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.
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 gulls 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.

![Foraging landscape of the herring gull breeding population of Texel, the Netherlands.](image)

**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.