at each nest, the difference between corticosterone-treated (mean ± SD: 0.35 ± 0.42) and sham-treated (0.56 ± 0.38) nests was only marginally significant (z = 0.55, P = 0.08). Breeding failures, i.e. the loss of all remaining chicks, occurred on average on June 21 ± 9 (mean ± SD), which was 16 ± 9 days after implant removal (Fig. 4-1).

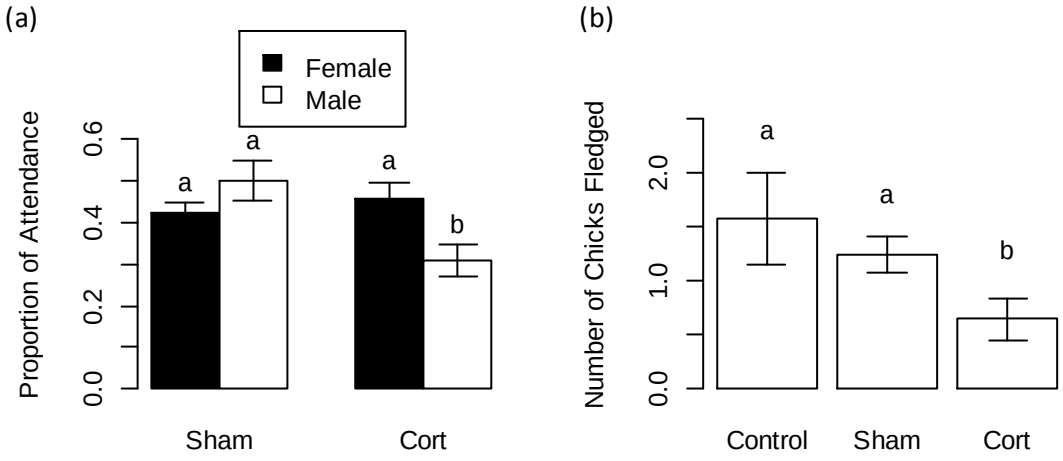


Fig. 4-3 (a) Nest attendance (proportion of visits; mean ± standard error) during chick-rearing of male (open bars) and female (filled bars) corticosterone- and sham-implanted kittiwakes. (b) Breeding success (mean ± standard error) calculated as number of chicks fledged for kittiwakes given no implants (Control: n = 7), sham implants (Sham: n = 21) and corticosterone implants (Cort: n = 17). Letters above bars indicate statistical significance between groups (mean values of bars with the same letter are not significantly different (a; P > 0.05); mean values of bars with different letters are significantly different (b; P < 0.05).

4.5 Discussion

Corticosterone concentrations, measured during chronically stressful conditions, have been associated with reductions in prolactin concentrations and body condition (Angelier and Chastel, 2009), and decreased reproduction and survival (Crespi et al., 2013). Our results support these findings in part, with exogenous corticosterone treatment to simulate chronic stress explaining some of the decrease observed in breeding success. However, we found no evidence for an effect on circulating prolactin or body mass after eight days of treatment.

The fact that there was no significant difference in corticosterone concentrations on day eight of the experiment compared to the time of implantation, yet there was a difference in breeding success between the treatment groups, suggests that corticosterone had been elevated, but for a shorter duration than we expected. Sustained low and medium doses of corticosterone were successfully administered to white throated sparrows using Alzet® osmotic pumps (Horton et al., 2007); however Fig. 2 in Horton et al. (2007) indicates that in both cases this initially resulted in elevated circulating concentrations of this hormone followed by a decline in concentrations. Medium doses peaked the day after implantation and low doses peaked four days after implantation. A similar pattern of change could have occurred in our experiment and would likely be explained by increased metabolism or clearance rates of circulating corticosterone and negative feedback (Newman et al., 2010). Clearance rates will be higher with higher concentrations of corticosterone in the bloodstream and in addition, the experimental manipulation may have caused exogenous corticosterone-induced negative feedback, thus decreasing endogenous production and returning circulating concentrations to pre-treatment values (Newman et al., 2010). We were unable to monitor change in corticosterone during the experiment by recapturing birds repeatedly due to the disturbance this would have caused the colony; we would have reduced our chances of recapture at the time of implant removal and caused additional acute stress, the effect of which would have been indistinguishable from our corticosterone manipulation.

If birds had fully recovered from the eight-day chronic stress manipulation by the time of breeding failures later in the season, we would have expected breeding success to be unrelated to treatment. Instead, treated birds fledged fewer chicks, suggesting that the treatment had a lasting effect. This effect may be partly due to a difference in clutch size between the treatment groups, because the effect was only marginally significant when breeding success was defined by the number of chicks fledged per egg laid. However, because there was still a marginal effect we can assume that treatment explains some of the variation seen in breeding success. The negative effect we found on breeding success may support the corticosterone induced reproductive conflict hypothesis (Love et al., 2004) and reflect the long-lived life-history strategy of the kittiwake, which favours self-maintenance over current reproductive investment to ensure survival for future breeding opportunities. Because our results show a negative effect of treatment on breeding success, it is unlikely that corticosterone was blocked, as has been found in other studies where exogenous corticosterone down-regulated endogenous corticosterone production (e.g. Goutte et al., 2011). However, it is possible that after implantation, endogenous corticosterone levels

may have dropped precipitously, impacting an individual's ability to maintain proper energy homeostatic functioning by down-regulating the glucocorticoid stress response (reviewed in Busch and Hayward, 2009). Such an inhibition of the stress response could have resulted in the observed reductions in breeding success later in the season.

Kittiwakes breeding on the Isle of May tend not to fail until the latter half of the chick-rearing period, when demands due to the energetic costs of rearing chicks often exceed the available food supply in the environment (e.g. Harris and Wanless, 1990, Harris and Wanless, 1997). Atlantic kittiwakes may be relatively prudent parents, abandoning breeding later in the season, compared to Pacific kittiwakes, which tend to have slower life-history strategies (Hatch et al., 1993, Frederiksen et al., 2005a, Suryan et al., 2009). In our corticosterone-implanted birds, failures also occurred during chick-rearing and no failures occurred until at least a week after implant removal. This suggests that the birds were able to continue to act as prudent parents until later in the season, at which point the corticosterone treatment had a delayed effect on the number of chicks fledged. Alternatively, as discussed above, the corticosterone treatment could have blocked corticosterone, resulting in a compromised stress response later in the season. We have data to suggest that on average breeding success was relatively high across the population in 2011 (2011: 0.9 chicks fledged per active nest; 1986–2011: 0.5 ± 0.1 chicks fledged per active nest) and that average baseline corticosterone concentrations were significantly lower in 2011 compared to 2010 (2010: 19.9 ± 19.2 (chapter one); 2011: 13.6 ± 8.4; Student's t test: $t = 2.22$, $df = 99$, $P = 0.03$), which further supports the idea that birds were relatively unstressed during most of the breeding season in 2011. Thierry et al. (2013) found a gradual effect of implanting Adélie penguins *Pygoscelis adeliae* with corticosterone pellets on incubation behaviour, with birds abandoning incubation several days after treatment. Our results suggest an even more gradual effect on breeding success of a corticosterone treatment during chick-rearing.

The lack of a reduction in the prolactin concentrations of corticosterone treated birds suggests that corticosterone does not have an immediate effect on prolactin. This is in line with our results that suggested a delayed effect on breeding success rather than an immediate abandonment of breeding. We speculate that prolactin would have declined following failure, when the stimulatory effects of the nest and chicks would have been removed (Hall and Goldsmith, 1983), and may have declined prior to failure when we were unable to catch kittiwakes. The study of kittiwakes breeding in Svalbard, Norway by Angelier et al. (2009a) showed that when corticosterone was administered using silastic

tubes, its concentration was elevated to supra-high levels 24 hours later, and whilst this caused a small but significant decline in prolactin concentrations, the decline did not occur until after corticosterone had returned to baseline values, on day three. We speculate that we might have found a similar decline in prolactin had we been able to blood sample birds at a later date. However, from our results we cannot assume that prolactin concentrations fall as a result of chronically raised corticosterone, or that low prolactin concentrations are necessary to induce breeding failure. Recently, Angelier et al. (2013) showed a lack of a mechanistic link between corticosterone and prolactin concentrations after an acute capture-restraint stress response. Our results suggest that the same is true in the short-term (one week) after a chronic stress treatment, proposing that corticosterone and prolactin may be mediating different aspects of the response to environmental perturbation.

Schultner et al. (2013) suggested that energy allocation is more dynamic than previous studies have often assumed, with an initial increase in baseline corticosterone concentrations being related to increases in body condition, used as a proxy for endogenous energy reserves, until a threshold level. A subsequent decline in body mass, below a critical threshold level, may cause breeding failure, as documented in Arctic terns *Sterna paradisaea* facing natural chronic stress (Monaghan et al., 1992). It is possible that we manipulated corticosterone concentrations within the range of values that maintained body mass rather than inducing a decline. Our results are also limited in sample size, which reduces the likelihood of detecting an effect over and above the natural variations in body mass due to time of feeding. We speculate that our corticosterone treated birds had lower resistance to further physiological or environmental stress later in the chick-rearing period compared to the sham-implanted or control birds. Our results are in agreement with Thierry et al. (2013) who found that elevated corticosterone was not sufficient to cause breeding failure, unless it was combined with other factors such as breeding experience, weather conditions and body condition at fledging.

Female corticosterone-implanted birds attended their nests more than sham-implanted females, whilst the reverse was true for males. This suggests that our prediction that corticosterone treatment would disrupt breeding behaviour and reduce nest attendance holds up in male kittiwakes but not females. Male and female seabirds have previously been shown to have differing patterns of change in baseline corticosterone concentrations, body condition, provisioning rates and nest attendance from incubation to chick-rearing, with females (e.g. Lormée et al., 2003) or males (e.g. Harding et al., 2004) acting more prudently during the chick-rearing period. Leclaire et al. (2011) showed that

experimentally handicapped male kittiwakes attended their nests less than control males but maintained the same rate of chick feeding, whilst their female partners compensated by reducing their provisioning rate and increasing their nest attendance. Our results suggest that female kittiwakes show greater prudence throughout the chick-rearing period following chronic stress than they would under normal conditions.

One limitation of our study is that we measured corticosterone concentrations rather than corticosterone binding globulin (CBG). CBG regulates the access of hormones to tissues and may reveal how much corticosterone is free and therefore biologically active, and how much is bound and therefore biologically inactive (Breuner et al., 2013, Desantis et al., 2013). We attempted to mimic chronic stress by administering corticosterone using Alzet osmotic pumps at a constant rate over a week. Previous studies have tended to use open-ended silastic tubes, or small incisions in silastic tubing, to facilitate the release of corticosterone, which results in rapid and uncontrolled release of the hormone and consequently higher clearance rates and negative feedback, shutting-down endogenous corticosterone secretion (Romero et al., 2005, Newman et al., 2010). This potential burst delivery of corticosterone is unlikely to mimic chronic stress, such as that experienced during adverse environmental conditions, which previous studies have attempted to emulate. Self-degradable corticosterone pellets do not work exactly as reported by the manufacturers (Müller et al., 2009), instead resulting in a peak elevation in circulating corticosterone over a shorter period than expected (Thierry et al., 2013). We were unable to recapture birds repeatedly during the treatment because of the readily disturbed nature of kittiwakes breeding on the Isle of May. Further studies are needed to measure the profile of change in corticosterone concentrations, after implantation with osmotic pumps, in order to determine the value of osmotic pumps as a method of mimicking chronic stress in a long-lived bird.

Chapter Five

Evaluating stress responses in captive Japanese quail

5.1 Abstract

The corticosterone stress response is an important mechanism by which birds and other organisms can cope with unpredictable perturbations in their environment. We were interested in the stress responsiveness of a captive bird, to see whether chronic stress experienced early in life, or selection for high productivity lines, has suppressed the stress response. We used a group of captive Japanese quail *Coturnix coturnix japonica* to assess whether the natural stress response is suppressed, by measuring corticosterone after a capture-restraint protocol. When capturing multiple individuals from the same group during an experiment, those captured latterly may have experienced disturbance during the capture of former individuals. Few studies consider the potential effect of this disturbance to the group prior to capture of an individual. We measured both time since first disturbing the group (group disturbance time) and time since capture of the individual (individual sampling time), and these showed no positive correlations with corticosterone concentrations. Our results suggest that the normal stress response to a capture-restraint protocol is suppressed in this captive bird.

5.2 Introduction

In vertebrates, glucocorticoid hormones are generally secreted when the hypothalamic-pituitary-adrenal (HPA) axis is activated by a stressor (Wingfield et al., 1998). Elevated glucocorticosteroids can cause an organism to enter the emergency life-history stage, in which non-essential behaviours and physiologies such as growth, reproduction, immune response and digestion are suppressed, and energy stores are mobilised (reviewed in Landys et al., 2006, Sheriff et al., 2011); this allows energy to be redirected towards survival (reviewed in Wingfield et al., 1998). This so called stress response is important for Darwinian fitness, especially in long-lived vertebrates. The stress response is a much studied area within ecophysiology because of its importance in ensuring survival in the face of environmental perturbations. In vertebrates, following perception of a stressor, corticotrophin-releasing hormone (CRH) is secreted from neurosecretory neurones within

the hypothalamus (Ricklefs and Wikelski, 2002). CRH passes from the median eminence to the anterior pituitary, where it causes the release of adrenocorticotropic hormone (ACTH). This targets the adrenal gland stimulating release of a glucocorticosteroid (Wingfield et al., 1998, Sapolsky et al., 2000). Corticosterone is the dominant glucocorticosteroid in amphibians, reptiles and birds and has been studied in a wide range of laboratory and field experiments (Holmes and Phillips, 1976, Fusani, 2008).

In the non-mammalian terrestrial vertebrates, the stress response involves a rapid rise from baseline concentrations to a peak concentration of corticosterone, followed by a return to baseline levels (Breuner et al., 2006). In mammals, this response usually involves cortisol rather than corticosterone. Baseline concentrations, the rate of increase, peak concentrations and the rate of decline in corticosterone all vary between species, among individuals and in relation to environmental conditions (Angelier et al., 2011 and examples cited therein).

Various studies have measured the time taken for corticosterone concentrations in birds to rise above baseline levels following a stressor. For example, in free-living white-crowned sparrows *Zonotrichia leucophrys gambelii*, captured via mist netting during the winter, there was a rapid increase in corticosterone within five to 10 minutes (Wingfield et al., 1982). However, the rate of increase was slower in male sparrows captured in summer and there was no increase in females captured in summer. The stress response may be suppressed during the breeding season, especially in birds that breed at high latitudes. This may be an adaptive mechanism by which the chances of reproductive success are increased despite harsh environmental conditions; for example, at high latitudes breeding seasons may be short and restricted and therefore it may be beneficial for an individual to breed despite less than favourable conditions in a given season (Wingfield et al., 1982). Dawson and Howe (1983) showed that there was no corticosterone increase within one minute of sampling in wild starlings *Sturnus vulgaris*, also captured via mist netting, but values increased thereafter. Corticosterone concentrations collected within one minute in starlings were lower than the within two minute values of white-crowned sparrows in the Wingfield et al. (1982) study. However, values were similar between these two studies and species after two minutes. Romero and Reed (2005) tested five avian and one reptilian species (n = 945) in an attempt to find a generalised time limit for baseline blood sample collection. They concluded that samples collected in less than two minutes could be reliably used to measure baseline corticosterone. Corticosterone measured in samples

collected within three minutes was consistently baseline or at least near baseline and beyond three minutes corticosterone concentrations may be stress-induced.

Depending on the severity of the stressor, glucocorticosteroid concentrations in vertebrates usually reach peak values 15–30 minutes after a stressor and return to basal concentrations within 60–90 minutes (de Kloet et al., 2005). This may be because the stressor is short-lived and corticosterone concentrations decline as the stressor disappears. Alternatively, elevated corticosterone may result in increases in the clearance rate of this hormone from the bloodstream and activation of negative feedback mechanisms that shutdown endogenous production. Different handling conditions during capture and restraint can result in differing durations of a stress response (e.g. Romero and Romero, 2002, Champagne et al., 2012). Romero and Romero (2002) compared the stress responses of three wild bird species—white-crowned sparrows, house sparrows *Passer domesticus* and Lapland longspurs *Calcarius lapponicus*—and found that corticosterone responses to stress can vary with species and trapping technique. After being left in mist nets for 15 minutes, both species of sparrow had raised corticosterone concentrations compared to birds immediately removed from the nets; however, there was no treatment effect in Lapland longspurs. Corticosterone concentrations then rose similarly over a 45-minute capture-restraint period in both treatment groups. When using seed-baited potter traps there was no difference in corticosterone response in birds removed immediately compared to those left in the trap for 15 minutes. However, in the case of Lapland longspurs, whilst there was no difference between treatment groups within the first 10 minutes of the capture-restraint protocol, the birds left in the trap had lower corticosterone concentrations at 30 and 60 minutes than those removed immediately. Seed-baited traps allow captured birds to feed, and this feeding behaviour may explain the suppression of plasma corticosterone concentrations.

Suppression of the stress response, as found in species breeding in harsh environmental conditions, might also occur as a consequence of being bred in captivity. This suppression might be an adaptive mechanism to reduce exposure to the damaging effects of chronic stress, or might be a by-product of selection for high productivity, in the case of a long domesticated species. Japanese quail *Coturnix coturnix japonica* (hereafter ‘quail’) are often used as laboratory animals for physiological and behavioural studies but relatively few studies of corticosterone have been carried out in this species to date. Captive zebra finches *Taeniopygia guttata* show normal stress responses (Evans et al., 2006, Wada et al., 2008, Monaghan et al., 2011) and a few studies to date have shown

similar results for quail. Malisch et al. (2010) reported a five- to 10-fold increase in corticosterone 60 minutes after an acute stress handling protocol and Cockrem et al. (2010) reported that corticosterone concentrations increased for 15 to 30 minutes after the onset of a handling protocol remaining elevated above baseline concentrations 60 minutes later. However, few studies have considered that a stress response may start prior to capture of a bird, particularly in captive birds that are housed in groups. Deciphering the timing of the onset of a stress response is difficult because external signals of stress are not always observable or measurable. However, vocalisations or sudden escape movements during attempted capture, or during capture of other birds in the group, can indicate stress long before capture is successful. Therefore, it is important to time the duration of an entire capturing and handling procedure, especially when measuring multiple individuals and potentially disturbing those measured latterly multiple times over.

The aim of this study was to evaluate the change in corticosterone in Japanese quail. We measured the stress response of birds that had experienced disturbance whilst others in the group were being captured (high group disturbance time) and that were blood sampled after longer than the recommended time to collect baseline values (high individual sampling time). We predicted that corticosterone concentrations would be elevated with high group disturbance time and high individual sampling time.

5.3 Methods

5.3.1 Study animals and housing

Quail (n = 20) were maintained in a single, indoor, climate-controlled aviary (2.2 m x 1.8 m x 2.1 m). Wood shavings covered the floor. Temperature was 13 °C and photoperiod was kept constant at 11 hours of light per day. Light intensity was 500 lux at floor level. Food (turkey starter crumbs) and water were provided ad lib. The quail had been housed in the aviary for four weeks prior to the study, allowing them sufficient time to become accustomed to their surroundings. All work was carried out under Home Office personal (Bethany Nelson: PIL 60/12426 and Alistair Dawson: PIL 70/1697) and associated project (Alistair Dawson: PPL 60/4176) licences.

5.3.2 Acute stress protocol

The quail (n = 20) were captured by hand sequentially from the aviary in order of ease of capture on November 24 between 14:00 and 15:30. After capture of a bird we removed it to a separate room out of sight from the aviary where the remaining birds were situated, and blood sampled the bird by puncturing the alar vein. A maximum of 1 ml of blood was

collected from each bird. For each bird we recorded the time since we first started working in the aviary until capture (group disturbance time) and the time from capture to the end of blood sampling (individual sampling time). We therefore considered the combined effect of disturbance to the colony throughout the experiment and disturbance through the handling and sampling of each individual. The quail were ringed and then returned to a second aviary, so that the same bird was not captured twice on the same day. This protocol was repeated using the same group of birds 56 days later (January 19; n = 19; one bird died of natural causes in the intervening period). This time period was due to logistical constraints but we can be confident that disturbance to the birds during the first sampling occasion would not still be in effect by the time of the repeat.

Across both sampling days (n = 39), birds were either blood sampled as soon as possible after capture (< 2 min, n = 21) or were restrained in a cloth bag before sampling (2–5 min, n = 18). These time periods reflect the recommended time to collect baseline blood samples (< 2 min) and handling beyond this time (2–5 min) (Romero and Reed, 2005). On the first sampling date of the experiment, the first eight birds were sampled in less than two minutes, the next 10 birds were sampled within two to five minutes, and the final two birds were sampled in less than two minutes. On the second date of sampling, the first 12 birds were sampled within two minutes and the final seven birds were sampled within four to five minutes. This means that on both sampling occasions group disturbance time and individual sampling time were correlated and therefore these two variables are confounded (linear mixed effects model: $t = 5.29$, $df = 18$, $P < 0.0001$). However, the order in which birds were captured varied between the two sampling occasions, which provided randomisation between, but not within, the two dates.

5.3.3 Hormone assay

Corticosterone concentrations were determined in March 2012 by a quantitative competitive enzyme-immuno assay (EIA). Plasma samples were equilibrated with 2000 cpm ¬3 H-CORT to measure recovery and extracted using diethyl ether. Extracted samples were analysed in duplicate using an EIA kit as described in Wada et al. (2007). A dose response curve of kittiwake plasma ran parallel to the standard curve. Values were corrected for sample dilution and recovery. The average extraction efficiency was 76 ± 1.5 %. The inter-assay variation was 6.8 % and the intra-assay variation ranged from 4.4 to 7.1 %.

5.3.4 Statistical methods

All statistical analyses were performed in the R computing environment (version: 3.0.1, R Development Core Team, 2013). Values presented are means ± standard error. To examine the effect of group disturbance time and individual sampling time on corticosterone levels, we used three linear mixed effects models each with bird identification (ring number) as a random effect. The first model had group disturbance time as the fixed effect; the second model had individual sampling time as the fixed effect; the third model had total time (group disturbance time + individual sampling time) as the fixed effect. These three models were used because we could not examine both group disturbance time and individual sampling time as separate variables in the same model. As corticosterone concentrations were constrained by being positive and the residuals were not normally distributed, we transformed this variable by taking the logarithm to base ten.

5.4 Results

The first bird was captured one minute after the first entry into the aviary and the last bird was captured 86 minutes after the first entry into the aviary (mean group disturbance time: 36.3 ± 4.0). Birds were blood sampled between 0.5 and five minutes (mean individual sampling time: 2.3 ± 0.4) after capture. Corticosterone values were on average 11.6 ± 1.7 ng/ml and ranged from 1.2 to 43.8 ng/ml. Neither group disturbance time (linear mixed effects model: $t = 1.44$, $df = 18$, $P = 0.17$; Fig. 5-1a) nor individual sampling time (linear mixed effects model: $t = 1.85$, $df = 18$, $P = 0.08$; Fig. 5-1b) significantly predicted corticosterone concentrations. Total time did not predict corticosterone concentration (linear mixed effects model: $t = 1.50$, $df = 18$, $P = 0.15$; Fig. 5-1c).

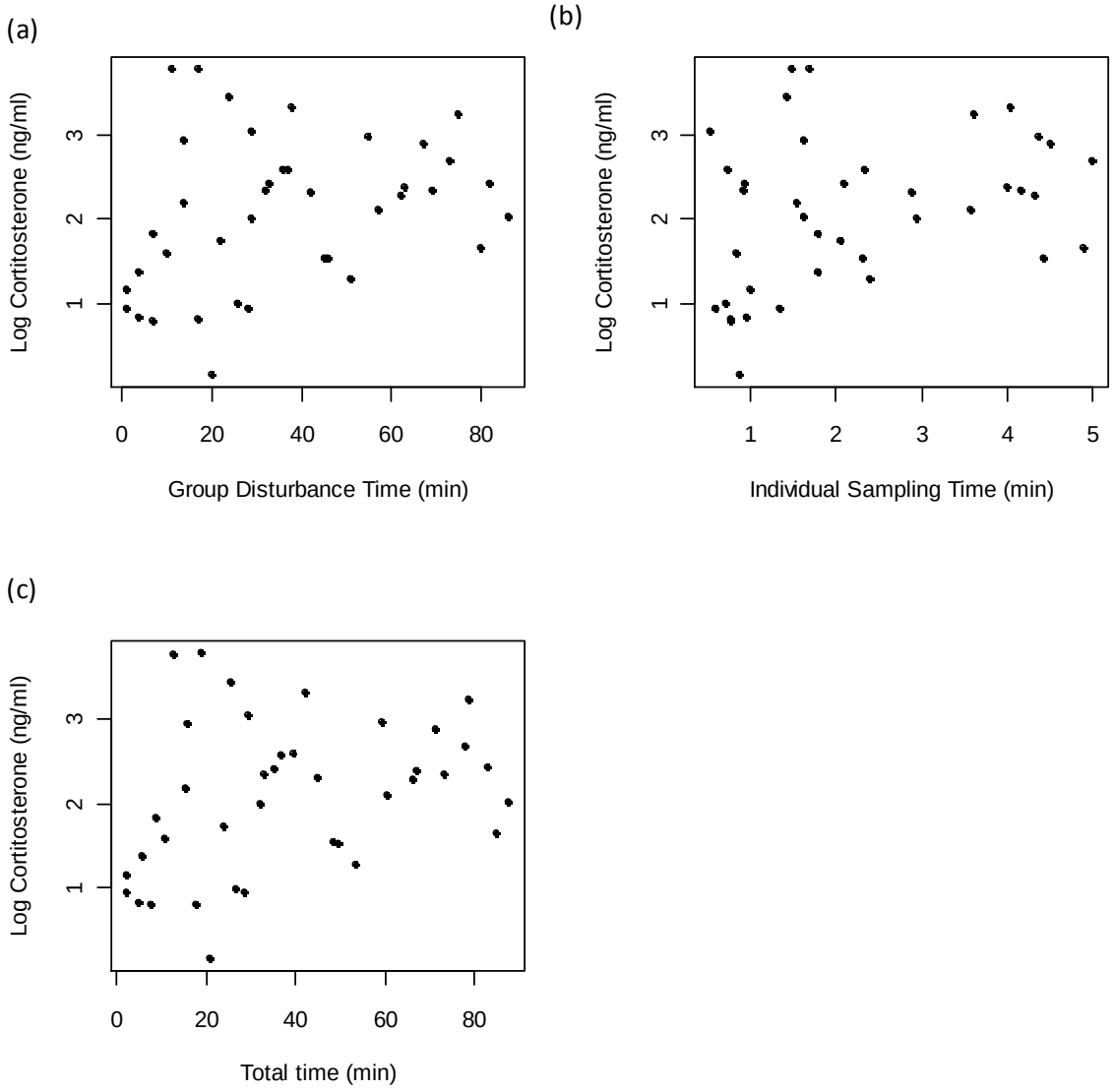


Fig. 5-1 Effects of (a) group disturbance time, (b) individual sampling time and (c) total time on the logged corticosterone concentrations of quail (first sampling date: n = 20; second sampling date: n = 19). No correlations were found.

5.5 Discussion

It is generally accepted that a rise in glucocorticosteroids is seen in organisms following an environmental stressor or a capture-restraint protocol (e.g. Sumpter et al., 1986, Widmaier and Kunz, 1993, Coddington and Cree, 1995, Romero and Reed, 2005; in fish, mammals, frogs and birds, respectively). This is because capture and handling are novel occurrences to wild animals, and therefore the HPA axis responds as it would to a stressful stimulus (Romero, 2002). However, some studies have shown cases where no elevation in corticosterone is detected during periods of capture (Ott et al., 2000, Kahn et al., 2007 and

examples cited therein). We found no apparent effect of group disturbance time or individual sampling time on the corticosterone concentrations of captive quail.

Romero and Reed (2005) found that seven datasets out of 14 (comprising five species: breeding redpolls, white-crowned sparrows, Lapland longspurs, snow buntings and iguanas) did not show any elevation in corticosterone within three minutes of capture. On the other hand, corticosterone started to rise after only two minutes in seven species, but values after three minutes still were closer to baseline concentrations than to the stress-induced concentrations measured after 30 minutes of a capture-restraint protocol. This shows that there is variation between species and populations in how fast stress responses can be detected. Although stress responses after a capture-restraint protocol have been previously recorded in quail (Cockrem et al., 2010, Malisch et al., 2010), we found no significant increase in corticosterone concentrations with increased group disturbance time and individual sampling time. Both Malisch et al. (2010) and Cockrem et al. (2010) used a capture-restraint protocol that involved lifting, inverting and then returning quail to a box repeatedly over five minutes, whereas our capture-restraint protocol involved holding captured birds with their heads in cloth bags. It is possible that the absence of a procedure involving repeated movement of the quail meant that the birds in our study were not sufficiently disturbed to show a significant increase in corticosterone concentrations over a five minute period. However, we might still expect to see an effect of capture regardless of the restraint protocol used.

It is possible that the birds in our study experienced some chronic stress early in life, which may have led to a down-regulation of their acute stress response in order to reduce the detrimental consequences of prolonged elevated corticosterone that they otherwise might have faced (Rich and Romero, 2005, Cyr and Romero, 2007). However, Evans et al. (2006) found that despite many generations in captivity, the stress responses of captive zebra finches were similar to those seen in wild populations. Monaghan et al. (2011) found that adult zebra finches exposed to elevated corticosterone in early life showed higher stress responsiveness. A recent study in quail showed no difference in the baseline or acute stress-induced concentrations of corticosterone between chronically stressed birds and controls (Calandreau et al., 2011). Studies in poultry have shown that birds selected for high stress responses have lower immunity, making them more susceptible to disease, and have lower growth rates than those selected for low stress responses (e.g. Gross and Colmano, 1971, Brown and Nestor, 1974). A long-term selection experiment of quail has shown that in lines selected for high stress, the high stress trait is

highly heritable, whereas in lines selected for low stress, the low stress trait is only moderately heritable (Satterlee and Johnson, 1988, Odeh et al., 2003). We can therefore speculate that as a long domesticated species, low stress quail might have been selectively bred as a by-product of selection for high productivity; presumably high stress birds would be less productive, and therefore selecting for high productivity would, by default, select for low stress responses. We can speculate that an adaptive or selective suppression of the stress response could be responsible for the lack of an increase in corticosterone seen during the relatively short period of handling (individual sampling time) and even the longer period of disturbance to the group prior to capture (group disturbance time).

On average corticosterone concentrations in our study were 11.6 ± 1.7 ng/ml, which is higher than the baseline concentrations typically reported in the literature for quail (e.g. < 3 ng/ml; Cockrem et al., 2010, 1.5 ± 0.3 ng/ml; Hazard et al., 2008). This may indicate that the birds were under relatively high levels of chronic stress and therefore our results may not apply to birds with lower baseline concentrations of corticosterone. Variation between individuals in corticosterone concentrations was marked in our study and may occur partly due to genotypic and phenotypic differences. Personality may also contribute to such variation. Cockrem (2007) found that birds with proactive personalities have lower corticosterone stress responses compared to those with reactive personalities. This suggests that within a population there may be high levels of variation in the physiological stress response due to the variation in the behavioural profiles of the birds. Genetic variability of HPA axis activity has been demonstrated in quail, with long and short tonic immobility genotypes having different corticosterone responses to acute stressors (Hazard et al., 2008). However, there was no difference between the responses of the two genotypes to lower intensity stressors.

In conclusion, we have shown that the corticosterone concentration of quail was not affected by a combination of increased group disturbance time and individual sampling time. We suggest that this could be a result of an adaptation to suppress the stress response due to chronic stress during captivity, or a by-product of selection for highly productive lines of this long domesticated species.

Chapter Six

General discussion

6.1 Overview

Changing environmental conditions are known to be impacting on the population dynamics of many organisms. Understanding the mechanisms and limitations of behavioural and physiological flexibility is crucial for predicting population viability (Komers, 1997, Jepsen and Topping, 2004, Hofmann and Todgham, 2010). This thesis aimed to investigate what mechanisms cause changes in breeding success of a top marine predator in response to marine environmental change. In order to address these questions, long-term dietary, body mass and productivity data were used alongside an experimental study to mimic chronic stress, using the black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake') as a model species. Essentially, the work that I have carried out shows that the mechanisms involved in the control of the breeding success of a top predator include changes in adult body mass, foraging trip duration and diet composition. This chapter discusses the wider context into which this thesis fits, as well as outlining potential applications and areas for future research.

6.2 Perspectives on environmental change using long-term data

There is an ever increasing need for researchers to investigate the impacts of environmental change on ecosystems; environmental change is occurring more or less continuously and the ways that species respond to change depend in part on the extent to which they have evolved coping mechanisms for the degree and nature of change occurring. Numerous studies are being carried out to investigate changes in the diet, foraging behaviour, body mass and breeding success of wild populations (e.g. Brown bears *Ursus arctos*; Hilderbrand et al., 1999, moose *Alces alces*; Herfindal et al., 2006, Atlantic cod *Gadus morhua*; Sherwood et al., 2007). Long-term studies are invaluable when tracking how individuals (Jones et al., 2008, Clutton-Brock and Sheldon, 2010) and populations (e.g. Chamberlain and Pearce-Higgins, 2013, van Asch et al., 2013) respond to changes in their environment. Whilst individual-level data were not available for my study, chapters two and three investigate long-term population changes in a marine top predator. Marine and terrestrial environments are affected by anthropogenic activities, including climate change, which occur over small and large-scales. Top predators can provide useful

indicators of ecosystem change and biodiversity through their life-history characteristics and position at the top of the food chain (Boyd et al., 2006, Sergio et al., 2008). However, top predators should only be considered indicators within a specific ecosystem or habitat where they occupy the top predator position, rather than across an entire heterogeneous region, since they may occupy this position only in certain areas depending on spatial variability in other predators (Sergio et al., 2008). Within the NW North Sea ecosystem kittiwakes act as top predators, occupying the top trophic level along with other seabirds and marine mammals. Adult kittiwakes are not predated within this geographical area of their distribution; however eggs and chicks can be vulnerable to low levels of predation.

Indicators of environmental change allow large-scale, long-term variability to be inferred from measurable indices and reveal information about the impacts of environmental change on the ecosystem as a whole. Changes in phenology provide useful indicators of environmental change because mismatches between predators and prey can indicate disruption between the trophic levels of an ecosystem (Visser et al., 1998) and temporal shifts in the timing of biological events point to shifts in climatic suitability for those events. Phenological mismatch may occur because of tradeoffs with the fitness benefits of breeding early (Verboven and Visser, 1998), photoperiodic constraints on the timing of breeding (Dawson, 2008) or because individuals may utilise alternative prey types instead of altering their phenology. The changes in the timing of the switch from adult (1+ group) sandeels to young of the year (0 group) sandeels in the diet of kittiwakes (chapter two) confirms the findings of previous studies that have suggested temporal variation in prey availability for kittiwakes (Lewis et al., 2001b). Long-term trends have shown changes in the estimated hatch date and juvenile growth rate of sandeels (Frederiksen et al., 2011) and in the timing of kittiwake breeding within the north-western (NW) North Sea (Wanless et al., 2009). Sandeels feed predominantly on the copepod *Calanus finmarchicus*, which has shown a long-term decline (1960–2010) at the southern end of its North Sea distribution (Frederiksen et al., 2013). This has had negative effects on seabird populations and these effects are likely to spread to populations breeding further northwards in the future. Changes in the localised availability of prey species for breeding seabirds have been found in other regions of the Atlantic and in the Pacific (e.g. Sydeman et al., 2001, Durant et al., 2003, Gasbjerg, 2010, Hatch, 2013).

The foraging trip duration of kittiwakes was associated with variation in adult body mass and breeding success, acting independently from the marginal effect of diet composition and masking this weaker effect (chapter three). The benefits of higher

proportions of 0 group sandeels during the chick-rearing diet of kittiwakes were predicted to be explained by fish being closer to the colony, or easier to capture close to the colony, and hence shorter foraging trip durations being required by adult birds. However, the results suggest instead that whilst foraging trip duration is of primary importance for breeding kittiwakes, the different age classes of sandeels did not differ in their distance from the colony nor in the time it took for birds to obtain them during a foraging trip. This has implications when predicting the foraging area used by kittiwakes, and other sandeel-dependent seabirds breeding in the NW North Sea, throughout different periods of the breeding season. The foraging range of kittiwakes breeding on the Isle of May, National Nature Reserve, Firth of Forth, south-east Scotland (56° 11‘ N, 02° 33’ W) has previously been estimated using purpose-built activity loggers (Daunt et al., 2002). The authors showed an upper limit on foraging range and a flexible foraging strategy, which were speculated to reflect the distribution and patchy availability of prey rather than energetic constraints on flight costs. Contrary to expectations, a positive relationship between breeding success and foraging range has previously been found for kittiwakes breeding in the NW North Sea (Camphuysen et al., 2006); however this relationship was explained by the fact that relatively small seabirds may avoid feeding in inshore areas where larger species such as *Larus* gulls dominate. Therefore, good breeding years may be associated with years when feeding conditions are favourable further from the colony, rather than close to the colony. Foraging areas used by seabirds are of particular monitoring importance, due to interactions with fisheries (Frederiksen et al., 2004) and current advances in off-shore wind farm developments in the NW North Sea (Fox et al., 2006). The foraging range of breeding birds is also important when identifying marine protected areas (MPAs) and whilst proposals can be made from reviewing general foraging range data for the North Sea, site-specific monitoring is vital to refine such proposals (Thaxter et al., 2012).

Changes in body mass during the breeding season can indicate breeding success, with precise thresholds of condition often determining either whether individuals will breed or not (e.g. asp viper *Vipera aspis*; Naulleau and Bonnet, 1996), or whether they will breed successfully or abandon breeding (e.g. Adélie penguins *Pygoscelis adeliae*; Ballard et al., 2010). How body mass relates to breeding activity depends partly on when measurements are taken. Body mass measured during the autumn or winter period may indicate the likelihood of a breeding attempt, whilst mass measured early during the breeding season, for example during pregnancy or incubation, may indicate the survivability of young (e.g. caribou *Rangifer tarandus*; Cameron et al., 1993). Body mass

change is also largely dependent on the condition of an individual. It is possible that during unfavourable environmental or foraging conditions, when an individual is at the lower end of its optimum condition, increasing body mass will benefit fitness ('fat and fit hypothesis'; Schultner et al., 2013). On the other hand, during optimal conditions fitness will benefit from mass loss, or the suppression of further mass increase, to avoid additional costs to mobility when foraging ('lean and fit hypothesis'; Schultner et al., 2013). The change in body mass of breeding kittiwakes outlined in chapter two acted as an indicator of fitness, with years of higher success at the end of each breeding stage associated with years of higher mass at the end of that stage.

One limitation of long-term population-level studies is that they are often restricted to non-causal correlations. Non-causal correlations are in danger of being spurious, if confounding variables are in fact driving the relationships. This explains why the results of chapters two and three may not be conclusive or exclusive in identifying the causes of breeding failure in the kittiwake.

6.3 Perspectives on environmental change using hormonal manipulations

Experimental manipulations avoid potentially spurious correlations between variables, instead allowing causal relationships to be determined. Hormonal studies are useful when investigating environmental change because rapid and effective physiological, as well as behavioural, responses reveal the ability of an organism to resist and recover from perturbations (reviewed in Wingfield, 2013). Specifically, environmental variation and the evolution of species-specific traits are revealed in part by the degree of variation in the glucocorticoid stress response among species (Jessop et al., 2013). Life-history traits such as age-specific life-history transitions, reproduction and survival can be influenced by glucocorticoid-induced changes in energy allocation, physiology and behaviour (reviewed in Crespi et al., 2013). However, the relationships between glucocorticoids and life-history traits are complex. In general, individuals with low baseline concentrations of glucocorticoids have higher reproductive success, but this relationship is inconsistent, as is that between stress-induced glucocorticoids and reproductive success (reviewed in Busch and Hayward, 2009). Busch and Hayward (2009) highlighted the fact that chronic exposure to stressors can result in the down-regulation of the glucocorticoid stress response, which will reduce an organism's coping mechanism during subsequent stress.

Chronic stress in nature may occur for different reasons and can refer to a range of physiological, behavioural and psychological responses. For example, within human populations chronic stress tends to refer to sustained psychological stress, and evidence suggests that a similar response may occur after long-term exposure to predators in laboratory animals and wild populations (Clinchy et al., 2013). If this is the case, predator-induced chronic stress may be better described as the 'ecology of fear' (Clinchy et al., 2013). Boonstra (2013) has raised the question of whether chronic stress occurs in a strictly maladaptive or pathological sense within wild populations. He argues that the responses of individuals to chronic stressors, such as poor food availability, poor weather conditions and high predation risk, tend to be adaptive and benefit fitness. Whilst poor food availability is likely to cause a direct physiological challenge to an organism for a prolonged duration of time, the direct stress associated with high predation risk may be short-lived but have longer-lasting consequences due to a resultant perceived risk. It has been suggested that chronic stress only arises in populations facing high predation risk if it is beneficial for fitness. For example, evidence suggests that chronic stress occurs adaptively in cyclic snowshoe hare *Lepus americanus* and ground squirrel *Urocitellus parryii* populations, but does not occur in cyclic vole *Myopus glareolus* or noncyclic elk *Cervus canadensis* populations (reviewed in Boonstra, 2013). From an evolutionary point of view this would explain why chronic stress occurs in some wild populations despite the often maladaptive or pathological consequences associated with it.

Correlational and experimental studies provide evidence for a negative association between food abundance and both baseline and stress-induced glucocorticoids (Clinchy et al., 2004, Schoech et al., 2004, Wasser et al., 2004, Jenni-Eiermann et al., 2008, reviewed in Busch and Hayward, 2009). Whilst poor feeding conditions tend to cause increased baseline and stress-induced glucocorticoids, severe food limitations have variable effects that cannot easily be predicted (reviewed in Busch and Hayward, 2009). Studies have highlighted the lack of any direct link or linear relationship between corticosterone concentrations and body mass (e.g. Golet et al., 2004, Chastel et al., 2005), which may be explained by the complexity of a breeding bird's optimum body mass depending both on lower and upper limits of condition (Schultner et al., 2013). The results in chapter four showed no immediate change in body mass after implantation with corticosterone to mimic chronic stress. This may have been because changes in body mass were only evident later in the season when limited food availability acted additively with the previous chronic stress treatment to reduce breeding success. Alternatively down-regulation of the stress response as a result of the chronic stress treatment may have had negative fitness

consequences during subsequent stress later in the season, resulting in reduced body mass and ultimately breeding failure.

Whilst no evidence was found in chapter four to support the hypothesis that prolactin mediates the effect of chronic stress on breeding failure, a decline in prolactin later in the chick-rearing period may have occurred. Alternatively, prolactin may decline only as a result of failure and the removal of the stimuli within the nest (Dawson and Goldsmith, 1985, El Halawani et al., 1986). A recent study of little auks *Alle alle* showed that prolactin concentrations increased in response to an acute stressor during chick-rearing, contrary to predictions (Wojczulanis-Jakubas et al., 2013). This may be explained by an adaptive mechanism allowing parent auks to maintain parental care despite being absent from the nest stimuli during long foraging trips, despite chronic stress due to fluctuating and often unfavourable foraging conditions, despite frequent stress due to predation from glaucous gulls *Larus hyperboreus*, or despite lower baseline concentrations of prolactin during chick-rearing compared to incubation (Wojczulanis-Jakubas et al., 2013). These possible explanations highlight the complexity of the relationship between corticosterone and prolactin, and more generally between stress and breeding behaviour. If prolactin concentrations were raised in little auks in order to prevent concentrations falling below a threshold for parental care, it is possible that a similar mechanism could have prevented prolactin concentrations from declining in the chronically stressed kittiwakes in chapter four.

6.4 Perspectives on the kittiwake as an indicator species

The kittiwake has previously been identified as a useful indicator of marine environmental change, largely due to its sensitivity to change in prey availability (Frederiksen et al., 2005a, Frederiksen et al., 2007b), which has been negatively and additively affected by increasing sea surface temperature and the activity of a fishery in recent years (Frederiksen et al., 2004). Both 1+ group sandeels (Rindorf et al., 2000, Frederiksen et al., 2004, Daunt et al., 2008) and 0 group sandeels (Harris and Wanless, 1997, Lewis et al., 2001b, Daunt et al., 2008) have been linked to kittiwake productivity. However, the results in chapter two show that the proportion of 1+ group relative to 0 group sandeels in diet samples of breeding adults collected during the chick-rearing period, but not the incubation period, is involved in determining breeding success, with productivity being marginally higher when the proportion of 0 group sandeels in the diet was higher. The suggestion that conditions in the NW North Sea during the chick-rearing period have greater influence on breeding success than those during incubation supports the findings of Lahoz-Monfort et al. (2013)

for common guillemots *Uria aalge* and razorbills *Alca torda* on the Isle of May, and previous studies of the kittiwake population (e.g. Harris and Wanless, 1997). In chapter four, the number of kittiwake chicks fledged at the end of the season was shown to indicate a chronic stress treatment during late incubation, emphasising the fact that conditions during chick-rearing act in concert with stress that may have occurred earlier in the season to determine the number of chicks successfully fledged. Despite the chronic stress treatment being implemented during incubation, failures tended to occur during late chick-rearing, as would be expected under natural environmental conditions due to peaks in energy demand, rather than occurring soon after the treatment.

Whilst kittiwake breeding success has previously been related to prey availability (Gill et al., 2002, Frederiksen et al., 2007a, Coleman et al., 2011), such studies did not include diet composition or foraging data. This gap in knowledge was addressed in chapters two and three, which highlighted a strong negative effect of foraging trip duration and a weaker independent effect of diet composition on kittiwake breeding success. This suggests that kittiwakes act as specific indicators of both the composition of the forage fish community (i.e. small shoaling fish such as sandeels) within the NW North Sea, and the spatial distribution of those species, in addition to prey availability more generally. The relationships between diet composition, foraging trip duration and breeding success were mediated via changes in adult body mass, with years of lower proportions of 1+ group relative to 0 group sandeels and shorter foraging trips during chick-rearing being associated with years of less adult body mass loss (chapters two and three). In addition, adult body mass at the end of each breeding stage was positively associated with the success of that stage. These results therefore suggest a key role for adult body mass in mediating the link between kittiwake predators and their piscivorous prey.

6.5 Recommendations for future research

6.5.1 Long-term monitoring of populations

Long-term studies that compare several contrasting seasons need to be further utilised in the understanding of how long-lived birds optimise their reproductive success in the face of changing environmental and foraging conditions (Weimerskirch et al., 2000, Clutton-Brock and Sheldon, 2010). Not only should long-term datasets be maintained and extended into the future, but seabird researchers should also seek to share past and future results within online databases, in order to facilitate collaborations on a global scale (Hatch, 2013). For example, kittiwakes have been studied in both the Atlantic and Pacific oceans,

allowing comparisons of geographically distinct populations and global-scale research collaborations (Hatch et al., 1993, Suryan et al., 2009).

The use of long-term data in conjunction with manipulative experiments is a vital combination when researching the effects of ecological parameters on population processes. The value of such datasets has been highlighted in the extent and complexity of the data analysed in chapters two and three of this thesis. Continuing such monitoring using often relatively inexpensive, low-technology, traditional methods, but requiring the time and effort of many researchers, is vital for future research. Important monitoring sites include Bird Island, Antarctic (e.g. Williams and Croxall, 1991, Phillips et al., 2004), Hornøya, Norway (e.g. Barrett and Krasnov, 1996, Sandvik et al., 2005, Sandvik et al., 2008), the Pribilof Islands, Alaska (e.g. Byrd et al., 2008, Sinclair et al., 2008, Renner et al., 2012) and the Isle of May, Scotland (e.g. Harris and Wanless, 1997, Wanless et al., 2009; chapters two and three); these and similar resources should be utilised in the future both to continue the complex analyses of existing historical data and to update these datasets for years to come.

Chapter two showed that years of higher proportions of 0 group relative to 1+ group sandeels were marginally associated with years of higher body mass of chick-rearing kittiwakes and higher breeding success. This may suggest that the recent trend towards greater proportions of 0 group sandeels relative to 1+ group sandeels in the diet of breeding kittiwakes should have resulted in a trend towards higher breeding success. However, trends over time have shown the opposite, with declining breeding success and population size. It is possible that the influence of increasing proportions of clupeids in the kittiwake diet could be contributing to this decline. However, there was no evidence to support a negative effect of higher proportions of clupeids on adult body mass or breeding success. Further years of data may reveal the implications of increasing proportions of clupeids on kittiwake breeding and whether this prey type could provide a beneficial alternative if sandeel availability and quality continues to decline (Frederiksen et al., 2013). It is also important to consider the lipid content of prey in addition to the prey type dominating the diet in order to test the junk food hypothesis (Alverson, 1992), which states that if prey are small in size and low in lipid content they may be of little calorific value to predators (Rosen and Trites, 2000, Wanless et al., 2005, Osterblom et al., 2008). Therefore, future work should incorporate assessment of the energetic content of each prey type (Wanless et al., 2007), in addition to diet composition.

6.5.2 Further studies of stress physiology

Future research should address the need to explore life-history decisions on a population-level as well as the individual-level. This would answer the question raised by Wingfield (2013) of whether populations that withstand environmental perturbations are more flexible in their stress responses and life-histories than populations that are in decline. Whilst the responses of individuals to environmental perturbations have been investigated, few studies to date have considered the responses of populations to increasing frequencies or intensities of perturbation. Future research should also address the current contention in the role of prolactin and corticosterone in brood desertion or breeding failure by further experimentation to link the regulation and action of these two hormones (reviewed in Wingfield, 2012, Angelier et al., 2013). Manipulating prolactin secretion and binding properties would be useful (Kosztolányi et al., 2012), but is not easy. Injections of the prolactin stimulating hormone, vasoactive intestinal peptide (VIP), lead to only short-term elevations (Vleck and Patrick, 1999), whilst treatment with prolactin would invoke an immune response. Immunization against VIP has worked but is difficult to implement (e.g. El Halawani et al., 1996). It would be useful to look for an interaction, or lack of, between corticosterone and prolactin in an experimental model, for example using bantams *Gallus gallus* or other captive birds that show strong incubation behaviour. Measurements of corticosterone binding globulin (CBG), which regulates the access of hormones to tissues, may reveal how much corticosterone is free and therefore biologically active, and how much is bound and therefore biologically inactive (Breuner et al., 2013, Desantis et al., 2013).

When assessing the effects of environmental stress on the reproduction of long-lived species, long-term studies need to monitor the lifetime reproductive success of different individuals within a population following an endocrine manipulation, rather than being restricted to monitoring a single breeding attempt (Vincenzi et al., 2013). Studies of kittiwakes breeding in Cook Inlet, Alaska have suggested that baseline corticosterone concentrations may be used as a proxy for adult survival, with an individual-level study showing increasing adult mortality with increasing corticosterone concentrations (Satterthwaite et al., 2010). On a population-level, corticosterone concentrations greater than 7.9 ng/ml (log corticosterone: 0.9 ng/ml) were associated with birds that either skipped breeding the following year or disappeared from the colony for the following three years (Kitaysky et al., 2010). Average baseline corticosterone concentrations for Isle of May breeding kittiwakes in both 2010 and 2011 were well above this threshold (2010 (mean ± SD): 19.9 ± 19.2 ng/ml; 2011: 13.6 ± 8.4 ng/ml). However, return rates the

following year were relatively high (2011: 80.0 %; 2012: 80.2 %; long-term average (1986–2013): 78.4 %; Newell et al., 2011, Newell et al., 2012). Fledging success was on average much lower (0 and 0.004 chicks fledged per number of chicks hatched) at the colonies on the two islands monitored in Cook Inlet (Kitaysky et al., 2010) compared to the Isle of May population (2010: 0.29; 2011: 0.87 chicks fledged per completely nest built). Differences between these studies may be explained in part by differences in life-history traits between Atlantic and Pacific kittiwakes, with Atlantic populations being characterised by higher fecundity and lower survival and Pacific populations by lower fecundity and higher survival (Hatch et al., 1993, Gill and Hatch, 2002, Frederiksen et al., 2005a, Suryan et al., 2009). Further studies should assess whether a threshold value of corticosterone can be used to indicate Atlantic kittiwake survival.

6.5.3 Validation of osmotic pumps

Further studies are required to test the value of osmotic pumps as a delivery mechanism of corticosterone to mimic chronic stress. Osmotic pumps could be tested in a captive bird so that the profile of corticosterone could be mapped, by taking blood samples to measure corticosterone concentrations every day after implantation for the full two weeks of delivery. This would enable a picture of the extent to which chronic stress is mimicked to be obtained. Japanese quail *Coturnix coturnix japonica* would be a useful captive study species to choose because we have shown this bird to have a suppressed acute stress response to handling (chapter five) and therefore handling stress would not mask changes in corticosterone due to exogenous corticosterone manipulation. However, quail are not good incubators and therefore bantams, which are good incubators, could be a useful alternative. It would also be beneficial to then test osmotic pumps using kittiwakes that are easier to recapture multiple times, for example individuals from colonies in Kongsfjoden, Norway (Angelier and Chastel, pers. comm.).

An alternative method of mapping the profile of change in corticosterone could utilise a method described in Arnold et al. (2008) in which blood samples are obtained from birds using blood sucking bugs (Heteroptera, Triatominae) which were contained within dummy eggs and placed in the target nests. This method of sampling allows baseline concentrations of corticosterone to be guaranteed and allows a minimally invasive technique for obtaining repeated blood samples.

6.5.4 Breeding failure of chronically stressed birds

The question remains, what determines the breeding failure of chronically stressed birds and what roles might adult body mass and prolactin play just before failure occurs? The

kittiwakes breeding on the Isle of May have been studied intensively in the past including capturing of individuals for morphometrics, body mass and diet sampling. This has resulted in many of the birds breeding on the Isle of May becoming increasingly agitated when researchers approach their colonies. Therefore capturing these birds is much harder than it has been in the past. Colonies of naive kittiwakes at less intensively studied locations may provide useful birds for future research (e.g. Kongsfjoden, Norway; Angelier and Chastel, pers. comm.). For example, it would be interesting to see how prolactin concentrations changed throughout the breeding period by capturing corticosterone implanted and sham implanted individuals later in the season and after failure occurred. Similarly it would be interesting to measure body mass more often through the breeding season and at the time of failure, in order to assess whether corticosterone implanted birds lost mass later in the season, resulting in lower breeding success. Alternatively electronic balances could be positioned on the cliff to allow repeated body mass measurements without the need to repeatedly disturb individuals through capture. No effect of body mass was detected in the time course of the study in chapter four because birds could not be captured near or at the time of failure.

It would be interesting to investigate further the nest attendance behaviour of kittiwakes. Specifically, future work could assess whether the unmanipulated partners of corticosterone implanted birds compensated for any changes in nest attendance behaviour of their stressed partner, and if so, at what point an individual's own condition becomes a priority above compensating for its partner to ensure the success of its current breeding attempt. To do this, individuals could be marked more clearly for ease of visual nest attendance checks and the body mass of both members of a pair could be measured regularly through the season to assess implications for the self-maintenance of chronically stressed individuals and their partners.

6.6 Concluding remarks

In this thesis I have shown firstly that changes in the breeding success of a top marine predator indicate changes in prey availability, which may be due to mismatches in phenology. Secondly, body mass is a key mechanism by which changes in diet composition determine changes in breeding success. Specifically, my data have shown what can be inferred from the breeding success of the kittiwake in terms of its physiology, body mass, foraging trip duration and diet composition, during natural inter-annual variation in environmental conditions and experimentally-induced chronic stress. Whilst these data may raise more questions than they can answer, future research could build upon

them with the use of continued long-term data collection and revised methodology for experimental studies.

Appendix A

Validation of corticosterone manipulation using captive Japanese quail

A.1 Abstract

Manipulating corticosterone is a commonly used method of assessing physiological and behavioural responses to stress. Studies to date have tended to use open-ended silastic tubes to manipulate corticosterone concentrations in vertebrates. However, this methodology may mimic acute stress better than chronic stress, due to the rapid and inconsistent release of this steroid hormone through the open-ends. We aimed to validate the use of Alzet® osmotic pumps, using captive Japanese quail *Coturnix coturnix japonica*, as a better means of releasing corticosterone consistently over a number of days. We demonstrate that virtually all the contents of the pumps were released into the birds. However, blood corticosterone concentrations were not significantly higher 11 days after implantation.

A.2 Introduction

Manipulating corticosterone concentrations in live vertebrates allows experimental studies to be carried out into physiological and behavioural responses to stress. External stressors can induce many changes in the behaviour of an organism, and direct manipulation of corticosterone tries to address this by identifying causal relationships between corticosterone and factors such as condition, behaviour and fitness. Silicon tubing (Silastic Medical Grade silicon tubing, Dow Corning Inc.) has been commonly used for administering substances subcutaneously (reviewed in Fusani et al., 2005). Silastic tubes are useful for the transfer of lipophilic hormones, for example the more non-polar steroid hormones such as testosterone, as these can be released through the tubing over a period of time, the rate of which depends on the thickness and length of the tubes. However, hydrophilic substances, for example more polar steroid hormones such as corticosterone, do not pass through silicon. Consequently, in such cases the tubes must be cut at the ends, or punctured with holes, to allow the hormone to be released, which results in a relatively fast and inconsistent release of the hormone (Fusani, 2008, Bonier et al., 2009). This rapid release of corticosterone may mimic acute stress or reach pharmacological concentrations.

Self-degradable corticosterone pellets have also been trialled as a method of delivery to mimic chronic stress; however, these do not work exactly as reported by the manufacturers (Müller et al., 2009), instead resulting in a peak elevation in circulating corticosterone over a shorter period than expected (Thierry et al., 2013). Acute stress involves a rapid peak in corticosterone, for example in response to a predation attack. High concentrations of corticosterone result in higher clearance rates, which passively clear corticosterone from the bloodstream. Supra-high short-term concentrations of corticosterone may also induce severe subsequent down-regulation of the hypothalamic-pituitary-adrenal axis (Rich and Romero, 2005, Romero et al., 2005). This is due to an endogenous feedback response to elevated exogenous corticosterone that often occurs in order to reduce the detrimental effects of prolonged raised corticosterone concentrations (Sapolsky et al., 2000, Romero, 2002, Newman et al., 2010). When the effects of stressors such as harsh environmental conditions are of interest, experimental manipulations of corticosterone must mimic chronic stress rather than acute stress. Chronic stress involves increased corticosterone over a long period of time, for example in response to poor food availability.

An alternative method of corticosterone delivery is via osmotic mini-pumps (Alzet®, Charles River), which can release substances for up to four weeks at a constant rate, resulting in an increase in baseline concentrations, in the case of corticosterone release, thus mimicking chronic stress (Fusani, 2008). Alzet® osmotic pumps work via the high osmolarity of the salt sleeve layer within the pump, which causes water to flux into the pump through the semi-permeable outer membrane surface (Alzet® osmotic pumps, www.alzet.com). As water enters the salt sleeve, the contents of the impermeable reservoir, which in our case is corticosterone dissolved in polyethylene glycol 400, is compressed and thus release out of the pump. The rate of this release is determined by the water permeability of the pump's outer membrane surface (Alzet® osmotic pumps, www.alzet.com). Osmotic pumps have been used successfully in some studies in birds (Sockman et al., 2000 to secrete ovine prolactin, Soma et al., 2000 to secrete gonadotropin inhibitory hormone, Fusani et al., 2001 to secrete aromatase inhibitor (fadrozole), Ubuka et al., 2006 to secrete gonadotropin inhibitory hormone). However, only one study to date has used these pumps to manipulate corticosterone concentrations in birds. This method was successful at administering sustained low and medium doses of corticosterone to captive white-throated sparrows *Zonotrichia albicollis* (Horton et al., 2007).

We used Alzet® osmotic pumps to manipulate corticosterone levels within the blood of Japanese quail *Coturnix coturnix japonica* (hereafter 'quail'). We checked that the

pumps successfully released corticosterone into the birds in order to validate the use of osmotic pumps as a delivery vehicle for corticosterone to mimic chronic stress.

A.3 Methods

A.3.1 Study animals and housing

See chapter five for details of housing. The birds were taken from the sample of individuals previously used in the stress response experiment (chapter five) and the corticosterone manipulation took place 83 days after the second stress response sampling occasion (n = 18; one bird died of natural causes between the two studies). All work was carried out under Home Office personal (Bethany Nelson: PIL 60/12426 and Alistair Dawson: PIL 70/1697) and associated project (Alistair Dawson: PPL 60/4176) licences.

A.3.2 Corticosterone manipulation using osmotic pumps

We followed the guidelines provided in the Horton et al. (2007) study of white-throated sparrows. Our study allowed us to test whether the osmotic pumps administered corticosterone successfully over an 11 day period in a larger bird (the quail) than the passerine used by Horton et al. (2007). This information was essential before we proceeded to use the same methodology later in kittiwakes (chapter four). Horton et al. (2007) used Alzet® 1007 osmotic pumps with a reservoir volume of 100 µl and delivery duration of seven days to successfully manipulate corticosterone within the natural range for this species throughout the seven-day period. Because quail have a body mass of approximately 150 g, we scaled up the dosage required for the 25 g white-throated sparrows and used Alzet® 2002 osmotic pumps (length: 3.0 cm; diameter: 0.7 cm; mass: 1.1 g). These pumps have a nominal volume of 200 µl, which is delivered over 14 days at a rate of 0.5 $\mu l.h^{-1}$. Some of the pumps contained corticosterone dissolved in polyethylene glycol 400 (PEG) at a concentration of 28 $mg.ml^{-1}$ (corticosterone-implanted birds; n = 10), which was calculated from Horton et al. (2007) accounting for increased body size (approximately 150 g) of the bird and delivery rate of the pump. The remaining pumps were shams, containing PEG only (sham-implanted controls; n = 8).

The pumps were inserted subcutaneously on the flank under general anaesthesia (Isoflurane). An initial blood sample (maximum of 1 ml) was taken before the implants were inserted (pre-implant), by puncturing the alar vein. A second blood sample was taken 11 days later (post-implant). Blood sampling was completed 2.0 ± 0.1 min after capture with the longest sample taking 3.7 min. In light of the results of chapter five, all samples were considered baseline. After the post-implant blood sample had been taken the implants

were removed under anaesthesia and the volume of corticosterone-PEG solution (or PEG only in the case of sham birds) remaining in the reservoir was measured. All processing of the birds, including implantation and blood sampling was carried out in a separate room out of sight from the aviary where the remaining birds were situated. The order of capture of the birds varied between the day of implantation and implant removal.

A.3.3 Hormone assay

Corticosterone concentrations were determined in March 2012 by a quantitative competitive enzyme-immuno assay (EIA). Plasma samples were equilibrated with 2000 cpm ¬3 H-CORT to measure recovery and extracted using diethyl ether. Extracted samples were analysed in duplicate using an EIA kit as described in Wada et al. (2007). Values were corrected for sample dilution and recovery. The average extraction efficiency was 76 ± 1.5 %. The inter-assay variation was 6.8 % and the intra-assay variation ranged between 4.4 and 7.1 %.

A.3.4 Statistical methods

All statistical analyses were performed in the R computing environment (version: 3.0.1, R Development Core Team, 2013). Values are presented as means ± standard error unless specified otherwise. When examining the effect of corticosterone administration via osmotic pumps, we used a Student's t test to check that there were no differences in corticosterone concentration between the treatment groups at the time of implantation. We used a linear mixed model fitted by restricted maximum likelihood and calculated P values using the Markov chain Monte Carlo (MCMC) method to test for any effect of treatment at the time of implant removal. The interaction between treatment (i.e. sham-implanted or corticosterone-implanted) and pre/post-implant (0 = pre-implant sample; 1 = post-implant sample) was fitted to the model, and this was the key variable of interest. Ring number was included as a random factor to account for repeated measures. As corticosterone concentrations were constrained by being positive and the residuals were not normally distributed, we transformed this variable by taking the logarithm to base ten.

We used a paired Wilcoxon signed rank test to compare the treatment groups before and after implantation with an extreme value included; using a non-parametric test meant that the extreme value had less leverage, as the data was ranked. Two birds had to be excluded from this paired non-parametric analysis: bird 7 died from natural causes before the post-implant sample had been taken; bird 20 had insufficient pre-implant sample for corticosterone to be measured. This meant that there were nine corticosterone-implanted birds and seven sham-implanted birds included in the analysis.

A.4 Results and discussion

A.4.1 Welfare and implant effects

There were no welfare issues, with no adverse effects on the quail evident. There was a 94 % survival rate with one bird dying of natural causes that were unrelated to the insertion of an osmotic pump. When removing the pumps 11 days after insertion, the incision area from the time of implantation had completely healed. Birds showed no visible signs of reduced body condition as found by Calandreau et al. (2011); however we did not measure the body mass of individuals to confirm this.

A.4.2 Delivery of corticosterone

On average only 7 ± 0.16 % of the solution remained in the pumps at the time of removal i.e. 93 % was released into the birds (mass at start: 0.25 ± 0.008 g; mass at end: 0.02 ± 0.001 g). The minimum amount of solution remaining at the time of implant removal was 0.003 g (95 % administered) and the maximum amount remaining was 0.025 g (78 % administered). Whilst virtually all the contents of the pumps were released, this occurred over 11 days rather than the 14 days indicated by the manufacturers. This may be due to birds having a body temperature three to four degrees higher than mammals.

Pre-implant corticosterone concentrations did not differ between birds allocated into the sham treatment and those allocated into the corticosterone treatment (Student's t test: $t = 1.20$, $df = 15$, $P = 0.25$). There was high variation between individuals in corticosterone concentrations (Table A-1). We expected that administration of exogenous corticosterone to captive quail using osmotic pumps would result in higher circulating concentrations of this hormone at the time of implant removal. However, there was no significant interaction between treatment and pre/post-implant (linear mixed effects model: $t = 1.29$, $P = 0.21$; Table. A-1). The post-implant corticosterone value for the corticosterone-implanted bird with ring number 11 was an extreme value (242.28 ng/ml; Mahalanobis distance: $MD = 30.85$, $df = 4$; critical value = 18.47). However, when this extreme value was included in a paired non-parametric test there was a significant increase in corticosterone between pre- and post-implant concentrations for corticosterone-implanted birds (Wilcoxon signed rank test: $V = 5$, $P = 0.04$) but not between pre- and post-implant concentrations for sham-implanted birds ($V = 9$, $P = 0.47$). Using a non-parametric test was appropriate in this case because the data is ranked and therefore extreme values have less leverage. It is possible that we did not see any effect of the treatment on corticosterone concentrations, unless the extreme value was included in the

dataset, because of a small sample size. We were unable to house greater numbers of quail in captivity due to practical and welfare issues.

Table A-1 Summary statistics of corticosterone concentrations of sham-implanted and corticosterone-implanted birds before (pre-implant) and after (post-implant) manipulation. One sham-implanted bird had insufficient blood sample for pre-implant corticosterone concentrations to be measured. One corticosterone-implanted bird died due to natural causes before a post-implant sample could be obtained. One influential extreme value, which relates to the post-implant sample for a corticosterone-implanted bird, was excluded in the values in brackets.

	Corticosterone concentration (ng/ml)			
	Sham-implanted		Corticosterone-implanted	
	Pre-implant	**Post-implant**	**Pre-implant**	**Post-implant**
n	7	8	10	9 (8)
Mean	3.62	3.97	6.80	38.90 (13.48)
SD	2.73	3.76	7.72	77.25 (13.16)
SE	1.03	1.33	2.44	25.75 (4.65)

It would have been ideal to measure the change in corticosterone during the days following implantation in order to record the timing and magnitude of corticosterone elevation to confirm the findings of Horton et al. (2007). However, we assumed that repeated sampling would have been stressful in itself for the quail. We were unable to analyse the data from the stress responsiveness study on quail (chapter five) until after we had to undertake the corticosterone manipulation study. Had we known at the time that capture and sampling quail had little effect on circulating corticosterone concentrations, we would have sampled birds at multiple intervals between implantation and implant removal.

Calandreau et al. (2011) showed that after a week of chronic stress, treated and untreated captive quail had similar corticosterone concentrations but treated birds had reduced body condition, indicating physiological stress. This suggests that birds can show signs of chronic stress without having measurably elevated corticosterone concentrations. Indeed, Cyr and Romero (2007) found that female European starlings *Sturnus vulgaris* actually had lower baseline corticosterone after nine days of a chronic stress protocol. It is possible that these studies demonstrate a powerful negative feedback in the hypothalamo-pituitary-adrenal system such that acute stress causes a measurable increase but this disappears with time as stress becomes chronic. This could account for the non-significant difference in corticosterone concentrations that we saw between corticosterone-implanted birds at the time of implantation and implant removal.

A.4.3 Conclusions

We show that corticosterone filled osmotic pumps implanted into quail did deliver virtually all of the corticosterone. However, implanted birds did not have significantly elevated concentrations of corticosterone 11 days after implantation, and we do not know the time course or the magnitude of an increase in corticosterone concentration in implanted birds during the experiment. Since the Alzet® osmotic pumps successfully delivered the exogenous corticosterone into quail we assumed that this procedure would work successfully in our subsequent kittiwake study and that values decreased, either because of an increased clearance rate, or because negative feedback shut-down endogenous corticosterone production.

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