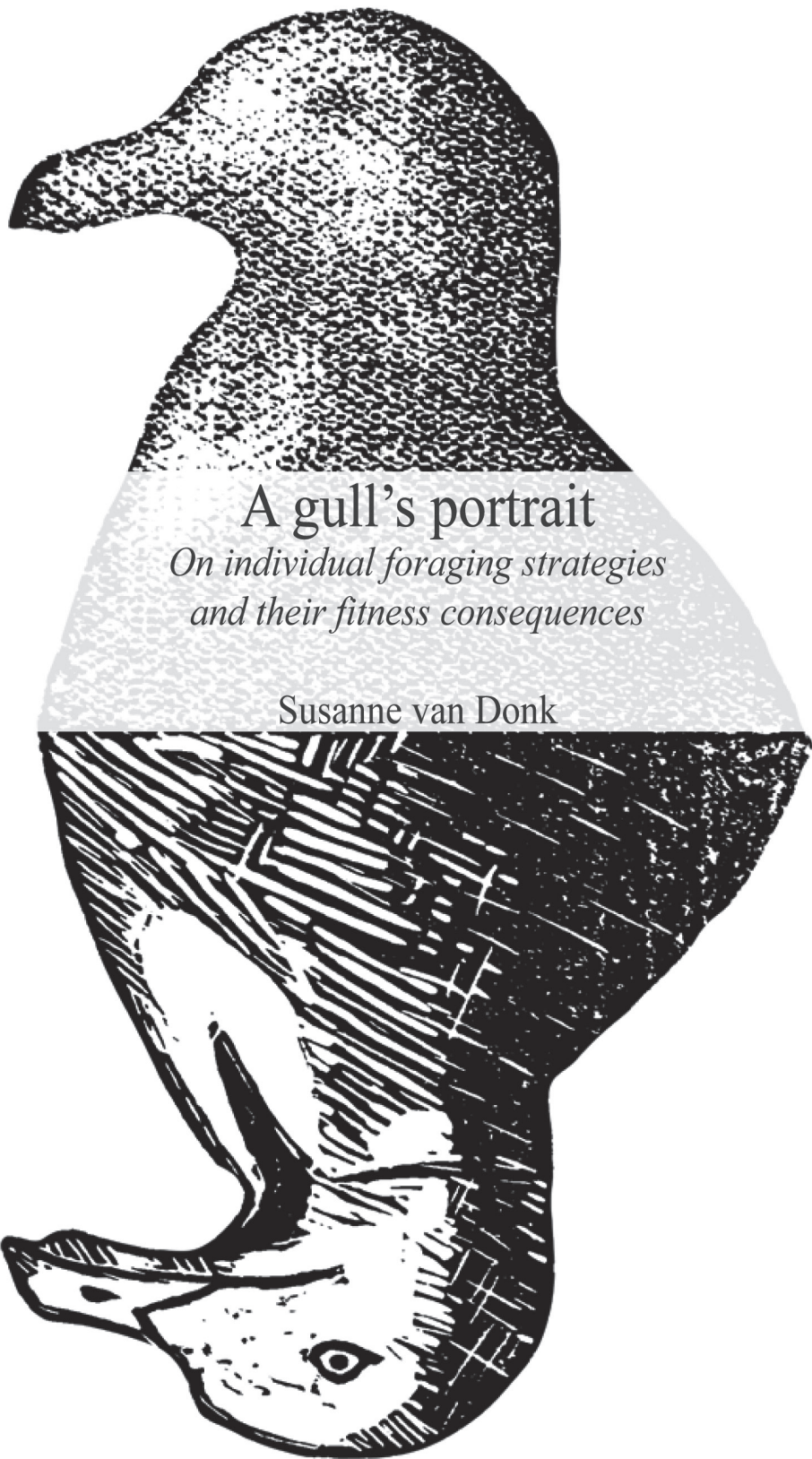




A gull's portrait

*On individual foraging strategies
and their fitness consequences*

Susanne van Donk

A gull's portrait

On individual foraging strategies and their fitness consequences

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VRIJE UNIVERSITEIT

A gull's portrait

On individual foraging strategies and their fitness consequences

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door

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Chapter 1

General introduction

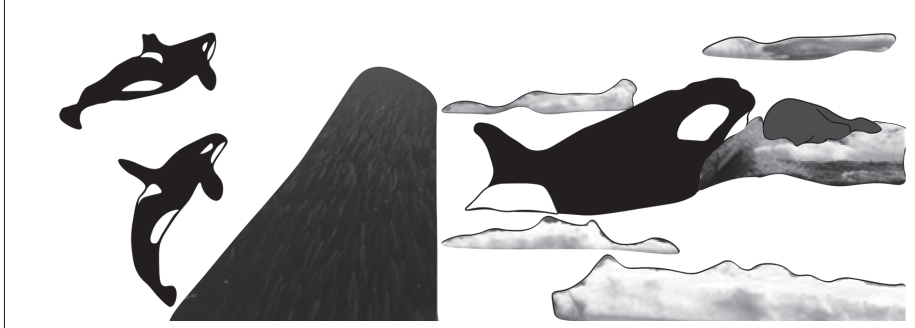
Nature offers a wide variety of species, that all have their specific characteristics. Looking closer to a single species, one may discover even more variety; individuals within one species often differ both in appearances as behaviour. This individual variation had already been observed as early as 350 BC by Aristotle, and is precisely described by Darwin (1859);

“The many slight differences which appear in the offspring from the same parents, or which it may be presumed have thus arisen, from being observed in the individuals of the same species inhabiting the same confined locality, may be called individual differences”

One interesting form of individual variation involves consistent differences in behaviour. Behaviour is probably the most flexible trait an animal has, so the fact that behavioural flexibility seems limited, attracts attention (Dall et al. 2012). Part of research on behavioural variation in animals is focused on how individuals forage. How to exploit food is fundamental in nature, as how well animals can acquire it, will affect survival and reproductive success. It appears that many populations exist of individuals that differ consistently in the way they gather food. These differences can encompass for instance the type of food individuals eat, the variety of food in their diet and where animals go to find it (Bolnick et al. 2003). Foraging strategies of animals have been and are still of high interest by ecologists to explore questions like: why are individuals in one population so different, how is variation maintained and when is variation important.

As evolution works on individual variation in traits, variety in foraging strategies can affect how populations evolve (Price et al. 2003). In extreme cases, it can even lead to the formation of new species (box 1.1). However, before one is able to understand these population dynamics, one should study the consequences of variation on the individual level. For instance, individuals with different strategies can vary in their reproductive success or survival. Or, alternatively, individuals can have similar fitness, which explains why variation stays in a population. The environmental conditions can also affect how successful certain strategies are; a strategy can for instance have high fitness in environment A but low fitness in environment B. However, knowledge on fitness consequences of having different foraging strategies is lacking (Ceia and Ramos 2015, Phillips et al. 2017). With this thesis I aim to contribute to the understanding of the wonderful complexity in behavioural variation within populations. More specifically, I will look at consequences of individual variation in foraging strategies on proxies of fitness.

Box 1.1 In extreme cases, individual differences in foraging might even lead to speciation and can thereby drive biodiversity (West-Eberhard 1989, Price et al. 2003). An example of possible speciation due to differences in foraging behaviour are killer whales *Orcinus orca*, where different groups, even when they populate overlapping areas, show very distinct hunting techniques. The ‘residents’ forage mainly for schools of fish by surrounding them with large groups (left picture), while ‘transients’ that mostly live in smaller groups forage mainly on sea mammals (right picture). Killer whales with different hunting techniques do not interbreed which was detected from their DNA. Ultimately, they might become distinct species due to ecological specialization (Morin et al. 2010).



Balancing energy

All animal behaviour involves the use of energy (Butler et al. 2004). The (limited) amount of energy animals can gather in a certain time, determines how they can allocate energy to different processes such as reproduction and survival. How efficient an animal gathers energy, can therefore impact fitness. For instance, it can increase its survival by decreasing the time it spends on the feeding grounds where the risk of predation might be high.

Efficient foraging is important for an individual's survival, but particularly so during reproductive periods. As individuals have a finite amount of energy they can gather, they are constrained in what is energetically feasible to maximize their fitness. When raising young requires parental care, it might cost more energy and thereby foraging time than just taking care of one's own (Drent and Daan 1980). This can cause a trade-off between current reproduction and reproduction in future (McNamara and Houston 1996). If animals want to increase their fitness, they have to balance the energetic effort on current reproduction with that of future reproduction (Williams 1966, Stearns 1992).

How an animal balances its energy between reproduction and survival, is partly determined by its life history strategy. On the extremes, there are species that are characterized by becoming mature at relatively young age, having many offspring at once and a low survival rate and species that are characterized by delayed maturity, only a few offspring and high survival rates (Sæther et al. 2004).

Concluding, how energy is gathered and allocated to different activities is of importance to understand the behavioural and evolutionary ecology of animals (McNamara and Houston 1996). Individuals have different strategies in how they gather and allocate their energy i.e. foraging strategies. This can affect the energetic balance between reproduction and survival (Fig. 1.1). How all individuals of one population reproduce and survive influences on the long-term population dynamics.

Morphological and environmental factors influencing energy intake

How animals can successfully gather energy, depends on both intrinsic as extrinsic factors (Fig. 1.1). Intrinsic factors are for instance morphological characteristics of an animal like size or body structure. For example, individual Darwin's medium ground finches *Geospiza fortis* with bigger beaks are able to crack larger seeds, while individuals with smaller beaks are not (Price 1987). Besides, sex or age could play a role in an individual's foraging behaviour (Araújo et al. 2011). Extrinsic factors also influences how well animals gather energy and are any factor related to the foraging environment, like for instance the amount of competitors (Svanbäck and Bolnick 2005), predators (Eklöv and Svanbäck 2006) or the predictability of the resources.

The predictability of the resources can determine what type of foraging strategy is most successful (Fig. 1.1 D). If resources are relatively stable, specializing on these can be beneficial. Returning regularly to the same resources increases the knowledge of an individual about that specific environment and its food situation. Individuals can use this knowledge to reduce search and/or handling time while increasing the energy gained per unit time (Golet et al. 2000, Masello et al. 2013, Potier et al. 2015, Phillips et al. 2017). However, specializing on one prey might be risky when resources are stochastic and unpredictable. In that case, having knowledge about a wider area and food situation might be beneficial (Marvier et al. 2004, Devictor et al. 2008, Clavel et al. 2011).

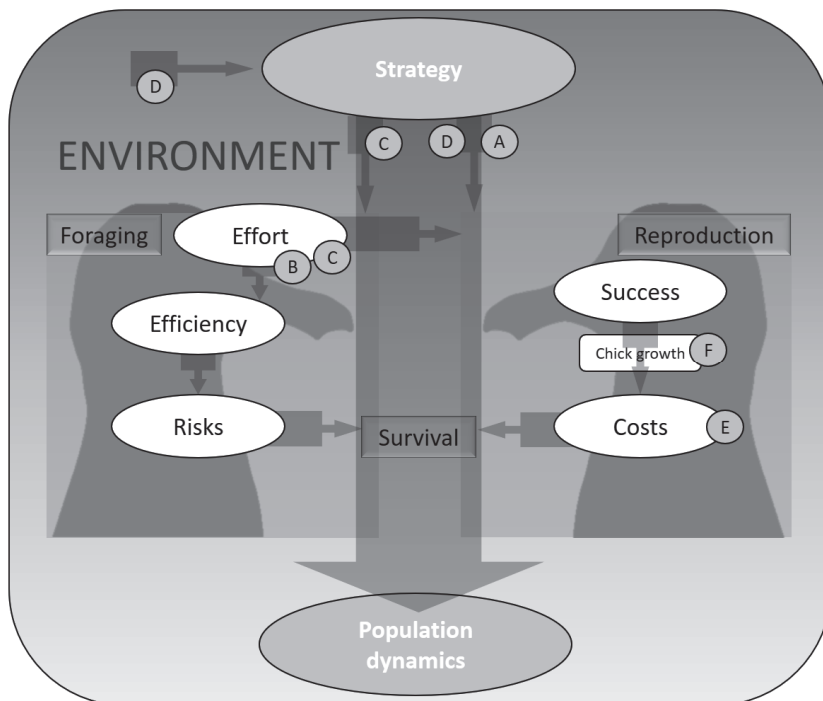


Fig. 1.1 Schematic overview of the framework on which the work in this thesis is based inspired by the schematic overview of (Ropert-Coudert and Wilson 2005). Individual strategies can affect population dynamics via differences in individual reproduction and survival, which is all dependent on the environment (grey background), but also on an individual's morphological characteristics. Foraging can affect both reproduction as survival and has thereby an indirect effect on population dynamics. The different studies done in this thesis are indicated with letters. A The relationship between diet choice and reproduction (chapter 2). B Differences in foraging effort between different habitats (chapter 3). C The relationship between foraging site fidelity and foraging effort (chapter 4). D The effect of habitat loss on foraging behaviour and reproduction (chapter 5). E The costs of reproduction (chapter 6). F Predicting energy intake of gull chicks using DEB modelling (chapter 7). The studies A-E were based on demographic data and/or GPS and accelerometer data of the herring gulls in the breeding colony on Texel. Study F was based on lesser black-backed gull data collected at Ghent University.

This thesis

Many factors can influence how an individual animal gathers energy as described above, and how it balances this (limited) energy between reproduction and survival. How animals forage can ultimately affect how well it reproduces and survives. As the environment is changing in a rapid way last decades, it is of extra importance to study how the environment and foraging strategies of individuals relate. Environmental changes might especially affect long-lived animals, as individuals encounter a relatively higher level of changes during their life than short-lived ones. In this thesis, we study therefore consequences of foraging strategies on proxies of fitness in a long-lived species, with an emphasize on the role of the changing environment.

In order to shed light on these complicated foraging choices animals have to make, regarding all factors involved, I set out studying several consequences of foraging strategies within one natural system. By trying to understand all facets of one natural system, one hopes to ultimately get a better understanding about other ecological systems as well. Below, I introduce the study system and explain why this system is of interest. The focus of the different studies in this thesis are shown in Fig. 1.1 and are discussed in more depth below. Roughly, we tested whether diet of individuals was related to breeding parameters (Fig. 1.1A), whether habitat use was related to energy expenditure and time budgets (Fig. 1.1B and C), how the environment and foraging strategies are related (Fig. 1.1D) and how animals balance their energy expenditure between current and future reproduction (Fig. 1.1E and F).

The herring gull as a model species

A suitable group of species to study the consequences of foraging strategies are generalist species. Generalists have a broad prey spectrum or habitat use but individuals within populations often differ consistently from each other (Bolnick et al. 2003). Generalist populations do therefore show more variation between individuals than specialist populations. This thesis is focused on the foraging behaviour of a long-lived (up to 30 years) coastal seabird, the herring gull *Larus argentatus*. The herring gull is a generalist on population level but individuals vary considerably in foraging behaviour (McCleery and Sibly 1986, Pierotti and Annett 1991, Bukacińska et al. 1996, Camphuysen 2013).

Herring gulls are an ideal species to study consequences of foraging strategies for a couple of reasons; they are relatively easy to study as they are an abundant species in Europe, and breed in often large populations in open coastal areas where breeding success can be measured and adults can be caught and observed. As males and females are both more or less equally involved in raising the brood, both sexes can be caught on the nest and followed throughout the breeding season. Moreover, diet can be monitored in a non-invasive way, as herring gulls regurgitate

hard and non-digestible parts of their prey, which can be collected and analysed. Herring gull are large enough to carry light-weight GPS trackers, which makes it possible to also follow (foraging) behaviour in more detail and over longer timespans.

Previous herring gull studies

The herring gull became an iconic species for the study of animal behaviour due to the work of Nobel prize winner Niko Tinbergen. He examined the role of red dots on the beaks of adult herring gulls in chick begging behaviour in a field experiment (Tinbergen and Perdeck 1950). Later, more studies investigated the ecology of the herring gull. Here, I shortly highlight some previous work on variation in foraging strategies in herring gulls, of which several studies were already carried out 40 to 50 years ago (Spaans 1971, Hunt 1972, Verbeek 1977, Sibly and McCleery 1983).

Researchers investigated the consequences of diet choice on reproduction and found that high caloric prey positively affected growth and survival of chicks (Spaans 1971, McCleery and Sibly 1986, Bukacińska et al. 1996). These beneficial high caloric prey types were often of human origin like fish discarded by the fishery industry or food remains of humans gathered at open dump sites and cities. However, not all studies found this relation, and the beneficial effect of prey types seem to be related to the characteristics of the study system. An example in which high caloric prey did not result in higher breeding success, is a study carried out in Newfoundland, Canada (Pierotti and Annett 1991). The researchers found that animals specializing on intertidal organisms had a better reproductive success than individuals that specialized on human waste, seabird chicks or consumed a mix of prey types. Intertidal organisms were the most abundant prey in the system but had the lowest energy, protein and fat content compared to other possible prey. Differences in foraging effort between the strategies were suggested to have played a role in explaining the variation in reproductive success in this case, as animals specializing on garbage were absent from the colony for longer periods per day (Pierotti and Annett 1991). However, foraging behaviour and foraging effort could not be measured. Another study investigated foraging effort between different specializations in more depth. By attaching radio-trackers to several gulls, they could follow and observe animals on known foraging grounds that could be visited by the researchers. Interestingly, gulls foraging on the most profitable food in terms of calories per gram coming from the open dump site, also spent the longest time foraging per day (McCleery and Sibly 1986).

These older studies on herring gulls already revealed some of the factors that play a role in foraging decisions of this species. However, most of these studies had a relatively short period of study of one to at most three years. As environmental conditions or natural fluctuations affect the availability and quality of prey, such conditions and fluctuations are probably important for

making foraging decisions. Furthermore, through technological innovation, light weight GPS trackers that take also acceleration measurement attached on the back of the birds enable gathering much more data per individual even in remote areas and over longer timespans sometimes up to several years. This enables us to answer question about habitat use, energy expenditure and time budgets in a level of detail which was not possible before. Besides, the environmental conditions have changed over the last decades compared to the studies done in the 70-ties and 80-ties, which offers the opportunity to also study the role of environmental change.

The herring gull on Texel; adapting to changes in a cultural food landscape

The chapters in this thesis focus on herring gulls of a well-studied breeding in a colony of about 4000 individuals that breed together with about 11.000 lesser black backed gulls *Larus fuscus* on the island of Texel, the Netherlands (Fig. 1.2)(Camphuysen 2013). The chosen colony is suitable for the study on the consequences of foraging strategies for several reasons. Demographic parameters and diet have been monitored systematically in the colony since 2006 (Camphuysen and Gronert 2010, Camphuysen 2013, Camphuysen et al. 2015, Shamoun-Baranes et al. 2017), so I could use ten years of data for analysis. Furthermore, the foraging landscape of this colony is quite diverse. It consists of marine areas like the North Sea and Wadden Sea, intertidal areas like mudflats in the Wadden Sea and breakwaters (coastal defence structures) along the coast, terrestrial areas like agricultural land and urban areas as cities and towns and one open dump site. Each prey type from these foraging habitats requires particular foraging skills and expert knowledge (Woo et al. 2008)(Fig. 1.3). Finally, there are several changes in the foraging landscape that happened over the last decades making this colony interesting for studying how changes in the environment can affect individuals. First, the amount of human waste that herring gulls scavenged on since early 20th century decreased a lot, particularly since the 1990s (p. 251 Camphuysen 2013). This is caused by a decrease in the number of open landfills due to changes in national and international legislation (Kohler and Perry 2005, Camphuysen 2013, European Environment Agency (EEA) 2016, Rijkswaterstaat 2016). Second, another important prey, discarded bycatch from fisheries, has also decreased. This is caused by a decline in fishing effort since the late 90ties (Rijnsdorp et al. 2008, Camphuysen 2013) and changed legislation towards discarding bycatch which were implemented before and during the course of this study (Poos 2010, Rijnsdorp et al. 2011); due to implementation of measures to get a Marine Stewardship Council between 2016 and 2020 in which a lot of shrimp fisherman engage, less discarded bycatch will be available for the gulls (Baer et al. 2017). A third change in the habitat that also occurred during this study, was the loss part of the coastal habitat that provides the main prey for these gulls (Fig. 1.2). These three environmental changes might shift the balance in for instance energetic profitability and

competition of some prey, and can teach us how animals deal with changes in their environment.

Study outline

In conclusion, the principal aim of this thesis is to get a better understanding of the fitness of different foraging strategies in a generalist seabird, the herring gull. This species forages in a landscape that is heavily and regularly modified by humans, which also offers possibilities to try to understand trade-offs of foraging decisions in a changing world. As mentioned, animals have to balance the (limited) energy they have between reproduction and survival. The second aim of this thesis focuses therefore on investigating the balance between current and future reproduction by studying foraging behaviour and energetic costs of breeding. By quantifying different factors that play a role in the foraging behaviour of this species, we hope to require more insight in the significance of variation in foraging strategies within populations. Below, I summarize the main aims of every study.



Fig. 1.2 Foraging landscape of the herring gull breeding population of Texel, the Netherlands. Latitude and longitude are indicated on the x and y axis in UTM zone 31 (x10.000), breeding colony is indicated with a circle (615201.4 E, 5873649 N). By the end of 2014, part of the intertidal coastal foraging habitat was lost (square).

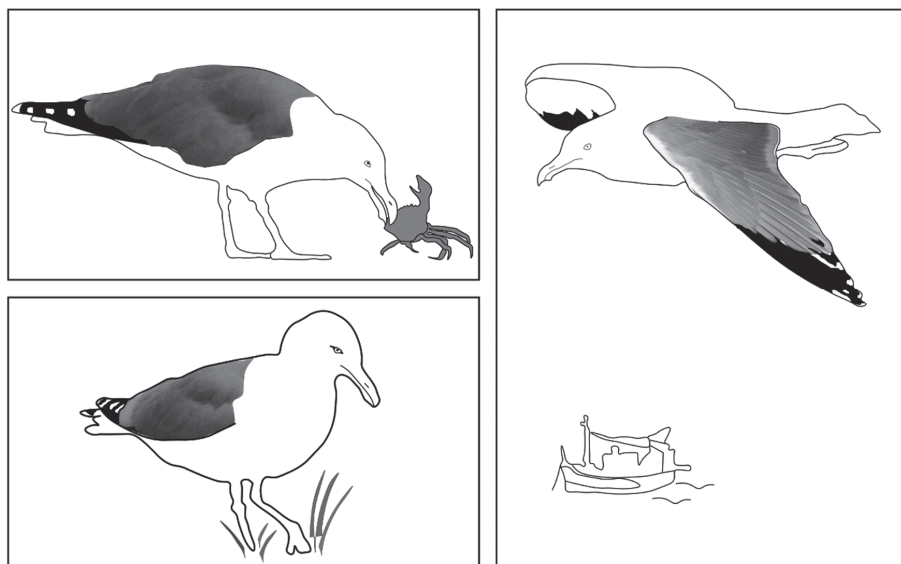


Fig. 1.3 The herring gull forages on a variety of prey types that all require specific foraging techniques. When foraging for crabs in the intertidal, herring gulls need to develop a technique to remove the dangerous claws (left upper corner). Birds that forage for bivalves along the coast need to learn that their prey is only available during low tide. Birds that forage for fishery discards have to be agile and quick to secure a fish in a highly competitive setting (right). Birds that forage for earthworms learn to trample in the grass, but these prey are unavailable in dry soil (left lower corner).

Part I Consequences of foraging strategies

In chapter 2, we used 10 years of data (2006-2015) to study the consequences of diet on reproduction (Fig. 1.1, A). For this study, prey remains collected at the nest sites were used to determine the diet per pair. Males and females can influence the growth and survival of chicks, as both parents provision their young. We hypothesized that breeding pairs that provision high caloric prey have a higher breeding success, as these are essential for proper chick growth. High caloric prey are typically from human origin in the foraging landscape around Texel, like human waste and fishery discards. In addition, we were also interested in whether breeding pairs that have a broader diet (generalists) would perform better in terms of breeding success, as they have more feeding options in a world that is changing and not always predictable. The strengths of this study were the long-term dataset that combined breeding and dietary measurements and our methodological approach that allowed us to analyse dietary selection along a continuum rather than discrete categories as done in earlier studies (Pierotti and Annett 1991, Watanuki 1992). The advantage of studying relationships along a continuum is the potential to detect subtle or non-linear changes in the data.

To understand the costs associated with time and energy invested in foraging for different resources, we investigated individual consequences of different foraging strategies in chapter 3 using GPS trackers (Fig. 1.1, B). We related habitat use with time and energy budgets of animals, using both the GPS positions and acceleration measurements, from which we could extract behaviour.

In addition to the differences in resource selection, individuals using the same resource do also differ in space use. In chapter 4, we examine whether site fidelity, i.e. repeatedly coming back to the same foraging patch, potentially influences foraging efficiency (Fig. 1.1, C). Our hypothesis was that increasing efficiency improves energy intake per time unit, which results in more time for resting or investing in reproduction. The foraging landscape around Texel was especially suitable to test this hypothesis, as the most common prey (blue mussels) of the breeding colony are growing on coastal defence structures along the coast. These breakwaters are clearly separated foraging patches that contain similar quality prey. Therefore, we could account for some variation like prey availability, quantity and quality, which is not common for a field study.

Environments are not always stable and predictable, but generalist species are thought to be quite resilient to changes in their environment compared to specialized species. However, less is known about how specialized individuals within the generalist population deal with changes. In chapter 5, we report the impact of habitat loss of part of the coastal habitat on reproduction and foraging behaviour by comparing different measures of reproduction and habitat use before and after habitat loss (Fig. 1.1, D). The long-term dataset enabled us to study foraging and breeding behaviour well before habitat loss took place.

Part II Consequences of breeding

Animals have to balance energy investment in current reproductive success with future reproductive success. Long-lived animals with a slow life history like herring gulls can do so by skipping a reproductive attempt, thereby avoiding the energetic costs associated with parental care. During parental care, individuals might spend temporally elevated levels amounts of energy allocated to locomotion, for instance to require territories and mates, producing eggs and feeding chicks. Yet, whether skipping a reproductive opportunity could be a mechanism to avoid reproductive costs associated with movement was not yet demonstrated, as skippers are generally difficult to monitor. We had several years of data of animals with GPS trackers, so we were able to test whether skipping breeding would lead to decreased energy expenses attributed to movement in chapter 6 (Fig. 1.1, E).

Parental costs are thought to be especially high during the period of chick care. In this period, gulls have to provide food for themselves as well as for their growing chicks. To be able to understand the reproductive costs in terms of energy needed to successfully raise chicks, one

needs to know the energy intake of chicks. However, measuring intake rates of chicks is very difficult in the field. We tested whether we could predict total food intake when only measuring the weight of a chick, which is more easily done, by constructing a Dynamic Energy Budget model (Kooijman 2010). This model integrates energetics and physiological processes of a whole-organism and can link it to the food environment. For this analysis, we made use of growth data of lesser black-backed chicks that were raised in the laboratory and tested the model with the actual food intake of the chicks in chapter 7 (Fig. 1.1, F). This model could be used by other seabird researchers to predict provisioning rates while only measuring growth rate.

In chapter 8, main findings of the studies described above will be summarized and placed in an ecologically and evolutionary context. I discuss how habitat change might affect animals in terms of foraging strategies or even personalities. This is of relevance to understand and possibly even predict whether and how animals will adapt to our rapidly changing world.



PART I

Consequences of foraging strategies



Chapter 2

The most common diet results in low reproduction in a generalist seabird

Susanne van Donk, Kees C.J. Camphuysen, Judy Shamoun-Baranes, Jaap van der Meer

Abstract

Dietary specialization has been described across a wide range of taxa in the animal kingdom. Fitness consequences are, however, not well documented. We examined the reproductive consequences of different dietary specializations in the herring gull *Larus argentatus*, an omnivorous seabird, using an extensive dataset which includes breeding and dietary data of 10 successive years. We hypothesized that pairs that focused on prey of higher energetic value would yield higher fledging rates. An alternative hypothesis is that pairs that relied on more resources simultaneously would reproduce better. The novelty of this study is that we used continuous measurements representing dietary composition and degree of specialization rather than restricting our analysis to predefined categories. By relating these two continuous measurements for diet to several proxies for reproductive success, we show clear consequences of dietary choice. Most pairs concentrated on bivalves, a prey type not particularly rich in energy. Pairs feeding on energy-rich prey (e.g., “domestic refuse and fishery discards”) during chick rearing were found to have a higher reproductive success, supporting the first hypothesis. Pairs that used more resources did not clearly have a higher reproductive success. The majority of the pairs did not switch to energy-rich prey during chick rearing, despite low breeding outcome. We discuss how trade-offs between factors such as resource availability, predictability, and the time and energy needed to obtain certain prey species may influence resource selection.

Ecology and Evolution (2017) 7 (13): 4620–4629.

Introduction

Generalist populations utilise a variety of resources or foraging areas, yet they may consist of individuals that specialise and use only part of the population-level niche breadth (Bolnick et al. 2002, Araújo et al. 2011). Evidence for individual, dietary specialisation is available for many species across a broad range of taxonomic groups (Heinrich 1976, Bolnick et al. 2003, Masello et al. 2013) and is frequently described (Roughgarden 1974, Bolnick et al. 2003, Eklöv and Svanbäck 2006, Layman et al. 2007, Huss et al. 2008, Araújo et al. 2011). However, the importance of specialisation for fitness is not well documented (Woo et al. 2008, Cucherousset et al. 2011, Ceia et al. 2014). Specialising on a particular resource may for instance have immediate consequences for reproductive success, due to prey-specific differences in provisioning rates or caloric values when raising young (Pierotti and Annett 1991, Golet et al. 2000, Votier et al. 2004). On the other hand, in a changing world (i.e., natural or human-induced changes of the food landscape), the predictability of particular resources could decline and generalists might be better off (Wakefield et al. 2015, Dehnhard et al. 2016).

Large gulls, *Laridae*, are a suitable group of species to study fitness consequences of dietary specialisation, as they are generalists at the species level, but individual birds have multiple foraging specialisations (Ceia and Ramos 2015). Moreover, their reproductive success and diet are relatively easy to study (Pierotti and Annett 1987, Watanuki 1992). Previous studies showed that diet can have a significant impact on the reproductive success of gulls (Hunt 1972, Pierotti and Annett 1991, Watanuki 1992, Weiser and Powell 2010). More specifically, the proportion of fish in diets was correlated with a higher reproductive success, probably due to the higher energetic value in fish compared to other prey types (Bukacińska et al. 1996, Annett and Pierotti 1999). The (positive or negative) effects of dietary biases towards marine prey, intertidal prey, or anthropogenic waste were partly colony specific (Hunt 1972, Ward 1973, Pierotti and Annett 1991, Watanuki 1992, Weiser and Powell 2011). Importantly, most aforementioned studies focused on the effect of diet on population-level characteristics, for example, by comparing reproductive success between populations with different diets (Hunt, 1972; Ward, 1973; Weiser & Powell, 2010), thereby ignoring dietary specialisations of individual pairs. Others investigated consequences of dietary specialisation at the individual level using a categorical definition of dietary specialisation. They used a threshold value to determine whether an individual is a specialist or generalist (Pierotti and Annett 1991, Watanuki 1992), hereby ignoring gradients and potentially losing valuable information.

In this study, we used two continuous measures to study the consequences of dietary specialisations of individual breeding pairs in the herring gull *Larus argentatus*, an omnivorous seabird (Fig. 2.1). The first measure focuses on the most prominent prey types in the diet (referred to further as ‘diet’) whereas the second measure emphasises the variation within the

diet (referred to further as ‘diversity’). In a long-term study of the breeding biology and demography of this breeding colony, both dietary preferences and reproductive parameters varied considerably among individual pairs (Camphuysen and Gronert 2010). However, the consequences of different diets were not explored. The population recovered from a prolonged period of decline, associated with major changes in resources during the 1980s and 1990s (Camphuysen 2013). During this decline, both breeding success and annual survival were low (Spaans et al. 1987, Camphuysen and Gronert 2010). Although the population decline recently came to a halt and numbers stabilised (Camphuysen 2013, Boele et al. 2014), the birds still experience changes in their food landscape, both within and between seasons such as fluctuations in bivalve quality and availability, changes in fishing fleet densities and changes in human waste management.

We hypothesised that dietary biases towards prey with higher calorific values would yield a higher reproductive success (Watanuki 1992). However, in a dynamic food landscape, a specialised lifestyle that relies on few resources might be a vulnerable strategy, especially when energy demands rise during chick care (Spaans 1971, Huig et al. 2016). An alternative hypothesis, therefore, is that birds with a more diverse diet (generalists) reproduce better (Masello et al. 2013). Using continuous measures for diet and diversity, we use extensive field data to test and compare the two partly contradicting hypotheses. We investigated the egg phase and the chick phase separately, because dietary shifts between phases have been noted in previous studies (Spaans 1971, Murphy et al. 1984, Annett and Pierotti 1989) as well as for our own study system (Camphuysen, 2013). We finally discuss breeding consequences of foraging specialisation in the context of natural and human-induced changes in the food landscape.



Fig. 2.1. Herring gull with prey. Photo credit: Maarten van Kleinwee

Methods

Study area

The study was conducted in a breeding colony on the island of Texel, the Netherlands (53°00'N, 04°43'E) at the crossroads of the western Wadden Sea and the southern North Sea. The main foraging areas include open sea (fish and benthic fauna, including fishery discards), intertidal areas (including mudflats and coastal breakwaters), freshwater ponds, agricultural land, rubbish tips and cities. Approximately 5000 herring gulls breed sympatrically with around 10,000 lesser black-backed gulls *Larus fuscus* in the colonies (Camphuysen and Gronert 2010).

Reproductive measurements

Breeding success within the colony was assessed over 10 consecutive breeding seasons (2006-2015) using study plots that were assumed to represent the colony at large. Only full adults (> 4 years old, no immature characteristics within the plumage) were monitored. To monitor breeding success, we marked nests during egg laying (April-May) and marked nests were monitored until hatching (May-June). A subset of these nests were randomly selected and monitored throughout the full breeding season until fledging (July-August). Nests controls were conducted every third day, throughout the breeding season (prospecting through hatching or fledging). When possible, we individually marked birds with a metal and colour ring with a unique code (for more details see (Camphuysen and Gronert 2010)).

We used six proxies of reproductive success; timing, egg size, growth rate, fledgling mass, hatching success, and fledging success. To determine timing of a nest, we recorded laying date and subsequently calculated the deviation in days of every individual nest from mean laying date of that particular year. For colony breeders, it is important to synchronise breeding (e.g. not deviating too much from mean laying date) to prevent predation (Patterson 1965, Parsons 1975, Hunt and Hunt 1976). Mean egg volume (egg size) within a clutch was used as a measure of egg quality, as egg size is correlated with chick survival (Krist 2011). Length (cm) and width (cm) of eggs were measured to the nearest 0.1 mm with Vernier callipers. Egg volume (V , cm^3) was estimated using the formula of Barth (1968) ($V = k \cdot L \cdot W^2$, using $k = 0.5035$ following (Spaans and Spaans 1975)). To be able to determine growth rate, fledgling mass and fledging success we enclosed selected nests with high chicken wire fence and marked hatchlings with uniquely numbered aluminium rings (replaced by uniquely numbered stainless steel rings and engraved colour-rings prior to fledging). During nest visits, we captured chicks from their enclosures. Chicks were measured (head, bill, wing, and tarsus) and weighed with an electronic balance on a quiet place in the colony and returned to the enclosure. Growth rate (g/day) was defined as the slope of the linear regression line between day 5 and 20 of age, as growth rate under optimal conditions is almost linear in this period (Oro et al. 1996, Camphuysen 2013).

Fledging mass was defined as the mass of a chick 40 days after hatching. Hatching success and fledging success were defined as the number of eggs that hatched and the number of chicks surviving until day 40, respectively.

Prey spectrum and prey characteristics

Our study is based on the analysis of regurgitates. Although this method is a widely used method to determine diet, non-invasive and fairly simple, there is a bias toward hard non-digestible parts so that certain soft tissue prey types that leave no remains at the nest site (such as bread or big bivalves from which gulls do not ingest the shell, like oysters) can be completely overlooked (Weiser and Powell 2011). Therefore, there is a chance that we missed important prey types. Occasionally, we have nests without prey remains and these birds probably feed solely on soft prey. These nests were excluded from analysis because of too few food samples.

The dietary analysis was based on regurgitated prey found near the nests of individual pairs. Regurgitates include pellets, boluses obtained when handling adult birds or chicks, and chick feed. Pellet analysis is a widely used method to determine diet in many species, as it is a non-invasive and simple way of collecting large samples over time. Furthermore, it is extensively tested both with captive birds and against other methods (Barrett 2007). The drawback of this method is that there is a bias towards hard non-digestible parts so that certain soft tissue prey types that leave no remains at the nest site might be underestimated, like for instance bread. Boluses and fresh chick feed helped to improve the chances of identifying soft digestible prey.

Chick feed that was still fresh and edible was preferably identified and measured in the field and put back in the enclosure of the corresponding chick. Prey samples were otherwise bagged, labelled and stored frozen before analysis. Each sample was assigned to the nest-specific breeding phases ('egg-phase' and 'chick-phase'). Samples were analysed with a microscope (Olympus SZ51, max. 40x magnification) when needed. Prey types were identified to the lowest possible taxon, measured and quantified when possible. Sample contamination (blown in or accidentally picked up when sampling, e.g. sand, mosses) were excluded from analysis and so were grasses expected to have been ingested to help regurgitate small indigestible remains (e.g. earthworm setae and polychaete jaws). Included plant materials were corn, countryside berries and plant material originating from domestic refuse.

Only nests that had 10 prey samples or more during the chick rearing phase or egg phase were included in the analysis; this resulted in 141 nests for the egg-phase with 16.38 ± 9.12 (mean $\pm$ SD) prey samples per nest (range 10-70) and 99 nests for the chick-phase with 22.11 ± 10.62 (mean $\pm$ SD) prey samples per nest (range 10-63). After identification, prey types were grouped in 13 main prey categories based on family and/or habitat where prey types could be found; oligochaetes, polychaetes, echinoderms, mammals, freshwater fish, plant matter, terrestrial arthropods (including spiders and woodlice), human waste in the form of domestic refuse, birds

(both passerines and non-passerines, the latter being mostly conspecifics and chicks of the sympatric Lesser Black-backed Gulls), fisheries discards (including marine fish and Brown Shrimp *Crangon crangon*), intertidal mudflat bivalves, crustaceans, and coastal bivalves (Table 2.1). We excluded five other dietary components, because of their very low occurrence (less than 0.1 percent occurrence in total diet): marine gastropods, terrestrial snails, cephalopods, barnacles and seaweed. One gull regurgitate often contained prey types from several prey categories. Proportions of the 13 prey categories (using frequency of occurrence) were first calculated per regurgitate and subsequently per nest.

The energy content of different prey categories differs considerably, as do other factors that contribute to the profitability of prey such as handling time, waste materials (digestion), and availability. It is difficult to quantify these proxies exactly, but we assessed the foraging distance, the prey availability, the risks or levels of competition involved while feeding, and the expected energetic gain in categories ranging from favourable (high score) to unfavourable (low score) for each prey category. Travelling distance required to feed ranged from short (<5 km) to long (>50 km) distances, prey availability was classified as ‘always’, ‘tidal cycle’, ‘weather dependent’, ‘unusually’ to ‘rare opportunities’, the risks or the competition ranged from low to high. The energetic gain ranged from high to low, incorporating several factors including the potential filling up time (prey size), the energetic value (kJ/g), and the processing time based on the amount of indigestible matter associated with that prey [Supplementary material]. For further details of the food landscape around the study colony, see Camphuysen (2013).

Analysing the impact of diet

In order to define the most prominent prey types in the population and aggregate prey categories to reduce the number of explanatory variables and facilitate model interpretation, we applied principal component analysis (PCA) to the proportion of prey categories per nest. We used the dietary data from the chick-phase in this analysis as the diversity in prey categories is higher in this period. The first two principal components (PC1 and PC2) explained 73 percent of the variance in the data and thus we used these principal components to group the prey categories. Loadings of these first two principal components showed us that especially prey categories coastal bivalves, crustaceans, domestic refuse and fishery discards explained most of the variance in the diet. Loadings of these categories are respectively for PC1 [principal component loadings (-0.918; 0.210; 0.220; 0.239) and for PC2 [principal component loadings (-0.020; -0.863; 0.411; 0.274). Prey categories domestic refuse and fishery discards (3rd and 4th values in the loadings) have both a positive and relatively high value for both PC1 as PC2; birds that have domestic refuse in their diet also tend to have more fishery discards in their diet. There seems to be no relation between the other groups (i.e., loadings of coastal bivalves and crustaceans have values that differ greatly from each other as well domestic refuse and fishery discards).

Based on these outcomes, we created three ‘diet components’ out of the 13 prey categories; ‘Coastal bivalves’ (C), ‘Domestic refuse and fishery discards’ (D) and ‘Crustaceans and remaining prey categories’ (R). The last group includes crustaceans as well as all the small groups that were of minor influence in explaining the variance in the data (Table 2.1). These three components (C, D, and R) were used in subsequent analysis.

As we worked with frequencies, all prey categories per nest sum up to one (compositional data). Data that sums up to a constant are not independent of each other. This sum constraint imposes some limitations on the variance and covariance of the data that are non-normally distributed, invalidating the use of most standard statistical approaches based on multivariate normality. Aitchison (1986) proposed a method that transforms data to remove this sum constraint allowing the use of standard statistical techniques. To transform the data we recalculated all proportions relative to one randomly chosen proportion (one of the three diet components) and took the log-transformation of these values. The three diet components in our study are thus described in two coordinates, z_1 and z_2 . (Pawlowsky-Glahn and Egozcue 2006).

$$(1) \ z_1 = \log(C/R), \ z_2 = \log(D/R)$$

The value of one proportion can be deduced from the proportions of the others in compositional data (i.e., food category C must have a value of $1-c$, if food categories D and R have together the value of c), and so it does not matter which of the three categories are taken as the denominator. To avoid the problem of calculating log-ratios over zeros, very small proportions (0.0001) were assumed instead.

The coordinates z_1 and z_2 were used to test our first hypothesis that states that pairs that focus on prey of higher energetic value yield a higher reproductive success. We used linear regression models to test how diet (the predictor) seemingly affected breeding success. During the egg-phase, we considered the effect of diet (predictor) during the egg phase on laying date and egg volume (response variables y). During the chick phase, diet during this phase was considered as the predictor of response variables chick growth and fledging mass. To test whether diet influenced hatching success and fledging success, we used a generalised linear model with a binomial distribution where zero was equal to, respectively, zero hatchlings or zero fledglings and one was equal to one or more hatchlings or fledglings. These models were compared with a null-model to test for significance. To visualise and measure the direction of the effect in relation to the three main dietary components, ternary diagrams were created using the ggtern library (Hamilton 2015) an extension of ggplot in R (Wickham 2009). Isoclines were included using the coefficients from the linear and generalised models. In a two-dimensional space where z_1 and z_2 are plotted against each other, the relationship between the response variables and the diet components can be described as follows;

$$(2) \ y = a_0 + a_1 \times z_1 + a_2 \times z_2$$

when incorporating formulas of z_1 and z_2 :

$$(3) y = a_0 + a_1 \times \ln(C/R) + a_2 \times \ln(D/R)$$

which is equivalent to the following:

$$(4) y = a_0 + a_1 \times \ln(C) + a_2 \times \ln(D) - (a_1 + a_2) \times \ln(R)$$

where z_1 and z_2 are the coordinates described in Equation (1), and y is the response variable, C , D , and R the three diet components in the ternary diagram, a_0 the intercept of the model, a_1 the coefficient belonging to C , a_2 the coefficient belonging to D and $-(a_1 + a_2)$ the coefficient belonging to R . The coefficients a_1 , a_2 and $-(a_1 + a_2)$ determine the direction of the response. For instance, when a_1 is big and positive and a_2 really small and negative, diet component C has a big positive influence while diet component D has a small negative influence on the reproductive success. Consequently, component R has a big and negative effect.

Previous studies on gull diet showed a change in diet from the egg-phase to the chick-phase (Annett and Pierotti 1989). To evaluate this, we used Hotelling's T^2 test to compare the means of the prey categories between the egg- and chick-phase. We used the vectors (z_1 and z_2) that are described above (1) as representation for a pair's diet.

Analysing diversity

We used the Shannon index for diversity (Roughgarden 1972) as a continuous measure for diversity to test the second hypothesis that states that pairs that rely on more resources reproduce better.

The Shannon index H' (Shannon and Weaver 1949) is given by the following equation:

$$(5) H' = - \sum [p_i \times \ln(p_i)]$$

where p_i is the proportion of each prey category in the diet of *pair i*. A high value of H' corresponds to a high diversity in the diet (i.e., generalised diet), while a low H' corresponds to low diversity in the diet (i.e., specialised diet).

We used linear regression models to test the effect of diversity (H') during the egg phase on laying date average and egg size and the effect of diversity during chick rearing on average chick growth and average fledging mass. We fit a generalised linear model with a binomial distribution to model the impact of diversity on the probability of hatching or fledging as described above.

In line with earlier studies documenting a change in gull diets from the egg-phase to the chick-phase, we measured whether there was a significant change in diversity between the two breeding phases using a Student's t-test.

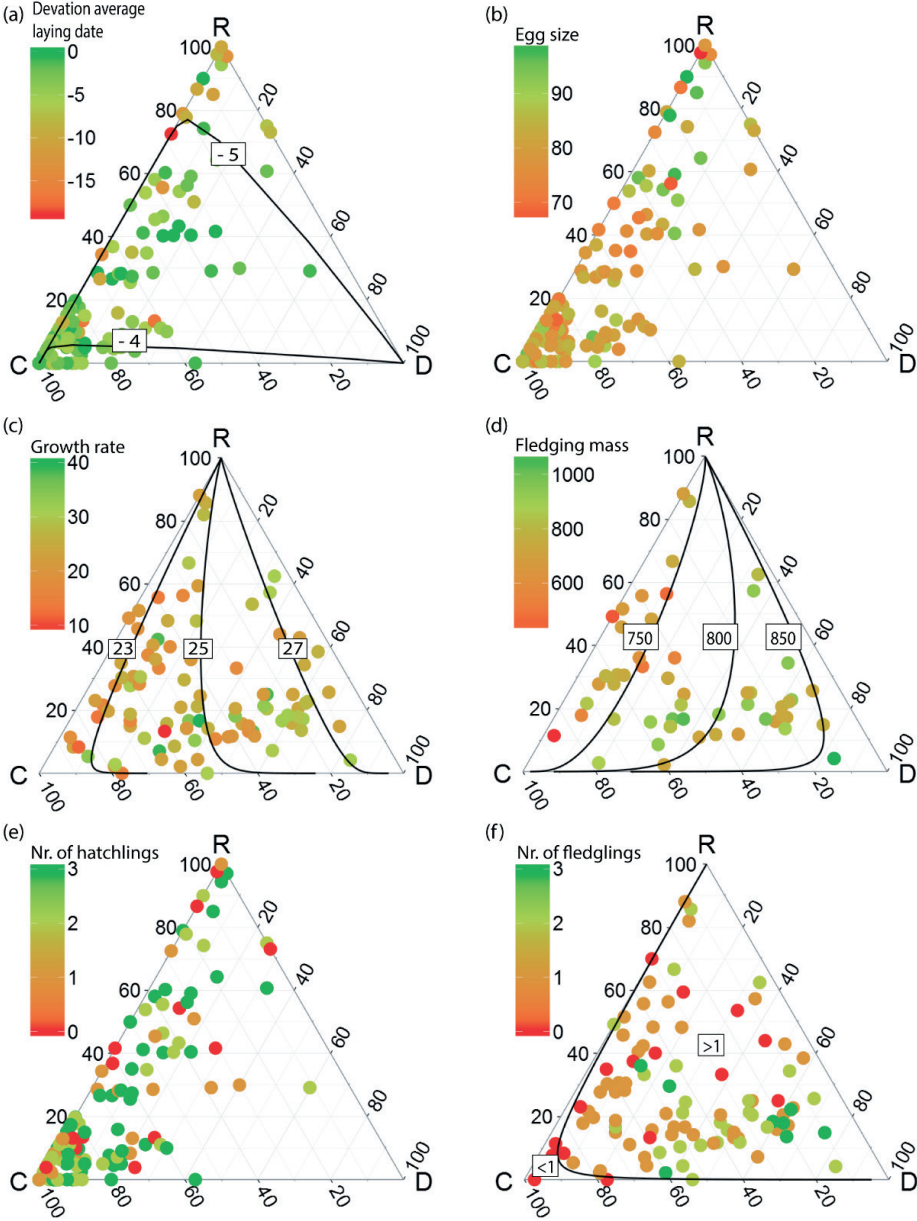
Results

Prey spectrum and prey characteristics

Contribution of the most important prey categories to the overall diet per breeding stage is summarised in Table 2.1. Coastal bivalves (mostly Blue Mussels *Mytilus edulis*) are the most prominent prey type in both the egg- and the chick-phase (Table 2.1, grey shade). Dietary composition significantly changed between the two breeding phases [Hotelling's T^2 test ($T.2 = 28.838$, $df1 = 2$, $df2 = 245$, $p\text{-value} < 0.0001$)]. The proportions of crustaceans (mostly common shore crabs *Crangon crangon* and common swimming crab *Liocarcinus holsatus*), domestic refuse (mainly chicken and pork remains and plastic packages of food), and fisheries discards (mainly flatfish like European plaice *Pleuronectes platessa* and common dab *Limanda limanda*, brown shrimp *Crangon crangon* and whiting *Merlangius merlangus*) increased. Note that the energetic content per unit mass of coastal bivalves -while found in the highest proportion in the diet- is lower than human refuse and fishery discards (Table 2.1).

Diet and reproductive output

Results are summarized in Table 2.2. The strongest relation that we found was that pairs with more 'Domestic refuse and fishery discards' in their diet in the chick-phase produced chicks with a higher fledging mass (Table 2.2; large positive a_2). Pairs with more 'Coastal bivalves' in their diet produced in contrast chicks with low fledging mass (Table 2.2; large negative a_1). Pairs that feed more on 'Crustaceans and remaining prey categories' produced chicks of more or less average size (Table 2.2; relatively small $-(a_1 + a_2)$). Interestingly, the two other models in the chick-phase (growth rate and fledging success) showed the same pattern; pairs that fed more on 'Domestic refuse and fishery discards' had the best reproductive success (highest growth rate, highest fledging success), while pairs feeding more on 'Coastal bivalves' a lower reproductive success (lowest growth rate, lowest fledging success). However, these two models only explained a low amount of the variance (Table 2.2). We also found that gull pairs feeding more on 'Coastal bivalves' during the egg-phase laid their eggs more closely to the mean laying date (more synchronization) than pairs that fed more on other prey types (Table 2.2), but this model only explained a low amount of the variance (Table 2.2).



The results are visualised in ternary diagrams in Fig. 2.2 in which also gradients in dietary composition are shown due to our continuous measurements for diet. These diagrams have three corners, one for each of the three primary diet components, referring, respectively, to ‘Coastal bivalves’ (C), ‘Domestic refuse and fishery discards’ (D), and ‘Crustaceans and remaining prey categories’ (R). The location of every point in the ternary diagram represents the diet of a single pair of gulls. When a point is in a corner, for instance near C, the pair fed predominantly on ‘Coastal bivalves’. When a point is in the middle of the diagram, that pair had equal proportions of all prey components in its diet. Each ternary diagram represents another proxy of reproductive success (timing, egg size, growth rate, fledgling mass, hatching success and fledging success). Significant correlations between diet and a proxy for reproductive success are plotted as isoclines with expected values. The colour of points corresponds to the value of the response variables, ranging from red (negative) to green (positive). The strongest results based on model outcomes in Table 2.2 are shown in Fig. 2.2(d): the relationship between dietary components and fledging mass. In this diagram, the transition from red (corresponding to a low fledging mass) close to dietary component ‘Coastal bivalves’ to green (a high mass) nearer to ‘Domestic refuse and fishery discards’ is most evident.

◀**Fig. 2.2.** Ternary diagrams that show the relationship between diet and reproductive measurements. The diet components (C, D and R) in every corner of the diagram correspond to respectively ‘Coastal bivalves’, ‘Domestic refuse and fishery discards’ and ‘Crustaceans and remaining prey categories’. When we found a significant relationship between diet and reproductive measurements, expected lines and values are plotted in the diagram. Figs. (a), (b) and (e) are results of the egg-phase while Figs. (c), (d) and (f) are results of the chick-phase. Every point corresponds to one pair. The colour of the point corresponds to the value of the response variable where green corresponds to a high value and red to a low value. Figs. (a)-(f) represent diet in relation to (a) the deviation of average laying date in days where a deviation closer to zero corresponds to a more synchronised laying date. (b) average egg size (cm³). (c) average growth rate (grams/day) (d) average fledging mass (grams) (e) hatching success (0-3 eggs hatched) and (f) fledging success (0-3 chicks fledged)

Diversity and reproductive output

There was no significant relationship between diversity in the diet and breeding output during the egg phase. During the chick phase, pairs with a more diverse diet had a higher reproductive success (higher growth rate and fledging success), however, the relation while statistically significant is very weak (Table 2.3).

Diversity in the diet increased from the egg- to the chick-phase, the average Shannon-index increased from 0.67 to 1.23 [t-test ($t = -10.600$, $df = 245$, $p\text{-value} < 0.0001$)]. The change in diversity can also clearly be seen in the ternary diagrams (Fig. 2.3). In the egg-phase most nests are situated in the corners of the ternary diagram with low diversity indicated in red (Fig. 2.3(a)), while in the chick-phase more nests are in the middle of the ternary diagram reflecting a more diverse diet (Fig. 2.3(b)).

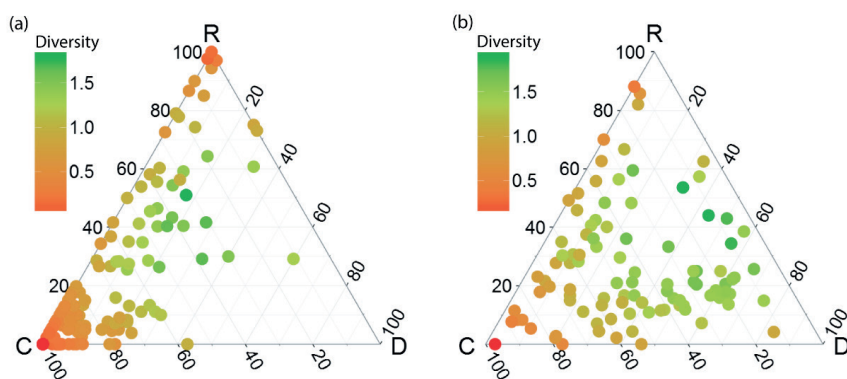


Fig. 2.3. Ternary diagrams that show the relationship between three diet components and the level of diversity of the diet (Shannon index). The diet components (C, D and R) in every corner of the diagram correspond to respectively ‘Coastal bivalves’, ‘Domestic refuse and fishery discards’ and ‘Crustaceans and remaining prey categories’. Every point corresponds to one pair. The colour of the point corresponds to the degree of diversity where green corresponds to a high diverse diet while red to a low diverse diet. (a) egg-phase, (b) chick-phase

Table 2.1 Prey categories and their mean percentages (%; frequency of occurrence) in the diet over all nests used in this study in the egg phase (n=141) and in the chick phase (n=107). Each prey category was assigned to one of three main diet components based on a principal component analysis. The main diet components ‘Coastal bivalves’, ‘Domestic refuse and fishery discards’ and ‘Crustaceans and remaining prey categories’ were noted as C, D and R respectively. Distance, availability, energetic gain and risk and competition of prey categories were qualitatively assessed (for details regarding the classification see Supplementary materials)

Prey category	Comp onent	Egg phase	Chick phase	Distance	Availability	Energetic gain	Risk and competition
Terrestrial arthropods	R	1.9	2.0	Short	Moderate	Rather high	Rather low
polychaetes	R	0.3	0.4	Moderate	Rather low	Rather high	Moderate
oligochaetes	R	0.2	0.5	Short	Moderate	Moderate	Low
echinoderms	R	0.5	2.2	Moderate	Moderate	Low	Moderate
coastal bivalves	C	69.2	43.7	Short	High	Moderate	Moderate
mudflat bivalves	R	5.2	0.5	Moderate	Moderate	Moderate	Moderate
crustaceans	R	6.3	12.1	Short	Rather high	Rather low	Moderate
freshwater fish	R	1.3	1.1	Long	Moderate	High	Moderate
fisheries discards	D	4.8	16.1	Moderate	Moderate	High	Rather high
birds	R	4.2	5.7	Short	Rather low	Moderate	High
mammals	R	1.1	0.5	Moderate	Low	Rather high	Rather high
domestic refuse	D	3.6	13.8	Long	Rather high	High	High
plant matter	R	1.4	1.5	Moderate	Moderate	Low	Low

Table 2.2 Relationships between diet and reproductive output. a_1 , a_2 and $-(a_1+a_2)$ are the three coefficients, corresponding to diet components ‘Coastal bivalves’, ‘Domestic refuse and fishery discards’ and ‘Crustaceans and remaining prey categories’ respectively. We used a linear regression model for the upper four response variables, and a generalised linear model with binomial distribution for the last two response variables.

Breeding phase	Response variable	Intercept	a_1	a_2	$-(a_1 + a_2)$	F-value	r^2	p-value	df
Egg	Laying date	-4.619	0.227	0.023	-0.250	4.828	0.068	0.009 **	2, 133
Egg	Egg size	82.052	-0.085	0.053	0.032	0.146	0.002	0.865	2, 134
Chick	Growth rate	25.362	-1.147	0.996	0.150	4.500	0.089	0.014*	2, 92
Chick	Fledging mass	787.408	-23.957	33.093	9.136	8.344	0.250	0.001***	2, 50

Breeding phase	Response variable	Intercept	a_1	a_2	$-(a_1 + a_2)$	Deviance	d^2	p-value	N
Egg	Hatching success	1.915	0.045	0.066	-0.111	-2.679	0.024	0.262	137
Chick	Fledging success	2.102	-0.418	0.236	0.182	-6.108	0.070	0.047 *	99

* = p-value < .05, ** = p-value < .01, *** = p-value < .001

Table 2.3 Relationship between diversity (Shannon index) and reproductive measurements. We used a linear model for the upper four response variables, and a generalised linear model with binomial distribution for the last two response variables.

Breeding phase	Response variable	Intercept	a_1	F-value	r^2	p-value	df
Egg	Laying date	-4.222	0.147	0.041	0.000	0.84	1, 134
Egg	Egg size	80.967	1.163	0.7616	0.005	0.384	1, 135
Chick	Growth rate	18.889	4.599	5.524	0.056	0.021*	1, 93
Chick	Fledging mass	636.03	104.47	2.592	0.048	0.114	1, 51

Breeding phase	Response variable	Intercept	a_1	Deviance	d^2	p-value	N
Egg	Hatching success	1.738	0.134	-0.060	0.001	0.806	137
Chick	Fledging success	-0.021	1.438	-3.787	0.043	0.052	99

* = p-value < .05

Discussion

Main findings

In this study, we investigated two partly contradicting hypotheses using a continuous measure for diet and diversity. The advantage of using continuous scales is that gradients in diet composition or diversity can be revealed. The first hypothesis assumed that pairs with a diet of higher energetic value yield in higher reproductive success. The second assumed a higher reproductive success for pairs with a diverse diet (generalists), as the prey landscape is dynamic in space and time. We found that pairs with a high percentage of energy rich prey in their diet (e.g. 'Domestic refuse and fishery discards'), have a higher reproductive success, mainly in terms of a higher fledging weight of the chicks, than individuals that continued foraging on energy poor prey such as mussels, thus supporting the first hypothesis. We did not find strong evidence for the second hypothesis. Higher diversity in the diet during the chick phase increased the probability of fledging chicks, but the relationship explained only a minor fraction of the total variation.

Diet

Pairs that fed on energy rich prey had heavier and more fledglings. However, there were also many pairs feeding mainly on energetically poorer prey (coastal bivalves; mainly mussels) in both breeding phases. Those pairs had smaller and fewer fledglings. To understand why numerous pairs do not switch to energy rich prey, it may be important to examine the resource characteristics and the costs involved to obtain and process particular prey types (Table 2.1; details and explanations in Supplementary material). Coastal bivalves, for example, have low intake benefits (low energetics with a lot of indigestible remains (Sibly and McCleery 1983)), but are predictable at short distances around the colony. Handling costs and risks involved are also low (Appendix S1). Energetically much richer prey types such as fishery discards are less predictable, require greater traveling distances, and have high handling costs (Appendix S1). Herring gulls obtain fishery discards exclusively from near-shore fleets of beam trawlers (targeting shrimp, with small fish as bycatch) within the western Wadden Sea and North Sea coastal zone (Berghahn and Rösner 1992, Camphuysen 1995). Anthropogenic (domestic) refuse is, like fishery discards, also not predictable compared to coastal bivalves. Most refuse is taken from cities or from a rather distant landfill area. Domestic refuse is probably also taken from recreational areas, mostly during public holidays and nice weather. Foraging on coastal bivalves might thus be a more predictable strategy and less energy-consuming. Such a 'slower' pace of life may result in a higher survival, which may compensate for the lower annual reproductive success (Réale et al. 2010). Strategies could have equal pay-offs in terms of lifetime reproductive success, and the population might be made up by several co-existing and successful strategies. To investigate this hypothesis we should study survival of individuals

with different strategies in addition to reproductive success. Variation in survival between different specialisations has been reported in birds (Durell et al. 2001).

The density of competitors could also explain the variation in strategies in the population (Bolnick 2004, Svanbäck and Persson 2009). When many individuals try to get to the most favourable prey types, competition increases. Individuals that forage on less favourable prey types have fewer competitors to share these resources with and so their overall fitness might be relatively high (Bolnick 2004). We should study interference competition of different prey types in our study to find out whether the density of competitors plays a role. Van de Pol and colleagues (2010) did test whether there was selective pressure on density in an extensive, long-term study on oystercatchers. They could not find evidence for this hypothesis although population size might have been too small for competition to take place. They did find strong fluctuations in survival between different strategies over years, suggesting that variation in strategies persists in the population due to changing conditions in the environment (van de Pol et al. 2010).

Diversity

We did not find strong evidence that higher diversity in the diet (more generalist diet) results in higher reproductive success. Higher diversity in the diet during the chick phase increased the probability of fledging chicks, but the relationship was statistically weak. However, we did report a strong significant increase in diversity in the diet from the egg-phase to the chick-phase. During the egg-phase, diversity in the diet is quite low (more specialisation) while during the chick phase the diet becomes more diverse. A higher diversity in prey items during the chick phase was primarily caused by a higher percentage of crustaceans, fisheries discards, and domestic refuse. This suggests that more diversity in the diet during chick phase indirectly results in a higher reproductive success, but only when the diet incorporates energy rich prey such as domestic refuse and fishery discards and not by adding for instance crustaceans. Diet composition also clearly changed between the two breeding phases (Table 2.1). An increase in the proportion of fish and domestic refuse was reported in the diet during the chick phase. This seems to be a switch in diet and not a change in the availability as fishing vessels are active in the same amount all year long (Camphuysen 2013, p.55) and there are also no indications that domestic refuse changes dramatically over the breeding season. Diet switches over the course of the breeding season have been frequently reported for seabirds (Ward 1973, Murphy et al. 1984). In some studies, birds switched to a diet with more fish as soon as the chicks were hatched (Spaans 1971, Annett and Pierotti 1989). Probably caused by an increase in the energetic demands or by special nutritional requirements of the chicks (Annett and Pierotti 1989).

Other variables

Age (Monaghan 1980, Elliott et al. 2006), individual characteristics (i.e., 'personality', morphology) (Sol et al. 2005, Patrick and Weimerskirch 2014b), and experience (Werner et al. 1981, Limmer and Becker 2009) can influence both reproductive success as well as foraging strategies. Life-history theory predicts for instance that effort toward reproduction increases with age in long-lived organisms (Paitz et al. 2007). We may be able to evaluate some of these factors in years to come when more individuals have been monitored for a number of years and their diet, morphology, and age assessed. Sex could also influence foraging strategies, but we were unable to distinguish between diets of males and females within a pair. Differences in foraging strategies between sexes have been reported in lesser black-backed gulls using GPS loggers, however (Camphuysen et al. 2015), suggesting in that case that males specialised more strongly on marine habitats and fish prey and females on a diversity of habitats closer to the shore and on land (suggesting a greater diversity of prey). Sex differences (associated with sexual dimorphism) in habitat use and diet were also reported in raptors and snakes (Andersson and Norberg 1981, Shine et al. 1998).

Our study is based on the analysis of regurgitates. Although this method is a widely used and excepted method to determine diet, non-invasive, and fairly simple, there is a bias towards hard non-digestible parts so that certain soft tissue prey types that leave no remains at the nest site (such as bread or big bivalves from which gulls do not ingest the shell, like oysters) can be completely overlooked (Weiser and Powell 2011). Therefore, there is a chance that we missed important prey types. Occasionally, we have nests without prey remains and these birds probably feed solely on soft prey. These nests were excluded from analysis because of too few food samples.

Conclusion and future directions

Our study shows that not all pairs have a diet that would lead to a higher fledging success (energy-rich prey including discards and/or human waste). Many pairs fed mainly on coastal bivalves even though this diet was related to a lower reproductive output. Differences in diet between individuals could also be reflected in differences in survival. Successful breeding birds - pairs that feed on human waste and fishery discards - might actually have a lower survival and lifespan as a result of higher costs involved with successful reproduction (Smith and Blumstein 2008, Creighton et al. 2009, Blomberg et al. 2013). Individuals that relied on lower energy, predictable prey throughout the breeding season could, by contrast, increase their survival by lowering foraging costs and potentially increasing lifetime reproductive success. Tracking individuals with GPS loggers with integrated accelerometers to estimate time energy budgets of different foraging specialisations and studying survival are likely to provide more insights into trade-offs associated with different foraging specialisations in future.

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Author Contributions

SvD carried out the statistical analysis together with JvdM, and drafted the manuscript with support from JSB, JvdM and CJC; CJC leads long term study on herring gulls; CJC and SvD conducted field work. All authors discussed results and contributed to the final manuscript.

Supplementary material

References supplementary of key documents regarding to calorific values of prey items

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Characterising Herring Gull prey										Original scores															
Group of prey		Typical species [Freq Occ]		Distance		Availability		Search time		Pot. filling up time		Indigestible remains		Energy (kJ g ⁻¹)		Handling time		Risk		Skills		Competition		Notes	
(1) insects (incl spiders and woodlice)	Coleoptera	4	3	3	3	1	5	3	5	3	5	3	4	weather dependent (swarming)											
(2) polychaetes	Nereis longissima/Virens	3	2	2	2	2	4	5	2	4	5	2	4	lunar cycles											
(3) oligochaetes	Lumbricus terrestris	4	3	3	1	5	2	5	5	5	5	5	5	weather dependent (rain)											
(4) echinoderms	Asterias rubens	3	4	2	2	1	1	1	4	3	5	3	4	tidal cycle											
(5) coastal bivalves	Mytilus edulis/Ensis directus	4	4	5	3	1	3	4	5	3	4	5	3	tidal cycle											
(6) intertidal mudflat bivalves	Cerastoderma edule	4	4	3	3	1	3	3	5	4	4	5	4	tidal cycle											
(7) crustaceans	Carcinus maenas	4	4	4	2	1	2	2	5	3	5	3	5	tidal cycle											
(8) freshwater fish	Rutilus rutilus	2	5	1	5	3	4	3	4	1	5	5	5	specialised skill											
(9) fisheries discards	Merlangius merlangus/Pleuronectes platessa	3	3	4	5	3	4	3	3	2	1	2	1	severe competition, fleet presence											
(10) birds (mostly cannibalistic)	Larus argentatus/fuscus	5	2	3	3	2	2	2	1	2	2	3	1	risk from parental defences											
(11) mammals	Oryctolagus cuniculus	3	2	1	4	2	4	2	2	2	3	1	1	disease risk											
(12) domestic refuse	packaging/chicken/bread/pork/foal	1	5	3	4	4	4	4	4	1	1	1	1	disease risk, car traffic, severe competition											
(13) plant matter	Zea mays , grain	3	2	5	1	1	1	5	5	5	4	4	4	low nutrition, partial digestion											

Factors			
Competition			
5 Low, solitary feeding	Risk		Distance
4 Low, loose flocks	5 Low, safe environment		5 Short (<5 km)
3 Moderate (interference)	4		4
2 High, large flocks	3 Moderate		3 Moderate (10-25 km)
1 Very high (fighting, klepto)	2		2
	1 Very high (hit & run, fights, traffic, bycatch)		1 Long distance (>50 km)
Potential filling up time			
5 Quick (large)	Handling time		Availability
4	5 Trivial		5 Always
3 Moderate	4		4 Tidal
2	3		3 Weather dependent
1 Slow (small items)	2		2 Unusually (e.g. lunar cycles)
	1 Long, manipulations, swallowing constraints		1 Rare occasions
Energy (kJ g⁻¹)			
5 High (>10 kJ)	Skills		Search time
4 Seasonally high	5 Low		5 Low (predictable)
3 Variable / moderate (~6 kJ)	4		4
2	3 Variable / moderate		3 Variable
1 Low (<4 kJ)	2		2
	5 High (e.g. manoeuvrability, killing)		1 Long (unpredictable/difficult)
Indigestible remains			
5 Nothing, or marginally			
4 Small excretion through pellets			
3 Fish bone/ bone pellet			
2 Carapax pellet / bone and fur pellet			
1 Shells to be excreted/largely indigestible prey			



Chapter 3

Foraging for high caloric anthropogenic prey is energetically costly

Susanne van Donk, Judy Shamoun-Baranes, Jaap van der Meer, Kees C.J. Camphuysen

Abstract

Background: Several generalist species benefit from food provided by human activities. Food from anthropogenic sources is often high in caloric value and can positively influence reproductive success or survival. However, this type of resource may require specific foraging skills and habitat experience with related costs and benefits. As a result, not all individuals utilize these resources equally, with some individuals preferentially foraging in habitats where natural resources of lower energy content are predominant, possibly due to lower energy expenditure of the specific foraging strategy.

Methods: Here we investigate whether foraging in habitats which contain high caloric resources of anthropogenic origin is energetically costlier than foraging in habitats with low caloric resources such as intertidal areas or agricultural and natural areas, for example due to increased flight costs, in a generalist seabird, the herring gull *Larus argentatus*. We use data from GPS trackers with tri-axial acceleration measurements that allow us to quantify time-energy budgets, representing energy expenditure during foraging trips of herring gulls for each habitat.

Results: We show that the rate of energy expenditure is on average 34% higher when individuals forage for high caloric prey in marine and urban areas compared to foraging for low caloric prey in intertidal and agricultural areas. Energetic estimates suggest that if birds would feed completely on these resources, they have to gather ~400 kJ per day more to compensate for the higher foraging costs.

Conclusions: Energy expenditure differs among foraging habitat and may thereby influence foraging decisions of individual herring gulls. As management of anthropogenic resources changes, so too may the costs and potential benefits of foraging strategies which are strongly tied to human activities.

Movement ecology (2019) 7 (1): 1-7.

Introduction

Many species experience a loss in resource availability due to human influences in their environment, but some species take advantage of resources that comes available due to human activities (Weiser and Powell 2010). For example, predators such as red foxes *Vulpes vulpes* and coyotes *Canis latrans* have expanded their foraging activities to urban areas in recent decades to profit from anthropogenic resources (Chautan et al. 2000, Gompper 2002, Contesse et al. 2004, Murray et al. 2015). Generalist species are especially suited to exploit human refuse, as they have a broad prey spectrum and exhibit flexibility in their behavior (Micheli 1995, O'Brien et al. 2005, Gompper and Vanak 2008, Angert et al. 2011, Plumer et al. 2014, Murray et al. 2015).

The resources or foraging patches individual animals choose to forage on may depend on the trade-off between costs and benefits of different foraging strategies (Houston et al. 1993, Hutchings et al. 2001, Patenaude-Monette et al. 2014). For instance, some prey might have benefits like a high energetic value or they are beneficial for breeding success, but they might be energetically costly to forage on due to special foraging skills that need to be learned (Hand et al. 2010), a long searching or handling time (Hawlena and Pérez-Mellado 2009) or a high level of predation (Houston 1993) or competition (Slotow and Paxinos 1997).

A specific example of a generalist species that has to make foraging decisions in a landscape which has changed by humans is the herring gull *Larus argentatus*. Herring gulls have adapted their foraging behavior to human activities, and forage at refuse dump sites, waste treatment centers and on fishery discards from commercial fisheries (Hunt 1972, Pons 1992, Camphuysen 1995, Pons and Migot 1995), profiting from relatively high caloric prey. Fishery discards and refuse were found to have a beneficial effect on reproductive success in several populations of gulls (Spaans 1971, Hunt 1972, Pons and Migot 1995, van Donk et al. 2017), which suggests that animals foraging on these prey have a higher net energy intake and are thereby able to offer more food in terms of kilojoules to their offspring. The net energy intake is determined by the energy intake per unit time as well as the energetic costs of foraging per unit time (Ydenberg and Welham 1992), which might differ per foraging habitat. However, assessing and comparing foraging costs in terms of energy expenditure associated with different foraging habitats in the wild remains challenging. Even in relatively well studied species, such as the herring gull, little is known about the energetic investments in different foraging strategies and how differential costs may influence foraging decisions.

In this paper, we investigate whether energetic costs of foraging varies between different foraging habitats. We conducted our study in a population of herring gulls that is studied thoroughly over the last 10 years on the island of Texel, the Netherlands (Camphuysen 2013). Intertidal areas provide bivalves, the predominant prey type for birds within this colony, but

during chick rearing the diet becomes more diverse (van Donk et al. 2017). As shown in other gull studies (Bukacińska et al. 1996, Annett and Pierotti 1999, Weiser and Powell 2010), high caloric prey are important to ensure sufficient chick growth in this population (van Donk et al. 2017); breeding pairs that provision their chicks more regularly with refuse and fishery discards fledged more and larger chicks. Still, many individuals continue to forage mainly in intertidal areas even during chick rearing, suggesting that there are higher costs involved in foraging for the more beneficial high caloric prey (Table 3.1). We hypothesize that foraging for high caloric prey of anthropogenic origin is energetically more costly than foraging for the more predominant low caloric prey, as foraging for anthropogenic prey might require costly flight and competitive behavior. The higher energetic costs of foraging for anthropogenic prey may at least partially explain why some individuals prefer other foraging habitats.

Bird-borne GPS trackers with tri-axial accelerometers, make it possible to measure behavior and estimate energy expenditure. Using more than 10 years of dietary data and color ring recordings, we link habitat use to prey types most likely to be acquired in each habitat (Table 3.1) (Woo et al. 2008, Masello et al. 2013). We tested whether the energy invested in foraging is higher in habitats containing prey of anthropogenic origin (marine and built up areas) than when foraging in habitats containing low caloric prey (intertidal areas and non-built up terrestrial areas) by comparing habitat use with energy expenditure during foraging trips. We quantified time energy budgets of herring gulls using GPS tracking and concomitant acceleration measurements. We show that more energy is invested in foraging in habitats with anthropogenic prey than when foraging in habitats with intertidal or terrestrial prey in our study system and we discuss the consequences of energetic costs of different foraging strategies in the context of a food landscape strongly influenced by humans considering what gulls have experienced over the past 40 years and what is expected in the coming decades.

Table 3.1 Overview of the diet of Herring Gulls breeding on Texel during the chick care of the breeding season. Frequency of occurrence of prey types are shown per foraging habitat based on all samples gathered (n = 3969), together with the most common species or prey types within each habitat groups. Furthermore, an indication is given about the availability, energetic value in kJ g⁻¹ wet weight and possible digestive constraints associated with these prey. The analysis was based on regurgitates gathered in the colony during fieldwork between 2006 and 2016, see for more information references (Camphuysen 2013, van Donk et al. 2017).

Habitat	Anthropogenic	Marine	Intertidal	Terrestrial	Other-Fresh water	Other-Colony
Frequency of occurrence	17.6%	33.2%	67.6%	9.9%	1.6%	8.0%
Number of samples	699	1319	2683	394	64	316
Common species/types	Plastic packaging (58%) Chicken (20%) Bread (16%) Pork (11%)	Flatfish (44%) Whitefish (37%) <i>Liocarcinus holsatus</i> (25%) <i>Crangon crangon</i> (20%) Small pelagics (12%)	<i>Mytilus edulis</i> (82%) <i>Carcinus maenas</i> (17%) <i>Ensis americanus</i> (11%) <i>Asterias rubens</i> (5%)	Insects (48%) Cattlefeed, grains (18%) Berries and seeds (17%) Earthworm (13%) Birds (13%) Rabbits & rodents (11%)	<i>Rutilus rutilus</i> (86%) <i>Perca fluviatilis</i> (9%)	<i>Larus</i> gull chicks (67%) <i>Larus</i> gull egg (32%)
Availability	Opening hours & waste cleaning operations	Nearby fishing fleets	Low tide	Variable	Unclear	Breeding season
Energetic value	Up to very high ~10-25 kJ/g	Moderate to high ~4-10 kJ/g	Low to moderate ~2-5 kJ/g	Variable ~2-9 kJ/g	Moderate ~4-6 kJ/g	Moderate ~4-8 kJ/g
Digestive constraint	Large bones, plastics, metals, glass	Fish bones, scales	Breaking shells with muscular gizzard	Bones, fur, chitin	Fish bones, scales	Bones, down, eggshells

Methods

The study was carried out between May 2013 and August 2016 at a breeding colony of approximately 4000 pairs of herring gulls which breed sympatrically with approximately 11,000 pairs of lesser black-backed gulls *Larus fuscus* at the island of Texel, the Netherlands (53°00'N, 04°43'E; 615201.4 E, 5873649 N UTM zone 31; Fig. 3.1).

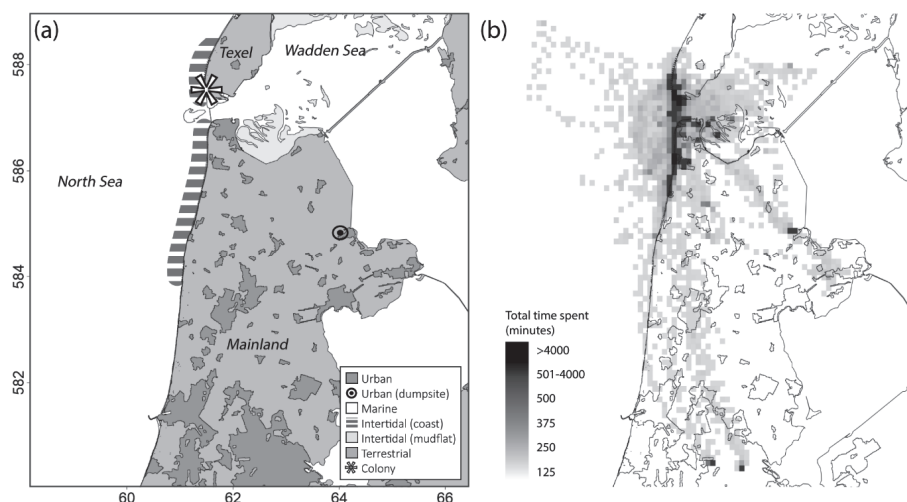


Fig. 3.1 Map of the study system and habitat use (a) Overview of the study area, latitude and longitude are indicated on the x and y axis in UTM zone 31 ($\times 10,000$), breeding colony is indicated with an asterisk (615,201.4 E, 5873649 N). Foraging areas of category urban which contain refuse are indicated in dark grey. Another source of human waste is the closest waste treatment center to the colony, indicated with a circle. Foraging area of category marine with main prey fishery discards are North Sea and Wadden Sea. Foraging areas of category intertidal are indicated in the dashed area, but herring gulls also forage in the Wadden Sea on intertidal mudflats indicated in light grey. Terrestrial foraging areas are found on Texel and the mainland and are indicated in grey. b Space use of all the herring gulls used in the study ($n = 17$) during chick care in breeding seasons of 2013–2016, expressed in total time spent in minutes per square kilometre.

GPS tracking

Thirty-one adult herring gulls (17 males and 14 females) were caught with walk-in traps during incubation between 2013 and 2015. Solar-powered GPS trackers of the UvA Bird Tracking System (Bouten et al. 2013, van Donk et al. 2018) were mounted to the birds with a 3-g non-flexible Teflon harness on the back of the birds. As recommended for seabirds (Phillips et al. 2003) GPS-tracker and harness together weighted less than 3% of the body mass of the birds which was on average 2.4 % of female body mass and 2.1 % of male body mass. These trackers measure, among others, the geographic location and time (UTC), and acceleration in three directions (surge, sway and heave). Tracking devices were calibrated to convert surge, sway and heave acceleration data to g-force ($1 g_n = 9.81 \text{ m/s}^2$). At time of capture, body mass (g), wing (mm), tarsus (mm), head (mm) and bill (mm) lengths were taken. The birds were sexed on the basis of head plus bill length (mm) (Coulson et al. 1983a). Birds were released after attaching the GPS tracker and taking body measurements, which took approximately 20 minutes. The tracking frequency was set to every 10 minutes inside the breeding territory and every 5 minutes outside the breeding territory. As we had the possibility to change measurement

frequency while the tracker was on the bird, we took occasionally higher resolution measurements. For better comparison, we resampled the data in this case to the standard measurement frequency. Tri-axial acceleration was periodically measured, only outside the breeding colony, at 20 Hz for 1 s directly following a GPS fix.

Data selection and processing

For our analysis, we used GPS data of individuals that had a nest with chicks for at least 5 days after hatching of the first egg and we only used data up to 10 days after hatching to control for differences in demands when chicks grow bigger. We studied the costs of foraging during chick care, as prey choice have shown to be important for reproductive success in this period (van Donk et al. 2017).

We compared the costs of foraging for different resources by analyzing foraging trips. We defined a foraging trip as a continuous period beginning when an individual travelled more than 100 meter from its nest and ending when the individual returned to within 100 meter of the nest. For each GPS location we attributed a ‘centered duration’ which was calculated by averaging the backward and forward time intervals between locations. The centered duration was used in further analysis to calculate trip duration and time spent in flight.

To calculate energy expenditure of foraging, we made use of acceleration data. Each acceleration measurement was attributed to one of 11 behaviors. We classified behaviors by training a random forest machine-learning algorithm for the classification of accelerometer data (Shamoun-Baranes et al. 2016, van Donk et al. 2018). We used two datasets to train the model on 11 different behaviors. The first is based on annotated accelerometer data of lesser black-backed gulls (Shamoun-Baranes et al. 2016), which is a species that is comparable in size and morphology, and most behavior with the herring gull. The second dataset contained accelerometer data of herring gull specific foraging behavior which was annotated with synchronized video recordings (van Donk et al. 2018). The final random forest model used had an accuracy for predicting the 11 behaviors of 94%. The 11 behaviors were then aggregated into four behaviors, which are inactive behavior (sitting, standing or floating), terrestrial movement (terrestrial locomotion, looking and standing while looking for food, handling prey and other), soaring flight (soaring and maneuvering) and flapping flight (regular and extreme flapping flight).

Gaps in the GPS measurements occurred, and we excluded trips from analysis when gaps were bigger than 20 minutes when outside the breeding colony. Besides, we only used trips of which at least 80% of the GPS fixes were accompanied with acceleration measurements. After data selection, 605 trips were included in the analysis of 17 different individual herring gulls. One herring gull was included in the analysis for three consecutive years.

Energetic costs

To compare energy expenditure of foraging in different habitat, we used three proxies for energy expenditure: (1) trip duration (h), (2) duration spent on flapping flight per trip (h) and (3) average estimated hourly energy expenditure per trip (kJ h^{-1}). Trip duration was calculated by summing all the ‘centered durations’ per trip.

The duration spent on flapping flight per trip was calculated by summing the ‘centered duration’ of measurements which were assigned to flapping flight. The duration of flapping flight per trip was used as a proxy for energy expenditure as flapping flight is thought to be the most energetically expensive form of locomotion compared to other behaviors (Tucker 1972).

We estimated the rate of energy expenditure per trip by estimating metabolic rates in kilojoules for the four classified behaviors per individual herring gull (van Donk et al. 2018). We calculated the basal metabolic rate (BMR) per individual in kJ day^{-1} as $2.3 \times \text{body mass (g)}^{0.774}$ at catching per individual (mean $\pm$ standard deviation of $19.64 \pm 1.31 \text{ kJ h}^{-1}$ for all animals in our study) (Bryant and Furness 1995). As the BMR does not account for thermoregulation when temperature is lower or higher than the thermo-neutral zone, digestion or little body movements, we calculated resting metabolic rate (RMR) as $1.7 \times \text{BMR}$ (Baudinette and Schmidt-Nielsen 1974, Furness 1978), with an average of $33.39 \pm 2.22 \text{ kJ h}^{-1}$ over all individuals. For the energetic cost of the behavior ‘inactive’ we used RMR. We estimated the energetic cost of ‘terrestrial movement’ as $2 \times \text{BMR}$. This estimation was based on a formula of costs for terrestrial movement of Bautista et al. (1998) (Bautista et al. 1998); costs terrestrial movement (kJ day^{-1}) = $(5.6 \times W_{\text{kg}}^{0.246} + 11.4 \times W_{\text{kg}}^{-0.285} \times v) \times 86.4$, where W_{kg} is body mass (kg) and v is velocity in m s^{-1} . As v we used 0.4 m s^{-1} which is the average velocity while walking of herring gulls with GPS trackers in this study. The formula of Bautista et al is based on data of starlings *Sturnus vulgaris*, but two studies in barnacle geese *Branta leucopsis* show similar energy expenditure of terrestrial locomotion compared to basal metabolic rate (Nolet et al. 1992, Nudds et al. 2010). The cost of soaring flight was estimated as $2 \times \text{RMR}$ (Baudinette and Schmidt-Nielsen 1974) and the cost of flapping flight was estimated as $7 \times \text{RMR}$ (Tucker 1972). We calculated energy expenditure by summing the ‘centered duration’ for the four classified behaviors per trip and multiplying these with the energetic estimations (hour^{-1}) of these four behaviors. To calculate energetic costs per hour, we divided energy expenditure of the whole trip by its trip duration.

Habitat use

To compare trips with different habitat use, we calculated the percentage of time gulls spent per trip in four foraging habitats which are termed (1) urban (2) marine, (3) intertidal and (4) terrestrial. We expect urban and marine environments to include predominantly high caloric

prey (e.g. refuse and fishery discards) whereas intertidal and terrestrial include mainly low caloric prey such as bivalves and crabs and terrestrial invertebrates (Table 3.1)(Fig. 3.1).

To calculate habitat use, we took all the GPS positions outside the colony into account, apart from when animals are commuting (i.e. when an individual is flying in a straight line from one place to the other). To select the commuting GPS positions, we made use of an expectation maximization binary clustering for behavioral annotation developed by Garriga et al. 2016 (Garriga et al. 2016a). This clustering algorithm uses turning angle and velocity obtained from successive locations to cluster GPS positions in four behavioral categories which are High velocity/Low turn (HL), High velocity/High turn (HH), Low velocity/Low turn (LL), Low velocity/High turn (LH). We assumed that an animal is commuting when velocity is high and turning angle low (HL category). We applied the clustering algorithm per individual in a given year using the *r* package *EmbC* and applied a pre-smoothing procedure which is provided by the packages to account for temporal associations.

Subsequently, we coupled every non-commuting GPS position to one of the four foraging habitats using several shapefiles of foraging areas around the colony and the behavioral classifications. We used the following shapefiles of foraging areas: North Sea and Wadden Sea, urban areas, breakwaters, beach & intertidal mudflats, agriculture & natural land (Table S 3.1). Often, the area around the breakwater, beach and intertidal mudflats is also available for foraging during low tide (personal observations) and therefore we also assigned GPS points which were assigned to North Sea or Wadden Sea closer than 50 meters to breakwater, beach or intertidal mudflats to the intertidal habitat type. GPS positions were assigned to urban habitat when in urban areas. GPS positions were assigned to the marine when in the North Sea and Wadden Sea and on intertidal mudflats with the behavioral mode flying or floating. Almost all fish that the herring gulls of this colony consume originates from fishery discards (Camphuysen 2013) (p.337). GPS positions were assigned to intertidal habitat when on breakwaters and beach and on intertidal mudflats when the behavioral mode was resting or terrestrial movement which indicates foraging on intertidal mudflats. GPS positions were assigned to terrestrial habitat when in agricultural or natural areas.

Statistical analysis

To test whether foraging costs differ depending on the foraging habitat, we divided all foraging trips in five habitat categories based on the time an animal spent in every foraging habitat. A foraging trip with 50% or more of its non-commuting GPS positions in one of the four foraging habitats, was assigned to category urban, marine, intertidal or terrestrial. A foraging trip with less than 50% of its non-commuting GPS positions in one of the four foraging habitats was assigned to a fifth category; mixed. Fig. 3.2 shows examples of foraging trips of four categories.

We tested the hypothesis whether trips of the five habitat categories differed in energy expenditure by fitting linear mixed-effect models. We fitted a separate model for each of the response variables: trip duration in hours, duration spent on flapping flight in hours and rate of energy expenditure per hour. We included habitat categories as fixed effect and bird ID as random intercept in the models. Response variables in the models were transformed to obtain normality and homogeneity of variance; trip duration and energy expenditure were transformed with the natural logarithm, duration in flapping flight was transformed with the square root. Commuting GPS fixes were included in the calculation of these response variables. The models were tested against a null model which only contained the random factor. When the model was significantly better than the null model, we performed post hoc Tukey testing for the fixed part of the model to test which habitat category differed using the *lsmeans* function from the *lmer* Test library (Kuznetsova et al. 2017). P-values, Δ AICc and the model estimates and standard errors were reported, as well as marginal and conditional R squared values for mixed models (Nakagawa and Schielzeth 2013). Although we did not have specific hypotheses about the role of sex, mass or sampling year in this study, we did explore these factors in the models by comparing the residuals of the model with sex, sampling year and mass. After this analysis, we concluded that we could ignore these factors in our analyses.

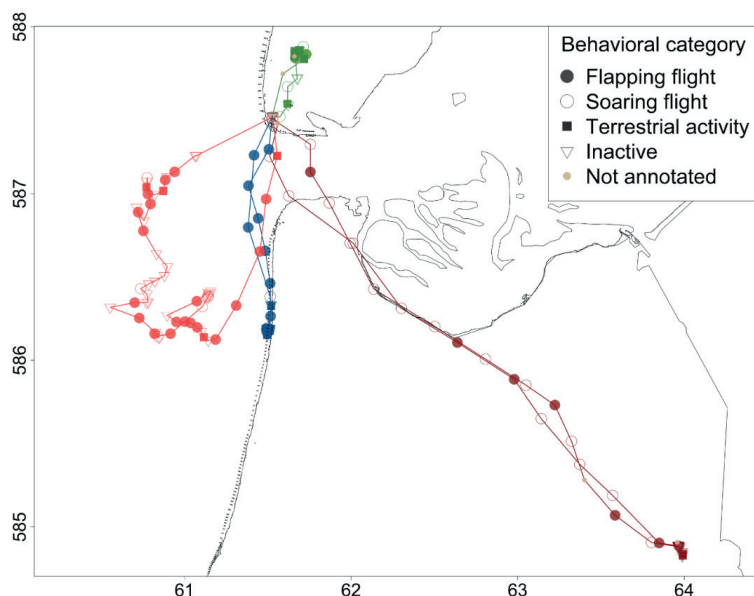


Fig. 3.2 Examples of four foraging trips which are indicated in four different colors. Latitude and longitude are indicated on the x and y axis in UTM ($\times 10.000$). Every point corresponds to one GPS fix and the shape of the points indicates the behavior of the animal (Flapping flight, soaring flight, terrestrial activity, inactive or not annotated). In dark red; a foraging trip of category urban. In light red; a foraging trip of category marine. In blue; a foraging trip of category intertidal. In green a foraging trip of category terrestrial.

Results

Habitat use and foraging trips

During the non-commuting phase of foraging trips, herring gulls spent most time in areas with relatively lower caloric prey; most time was spent in the intertidal habitat followed by terrestrial habitat (Table 3.2). Less time was spent in areas with relatively high caloric prey; gulls spent from these habitat types a bit more time in marine habitat than in urban habitat (Table 3.2). As a result, the number of foraging trips per category were also not evenly distributed; most trips were assigned to intertidal and least to category mixed (Table 3.2).

To test whether habitat use differed in energy expenditure per trip, we made use of three proxies for energy expenditure which were trip duration, time spent on flapping flight and energy expenditure for which we also included the time spent on commuting. Duration of foraging trips varied widely (range: 0.6 – 14.4 h, mean $\pm$ SE: 2.8 $\pm$ 1.9 h) and mean foraging duration was highest for urban and mixed foraging trips. Similarly, we found high variation in the proportion of time spent on flapping flight per trip (range: 0 – 1 per h trip, mean $\pm$ SE: 0.21 $\pm$ 0.15 h) and the estimated energy spent per trip (range: 11 – 1006kJ, mean $\pm$ SE: 224 $\pm$ 163 kJ) and they were both highest for urban trips. But the estimated energy spent per hour (range: 26 – 252kJ, mean $\pm$ SE: 78 $\pm$ 29 kJ) was highest for marine foraging trips. Mean trip duration, time spent on flapping and the estimation of energy expenditure per trip were lowest for terrestrial trips, but estimated energy expenditure per hour was lowest for both terrestrial and intertidal trips.

Link between energetic costs and habitat use during foraging trips

Foraging costs were also significantly higher in urban and marine habitats than foraging in intertidal or terrestrial foraging habitats, while mixed foraging trips had similar energetic costs as trips to urban and marine habitat (Table 3.3). Duration of trips differed between the categories; urban and mixed trips were significantly longer than trips to marine and intertidal habitat and trips of category terrestrial were shorter than trips of all other categories (Fig. 3.4a). But the higher energetic costs of urban, marine and mixed trips are mainly caused by relatively more time spent on flapping flight per trip (Figs. 3.3 & 3.4). More specifically, the trips in category urban, marine and mixed included more time spent on flapping flight and a higher estimated energy expenditure per hour than trips in category intertidal and terrestrial (Table 3; $p < 0.05$), while energy expenditure per hour did not differ between intertidal and terrestrial trips (Figs. 3.4b & 3.4c).

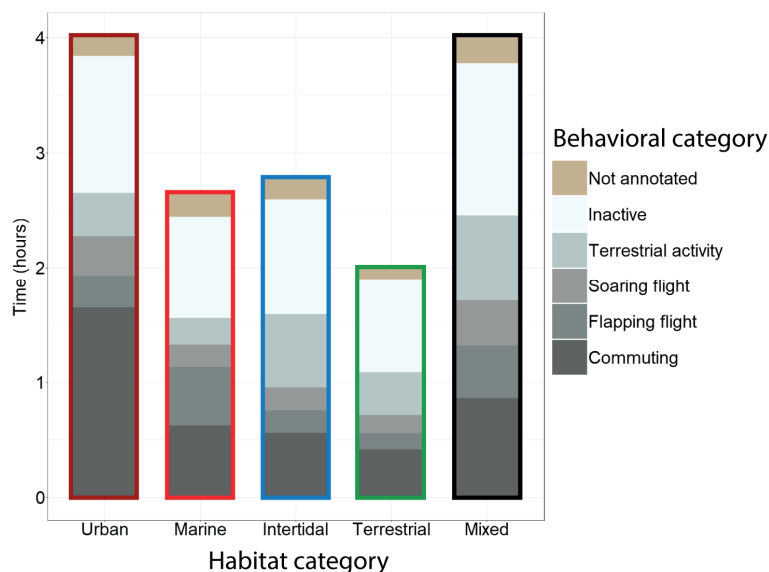


Fig. 3.3 Trip duration and time spent (h) on the different behavioral categories per habitat category ($n = 605$ foraging trips). Trips on which individuals spent more than 50% in one habitat were assigned to main habitat category urban, marine, intertidal or terrestrial. Trips on which individuals spent less than 50% in one habitat were assigned to main habitat category mixed

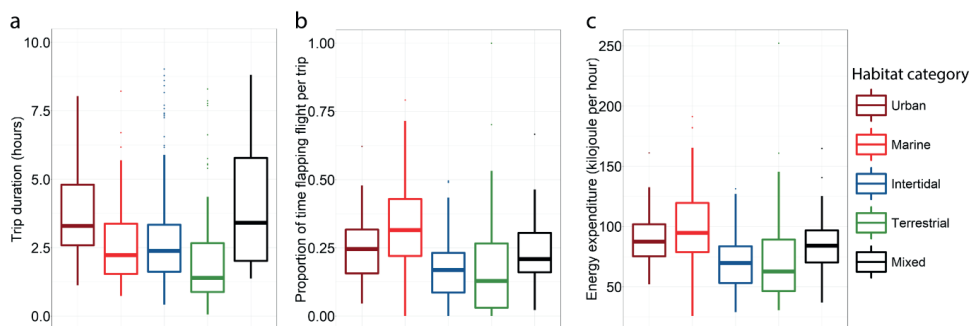


Fig. 3.4 The relationship between habitat use per habitat category and energetic costs. The boxplots show the median values of energetic costs per habitat category. a-c represents habitat category in relation to (a) trip duration in hours (b) Proportion of time in flapping flight and (c) energy expenditure in kilojoules per hour

Table 3.2 Habitat use outside the breeding colony of non-commuting GPS data of all herring gulls used in this study (n = 17) and foraging trip details (n = 605). Total time in hours (Time (h)) and percentages (Time (%)) of non-commuting GPS data of all herring gulls used in this study, the number of trips per habitat category (Nr. Trips), mean $\pm$ standard error of the trip duration per habitat category (Mean trip duration; h), the proportion of flapping flight per trip per habitat category (Proportion flapping trip⁻¹) and the average energy expenditure per time (Rate of energy expenditure; kJ h⁻¹) and per trip (Total energy; kJ) per habitat category.

Habitat	Time (h)	Time (%)	Nr. trips	Mean trip duration	Proportion flapping trip ⁻¹	Rate of energy expenditure	Total energy
Urban	155	14	66	4.02 $\pm$ 2.28	0.25 $\pm$ 0.11	89.41 $\pm$ 21.88	357.17 $\pm$ 205.50
Marine	199	18	86	2.66 $\pm$ 1.46	0.34 $\pm$ 0.17	100.70 $\pm$ 33.97	261.52 $\pm$ 152.22
Intertidal	535	48	271	2.78 $\pm$ 1.70	0.17 $\pm$ 0.11	69.88 $\pm$ 21.78	196.65 $\pm$ 127.88
Terrestrial	232	21	127	2.01 $\pm$ 1.67	0.17 $\pm$ 0.17	71.96 $\pm$ 34.63	146.89 $\pm$ 138.62
Mixed	-	-	55	4.00 $\pm$ 2.23	0.24 $\pm$ 0.12	85.10 $\pm$ 23.27	323.52 $\pm$ 180.79

Table 3.3 Model results of the relationship between habitat use and response variables the logarithm of trip duration in hours (Log(Duration)), the square root of duration of flapping flight in hours (sqrt(Flapping)), and the logarithm of energy expenditure in kJ per hour (log(energy)). We used linear mixed-effect models with habitat category as fixed effect and bird ID as random intercept. Model estimates and standard error (SE) are shown for the five categories; Intercept U is the intercept and the estimate for category urban. When the estimates for the other fixed factors are negative, this category has a lower output of the response variable than the Intercept U. When the estimates of the other fixed factors are positive, this category has a higher output of the response variable than the Intercept U. The fixed factor with the highest model estimate per model is printed in bold and the statistical differences of the groups are indicated with letters. We provided the marginal (R²m) and conditional (R²c) for every model which represents, respectively, the variance explained for the fixed factors alone or the variance explained taking by both the fixed and random factors (individual birdIDs).

Response variable	Fixed factors	Model estimates	Chisq	Δ AICc	p-value	df	R ² m	R ² c
Log(Duration)	Intercept U.	1.22$\pm$0.09^a	89.55	81.55	<2e-16	4	0.13	0.23
	Marine	-0.40 $\pm$ 0.10 ^b						
	Intertidal	-0.35 $\pm$ 0.09 ^b						
	Terrestrial	-0.77 $\pm$ 0.09 ^c						
	Mixed	-0.06 $\pm$ 0.11 ^a						
Sqrt(Flapping)	Intercept U.	0.92$\pm$0.05^a	120.58	112.58	<2e-16	4	0.18	0.25
	Marine	-0.06 $\pm$ 0.05 ^a						
	Intertidal	-0.30 $\pm$ 0.05 ^b						
	Terrestrial	-0.43 $\pm$ 0.05 ^c						
	Mixed	-0.05 $\pm$ 0.06 ^a						
Log(Energy)	Intercept U.	4.46 $\pm$ 0.04 ^a	96.20	88.20	<2e-16	4	0.15	0.16
	Marine	0.09$\pm$0.06^a						
	Intertidal	-0.27 $\pm$ 0.05 ^b						
	Terrestrial	-0.29 $\pm$ 0.05 ^b						
	Mixed	-0.05 $\pm$ 0.06 ^a						

Discussion

By comparing foraging trips of different habitat use, we found, in line with our expectations, that foraging at sea for discards or in dumps or cities where most human refuse is obtained was energetically costlier (about 34 higher costs per hour) than foraging in other habitats. Mixed foraging strategies (the use of more foraging habitats) had a similar energy expenditure as foraging trips towards anthropogenic resources (urban and marine trips). Higher costs resulted in particular from the time spent in flapping flight, but mixed and urban foraging trips were also longer in duration. Foraging in terrestrial or intertidal habitats was comparable in energetic costs per hour, but foraging in terrestrial habitat was least costly per trip, because the duration of these trips was shorter. We discuss the consequences of these foraging costs considering the past and future changes in the food landscape and costs and benefits of prey.

We used rough estimates for energy expenditure in this study, and compare them with other studies to determine whether our estimates were biologically meaningful. These studies described below measured food intake or energy expenditure of adult seabirds. A study on lesser black-backed gulls in captivity measured a fish intake of 900-1400 kJ per day (Hilton et al. 2000) and with an assimilation efficiency of 75% (Castro et al. 1989), these gulls used 28-44 kJ per hour. This gull species is smaller than the herring gull and the birds were not able to show energetically costly behavior like searching for food and flying. Another study on black-legged kittiwakes *Rissa tridactyla*, seabirds which are half the weight of herring gulls, found that birds used 41 kJ per hour during foraging trips (Gabrielsen et al. 1987). Our estimations of an average energy use of 78kJ per hour during foraging trips seem to be quite reasonable, compared to measurements from other seabirds.

Foraging for anthropogenic resources is energetically expensive in our system but how big are these costs in terms of quantity of prey? The average length of discarded flatfish that is found in the breeding colony is 12-13 centimeter with an energetic value of 84 kJ per fish (Garthe et al. 1996, Camphuysen and Henderson 2017). Daily energetic costs per day for an animal solely foraging for fishery discards are 1462 kJ per day, assuming 14 hours in the colony spending 33 kJ per hour and 10 hours outside the colony spending 100 kJ per hour (Table 3.2). The average assimilation efficiency is 75% (Castro et al. 1989), so such an animal has to catch 23 fishes (1949 kJ) for its own subsistence. The amount of prey that it catches should be higher, as birds also have to gather food for chicks. Compared to an animal foraging solely in intertidal or terrestrial habitat which costs about 70 kJ per hour (daily costs about 1162 kJ), it would need to catch 5 flatfish more per day to compensate for the higher foraging costs.

When animals forage for anthropogenic prey, they have to catch more prey to compensate for higher foraging costs. However, the differences in energetic costs per hour between resting metabolic rate and foraging are in fact considerably larger, respectively 33 kJ and 70-100 kJ

depending on foraging habitat (Table 3.2). The total time a gull spends on foraging might actually be more important in terms of its energetic costs than in which habitat a gull forages. A gull that mostly forages in urban or marine habitat could compensate for its higher foraging costs by conducting fewer foraging trips per day and can thus have similar daily costs compared to a gull that mostly forages in terrestrial or intertidal habitats. Among individuals in our study, this does not seem to be the case. The average number of trips per day differs considerably per individual, but individuals that forage more for anthropogenic resources do not have less trips per day (Table S3.1). Interestingly, there does seem to be a correlation between the number of trips per day and the time spent in intertidal area. Individuals that spent most of their trips in intertidal areas seem to have a higher amount of trips per day compared to individuals that do not forage often in intertidal habitat (Table S3.2 & Fig. S 3.1), suggesting that the low hourly costs of foraging in intertidal area are cancelled out by foraging more times a day. This relationship is mainly caused by two individuals, so a larger sample size would be needed to investigate this relationship more thoroughly.

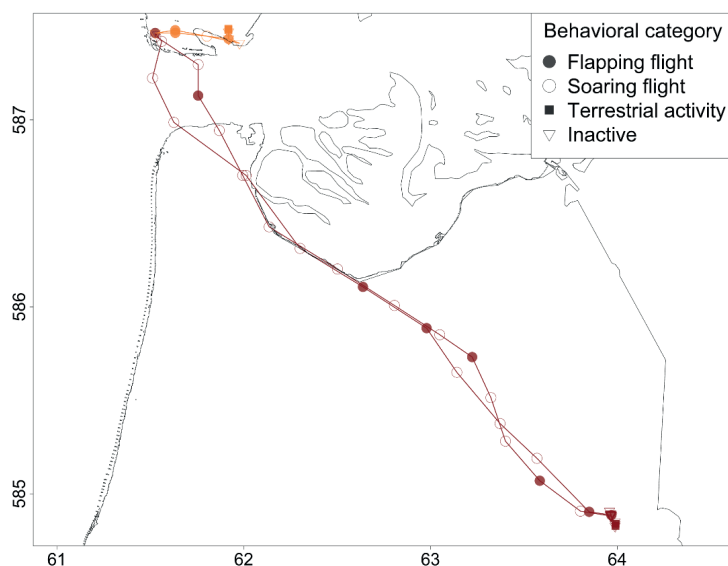


Fig. 3.5 Comparison between imaginary foraging trip to the closest refuse dump 30 years ago (4 km distance of the colony; in orange) and a foraging trip to the closest waste treatment center (35 km distance of the colony; in dark red). Latitude and longitude are indicated on the x and y axis in UTM ($\times 10.000$). Breeding colony is situated at 615201.4 E, 5873649 N UTM. Every point corresponds to one GPS fix and the size of the points indicates the behavior of the animal (resting, terrestrial locomotion, soaring flight or flapping flight). Estimated energetic costs of these trips of an animal with a body mass of 1000 g are respectively 160 kJ and 362 kJ

Individual animals have to make foraging decisions based on the advantages and disadvantages between different foraging strategies (Oudman et al. 2014, Patenaude-Monette et al. 2014, Rozen-Rechels et al. 2015). One of the main benefits of foraging for refuse and fishery discards for herring gulls is the high caloric value per gram prey which helps reaching energetic demands of growing chicks (Table 3.1) (Spaans 1971, Hunt 1972, Pons and Migot 1995, van Donk et al. 2017). We found that herring gulls spent more energy to obtain these high quality prey by making longer trips and flying more (Table 3.2). That central-place foragers like breeding gulls spent more energy to obtain prey of higher quality has been found before. For example, Ring-billed gulls *Larus delawarensis* travelled further for foraging patches that provided higher mean energy intake, like refuse dumps (Patenaude-Monette et al. 2014), while foraging patches with lower mean energy intake, like agricultural fields, were only visited closer to the breeding colony.

To understand the net energy gain, it is also important to learn about the food intake per unit time. Although we have indirect proof that animals foraging for high caloric prey like fishery discards and human waste have a higher net energy gain, because of their better growing and surviving chicks (van Donk et al. 2017), we miss a direct measurement of food intake per unit time. In future, we hope to be able to measure food intake per habitat by using detailed accelerometer data and video recordings of the different habitats. Another possibility to estimate energy intake is to use the dynamic energy budget model (DEB) (Kooijman 2010). This model can be used to estimate energy intake of growing chicks based on their weight, which will give a more precise estimate of prey intake in terms of kilojoules brought to the nest, even on a daily basis (Teixeira et al. 2014).

Characteristics of prey other than energetic gain and loss are also important for gulls, like the availability and predictability of prey (Table 3.1). Prey in terrestrial habitat are not always available during the breeding season. Earthworms, for example, are only available when the soil is moist, and agricultural areas provide most food when farmers are ploughing (Kruuk 1978, Sibly and McCleery 1983, Patenaude-Monette et al. 2014). This might explain the shorter time herring gulls spent in this habitat, despite the low foraging costs, compared to intertidal foraging habitat (Table 3.2; 21% of foraging time). On the contrary, prey of the intertidal habitat (mostly bivalves) are very predictable (during low tide) and available in large amounts every day which might be the reason that most of the foraging time is spent in this habitat.

Although herring gulls have been benefiting from human resources, this situation is changing and resources have been decreasing the last decades. National and international legislation caused the decrease of the number of refuse dumps and the amount of refuse in most European countries including the Netherlands (Kohler and Perry 2005, Camphuysen 2013, European Environment Agency (EEA) 2016, Rijkswaterstaat 2016). Furthermore, fishing fleet densities

in the region have decreased and legislation towards discarding bycatch became stricter (Rijnsdorp et al. 2008, 2011, Poos 2010, Borges 2015). Resource availability for the herring gulls breeding on Texel have changed in a similar way as the number of fishing vessels and refuse dumps in the close surroundings decreased a lot (Spaans 1971, Camphuysen 2013). Only 30 years ago, there was still a refuse dump within 4 kilometers of the breeding colony (Fig. 3.5), whereas now the closest waste treatment center is 35 km away. Unfortunately, we cannot compare foraging costs between the past and now, but using the knowledge we have gained in the present study, we could compare an hypothetical foraging trip to the disappeared refuse dump with a foraging trip to the closest waste treatment center now, which is presented in Fig. 3.5. When we assume that foraging time is similar between the two places (about 1.5 hours), the costs of foraging on refuse dumps might have more than doubled for these gulls due to the increased cost of flight. In future, the amount of refuse and fishery discards will probably be even less. Fishing effort is still decreasing and a more sustainable way of fishing is in development (Bicknell et al. 2013). This will probably increase time and energy needed for foraging because of higher competition.

If the foraging costs for these resources become higher than the reproductive gains, gulls might have to change their behavior. Gulls could decrease foraging costs, for instance by decreasing the distance that they have to commute between breeding territory and foraging areas by breeding closer to urban areas or refuse dumps. Gulls do breed on rooftops in increasing numbers, with sometimes higher breeding performance (Monaghan 1979, Mitchell et al. 2004, Rock 2005, Soldatini et al. 2008). Although the foraging behavior of these gulls is largely unknown, the proximity of foraging possibilities to a colony does affect the composition of the diet of that colony (Washburn et al. 2013, O'Hanlon et al. 2017, Fuirst et al. 2018). A recent study on breeding colonies of herring gulls in the USA, showed that birds breeding closer to urbanization had shorter foraging trips (Fuirst et al. 2018). But whether gulls will move between breeding locations is questionable, as gulls of this colony rarely move to another breeding colony, even though breeding success is low (Camphuysen 2013) (p.326). The location of the breeding site on Texel does not seem very favorable anymore in terms of food sources compared to 30 years ago (Spaans 1971). Still, there are no indications of a decrease in breeding pairs over the last decade. Whether individual herring gulls of this colony will adapt their behavior is unclear, but these human induced changes in the environment create a natural experiment to study the effect on animals' behavior. In future, we could use these environmental changes to look into whether individuals will respond to these changes by adapting their foraging or breeding behavior.

Conclusions

We studied costs of foraging in different habitats in the herring gull, to get a better understanding of the factors that can shape animals' foraging decisions in an environment which is highly affected by humans. We found that foraging for high caloric prey of anthropogenic origin is costly in terms of foraging effort compared to other foraging options, but these prey are beneficial for chick growth and survival. Foraging for less beneficial prey for reproduction, like terrestrial and intertidal prey, were less costly in terms of foraging effort. Recent and future alterations in fishery discards and garbage management will increase foraging costs of these prey, which will affect the balance between costs and benefits. Gulls might have to adapt or change foraging or breeding behavior, although it is not clear whether they will be able to do this due limited flexibility.

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Author Contributions

SvD carried out the statistical analysis, and drafted the manuscript with support from JSB, JvdM and CJC; CJC leads long term study on herring gulls; CJC and SvD conducted field work, JSB assisted with GPS tracking. SvD, JSB, JvdM and CJC discussed the analytical approach; All authors discussed results and contributed to the final manuscript.

Supplementary material

Table S3.1 Habitat types and shapefiles used in the analysis.

Habitat	Shapefile
North Sea and Wadden Sea	GDAM January 2012 European boundaries polygon (Hijmans 2012)
Urban areas	OpenStreetMap data (OpenStreetMap contributors 2017) CORINE Urban morphological zones 2006 (European Environment Agency (EEA) 2017)
Beach	LGN5 (Landelijke Grondgebruikskartering 5) (Hazeu 2005)
Breakwaters	Delineated based on QGIS openlayer plugin google earth (QGIS Development Team 2009)
Tidal flats	Rijkswaterstaat (http://www.rijkswaterstaat.nl)
Agricultural and natural	OpenStreetMap data (OpenStreetMap contributors 2017) Netherlands Natural Features shapefile (MapCruzin 2017)

Table S3.2 Average number of foraging trips per individual bird ID per habitat category and the total number of trips per day. The table is ordered in ascending order of total number of trips per day. The highest value per individual (favored habitat category) is underlined.

Bird ID	Average number of trips per day					Total
	Urban	Marine	Intertidal	Terrestrial	Mixed	
6217	<u>0.72</u>	0.31	<u>0.72</u>	<u>0.72</u>	0.62	3.10
6206	0.96	0.48	<u>1.44</u>	0.24	0.72	3.83
1600	0.00	0.91	<u>2.73</u>	0.13	0.13	3.90
6004	0.56	0.42	<u>1.25</u>	1.11	0.56	3.90
6006	<u>1.95</u>	0.00	0.43	1.19	0.33	3.90
6009	0.00	0.42	1.58	<u>2.00</u>	0.00	4.00
6076	0.10	0.50	<u>1.80</u>	0.90	0.70	4.00
6073	0.00	0.99	1.44	<u>1.66</u>	0.11	4.20
6080	<u>1.56</u>	0.78	0.39	1.17	0.39	4.29
6014	0.80	<u>1.60</u>	0.40	1.00	0.60	4.40
6205	0.00	0.39	<u>2.70</u>	0.64	0.77	4.50
6210	1.07	0.59	<u>2.13</u>	0.36	0.36	4.50
6202	1.02	0.87	<u>1.60</u>	0.87	0.44	4.80
6015	<u>1.61</u>	1.38	0.69	1.15	0.00	4.83
6071	0.00	0.83	<u>2.50</u>	1.04	0.52	4.90
6016	0.05	0.56	<u>3.63</u>	0.87	0.31	5.42
6208	0.00	0.63	<u>4.28</u>	0.32	0.48	5.70

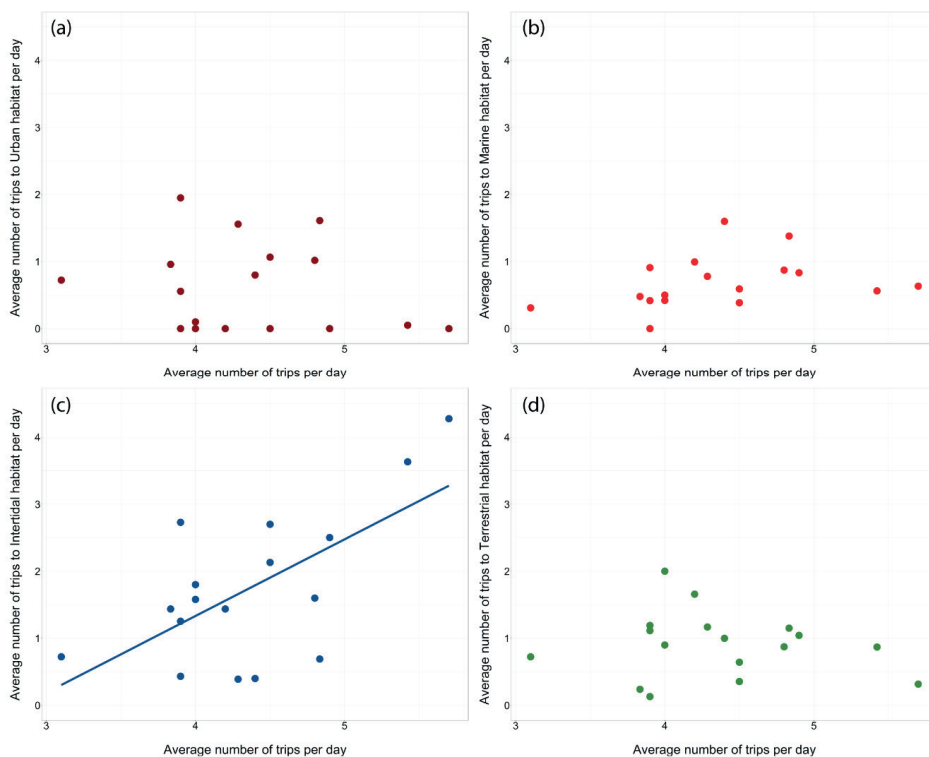


Fig. S3.1 Relationship between average number of trips per day on the x-axis and average number of trips to the specific habitats per day per bird ID on the y-axis per bird-ID. Every point represents one Bird ID. Figs (a)-(d) show average trips per day against average trips to (a) urban habitat, (b) marine habitat, (c) intertidal habitat and (d) terrestrial habitat. Only the relationship between average number of trips per day and average number of trips to intertidal habitat is statistically significant (linear model intercept= 3.74 ± 0.23 , estimates = 0.36 ± 0.11 , $p=0.006$, $R^2=0.37$).



Chapter 4

Individual differences in foraging site fidelity are not related to time-activity budgets in Herring Gulls

Susanne van Donk, Judy Shamoun-Baranes, Willem Bouten, Jaap van der Meer, Kees C.J. Camphuysen

Abstract

Many populations consist of individuals that differ consistently in their foraging behaviour through resource or foraging site selection. Foraging site fidelity has been reported in several seabird species as a common phenomenon. It is considered especially beneficial in spatially and/or temporally predictable environments in which fidelity is thought to increase energy intake, thereby affecting time-energy budgets. However, the consequences for activity and energy budget have not been adequately tested. In this paper, we studied the consequences of fine-scale foraging site fidelity in adult Herring Gulls *Larus argentatus* in a highly predictable foraging environment with distinct foraging patches. We measured their time-activity budgets using GPS tracking and tri-axial acceleration measurements, which also made it possible to estimate energy expenditure. Individual variation in foraging site fidelity was high, some individuals spending most of their time on a single foraging patch and others spending the same amount of time in up to 21 patches. While time and activity budgets differed between individuals, we found no clear relationship with foraging site fidelity. We did find a relationship between the size of the birds and the level of site fidelity; faithful birds tend to have a larger body size. Although differences in foraging time and habitat use between individuals could play a role in the results of the current study, short-term consequences of variation in foraging site fidelity within a population remain elusive, even when focusing on individuals with a similar foraging specialization (Blue Mussels *Mytilus edulis*). Studying individuals over multiple years and under varying environmental conditions may provide better insight into the consequences and plasticity of foraging site fidelity

Introduction

Many populations consist of individuals that differ consistently in their food choice and foraging strategy. A common form of such variation is foraging site fidelity, where some individuals exploit a more limited set of foraging sites than others (Switzer 1993, Bradshaw et al. 2004, Piper 2011, Wakefield et al. 2015, McIntyre et al. 2017, Patrick and Weimerskirch 2017). Despite the important role of site fidelity in space use, proximate causes and associated fitness consequences are only reported in a few cases (Piper 2011). Site fidelity may increase energy intake and thereby affect time-activity budgets. For example, site-faithful individuals could reach higher energy intake rates through improved local knowledge about the quality and availability of prey (Irons 1998, Hamer et al. 2001). In addition, foragers will learn to know their immediate competitors, when the majority of them are also site-faithful, and eventually spend less time on aggression and interference competition (Eason and Hannon 1994, Leiser and Itzkowitz 1999, Wolf and Trillmich 2007), while leaving more time for self-maintenance or investing in offspring.

The occurrence of foraging site fidelity has been related to characteristics of the environment and resources within it. For fidelity to be an advantageous strategy, prey should be spatially and/or temporally predictable and not likely to be depleted for fidelity to be an advantageous strategy (Andersson 1980, Irons 1998, Arthur et al. 2015). However, even when environments seem to be predictable and have abundant resources, some animals within the same population show a low degree of site fidelity (Piper 2011, Patrick and Weimerskirch 2014a, Wakefield et al. 2015, McIntyre et al. 2017). This raises the question of whether there are negative consequences of having lower site fidelity for time-energy budgets. Foraging site fidelity has been widely reported in seabirds at coarse to mesoscale (tens to hundreds of kilometres) (Irons 1998, Weimerskirch 2007, Wakefield et al. 2015) and at a finer scale (< 10km) (Kotzerka *et al.* 2011). However, the relationship between site fidelity and time-energy budgets has barely been studied in these systems.

Understanding the extent to which individual differences in site fidelity influences time-energy budgets can be extremely challenging in free-ranging birds. For example, foraging site fidelity could be a consequence of specialization in diet or habitat (Woo et al. 2008, Wakefield et al. 2015) or demands on time, energy and food quality may change during the annual cycle and subsequently affect foraging site fidelity (Annett and Pierotti 1989, Votier et al. 2017). Some of these factors can be accounted for when working with systems that have been extensively studied. One well-studied species of seabird, is the herring gull *Larus argentatus*. Herring gulls, like many other *Larus* species, are dietary generalists on the species level, but individuals have different foraging strategies (Morris and Black 1980, Gorke and Brandl 1986, McCleery and Sibly 1986, Pierotti and Annett 1990, Irons 1998). Herring gulls breeding on the island of Texel,

the Netherlands, forage during incubation mainly on a predictable and abundant resource, blue mussels *Mytilus edulis* (Camphuysen 2013, van Donk et al. 2017). These mussels grow on breakwaters which are human-made coastal defence structures. Breakwaters form discrete foraging patches which are linearly arranged and equidistant from each other, with similar resource quality and quantity between patches. This provides an opportunity to study individual differences in foraging behaviour and consequences of site fidelity while foraging on the same predictable resource.

We studied foraging site fidelity and time-activity budgets of adult breeding gulls during the incubation period, in which both sexes are involved equally, for three reasons. First, we focus on incubation to control for possible changes in demands during different breeding phases. Second, we can control for differences in diet by selecting individuals with a similar dietary specialization, as gulls in this system feed primarily on blue mussels during incubation (Camphuysen 2013, van Donk et al. 2017). Finally, incubation is an important period for increasing energy reserves, as herring gulls recover from the physical impacts of egg-laying (females) and extra food provisioning in the pre-laying phase (males to females) (Hario et al. 1991). Therefore, the time and energy spent on foraging is of great importance during incubation.

The aim of the study was to investigate whether fine-scale foraging site fidelity is related to time-activity budgets by focusing our analysis on individuals that primarily use the same resource organized in discrete patches. We quantified time-activity budgets of individual herring gulls and estimated energy expenditure using GPS tracking and tri-axial acceleration measurements. We expected that site-faithful individuals spend more time in the breeding territory as they need less time for foraging (supplementary fed Herring Gulls stay longer in the colony (Niebuhr 1983)), spend a larger proportion of time on inactive behaviour during foraging (self-maintenance) or use less energy during foraging as they spend less time on searching, social interactions or commuting between patches. Herring gulls are sexually dimorphic, and both sex and body size can influence their hierarchy (Monaghan 1980, Sibly and McCleery 1983). This may result in competitive interference within feeding patches, with females or smaller individuals being displaced more frequently than males and hence being less site-faithful. We therefore also tested whether body size or sex influenced the level of site fidelity or time-activity budgets.

Methods

Study system

The study was based on a breeding colony on the island of Texel, the Netherlands (53°00'N, 04°43'E), between the western Wadden Sea and the southern North Sea (Fig. 4.1a). Approximately 4000 pairs of herring gulls breed sympatrically with around 11 000 pairs of

lesser black-backed gulls *Larus fuscus* (Camphuysen and Gronert 2010). We have permission to work in the colony and catch, ring and tag herring gulls under the permit of Art 75 of the Dutch "Flora & Faunawet" FF/75A/2014003, an annually renewed ringing permit issued by Vogeltrekstation Wageningen for ringer-licensed E29 Camphuysen, an annually renewed research permit issued by Saatsbosbeheer Divisie grond en gebouwen, and a permit for animal experiments (tracking Herring Gulls) issued by the "Nederlandse Voedsel- en Warenautoriteit", Ministry of Economics, TRC/VWA/20132090. The foraging and breeding ecology of herring gulls breeding on the island have been studied for over 10 years. Based on analysed prey remains found on breeding territories over the study period, the main foraging habitat includes arable land, urban areas, sea (North Sea and Wadden Sea) and coastal areas including beach and breakwaters. Breakwaters are human-made coastal defence structures colonised by blue mussels (*Mytilus edulis*) which are expected to provide the main diet during the incubation period (up to 70% of pellets contained mussels) (Camphuysen et al. 2008, Camphuysen 2013, van Donk et al. 2017). These foraging patches are found in a range of 35 kilometres of the colony, along the North Sea coast between Texel and Schoorl (Fig. 4.1a) and are organized in discrete patches, comparable in structure and size and linearly arranged with similar distance (~200 m along the coast of Noord-Holland and ~400 m along the coast of Texel) in-between neighbouring breakwaters (Fig. 4.1b). The quality of blue mussels is generally similar between different breakwaters and there is no indication of depletion of resources through the year (Dekker et al. 2014). Although there is no evidence of resource depletion, the number of birds can cause interference competition (Vahl et al. 2005). Furthermore, gulls are uniformly distributed over the breakwaters, with more or less similar numbers of gulls per breakwater.

Data collection

To obtain time-activity budgets of herring gulls at fine spatial and temporal scale, GPS trackers of the UvA Bird Tracking System were used (Bouten et al. 2013). These trackers measure the geographic location (with a mean position error of 3 m for measurement intervals of 60 s and 30 m for interval of 600 s), time (UTC), altitude above mean sea level (m), ground speed (km/h) and acceleration in three directions (surge (x), sway (y) and heave (z)). Tracking devices were calibrated to convert x, y and z acceleration data to gravitational force ($1\text{ g}_n = 9.81\text{ m/s}^2$). A total of 31 adult herring gulls (17 males and 14 females) were equipped with GPS trackers between 2013 and 2015. Birds were trapped during incubation using a walk-in trap. The birds were colour-ringed and a solar-powered GPS tracker (ranging from 17.1-19.7 g) was mounted with a 3-g non-flexible Teflon harness on the back of the bird. We sexed each bird on the basis of biometrics (head plus bill length) with only 5% expected misidentification (Coulson *et al.* 1983) and made size measurements including bill depth (at base, 0.1 mm), tarsus length (mm),

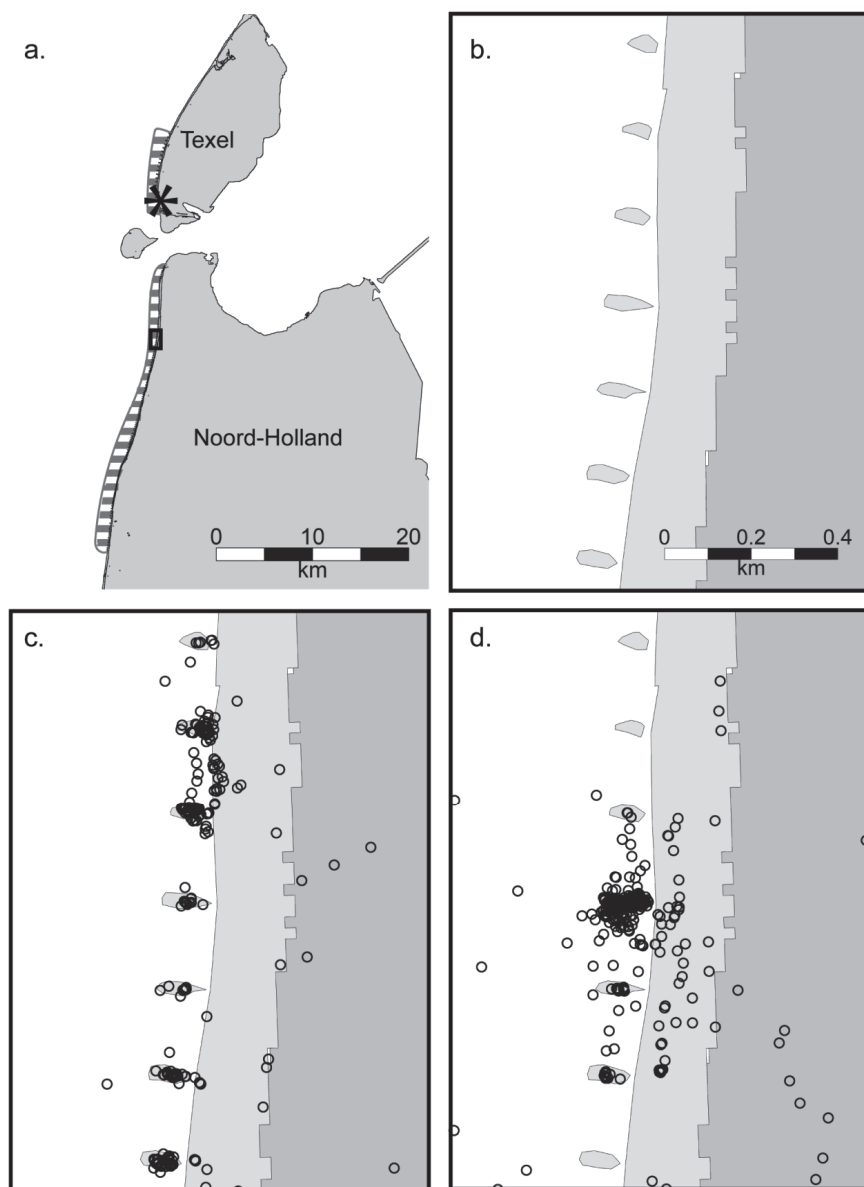


Fig. 4.1 Map of the study system at different spatial scales. (a) Overview of the study area, breeding colony is indicated with an asterisk. Breakwaters are situated along the North Sea coast (both at the island of Texel and the mainland). The dashed area indicates where breakwaters are situated. The square on map 1a indicates the area which is shown on a larger scale in 1b, c and d. b. Map of 7 breakwaters along the coast of Noord-Holland c. and d. Examples of area use of respectively an individual with low foraging site fidelity (bird-year 1600_2013, SFI 2.36) and a very site-faithful individual (bird-year 6016_2013, SFI 0.52) on a selection of breakwaters (which are shown in 1b) during 14 days of incubation. Every point corresponds to one GPS fix.

wing length (mm), and body mass (g). We calculated a body size index to analyse the effect of size in later analyses using the first principal component (PC) of tarsus length, wing length and head plus bill length (Benson et al. 2003). To associate a high body size index score with a large body size, we multiplied the PC with -1 (Table S4.1). The mean body mass ($\pm$ standard deviation) of tagged females was 887 ± 49 g and that of males 1016 ± 59 g. Birds were released immediately after being instrumented, which was usually within 20 min of capture. As recommended for seabirds (Phillips et al. 2003), the GPS tracker and harness weighed $< 3\%$ of the body mass of the birds (average mass of tracker and harness combined 2.4% of female body mass, 2.1% of male body mass). Although the mass of the trackers is not excessive, we cannot exclude the possibility that the devices affected the birds in another way. Thaxter et al. (2016) showed that GPS trackers, which were attached in the same way as the trackers in our study, did not affect (short-term) breeding productivity and winter return rates in the closely related lesser black-backed gull.

In our study, there was some indication that birds with GPS trackers had lower return rates than expected; 70% of individuals with a GPS tracker were seen again the next year, which is lower than a rough estimate of 90% survival of adult herring gulls of this colony. Also, birds with a GPS tracker appeared to have a lower likelihood of breeding again in the next season; 62% of the birds bred again in the next season, which is lower than expected. Roughly, birds of this colony breed once every 1.5 year, which is 75% of breeding individuals. Here, we saw a difference between the sexes, as only 30% of the females bred again the following season, compared with 82% of the males. However, birds with a tracker did not have a lower hatching success than the average hatching success of the breeding colony in the same period (65.5% for the colony compared to 65.6% for bird with GPS tracker). Besides, we attached some GPS trackers to birds which had already been colour-ringed ($n=7$) in earlier breeding seasons. This gave us the opportunity to compare foraging sites and sometimes even winter areas before and after attachment of the tracker. These birds still visited the same foraging and wintering areas, suggesting that foraging behaviour had not changed.

A GPS location was taken every 10 min inside the breeding territory and every 5 min outside the breeding territory. We occasionally took higher resolution measurements on trackers with an empty memory and full battery for other analyses. As differences in resolution might influence comparison between individuals, we resampled the data to once every 5 min before analysing the data. Tri-axial acceleration was periodically measured at 20 Hz for 1 s immediately following a GPS fix.

Habitat use and selection of birds

We made use of bird-year combinations in our analysis, as two birds were tracked over 2-3 years (bird ID 1600 and 6016). We will therefore use the term ‘bird-year’ for the rest of the

methods and results section. To focus on the potential impact of site fidelity without confounding effects of time and energy constraints that may differ across the breeding season, we compared breeding birds during incubation only. We assumed that individuals that breed and have a nest with eggs are in comparable physical condition. During this period, both males and females return regularly to the colony to defend the territory and incubate the eggs. This is also the period during which blue mussels are the most predominant part of herring gull diet (van Donk et al. 2017). We only used GPS and accelerometer data of breeding birds that had a nest with eggs for at least 5 days after tagging, or the full breeding period of birds that had a nest with eggs which received a tracker in earlier breeding seasons (range 5-31 days). Herring gulls are considered a generalist species; they have a broad prey spectrum and habitat use (Morris and Black 1980, Gorke and Brandl 1986, McCleery and Sibly 1986, Pierotti and Annett 1990, Irons 1998). To remove the potential confounding effect of diet, we compared site fidelity amongst birds in a given year of which the breakwaters are the most visited foraging habitat compared to other potential foraging habitats.

Habitat use was calculated by assigning every GPS fix to either the breeding territory (< 100 m around the nest), or potential foraging habitats around the colony. We took every GPS position into account, apart from when an animal was commuting (i.e. when an individual was flying in a straight line from one place to the other). To select these GPS positions, we made use of an expectation maximization binary clustering for behavioural annotation, which used turning angle and velocity obtained from successive locations to cluster GPS positions in four behavioural categories (Garriga et al. 2016a). The categories are high velocity/low turn (HL), high velocity/high turn (HH), low velocity/low turn (LL) and low velocity/high turn (LH). We assumed that an animal was commuting when velocity was high and turning angle low (HL category). We applied the clustering algorithm per individual in a given year using the R package *EmbC* and applied a pre-smoothing procedure which is provided by the packages to account for temporal associations (Garriga et al. 2016b). Subsequently, we assigned every non-commuting GPS position to a habitat. We defined the following habitats: sea (North Sea and Wadden Sea), breakwaters, beach, arable land (including ponds, forest and nature areas) and urban areas. Sea and arable land were defined using GDAM January 2012 European boundaries polygon shapefiles (Hijmans 2012). The beach habitat was based on LGN5 (Landelijke Grondgebruikskartering 5) (Hazeu 2005), which provides information about land use in the Netherlands. Urban areas were based on QGIS openlayer plugin of OpenStreetMap Humanitarian Data Model in which cities, towns and dump sites around the breeding colony were selected. The breakwaters were delineated based on QGIS openlayer plugin Google Earth which uses Google Earth images. Every breakwater along the coast of Texel and Noord-Holland was given a unique number (QGIS Development Team 2009, version 2.18). A total of 165 breakwaters were available for the birds until 2014, after 2014 there were 119 breakwaters left

due to coastal protection activities. Often, the area around the breakwater is also available for foraging gulls during low tide (pers. obs.) and therefore we also assigned GPS points closer than 50 m to the breakwater to the habitat breakwater. Each GPS location was also assigned a duration (s) which was calculated by averaging the backward and forward intervals between relocations, providing a 'centred duration'. Gaps in the data occurred and the 'centred duration' of GPS measurements before and after gaps was sometimes disproportionally long. We therefore removed the GPS measurements which had a 'centred duration' deviating more than 10 min from the measurement scheme. Using the centred duration and habitat class assigned to each location, we calculated the percentage of time spent outside the breeding territory while not commuting in every foraging habitat by dividing total time spent in a habitat by the total time spent outside the breeding colony per bird-year. The percentage of time spent in each habitat was then ranked from high to low and birds that preferred the breakwaters (most time spent) over other foraging habitats were selected for further analysis (Fig. 4.2, $n = 17$, eight females and nine males). The selected animals spent 39-70% of their time outside the colony while non-commuting on breakwaters (Table 4.1). The distribution of GPS locations around the breeding territory of all incubating animals and the selected individuals are shown in Figs. 4.3a and 4.3b, respectively. We defined foraging trips as the first location outside the breeding territory until the next location within the breeding territory. The maximum (great circle) distance (km) travelled from the breeding colony was calculated per trip.

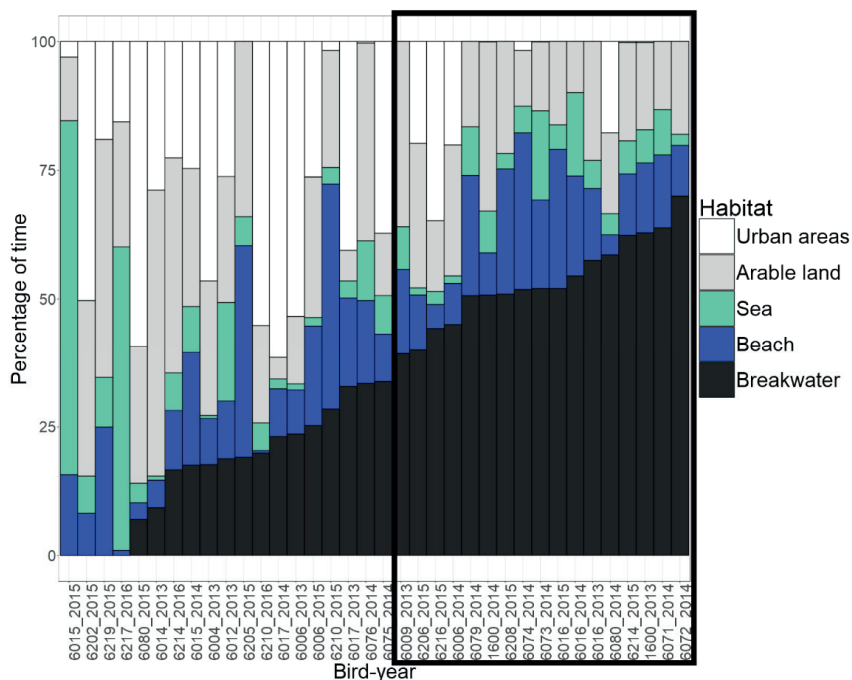


Table 4.1 Overview of bird-year combinations used in the study with their site fidelity index (SFI) and their time-activity budget. Average hours per day spent in the breeding territory (Colony), the proportion of time spent during foraging trips on either inactive behaviour (Prop. Inactive), terrestrial movement (Prop. Terr), soaring flight (Prop. Soar) or flapping flight (Prop. Flap), daily energy spent while on foraging trips (kJ/day), the proportion of foraging trips on which birds return to the favourite breakwater (Prop. return) and the percentage of time outside the breeding territory spent on breakwaters (B. time). The table is organized in descending order according to SFI score. A high value of SFI corresponds to an animal with low site fidelity ('diverse' patch use), while a low SFI corresponds to an animal with high site fidelity ('non-diverse' patch use). The two example bird-year combinations shown in Fig. 4.1c, d are highlighted in grey, representing two individuals with similar daily energy expenditure during foraging trips but contrasting SFI. * = bird-year that was excluded from some analysis, because of too little acceleration measurements.

Bird-year combination	SFI	Colony (h/day)	Prop. Inactive	Prop. Terr.	Prop. Soar	Prop. Flap	Energy (kJ/day)	Prop. return	B. time (%)
1600_2014	2.65	12.56	0.55	0.27	0.07	0.11	623	0.20	51
1600_2013	2.36	13.39	0.37	0.34	0.12	0.17	701	0.21	63
6074_2014	2.33	13.37	0.59	0.20	0.12	0.09	554	0.29	52
6208_2015	2.31	12.06	0.62	0.23	0.09	0.06	602	0.16	51
6079_2014	2.28	12.24	0.57	0.26	0.09	0.08	637	0.37	51
6006_2014	2.04	13.85	0.58	0.21	0.08	0.13	653	0.29	45
6216_2015	2.01	14.63	0.53	0.31	0.07	0.09	520	0.47	44
6206_2015	1.76	15.21	0.54	0.20	0.16	0.10	471	0.75	40
6009_2013	1.70	11.75	0.44	0.40	0.13	0.02	534	0.33	39
6214_2015	1.62	16.30	0.46	0.32	0.11	0.11	478	0.58	62
6016_2015	1.51	15.31	0.59	0.27	0.09	0.07	515	0.49	52
6072_2014	1.43	16.94	0.50	0.38	0.07	0.05	305	0.42	70
6073_2014	1.29	14.83	0.60	0.20	0.08	0.11	505	0.49	52
6071_2014	1.10	13.91	0.45	0.29	0.12	0.14	709	0.70	64
6016_2014	0.63	15.82	0.62	0.23	0.06	0.09	500	0.43	55
6016_2013	0.51	14.24	0.55	0.31	0.07	0.07	561	0.48	58
6080_2014	0.19	9.72	-	-	-	-	-	0.70	59
*									

Fig. 4.2 Overview of habitat use outside breeding territory while not commuting per bird-year combination. Habitat use is shown in percentage of time spent in different possible foraging habitats near the colony which are urban areas, arable land, sea, beach and breakwaters. Data is organized on the ascending percentage of time spent on breakwaters, where Blue Mussels are the primary resource. Individuals that spent most of their time on breakwaters compared to other habitats within a given year and that are used in further analysis are shown within the black square.

Site fidelity index (SFI)

Site fidelity of birds was determined per bird-year by analysing the time an individual spent near every breakwater. For each bird-year, we first calculated the time spent in the proximity (i.e. closer than 50 m) of every breakwater when not commuting, using the *rgeos* package in R (Bivand and Rundel 2016). We calculated the percentage of time spent on each breakwater as the time spent near each breakwater divided by the total time spent on all breakwaters. To only include breakwaters which were of significance in the total time, we excluded from the calculation breakwaters on which individuals spent $< 2\%$ of their total time spent on breakwaters. Site fidelity was calculated per bird-year as the Shannon index, which is given as $SFI = -\sum_i p_i \ln p_i$ where p_i is the percentage time spent on each breakwater (Shannon and Weaver 1949). A high SFI value corresponds to an animal with low site fidelity ('diverse' patch use), whereas a low SFI corresponds to an animal with high site fidelity ('non-diverse' patch use) (Fig. S4.1). Breakwaters are used as foraging habitat, however, animals also rest and digest their food on breakwaters. To check whether the breakwaters were not used solely for resting by some individuals, we also calculated the site fidelity index based on foraging behaviour ('terrestrial movement') solely. The two measurements were highly correlated and thus we decided that it was valid to use all behaviours for the calculation of site fidelity (Fig. S4.2).

Relationship between SFI and time-activity budgets

We expected that highly site-faithful individuals with breakwaters as their principle feeding area can spend more time in the breeding colony to defend their territory or can spend less energy outside the breeding territory by spending more time resting. To test whether site fidelity is related to the time and energy budget of individual herring gulls, we calculated: (1) time spent in the breeding territory, (2) proportion of time spent on inactive behaviour outside the breeding territory and (3) daily energy expenditure outside the breeding territory; these are explained further below. For analysis (2) and (3) we excluded one bird-year because of missing acceleration measurements (see Table 4.1). For the calculation of SFI we only used GPS locations close to and on the breakwaters, but we used all GPS locations to calculate the time-activity budget. As we selected individuals with breakwaters as their principle feeding area, we assumed that most of the time dedicated to foraging was done on breakwaters. As breakwaters are intertidal foraging habitat, they are only available at low tide, which should be taken into consideration. Habitat around the breakwaters is also often used (Fig. 4.3b), for instance for waiting, preening or digesting.

(1) Time spent in the breeding territory

We calculated the average hours per day spent in the breeding territory for every bird-year combination calculated as every GPS position that was closer than 100 meters to their nest-site. To analyse whether SFI was correlated to the time individuals per bird-year spent in their

breeding territory, a linear mixed-effect model was fitted. The full model contained SFI and sex as fixed effects, average hours per day in breeding territory as the dependent variable, and random intercepts for bird ID and year to account for differences between individuals and yearly fluctuations in foraging effort.

(2) Proportion of time spent on inactive behaviour outside the breeding territory

To calculate the activity budget of birds within a given year we trained a random forest machine-learning algorithm for the classification of accelerometer data (Shamoun-Baranes et al. 2016) using two datasets. The first dataset is based on annotated accelerometer data of lesser black-backed gulls (Shamoun-Baranes et al. 2016). The second dataset contained annotated accelerometer data of six herring gulls (three males and three females) with synchronized video recordings while foraging on breakwaters. The two species are comparable in size and morphology, and most behaviour and accelerometer patterns were clearly similar. We first distinguished 11 different behaviours (Table S4.2) which we aggregated into four behavioural classes: (1) inactive behaviour (sitting or standing and floating on the water), (2) terrestrial movement (walking, looking for food, standing while looking for food, handling prey, other movements) and two types of flight (3) flapping flight (regular and extreme flapping flight and (4) soaring flight (regular soaring and manoeuvring). In total, 8472 segments of acceleration measurements lasting 0.5 s were used for annotation. We calculated 37 data features from the tracking data that could be used to classify behaviour and reduced the number of features to 17 (Table S4.2) (Shamoun-Baranes et al. 2016). The random forest classifier used 50 trees and was trained on a random subset of 70% of the annotated data. Accuracy was tested with the remaining 30% of the data. The final model, with an overall accuracy of predicting the 11 behaviours of 94%, was used to classify all unclassified accelerometer data.

Proportions of the different behavioural classes were calculated by the accumulated time spent on one of the activities divided by the total duration of measurements per bird-year. As proportions always sum up to one, they impose some constraints on the variance and covariance of the data. To allow the use of standard statistical techniques we transformed the data by taking the log transformation of the proportion of inactive behaviour over the proportion of active behaviour (terrestrial movement, flapping flight and soaring flight) (Aitchison 1986, Warton and Hui 2011).

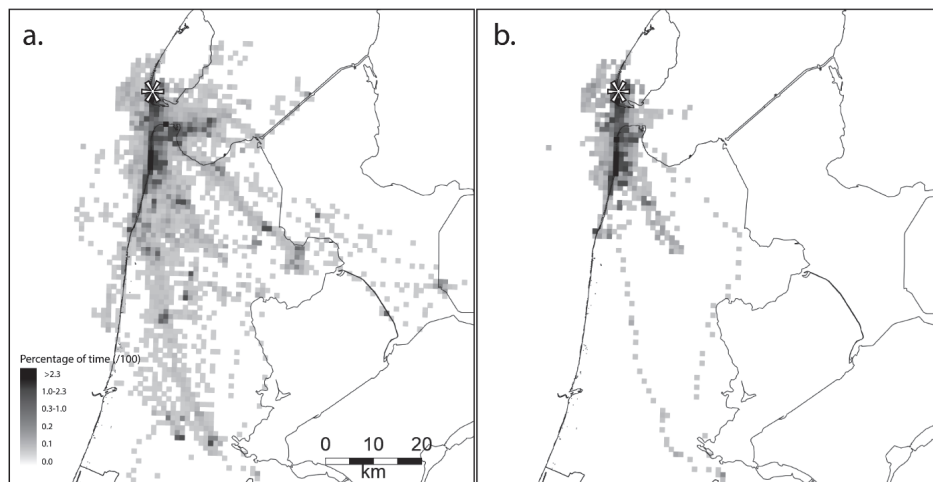


Fig. 4.3 Distribution of all GPS locations of incubating Herring Gulls carrying a tracker and a nest with eggs for at least five days (a.) and distribution of the animals that favoured breakwaters over other foraging habitat (b.). Breeding colony is indicated with an asterix.

A linear mixed-effect model was fitted that contained SFI, sex and body size index as fixed effects, the (transformed) proportion of inactive behaviour as the dependent variable, and random intercepts for bird ID and year to account for differences between individuals and yearly fluctuations in foraging effort. In this model, we also added average maximum distance from the colony as a fixed effect, calculated as the average of the maximum distance travelled away from the colony per foraging trip (Table S4.1), as this might affect the time spent on flying and thus the total time spent on active behaviour.

(3) Daily energy expenditure outside the breeding territory

To estimate energy expenditure outside the breeding territories, we made estimations of metabolic rates (kJ) for the four classified behaviours (Collins et al. 2016). Inactive behaviour has low energetic cost, whereas flapping flight is estimated to be the most costly form of locomotion. Variation in time spent on flapping flight might therefore drive variation in energy expenditure (Norberg 1990, Collins et al. 2016). We calculated the basal metabolic rate (BMR) in kJ/day as $2.3 \times \text{body mass(g)}^{0.774}$ at capture (Bryant and Furness 1995). As the BMR does not account for thermoregulation when temperature is lower or higher than the thermo-neutral zone, digestion or small body movements, we calculated the costs for the behaviour 'inactive' as the resting metabolic rate (RMR); $1.7 \times \text{BMR}$ (Baudinette and Schmidt-Nielsen 1974, Furness 1978). We estimated the cost of terrestrial movement as $2 \times \text{BMR}$ (based on the formula for cost of walking in (Bautista et al. 1998)) using 0.4 m/s, the average speed measured by the GPS of all

bird-year combinations during terrestrial movement. For the cost of flight, we calculated energetic expenditure as $2 \times \text{RMR}$ for soaring flight (Baudinette and Schmidt-Nielsen 1974) and $7 \times \text{RMR}$ for flapping flight (Tucker 1972). We calculated the average number of hours birds in a given year spent on the four classified behaviours (using values from Table 4.1) and multiplied these values by the energetic estimations we made to calculate the average energy expenditure outside the breeding colony (kJ/day).

To analyse whether energetic expenditure was correlated to SFI, we fitted a linear mixed-effect model. The full model contained SFI and sex as fixed effects, daily energy expenditure outside the breeding territory as the dependent variable, and random intercepts for bird ID and year to account for differences between individuals and yearly fluctuations in foraging effort. We also added average maximum distance from the colony as a fixed effect, calculated as the average of the maximum distance travelled away from the colony per foraging trip, as it might affect the time spent on flying and thus energy expenditure.

The relationship between SFI, body size, sex

To analyse whether SFI is determined by sex or size, a linear mixed-effect model was fitted. The full model contained sex and body size index as fixed effects and SFI as the dependent variable and random intercept for bird ID.

Statistical analysis

All models were fitted using the `lmer` function from the `lme4` package in R version 3.3.2 (Bates et al. 2015). Full models were compared with models containing all possible combinations of fixed effects using the `aictab` function from `AICcmodavg` package (Mazerolle 2017). To assess whether the final model was valid in explaining the data, a comparison between the final model and a null model which only contained the random factor was made using ANOVA and *p*-values were obtained by likelihood-ratio tests. We reported the model estimates with standard errors and marginal *R*-squared values for mixed models (Nakagawa and Schielzeth 2013) of the best models (lowest Akaike information criterion *AIC*) as well as the models in which the *AIC* difference with the best model is < 2 in the text. Full models and *AIC* values are reported in Tables S4.3-S4.6).

Results

Habitat use and selection of birds

The percentage of time spent in the main habitat zones outside the breeding territory per bird-year combination varied greatly between individuals (Fig. 4.2, $n = 36$). For further analysis, we selected bird-year combinations for which the preferred foraging habitat (most time spent compared to other foraging habitats) are breakwaters ($n = 17$ bird-years, 14 individual birds, seven females and seven males). The selected birds spent 39 - 70% of their time outside the

breeding territory while not commuting on breakwaters (Fig. 4.2, Table 4.1). Fig. 4.3 shows the distribution of GPS locations during the incubation period of all herring gulls with a GPS tracker (Fig. 4.3a) and the GPS locations of the selected birds (Fig. 4.3b). Although the selected birds still spent considerable time in other habitats (Fig. 4.2), most locations in other foraging habitat are concentrated around the breakwaters at sea and on the mainland (Fig. 4.3b).

Site fidelity index

The SFI differed between bird-year combinations that have breakwaters as their preferred foraging habitat (Table 4.1), ranging from an SFI of 0.19 to 2.65. The most site-faithful bird spent 92% of its time on breakwaters on a single breakwater. All birds returned regularly to their most visited breakwater (16 - 75% of their foraging trips, Table 4.1). Two extreme examples are shown in Figs. 4.1c and 4.1d, in which the space use of two individual herring gulls in 2013 is plotted on the same selection of breakwaters. These two birds spent the same percentage of time on breakwaters (Table 4.1, highlighted) but have very different SFI scores. The bird shown in Fig. 4.1c (1600_2013) divided its foraging time over several breakwaters and had thus a high SFI score (SFI = 2.36). The bird shown in Fig. 4.1d (6016_2013) was highly site-faithful, spending 79% of its breakwater-time on one breakwater (SFI = 0.51).

The relationship between SFI and time-activity budgets

(1) SFI and time spent in the breeding the territory

The average time spent per day in the breeding territory varied among bird-year combinations ($13.76 \text{ h} \pm 1.85 \text{ h}$). The two most extreme birds differed by 7 h/day in the time spent in the colony (minimum = 9.7 h/day, maximum = 16.9 h/day, Table 4.1). However, we did not find a significant linear relationship with SFI or an effect of sex (Table 4.2).

(2) SFI and proportion of time spent on inactive behaviour outside the breeding territory

Time spent inactive outside the breeding territory differed among bird-years, ranging from 37% to 62% ($54\% \pm 7\%$, Table 4.1). The most active bird (1600_2013) was moving around 63% of the time during foraging trips, whereas other birds were active less than half of the time outside the colony (Fig. 4.4, Table 4.1). However, the time that birds spent inactive was not related to SFI or the other fixed factors in the model (Table 4.2).

(3) SFI and daily energy expenditure outside the breeding territory

The estimated daily energy expenditure outside the breeding territory ranged from 305 to 709 kJ/day (554 ± 101 , Table 4.1). We did not find a significant linear relationship between daily energy expenditure outside the breeding territory and SFI or other fixed factors in the model (Table 4.2).

The relationship between SFI, body size, sex

We investigated whether foraging site fidelity may be driven in part by body size or sex, given differences in competitive strength (interference competition). Highly site-faithful birds had a larger body size (Fig. 4.5). The best model included body size index as a fixed factor and significantly differed from the null model (Table 4.3).

Table 4.2 Model results of the relationship between SFI and proxies for time-activity budgets; (1) time spent in the breeding territory in hours (Colony time), (2) transformed proportion of time spent on inactive behaviour outside the breeding territory (Inactive behav.) and (3) daily energy expenditure outside the breeding territory in kJ (Energy exp.) tested using a mixed model with random intercept for birdID and year. Model estimates and model results, among which marginal R squared ($m.R^2$) of best models are shown (lowest AIC) and the models in which the AIC difference with the best model is < 2 . Models with an $\Delta AIC > 2$ are shown in the supplementary material (Tables S4.3, S4.4 & S4.5). For the fixed effect Sex, category female was used as reference level (Intercept) and the fixed effect estimate is thus the value for males (M).

Dependent variable	Fixed effect	AIC	Intercept $\pm$ SE	Fixed effect estimate $\pm$ SE	df	X^2	p	$m.R^2$
(1) Colony time	Sex (M)	81.05	13.98 $\pm$ 0.70	-0.56 $\pm$ 0.99	1	0.32	0.57	0.02
(1) Colony time	SFI	81.36	13.72 $\pm$ 1.13	-0.01 $\pm$ 0.61	1	0.00	0.98	0.00
(2) Inactive behav.	Sex (M)	19.27	0.03 $\pm$ 0.12	0.13 $\pm$ 0.13	1	0.70	0.40	0.05
(2) Inactive behav.	Distance	19.56	0.18 $\pm$ 0.21	-0.01 $\pm$ 0.02	1	0.41	0.52	0.02
(2) Inactive behav.	SFI	19.93	0.03 $\pm$ 0.24	0.02 $\pm$ 0.12	1	0.03	0.86	0.00
(2) Inactive behav.	Size	19.95	0.07 $\pm$ 0.13	0.00 $\pm$ 0.00	1	0.02	0.89	0.00
(3) Energy exp.	Distance	201.78	459.96 $\pm$ 69.59	10.62 $\pm$ 6.47	1	1.88	0.17	0.13
(3) Energy exp.	Sex (M)	201.83	527.90 $\pm$ 41.38	76.17 $\pm$ 54.23	1	1.84	0.18	0.13
(3) Energy exp.	Size	202.99	566.87 $\pm$ 34.34	1.52 $\pm$ 1.83	1	0.67	0.41	0.06

Table 4.3 Model results of the relationship between SFI and body size tested using a mixed model with random intercept for birdID. Model estimates and model results of best model is shown (lowest AIC). Models with an $\Delta AIC > 2$ are shown in the supplementary material (Table S4.6).

Dependent variable	Fixed effect	AIC	Intercept $\pm$ SE	Fixed effect estimate $\pm$ SE	df	X^2	p	$m.R^2$
SFI	Size	31.20	1.71 $\pm$ 0.11	-0.02 $\pm$ 0.01	1	6.21	0.01	0.47

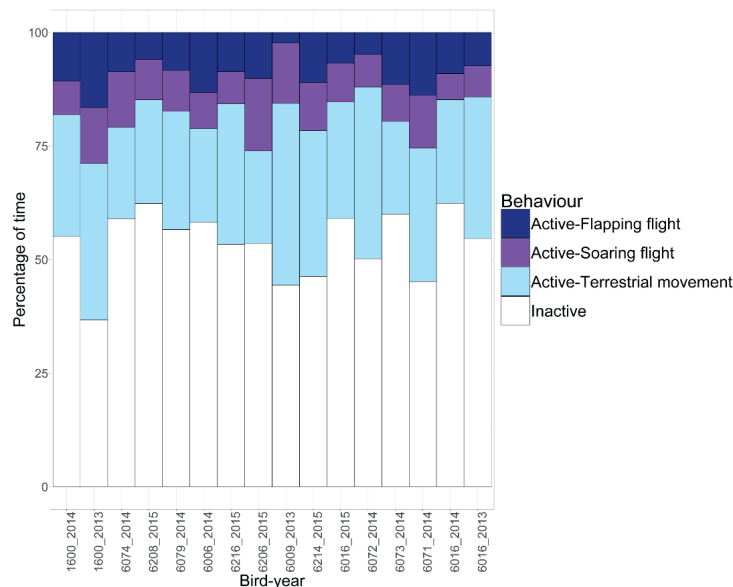


Fig. 4.4 Behaviour outside the breeding territory per bird-year combination of selected birds. Behavioural classes are shown in percentage of time spent on inactive behaviour (sitting, standing, floating) or active behaviour; flapping and soaring flight and terrestrial movement. Bird-year combinations are ordered from left to right on descending SFI (for values see Table 4.1). Bird-year 6080_2014 was excluded from this graph due to too little acceleration measurements.

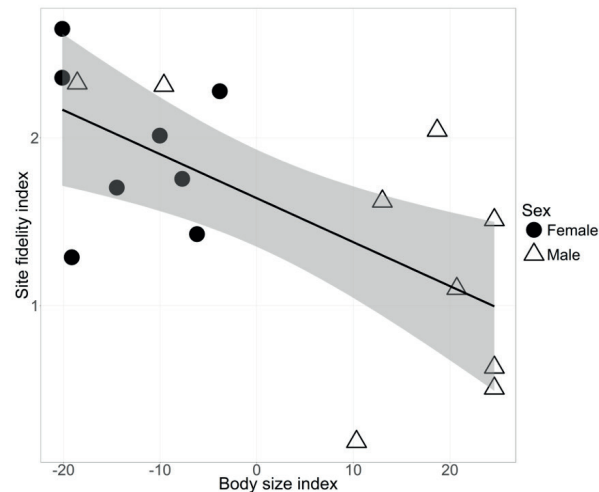


Fig. 4.5 The relationship between body size and SFI. A low body size index indicates a bird with a small body size. A low SFI indicates a bird in a given year with high foraging site fidelity. Every point represents one bird-year combination ($n = 17$). Linear regression is shown (line) with standard error (shaded area). The shape of the point indicates the sex of the bird.

Discussion

We investigated the consequences of fine-scale foraging site fidelity in adult herring gulls with similar dietary specialization during incubation. The study system was especially suitable for investigating this question in free-ranging animals because of the predictable and homogenous foraging environment organized in distinct foraging patches and the technical ability to measure fine-scale behaviour 24 h/day and across an entire breeding season. By making a detailed description of time-activity budgets of the birds using GPS trackers with tri-axial acceleration, we showed remarkable differences between individuals in habitat use (Fig. 4.2), fine-scale foraging site fidelity on breakwaters (Fig. 4.1c & 4.1d, Table 4.1), and time and energy use (Fig. 4.4, Table 4.1). Highly site-faithful birds tend to have a larger body size (Fig. 4.5). In this study we focused on the incubation phase, during which individuals face similar time and energy constraints. We found no clear (short-term) consequences of fine-scale foraging site fidelity; highly site-faithful individuals did not spend more time in the breeding territory or more time inactive, and did not have a lower daily energy expenditure outside the breeding territory. Although this result was contradictory to our expectations, there are several possibilities as to how variation in site fidelity could exist in populations without clear short-term benefits, as discussed below.

The importance of other foraging habitats

Herring gulls are generalist species and have many ways of foraging - flying, walking, pulling or fighting, as well as standing still and observing the environment, waiting for a feeding opportunity. We therefore chose to use all GPS locations outside the breeding territory, independent of behavioural class and habitat, to calculate time-activity budgets. For the animals with breakwaters as their principle feeding habitat, we assumed that most of the time dedicated to foraging is spent on breakwaters. Animals that eat bivalves such as blue mussels have to spend time digesting these prey to break the shells in their stomach. They do this on breakwaters during low tide, but they may also move to other places such as agricultural fields or nearby on rooftops nearby to rest and digest, especially at high tide, when breakwaters are not available. In addition, these animals often spent time on the beach, waiting for the breakwaters to appear at low tide, or at sea, when disturbed by people or dogs (CJC, SvD & JSB pers. obs., Fig. 4.1c & 4.1d). Fig. 4.3b seems to confirm this idea, as most of the GPS locations which are not situated on breakwaters are concentrated around the coastline. As we did not include waiting and digesting time around breakwaters to the total time spent on breakwaters, the relative time spent outside the colony on foraging-related behaviour on breakwaters is probably higher than we reported (Table 4.1) compared to other foraging habitat that does not disappear at high tide, such as sea, urban areas and arable land. Nevertheless, the time spent in other foraging habitats could influence time-activity budgets, especially when animals forage in an 'urban area' which

contains prey types of high caloric value that are important for reproductive output and condition (Pons 1992, van Donk et al. 2017). However, we did not find evidence for this in our data, as there was no relationship between the time our selected animals spent on breakwaters and the level of site fidelity (Table 4.1) or the time-activity budget (Fig. S4.3, Table 4.1).

How can variation in site fidelity be maintained in populations?

We did not find clear consequences of fine-scale foraging site fidelity in our study. However, we did see differences in the level of fine-scale foraging site fidelity between individuals. We discuss three other hypotheses, besides the variation spent on breakwaters, as to why this variation may exist in the population with no apparent proximate advantages or disadvantages.

Fitzpatrick et al. (2007) suggested that variation in certain traits remains in populations due to negative frequency-dependent selection. This mechanism selects against common phenotypes, thereby creating fitness advantages for the rarer phenotypes (Maynard Smith and Price 1973, Wilson and Yoshimura 1994, Pruitt and Riechert 2009, Patrick and Weimerskirch 2017). For birds, negative frequency-dependent selection is often suggested to be an important mechanism in regulating consistent variation in behavioural traits, but evidence for this is largely absent (Kurvers et al. 2012). The few studies that have investigated this mechanism (in oystercatchers *Haematopus ostralegus ostralegus* and barnacle geese *Branta leucopsis*) could not find evidence for this hypothesis (van de Pol et al. 2010, Kurvers et al. 2012). Currently, we do not have any evidence to support this hypothesis.

A second hypothesis is that there are pros and cons associated with foraging site fidelity. Site-faithful individuals might have higher food intake on their specific foraging spot but have less flexibility to respond to environmental change because they have less knowledge about their wider environment and therefore cannot easily switch between foraging patches or resources (Wilson and Yoshimura 1994, Bolnick et al. 2003, Wakefield et al. 2015). For instance, in our study system, highly site-faithful individuals might profit less from unexpected food bonanzas such as mass mortality of razor clams *Ensis directus* that sometimes wash ashore (Armonies and Reise 1999). Besides missing food bonanzas, site-faithful individuals may be more vulnerable to environmental change (Kotzerka et al. 2011). Changes in the environment are also taking place in our system. Due to coastal protection activities, the creation of new dunes and sand supplementation has already covered important foraging patches (breakwaters) (van Koningsveld and Mulder 2004, Freriks 2015, Wenneker et al. 2016). These changes create a natural experiment in which we can test whether individuals with high site fidelity can adapt less well when their foraging habitat is disappearing.

A third hypothesis to explain our findings is that individuals benefit from being site-faithful in the long term or even over an individual's lifetime, as foraging behaviour is often consistent over years in marine animals (Bradshaw et al. 2004, Wakefield et al. 2015). The importance of

foraging site fidelity might only become apparent in very demanding times of an animal's life cycle, for instance when animals have to feed their young. In a study on black-browed albatrosses *Thalassarche melanophris*, site fidelity within a certain year was positively associated with reproductive success (Patrick and Weimerskirch 2017). Measuring foraging site fidelity and analysing potential consequences during longer periods, might help to elucidate the mechanisms and consequences of site fidelity. In the current study, sample size was too low to measure consequences of site fidelity over years. However, the two individual birds that were measured over more than 1 year (bird ID 1600 & 6016, Table 4.1) were quite consistent in their level of site fidelity; bird ID 1600 had the lowest site fidelity measured over 2 years of all individual birds in this study, whereas, by comparison, bird ID 6016 was very site-faithful over 3 years (Table 4.1).

The role of size in the level of foraging site fidelity

Individual differences in foraging strategies are often related to morphology or sex (González-Solís et al. 2000, Lewis et al. 2002, Camphuysen et al. 2015). In our study, variation in foraging site fidelity was also not randomly distributed over the population. We found a significant relationship between foraging site fidelity and size, larger individuals tending to be more site-faithful. Herring gulls are sexually dimorphic and therefore sex and size are difficult to disentangle. Also, body size is clearly not the only variable that influences the variation in foraging site fidelity, as some large individuals in our study are not highly site-faithful (Fig. 4.5). Although the results are not conclusive, they do suggest that larger individuals are better able to deal with competition and defend their specific foraging patch, whereas smaller individuals are displaced more frequently from feeding patches. However, it is also possible that larger individuals have to balance other trade-offs compared with smaller individuals. For instance, flying is more expensive for larger/heavier individuals and therefore it might be more rewarding to be site-faithful compared with smaller individuals with lower costs of moving between foraging patches. In the current study, we used rough estimations for energy expenditure of different behaviours based on literature values. Investigating energetic costs among individuals with different morphology and time-activity budgets would benefit from a method in which energy expenditure can be investigated on the level of an individual. Several studies investigated the relationship between overall dynamic body acceleration (ODBA), measured with GPS devices, and energy expenditure, and ODBA has been used as a proxy of energy expenditure (Wilson et al. 2006, Gleiss et al. 2011, Hicks et al. 2017). However, ODBA is not comparable between terrestrial movement and flight, probably due to different muscle groups involved in each kind of behaviour (Laich et al. 2011). Improving estimates of energy expenditure based on body acceleration which can be measured throughout an annual cycle

may help to gain more insight into individual differences in energy expenditure (Hicks et al. 2017).

Conclusion and future directions

We studied herring gulls foraging in a food landscape that is heavily shaped by humans. This created a unique situation to study individual differences in fine-scale habitat use. In this way, we were able to add empirical data to increase knowledge on the consequences of fine-scale foraging site fidelity, an important phenomenon in space use (Wolf and Trillmich 2007, Brischoux et al. 2009, Lowther et al. 2012). Although individuals varied in their foraging site fidelity, we did not find evidence that this behaviour comes with an advantage in terms of their time-activity budgets in the system we studied. As discussed, many environmental and individual processes can be involved in shaping variation in foraging site fidelity. Bio-logging, especially with GPS, has created new opportunities for studying the consequences of foraging site fidelity at a level of detail that was not possible in the past. Where feasible, future studies should focus on the consequences of site fidelity within individuals over longer time-spans, to explore different constraints within the annual cycle. In addition, we recommend studies on the consequences of different strategies under changing food conditions, and comparing consequences not only within but also between species.

Acknowledgement

These studies are part of a long-term demographical and ecological study on sympatric breeding gulls by the Royal Netherlands Institute for Sea Research (NIOZ) at Texel. We thank Staatsbosbeheer Texel for permission to work in Kelderhuispolder, a nature reserve closed for the general public. Particularly, we thank Aris Ellen, Glenn van Ginkel, Marcel Groenendaal, and Erik van der Spek for help and cooperation. We thank all the volunteers that helped in catching the gulls and other fieldwork over the years. We thank Edwin Baaij for his technical support of UvA-BiTS, Roeland Bom for helping with some analytical problems, Stacy Shinneman for help with the LGN5 data set, Alice Driesen for sharing some very helpful r-codes, Tristan Bakx and Margot Maathuis for making videos of Herring Gulls with GPS trackers used for annotation. We thank two referees for useful and constructive comments. The UvA-BiTS infrastructure was facilitated by Infrastructures for E-Science, developed with the support of the Netherlands eScience Centre (NLeSC) and LifeWatch, and conducted on the Dutch National E-Infrastructure with support from the SURF Foundation.

Author Contributions

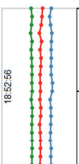
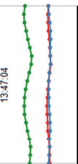
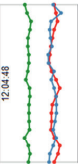
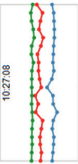
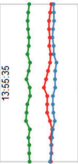
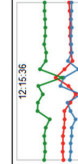
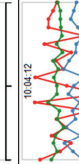
SvD carried out the statistical analysis and drafted the manuscript with support from JSB, JvdM and CJC; CJC leads a long-term study on Herring Gulls; CJC and SvD conducted fieldwork, JSB assisted with GPS tracking; WB supported the collection and analysis of acceleration data; SvD, JSB, JvdM and CJC discussed the analytical approach. All authors discussed results and contributed to the final manuscript.

Supplementary material

Table S4.1 Overview of bird-year combinations used in the study with their sex and size measurements (size index calculated as inverse of first principal component of tarsus, wing and head+bill), site fidelity index (SFI) and average furthest point from the colony when outside the colony. The table is organized in descending order according to SFI score. The two example bird-year combinations shown in Fig. 4.1c, d are highlighted in grey, representing two individuals with similar time spent on breakwaters but contrasting SFI. All birds delineated in the box in Fig. 4.1 are shown in this table. * = bird-year that was excluded from some analysis, because of too little acceleration measurements.

Bird-year combination	Sex	Mass (kg)	Tarsus (mm)	Wing (mm)	Head +bill (mm)	Body size index	SFI	Ave. travel distance (km)
1600_2014	F	-	-	-	-	-20.88	2.65	9.58
1600_2013	F	0.850	64	408	114	-20.88	2.36	9.54
6074_2014	M	0.885	64	408	119	-19.36	2.33	8.90
6208_2015	M	0.990	63	418	118	-10.36	2.31	4.86
6079_2014	F	0.910	64	425	115	-4.53	2.28	12.00
6006_2014	M	0.960	66	445	126	17.94	2.04	12.30
6216_2015	F	0.985	62	420	111	-10.73	2.01	12.03
6206_2015	F	0.835	63	421	115	-8.44	1.76	17.32
6009_2013	F	0.935	64	414	114	-15.22	1.70	4.99
6214_2015	M	0.995	68	440	122	12.27	1.62	9.40
6016_2015	M	-	-	-	-	23.87	1.51	8.25
6072_2014	F	0.855	65	423	113	-6.90	1.43	3.07
6073_2014	F	0.865	62	409	115	-19.90	1.29	8.61
6071_2014	M	1.030	67	448	123	20.00	1.10	13.00
6016_2014	M	-	-	-	-	23.87	0.63	6.35
6016_2013	M	1.070	68	451	126	23.87	0.51	7.72
6080_2014*	M	1.090	67	435	129	9.54	0.19	21.42

Table S4.2 Definition of 11 activity classes of herring gulls and lesser black backed gulls, used to annotate tri-axial acceleration data. Two 1 second segment of 20Hz tri-axial data is presented, green represents heave (z-axis), red represents surge (x-axis), blue represents sway (y-axis), the x and y axis of all figs are on the same scale and range from -1.5 – 2.5 g. Activities 'Looking for food', 'stand looking for food' and 'pulling mussels' are annotated exclusively from herring gull accelerometer data, while the general activity class flight is exclusively annotated from lesser black backed gull accelerometer data (see Supplementary material S1: Shamoun-Baranes et al. 2016). A mix of accelerometer data of the both species is used for the remaining activity classes. Features calculated from accelerometer data that are used in classification are mean x, standard deviation of x, y and z, the mean pitch, gps speed, the mean of the absolute value of the derivative of x, y and z, noise in x and y signal, noise in signal of x divided by the mean of the absolute derivative of x, the fundamental frequency of the z signal, the magnitude of the highest peak in the frequency domain of the Fourier transformation of the x, y and z signal and the first value of the x signal.

General activity	Activity label	Activity description	1) Accelerometer characteristic and 2) additional GPS information used to distinguish behaviour	Example of typical tri-axial signal	Number of annotations
1) Inactive behaviour	Sit or stand	Sitting or standing on land or static structure at sea	1) constant value for all 3 axes, 2) speed is close to zero.		2948
	Floating	Floating with the currents at sea	1) smooth undulating patterns (caused by waves)		1624
2) Active - Terrestrial movement	Walking	Walking	1) typical periodic pattern of the surge (x axis)		608
	Looking for food	Body tilted forward to look for food while standing or walking	1) high value for the surge (x axis) and not too much change in the other axes, 2) low speed		277
	Standing while looking for food	Transition from standing to looking for food while stationary	1) surge (x axis) gradually increases while other values stay constant, 2) lower value for surge axis than looking for food		25
	Other	Other terrestrial movements like shaking or social interactions	1) all other terrestrial movements that do not fit in the other categories		65
	Handling prey	Pulling mussels from the breakwater to be able to ingest them	1) Heavy movement in especially surge (x axis), 2) low speed		235

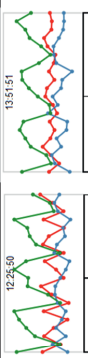
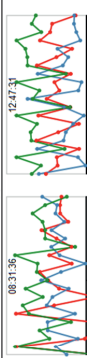
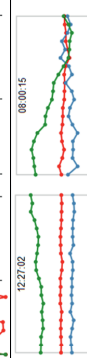
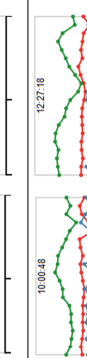
3) Active – Flapping flight	Regular flapping flight	Flapping flight with regular wing beat	1) repeated and correlated oscillations, strongest in heave		1297
	Extreme flapping flight	Irregular and intense wing beat, during take-off or aerial interactions			78
4) Active – Soaring flight	Soaring	Flight with no wing beat, includes climbing and gliding	1) gradually changing pattern, 2) distinguished from float by either speed, or lack of typical float GPS patterns		1010
	Manoeuvre	Manoeuvre while flying due to for instance wind conditions	1) sudden changes in pattern while soaring, no flapping		305

Table S4.3 Full models and their AIC values testing the relationship between SFI and dependent variable average time spent in the breeding territory per bird in a given year (Hours/day). The best model (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red.

Model	Random intercept	Fixed effect		AIC
		Size	Sex	
Model 2	birdID, Year		X	81.05
Model 1	birdID, Year	X		81.36
Model 3	birdID, Year	X	X	85.97

Table S4.4 Full models and their AIC values testing the relationship between SFI and dependent variable transformed proportion of time spent on inactive during foraging trips. The best model (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red.

Model	Random intercept	Fixed effect				AIC
		SFI	Size	Max. distance colony	Sex	
Model 4	birdID, Year				X	19.27
Model 3	birdID, Year			X		19.56
Model 1	birdID, Year	X				19.93
Model 2	birdID, Year		X			19.95
Model 8	birdID, Year		X		X	24.01
Model 10	birdID, Year			X	X	24.30
Model 6	birdID, Year	X			X	24.53
Model 7	birdID, Year	X		X		24.85
Model 9	birdID, Year		X	X		24.89
Model 5	birdID, Year	X			X	25.26
Model 14	birdID, Year			X	X	30.54
Model 11	birdID, Year	X	X		X	30.65
Model 13	birdID, Year	X		X	X	30.87
Model 12	birdID, Year	X	X	X		31.50
Model 15	birdID, Year	X	X	X	X	39.11

Table S4.5 Full models and their AIC values testing the relationship between SFI and dependent variable daily energy expenditure during foraging trips. The best model (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red.

Model	Random intercept	Fixed effect				AIC
		SFI	Size	Max. distance colony	Sex	
Model 3	birdID, Year			X		201.78
Model 4	birdID, Year				X	201.83
Model 2	birdID, Year		X			202.99
Model 10	birdID, Year			X	X	204.46
Model 1	birdID, Year	X				205.68
Model 6	birdID, Year	X			X	206.57
Model 9	birdID, Year		X	X		206.76
Model 7	birdID, Year	X		X		206.90
Model 8	birdID, Year		X		X	207.16
Model 5	birdID, Year	X	X			207.40
Model 13	birdID, Year	X		X	X	209.07
Model 14	birdID, Year			X	X	210.66
Model 12	birdID, Year	X	X	X		211.89
Model 11	birdID, Year	X	X		X	212.98
Model 15	birdID, Year	X	X	X	X	217.61

Table S4.6 Full models and their AIC values testing the relationship between SFI, body size and sex. Dependent variable in this model: SFI. The best model (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red.

Model	Random intercept	Fixed effect			AIC
		Size	Sex	Size*Sex	
Model 1	birdID	X			31.20
Model 2	birdID		X		34.43
Model 3	birdID			X	36.85

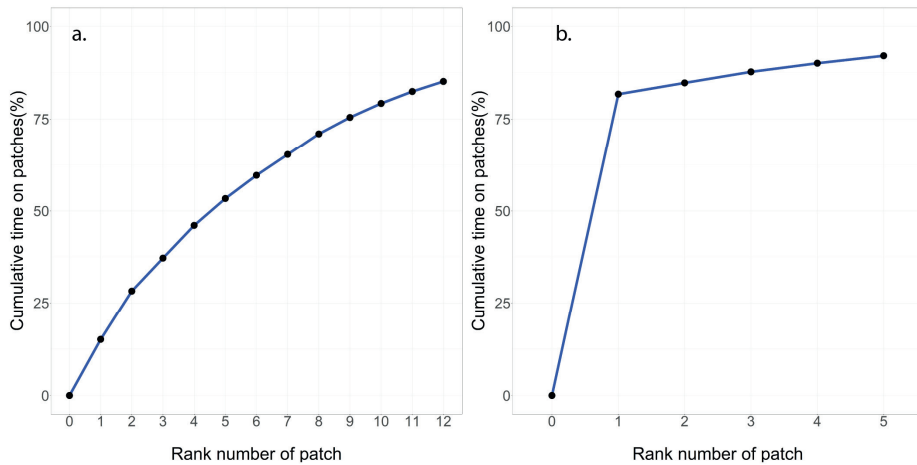


Fig. S4.1 Example of two individuals with contrasting foraging site fidelity with bird-year combination 1600_2013 (a.) and 6016_2013 (b.). On the y-axis the cumulative time on breakwater patches (%), on the x-axis the number of visited patches ranked from most visited to least visited patch. a. Bird 1600_2013 visited several breakwaters b. Bird 6016 spent ~80% of its total time on breakwaters on one breakwater. Foraging site fidelity was calculated as the Shannon index of the percentage of time on every breakwater. As a consequence, the bird of Fig. a. has a high SFI (2.36) while the bird of Fig. b has a low SFI (0.51). Breakwaters on which individuals spent less than 2 percent were excluded from calculations.

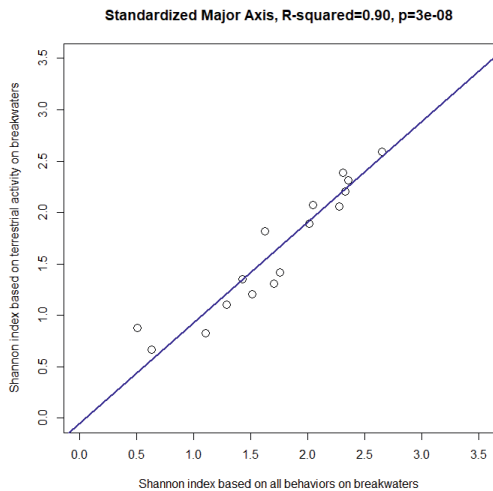


Fig. S4.2 Standardized major axis analysis between the Shannon index based on all data points on and near (< 50 meters) to the breakwaters (x-axis) and the Shannon index based on all terrestrial activity on and near (< 50 meters) to the breakwaters (y-axis) (*intercept* = -0.05, *slope* = 0.98, *r-squared* = 0.90, *p* = 3e-08).

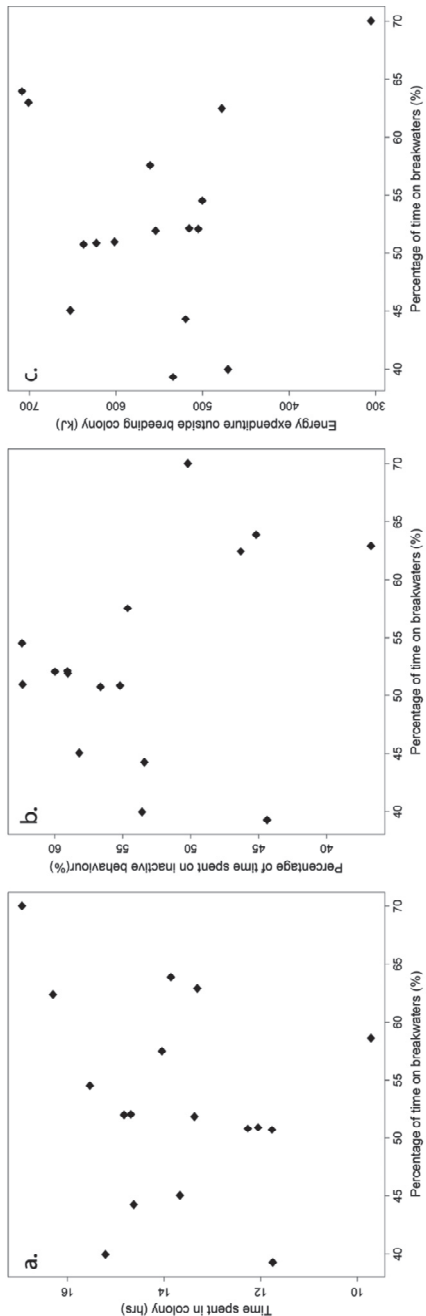


Fig. S4.3 Relationship between the percentage of time on breakwaters and time-activity budgets of individuals with breakwaters as principle foraging habitat. Every point represents one individual in a given year. Time-activity budgets are expressed as (1) time spent in the colony (hrs), (2) the percentage of time spent on inactive behavior (%) and (3) energy expenditure outside the breeding colony (kJ).



Chapter 5

Behavioural and reproductive consequences after elimination of coastal foraging habitat in a generalist seabird

Susanne van Donk, Judy Shamoun-Baranes, Jaap van der Meer, Kees C.J. Camphuysen

Abstract

In light of rapid environmental change driven by human activities, it is increasingly important to understand how animals deal with changes in their environment. Understanding species resilience to change is especially needed in coastal areas, as human pressure and ecosystem degradation in these areas is often more pronounced compared to other ecosystems. Whether species can deal with change depends on the breadth of their ecological niche; generalist species seem to respond better to landscape fragmentation and disturbance compared to specialized species. However, individuals of generalist species often differ consistently in their foraging behaviour and use only a limited selection of available foraging habitat. These specialized individuals might have difficulties to adapt, but not much is known on how these individuals respond on changes in their environment. We studied the consequences of the elimination of a reliable coastal resource in a population of herring gulls *Larus argentatus*, a generalist seabird. We quantified how habitat use, diet and reproductive success varied on population level and describe individual patterns. For the analysis, we used a long-term dataset of 10 years which enabled us to study behaviour and habitat use for 8 years before habitat loss. We found that herring gulls are relatively resilient on the population level, as reproductive success and the frequency of prey from the coastal area did not decline. However, we found that individuals within the population can have difficulties adapting to habitat loss. Some individuals switched to an uncommon diet for this colony, probably due to higher competition on the remaining coastal habitat. These individuals had lower reproductive success than others. We discuss the role of individual variation in foraging strategies on population dynamics and potential consequences of coastal habitat alterations.

Introduction

How animals respond to changes in their environment, is an important question in ecology and became more prominent in recent times of rapid environmental change. The degradation of wetland areas like coastal areas is even going more rapid than that of other ecosystems, while coastal areas provide important ecosystem services and are amongst the most productive ecosystems in the world (Jackson et al. 2001, Lotze et al. 2005, Millennium Ecosystem Assessment 2005). It is therefore of great interest whether the species living in these areas possess the flexibility to adapt to rapid environmental change (Chevin et al. 2010). Different species are not equally at risk when their environment changes and some species are better able to adapt than others. One of the factors that can play a role is their realized niche width, as generalists seem more capable to landscape fragmentation and disturbance (Marvier et al. 2004, Beck and Airolidi 2007, Devictor et al. 2008, Clavel et al. 2011).

While generalist species may be more resilient to change than specialist species, individuals within a species may not respond in the same way. Several studies have shown that individuals of generalist species often differ consistently in their food choice and foraging strategy (Lewis et al., 2006; Bolnick et al., 2002). Such specialised animals use a subset of prey items that are available to the population as a whole. By doing so they invest in prey-specific foraging techniques, which can increase foraging efficiency (Woo et al. 2008). As a consequence, specialized individuals within generalist populations could have difficulties to adapt, because they will need to familiarise themselves with new foraging techniques and/or prey types. While the issue of individual specialisation within populations of generalists has received considerable attention (Bolnick et al. 2003, Araújo et al. 2011, Ceia and Ramos 2015), not much is known about the flexibility of specialised individuals in response to changes in their environment.

Herring gulls *Larus argentatus* forage traditionally in marine coastal habitats, especially in intertidal areas, but also forage offshore or in terrestrial habitat (O'Hanlon and Nager 2017). They are generalist species on population level, but individuals vary in their foraging strategies (McCleery and Sibly 1986, Pierotti and Annett 1991, Bukacińska et al. 1996, Bosch et al. 2019). We studied herring gulls breeding on the island of Texel, the Netherlands (Camphuysen 2013). This population uses a variety of foraging options during the breeding season ranging from coastal intertidal, mudflat intertidal and marine prey types to terrestrial food including anthropogenic refuse. Their main prey are blue mussels *Mytilus edulis* from the intertidal coastal habitat growing on breakwaters constructed for coastal defence in the beginning of the 20th century (Endema 1979, van Donk et al. 2017). Mussels provide a predictable resource throughout the breeding season and are available in large quantities.

Recently, governmental decisions were taken to strengthen the coast with high dunes through sand nourishments along parts of the coastline. This coastal defence project was finished by the

end of 2014 (van Koningsveld and Mulder 2004, Freriks 2015, Wenneker et al. 2016) and resulted in the coverage of part of the breakwaters by sand. For the herring gulls, this meant that 46 out of 165 of their foraging patches were eliminated (28%; Fig. 1). The habitat loss created a natural experiment in which we could test how this generalist species and (specialized) individuals respond to major environmental change.

The aim of this paper is to study the short-term consequences of the reduction of coastal foraging habitat. Measuring the effect of habitat loss in free-living animals is challenging, as regular behaviour and habitat use should be studied well before and after the habitat loss occurred to draw conclusions about possible effects of the environmental impact. In the current study, we made use of long-term behavioural and breeding data (diet, breeding parameters and habitat use), on both the individual and population level, eight years before and two years after the habitat loss. To study more fine-scale behaviour, we also used bio-logging data a year before and after habitat loss. Habitat loss may have increased interference competition in the remainder of the intertidal coastal habitat, assuming that the intertidal coastal foraging area as a whole was fully used by birds before the impact occurred, leading to shifts from one resource to another for birds that failed to establish a position within the dominance hierarchy.

We expect considerable resilience to coastal habitat loss on the population level, but expect that specialized individuals will have difficulties to adapt. We expect to measure this as a reduction in reproductive success, such as smaller eggs and less fledglings per nest and a later onset of breeding in some individuals due to the lack of sufficient prey. In addition, we expect marked changes in foraging behaviour in the years following habitat loss. As many individual herring gulls possess a high degree of site fidelity to their foraging site (van Donk et al. 2018, Bosch et al. 2019), we also expect individuals to be less site faithful on the intertidal coastal habitat after habitat loss due to higher interference competition. By looking at changes in foraging behaviour and breeding success over multiple years after coastal habitat loss, we show that also individuals of a generalist species can have difficulties to adapt.

Methods

Study site and loss of coastal foraging habitat

To study the effect of coastal habitat loss, we used a study site situated on the south-tip of the island of Texel, the Netherlands (53°00'N, 04°43'E) where about 4000 herring gulls are breeding among with approximately 11.000 lesser black-backed gulls *Larus fuscus* (Fig. 5.1). A part of this colony is intensively monitored for over more than 10 years on foraging and breeding ecology.

The main foraging habitats of the herring gulls during the breeding season (April-August) are terrestrial areas like (natural) parks, agricultural areas, and urban areas, marine habitat (North

sea and Wadden sea), intertidal coastal areas as beach and breakwaters and intertidal mudflats. But the main prey for this colony are mussels *Mytillus edulis* that grow on breakwaters which are coastal defence structures made of concrete (Camphuysen 2013, van Donk et al. 2017). The 165 breakwaters are found in a range of 35 kilometres to the colony along the North Sea coast between Texel and Schoorl (Fig. 5.1) and provide reliable and predictable prey during the breeding season since the beginning of the 20th century (Endema 1979). Between the breeding season of 2014 and 2015, 46 out of 165 foraging patches (28%; Fig. 5.1) were eliminated due to coastal protection activities. The lost habitat was visited by 11.9 % of animals foraging in the intertidal coastal habitat, which was recorded by colour ring recordings.



Fig. 5.1 Overview of the habitat and main foraging areas around the colony. Latitude and longitude are indicated on the x and y axis in UTM zone 31 (x10.000), breeding colony is indicated with a double circle (615201.4 E, 5873649 N). Intertidal coastal foraging habitat is available for the gulls along the coast of Texel and the mainland and is indicated with dashed lines. The intertidal coastal foraging habitat, which was removed between 2014 and 2015, is indicated with a square. Other foraging habitats include North Sea and Wadden Sea, intertidal mudflats indicated as light grey areas in the Wadden Sea, urban areas indicated in darker grey on Texel and the mainland and (natural) parks and agricultural area indicated in grey on Texel and mainland.

Monitoring changes in diet

We measured the diet of gulls in May and June in the breeding colony before (2006-2014) and after (2015-2016) habitat loss. The dietary analysis was based on regurgitated prey at the nest sites of breeding gulls, which include pellets, boluses collected when handling adult birds or chicks, and prey brought to the nest as chick feed. As the diet of these gulls differs between breeding phase, we analysed the data in the early phase (when most animals lay eggs, or incubate them) and late breeding phase (when animals feed their chicks or failed breeding) separately. Breeding phase was determined by regular checks of a selection of nests in the breeding colony (as described in van Donk et al. 2017). The median date of egg laying calculated for the entire study period is the 8th of May and median hatching date is the 3rd of June. Prey samples were classified as 'Early season' when gulls were laying eggs, relaying after failure of a nest due to predation or other causes or incubating eggs, but also after failure of a nest in the month May. Prey samples were classified as 'Late season' when the eggs of breeding gulls were hatching and when gulls were taking care of their chicks or after failure of the nest due to predation or starvation of chicks in the month June.

Some prey were analysed directly in the field, but most prey were bagged and labelled with date and location and stored frozen before analysis. The samples were analysed in the laboratory and when needed using a microscope (Olympus SZ51, max. 40× magnification). We identified the prey to the lowest taxon possible and grouped every prey item in seven main prey categories after identification based on family and/or habitat where prey types occur (as in van Donk et al. 2017). These groups were intertidal coastal bivalves which are mainly mussels *Mytilus edulis* from breakwaters, intertidal mudflat bivalves which are mainly cockles *Cerastoderma edule*, crustaceans which are mainly shore crabs *Carcinus maenas*, marine fishery discards including marine fish and brown shrimp *Crangon crangon*, human waste like domestic refuse and food remains, birds both passerines and non-passerines which were mainly chicks of conspecifics and of the sympatric lesser black-backed gulls, and remaining prey items like mammals, terrestrial invertebrates and woodlice, plant matter, oligochaetes, polychaetes and echinoderms.

We calculated the proportion of every prey category per year as the frequency of occurrence a prey was found in separate regurgitates divided by all prey found. We compared whether the dietary spectrum changed after the habitat loss, and tested whether the proportion of coastal bivalves in the diet decreased after this period.

Proportional data induces some constraints on the variance and the covariance of the data (Aitchison 1986, Warton and Hui 2011), which was the reason to do a data transformation to be able to use standard statistical techniques. We took the logarithm of the proportion of all prey types excluding coastal bivalves divided by the proportion of coastal bivalves. We used a

Student's t-test to compare the proportion of coastal bivalves before and after habitat loss, for the early and late breeding phase separately.

During our analysis, we also saw an increase in the proportion of intertidal mudflat bivalves in the diet compared to other years. Therefore, we also tested whether the logarithm of the proportion intertidal mudflat bivalves divided by the proportion of coastal bivalves was significantly different.

We excluded both breeding phases for the year 2013 and the early phase for the year 2011 due to low sample size ($n < 100$).

Measuring changes in reproductive success

Reproductive success was monitored in study plots within the colony between April and August 2006-2016. We assessed four reproductive parameters: timing of egg laying, egg volume, hatching success, and fledging success. Loss of habitat can affect the body condition of adult birds and can thereby delay the timing of breeding. Delayed breeding can negatively affect chick survival (Hunt and Hunt 1976, Brouwer et al. 1995). To define timing of egg laying, we measured laying date and calculated the deviation of the mean laying date measured for the entire study period in days. Egg volume is a measure for egg quality because it is positively correlated with chick survival (Krist 2011). Length (L) in cm and width (W) in cm of eggs were measured to the nearest 0.1 mm with Vernier callipers and egg volume was calculated as volume as $V \text{ (cm}^3\text{)} = kLW^2$, using $k = 0.5035$ (Barth 1968, Spaans and Spaans 1975). Hatching success was determined by checking nests within the study plots every third day until hatching date and scoring the number of hatched, predated and dead eggs (e.g. not hatched after more than 4 weeks) after which we calculated hatching success in percentages per nest ($\% \text{ nest}^{-1}$). To determine fledging success, randomly selected nests were enclosed with chicken wire fence and hatchlings within the enclosure were individually marked. Fledging success was defined as the number of chicks that survived until day 40 per nest (for more information see van Donk et al. 2017). We compared all four proxies for reproductive success per nest site before (2006-2014) and after (2015-2016) the disappeared foraging habitat using a Student's t-test. In case of a significant difference, we performed an ANOVA followed by a Tukey's honestly significant difference (HSD) post hoc test, to test whether the difference before and after habitat loss is consistent for the entire study period.

The year after habitat loss, we observed a sudden increase in the proportion of intertidal mudflat bivalves (cockles *Cerastoderma edule*) during the early phase when most animals were laying their eggs. We therefore also tested whether breeding pairs with this uncommon prey in their diet had poorer breeding success measured as timing of breeding, egg volume and hatching success than individuals with mainly coastal bivalves in their diet using a Student's t-test.

Measuring changes in habitat use

We used two methods to compare habitat use before and after the habitat loss. We analysed movements based on colour-ring re-sightings and, to study habitat use in more detail, we made use of animals with GPS trackers to see whether habitat used corresponds to the prey remains found in the colony.

Colour ring re-sightings were used to monitor habitat use and site fidelity to intertidal coastal habitat of a large amount of individuals. Adult herring gulls were caught with walk-in traps during incubation between 2006 and 2016 and body mass (g), wing (mm), tarsus (mm), head (mm) and bill (mm) lengths were measured. Birds were sexed based on head plus bill lengths (mm) (Coulson et al. 1983a). Birds received a colour ring around their tarsus with unique codes which can be read from a distance when using binoculars or a telescope. Colour rings were read in the breeding colony and surroundings, but also by several volunteers, who reported colour code, time, date and place. Subsequently, we grouped these places in different habitat categories which were (natural) parks and agricultural land, urban areas, intertidal coastal area (including beach and breakwaters) and the lost intertidal coastal area.

We analysed the colour-ring sightings in two ways. The first analysis was executed to analyse whether gulls that made use of the lost coastal habitat made use of different habitat categories after habitat loss, indicating a shift in foraging habitat. The second analysis was done to analyse whether gulls foraging on the remaining intertidal coastal habitat decreased site fidelity, indicating an increase in interference competition in that area. The first analysis was done by comparing all the sightings in the habitat categories of individuals that had been observed in the lost intertidal coastal habitat in 2014 and compare the same individuals with where they had been sighted the year after. Here, we have to take into account that not all foraging habitat is accessible for reading rings; foraging areas like Wadden or North Sea or intertidal mudflats, are barely accessible. Also the lost intertidal coastal area has been less accessible during the coastal protection work (~half a year), whereas the non-changed intertidal coastal foraging habitat along the coast was suitable for reading rings during the complete period of the study. Therefore, the second analysis was focused on sightings of birds that were seen in the intertidal coastal foraging habitat that did not undergo changes (Fig. 5.1, area outside the square). For this analysis, we compared re-sightings of individuals that were seen in intertidal coastal foraging habitat to where they were seen in the following year. We reported whether they were seen again at the intertidal coastal habitat, whether they were seen somewhere else, or not re-sighted in that year. In this way, we could monitor movements and site fidelity before and after habitat loss. We tested movements before and after habitat loss by comparing the logarithm of the proportion of animals seen elsewhere divided by the proportion of animals that were seen

again in the coastal foraging habitat using a Student's t-test. We only used data from 2009-2016 as sample size was too low before 2009.

To determine more detailed habitat use, a selection of 31 herring gulls were equipped with GPS trackers (14 female and 17 male) between 2013 and 2015 (van Donk et al. 2018). GPS trackers with solar-panels of the UvA Bird Tracking System (Bouten et al. 2013) were mounted on the back of the birds with a 3-g non-flexible Teflon harness, after taking body measurement as described above. For seabirds, it is recommended to keep the weight of trackers below 3% of the body weight (Phillips et al. 2003). In our study, GPS tracker and harness together weighted less than 3% of the body mass of the birds, which was on average 2.4 % of female body mass and 2.1 % of male body mass. The trackers measure the geographic location and time (UTC) and provide the possibility to change measurement frequency while the tracker is on the bird. Measurement frequency was generally set to every 10 minutes inside the breeding colony and every 5 minutes outside the breeding colony. We took higher resolution measurements occasionally (~every 3 seconds) outside the breeding colony, when the memory of trackers was empty and the battery fully loaded. We resampled all the data to every 5 minutes, as measurement frequency could influence precision of GPS fixes. Subsequently, we coupled every GPS position outside the breeding colony to a foraging habitat category. The foraging habitat categories are parks and agricultural land, urban areas, North Sea and Wadden Sea, intertidal mudflats, intertidal coastal beach and intertidal coastal breakwaters. We used several shapefiles for every habitat category which are; (MapCruzin 2017, OpenStreetMap contributors 2017) for (natural) parks and agriculture land, (European Environment Agency (EEA) 2017, OpenStreetMap contributors 2017) for urban areas, (Hijmans 2012) for North Sea and Wadden Sea, (www.rijkswaterstaat.nl) for intertidal mudflats, beach (Hazeu 2005) for beach, and (QGIS Development Team 2009) for breakwaters which were delineated based on QGIS openlayer plugin google earth. Due to tidal fluctuations, areas close to breakwaters, beach and intertidal mudflats are also often accessible for the gulls during low tide. We therefore assigned GPS positions in North or Wadden Sea which were closer than 50 meters to breakwater, beach or intertidal mudflats to these habitat types (van Donk et al. 2018).

We calculated the proportion of time all herring gulls with a tracker spent in these different foraging areas. We compared habitat use between 2014 and 2015 for all individuals carrying a GPS tracker, but also for individual birds that carried a GPS tracker in both 2014 and 2015. For the repeated individuals, we only selected dates on which we had tracking data between the beginning of April and the end of June for both years, excluding the possible effects of time of the year on habitat use.

Results

Dietary changes per breeding stage

Herring gulls of the colony of Texel feed on many different prey types originating from a range of sources like agricultural lands, anthropogenic refuse from cities or dumpsites, the marine environment, intertidal mudflats and intertidal coastal habitat. In most years, the proportion of intertidal coastal bivalves in the diet was larger during the early compared to the late phase when many breeding pairs are feeding their young (Fig. 5.2). Over the course of the study, the proportion of intertidal coastal bivalves increases and other prey categories decrease, in particular crustaceans, fishery discards, mammals and plant matter. This change is stronger in the early phase. Interestingly, loss of coastal habitat did not result in a lower proportion of intertidal coastal bivalves in the diet in the early phase of the breeding season (two-sample t (4.83) = -1.57, $p = 0.18$). In the late phase, we found a significant difference for the proportion of coastal bivalves in the diet (two-sample t (7.79) = -2.50, $p = 0.04$); but, contrary to our expectations, the proportion of intertidal coastal bivalves was significantly higher after habitat loss. However, the increase in coastal bivalves in the diet seems to have happened in the early years of this study (Fig. 5.2: after 2008) and is highly likely not caused by the loss of habitat. After the habitat loss we observed a relatively high amount of intertidal mudflat bivalves in the diet during the early breeding season (Fig. 5.2); the frequency of intertidal mudflat bivalves was significantly higher after habitat loss (two-sample t (6.55) = -4.84, $p = 0.002$).

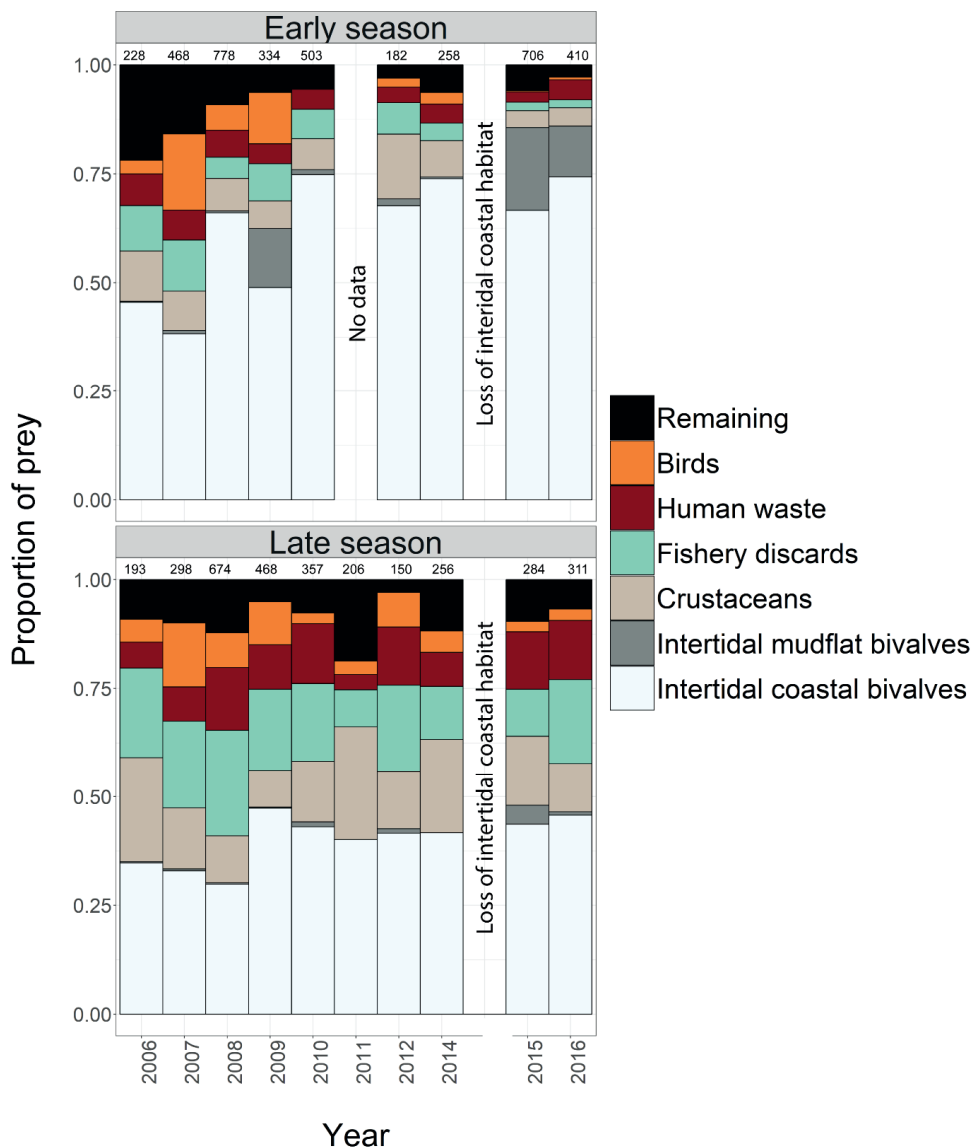


Fig. 5.2 Time series of the distribution of prey categories shown as proportion of the diet of herring gulls breeding in the colony on Texel per year and per breeding phase, which are either during egg-laying and incubation (early phase) or during the period of chick-rearing (late phase), prey types of failed individuals were also taken into account. Prey types are measured as frequency of occurrence ($n=8007$ samples). The time series show that loss of coastal habitat (between autumn 2014 and spring 2015) did not have an effect on proportion of coastal bivalves in the diet. Sample sizes are shown above every year and breeding phase. Both breeding phases for year 2013 and the early phase for year 2011 were left out the analysis due to low sample size.

Table 5.1 Reproductive success of the breeding colony of Texel measured over 11 years. The mean and standard deviation for four proxies for reproductive success are shown per year which are average laying date and relative laying date compared to the overall laying date of the study period of the 9th of May, average egg volume in cm³, the percentage of eggs that hatched and the number of fledged chicks per pair. Averages over the period before (2006-2014) and after (2015-2016) habitat loss are shown in bold. Lowest values per reproductive success are underlined.

Year	Laying date	Relative laying date	Egg volume (cm ³)	Hatching success (%nest ⁻¹)	Fledgings pair ⁻¹
2006	11 May	1.73±5.35	82.19±9.05	76.98±35.49	0.62±0.77
2007	09 May	-0.02±8.81	81.16±8.27	61.26±38.53	0.93±0.80
2008	08 May	-0.65±5.84	82.57±8.63	66.89±36.47	1.10±0.97
2009	06 May	-2.53±4.47	79.91±9.49	69.74±35.46	0.81±0.81
2010	04 May	-3.91±4.71	82.69±9.13	82.34±28.11	1.33±1.05
2011	04 May	-4.25±4.95	81.20±9.85	63.69±41.69	<u>0.48±0.73</u>
2012	07 May	-1.25±6.08	81.23±8.93	66.67±36.53	1.09±0.95
2013	11 May	3.13±7.68	79.98±9.25	61.03±42.35	0.65±0.79
2014	09 May	1.34±6.84	80.14±9.12	68.50±35.87	0.67±0.84
2006-2014	08 May	-0.72	81.20	68.13	0.87
2015	11 May	<u>4.12±7.35</u>	<u>79.87±10.33</u>	<u>54.73±39.97</u>	0.68±0.99
2016	10 May	1.91±6.68	81.36±9.75	69.22±38.62	0.67±0.89
2015-2016	11 May	2.81	80.75	62.83	0.67

Changes in reproductive success

Reproductive success varied over years (Table 5.1). Relative laying date calculated as the difference with average laying date measured over the entire study period was significantly later after habitat loss (two-sample t (576.09)=8.89, $p < 0.001$). A posthoc test showed that laying date was not consistently later after habitat loss and earlier before habitat loss. For instance, the relative laying date of 2015 and 2016 did not differ from the year 2006 and 2013 and relative laying date of 2016 did also not differ from the year 2007 and 2014 ($p > 0.05$). Both egg volume (two-sample t (559.01)= -0.79, $p = 0.428$), hatching success (two-sample t (228.02)= -1.48, $p = 0.141$) and number of fledglings per pair (two-sample t (95.25)= -1.45, $p = 0.152$) did not significantly differ before and after habitat loss. Although we did not find convincing evidence that reproductive success was lower after habitat loss, we did observe the latest relative laying date, the smallest average egg volume and the lowest hatching success in the year directly after habitat loss compared to all other years, suggesting a small effect on population level with a small recovery in the year 2015 (Table 5.1; year 2015).

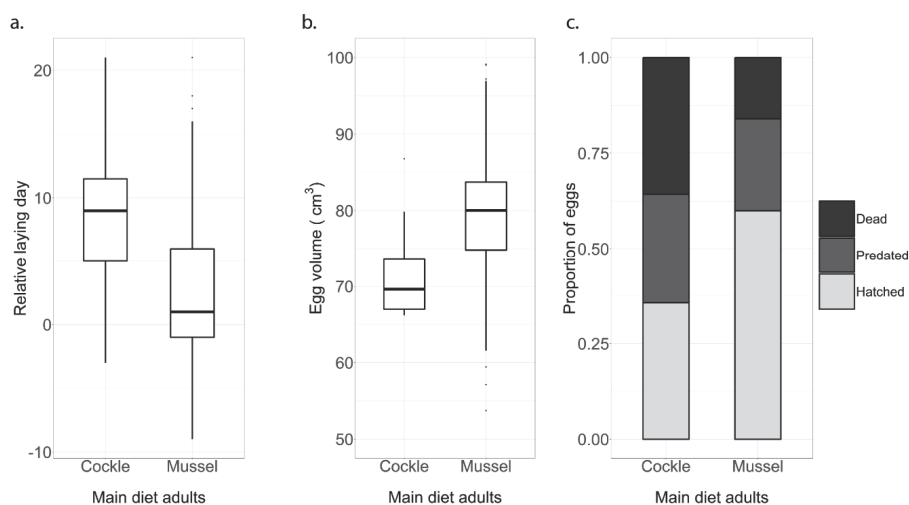


Fig. 5.3 Diet related to different proxies for reproductive success of the year 2015, directly following habitat loss. On the x-axis, the two dietary groups we selected for this analysis. Main diet of breeding pairs was based on the proportion of cockles and mussels. Breeding pairs of which the diet contained more than 40% cockles were assigned to 'Cockle', breeding pairs of which the diet contained more than 40% mussels, and less than 40% cockles were assigned to 'Mussel'. Main diet of adults in relation to a. relative laying date calculated as the difference with average laying date over all monitored years (9th of May = 0) b. average egg volume (cm³) c. proportion of eggs that hatched, were predated or were dead. When birds had a diet which contained relatively a lot of cockles, they laid there eggs relatively late, had smaller eggs and the eggs had a lower hatching success although the latter difference was not significant. But sample sizes for cockle nests were low ($n = 6$ cockle nests with 14 eggs versus $n = 49$ mussel nests with 125 eggs).

Reproductive success did not significantly differ before and after habitat loss, but it was related to the diet. Breeding pairs which had more than 40% of the mudflat bivalves (cockles) in their diet, had a relatively late laying day (Fig. 5.3a; two-sample $t(15.87) = 3.04$, $p = 0.007$) and smaller eggs (Fig. 5.3b; two-sample $t(21.35) = -3.91$, $p < 0.001$) compared to breeding pairs that had 40% or more of common coastal bivalves (mussels) in their diet. The proportion of hatched eggs also seemed to be lower (Fig. 5.3c), but the difference was not significant (two-sample $t(5.71) = -0.59$, $p = 0.58$). Here should be considered that the sample size for cockle nests was quite low (6 nests with 14 eggs), partly because pairs on territories with a lot of cockles often did not start laying (CJC and SvD pers. obs.).

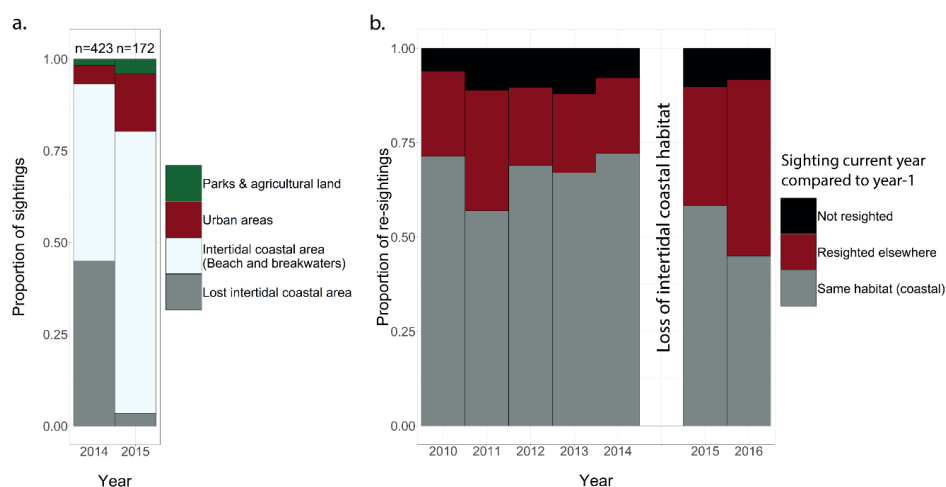


Fig. 5.4 Habitat use per year based on ring recordings. a. Colour-ring sightings of individuals that were seen in the lost intertidal coastal habitat in 2014 compared to where these individuals have been reported in 2015 (30 individuals). Sample sizes of re-sightings are shown above every bar. b. Re-sightings are shown of animals that were seen at the coastal breakwaters the previous year. For instance, animals that were seen at the coastal breakwaters in 2009, are shown in the bar for the year 2010. On the y-axis is the proportion of animals shown, the colour represents where the animal has been seen; again at the coastal breakwaters or somewhere else, or the animal has not been re-sighted that year. The time series shows that loss of coastal habitat (between autumn 2014 and spring 2015) resulted in lower re-sighting probability on coastal habitat.

Changes in habitat use

1. Habitat use of colour ringed individuals

We summarized the colour ring re-sightings in two ways. First, in order to explore how individuals may have altered their habitat use, we compared the proportion of observations in different habitats in 2014 and 2015 (before and after habitat loss respectively) for those individuals that were observed in 2014 in the intertidal coastal area that was eliminated (Fig. 5.4a). Many individuals were re-sighted in 2015 in the remaining intertidal coastal area, but the proportion of sightings in parks and agricultural land and urban areas also increased slightly. However, with these results one should consider that the presence and effort of bird watchers between foraging areas can differ, as mentioned in the methods section.

Second, we analysed the colour-ring sightings of the intertidal coastal area that was not lost. We tested whether animals changed in the use of coastal habitat. Most individuals were site-faithful to this part of coastal habitat: individuals that were seen on and around coastal habitat (breakwaters) were very often seen again in the same habitat the following year (Fig. 5.4b). On average, 70% of the animals were seen in the same coastal habitat again, while 25% was seen in different places, like for instance the colony, on roosting sites or other foraging habitat. About 5% of the animals were not seen the year after. In the year of the start of coastal habitat loss (end of 2014), the likelihood of re-sightings in the intertidal coastal habitat decreased; individuals were re-sighted in only 60% of the cases which decreased to 50% in 2015 and 40% in 2016. These results suggest that interference competition increased in the remaining intertidal coastal habitat, and that individuals were replaced more often from their spot resulting in a lower re-sighting probability. However, the difference between the amount of re-sighted individuals on the coastal habitat compared to individuals re-sighted elsewhere was not statistically different before and after habitat loss (two-sample t (1.320) = 2.260 , $p = 0.21$).

2. Habitat use of animals with GPS trackers

When examined at the population level, habitat use differed between the year before and the year after loss of intertidal coastal habitat (Fig. 5.5). Animals with GPS trackers spent more time on intertidal mudflats, which confirmed the results of the dietary study (Fig. 5.2). These results were measured in all individuals with GPS tracker as individuals tracked in both years (Fig. 5.5). As individuals might differ in their response to habitat loss, we also showed habitat use of all individuals that we monitored in both years separately (Fig. 5.6). Some individuals change their habitat use dramatically (bird ID 6015, 6072, 6077 and 6080), while others are remarkably consistent (1600, 6016, 6017). Of these, individual with code 6080 was directly affected by the habitat loss.

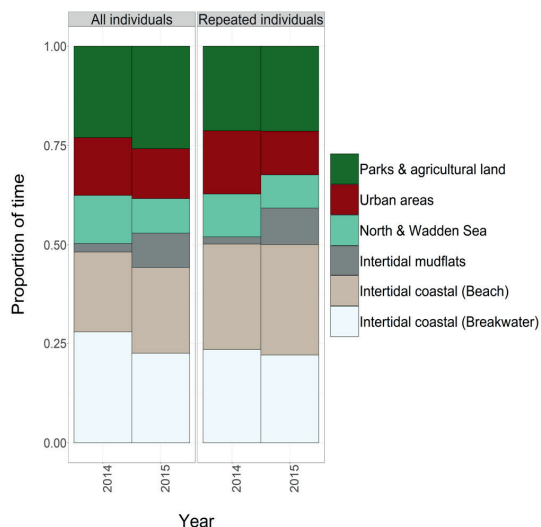


Fig. 5.5 Proportion of time spent in different habitats outside the breeding territory in 2014 and 2015 in April – June. Left, all GPS-tracked individuals ($n = 27$) and right, individuals that were tracked in both years (right; $n = 10$). Loss of coastal habitat happened between autumn 2014 and spring 2015. After habitat loss, animals spent more time in intertidal flats.

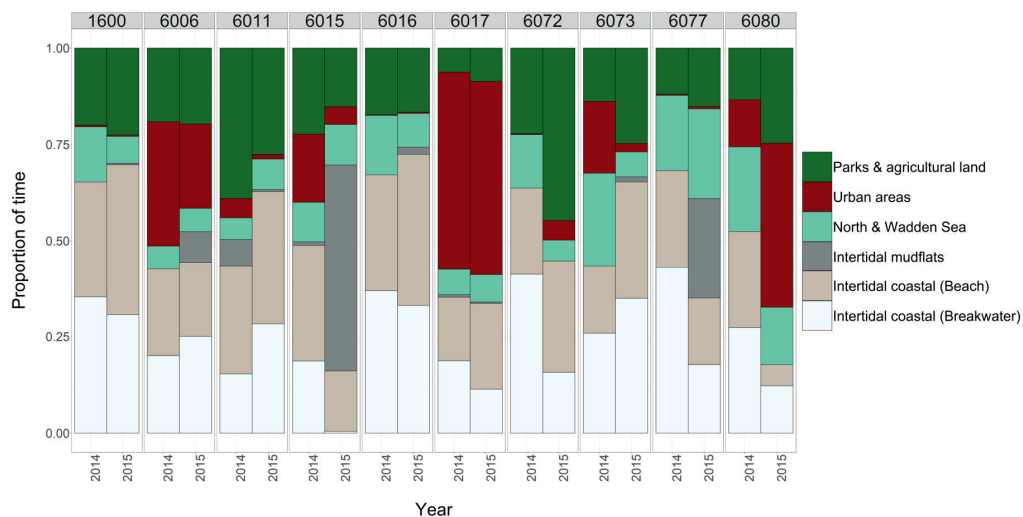


Fig. 5.6 Habitat use in proportion of time outside the breeding territory in 2014 and 2015 in April - June of individuals that were carrying a tracker in both years ($n = 10$). The top shows the unique code per individual. Some gulls are remarkably stable in their habitat use (1600, 6016, 6017), while others differ in their habitat use between the two years (6015, 6072, 6077, 6080). Only individual 6080 was directly affected by the habitat loss.

Discussion

In this study, we used a long-term dataset of reproductive measurements, dietary data and habitat use to study how a population of generalists deals with a sudden loss of part of its coastal foraging habitat. We found no significant effects of habitat loss on the population level. The frequency of occurrence of intertidal coastal bivalves (mussels), which are the main prey in the lost foraging habitat, did not decline (Fig. 5.2) and mean breeding success (fledglings nest⁻¹) was similar in the years before and after the loss of feeding habitat (Table 5.1), but we found the lowest hatching rates measured over 11 years. We did find a sharp increase in the proportion of mudflat bivalves (mainly cockles), a thus far highly unusual prey during the early phase of breeding (prospecting, egg-laying and incubation periods, Fig. 5.2). GPS data reflected this dietary shift with an increase in time spent on the habitat that contains cockles, the intertidal mudflats in the Wadden Sea, in the year immediately following the habitat loss along the coast (Fig. 5.5). Individual breeding pairs with cockles in their diet, had lower success in the early breeding phase (Fig. 5.3). We expect this shift in habitat use and diet to represent an immediate and potentially short-term response to the loss of coastal foraging habitat. Our results indicate that while this generalist population shows the expected resilience on population level (Devictor et al. 2008, Sih et al. 2011, Tuomainen and Candolin 2011), certain individuals within the population had difficulties to adapt. This finding questions the general idea that generalists are flexible by definition. Here, we discuss consequences of coastal habitat loss on a population level and individual level.

Behavioural plasticity or changes in population composition

We made use of a long-term dataset, which enabled us to study breeding and foraging behaviour of the birds well before the loss of foraging habitat took place. Although we gathered a lot of data, we did in general not follow behaviour and breeding success within individual birds over multiple years. Also, even if individuals breed regularly in the colony, their diet or breeding success is not always measured as only a random selection of nests are taken into complete monitoring every year. It is possible that the increase of cockles in our samples and the observed low breeding success of birds feeding on these prey are in fact new breeding individuals entering the population.

There are several reasons why this is unlikely. First, cockles are a rare prey throughout the colonies on Texel and only very occasionally encountered, nearly always around nests of specialized individuals or pairs. Within the zone of monitoring, the frequency of occurrence of cockles in the early season prior to the year of impact was on average only 2.6%. Second, animals with GPS trackers that provided data in both years showed that indeed some individuals started to utilize in the intertidal mudflats, the cockles banks, after the loss of intertidal coastal

habitat (Fig. 5.5). This is further evidence that the same individuals indeed changed their foraging behaviour.

Consequences on population and individual level

Whether a generalist population is affected by environmental change, depends on several factors. First, the size of the effect will be related to the importance of the foraging area for the breeding colony. Only 12% of the colour-ringed birds foraging for mussels used the area that was lost and were affected directly. Birds foraging on mussels in intertidal coastal habitat north of the area that was lost, were highly likely affected indirectly from an increase in intra-specific competition (Fig. 5.4b); the likelihood that individuals were re-sighted in the remaining intertidal coastal habitat decreased after habitat loss, suggesting a higher replacement of individuals. Second, the effect size of habitat loss can be related to the diversity and types of strategies the population is composed of (Phillips et al. 2017). A population can for instance consist of specialists, or generalists only (Sjödin et al. 2018) or potentially consist of a mix of specialists and generalists. Only the individuals that are specialized on lost or changed habitat will be affected while generalists would have other options. Data from GPS trackers suggest that specialists (narrow range) and generalists (wide range) co-exist (Fig. 5.6). Third, the effect depends on the importance of a (lost) prey in the context of breeding success. Herring gulls foraging on high caloric prey of anthropogenic origin in the chick phase have a higher breeding success in this population than herring gulls foraging mainly on low caloric intertidal coastal bivalves (van Donk et al. 2017). Losing prey related to higher breeding success, like anthropogenic prey in this colony, will have a greater impact than losing an area related to low breeding success, like the low caloric intertidal coastal bivalves. This might explain why habitat loss did not result in a large impact on the breeding success.

Nevertheless, when studying not only the population but also the individual, we show that individual birds of a generalist species can struggle with habitat loss. Individual birds that changed their foraging diet to an otherwise rare prey in this colony, intertidal mudflat bivalves (mainly cockles), had a lower breeding success. In addition, we observed that breeding pairs on territories with many cockle remains often did not lay eggs (pers. obs.). While not part of our study protocol, monitoring dietary selection of territorial birds that do not lay eggs could improve our understanding of non-successful strategies that reduce the probability of breeding. Our findings show that individuals of generalist species may not always be highly adaptable to changing environmental conditions.

It is not clear why animals feeding on intertidal mudflat bivalves are unsuccessful in reproducing. One reason could be that weaker/less dominant animals are replaced from better foraging habitat with higher quality prey. Cockles from intertidal mudflats of the size found in the colony were for instance of lower quality than mussels of the coastal breakwaters in the

same period; sampled cockles had a lower meat shell ratio than mussels (Fig. S5.1). Animals foraging on cockles might therefore be in worse body condition, resulting in a lower breeding success or more frequent breeding sabbaticals.

Apart from the relative lower prey quality of cockles compared to mussels, changing foraging strategy might also be costly. Juvenile birds get progressively better over time in handling and finding prey (Verbeek 1977, Riotte-Lambert and Weimerskirch 2013, Cristol et al. 2017), which suggests learning new strategies later in life also takes time and energy. Individual herring gulls are highly site faithful to their foraging habitat, which was shown in an earlier study (van Donk et al. 2018). Sometimes, individuals can even stay site faithful to their spot when their foraging habitat is lost, which was shown by a gull which received a GPS tracker in 2014 (Fig. S5.2). This gull was very regularly observed in the colony and on breakwaters in the foraging area that disappeared by the end of 2014. Although this animal was forced to move to other foraging habitat, it still regularly returned to its old foraging area despite the lack of suitable prey and the long distance to the colony. Concluding, individuals that foraged on cockles may not be particularly successful, due to costs associated with digesting cockles or due to conservative foraging behaviour of adult herring gulls that have difficulties changing their habits.

Environmental change and the consequences of foraging strategies

As already mentioned, individuals within the same population can show consistent differences in (foraging) behaviour (Reviews: Bolnick et al. 2003; Sih et al. 2004). Besides differences in foraging strategies in gulls, individuals also differ in the level of specialization in habitat use or prey (van Donk et al. 2018, Bosch et al. 2019). Specializing might be beneficial for foraging efficiency (Werner et al. 1981, Persson 1985) and can decrease competition with conspecifics (Svanbäck and Bolnick 2005). However, in a changing world, individuals that are less specialized might be more flexible and hence successful than specialized individuals (Sih et al. 2011, Tuomainen and Candolin 2011). In the current study, we also see large differences in foraging behaviour between years, which might have affected how animals have dealt with the changes in their environment (Fig. 5.6). Two individuals with birdIDs 1600 and 6016 spent a lot of time in the coastal foraging habitat on breakwaters and beach stay remarkably consistent after the habitat loss. Individual with bird ID 6015, on the contrary, changes its habitat use completely after habitat loss and starts foraging on intertidal mudflats in 2015 instead of on breakwaters in the intertidal coastal habitat.

In the current study, a large foraging patch was destroyed due to changes in coastal defence management. Important coastal ecosystems are being destroyed in a very rapid pace in many places over the world. For instance, fixed structures are built in some areas and removed in others, which drastically changes the coastal ecosystems. Some species or individuals are

expected to come out as winners and others as losers. Combining long term demographic research with dietary analysis and movement data including bio-logging can help elucidate why some species or individuals may fair well under such changes and others not. In future, it would be interesting to test whether generalized individuals within populations do better in rapidly changing coastal environments in both reproductive success but also survival.

Author Contributions

SvD carried out the statistical analysis, and drafted the manuscript with support from JSB, JvdM and CJC; CJC leads long term study on herring gulls; CJC and SvD conducted field work. All authors discussed results and contributed to the final manuscript.

Supplementary material

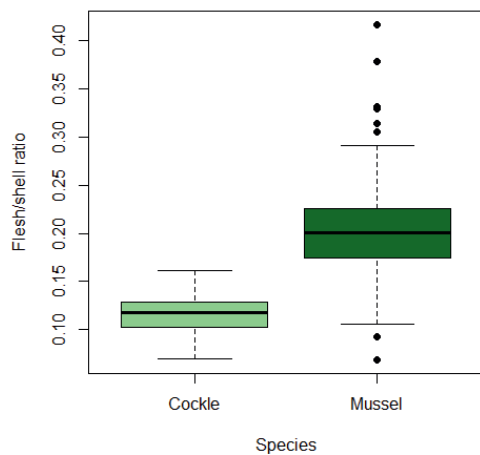


Fig. S5.1 The flesh/shell ratio of mussels on the breakwaters was higher than that of cockles sampled in June 2015 (t-test: -24.73, $df = 171.02$, $p < 0.001$). Flesh and shell weight is measured after drying it in an incubator by 560 °C degrees Celsius for 3 days.

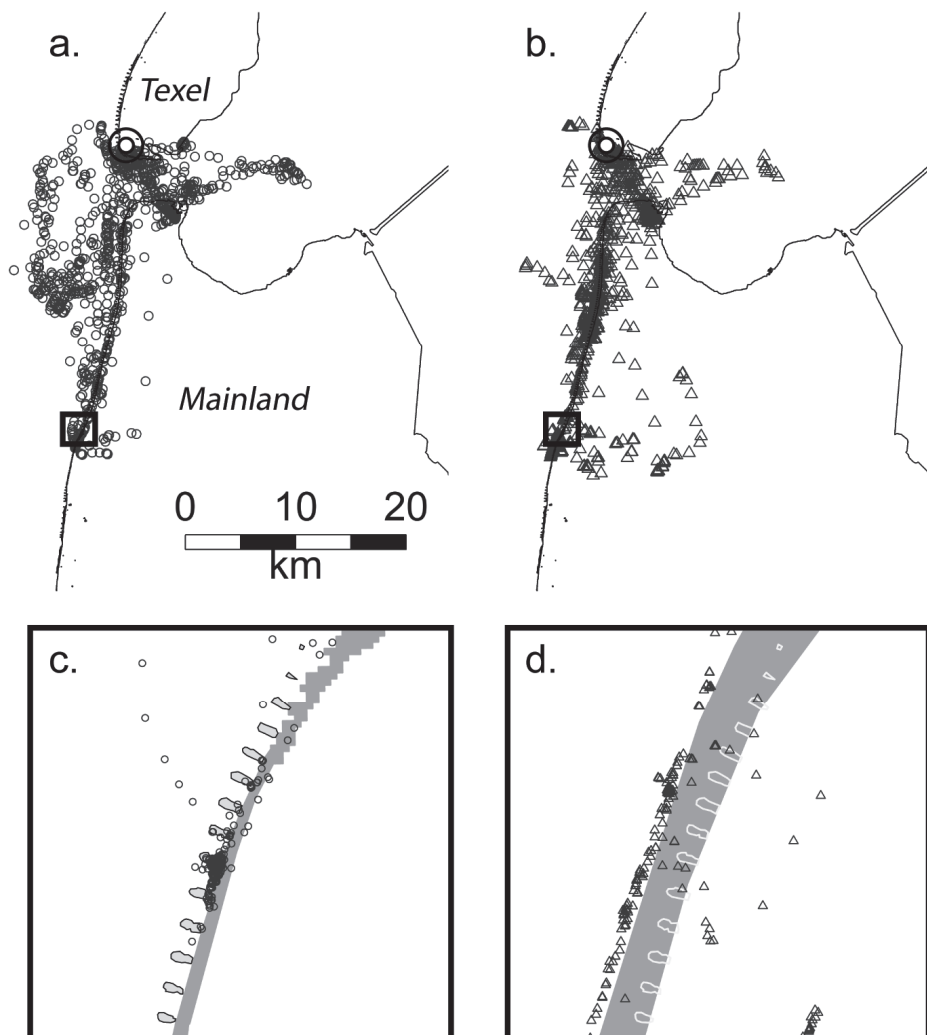


Fig. S5.2 Distribution of GPS locations of one herring gull from the first until the 20th of June of 2014 (a. & c.; circles) and 2015 (b. & d.; triangles) at different spatial scales. The breeding colony is indicated with a double circle (615201.4 E, 5873649 N). The square on a. and b. indicates the area shown on a larger scale in c. and d. After habitat loss, many breakwaters (light grey in c.) disappeared under a new created beach (darker grey in c. and d.), but the herring gull still visited the disappeared foraging habitat (d.). Every point corresponds to one GPS fix which was taken ~every 5 minutes.



PART II

Consequences of breeding



Chapter 6

Energy expenditure of movement is higher for breeders than for non-breeders, but only during offspring care

Susanne van Donk, Judy Shamoun-Baranes, Jaap van der Meer, Kees C.J. Camphuysen

Abstract

Long-lived species with multiple reproductive opportunities over a lifetime may skip or abandon reproductive attempts. Skipping reproduction might reduce energetic investment in reproduction and increase energy available for self-maintenance and survival. However, testing whether energetic costs differ between reproducing and non-reproducing individuals and among reproductive phases is challenging in the wild, as ‘skippers’ are often difficult to monitor. We examined the energetic costs associated with movement of a long-lived seabird, the herring gull *Larus argentatus* during the reproductive period of breeding and non-breeding individuals. We measured the daily activity budgets of adult herring gulls using GPS trackers with tri-axial accelerometers and concomitantly monitored the reproductive state and phase of each individual in the field. Bio-logging data were used to quantify activity of the herring gulls and estimate energy expenditure attributed to movement over the complete reproductive season (prospecting, incubation, chick care) over several years. We compared the energy invested in movement during different breeding phases and measured whether energy investment increased over the period of chick care, as energetic demands increase with chick age. Breeders and non-breeders did not differ in energetic cost of movement during the prospecting and incubation phases of the reproductive season. However, the energy expenditure during chick care was 25-30% higher compared to non-breeders in the same period. The elevated energy expenditure during chick care was stable over time and did not increase during chick development. Our study showed that if birds were to skip or abandon reproduction, the most energy allocated to movement would be saved during chick care. Chick care could therefore be the energetic bottleneck in the reproductive season of the herring gull. Despite low breeding success in this colony, individuals did not increase their foraging effort during chick development. This suggests that breeding individuals have an energetic ceiling to avoid negative impacts on future reproductive success. Combining long term bio-logging and demographic measurements across periods of environmental variability can provide insights into life history decisions and the trade-off between current and future reproductive success.

Submitted

Introduction

Life-history theory predicts that producing offspring should be costly, as energy reserves are in general limited (Stearns 1992, Williams and Fowler 2015). As a consequence, energy invested in offspring is not available for self-maintenance (Williams 1966). Therefore, it is assumed that reproducing would lead to a lower survival, causing a trade-off between reproduction and survival (Williams 1966; Pugesek and Diem 1990; Cayuela et al. 2014).

Animals that have multiple reproductive events in their lifetime can deal with this trade-off by skipping a breeding event, which is a widespread phenomenon in the animal kingdom (Bull and Shine 1979, Pilastro et al. 2003, Shine and Brown 2008, Skjaeraasen et al. 2012, Blomberg et al. 2013, Cayuela et al. 2014). Animals could decide not to reproduce, for instance when physical or environmental conditions are poor (Williams 1966, Shaw and Levin 2013). By skipping a breeding opportunity, animals might be able to avoid survival costs which can positively affect future reproductive success (Pugesek and Diem 1990, Stearns 1992, Candolin and Voigt 2001, Blomberg et al. 2013, Shaw and Levin 2013).

Skipping reproduction should be especially beneficial in species that invest a lot in parental care, which is all behaviour associated with increasing the survival of offspring (Williams 1966, 2018, Royle et al. 2012). During parental care, individuals might spend temporarily elevated amounts of energy allocated to locomotion, for instance to migrate to breeding grounds, acquiring territories and mates, producing offspring and feeding young (Williams and Fowler 2015). Yet, whether skipping a reproductive opportunity could be a mechanism to avoid reproductive costs associated with movement is not easily demonstrated, as skippers are generally difficult to monitor (Cubaynes et al. 2011).

In the current study, we were able to investigate the hypothesis that individuals that skip a reproductive opportunity can save energy associated with movement, by monitoring both skippers and breeders using animal-borne trackers which measure 3D position, speed and tri-axial acceleration. These trackers have made it possible to monitor individual animals over multiple breeding seasons, measuring behaviour remotely and enabling an estimate of energy expenditure attributed to movement (Gleiss et al. 2011, Elliott et al. 2013, Collins et al. 2016, Jeanniard-du-Dot et al. 2017). We focused our study on the herring gulls *Larus argentatus*, which are coastal seabirds that skip breeding events regularly in their adult life (Pons and Migot 1995; Calladine and Harris 1997; Camphuysen 2013).

The reproductive season of herring gulls can be divided into different phases, which is comparable to many other species with parental care (Cramp and Simmons 1983). Phases can vary in costs, which can have consequences for the decision of an animal to abort a reproductive attempt when current costs exceed long-term benefits (Williams 1966). We distinguished the phases prospecting, egg and chick phase. The prospecting phase is expected to be energetically

costly, as territories are established and defended and pair bonds are formed or reinforced (Burger 1984). In addition, females have to build up reserves to produce eggs, while males provide the females with extra food (Wiggins and Morris 1986, Hario et al. 1991, Helfenstein et al. 2003), resulting in similar costs between the sexes (Hario et al. 1991, Ramírez et al. 2010). The egg phase is expected to be less costly, as birds only need to forage for themselves with some additional energetic costs to incubate the eggs, an activity shared by the sexes (Bech et al. 2002, Niizuma et al. 2005, Rønning et al. 2008). The chick phase is thought to be the most energetically demanding phase, as both partners need to provision for themselves and for their chicks until independence (Drent and Daan 1980, Ricklefs 1983). During chick care energetic costs are expected to increase over time as chicks are growing. As energetic demands of chicks increases with age the parental foraging activities are expected to increase as well (Grémillet 1997).

From the above, we formulate three main research aims; (1) to determine whether daily energy expenditure is higher in individuals that are actively breeding compared to individuals which skipped a reproductive opportunity, (2) to determine whether energy expenditure differs among different phases of the reproductive cycle and (3) to determine whether energy expenditure increases with the energy demands of chicks. Because food supply varies over time, and hence the associated foraging costs, we compared breeding with non-breeding animals within the same period for each of the breeding phases. We expect energy expenditure due to movement to be higher in breeding adults compared to non-breeding adults. We expect energetic costs to differ among the reproductive phases with especially high costs during prospecting and chick phase. Furthermore, we expect the time and energy invested in movement to increase during the chick phase. We discuss the relevance of individual differences in time-activity budgets as individual animals differ consistently in this species and show how bio-logging data collected over multiple years can be used to compare the cost of reproduction and the different reproductive states attributed to movement.

Methods

Study system

The study was carried out in a breeding colony of approximately 4000 breeding pairs of herring gulls that breed together with approximately 11,000 pairs of lesser black backed gulls *Larus fuscus* at the island of Texel, the Netherlands (615201.4 E, 5873649 N UTM zone 31). Data was collected during breeding seasons of 2013 through 2016 between April and July.

GPS tracking

To investigate the costs of breeding, we used 21.43 ± 0.67 g solar-powered GPS trackers of the UvA Bird Tracking System (Bouten et al. 2013) that were mounted to the back of the birds with

3-g non-flexible Teflon harness. The trackers measure geographical location, time and body acceleration in three axes (surge, sway and heave). Trackers were attached to 31 adult herring gulls, of which one was not used in the analysis. Birds were caught with walk-in traps placed on the nest during incubation of the eggs in 2013 (10 individuals), 2014 (11 individuals) and 2015 (10 individuals) (Table S6.1). Thus in the first year of tracking all birds were active breeders and incubating at the time of capture. At capture, body mass (g), wing (mm), tarsus (mm), head (mm) and bill (mm) lengths were measured and birds were sexed based on the head plus bill length (mm) (Coulson et al. 1983b). Birds were also ringed with engraved colour rings and stainless steel rings for individual identification in the field. For seabirds, it is recommended to keep the weight of GPS trackers below 3% of the bird's body mass (Phillips et al. 2003). The average weight of the gulls used in this study was 887 ± 49 g for females and 1016 ± 59 g for males and GPS trackers plus harness in our study weighted on average 2.4 % and 2.1 % of the body mass of females and males respectively (Table S6.1). In the closely related lesser black-backed gull, Thaxter *et al.* (2016) did not find an effect of GPS trackers attached with a harness on breeding success in the year of tagging nor on winter return rates. Fitting the GPS tracker to the bird and body measurements took approximately 20 minutes after which the birds were released.

The tracking system allows changing the measurement frequency and downloading data while the tracker is on the bird and in the proximity of a ground-based receiving system, which was set up in the breeding colony (for more technical details about the tracking system see (Bouten et al. 2013)). For birds that were actively breeding or often present in the colony, tracking frequency was set to every 10 minutes inside the colony and every 5 minutes outside the colony. Tracking frequency of birds that were only occasionally in the colony, for instance because they failed breeding, was set to every 20 minutes outside the colony. When battery and tracker memory allowed, we occasionally took measurements every 3 seconds. Tri-axial acceleration was periodically measured outside the breeding colony, at 20 Hz for 1 s directly following a GPS fix. Sometimes, acceleration measurements outside the colony were missing due to technological failure.

Pre-processing of tracking data

The original dataset included 555,516 tracking measurements and 2867 bird-days (total number of days with tracking data per individual). As large differences in resolution could potentially affect estimated energy budgets, we first resampled the data to every 5 minutes outside the colony. For each resampled tracking point, we then calculated the 'centred duration' by summing the backward and forward time intervals between locations and taking the average of these. In our analysis, we only used tracking days for which at least 80% of the GPS measurements outside the colony were accompanied with acceleration measurements, 438

tracking days were removed because of this selection. The ‘centred duration’ can become disproportionately long when there are gaps in the tracking data due to low battery power, which can affect the analysis of energy expenditure. Therefore, we removed the tracking measurements which had a ‘centred duration’ of more than 30 minutes outside the colony and of more than 60 minutes inside the colony. Furthermore, if animals failed breeding, we removed tracking days from the day that breeding failed until the end of the season (see section 2.4), 472 tracking days were removed because of failure. After data selection, we used 1904 tracking days of 30 individuals, of which 18 individuals were tracked for 2-4 breeding seasons (Table 6.1).

Breeding state and breeding phase

Foraging and breeding ecology was monitored for over 10 breeding seasons in the colony on Texel using several study plots, and the birds with GPS trackers were included in this monitoring program. Study plots were visited every 3 days, and all nests with eggs were marked and followed until hatching. This allowed us to record laying date per nest and calculate average laying date per year. Birds that were equipped with a GPS tracker the previous year, were observed in the field on the basis of their colour ring. Locations of these sightings were regularly visited to check for nests and when eggs were laid, laying date was recorded. Before the eggs hatched, we enclosed the nests of birds with GPS trackers with a chicken wire fence in order to determine the fledging success. Every 3 days, chicks were caught from the enclosures and weighed and measured. We recorded when chicks were found dead or not found at all.

Table 6.1 Sample size in tracking days per breeding state of 31 different individuals, number of individuals per state and phase per sex and the mean and standard error for hours spent on flapping flight per day (h day^{-1}), hours spent active per day (h day^{-1}) and estimation energy expenditure per day (kJ day^{-1}). Highest values per energy expenditure proxy are shown in bold.

Breeding state	Breeding phase	Tracking days	F	M	Flapping $\pm\text{SE}$	Active $\pm\text{SE}$	Energy $\pm\text{SE}$
Breeding	Prospecting	275	2	7	1.02 $\pm$ 0.39	4.52 $\pm$ 1.13	1097.48 $\pm$ 117.88
Not breeding	Prospecting	202	4	4	1.09 $\pm$ 0.62	4.52 $\pm$ 1.42	1053.54 $\pm$ 152.40
Breeding	Eggs	560	12	16	1.08 $\pm$ 0.62	4.15 $\pm$ 1.65	1093.23 $\pm$ 154.25
Not breeding	Eggs	297	5	4	1.11 $\pm$ 0.58	4.88 $\pm$ 1.62	1065.30 $\pm$ 152.40
Breeding	Chicks	361	9	12	2.05$\pm$1.02	5.65$\pm$2.05	1352.51$\pm$258.99
Not breeding	Chicks	209	5	4	1.02 $\pm$ 0.54	4.74 $\pm$ 1.32	1012.38 $\pm$ 156.51

Breeding state and phase of birds with GPS trackers was assessed over 4 breeding seasons between 2013 and 2016. We assigned a breeding state and a breeding phase to every tracking day between the 15th of April and the last day of June per individual per bird per year. Breeding state was defined as whether an animal was breeding or skipping breeding in a given year. We assigned state “Not breeding” to tracking days of individuals that did not have a nest with eggs in that year. “Breeding” was assigned to tracking days of individuals that had a nest with eggs in that year as well as to tracking days of individuals that had chicks, until the chicks died or when chicks stayed alive until the 30th of June (Fig. S6.1). For individuals that failed during the egg or chick phase, all data from the moment an individual lost their eggs or chicks were removed from analysis. Breeding phase was defined as the 3 periods of the breeding season; prospecting phase, egg phase or chick phase. We assigned phase “Prospecting” from the 15th of April until the average laying date of that year for non-breeding individuals or until the laying date of the nest for breeding individuals. Breeding individuals that were assigned prospecting were tracked by default for more than one breeding season, as individuals were caught on the nest during incubation for tracker attachment. We assigned phase “Eggs” from the average laying date until the average hatching date of that year for non-breeding individuals or from the laying date of the nest until hatching date for breeding individuals. We assigned phase “Chicks” after the average hatching date of that year until the 30th of June for non-breeding individuals and after hatching date of the first egg until the 30th of June for breeding individuals.

To estimate energy expenditure during chick development, we assigned consecutive ascending numbers starting from the first day that a nest had a hatchling until the first chick reached 25 days of age or until all chicks died. In general, chicks of this colony fledge from 40 days of age and chick body mass at 25 days is approximately two thirds of the body mass at fledging with normal growth (Camphuysen 2013).

Time budget and estimated energy expenditure per breeding state and breeding phase

To investigate whether birds differ in their energy expenditure depending on the breeding state and phase or age of their chicks, we first calculated the time birds spent on different behaviours per day and then attributed an energetic cost to each behaviour (Fig. 6.1). For instance, flapping flight is energetically costly, while sitting or standing is energetically cheap (Tucker 1972). For our analysis, we used three proxies for energy expenditure which are all based on the behaviour measured using GPS and acceleration data. The proxies are hours spent on flapping flight per day, hours spent active per day and estimated energy expenditure per day.

To calculate the time spent on different behaviours per day, we first trained a random forest machine-learning algorithm for the classification of accelerometer data (for more details on the exact methods see van Donk et al. 2018). Subsequently, we used this algorithm to assign a behaviour to every GPS position that was accompanied with acceleration measurements. The

five main behaviours in this study are inactive (sitting or standing), floating, terrestrial activity (terrestrial locomotion, handling prey), soaring flight and flapping flight (Fig. 6.1). GPS positions within the colony were generally not accompanied with acceleration data and could therefore not be assigned to a behaviour. These GPS positions were therefore assigned as “Colony”, using a polygon with the borders of the breeding colony. Also outside the breeding colony, some tracking data was not accompanied with acceleration data. These tracking points were assigned as “Not annotated”. For each behavioural class, we calculated the hours spent per day by summing all data (centred duration) per behaviour per day for each individual.

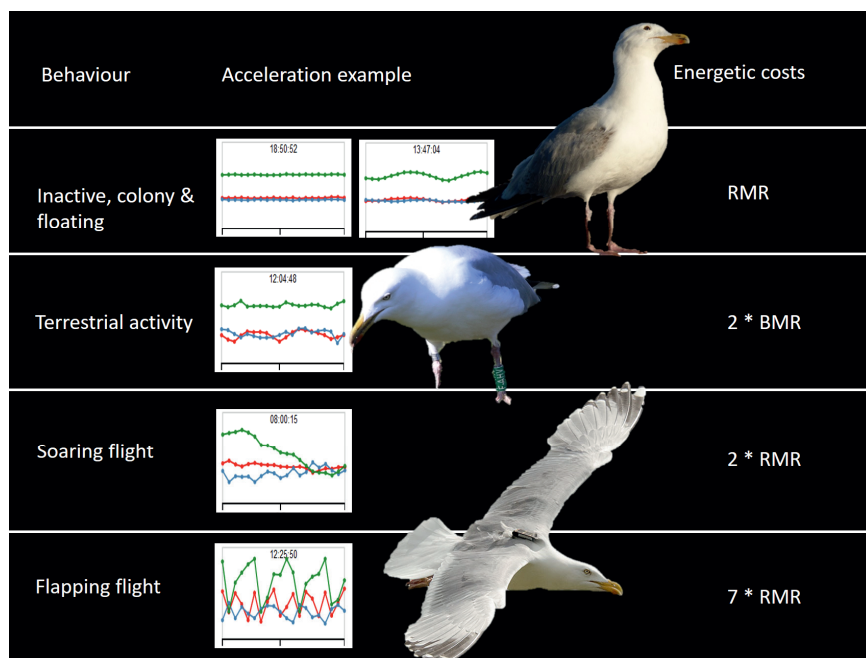


Fig. 6.1 Behavioural classes used in this study and examples of 1 second segment of 20Hz tri-axial data, green represents heave (z-axis), red represents surge (x-axis), blue represents sway (y-axis). The x and y axis of all Figs are on the same scale and range from -1.5 – 2.5 g. Estimation of the energetic costs per behavioural class is shown at the right, BMR = basal metabolic rate and RMR = resting metabolic rate calculated as $1.7 * \text{BMR}$. When estimating the energetic costs, we did some assumptions that are listed in Table S6.2.

To calculate the first proxy for energy expenditure, hours spent on flapping flight per day, we summed the time spent on flapping flight per day per individual. To calculate the second proxy for energy expenditure, which is hours spent active per day, we summed all the time an individual spent on terrestrial activity, soaring flight and flapping flight per day. To calculate the third proxy, which is estimated energy expenditure per day, we made an estimation of metabolic rates for the different behaviours per individual herring gull (Fig. 6.1, Table S6.1) (as in van Donk *et al.* 2018). We made some assumptions in our estimation of energy expenditure (summarized in Table S6.2); for example, we assumed that RMR was constant throughout the season and did not fluctuate in relation to environmental conditions. The average temperature in the time period used is between 10 and 16 degrees °C (<https://weerstatistieken.nl>, weather station 'De Kooy') and resting adult herring gulls have a relatively constant energy expenditure within these air temperatures (Baudinette *et al.* 1976, Lustick *et al.* 1978). We also assumed that RMR does not differ between breeding and non-breeding birds, nor between breeding phases. As we did not have acceleration data in the colony, we assumed that individuals are mostly inactive while in the colony and used RMR to estimate energetic costs for time spent in the colony. For each individual, we calculated the basal metabolic rate (BMR) with the formula $\text{BMR (kJ day}^{-1}\text{)} = 2.3 \times W^{0.774}$ where W is body mass (g) at catching (Bryant and Furness 1995). BMR does not account weather conditions, digestion or small body movements. To account for some of these factors, we calculated a resting metabolic rate (RMR) as $1.7 \times \text{BMR}$ (Baudinette and Schmidt-Nielsen 1974, Furness 1978). RMR was used to estimate the energetic cost of the behaviours inactive and floating. The energetic cost of terrestrial activity was based on the formula of Bautista *et al.* (2001); Costs terrestrial movement (kJ day^{-1}) = $(5.6 \times W_{\text{kg}}^{0.246} + 11.4 \times W_{\text{kg}}^{-0.285} \times v) \times 86.4$, where W_{kg} is body mass (kg) and v is velocity in m s^{-1} . We used 0.4 m s^{-1} as average walking speed which is the average walking speed measured in this study. This formula gave us an estimation of approximately $2 \times \text{BMR}$ for terrestrial activity. Based on aerodynamic theory (Rayner 1982, Pennycuick 1996) and wind tunnel experiments (Tucker 1972, Baudinette and Schmidt-Nielsen 1974), soaring flight is energetically cheaper per unit time than flapping flight. Based on findings from wind tunnel experiments on herring gulls, we estimated the energetic cost of soaring flight as $2 \times \text{RMR}$ (Baudinette and Schmidt-Nielsen 1974). We estimated the energetic cost of flapping flight as $7 \times \text{RMR}$ based on findings from wind tunnel experiments on laughing gulls *Larus actricilla* (Tucker 1972). Estimated energy expenditure per day was calculated per individual by multiplying the time spent on each behaviour with that behaviour's respective energetic estimate.

As mentioned, some acceleration data outside the colony was missing and could not be assigned to a behavioural class (on average 3% per day). As ignoring missing data would result in a lower estimated energy expenditure per day, we replaced these missing values with average

energy expenditure for that animal outside the colony. For the other two proxies for energy expenditure, we ignored these missing data.

Statistical analysis

We tested whether animals in different breeding states and phases differ in their time energy budget by fitting linear mixed-effect models using the `lmer` function from the `lme4` package in R (Bates et al. 2015). In the models we used one of three proxies for energy expenditure as response variables: hours spent on flapping flight per day, hours spent active per day and estimated energy expenditure per day. For each response variable, the full model included breeding state, breeding phase, sex and the interaction term of breeding state and breeding phase as fixed effects and bird ID as a random intercept to account for repeated measures within individuals. Herring gulls are sexually dimorphic (males are slightly larger than females) resulting in a higher BMR for males which probably results in a higher energy expenditure (Bryant and Furness 1995). Full models were compared with models containing all combinations of fixed effects using the `aictab` function from `AICcmodavg` package (Mazerolle 2017). The best model was compared with a null model that only contained the random factor using ANOVA. We reported p-values obtained by likelihood tests and the model estimates of the best model, as well as marginal and conditional R squared values for mixed models (Nakagawa and Schielzeth 2013). The marginal R squared values show how well the model explained the variance for the fixed factors alone, which is of importance for answering the main question in this paper. The conditional R squared takes the fixed factors and the random factors (individual) into account, which is of importance to assess the variation explained by individual differences. Full models, marginal R squared and AIC values of other models are reported in the supplementary material (Tables S6.3-S6.5).

We tested whether energetic costs increased with age of the chicks by fitting linear mixed-effect models with each of the three response variables described above and sex as fixed factor. We only used chicks until day 25 of age, as growth curves are generally linear in this period and therefore we expect that the energetic needs of the chicks also increase linearly (Camphuysen 2013, p. 280). Day after hatching of the chicks was included as an independent variable and bird ID in a given year as random intercept in the model. Full models were compared with models containing all combinations with the independent variable and fixed effect and the best model was selected by its AIC value. We compared the best model with a null model only containing the random effect using ANOVA. We reported p-values and the model estimates of the best model, as well as marginal and conditional R squared values for mixed models. Full models, marginal R squared and AIC values of other models are reported in the supplementary material (Tables S6.6-S6.8).

Results

Energetic costs of breeding state and phase

Time spent in the colony differed among breeding states; breeders spent on average 14 hours per day in the colony while non-breeders spent only 3-7 hours per day in the colony during the egg and chick phase (Fig. 6.2). For all breeding phases, non-breeders spent most of their time outside the colony inactive. Assuming birds are also inactive in the colony, the total time spent inactive (time spent in the colony and inactive outside the colony) was higher for non-breeders than breeders during chick care.

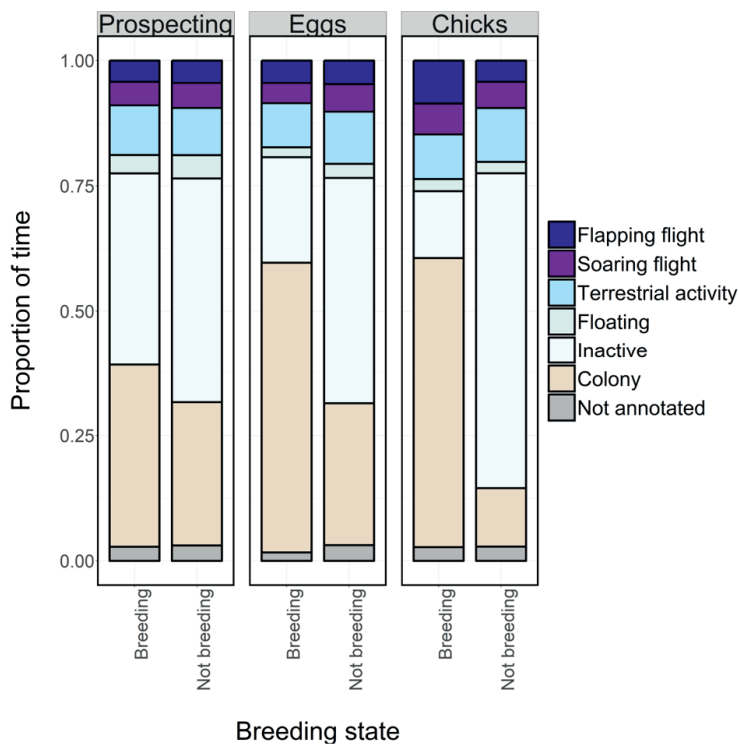


Fig. 6.2 Per breeding state and phase, the proportion of time spent on the five behavioural classes: flapping flight, soaring flight, terrestrial activity, floating and inactive as well as the time spent in the colony and the time not annotated.

Models revealed that all three proxies for energy expenditure, measured as hours spent on flapping flight per day, hours spent active per day and estimated energy expenditure per day, were statistically higher in breeding animals, but only during the chick phase (Figs 6.2 and 6.3, Tables 6.2, S6.3-S6.5). The model that predicted the most variance (38%), was the effect of breeding state, phase and sex on the estimated energy expenditure per day (Table 6.2). Both females and males spent about 300 kJ day⁻¹ more when they had to take care of chicks compared to not having chicks, which is an increase in estimated daily energy expenditure of 26% for females and 30% for males (Table 6.2). The models estimated that individuals would spend 2.13 hours per day more on flapping flight and 1.06 hrs per day more active, when caring for chicks compared to individuals in the same period that were not breeding. In these models, sex was not included. However, AIC values showed that a model explaining hours spent on flapping flight which also included sex, was comparable to the model without sex (Table S6.3, <2 AIC difference); during chick care, males spent more time in flight than females (on average 9 minutes more per day) (Fig. S6.2).

Although all models with the proxies of energy expenditure explained some variation in the data, the variation explained by the fixed factors was lower than the variation explained when individuals were also taken into account (Table 6.2).

Table 6.2 Predictions $\pm$ standard error and model performance of the mixed linear models testing the effect of breeding state and breeding phase on proxies of energy expenditure. Response variables are hours spent on flapping flight per day (Flapping: h day⁻¹), hours spent active per day (Active: h day⁻¹) and estimated energy expenditure per day (Energy: kJ day⁻¹). As the best model for estimated energy expenditure per day also included the variable sex, the estimated energy expenditure is shown for females and males separately (Energy F and Energy M respectively). Highest values per energy expenditure proxy are shown in bold. The marginal and conditional R² are provided for each model.

State	Phase	Flapping	Active	Energy F	Energy M
Breeding	Prospecting	0.92 $\pm$ 0.08	4.69 $\pm$ 0.19	976.10 $\pm$ 31.68	1135.90 $\pm$ 27.61
Not breeding	Prospecting	1.06 $\pm$ 0.09	4.58 $\pm$ 0.20	1000.47 $\pm$ 32.12	1160.27 $\pm$ 28.80
Breeding	Eggs	1.03 $\pm$ 0.07	4.27 $\pm$ 0.17	987.13 $\pm$ 30.47	1146.93 $\pm$ 26.49
Not breeding	Eggs	1.12 $\pm$ 0.08	4.96 $\pm$ 0.19	1015.37 $\pm$ 31.59	1175.17 $\pm$ 28.27
Breeding	Chicks	2.13$\pm$0.08	5.90$\pm$0.18	1265.44$\pm$31.08	1425.24$\pm$27.03
Not breeding	Chicks	1.00 $\pm$ 0.07	4.84 $\pm$ 0.20	968.83 $\pm$ 32.01	1128.63 $\pm$ 28.87
Model performance					
p-value		0.0001	0.0001	0.0001	
R ² marginal		0.28	0.10	0.38	
R ² conditional		0.46	0.32	0.59	

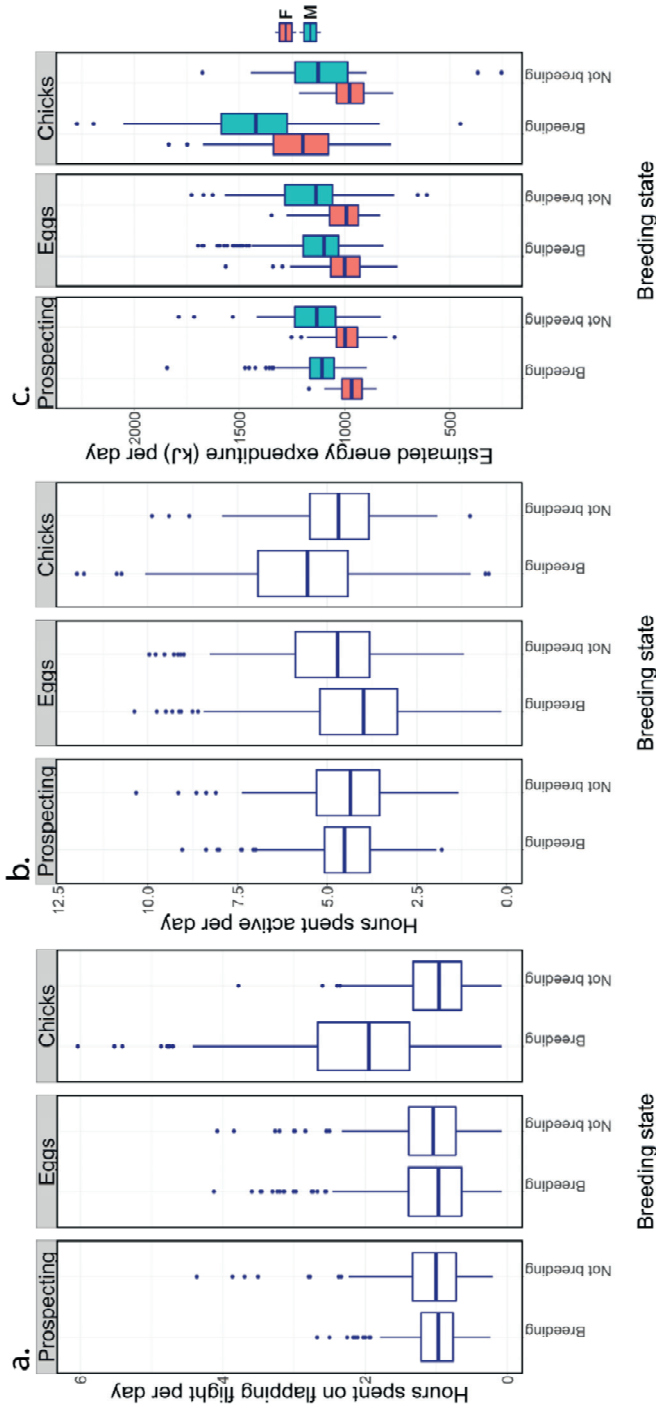


Fig. 6.3 Proxies for energy expenditure per breeding state and phase. Boxplots show median values per breeding state and phase. We used 1904 days of 31 individuals in our analysis. (a.) hours spent on flapping flight per day (h day^{-1}), (b.) hours spent active per day (h day^{-1}), terrestrial activity and flying) and (c.) estimated energy expenditure per day (kJ day^{-1}), per sex.

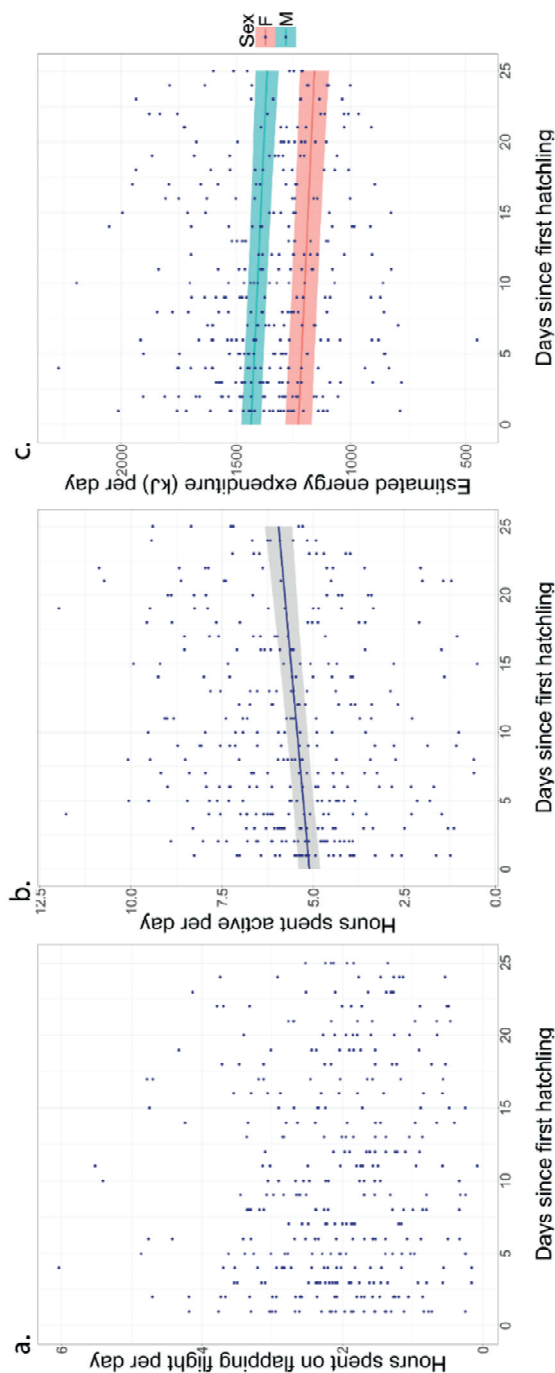


Fig. 6.4 Relationship between age of chicks in days since hatching and (a.) hours spent on flapping flight per day (h day^{-1}), (b.) hours spent active per day (h day^{-1} ; terrestrial activity and flying) and (c.) estimated energy expenditure per day (kJ day^{-1}). Every point represents one day ($n=343$) of 21 different individuals. When a significant relationship was found, the estimates of the fixed effects in the linear mixed models (line) and standard error (shaded area) of the model are shown.

Energetic costs of age of chicks

During chick care, proxies for energy expenditure varied greatly among days (Fig. 6.4). However, days since the first hatchling barely affected proxies for energy expenditure (Tables 6.3, S6.6-S6.8). Hours spent on flapping flight per day did not statistically differ over hatchling days (Fig. 6.4a). Hours spent active per day increased with hatchling day but the variance explained by this proxy is marginal (Fig. 6.4b, Table 6.3). Also estimated energy expenditure per day was barely affected by hatchling day (Fig. 6.4c, Table 6.3). Estimated energy expenditure even decreased slightly with hatchling day (2.8 kJ per hatchling day). The best model for estimated energy expenditure per day also included sex; males had a significant higher estimated energy expenditure than females (Fig. 6.4c).

Table 6.3 Model results of the relationship between age after hatching and the response variables hours spent on flapping flight per day (h day^{-1}), hours spent active per day (h day^{-1}) and estimated energy expenditure per day (kJ day^{-1}). As the best model for estimated energy expenditure per day also included the variable sex, estimates are also shown for this fixed factor. Model estimates $\pm$ standard error (SE) are shown. The marginal and conditional R^2 are provided for each model.

Model estimates and model results	Response variables		
	<i>Flapping</i>	<i>Active</i>	<i>Energy</i>
Intercept	2.09 $\pm$ 0.15	5.10 $\pm$ 0.30	1228.41 $\pm$ 57.89
Sex (M)			206.09 $\pm$ 69.30
Days (since 1 st hatchling)	-0.01 $\pm$ 0.01	0.03 $\pm$ 0.01	-2.80 $\pm$ 1.69
p-value	0.10	0.02	0.01
R^2 marginal	0.01	0.01	0.14
R^2 conditional	0.36	0.41	0.47

Discussion

In line with our expectations, we found that breeding individuals spent more hours in flight per day, more hours active per day and had a higher estimated energy expenditure per day than non-breeders, but only in the period of chick care. This is not influenced by environmental conditions related to the time of the year as non-breeding birds within the same period spent significantly less energy than birds caring for chicks. The increased energy expenditure is predominantly due to an increase in time spent in flight per day during chick care. However, estimated energy expenditure did not differ between breeders and non-breeders during either the prospecting phase or egg laying. Contrary to our expectations, proxies for energy expenditure attributed to movement of active breeders did not increase with increasing chick age, but it fluctuated considerably from day to day and differed among tracked individuals.

Energy expenditure estimates

While the main question of this studies was to compare proxies of energy expenditure among individuals in different breeding states and phases, it is interesting to explore whether our derived energy estimates are biologically meaningful. Depending on the breeding state, we estimated a daily energy expenditure of ~1000-1350 kJ per day. Studies of energy expenditure in other gull species show quite some variability, but most of them are in the range of our findings. A study on lesser black-backed gulls in captivity, a slightly smaller species than herring gulls, measured an energy intake of 900-1400 kJ per day (Hilton et al. 2000), which leads to a potential daily energy expenditure of 675-1050 kJ per day when taking a digestive assimilation efficiency of 75% (Castro et al. 1989). Note however, in contrast to our study, these gulls were not able to show expensive behaviour like flying. Energy expenditure was also estimated in ring-billed gulls *Larus delawarensis*, a species that is also smaller than herring gulls, by measuring oxygen consumption with doubly labelled water (Marteinson et al. 2015). With a nest attendance of ~50%, these gulls spent 0.9 kJ per day per gram body weight, assuming the same relationship with body mass leads to a relatively low daily energy expenditure for a herring gull male of about 900 kJ per day. Black-legged kittiwakes *Rissa tridactyla*, a species which is half the size of a herring gull, spent 794 kJ per day when spending 50 % of the day foraging (Gabrielsen et al. 1987). A recent study that modelled the expected energy use of several seabird species in different breeding phases, shows daily energy expenditure most close to our estimates; depending on the breeding phase a herring gull of 1000 grams would spend between ~1000 and 1200 kJ per day (Dunn et al. 2018). We assumed that RMR stayed constant over the breeding season. However, some studies have shown variation of RMR over the course of the breeding season (Welcker et al. 2015). For instance, RMR of incubating birds might be higher to enable heating of the eggs compared to birds that take care of chicks (Shoji et al. 2015). In addition, RMR could be higher in the colony compared to other

places due to the threat of possible territorial conflicts (Kanwisher et al. 1978). A study on Australasian gannets *Morus serrator* showed that RMR increased progressively from incubation to chick care but the proportion of time spent foraging did not change (Green et al. 2013). The authors suggest that gannets meet their own and their chicks' energetic demands without increasing foraging effort via a decrease in body weight. However, food availability could also have been higher during the period of chick care, but diet and energetic costs of non-breeders in the same period were not measured in this study. Concluding, as birds in the current study spent a large part of their time inactive, energy estimates would benefit from an improved understanding of RMR.

Estimates of energy expenditure may also be influenced by variation in individual traits. Individuals clearly differ in their energy expenditure; the variation in the data explained is more than double when taking individual into account in almost all models (Tables 6.2 and 6.3). The variation that is explained by individual, may be due to a combination of factors, like for instance the foraging strategy of an individual or their age. For instance, individuals from the same study system foraging for anthropogenic resources spend more energy on movement than individuals foraging on other resources (van Donk et al. 2019). Furthermore, reproductive behaviour has been shown to change with age in several species (Clutton-Brock 1984, Velando et al. 2006, Sparkman et al. 2007), and thus could potentially influence energy expenditure as well. In the current study, all birds were sexually mature and at least four years old but their exact age was unknown. Nevertheless, the pattern of energy expenditure over a complete reproductive cycle seems to be very similar among individuals in the same breeding state (Fig. S6.3), suggesting that the relative increase in reproductive investment did not differ much among individuals.

4.2 Higher energy expenditure during chick care

In species with a long life expectancy, such as herring gulls, a small reduction in the likelihood of survival could greatly affect future lifetime reproductive success. During chick care, herring gulls in our study spent about 300 kJ day⁻¹ more compared to non-breeding birds during this same period (Table 6.2), which is an increase of approximately 26-30%, depending on the sex, compared to non-breeding individuals in the same period. The increase in energy expenditure was also found in breeding individuals between phases (from prospecting/incubation to chick care). These values are in the same order of magnitude as other studies in seabirds comparing the energetic costs of incubation with that during chick care (Bevan et al. 1995, Dunn et al. 2018). To compare this energetic cost with the amount of common prey of herring gulls from this population, 300 kJ is comparable to eating about 4-5 plaice *Pleuronectes platessa* of 12-13 cm total length (Kühn et al. 2017) or 160 blue mussels *Mytilus edulis* of about 20 mm per day (Petersen 1981, van der Veer et al. 2006)(Table S6.9), when considering an assimilation efficiency of 75% (Castro et al. 1989). These additional amounts of food have to be consumed

by individuals with chicks, *only* to compensate for the higher daily energetic costs attributed to movement.

Consequences of increased energy expenditure

The increase in energy expenditure and movements necessary for reproduction may have negative effects on future reproductive success. For example, in adders *Vipera berus*, females have higher chance to be predated after they reproduced as they have to forage actively to regain their lost energy reserves (Madsen and Shine 1993). European Kestrels *Falco tinnunculus* with increased daily workload by experimentally enlarged brood size experienced significantly increased winter mortality (Daan et al. 1996). In kittiwakes *Rissa tridactyla*, females but not males with experimentally enlarged broods had lower body weight and lower survival during the next breeding season (Jacobsen et al. 1995).

Contrary to our expectations, breeders and non-breeders did not differ in energy expenditure attributed to movement in the prospecting and egg phase (Table 6.1). Our results suggest that the bottle-neck in terms of energetic costs for these animals is the period of chick care and that abandoning a reproductive attempt before this period, for instance when physical state or environmental conditions worsened, can prevent negative consequences in future. This is reported in the blue petrel *Halobaena caerulea*, where a reduction of body condition early in the season resulted in a higher proportion of animals deserting their eggs (Chastel et al. 1995). Similar results were found for megallanic penguins *Spheniscus magellanicus*, and showed that individuals with lower body condition deserted their eggs more often (Yorio and Boersma 1994). Depending on the reproductive system, other species might have similar or other reproductive bottle-necks. For instance, the prospecting phase might be more energetically costly in male elephant seals *Mirounga angustirostris* which have intensive male-male combats at the start of the reproductive season (Sharick et al. 2015).

Consequences of prey availability on reproductive success

Animals have been shown to skip reproduction when environmental conditions deteriorate or when their own physical condition is suboptimal (Wingfield 1984, Aebischer and Wanless 1992, Erikstad et al. 1998, Pilastro et al. 2003, Cubaynes et al. 2011, Skjaeraasen et al. 2012, Cayuela et al. 2014). In long-lived species, skipping reproduction is common, but proximal causes that make animals decide whether or not to breed are poorly known (Giudici et al. 2010). Animals could save energy by skipping reproduction in years with low expected reproductive success thereby enhancing their own survival. In the current study, we did not relate environmental conditions with the proportion of animals that skipped a reproductive attempt. However, breeding conditions are not very favourable within the studied colony for the last decade. Fledging weight is low compared to a colony in the same area 40 years ago (Spaans 1971, van Donk et al. 2017) and fledging rate is relatively low (<0.8 chicks nest⁻¹). The low

reproductive success is likely related to the current carrying capacity of the surroundings. Availability of resources which are important prey for gulls to raise chicks (van Donk et al. 2017) have declined over the last decades including: the availability of high caloric prey from human refuse dumps due to changes in waste management (Kohler and Perry 2005, European Environment Agency (EEA) 2016) and discarded fish from the declining commercial fishing fleet (Poos 2010, Rijnsdorp et al. 2011, Camphuysen 2013, Borges 2015).

Energetic ceiling

Despite the low reproductive success observed in this colony, birds with chicks barely increased their energy expenditure when energetic demands of chicks increase (Fig. 6.4). This suggests that gulls with chicks have a ceiling of a relatively fixed maximum workload which they do not exceed- An energetic ceiling has proposed as a mechanism to prevent harming lifetime reproductive success (Drent and Daan 1980). That animals have a ceiling in maximum workload has been shown in thick-billed murre *Uria lomvia* in which handicapped birds had similar daily energy expenditure as non-handicapped birds through behavioural adjustments (Elliott et al. 2014). Also a study on Adélie penguins *Pygoscelis adeliae* showed a possible ceiling effect. Animals from larger breeding colonies, made longer foraging trips and spent more energy while foraging, but animals from the largest colonies seem to approach an energetic ceiling, with possibly negative consequences on chick survival (Ballance et al. 2009). Thus gulls might also maintain a maximum workload to avoid a negative impact on physical state and future reproductive success.

Conclusions

In this study, we used bio-logging to investigate the extra energetic costs that can be attributed to breeding and thus the energetic gain of not breeding in wild birds. By combining behavioural measurements from bio-logging data, estimating energy expenditure per behaviour and monitoring breeding status in the field over multiple years, we were able to quantify that gulls which are taking care of chicks invest more energy attributed to movement compared to gulls that do not take care of chicks in the same period. Despite the low reproductive success of the studied breeding colony, gulls do not increase their investment when the energetic need of chicks increases. This suggests that gulls have a ceiling of maximum energetic expenditure. In the future, we should study whether survival is impaired when gulls invest a lot in parental care. In order to identify energetic thresholds for investment in breeding and understanding the driving factors of reproductive investment in relation to environmental factors, individuals should be studied over longer timespans to capture inter-annual environmental variability. Furthermore, comparative analyses of different breeding populations of the same species with a range of resource availability should be compared. Long term bio-logging and concomitant

demographic analysis can facilitate comparative analysis within individuals and among populations and species.

Acknowledgements

These studies are part of a long-term demographical and ecological study on two species of gulls by the Royal Netherlands Institute for Sea Research (NIOZ) at Texel. We thank Staatsbosbeheer Texel for permission to work in Kelderhuispolder, a nature reserve closed for the general public. Particularly, we thank Aris Ellen, Glenn van Ginkel, Marcel Groenendaal, and Erik van der Spek for help and cooperation. We thank Edwin Baaij for his technical support of UvA-BiTS and Willem Bouten for his advice on the analysis of acceleration data. We are thankful for the help of volunteers and students assisting in the fieldwork over the years. The UvA-BiTS infrastructure was facilitated by Infrastructures for E-Science, developed with the support of the Netherlands eScience Centre (NLeSC) and LifeWatch, and conducted on the Dutch National E-Infrastructure with support from the SURF Foundation.

Author Contributions

SvD carried out the statistical analysis, and drafted the manuscript with support from JSB, JvdM and CJC; CJC leads long-term study on herring gulls; CJC and SvD conducted field work, JSB assisted with GPS tracking. SvD, JSB and JvdM discussed the analytical approach; All authors discussed results and contributed to the final manuscript.

Supplementary material

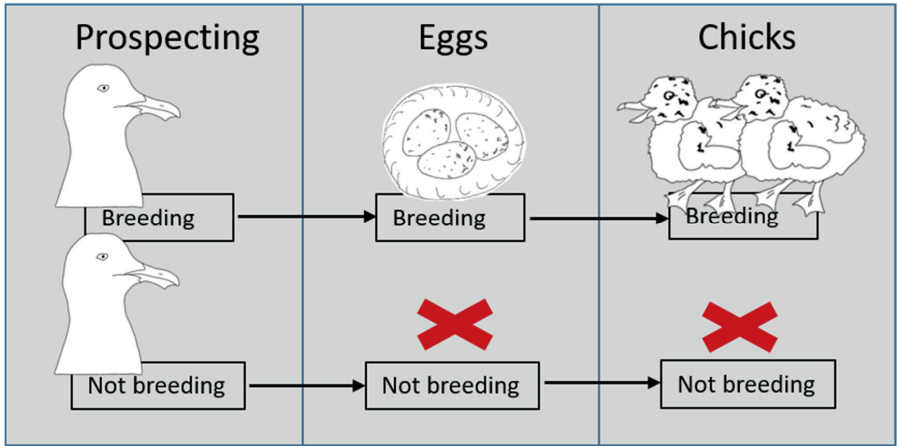


Fig. S6.1 Schematic explanation of the different breeding states (breeding, not breeding and breeding phases (prospecting, eggs, chicks) used in this study. Animals which had no nest with eggs where assigned to state “Not breeding” in all breeding phases, while animals that did have a nest with eggs where assigned to state “Breeding” in the prospecting and egg phase. The state “Breeding” in the chick phase was only assigned to animals which were taking care of offspring. When animals failed, for instance due to predation or mortality of eggs or losing their eggs or chicks, the days after losing the brood were removed from the analysis and not added to the “Not breeding” group.

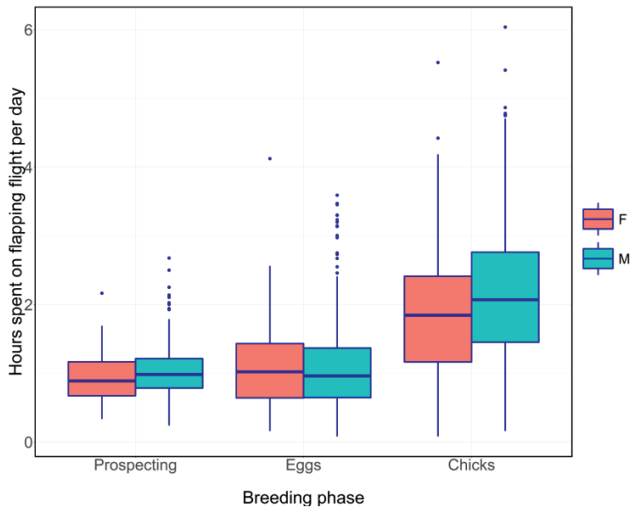


Fig. S6.2 Boxplots showing median values of time spent on flapping flight (h day⁻¹) of active breeding individuals during different breeding phases. Results are shown separately for females and males. Males spent more time on flapping flight which is only apparent in the breeding phase “Chicks”.

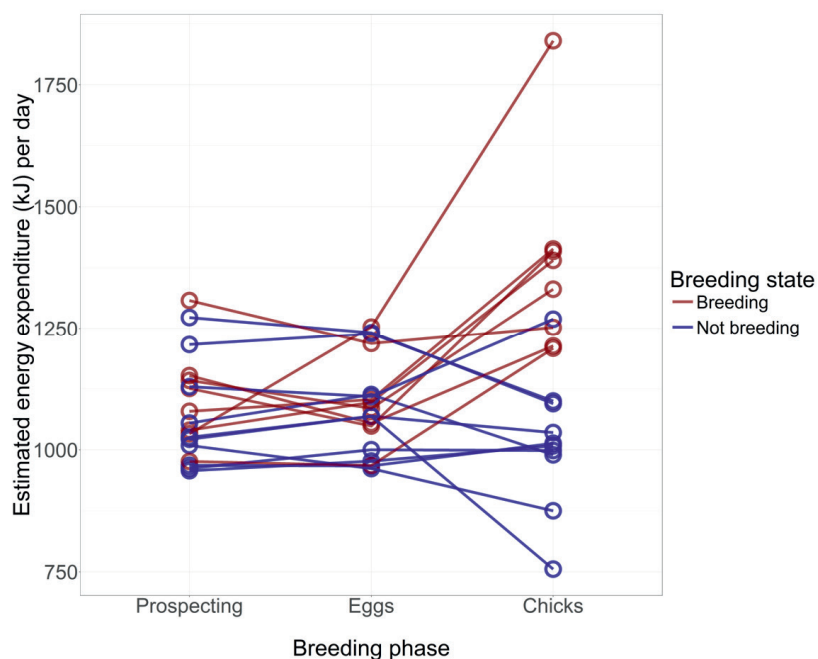


Fig. S6.3 Average energy expenditure (kJ day^{-1}) of individual birds for which data over the full reproductive cycle (Prospecting, Eggs, Chicks) was available ($n=18$ individuals in a given year). For every individual, the average daily energy expenditure is shown with a circle for every breeding phase separately and data points of one individual are connected with a line. Red circles and lines represent breeding individuals and blue lines and circles represent non-breeding individuals.

Table S6.1 Overview of the individual birds used in this study with the year of GPS deployment, sex, mass (g), BMR (kJ day⁻¹) years of tracking data used and total tracking days per bird ID.

Bird ID	Start tracking	Sex	Mass	BMR	Number of years	Tracking days
1600	2013	F	850	426	3	146
6004	2013	M	1090	516	1	37
6006	2013	M	960	468	4	170
6009	2013	F	935	458	1	37
6100	2014	F	855	428	1	0
6011	2013	F	895	443	2	128
6012	2013	F	820	414	1	14
6014	2013	M	980	475	1	22
6015	2013	M	965	470	3	166
6016	2013	M	1070	509	3	129
6017	2013	M	1075	511	2	113
6071	2014	M	1030	494	1	42
6072	2014	F	855	428	2	60
6073	2014	F	865	431	3	182
6074	2014	M	885	439	1	19
6075	2014	M	945	462	1	18
6076	2014	F	915	451	1	22
6077	2014	M	1085	514	1	55
6079	2014	F	910	449	1	10
6080	2014	M	1090	516	2	52
6082	2014	F	860	430	1	2
6202	2015	M	1065	507	1	36
6205	2015	F	965	470	1	22
6206	2015	F	835	420	2	91
6208	2015	M	990	479	1	35
6210	2015	M	1015	488	2	80
6212	2015	M	990	479	2	59
6214	2015	M	995	481	2	67
6216	2015	F	985	477	1	16
6217	2015	F	875	435	1	73
6219	2015	M	1035	496	1	1

Table S6.2 List of assumptions in calculating the estimated energy expenditure per day. In the discussion, the potential impact of these assumptions are discussed.

Assumptions
Estimated energy expenditure is representative for actual energy used
Weather conditions do not affect energy expenditure
Flight costs are constant
Flight costs in a wind tunnel are comparable with flight costs in the wild
RMR did not differ among breeding states or breeding phases
Body mass changes do not change metabolic rate
Animals are mostly inactive in the colony

Table S6.3 Model results and comparisons testing the relationship between different combinations of predictors and hours spent on flapping flight per day. The dependent variable in this model: hours spent on flapping flight per day (h day^{-1}) with random intercept for bird ID. The independent variables (fixed effects) included in each model are indicated with an X. The table is organized on descending AIC value. The best model is shown in bold (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red. R^2 shows the marginal R squared value, which shows how well the model explains the variance for the fixed factors in the model.

Model	Random intercept	Fixed effect				AIC	R^2
		Phase	State	Phase*State	Sex		
Model 1	birdID	X	X	X		3624.42	0.28
Model 2	birdID	X	X	X	X	3625.30	0.28
Model 3	birdID	X	X			3928.14	0.15
Model 4	birdID	X			X	3949.80	0.13
Model 6	birdID	X				3950.27	0.12
Model 7	birdID		X			4185.94	0.02
Model 5	birdID		X		X	4186.67	0.04
Model 8	birdID				X	4204.13	0.01

Table S6.4 Model results and comparisons testing the relationship between different combinations of predictors and hours spent active per day. The dependent variable in this model: hours spent active per day (h day^{-1}) with random intercept for bird ID. The independent variables (fixed effects) included in each model are indicated with an X. The table is organized on descending AIC value. The best model is shown in bold (lowest AIC). R^2 shows the marginal R squared value, which shows how well the model explains the variance for the fixed factors in the model.

Model	Random intercept	Fixed effect				AIC	R^2
		Phase	State	Phase*State	Sex		
Model 1	birdID	X	X	X		6946.41	0.10
Model 2	birdID	X	X	X	X	6948.43	0.10
Model 6	birdID	X				7042.56	0.05
Model 3	birdID	X	X			7044.55	0.05
Model 4	birdID	X			X	7044.55	0.05
Model 8	birdID				X	7156.81	0.00
Model 7	birdID		X			7156.81	0.00
Model 5	birdID		X		X	7158.81	0.00

Table S6.5 Model results and comparisons testing the relationship between different combinations of predictors and estimated energy expenditure per day. The dependent variable in this model: estimated energy expenditure per day (kJ day^{-1}) with random intercept for bird ID. The independent variables (fixed effects) included in each model are indicated with an X. The table is organized on descending AIC value. The best model is shown in bold (lowest AIC). R^2 shows the marginal R squared value, which shows how well the model explains the variance for the fixed factors in the model.

Model	Random intercept	Fixed effect				AIC	R^2
		Phase	State	Phase*State	Sex		
Model 2	birdID	X	X	X	X	24373.11	0.38
Model 1	birdID	X	X	X		24383.92	0.24
Model 3	birdID	X	X			24766.54	0.11
Model 4	birdID	X			X	24781.56	0.23
Model 6	birdID	X				24793.28	0.09
Model 5	birdID		X		X	25012.41	0.18
Model 7	birdID		X			25021.46	0.02
Model 8	birdID				X	25033.15	0.15

Table S6.6 Model results and comparisons testing the relationship between time since first hatchling and hours spent on flapping flight per day. The dependent variable in this model: hours spent on flapping flight per day (h day⁻¹) with random intercept for bird ID. The independent variables (fixed effects) included in each model are indicated with an X. The table is organized on descending AIC value. The best model is shown in bold (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red. R² shows the marginal R squared value, which shows how well the model explains the variance for the fixed factors in the model.

Model	Random intercept	Fixed effect			AIC	R ²
		Days since hatching	Sex			
Model 1	birdID	X			930.57	0.01
Model 2	birdID	X	X		932.12	0.01
Model 3	birdID		X		932.68	0.01

Table S6.7 Model results and comparisons testing the relationship between time since first hatchling and time since first hatchling and hours spent active per day. The dependent variable in this model: hours spent active per day (h day⁻¹) with random intercept for bird ID. The independent variables (fixed effects) included in each model are indicated with an X. The table is organized on descending AIC value. The best model (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red. R² shows the marginal R squared value, which shows how well the model explains the variance for the fixed factors in the model.

Model	Random intercept	Fixed effect			AIC	R ²
		Days since hatching	Sex			
Model 1	birdID	X			1358.86	0.01
Model 2	birdID	X	X		1360.87	0.01
Model 3	birdID		X		1364.69	0.00

Table S6.8 Model results and comparisons testing the relationship between time since first hatchling and time since first hatchling and estimated energy expenditure. The dependent variable in this model: estimated energy expenditure per day (kJ day⁻¹) with random intercept for bird ID. The independent variables (fixed effects) included in each model are indicated with an X. The table is organized on descending AIC value. The best model is shown in bold (lowest AIC) and the models in which the AIC difference with the best model is < 2 are shown in red. R² shows the marginal R squared value, which shows how well the model explains the variance for the fixed factors in the model.

Model	Random intercept	Fixed effect		AIC	R ²
		Days since hatching	Sex		
Model 2	birdID	X	X	4661.70	0.14
Model 1	birdID		X	4662.37	0.14
Model 3	birdID	X		4667.12	0.01

Table S6.9 Two common prey types for the herring gull on Texel, plaice *Pleuronectes platessa* and blue mussel *Mytilus edulis* with the average size eaten by gulls of this colony, the fresh weight of the meat (ignoring the shell of the mussel) and the energetic value in kJ per individual prey. We calculated fresh weight of plaice by using a formula of Kühn, Velilla & Camphuysen (2017); Fresh weight = (0.22*Length Plaice)^{3.02} and multiplied this with the energetic value of a plaice (Kühn, Velilla & Camphuysen 2017). For the blue mussel, we first calculated the ash free dry weight (AFDW) of mussel meat for a mussel with a shell length (SL) of 20mm, using a calibration line based on freshly taken samples in the field (AFDW = -0.0128*SL+ 0.0005*SL² + 0.0839). We calculated the fresh weight by multiplying the ASFW with 8.333 (van der Veer, Cardoso & van der Meer 2006) and the energetic value per individual mussel using energetic values taken from Petersen (1981).

Prey type	Average size (mm)	Fresh weight (g)	Energetic value (kJ)
Plaice	12.5	21.22	84.88
Blue mussel	20.0	0.39	2.15



Chapter 7

Predicting post-natal energy intake of lesser black-backed gull chicks by Dynamic Energy Budget Modeling

Jaap van der Meer, Susanne van Donk, Alejandro Sotillo, Luc Lens

Abstract

The standard Dynamic Energy Budget (DEB) model is widely used to describe the physiology of individual animals. Here we parametrized the DEB model for the lesser black-backed gull *Larus fuscus* mainly on the basis of literature data. Next we performed an inverse modelling approach to predict the food intake rate of gull chicks (model input) on the basis of their growth trajectory from hatching to fledging (model output). Food intake rate and growth were also measured for this period in an aviary experiment, where three different diet treatments resulted in a large range in overall intake rate. These measured food intake rate data were not used in the parameter estimation procedure, but rather to validate model results. Model predictions of food intake rate were systematically only about 10% below the observations, but predictions and observation correlated strongly. The DEB model might be used to predict food provisioning rates in the field, which are difficult to obtain, on the basis of growth data, which are much easier to get.

Introduction

In vertebrate species with parental food-provisioning, post-natal growth of the young strongly depends upon the amount of food that the parents are able to deliver. If food availability or parental effort is insufficient, the new-borns may show reduced growth rates and even starve to death, with negative effects on the population renewal rate. For a deeper understanding of the dynamics of such populations in relation to the abundance of their prey, one therefore needs to know both the link between food availability and provisioning rate, and the link between food intake rate and growth rate of the young. Measuring the provisioning or intake rate in the field is, however, a laborious and costly exercise.

Here we examine whether the Dynamic Energy Budget (DEB) model is capable of predicting the food intake rate of the young on the basis of their growth trajectory. One might call this an inverse modelling exercise, as the model input (food intake rate) is predicted from the model output (growth rate). The dynamic energy budget (DEB) theory, developed by Kooijman (2010), is the most comprehensive theory that links the food environment to the major physiological processes of individual organisms, such as feeding, growth, and reproduction. The inclusion of reserves acting as metabolic memory, the full-life cycle of individuals (embryo, juvenile, adult) and the explicit use of conservation laws (energy, chemical elements and isotopes) sets the DEB theory apart from other approaches.

The standard DEB model can already be parametrized for a particular species on the basis of a very restricted data set. A set of data that contains only eight so-called zero-variate data and one so-called univariate data set already suffices for estimating the 8 most important DEB parameters. A feasible zero-variate data set might include, for example, age at birth, age at first reproduction, lifespan, weight at birth, weight at first reproduction, maximum weight, maximum length, and maximum reproduction rate. Weight at age data is an example of a useful univariate data set. Over the last few years a wealth of published (see, for example, van der Meer et al. (2014) and references therein) and unpublished (compiled at <https://www.bio.vu.nl/thb/deb>) parameter estimations of the DEB model were done for a rapidly growing number of species. This collection of species, which comes under the name of the add my pet collection has presently about 2500 entries, including over 400 different bird species.

DEB theory provides an integrated look at whole-organism energetics and it is therefore possible to predict specific process rates without ever having measured these rates. This sets this mechanistic and theory-based modelling approach apart from a statistical approach, e.g. by fitting allometric relationships, which is still prevalent in most ecological research. One previous example of the strength of the DEB approach is the case of the Atlantic hagfish *Myxine glutinosa*, a species that has no otoliths, which makes aging them impossible. It furthermore tends to behave abnormally in captivity, as it, for example, refuses to eat, and growth and

reproduction rates cannot be obtained in the laboratory either. Data on oxygen consumption versus weight were, however, available, and this allowed the estimation of growth rates and age at maturity by using DEB modelling (van der Meer and Kooijman 2014). A major though inevitable shortcoming of the exercise was that the predictions could not be tested, as true data on hagfish growth rates were not available. Other examples of DEB predictions are food intake reconstructions on the basis of growth trajectories for emperor penguins *Aptenodytes forsteri* (Kooijman 1993) and for various bivalve and fish species (Kooijman 1993, Cardoso et al. 2006, Freitas et al. 2009, Troost et al. 2010, Pecquerie et al. 2012, Jusup et al. 2014, Lavaud et al. 2019). Most of these studies suffered from the same shortcoming that food intake predictions could not be tested, with the exception of Jusup et al. (2014) who were able to correlate predicted and measured annual food intake for captive Bluefin tuna.

Here we present a food intake reconstruction study in which DEB predictions are tested. For this, we use data of an aviary experiment where food intake rate of lesser black-backed gull *Larus fuscus* chicks was manipulated and precisely measured for almost the entire growth period of the chicks. Additionally, the growth response was measured. We first estimate the parameters of the standard DEB model for the lesser black-backed gull using a limited data set mainly gathered from the open literature. Next we apply an inverse modelling approach to predict the food intake rate over the entire growth period for all experimental chicks on the basis of their observed growth patterns (mass versus age). Hence we do not use any feeding data in fitting the DEB model parameters. Finally, we compare model predictions to true measurements of food intake.

As measuring growth of bird chicks in the field is much easier than measuring food intake rate during the entire growth period, the inverse modelling approach, as applied here, is of practical use for field ornithologists to predict the required overall food intake for obtaining a specific fledging weight.

Methods

DEB modelling

Below we will give a very short introduction to the standard DEB model for the individual organism. A more extensive introduction is given in the Supplementary material, but we refer the reader also to Kooijman (2010) for a detailed description of underlying DEB assumptions and derivations, or to van der Meer (2006, 2016, 2018), who provides easier accessible introductions.

The model organism has three succeeding life stages, the embryo, which neither feeds nor reproduces, the juvenile, which feeds but does not reproduce, and the adult, which feeds and reproduces. The organism is described by three state variables: (1) structural body volume, (2)

reserve density, which is the amount of reserves per unit of structural body volume, and (3) maturity, which is the cumulative energy allocated to development. Embryos and juveniles develop, i.e. build up maturity. Transitions between embryo and juvenile and between juvenile and adult occur at fixed levels of maturity. Once the animal has become adult, it has reached its maximum maturity and starts to reproduce. The present application focuses on changes in the structural body volume and reserve density of the juvenile stage.

The standard DEB model can be entirely re-written in a dimensionless form, meaning that all state variables and time are scaled by some quantity that has the same physical dimension as the original variable. For example, structural body length (the cubic root of structural body volume) is scaled by maximum body length. Such scaling has the advantage that the equations look much simpler, and the dynamical behaviour of the system of coupled differential equations can be more easily studied without any loss of generality.

The dynamics of the scaled reserve density e in scaled time τ are given by

$$\frac{de}{d\tau} = \frac{f-e}{l} \quad (1)$$

where f is the so-called scaled functional response that relates the assimilation rate to the food density, and takes a value between zero (no food) and one (ad libitum). Note that food density is the only environmental variable. The variable l stands for scaled length. Growth is given by the differential equation for scaled length

$$\frac{dl}{d\tau} = \frac{1}{e+g} \frac{e-l}{3} \quad (2)$$

where the compound parameter g is called the ‘energy investment ratio’. It stands for the energetic costs of new structural volume relative to the maximum energy within the reserves that is available for growth and maintenance.

Parameter estimation

The DEB parameter estimation procedure starts with 8 so-called zero-variate data points and 6 pseudo-data points (Table 7.1). These pseudo-data are in fact standard values for a selection of DEB parameters and these values are taken from Kooijman (2010), Table 8.1. The pseudo-data are used in the fitting procedure to avoid non-convergence problems. The procedure further uses one so-called univariate data set, i.e. body weight obtained at various ages. Zero-variate data on length and mass at birth and at first reproduction, on maximum reproductive rate and on maximum length and mass are all taken from published or unpublished work by Camphuysen (see Table 7.2 for references). The assumed maximum age of 34 years and 10 months is based on the EURING list of longevity records for European birds (Fransson et al. 2017). Maximum age only affects the estimate for the Weibull aging acceleration parameter $\hat{h}_a$, whose value is irrelevant for the present exercise. Hence the precise maximum age value

does not matter here. The univariate data on wet weight versus age are the only data that were taken from the aviary experiment (see below). For each day the maximum observed wet weight was taken.

The standard DEB model provides predictions for all data. We do not repeat the relevant equations that have been used to provide these predictions, but refer the reader to Kooijman (2010). Detailed references to the equations are given in Table 7.1. For completeness, several conversion coefficients should be mentioned here: wet mass-volume 1 g per cm^3 , dry mass-volume 0.28 g per cm^3 , energy per C-mole in the reserves 550 kJ per C-mole (Kooijman, 2010), and dry mass 23.9 g per C-mole (Kooijman, 2010). Combined these coefficients reveal an energy content within the reserves of 3.9 kJ per gram wet mass.

DEB model parameters are estimated according to a procedure described by Lika et al. (2011). Not all parameters were estimable, and we have chosen to set the estimates for a few parameters at predefined values (Table 7.3), taken from Table 8.1 from Kooijman (2010). The goodness-of-fit function that is minimized in the procedure by Lika et al. (2011) is a weighted sum of squares. Apart from the symmetric mean squared error (SMSE), the mean relative error (MRE) is also reported, see Lika et al. (2011) for details. We have chosen to put more emphasis on the univariate data and on data on maximum weight and maximum feeding rate. The DEB model routines and the parameter estimation routine are part of the software packages DEBtool and Add-my-pet and can be downloaded from the Theoretical Biology website of the VU University Amsterdam <https://www.bio.vu.nl/thb/deb>

Table 7.1 Data used to fit the standard Dynamic Energy Budget model. Data in the upper part of the table are true zero-variate data, the middle part gives pseudo-data. These pseudo-data are a-priori estimates of the parameters and might be needed to avoid overfitting. The lower part gives true univariate data. The last column gives the model equations that link the data to the model parameters; L_∞ is the ultimate structural body length, δ_M the shape coefficient. Section (Sn) and equation (Eq) numbers refer to Kooijman (2010).

Variable	Explanation	Model
a_b	Age at birth	Sn 6.1.1
t_X	Time since birth at fledging	
t_R	Time since birth at first brood	
a_m	Life span	Sn 6.1.1
$L_{\omega,\infty}$	Ultimate physical length	L_∞ / δ_M
W_b	Wet mass at birth	Sns 1.2.3, 2.6.2; Eq. 3.2
W_p	Wet mass at first brood	Sns 1.2.3, 2.6.2; Eq. 3.2
W_∞	Ultimate wet mass	Sns 1.2.3, 3.2.1; Eq. 3.2
$\dot{R}_\infty$	Ultimate reproductive rate	Eq. 2.58
$\dot{v}$	Energy conductance	
κ	Allocation fraction to soma	
$[\dot{p}_M]$	Volume-specific somatic maintenance rate	
κ_G	Growth efficiency	
W_ω, t_x	Wet mass versus time since birth	Sns 1.2.3, 3.2.1; Eq. 3.2

Aviary experiment

Data from a previously published aviary experiment are used (Gupta et al. 2016). Forty eggs of lesser black-backed gull were collected from the wild in 2015 and taken to the Wildlife Rescue Centre in Oostende, Belgium. The eggs were incubated and after hatching randomly assigned to one of four diet treatment groups. Here we use data from three treatments. The first is called terrestrial, and contains 80% terrestrial food plus 20% marine food. It was called S1 in Gupta et al. (2016). The second is called marine, previously named S2, and contains 20% terrestrial plus 80% marine food. The last one is called mixed, and contains 50% of both types of food. This treatment was not discussed in Gupta et al. (2016). All marine (consisting of cod *Gadus morhua*, mackerel *Scomber scombrus* and whiting *Merlangius merlangus*) and terrestrial food items (mealworm larva *Tenebrio molitor*, potato crisp and broiler chicken *Gallus gallus domesticus*) were homogenised, mixed and embedded in gelatine to avoid selective feeding. Gelatine contributed 20% of total pellet dry weight. Food pellets were offered in an unrestricted amount and food taken was measured on a daily basis. The total time until fledging was split up in periods of 3-5 days. Length and weight measurements were done at the end of each period. For further details we refer to Gupta et al. (2016).

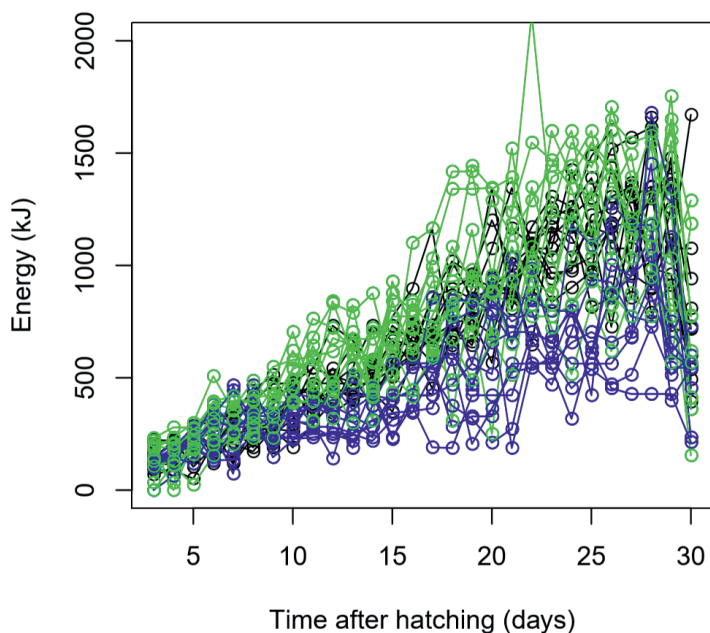


Fig. 7.1 Food intake versus time after hatching. Green dots and lines for a terrestrial diet, black for mixed and blue for marine.

Inverse modelling

The standard DEB model was simulated for each bird separately. The initial value of scaled structural length for the first observational period was derived from the observed physical length. Initial scaled reserve density for this first period was set to 1, which means that unscaled reserved density is equal to the maximum reserve density, i.e. to the ratio $\{\dot{p}_{Am}\}/\dot{v}$. The model was subsequently run for a series of scaled functional response f values. The f value that ‘exactly’ predicted the observed physical length at the end of each observation period, was selected. A quadratic function between f and physical length was used for interpolation. The predicted physical length and reserve density at the end of the period were used as initial values for the next observation period. This way the length predictions exactly followed the observations.

Results

The aviary experiment showed that food intake rates in terms of energy per time were highest for those birds feeding on terrestrial food and lowest for those that were restricted to marine food (Fig. 7.1). A similar difference was observed in the growth trajectories (Fig. 7.2). The mixed diet took an intermediate position in both food intake and growth rates.

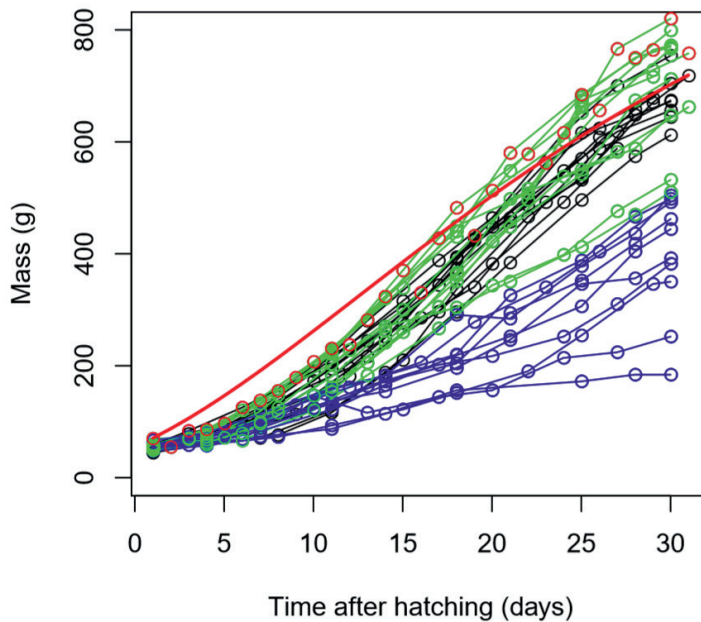


Fig. 7.2 Wet mass versus time after hatching for lesser black-backed gulls fed with three different diets. The red dots give the maxima per day and the red line gives the DEB prediction at ad libitum food. Green dots and lines for a terrestrial diet, black for mixed and blue for marine.

Table 7.2 Observed versus predicted zero-variate data for the lesser black-backed gull. Data in the upper part of the table are true data, the lower part gives pseudo-data. Weight refers to the weighing of the squared relative differences in the optimization procedure. Egg development occurs at a temperature of 6 °C, after hatching body temperature equals 41.2 °C, whereas the pseudo-data are given for a reference temperature of 20 °C.

Variable	Observed	Predicted	Unit	Weight	Source
a_b	29	29	d	1	Camphuysen (2013)
t_x	37	37.52	d	1	Camphuysen (2013)
t_R	1095	562	d	1	Camphuysen (2013)
a_m	12714	12720	d	1	Fransson et al. (2017)
$W_{\omega,b}$	55.32	55.23	g	1	Camphuysen (2013)
$W_{\omega,R}$	1065	1092	g	1	Camphuysen (2013)
$W_{\omega,\infty}$	1065	1091	g	20	Camphuysen (2013)
L_∞	55	55.01	cm	1	Camphuysen (2013)
$\dot{R}_m$	0.008219	0.008191	d ⁻¹	1	Camphuysen (2013)
$\dot{v}$	0.02	0.3801	cmd ⁻¹	0.004	Kooijman (2010)
K	0.8	0.9499	-	0.2	Kooijman (2010)
$[\dot{p}_M]$	18	244.8	Jd ⁻¹ cm ⁻³	0.1	Kooijman (2010)
κ_G	0.8	0.8005	-	1	Kooijman (2010)

Table 7.3 Parameter estimates of the standard Dynamic Energy Budget model for the lesser black-backed gull. All rates are given for a reference temperature T_{ref} of 293 K. Parameter values printed in italics were set at a predefined value that was taken from Kooijman (2010), Table 8.1.

Parameter	Value	Unit	Explanation
T_A	<i>9000</i>	K	Arrhenius temperature
f	<i>1</i>	-	Scaled functional response
δ_M	0.1517	-	Shape parameter
t_0	22.97	d	Time at start development
$\{\dot{p}_{Am}\}$	2150.6	Jd ⁻¹ cm ⁻²	Area-specific assimilation rate
$\dot{v}$	0.3801	cmd ⁻¹	Energy conductance
κ	0.9499	-	Allocation fraction to soma
κ_X	<i>0.8</i>	-	Assimilation efficiency
κ_{Xp}	<i>0.1</i>	-	Faeces efficiency
κ_R	<i>0.95</i>	-	Reproduction efficiency
$[\dot{p}_M]$	244.8	Jd ⁻¹ cm ⁻³	Volume-specific somatic maintenance rate
$\dot{k}_l$	<i>0.002</i>	d ⁻¹	Maturity maintenance rate coefficient
$[E_G]$	7318	Jcm ⁻³	Specific costs for structure
E_{Hb}	1590	J	Maturity at birth
E_{Hx}	888900	J	Maturity at fledging
E_{Hp}	3.493e6	J	Maturity at puberty
$\dot{h}_a$	1.327e-29	d ⁻¹	Weibull aging acceleration
s_G	<i>0.01</i>	-	Gompertz stress coefficient

Parameter estimation resulted in a fit with a symmetric mean squared error (SMSE) of 0.141, and a mean relative error (MRE) of 0.066. Compared to other species, these goodness of fit measures pointed to a good fit, see the add-my-pet website https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/about.html for an overview. All predictions for zero-variate data were close to observations, except for time since birth at first brood (Table 7.2). Observed time at first brood is three years (1095 days), but the prediction equalled only 562 days. This discrepancy is usually observed for birds, where the actual age of first breeding seems to be merely determined by behavioural constraints and not so much by physiological ones. The fitted growth trajectory, making the assumption that the scaled functional response equalled 1 for the entire growth period, initially overestimated the mass of the birds (Fig. 7.2). This observation is also in line with that for other bird species and it may be that the newly hatched chick needs a few days to get adapted to feeding itself. The parameter estimates (Table 7.3) are also in line with those for other bird species (Teixeira 2016).

The inverse modelling also pointed to a lower intake rate during the first few periods than the maximum achievable, even for the terrestrial treatment. After these initial periods the scaled functional response varied around 1 for the terrestrial treatment, slightly lower for the mixed, and around 0.7 for the marine treatment (Fig. 7.3).

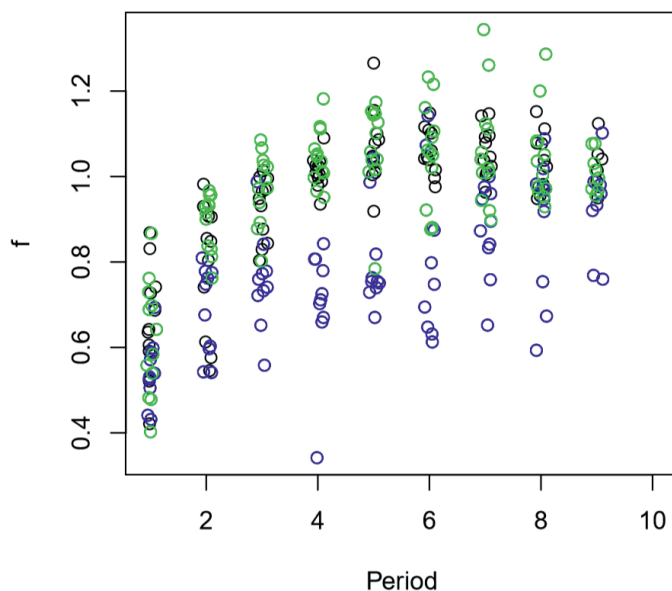


Fig. 7.3 Relative food level, as expressed by the scaled functional response f , versus observation period. Green dots for a terrestrial diet, black for mixed and blue for marine.

Fig. 7.4 shows, as an example, the results of the inverse modelling for one haphazardly chosen bird that obtained a mixed diet. The growth curve fits of course exactly through the data, as the scaled functional response f is fitted for each period separately (Fig. 7.4, upper panel). The predicted daily food intake followed the observations remarkably well (Fig. 7.4, middle panel). The scaled reserve density follows the scaled functional response with some delay (Fig. 7.4, lower panel). Plots for other birds are not shown, but revealed similar goodness of fits. Overall the measured food intake was about 10% higher than the predicted intake (Fig. 7.5).

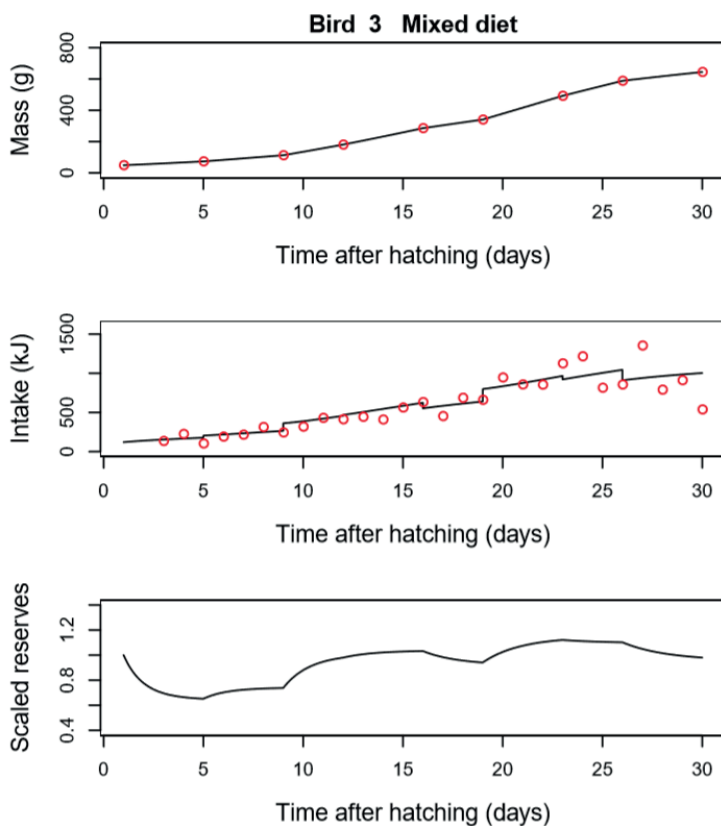


Fig. 7.4 Wet mass versus time after hatching for a particular individual (upper panel), predicted food intake rate per day and observed food intake rate per day (middle panel), predicted scaled reserve density (lower panel).

Discussion

A major goal in ecology is to understand how fitness-related performance of organisms responds to the environment. The availability of food is without doubt one of the most crucial environmental variables. It is therefore not surprising that numerous studies have been performed, though mainly in the laboratory, to determine the functional response that relates food availability to food intake rate, and to estimate the parameters of the appropriate type of functional response model (Jeschke et al. 2002). Much less attention has, however, been paid to study the next step, that is the relation between food intake rate and fitness-related characteristics such as growth rate, reproduction rate and survival. A likely reason for this discrepancy in research attention is that functional response experiments can be performed over relatively short time periods, i.e. for most species trials of minutes to hours will suffice, whereas studies of the link between food intake rate and growth or reproduction ideally last for the entire growth or reproductive period, which may take weeks to years.

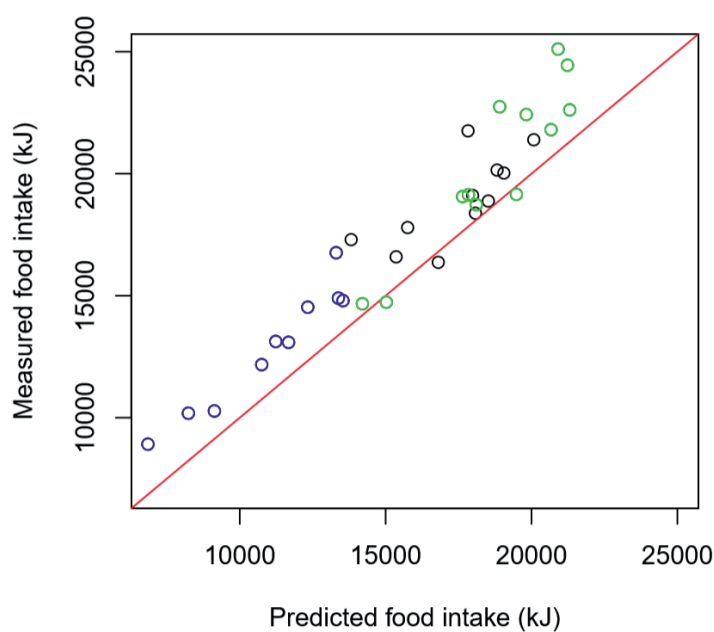


Fig. 7.5 Predicted versus observed food intake, as measured over the first 30 days after hatching. Green dots for a terrestrial diet, black for mixed and blue for marine.

Table 7.4 Various energy expenditures (kJ), that is powers integrated over the first 30 days after hatching, predicted by the standard DEB model for abundant ($f = 1$) and limited ($f = 0.7$) food. Maturity includes maturity maintenance.

Type	Integral	$f = 1$	$f = 0.7$
Feeding	$\int \dot{p}_x da$	19717	8891
Assimilation	$\int \dot{p}_A da$	15774	7113
Mobilization	$\int \dot{p}_C da$	13973	6682
Maintenance	$\int \dot{p}_M da$	10943	5530
Growth	$\int \dot{p}_G da$	2329	817
Maturity	$\int \dot{p}_J da$	700	335

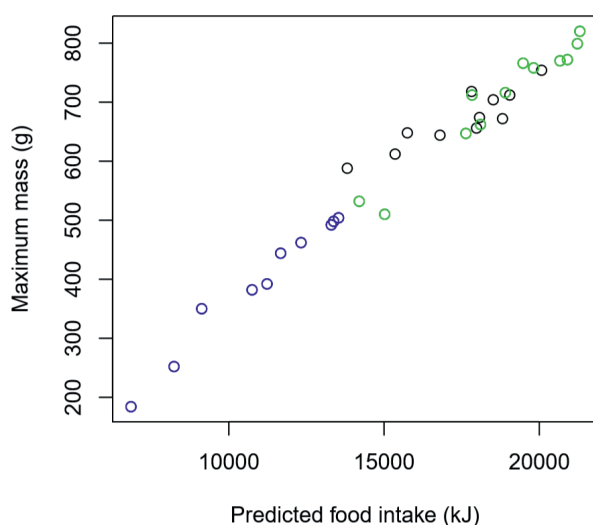


Fig. 7.6 Predicted food intake over the first 30 days after hatching versus mass at the age of 30 days after hatching. Green dots for a terrestrial diet, black for mixed and blue for marine.

Measuring food intake is, as already said, a laborious and costly exercise, particularly in the field. It is therefore encouraging that the modeling approach based on DEB theory, as presented here, enables a rather accurate prediction of food intake rate of the chicks on the basis of their growth trajectory. This enables ornithologists to study the functional response (i.e the link between food availability and food gathering rate) in the field in probably the most important period of the year, that is in the chick raising period. Provisioning rate, or at least intake rate of the chicks can now directly be derived from the growth trajectory of the chicks, which is much easier to obtain. Of course, feeding rate of the adults themselves has to be added to obtain the total food gathering rate. Adult feeding rate can be obtained in a similar fashion, if changes in

adult weight are available. These weights will probably only vary to a minor extent, implying that adult feeding rate is more or less constant.

Apart from predicting the intake rate required for obtaining a specific fledging weight, the DEB model keeps track of all energy fluxes. The huge difference in weight increase as a result of a much smaller difference in food availability ($f = 1$ versus $f = 0.7$), is not just the result of the difference in structural size but also to a great extent of the difference in reserves (Table 7.4). Note that the build-up of the reserves is given by the integrated assimilation minus the integrated mobilization, and thus equals 1801 kJ and 431 kJ for the two example feeding levels. This difference is relatively larger than that in structural growth: 2329 kJ versus 817 kJ.

Our food intake predictions were systematically about 10% below the observations. We refrained from using these food intake data in the parameter estimation procedure, but when we would have done that, it would have resulted in an almost perfect fit. Lowering the assimilation efficiency (which was set at 80%) would as well have yielded such perfection. A slightly lower efficiency of 75% has indeed been observed in birds (Castro et al. 1989). The slow initial growth observed might also be related to a low initial assimilation rate, similar to a lowered digestive performance after diet switching (Hilton et al. 2000).

Generally speaking, the problem of overfitting (too many parameters, too few data types) is always a serious one, particularly in such complex parameter estimation procedures as the add-my-pet procedure for DEB models. Testing the predictions of a parametrized model on an independent data set, as was done here, is therefore of utmost importance in modeling. We strongly encourage such tests for DEB models. As a next step, it might be rewarding to repeat our exercise for a variety of bird species for which data on intake rate during the chick raising phase are available.

Acknowledgements

Ghent University, Bird Rescue Center (VOC) Oostende, and the Flanders Marine Institute (VLIZ) provided the infrastructure for the aviary experiment.

Author Contributions

AS and LL designed the feeding experiments; JvdM and SvD fitted the DEB model to the data; JvdM developed and applied the inverse modeling procedure; JvdM wrote the manuscript, with the help of SvD. All authors contributed to the drafts.

Supplementary material

This appendix provides further details and derivations for the standard DEB model. The model has three state variables, structural body volume V , reserve density $[E] = E/V$, which is the amount of reserves per unit of structural body volume, and maturity E_H , which is the cumulative energy allocated to development. The most important environmental variable is the food density X (Table 7.5).

A list of assumptions gives rise to a set of coupled ordinary differential equation for the three state variables. Assumptions for the standard DEB model are, among other things, that (1) assimilation rate is proportional to the surface area of the structural body $\dot{p}_A = \{\dot{p}_{Am}\} f V^{2/3}$, (2) all assimilated energy enters the reserves and is then mobilized from the reserves (the rate of changes of the reserves is thus the difference between the assimilation rate and the mobilization rate), (3) a fixed fraction κ of the mobilization rate is spent on maintenance, which is assumed proportional to structural body volume, and on growth, assuming fixed costs for growth per unit volume, (4) the rate of change of maturity equals $1-\kappa$ times the mobilization rate minus the maturity maintenance costs, which are proportional to maturity.

Table 7.5 State variables of the standard DEB model and environmental variables. L stands for the dimension length of the structural body, e for energy, $\#$ for mass measured in terms of C-moles, and l for the dimension length of the environment.

Symbol	Dimension	Interpretation
V	L^3	Structural body volume
$[E]$	eL^{-3}	Reserve density
E_H	e	Maturity
T	T	Temperature
X	$\#l^{-3}$	Food density in the environment

The ordinary differential equation for reserve density is

$$\frac{d[E]}{dt} = V^{-1/3} (\{\dot{p}_{Am}\} f - \dot{v}[E]) \quad (3)$$

The area-specific assimilation rate $\{\dot{p}_{Am}\}$ and the energy conductance $\dot{v}$ are so-called primary parameters of the standard DEB model. They are explained, together with quite a few others such as $\{\dot{F}_m\}$ and κ_X , in Table 7.6; f is the so-called scaled functional response that relates the assimilation rate to the food density, and is given by

$$f = \frac{X}{\frac{\{\dot{p}_{Am}\}}{\{\dot{F}_m\}\mu_X\kappa_X} + X}$$

and μ_X is the chemical potential of the food.

The growth equation is given by

$$\frac{dV}{dt} = \frac{\kappa \dot{v}[E]V^{2/3} - [\dot{p}_M]V}{\kappa[E] + [E_G]} \quad (4)$$

It follows from

$$\frac{dE}{dt} = \frac{d[E]V}{dt} = \dot{p}_A - \dot{p}_C \quad (5)$$

which tells that the rate of changes of the reserves is the difference between the assimilation rate $\dot{p}_A$ and the mobilization rate $\dot{p}_C$. A fraction κ of the mobilization rate is spent on maintenance, which is assumed proportional to structural body volume, and on growth, assuming fixed costs for growth per unit volume. Using this so-called κ -rule and the product rule for differentiation, equation 5 can be re-written as

$$V \frac{d[E]}{dt} + [E] \frac{dV}{dt} = \{\dot{p}_{Am}\}fV^{2/3} - \frac{1}{\kappa}[\dot{p}_M]V - \frac{1}{\kappa}[E_G] \frac{dV}{dt}$$

Combining with equation 3 and some re-arranging yields the growth equation 4.

The rate of change of maturity equals $1-\kappa$ times the mobilization rate minus the maturity maintenance costs, which are proportional to maturity.

Hence

$$\frac{dE_H}{dt} = (1 - \kappa)\dot{p}_C - \dot{k}_J E_H \quad (6)$$

for $E_H < E_H^p$. Else, that is when the animals have become mature and $E_H = E_H^p$, maturity does not change anymore and $dE_H / dt = 0$.

It can be shown that the mobilization rate $\dot{p}_C$ equals

$$\dot{p}_C = \frac{[E]}{\kappa[E] + [E_G]} (\dot{v}[E_G]V^{2/3} + [\dot{p}_M]V)$$

The system of differential equations for reserve density (Equation 3), structural volume (Equation 4), and maturity (Equation 6) describe the standard DEB model.

Table 7.6 Primary parameters of the standard DEB model. See further Table 7.5.

Symbol	Dimension	Interpretation	Process
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	Surface-area-specific maximum assimilation rate	Assimilation
$\{\dot{F}_m\}$	$l^3L^{-2}t^{-1}$	Surface-area-specific searching rate	Feeding
κ_X	-	Digestion efficiency	Digestion
$\dot{v}$	Lt^{-1}	Energy conductance	Mobilisation
κ	-	Fraction of mobilisation rate spend on maintenance plus growth	Allocation
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	Volume-specific maintenance rate	Turnover/activity
$\{\dot{p}_T\}$	$eL^{-2}t^{-1}$	Surface-area-specific maintenance rate	Heating/osmosis
$[E_G]$	eL^{-3}	Volume-specific costs of growth	Growth
$\dot{k}_j$	-	Specific maturity maintenance	Regulation/defence
κ_R	-	Reproduction efficiency	Egg formation
E_H^b	e	Maturity at birth	Life history
E_H^p	e	Maturity at puberty	Life history

The standard DEB model can be entirely re-written in a dimensionless form. In order to arrive at a dimensionless model one has to re-scale all dimensions, that is energy, length (or volume) and time. The choice of scaling coefficients is rather arbitrary, as we will see. Yet, for energy an obvious choice is the maximum amount of energy in reserve E_m , and for volume it is the maximum volume of the structural body $V_m = (\kappa\{\dot{p}_{Am}\} / [\dot{p}_M])^3$. The maximum amount of energy in reserve equals the product of the maximum reserve density and the maximum volume $E_m = [E_m] V_m$, where $[E_m] = \{\dot{p}_{Am}\} / \dot{v}$ as follows from eqn. 3 with $f = 1$. These choices ensure that the new dimensionless state variables, which are scaled reserve density $e \equiv [E] / [E_m]$ and scaled length $l \equiv (V/V_m)^{1/3}$ are easy to interpret and to remember. The same holds for scaled maturity $e_H \equiv E_H / E_m$. The choice of a scaling coefficient for time is less obvious. But it helps to first look at power, which is given in energy per time. One option is to scale power by the maximum assimilation rate, which equals $\dot{p}_{Am} = \{\dot{p}_{Am}\} V_m^{2/3}$. This choice implies that time is scaled to κ times the ratio of the maximum reserve density and the volume-specific maintenance rate, resulting in $\tau \equiv t[\dot{p}_M] / (\kappa[E_m])$.

Not just the state variables, but all parameters (Table 7.7) and model equations can now be re-scaled. Equation 3, which describes the dynamics of the reserve density, turns into

$$\frac{de}{d\tau} = \frac{d[E]}{dt} \frac{1}{[E_m]} \frac{\kappa[E_m]}{[\dot{p}_M]} = \frac{f-e}{l} \quad (7)$$

Similarly, the growth equation 4 becomes

$$\frac{dl^3}{d\tau} = \frac{dV}{dt} \frac{1}{V_m} \frac{\kappa[E_m]}{[\dot{p}_M]} = \frac{1}{e+g} l^2 (e-l) \quad (8)$$

which is equivalent ($\frac{dl^3}{d\tau} = \frac{dl^3}{dl} \frac{dl}{d\tau} = 3l^2 \frac{dl}{d\tau}$) to

$$\frac{dl}{d\tau} = \frac{1}{e+g} \frac{e-l}{3} \quad (9)$$

where the compound parameter g is given by the ratio $[E_G]/(\kappa[E_m])$. This is one of the most important compound parameters in DEB theory and is called the ‘energy investment ratio’. It stands for the energetic costs of new structural volume $[E_G]$ relative to the maximum available energy for growth and maintenance $\kappa[E_m]$. Equation 6 can be re-written as

$$\frac{de_H}{d\tau} = \frac{dE_H}{dt} \frac{1}{[E_m]V_m} \frac{\kappa[E_m]}{[\dot{p}_M]} = (1 - \kappa)l^2 \frac{e}{e+g} (g + l) - \frac{\dot{k}_J}{\dot{k}_M g} e_H \quad (10)$$

where the compound parameter $\dot{k}_M$, called the ‘maintenance rate coefficient’ is given by the ratio $[\dot{p}_M]/[E_G]$. It stands for the maintenance costs of structure relative to the investment. When $\dot{k}_J = \dot{k}_M$, which means that the relative maintenance costs of maturity equal those of the somatic body, it can be shown that

$$E_H = \frac{1-\kappa}{\kappa} [E_G]V$$

or, in dimensionless form, $e_H = (1-\kappa)gl^3$. The main result of setting $\dot{k}_J = \dot{k}_M$ is thus that maturity occurs at a fixed length, that is $e_H^p = (1-\kappa)gl_p^3$. The consequence is that equation 10 simplifies to

$$\frac{de_H}{dt} = (1 - \kappa) \left(\frac{e}{e+g} l^2 (g + l) - l^3 \right) \quad (11)$$

Table 7.7 Rescaling the primary parameters of the standard DEB model written in an energy-length framework into a dimensionless framework. Energy is scaled to the maximum energy in reserves $[E_m] V_m$, volume to the maximum volume V_m , and power to the maximum assimilation rate $\{\dot{p}_{Am}\} V_m^{2/3}$. Hence time is scaled to one over the product of the energy investment ratio and the maintenance rate coefficient $(g\dot{k}_m)^{-1}$.

Energy-length	Dimension	Dimensionless
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	1
$\dot{v}$	Lt^{-1}	1
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	κ
$\{\dot{p}_T\}$	$eL^{-2}t^{-1}$	κl_T
$[E_G]$	eL^{-3}	κg
E_H^b	e	e_H^b
E_H^p	e	e_H^p



Chapter 8

Synthesis

In this dissertation, herring gulls of a breeding colony on Texel were studied to better understand how behavioural differences among individuals affect fitness, with a special attention on how animals gather and allocate energy. We used 10 years of field data, supplemented with detailed GPS and behavioural data, to unravel the factors that play a role in behavioural decisions of free-living animals in a complex and changing foraging area. Studying different facets within one ecological system, helps to understand the importance of behavioural variation.

First, I will summarize the main results of each chapter and put my findings in a broader context. Then I will discuss the methodology used and consider possible alternatives. Finally, I arrive at the overall conclusions and will make some recommendations for further research.

Discussion of main results

The main findings of this dissertation are summarized below and in Fig. 8.1, in which the numbers correspond with those in the text below.

Part I

1. Dietary choice influences the reproductive success of herring gulls (Chapter 2). High caloric prey of anthropogenic origin are beneficial for reproductive success, while low caloric prey like blue mussels result in lower breeding success. However, despite the reproductive disadvantage most birds feed predominantly on low caloric mussels.
2. While high caloric prey of anthropogenic origin is beneficial for reproductive success, foraging effort required is higher than for other resources (Chapter 3). Gulls foraging for high caloric foods at sea (fishery discards) or in urban area (human food remains) spent more energy per hour because of more time in flapping flight per foraging trip than gulls foraging on low caloric prey (bivalves and terrestrial prey).
3. Individual herring gulls do not only differ in the diet they eat, but also in how faithful they are to their foraging patches (Chapter 4). Larger herring gulls had a higher level of site fidelity than smaller individuals. Nevertheless, there was no clear relation to energy expenditure; site faithful individuals neither spent more time in the breeding colony, nor had a lower energy expenditure compared to other strategies.
4. Habitat loss did not affect reproductive success on population level (Chapter 5). However, individuals within the population switched to an uncommon diet for this colony, probably due to higher competition on the remaining foraging habitat. These individuals had lower reproductive success than others.

Part II

5. Breeding is costly in terms of energy expenditure attributed to movement, but only during the period of chick rearing (Chapter 6 and 7). Herring gulls that skip a breeding opportunity can save 300 kJ per day compared to herring gulls that raise chicks. Saving energy one year can help to improve body condition for the next breeding opportunity.
6. Mass at age data were used to predict the total energy intake of growing chicks using the dynamic energy budget model (DEB). Predictions correlated strongly with measurements, which makes measuring food intake in the field not necessary. Total energy intake estimates of chicks can be used to calculate foraging effort of adult herring gulls with different foraging strategies.

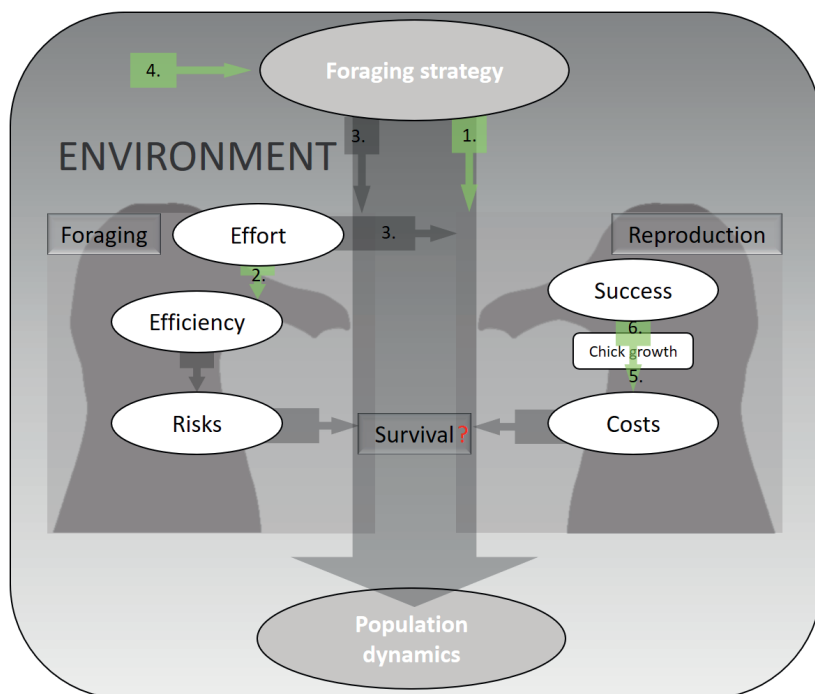


Fig. 8.1 Adjusted schematic overview of the framework of this thesis, which was presented in Chapter 1. A summary of the results are listed in the text on the previous page, the numbered results correspond with the numbers in this overview. Foraging strategy in this dissertation is studied as diet (1 & 4), habitat use (2) and as foraging site fidelity (3). When a relationship was found between two links in the scheme, the arrow is coloured green. When no relationship was found, only the number is indicated. Survival differences between individuals with different strategies is not known yet, and is a direction for future research.

Discussion of results

We showed that individual herring gulls differ in their diet, the habitat they visit and how faithful they are to foraging areas. Here, I discuss (1) how such variation in foraging strategies can be maintained in a population such as the herring gulls on Texel, (2) how variation in the population can be adaptive in a heterogeneous or changing environment, and (3) possible reasons why animals do not always adapt their behaviour according to changes in the environment.

1. Variation within a population

Herring gulls on Texel have a higher reproductive success when feeding their chicks with high caloric prey of anthropogenic origin, but foraging for these prey is energetically more expensive (Chapter 2 and 3). In contrast, herring gulls feeding their chicks with mainly low caloric bivalves, have a lower reproductive success but foraging on these prey is energetically cheaper. At the two extreme ends of the population, we have in theory individuals that breed successfully

and invest more energy in foraging and individuals that invest less in foraging and reproduce less successfully in a given year.

The differences between these two foraging strategies could be reflected in differences in life history traits (Stearns 1976). Life history traits reflect the trade-off between reproduction and survival in an environment with limited time and energy to support both (Williams 1966). This results in different life-history strategies between populations (Stearns 1992), but possibly also within populations (Réale et al. 2010). A ‘slow-living’ strategy is characterized by high survival and relatively low investment in reproduction while a ‘fast-living’ strategy is characterized by prioritizing reproduction over survival. A ‘fast-living’ life history is associated with more risk-taking behaviour which possibly results in their shorter lifespan (Réale et al. 2010).

The differences in life history strategies that are mainly studied on species level, can also explain variations in behaviour within the herring gull population on Texel. The successful breeders in our study system might suffer survival costs because of their high energy expenditure. Besides, they might suffer from risks associated with foraging for fishery discards or in urban areas, like possible injuries or entanglement in fishing gear (Favero et al. 2010) or a potentially higher risk of infection by diseases in urban areas (Bradley and Altizer 2007). While the less successful breeders do not suffer from these survival costs of energy expenditure and risks while foraging on predictable bivalves, possibly resulting in a longer lifespan. In the long-run, both strategies may result in similar lifetime reproduction and might thus be equally good strategies in terms of fitness.

Foraging strategies can also have similar fitness, when there are no clear short-term benefits or differences in life history traits. The results of chapter 4 of this dissertation show that individuals that differ in the level of site fidelity do not differ in the time they spent foraging or the time invested in reproduction, but larger gulls are more likely to be site faithful. Foraging strategies can be determined by morphology. Size affects energy expenditure in gulls and other species (Speakman 2005) and larger individuals are more likely to be dominant (Monaghan 1980). Therefore, they can more easily secure a foraging site in a competitive situation. Besides, flying is more expensive for them in terms of energy expenditure. It might be more rewarding for these larger individuals to be site faithful to avoid costly flight costs. For smaller individuals, moving between foraging patches is less expensive and therefore possibly less rewarding to invest energy in requiring a position in the dominance hierarchy.

Behavioural variation between individuals without clear fitness consequences can also be maintained by a mechanism called ‘negative frequency dependent selection’. This mechanism suggests that as long as a population consists of different phenotypes in a certain frequency, individuals have the same fitness. As soon as one strategy increases in frequency in the population, individuals with that strategy experience disadvantages in for instance food intake

and ultimately fitness, creating advantages for individuals with other strategies (Fitzpatrick et al. 2007). However, I do not think that this mechanism influences variation between individuals in gulls. The examples of populations in which this mechanism plays a role often consist of individuals with extreme differences in their strategy resulting in a bimodal distribution. In our study on foraging site fidelity, the gulls show a unimodal distribution in their strategies, instead of a bimodal one. Two studies that investigated this mechanism in birds, could also not find evidence for this theory (van de Pol et al. 2010, Kurvers et al. 2012).

2. Variation in a fluctuating or heterogeneous environments

The advantages and disadvantages of strategies are not static and can fluctuate over time, as the environment fluctuates by natural causes or human disturbances. As such, a strategy that is very advantageous in one environment can have disadvantages when its environment has changed, resulting in fluctuating selective pressures. For instance, a long-term study of 26 years on a population of oystercatchers *Haematopus ostralegus ostralegus* showed that selection fluctuated between years. Generalists were slightly in favour in most years in terms of survival, but were strongly selected against in rare harsh winters (van de Pol et al. 2010). Another study on this species, but in a different region did not find differences in survival between individuals that varied in strategies (Durell 2007). In black-browed albatrosses *Thalassarche melanophrys*, females that foraged closer to the colony had higher fitness than females foraging further away, but only in years with high estimated food availability. In years with low estimated food availability, females foraging further away were in favour in terms of fitness (Patrick and Weimerskirch 2014b).

In a similar way, particular prey types can be relatively stable or unpredictable in amount or quality and thus require a different foraging approach. In the studied population, bivalves provide a predictable and stable food source, and are available during low tide. Other prey items have a less predictable rhythm; fishery discards are primarily available on weekdays and the availability of earthworms is dependent on rain. Individuals that forage on less predictable prey, should logically have other foraging options available, while this is not necessary for individuals that forage on more predictable prey. The first should therefore have a wider knowledge of the environment, while the second has possibly a competitive advantage in knowing one specific environment very well.

3. Pre-programmed individuals in a changing world

Above, I described several mechanisms in which variation can be maintained in a population, and how this can actually be advantageous to deal with a heterogeneous or changing environment. Several studies have suggested that generalist predators are increasing in urban areas because they have a broad diet spectrum and are thought to be more flexible and thus better in exploiting new food resources than specialist species (Chautan et al. 2000, François

2002, Gompper 2002, Contesse et al. 2004, Mitchell et al. 2004, Rock 2005, Soldatini et al. 2008). The foraging environment of herring gulls is also changing. Two decades ago, open dump sites and fishery discards provided still plentiful foods for gulls. However, open landfills have decreased particularly since the 1990s; the open dumpsite on Texel was closed in 1991 and so were many others in the Netherlands and Europe (Kohler and Perry 2005, Camphuysen 2013, European Environment Agency (EEA) 2016, Rijkswaterstaat 2016). Similarly, the availability of fishery discards declined due to a lower fishing effort since the late 1990's and stricter legislation towards discarding bycatch (Poos 2010, "Factsheet: North Sea brown shrimp" 2011, Camphuysen 2013, Borges 2015). Are the generalist herring gulls able to quickly adapt as suggested for other generalist predators (Devictor et al. 2008, Clavel et al. 2011)?

The gulls have indeed changed their foraging behaviour, their diet contains now proportionally more mussels and less anthropogenic prey than at the start of the monitoring on Texel (Chapter 5, Fig. 5.2). However, they did not change in such a way to prevent a decrease in fitness over time, as mussels are insufficiently nutritious for chick growth (Chapter 2). Second, we show that raising chicks is costly in terms of energy expenditure (Chapter 6), but individuals do not increase their foraging effort when energetic needs of their chicks grow despite low reproductive success of the breeding colony. Third, we show that individual herring gulls do change their (short-term) foraging behaviour when part of the foraging habitat is lost, but some individuals switched to a clearly unsuccessful strategy (Chapter 5).

One way to adapt to the worsened conditions in resource availability around the breeding colony on Texel would be to move to another breeding location closer to high caloric food and reduce foraging costs. However, the number of breeding birds stayed stable over the time that this breeding colony was monitored and colour ringed adult birds are very faithful to their breeding colony, often even coming back to the exact location of their former territory (Camphuysen 2013). Why do herring gulls, as a species, seem to adapt well to increasing urbanization and landscape fragmentation, but on an individual level appear to have difficulties changing foraging habits and do not move to a better breeding location that is situated closer to the food they need for reproduction? Here, I hypothesize that plasticity of gull behaviour is limited during the lifetime of an individual.

Seabirds have a long period of immaturity (Dobson and Jouventin 2007), in which they are generally more explorative than adults (Riotte-Lambert and Weimerskirch 2013, Orben et al. 2018). This explorative behaviour might help them to gain experience that they can use later in life; for example, seabirds gain knowledge during immaturity which makes them more efficient foragers as adults (Maclean 1986, Riotte-Lambert and Weimerskirch 2013). Over time, birds often become less variable and more repeatable in their (foraging) behaviour with increasing age and experience (Wakefield et al. 2015, Votier et al. 2017, Campioni et al. 2019, Kok et al.

2019) thereby developing distinct migration and foraging strategies (Phillips et al. 2017, Campioni et al. 2019). This so-called behavioural canalization suggests that animals develop behavioural traits based on the conditions experienced at the start of development, but become less flexible at a later age. Environmental information gathered during the early life can thus have lifetime consequences on foraging behaviour (Dall et al. 2012). The increase in repeatability and decrease in flexibility might be adaptive, when birds forage in areas that yield predictable prey availability over longer timescales (Bradshaw et al. 2004, Wakefield et al. 2015). For instance, reproductive success in black-browed albatrosses *Thalassarche melanophrys* was higher in females that were site faithful to their foraging habitat in a given year, and between years individuals with higher site fidelity tended to have higher reproductive success (Patrick and Weimerskirch 2017). Behavioural canalization can be adaptive in an environment that is relatively predictable, but when the environment changes rapidly there may be dire consequences for individuals that do not retain enough behavioural plasticity to adapt to environmental change within their lifetime.

Implications for methods

Studying animals in their natural environment allows one to observe how animals adapt their behaviour to a variety of biotic and abiotic factors, which makes studying free-living animals challenging. However, studying animals in their natural environment is important, because an animal has to adapt its behaviour based on all these biotic and abiotic factors and not on stable laboratory conditions. We applied standard field methods, already in use for decades, but also used recently developed approaches. Here, we discuss shortly some of these methods and compare them to possible alternatives.

In chapter 2, we used the analysis of regurgitates to investigate the diet of herring gulls in relation to reproductive success. This method is non-invasive for the gulls as animals do not have to be caught and it is possible to gather many regurgitates per nest site. Also, it gives a good indication of the diversity of prey in the diet. However, it is possible to miss prey types that do not have hard non-digestible parts that are regurgitated by the gulls. The pacific oyster *Magallana gigas* is such a prey that will be missed by the regurgitate method, as gulls drop these large shells on hard substrate and only eat the soft flesh. The pacific oyster is an invasive species that has spread rapidly in the Wadden Sea. Learning about the frequency of this specific prey type in the diet of predators is of interest, as that can tell us something about the importance of this new species in the ecosystem.

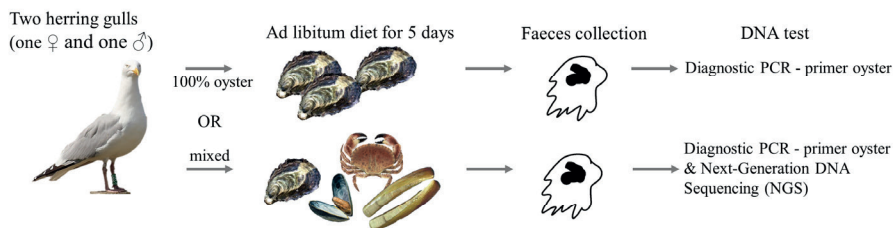
We tested the use of DNA markers on faeces to detect soft prey types like the pacific oyster in a small laboratory study with two herring gulls (Box 8.1). Both birds received two types of treatment for several days in a row; they were either fed with 100% oyster meat, or received a mixed diet which contained 25% oyster for several days to imitate a more natural setting, as

gulls often eat more than one type of prey. Faeces of these two gulls were collected daily and stored. Subsequently, a diagnostic PCR (Philippart et al. 2014) with a tested oyster-primer was done. With this method, it was possible to detect oyster DNA in the faeces. However, not all faeces of the 100% diet gave a positive result. Besides, we found a big difference between the two tested individuals. This finding suggests that individuals vary in their gut flora which can influence the results. Therefore, using diagnostic PCR to identify prey in faeces needs to be tested more thoroughly in the laboratory before it can be used in the field. Another way of measuring the diet by using DNA in the faeces is by performing next generation DNA sequencing in combination with metabarcoding (Pompanon et al. 2012)(Box 8.1). With this method, one can test for multiple prey, but only the species of which the genetic barcode is known.

Gathering regurgitates at a nest site has another disadvantage; one is only able to learn about the diet of a herring gull pair and not about the diet of an individual. A way of gathering information about the individual, is by monitoring habitat use. We used two methods to monitor habitat use; colour rings and GPS trackers. Colour rings can be used to measure both survival and habitat use and are instrumented in large numbers because of their low price and little impact on the animals. However, the re-sighting rate is dependent on the effort of observers; some areas are more accessible than other areas. Also, it is very hard to re-construct how animals spend their time by only observations. Monitoring time-energy budgets is possible with bio-logging. In this dissertation, several studies were based on the data of GPS trackers. GPS trackers with accelerometers provide information on the habitat use of the gulls (independent of observer effort) and on time and energy budgets. These trackers have provided new information and insights on the behaviour of animals that could not be measured before. However, there is still a lot to discover. Data gathered during the study period of this thesis consists of a wealth of information on detailed behaviour of gulls. Individuals with different strategies do for instance differ in daily foraging patterns (Box 8.2). This can have implications on the co-operation with the breeding partner during parental care. For instance, breeding pairs that both forage on intertidal prey are constrained by the tide and thus have to cooperate in such a way that they can both go out for foraging during low tide without leaving brooded eggs unattended. Breeding pairs that do have the same daily rhythm might be able to share foraging and breeding time in a better way. Good cooperation between breeding pairs is important and seems to be related to reproductive success in a recent study on lesser black-backer gulls *Larus fuscus*. Breeding pairs that had a more equal division of parental care during incubation, had a greater reproductive success when their brood was experimentally enlarged compared to pairs that divided the work less equally (Kavelaars et al. 2019).

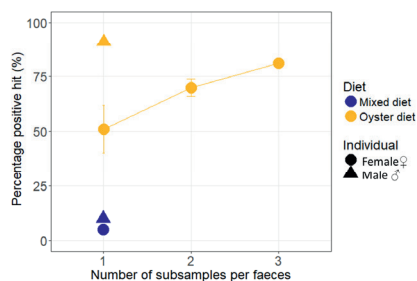
Box 8.1 Overview of an exploratory study on diagnostic DNA tests on gull faeces. This study was conducted in collaboration with Rohy Berghuis, Kees Camphuysen, Boukje Heidstra and Judith van Bleijswijk.

AIM: to evaluate a diagnostic DNA test on gull faeces to detect oyster consumption



RESULT diagnostic PCR - primer oyster

- 80-90% positive hit on oyster diet by using 3 subsamples
- About 10% positive hit on mixed diet
- Individual differences in success rate (confirmed with diagnostic PCR on 100% mussel faeces)

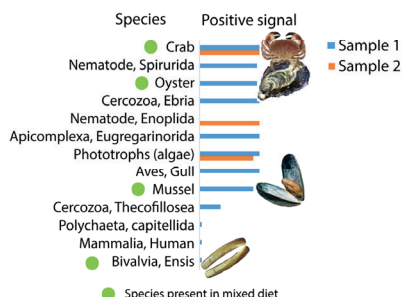


Faeces (% positive hit for oyster) after analyses of 1, 2 or 3 subsamples. Gulls were fed on oyster diet (#faeces 23 for ♀ and 27 for ♂) and mixed diet (#faeces 49 for ♀ and 37 for ♂).

- DNA markers can be used to detect oyster, but more subsamples are needed for optimal detection
- Individual differences are found in the success rate of the PCR, differences in gut flora might influence the result

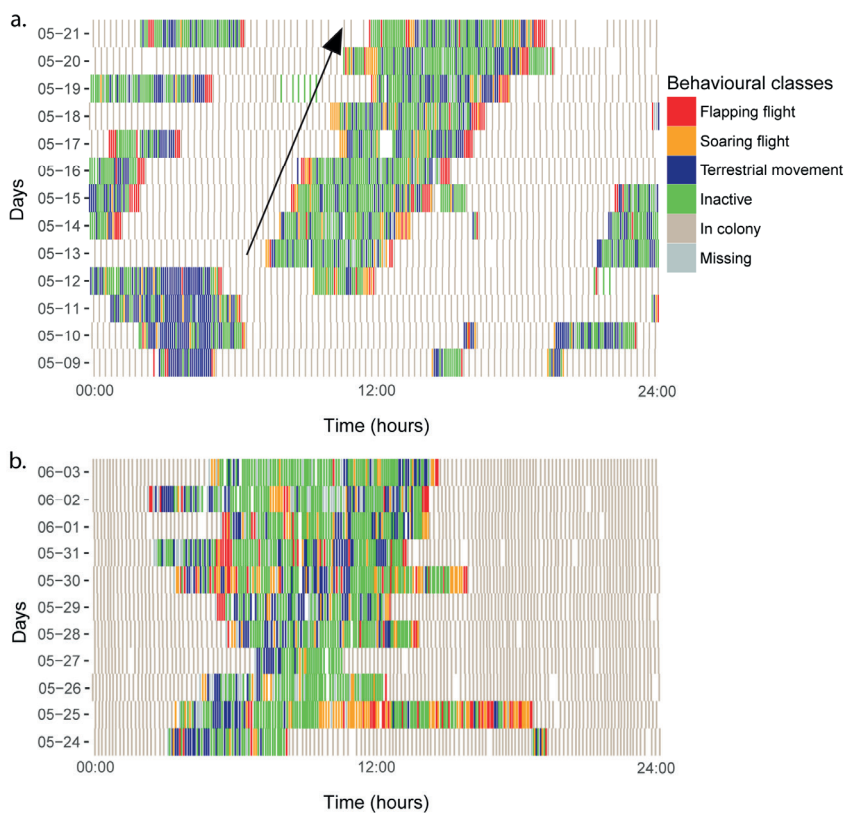
RESULT Next-Generation DNA Sequencing of mixed diet

- NGS on 2 faeces samples of ♀
- All prey types of mixed diet are detected in sample 1
 - Results NGS correspond with diagnostic PCR (positive for sample 1 and negative for sample 2)



- NGS results correspond with the diagnostic PCR results of the same faeces samples
- NGS does not show all prey types of the mixed diet in both faeces samples. Even in a mixed diet, gulls might have faeces with remains and DNA of only one prey type

Box 8.2 Daily rhythms of two individual herring gulls carrying GPS trackers during the incubation period. On the Y-axis from low to high preceding calendar days. On the x-axis time of the day from 00:00 until 24:00. Colours indicate the behaviour of the two individuals, or the time they spent in the colony when no behaviour was registered. a. An individual that forages mainly at breakwaters on blue mussels. The arrow indicated that the bird left the colony on average an hour later every day, following the changing tide over the days. b. An individual that has a more mixed foraging strategy using both urban areas as breakwaters. This bird has a more repetitive daily rhythm; leaving the colony in the middle of the night and coming back in the early afternoon.



Conclusions and outlook

The work presented in this dissertation shows the consequences of different foraging and breeding decisions for proxies for fitness. In this final chapter, several possible mechanisms which could promote variation in these decisions were discussed. Furthermore, recent environmental change can result in natural selection of generalist species or individuals. However, to be able to make conclusions about mechanisms and to predict possible selection due to environmental change, more studies are needed.

In this thesis, we were interested in foraging strategies in relation to fitness proxies, which was the reason to study individuals while breeding. However, the breeding season is only a short part of an animal's life. The conditions that an animal experiences outside the breeding season, can also highly influence the body condition of an animal (Harrison et al. 2011). The tracking data gathered during this dissertation, opens up possibilities to study this so-called carry-over effects. For instance, are individuals that are site faithful during the breeding season also site faithful at other foraging sites and provides this behaviour them with a long-term energetic advantage (in contrast to our findings during the breeding season, Chapter 4).

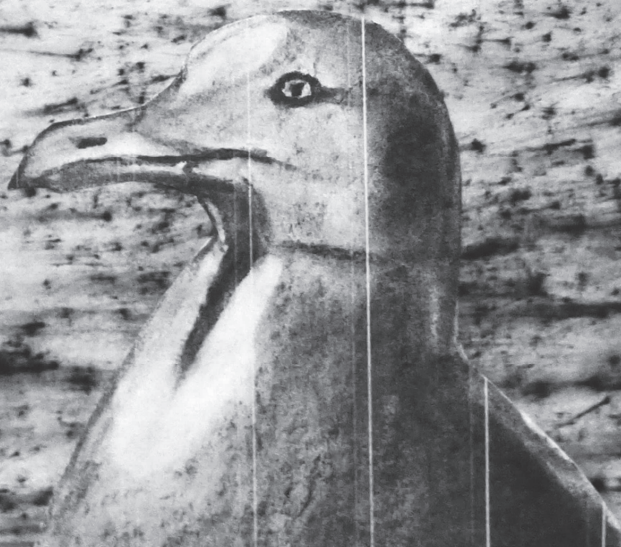
Another line of research should focus on survival of individuals with different foraging strategies (Fig. 8.1). In this way, we could answer the question whether animals foraging on high caloric prey with high breeding success have indeed a lower life expectancy than animals that forage on low caloric prey. And whether this results in similar lifetime reproductive success. Or we may find out that individuals that vary in foraging strategies do not differ in survival. Some herring gulls might just have a competitive advantage, and are able to claim better quality food for their young. This could be important when certain habitat is affected by human activities. Recently, several wind parks are being built in the North Sea and there are concerns whether seabirds foraging at sea are affected (Dierschke et al. 2016). When fishery discards-specialists have a higher lifetime reproductive success, because they are able to claim the beneficial prey types for chick growth, loss of such an individual has a larger effect on population level than the loss of a mussel specialist with potentially lower lifetime reproductive success. Survival analyses are already within reach with the large amount of re-sighting data of individuals with colour rings that have been gathered over the last 14 years.

Such analyses have been done on oystercatchers in which two papers examined whether survival differed between individuals (Durell 2007, van de Pol et al. 2010). For instance, van de Pol and colleagues (2010) found that survival can differ between individuals depending on their foraging strategy, but which strategy is selected against depends on the weather conditions. Also survival between spoonbills *Platalea leucorodia leucorodia* that vary in migration strategies has been examined with the use of re-sighting data (Lok et al. 2015). Understanding

both the survival and the breeding consequences of foraging strategies, could give us a better understanding of what the implications of these different strategies are on a population level.

General reflection

Humans have a curious nature and they love to find reasoning in animal behaviour on the basis of environmental and genetic criteria. But maybe we have to admit that an individual animal has just as much complexity as any individual human. Environmental conditions can affect us, sometimes in similar directions, but even identical twins growing up in the same family develop as individuals with different personalities (Torgersen and Janson 2002). Every individual, both human and non-human, will experience the environment in a different way. It will unfortunately be very difficult - if not impossible - to find rules and algorithms that explain all variation in animal behaviour. However, we might be able to shed some light on the patterns and mechanisms, which will enable us to admire and enjoy the diversity and complexity in populations and societies even more.



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Publications

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Published

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- van der Meer, J., van Donk, S., Sotillo, A., Lens, L. 2019. Predicting post-natal energy intake of lesser black-backed gull chicks by Dynamic Energy Budget Modeling. - *Ecol. Model.*

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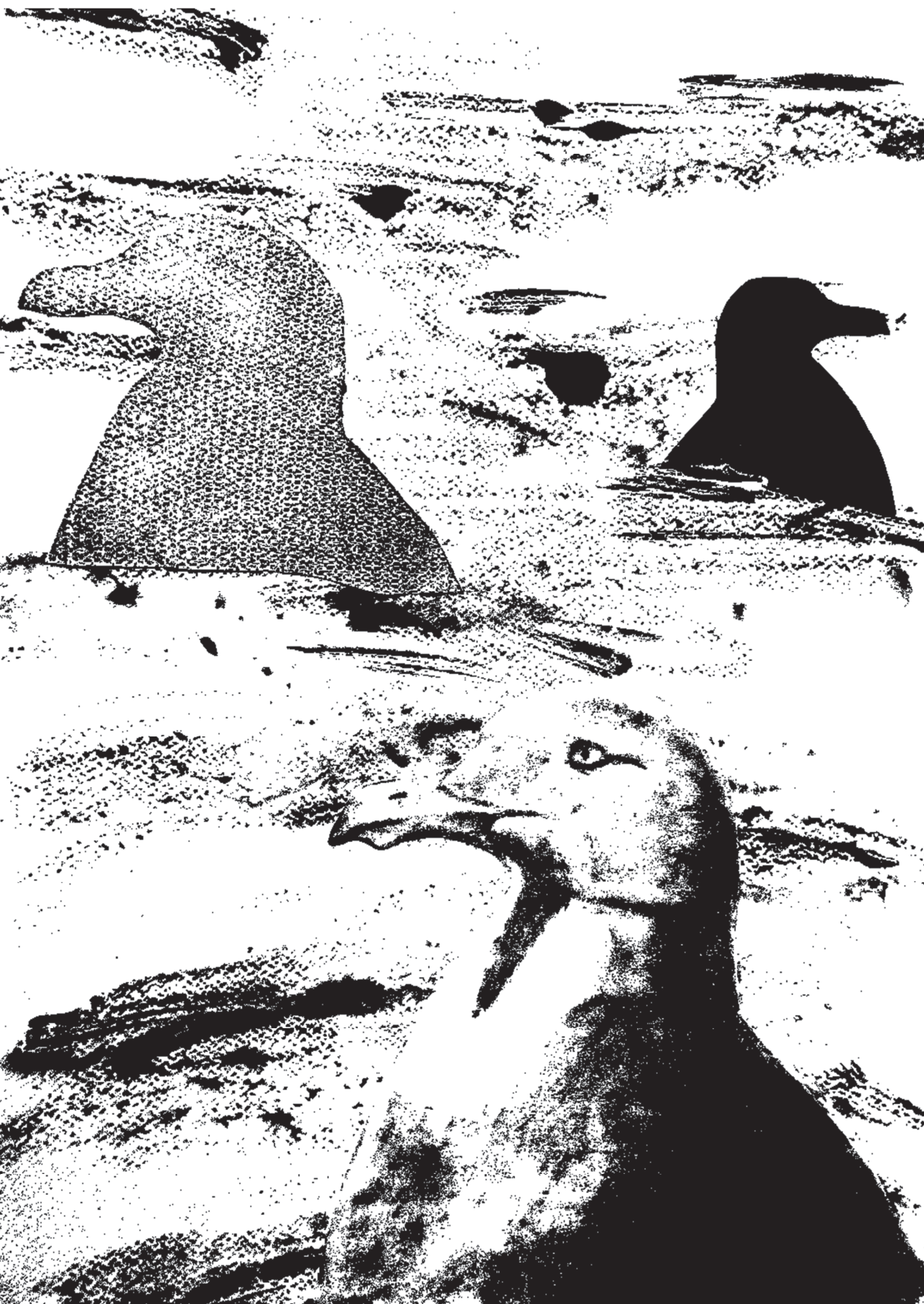
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- van Donk, S., Camphuysen, C. J., Shamoun-Baranes, J. and van der Meer, J. Behavioural and reproductive consequences after elimination of coastal foraging habitat in a generalist seabird

Other

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Summary

Nature offers a tremendous array of diversity, at many different levels of biological organization. Variation can for instance be found among ecosystems, among species or among individual genotypes or phenotypes of the same species. Individual variation in phenotypic traits is beautifully described by one of the most famous observers of the natural world, Charles Darwin. He recognized the importance of individual variation in observable traits as a driver of evolution.

One form of individual variation is the way animals forage. Individual variation within the same population may cause individuals to experience similar environmental conditions differently, possibly resulting in differences in fitness. In such a way, variation in foraging strategies can ultimately affect population dynamics. Therefore, understanding population dynamics must be preceded by knowledge of the individual foraging behaviour and its fitness consequences. In this thesis, fitness consequences of differences in foraging behaviour among individuals were studied. The main questions were: Do individuals differ in their reproductive success? Do individuals differ in how they spent their energy on foraging or reproduction? And how do individual animals behave when the environment changes?

A generalist seabird

To address these research questions, we studied a generalist seabird breeding on the island of Texel, the Netherlands. These herring gulls present an excellent system for the study of individual differences in foraging behaviour, because the population forages on a wide range of prey species. Furthermore, the population has been studied since 2006, which offered the possibility to study the population and individual differences over longer timespans than would be possible within a single PhD. Over this period, some changes in the foraging habitat took place, which enabled to additionally study consequences of foraging behaviour in a changing environment.

Herring gulls of Texel vary in diet, habitat use and site fidelity

Individual foraging behaviour was studied in one population, to shed light on several consequences of individual foraging behaviour. To do so, we used 10 years of breeding data and dietary analysis, next to advanced trackers measuring daily movements and behaviour. This revealed that individual herring gulls breeding on Texel differ in the type of prey and the diversity of prey they eat, which was shown by analysing regurgitates at the nest sites. Additionally, chapter 3 and 4 of this thesis showed that individuals differ both in the type of

habitat used as well as in the level of site fidelity regarding particular foraging patches. Furthermore, the acceleration measurements showed that individuals differ in the amount of time they invested in movement, with some individuals moving a lot and others resting more frequently.

Individual foraging behaviour relates to proxies of fitness

Differences in foraging strategies among individuals were found to have wide-ranging consequences. Herring gulls feeding their chicks with high caloric prey of anthropogenic origin like fishery discards and human waste have better reproductive success than herring gulls that feed their chicks with lower caloric prey (Chapter 2). The positive effect of these prey types is achieved despite the fact that foraging at sea and in urban areas is more expensive in terms of energy expenditure per foraging trip than foraging on terrestrial or intertidal habitat (Chapter 3). Besides variation in diet and foraging habitat, individuals were also found to vary greatly in the level of site fidelity to foraging patches when foraging on the same resource. However, site fidelity was not related to time and energy investment in breeding or foraging (Chapter 4). In conclusion, some behavioural differences between individual herring gulls have consequences on fitness proxies and can thus potentially affect population dynamics.

Foraging can be an expensive activity, especially during the reproductive period; gulls have to work considerably harder than others that are not breeding to gather enough food to raise chicks (Chapter 6). Herring gulls can avoid these higher foraging costs by skipping a breeding event, thereby potentially improving their lifetime reproductive success. It is important that adults gather enough food for their chicks; the model study showed that a relatively small decrease in food supply can already cause a sharp decline in growth, which reduces the chances of chick survival (Chapter 7). Hence, it might be better to skip a breeding event in years of unreliable food supplies.

Individual foraging behaviour and environmental changes

Large parts of the natural environment, particularly coastal habitats, are rapidly changing due to human activities. If herring gulls are to persist they must find ways of adapting to human induced environmental change. The herring gulls breeding on Texel have adapted to several human activities in the past and acquired new ways of foraging by starting to eat fishery discards, exploring cities and dumpsites and foraging on coastal defence structures as breakwaters. Over the years, less household waste became available to them and the amount of fishery discards declined. Besides, changes in coastal protection methods caused a decrease in coastal foraging habitat. In fact, herring gulls do change their foraging behaviour over time after changes in the environment (Chapter 5); their diet contains now proportionally more mussels and less anthropogenic prey than at the start of the monitoring on Texel. In addition, some

herring gulls changed their prey type in the first year after loss of the coastal foraging habitat. However, they did not change in such a way to prevent a decrease in reproductive success.

Synthesis

This thesis showed that individuals differ in fitness proxies depending on their foraging strategy. Differences in fitness between individuals can have implications on the dynamics and composition of a population. One hypothesis for future research is that individuals differ in life history traits. Successful breeders that forage on high caloric prey might suffer survival costs because of their higher energy expenditure and risks involved. This could potentially result in similar lifetime reproductive success compared to individuals with other foraging strategies and lower annual reproductive success. In this way, individuals with different strategies do stay in the population, as their fitness is similar. An alternative hypothesis is that some herring gulls have higher fitness because they are just better able to gather high quality food for their young. This could have implications on the population level when one type of habitat changes or is entirely removed. The population can be affected more severely, when foraging habitat of high producing herring gulls is affected.

For these types of questions, it is important to understand how animals respond to change. Some herring gulls do change their foraging behaviour but experience negative consequences on reproductive success. The failure of gulls to prevent reproductive consequences, for instance by moving to breeding sites closer to food sources, suggests that adult herring gulls have difficulties changing their habits. A hypothesis is that herring gulls develop their foraging strategies early in life, adapting to an environment that is assumed predictable over their lifespan. This implies that when the environment is changing rapidly, there will be fitness consequences for individuals that do not exhibit enough behavioural plasticity.

General reflection

This thesis shows that individual differences in foraging behaviour are affected by the environment and can result in variation in fitness proxies. In this way, individual differences in foraging strategies may steer population dynamics. For instance, by selection for individuals with beneficial diets in terms of reproduction or the ability to respond to environmental changes. To understand these processes better, it is necessary to determine how individual differences in foraging behaviour influences survival.

This thesis contributes to our understanding of the impact of individual differences in foraging behaviour on individual energy budgets and breeding success and can provide valuable input to understanding the impact of behavioural diversity on population dynamics. But above all, it presents a viewpoint from which to admire the stunning variation the natural environment offers us.

Samenvatting

De natuur biedt een enorme diversiteit, op verschillende niveaus van biologische organisatie. Zo is er variatie tussen ecosystemen, tussen soorten en in het genenpakket en de kenmerken van individuen binnen eenzelfde soort. Deze individuele variatie in kenmerken is prachtig beschreven door een van de bekendste natuurvorsers, Charles Darwin. Hij observeerde dat individuele variatie in eigenschappen een cruciale rol speelt in de evolutie.

Individen kunnen onderling op vele manieren verschillen, waaronder de manier waarop ze hun voedsel zoeken (foerageren). Hierdoor kunnen individuen dezelfde omgeving op verschillende manieren ervaren, wat kan leiden tot verschillen in de mate van geschiktheid van een individu de eigenschappen door te geven aan de volgende generatie (fitness). Variatie in foerageerstrategieën kunnen daarmee invloed hebben op het niveau van de populatie. Om deze populatie dynamiek beter te kunnen begrijpen, moeten we dus meer weten over welke consequenties de verschillen in foerageergedrag op fitness hebben. In dit proefschrift worden daarom de fitness consequenties van verschillen in foerageergedrag van individuen bestudeerd. De voornaamste vragen waren: Verschillen individuen in hoeveel nakomelingen ze groot brengen? Verschillen individuen in hoe ze hun energie gebruiken voor foerageren en reproductie? En hoe gedragen individuele dieren zich wanneer hun omgeving verandert?

Een generalistische zeevogel

Voor het beantwoorden van mijn onderzoeksvragen, bestudeerden we een generalistische zeevogel die broedt op de zuidpunt van Texel. Deze zilverbreeuuen zijn zeer geschikt voor het bestuderen van verschillen in foerageergedrag, omdat binnen de populatie een breed scala aan prooi-soorten wordt gegeten. Daarnaast wordt de populatie al bestudeerd sinds 2006, wat de mogelijkheid bood om langere tijdsreeksen aan gegevens te gebruiken dan mogelijk zou zijn binnen een enkel promotietraject. Gedurende deze periode vonden er ook een aantal veranderingen plaats in het foerageergebied van deze vogels, wat tevens de gelegenheid gaf om de aanpassing van individuen aan deze veranderende omgeving te bestuderen.

Zilverbreeuuen verschillen in dieet, habitat gebruik en plaats-trouwheid

Het foerageergedrag van individuele zilverbreeuuen is bestudeerd binnen één populatie, om duidelijkheid te scheppen over enkele consequenties van individueel foerageergedrag. Hiervoor maakten we gebruik van 10 jaar aan broedresultaten en dieet analyses, maar ook van geavanceerde trackers die verplaatsingen en gedrag vastlegden. Braakballen verzameld bij de nesten lieten zien dat Texelse individuele zilverbreeuuen verschillen in wat en hoe divers ze

eten. Daarnaast toonden we aan dat individuen ook verschillen in zowel habitatgebruik als de mate van trouwheid aan specifieke foerageerplekken. Tenslotte liet de analyse van gegevens van bewegingmeters in de trackers zien dat sommige individuen meer tijd besteden aan bewegen terwijl anderen meer tijd besteden aan rusten.

Individueel foerageergedrag is gerelateerd aan fitness

Individuele verschillen in foerageerstrategieën bleken uiteenlopende consequenties te hebben. Zilvermeeuwen die hun kuikens calorisch hoogwaardig voedsel met een aan mensen gerelateerde oorsprong gaven, zoals bijvangst van de visserij of (huishoudelijk) afval, brachten meer en grotere jongen groot dan zilvermeeuwen die hun kuikens prooi-soorten gaven van calorische lage waarde (hoofdstuk 2). Het positieve effect van dit type voedsel op reproductie werd bereikt hoewel het foerageren op zee (bijvangst) en in stedelijk gebied (afval) zilvermeeuwen meer energie kost per foerageertocht dan in landelijk of intergetijdengebied (hoofdstuk 3). Naast variatie in dieet en foerageergebied verschilden individuen ook enorm in de mate van plaatstrouwheid aan foerageerplekken voor een bepaalde type voedsel. Echter, de verschillen in plaatstrouwheid tussen individuen was niet gerelateerd aan de tijd en energie die werden geïnvesteerd in broeden of foerageren (hoofdstuk 4). Concluderend kunnen we zeggen dat individuele gedragsverschillen consequenties hebben op fitness van zilvermeeuwen en, mogelijk, de populatie dynamiek kunnen beïnvloeden.

Foerageren kost behoorlijk wat energie voor dieren, met name tijdens de reproductieve periode. We laten zien dat zilvermeeuwen zich aanzienlijk harder moeten inspannen wanneer zij voedsel moeten verzamelen voor hun opgroeiende kuikens dan dieren die dat niet doen (hoofdstuk 6). Zilvermeeuwen kunnen deze hoge energetische kosten vermijden door een broedseizoen over te slaan en hiermee hun conditie voor een volgend jaar te verbeteren. Hierdoor kunnen zij mogelijk het reproductieve succes tijdens hun leven verhogen. Het is namelijk belangrijk dat ze genoeg voedsel verzamelen voor hun kuikens: onze modelleerstudie laat zien dat een relatief kleine afname in voedselinname al kan leiden tot een significante afname in groei (hoofdstuk 7). Achterblijvende groei van kuikens vermindert hun overlevingskans. Daarom is het wellicht beter als zilvermeeuwen een broedseizoen overslaan in jaren dat zij niet kunnen vertrouwen op genoeg voedsel.

Foerageergedrag en omgevingsveranderingen

Grote delen van de natuur ondergaan veranderingen door menselijk handelen, met name de kustgebieden. Zilvermeeuwen in kustgebieden moeten zich zien aan te passen aan deze veranderingen. De zilvermeeuwen van Texel hebben zich in het verleden aangepast aan een aantal van deze veranderingen, en ze hebben zichzelf nieuwe manieren van foerageren eigen gemaakt. Zo zijn ze bijvangst van de visserij gaan eten, zijn ze steden en vuilnisbuilen gaan exploreren en foerageren ze op door de mens aangelegde dijken en strekdammen. Maar door

de jaren heen is er minder huisvuil beschikbaar gekomen voor de meeuwen en ook de hoeveelheid bijvangst is afgenomen. Daarnaast hebben veranderingen in de methodes om de kust te beschermen ervoor gezorgd dat een heel stuk foerageergebied langs de kust is verdwenen. De zilverbmeeuwen van Texel hebben hun foerageergedrag aangepast aan deze veranderingen (hoofdstuk 5); hun dieet bevat meer mossels en minder anthropogene prooi-soorten dan aan het begin van de studie op Texel. Daarnaast hebben een aantal zilverbmeeuwen hun prooi-keuze veranderd in het jaar na de verdwijning van foerageergebied langs de kust. Zij konden zich echter niet zodanig aanpassen dat zij een afname in hun reproductieve success konden voorkomen.

Synthese

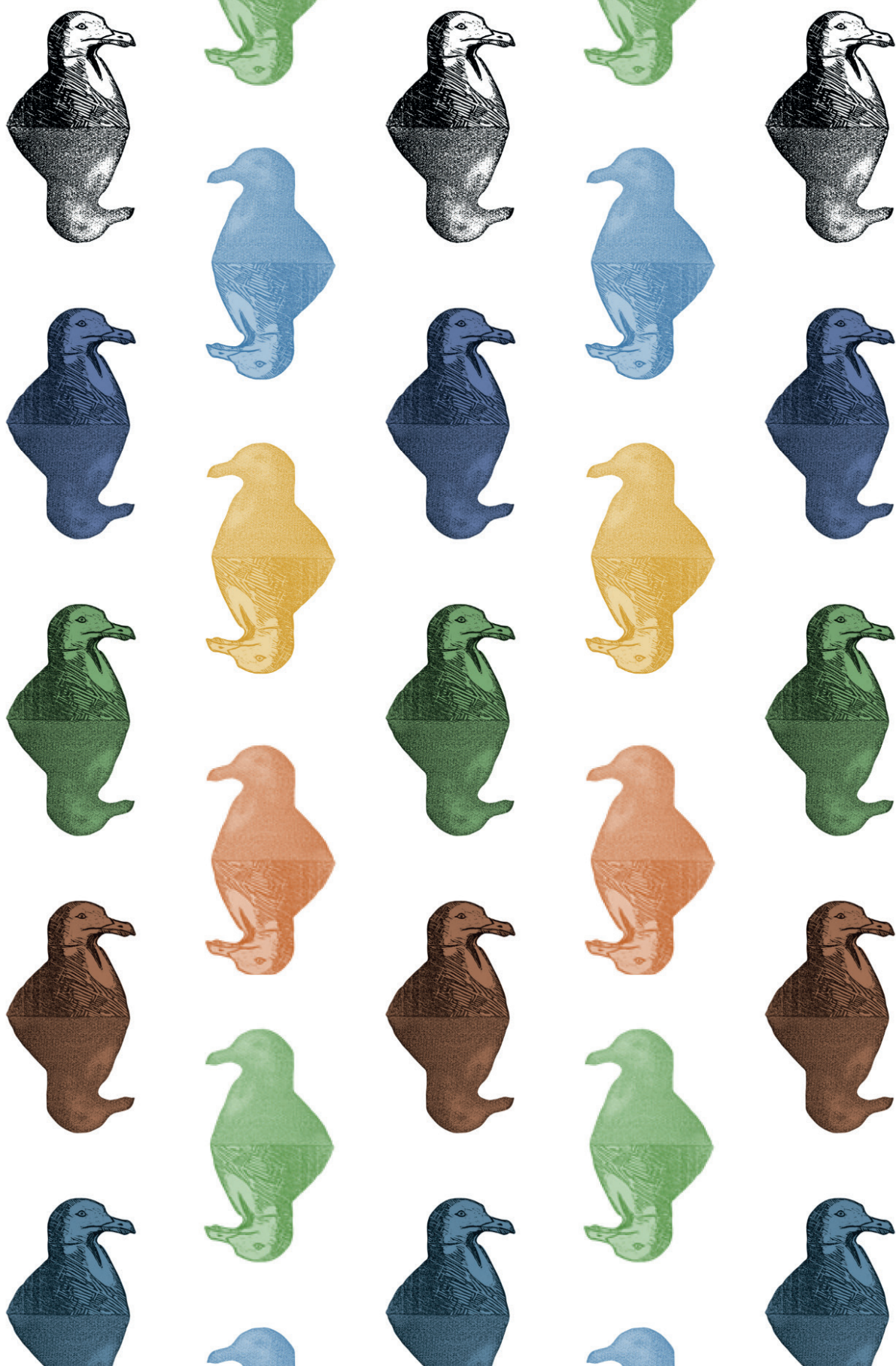
Dit proefschrift liet zien dat individuen verschillen in hun fitness afhankelijk van hun foerageerstrategieën. Verschillen in fitness tussen individuen kunnen effect hebben op de dynamiek en samenstelling van een populatie. Een hypothese voor toekomstig onderzoek hierover is dat individuen verschillen in hun levenscyclus. Succesvol reproducerende individuen die hoogwaardig calorisch voedsel eten zouden een lagere levensverwachting kunnen hebben vanwege de hogere energetische kosten en risico's die zij nemen tijdens het foerageren. Op die manier kunnen deze individuen en individuen met andere foerageerstrategieën en lager jaarlijks reproductief succes toch over het totale leven een vergelijkbaar reproductief succes hebben. Zo blijven individuen met verschillende strategieën in de populatie, aangezien ze een gelijke fitness hebben. Een alternatieve hypothese is dat sommige zilverbmeeuwen een hogere fitness hebben omdat ze beter zijn in het verzamelen van hoog kwalitatief voedsel voor hun jongen. Dit zou implicaties kunnen hebben op populatie niveau, wanneer een bepaald type prooi of habitat verandert of verdwijnt. Immers, de populatie wordt zwaarder getroffen wanneer foerageergebied van hoog reproducerende individuen wordt aangetast.

Voor dit soort vragen is het belangrijk om te begrijpen hoe dieren op veranderingen reageren. Dit proefschrift laat laten zien dat sommige zilverbmeeuwen hun foerageergedrag aanpassen aan veranderingen, maar dat dit resulteert in een lager broedsucces. Dat aanpassing van de Texelse meeuwen zonder negatieve consequenties op de reproductie niet lukt, suggereert dat adulte zilverbmeeuwen moeite hebben om hun gewoontes te veranderen. Bijvoorbeeld, verhuizing naar een broedgebied dicht bij (nieuwe) voedselbronnen lijkt niet te gebeuren. Het zou kunnen dat zilverbmeeuwen hun foerageerstrategieën vroeg in het leven ontwikkelen, waarbij ze zich aanpassen aan een omgeving waarvan ze aanneemen dat deze gedurende hun leven redelijk voorspelbaar is. Dit betekent dat wanneer de omgeving snel verandert, er fitness consequenties zijn voor individuen die niet genoeg flexibiliteit bezitten.

Reflectie

Individuele verschillen in foerageergedrag worden beïnvloed door de omgeving en dit kan leiden tot variatie in fitness. Op die manier kunnen individuele verschillen in foerageerstrategieën populatie dynamiek sturen. Bijvoorbeeld doordat individuen met een gunstig dieet voor hun reproductie of individuen die het vermogen hebben te reageren op veranderingen geselecteerd worden. Om deze processen beter te begrijpen, moeten we bestuderen of individuele verschillen in foerageergedrag overleving kunnen beïnvloeden.

Dit proefschrift draagt bij aan ons begrip hoe verschillen in foerageergedrag effect kunnen hebben op het energiebudget en het broedsucces van individuen. Daarnaast kan het waardevolle informatie leveren voor vervolgstudies naar de rol van diversiteit in gedrag op populatie dynamiek. Maar bovenal toont mijn studie wederom hoe rijk aan variatie onze wereld is, een rijkdom die wij vooral zouden moeten koesteren.

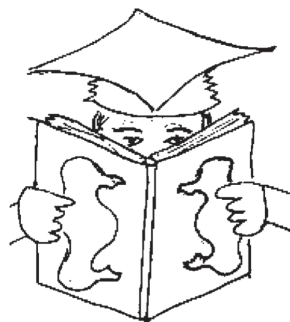


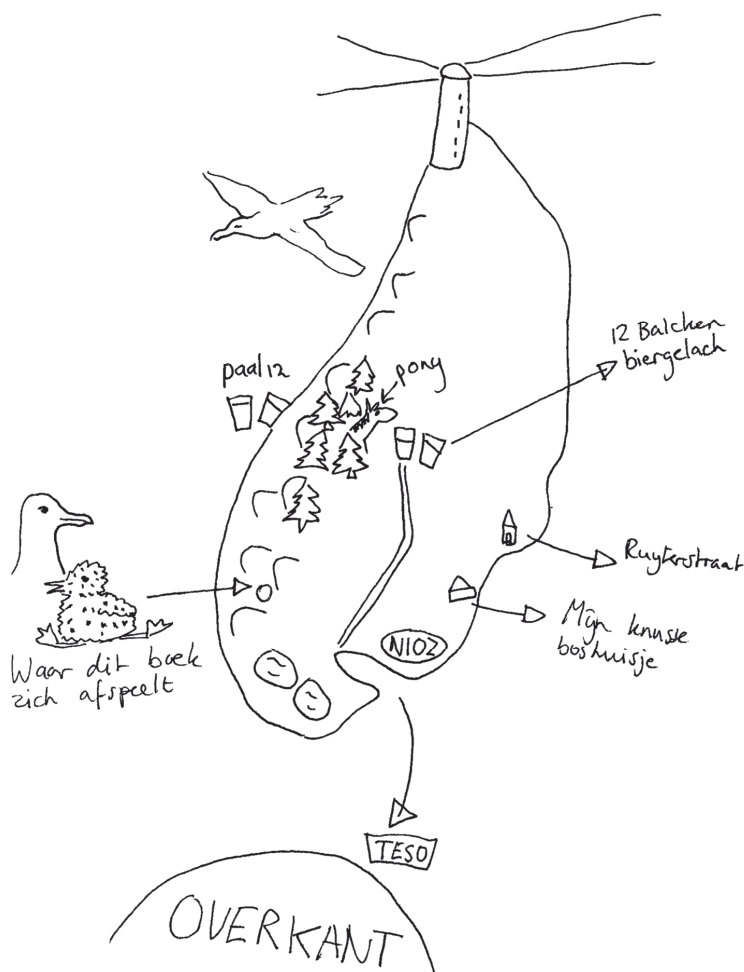
Acknowledgements

Ten eerste wil ik mijn drie begeleiders van harte bedanken voor hun begeleiding en enthousiasme. Kees, bedankt voor alle prachtige velddagen in de duinen, waar je me hebt geïntroduceerd bij alle meeuwen inclusief hun geschiedenis in bezochte plekken en partners. Ik vond het heel leuk dat we altijd de tijd namen om grappige of opmerkelijke gebeurtenissen te bestuderen en te becommentariëren (meeuw zonder stem, gekke rupsen, jonge gansjes etc). Het opzetten van de veldstudie en alle data die je al verzameld had voor het begin van mijn proefschrift waren van onschatbare waarde voor mijn werk. Ook naast het werk hebben we veel leuke ondernomen, je was de drijvende kracht achter ‘the-lonely-pity-people-dinner-club’ en naast ecologie delen we ook onze interesse in klassieke muziek en gingen we naar concertjes in het kerkje van Den Hoorn. Judy, ik kijk met veel plezier terug op de intensieve, altijd warme maar gezellige ‘tag-dagen’ in het veld en mijn bezoeken aan Amsterdam waar we goede discussies hadden over de wetenschap en ‘t persoonlijke leven. Je kritische blik en je niet aflatende doortastendheid hebben mij erg geholpen om de artikelen te schrijven. Jaap, bedankt voor de inspirerende discussies en gedachtewisselingen over populatie dynamica. Ik vond het leuk om met je na te denken over hoe de studies in een breder perspectief te zetten. Je hebt een jaloersmakende kennis over...van alles en nog wat! Leuk dat we nog wat langer gaan samenwerken bij WMR. Verder wil ik Willem Bouten bedanken voor zijn hulp met het annoteren van data, wat geleid heeft tot 2 leuke publicaties.

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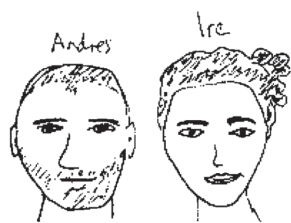
Dank aan de allerleukste ouders Joske en Dirk Pieter voor hun aangename gezelschap en interesse. Naast dat ik altijd op jullie kan rekenen, hebben jullie ook aanwijsbaar bijgedragen aan dit boekje door het lezen van de samenvattingen (en DP ook andere teksten) en hebben jullie meegedacht over de vormgeving. DP, ik vond het heel leuk om afgelopen periode te babbelen over de wetenschap en wetenschappelijke wereld, ook al werken we in zulke verschillende richtingen. Ook mijn beste broers, Adriaan & Olivier, bedankt voor jullie jolige gezelschap en adviezen, toch best leuk om nu iets regelmatig suffe dingen te delen in onze ‘moderne-familie-app’! Lieve Paulien en Dick, bedankt dat ik altijd bij jullie terecht kon als ik in Amsterdam op de UvA of VU moest zijn, en dat we dan gezellig met ‘n wijntje/whiskeytje de dag nog even doorspraken. En extra leuk dat de linosnede op de voorkant gemaakt is op een workshop samen met jou Paulien!





How special it is to live on this island for a while! A sea-breeze, numerous amounts of bird species, sea, dune and forest-scents, the beautiful gull colony, days of darkness and wind and then suddenly a stunning sunset.

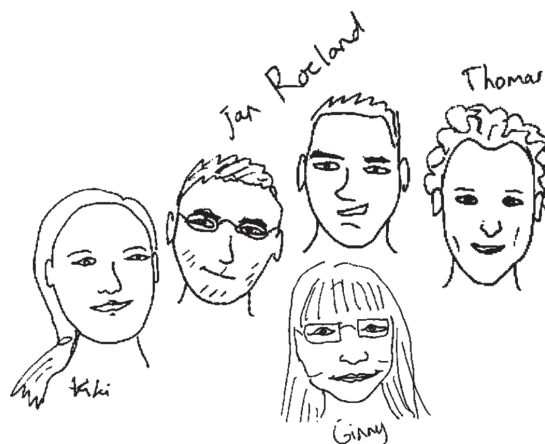
It is a great privilege to work at a place with so many nice colleagues, that became dear friends with whom I enjoyed spending time in the pub (12 Balcken), at the beach (Paal 12, or 13.5), in the forest or dunes, the Hors and occasionally at 'de overkant'.



Irene and Andres, thank you for being so extremely hospitable and always welcoming me on your couch at the Ruyterstraat. Irene, you are my PhD-buddy. Thanks for all the help with PhD-troubles and the great and annoying programs like R and Illustrator. Emma and Eva, thanks for the (ecology) discussions,

fieldwork and help with PhD issues. So comforting that you accompany me during this exciting day as paranymphs. Roeland, thanks for your cheerful company and helping me out with R codes. I hope that we (Eser...?) will continue sending stupid e-mails.





Ginny, thanks for your always down-to-earth support. Kiki, thanks for cooking delicious meals! Jan vG, so great that I could join to Mauritania. Anieke, thanks for your very helpful writing advice and reviewing the abstract and chapter 5. Rob Dekker, thanks for helping to collect cockles at the mudflat (chapter 5). Jan Drent, thanks for your interest and advice in my work. Anne and Job, thanks for the help in the field. Judith, thanks for the DNA extraction work from faeces. Selin & Nino, we should have dinner more often! Estefania, secretly still a great Texel

chick, Eldar & Julia, I enjoy our late dinner evenings a lot, Pascalle, for all good conversations about sustainability. Furthermore, I want to thank input in my work and creating a great working environment to all other COS colleagues; Eelke, Suzanne, Misha, Hebo, Carlijn, Clea, Jeroen H., Lise, Mark, Patrick, Tim, Tom, Theunis, Petra, Thomas O, Thomas L, Jeroen R, Henk, Allert, Roos (zo tof dat jij verder gaat met 't meeuwen werk!), Tamar, Paolo, Olivier, Lodewijk, Katja, Anita, Andreas, David, Luc, Loran, Dennis, Andre, Johan, Sonja, Sophie, Geert, Valerie, Piet vdH, Jim, Pieterella, Tanya, Jorge, Anouk, Bruna, etc. and colleagues from UvA Morgan and Elspeth.

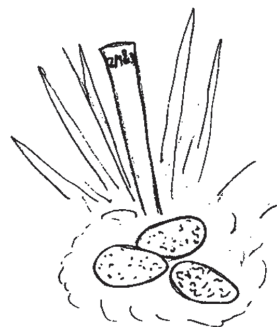
Friends from other departments enriched my life with their culture, dinners, parties, cheerful chats at the coffee machine or doorway, interesting science and joyful conversations. Thanks Zeynep, Michele, Diana, Alejandro, Jaime, Clara, Saara, Eveline, Esmee and many more.



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Daarnaast wil ik nog alle vrijwilligers die ringen hebben afgelezen, hebben geholpen met het veldwerk en uitzoeken van monsters hartelijk bedanken. Zonder jullie hulp was het veldwerk heel wat lastiger geweest! Speciale dank aan ‘vaste’ vrijwilligers: Arnolt Gronert, Caroline Walta, Miranda Zutt, Maarten van Kleinwee, Marian Dekker en Harmke De Hoogh. Ook wil ik de studenten die hun stage liepen bij ons bedanken: Evert Boesenkool, Tristan Bakx, Margot Maathuis, Lyce Saathof, Anne Ausems, Lotte Hazeleger en Boukje Heidstra (ook bedankt voor de mooie paardrij-ritten!).



Dear gulls, thanks for being so unique! When people are speaking bad about you, I almost feel personally addressed. Don't they see how elegant you can pick up a fish from the water, or how rich your courtship behaviour is, how peaceful you can eat mussels at breakwaters, how many personalities you have, how well you know the rhythm of the tides or the rhythm of people. Special attention to some of them; the gull that is carrying my name SUUS, she unfortunately lost her partner MAWF, but gathered several years of valuable data with her tracker. Also MANM (p.22) was an icon with its breeding territory clearly visible when entering the colony and extremely site faithful to its breakwater at Julianadorp. Jut (with voice) en Jul (voiceless) at the depot accompanied us always when drinking coffee. Two gulls served as models for the drawings & linocut in this thesis: MAVT (p. 64) and a ring-less female from ‘the roughs’ in the colony.

