# Life-history variation within and between two closely related gull species

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# Table of contents

# 1

# General Introduction

## 1.1. INTRODUCTION

Animal species differentially invest in growth, reproduction and survival throughout their lifetime and the balance between these energetically conflicting demands is what we refer to as ‘life-history’ (Stearns 1992, Bennett and Owens 2002). Life-history theory aims at understanding why species vary so extensively in life-history strategies, defined as complex patterns of life-history traits co-evolved to optimize these opposing challenges for a particular environment (Rochet 2000). In one way or another, all free-living animals are exposed to environmental fluctuations and will have to adjust their life-cycle accordingly to optimize their chances of reproduction and survival (Barta et al. 2008). The life-cycle of an animal, includes all of the stages from birth to death, i.e. from early development and maturation, over the adult life-stage to senescence. Based on the assumption that natural selection cannot maximize investment in relation to growth, reproduction and survival at all stages, it appears that investment in one life-history trait necessitates evolutionary compromises in others. Evolutionary models predict that selection will create particular life-histories in particular environments as a result of trade-offs between different traits (Linden and Moller 1989). For instance, r/K selection theory relates to the selection of combinations of traits in an organism that trade-off between quantity and quality of offspring, seemingly to optimize fitness in particular environments (Stearns 1992). These terms, r and K, are drawn from population growth models, where r is the maximum growth rate of the population, K is the carrying capacity of its local environment. As the name implies, r-selected species are those that place an emphasis on a high growth rate, tend to live in unstable or unpredictable environments and are more likely to go through early maturation, high reproductive output and short life-cycles. Organisms that exhibit r-selected traits range from bacteria and diatoms, to insects and grasses, to various semelparous cephalopods and small mammals, particularly rodents. By contrast, K-selected species predominates in stable or predictable environments where the ability to compete successfully for limited resources is crucial as population numbers are always close to the maximum that their environment can bear. K-strategists have a long life expectancy, have multiple reproductive cycles with few young, which often require extensive parental care and mature much more slowly. Organisms with K-selected traits include large organisms such as elephants, humans and whales, but also smaller, long-lived organisms such as Arctic terns (*Sterna paradiseae*).

### Seasonality and the annual cycle

Many long-lived species inhabit areas with strong seasonality where environmental conditions such as resource availability and temperature may change in a predictable manner within the year, and consistently from year to year within the period of a single lifespan (Wingfield 2008, Newton 2011). To cope with such temporal variability, animals are likely to experience selection pressures to carry out different activities related to reproduction and survival at favorable times of the year, i.e. an optimal annual routine (McNamara and Houston 2008) or life-history staging (sensu Piersma and Drent 2003). These routines vary according to the annual pattern of environmental conditions animals experience and show great variation in the timing, duration and sequence of major activities through the year. Breeding is a crucial stage in the annual cycle of animals and in terms of food requirements probably the most demanding. Not only do individuals have to collect food for self maintenance, but they also have to provide food for offspring (Newton 2011). With few exceptions (e.g. some baleen whales that feed at high latitude during summer when plankton is abundant while calving takes place at lower (warmer) latitudes where there's much less food), breeding will occur at that time of year when food is sufficiently available to raise offspring (Lack 1950). The ultimate example of timing relative to the seasonal environment is the timing of breeding of Great Tits (*Parus major*) relative to caterpillar abundance (Verhulst and Nilsson 2008). Hence, from a fitness perspective, the choice of when to breed is a key indicator of being well adapted to an environment. The timing of breeding affects both  the likelihood of producing high-quality young and the probability of adult survival owing to a seasonal decline in rearing conditions, i.e. lower quality food for a higher parental effort (Drent and Daan 1980). Logically, the timing of breeding takes precedence over other activities of the annual cycle that are then scheduled around it.

### Trade-offs and carry-over effects

All activities have costs and benefits. More specifically, activities related to growth, survival and reproduction have fitness consequences and form the basis of trade-offs and carry-over effects.

The timescale over which these consequences manifest themselves vary from immediate, to relatively short term to long term. (McNamara and Houston 2008). For instance, if an animal leaves cover to attract or find a partner to mate with, one immediate consequence might be that it is killed by a predator. Consequences that are not immediate in terms of survival, but have future implications for fitness later on in life are referred to as carry-over effects in literature. While trade-offs encompass, by definition, only negative relationships between traits and life-history stages, carry-over effects can be both positive and negative. The term 'carry-over effect' within the framework of ecological and evolutionary studies, has often been applied in migratory study systems, principally in birds, which has led to an emphasis on non-lethal effects across seasons (Harrison et al. 2011, O'connor et al. 2014). In this context, Harrison et al. (2011) defined carry-over effects as any events and processes occurring in one season that result in individuals making the transition between seasons in different states (levels of condition) consequently affecting individual performance in a subsequent period. However, O'connor et al. (2014) suggested that ecological carry-over effects can also occur between life-history stages, developmental stages, physiological states, or social situations, and each will be associated with a discrete time-scale. Therefore, they proposed the working definition that carry-over effects occur in any situation in which an individual's previous history and experience explains their current performance in a given situation. This more general concept allows one to identify carry-over effects in a broader range of situations, e.g., within and across life-history stages, seasons, years,... and to examine the mechanisms that drive non-lethal interactions between distinct periods of an organism's lifetime.

Fitness consequences are minimized by weighing benefits against costs to reproduction and survival. For example, on the long term, events and processes procuring beneficial effects during early development may incur fitness costs during the adult stage of the life-cycle (Cam and Aubry 2011). Such as permanent phenotypic changes in the structure and functioning of the body that promote survival under poor conditions during the developmental stage (e.g. changes to the endocrine system that serve to protect the supply of glucose to the developing brain in humans), but which become disadvantageous in adulthood (e.g. impaired glucose tolerance, Monaghan 2008). The sequential nature of life-history organization means that virtually every activity an individual initiates during its lifetime will have downstream consequences (Harrison et al. 2011). Short-term consequences involve carry-over effects between life-history stages of the annual cycle. Due to variation in access to resources and the manner in which they are allocated, individuals make the transition between these stages in different levels of physical condition with downstream consequences for reproduction and survival. Owing to the intertwinement of life-history stages and seasons in the annual cycle, these kind of carry-over effects are also called cross-seasonal effects, e.g. the trade-off between winter survival and spring breeding. Individuals that occupy high-quality territories during winter will make the transition to the breeding season with more energy reserves than others positively affecting subsequent reproductive performance. For example, dens of Artic Foxes (*Alopex lagopus*) receiving supplemental food over winter had higher breeding success than control (unsupplemented) dens (Angerbjörn et al. 1995).

### Life-history variation and age

Age commonly explains a large part of the life-history variation between and within individuals. For example, long-lived species that reproduce on several occasions during their lifetime exhibit age-related patterns of reproductive rates. The general pattern is that reproductive performance increases with age during the first reproductive years to reach a plateau at middle age, sometimes followed by a decline in old age as an expression of senescence (Forslund and Pärt 1995). For example, Using an 18-year data set, Dugdale et al. (2011) show an initial improvement in breeding success with age, followed by a later and steeper rate of reproductive senescence in male than in female badgers (*Meles meles*).

Long-lived species mature slowly and individuals will delay age of first reproduction to a point that it no longer increases survival and lifetime reproductive success (Bennett and Owens 2002). At this point they will have to face the trade-off between investment in current reproduction at the expense of future reproduction and/or survival (Stearns 1992). In other words, high investment will compromise the chances of surviving to breed again. Within a population, individuals will differ both in their inherent reproductive ability and probability of survival due to a variety of genetic, maternal and environmental factors (Aubry et al. 2011). If individuals of different breeding quality differ in age of first breeding or survival probability, a progressive appearance and/or disappearance of phenotypes can lead to differences in average reproductive performance between age classes (Forslund and Pärt 1995). Increasing reproductive performance with age can also be explained by age-related improvements in individual's ability to reproduce. Owing to e.g. previous breeding experience or better foraging skills, a given investment in reproduction might have a higher return in older than in younger individuals. Alternatively, individuals may enhance their reproductive performance as they get older because they allocate more resources to reproduction as future reproductive potential and life expectancy decreases (Forslund and Pärt 1995). Understanding life-history variation requires examining the performance of individuals and changes in performance over life, and thus it is important to determine the extent to which these changes are driven by both between- and within-individual variation. It is very likely that several factors act in concert to create age-specific variation in life-history traits.

## 1.2. AVIAN LIFE-HISTORIES

Birds are remarkably consistent in their basic life-cycle (Bennett and Owens 2002). Unlike mammals, reptiles and fish which all contain both oviparous and viviparous species, all birds start life as eggs. Again unlike many species of reptiles, fish and amphibians, they do not carry their egg or eggs around with them, instead they deposit them in purpose-built sites called nests. These eggs are warmed until they hatch. After a variable period of growth (i.e. the nestling period), birds leave the nest and learn to fly (i.e. fledging period). Most birds experience a rapid and determinate growth and reach their definite adult size at the time of fledging. This is unlike mammals, for example, where juveniles are usually much smaller than adults at weaning, and unlike reptiles and fish, which may continue to grow through life. Once sexually mature, all birds typically attempt to breed for more than one season during their adult life. So there is a complete lack of viviparity and semelparity in avian life-histories (Bennett and Owens 2002).

### Why birds?

Birds are an excellent group for investigating patterns of life-history variation. While the avian life-cycle is fairly consistent, birds display a great deal of variation in each aspect of their life-cycle (Bennett and Owens 2002). Furthermore, birds are an exceptionally well-studied group compared to other vertebrate groups, particularly in the wild. The huge body of literature on life-history diversity in birds has acted as a catalyst for an enormous range of theories in ecology, behavior and evolution. Much research, for example, has focused on the significance of this variation. Do these patterns have adaptive value or are they the result of constraints (i.e. limitations) working on the individual, or even restraint performed by the individual as the net result of benefits versus costs to fitness. In the following paragraphs, we will elaborate on the patterns of life-history variation that are specifically dealt with under the relevant data chapters.

### Patterns of egg size variation

Females can manipulate the quality of their offspring by depositing more nutrients in their eggs (Clutton-Brock 1991). Because larger eggs contain higher absolute amounts of nutrient reserves than do smaller eggs, egg size is positively related to several individual components of fitness, such as mass, growth rate and to a lesser extent survival of hatchlings (Krist 2011). Hence, egg size is a vital life-history trait under maternal control and constitutes an essential measure of parental investment in offspring (Roff 2002). However, eggs vary greatly in size across bird species, both in terms of absolute size and relative to female size (Bennett and Owens 2002). Within bird species, egg size varies both among and within clutches. Egg size variation between clutches accounts for most of the observed intraspecific variation, with the largest egg in a population being at least 50-100 per cent bigger than the smallest (Christians 2002). However, the causes leading to and maintaining this level of variation in natural populations still remain unclear (Williams 1994, Christians 2002). Life-history theory predicts a trade-off between egg size and number and this implies that females should maximize their reproductive output by adjusting the amount of resources invested in particular eggs. Albeit, in birds, such a trade-off between egg size and number is often weak or non-existent (Roff 2002). Even if there exists such an optimal level of resource investment, the inherent stochasticity of environments causes unpredictability in the availability of resources and may affect egg size through female adaptive adjustments or constraints during egg formation. For example, females could be expected to adaptively increase egg size when conditions are poor and reduce egg size under favorable conditions (Yampolsky and Scheiner 1996). On the other hand, egg size may be reduced under poor environmental conditions due to environmentally reduced female condition (Christians 2002). Despite the smaller variation in egg size within clutches, intraclutch variation may likewise result from nutritional/energetic constraints acting on laying females or may reflect adaptive differential investment in offspring in relation to laying order. In most birds, eggs hatch asynchronously because incubation begins before the clutch is complete, resulting in a hierarchy by age and size within the brood, with the youngest sibling being at a significant initial disadvantage (Howe 1978). Slagsvold et al. (1984) hypothesized that female birds might adaptively vary egg size to influence the degree of sibling competition. An increase in egg size with laying order should then represent an adaptation to counteract the effect of asynchronous hatching ("brood-survival strategy"), whereas a decline with sequence of laying should accentuate the effect of asynchronous hatching, facilitating brood reduction ("brood-reduction strategy"). Alternatively, nutritional or energetic constraints operating on the laying female may explain intraclutch egg-size variation (Slagsvold et al. 1984). Such constraints may be especially applicable in cases where, within a clutch, an egg's size declines with the order in which it was laid because the relative size of the last eggs is presumed to depend on the female's energy reserves (Sydeman and Emslie 1992). Because these hypotheses are not mutually exclusive, egg size may be subject to both constraints and adaptive adjustments in accordance with the prevailing environmental conditions.

### Variation in the age of first reproduction

Once fully fledged and independent from their parents, birds spent variable periods of time before they reach sexual maturity, find a mate and breed for the first time (Bennett and Owens 2002). Between bird species, most of this variation occurs along the axis of the slow-fast life-history continuum. Relatively short-lived species such as Common Quail (*Coturnix coturnix*) and Zitting Cisticola (*Cisticola juncidis*) are able to produce offspring in their first year of life from 1-2 months old (Snow et al. 1998), while long-lived seabirds like albatrosses and petrels do not begin breeding for many years, with some first breeding in their teens (Dillingham et al. 2012). But why do some birds postpone reproduction at all? Intuitively, breeding as early as possible should be the best strategy because it increases the number of lifetime reproductive attempts, and hence, at first glance should be favored by natural selection (Fay et al. 2016). However, reproductive activities carries both benefits and costs and the advantages of early first reproduction can be outweighed by negative effects on survival and future reproduction. Therefore, there should be selection pressures to minimize the net fitness costs by weighing the risk of premature breeding, associated with a lowered survival probability, against the advantage of presumed increased breeding opportunities with a consequent gain in lifetime reproductive success (Frederiksen and Bregnballe 2001). Indeed, in long-lived species, the age of first breeding is a key life-history decision since an increase in life-time reproductive success varies primarily with breeding longevity, and thus early mortality is very costly (Reid et al. 2003). Once delayed sexual maturity has evolved, there is generally a substantial degree of flexibility/variability in the age at which individuals start breeding. It has been suggested that the life-history continuum hypothesis described at the interspecific level may occur at the intraspecific level, with some individuals favoring survival compared to others investing more in reproduction (Reid et al. 2010). In this context, age at first breeding could be linked to individual life-history strategies, early recruitment occurring in individuals investing more in reproduction and late recruitment occurring in individuals favoring survival. Alternatively, variations in the age at first reproduction may be explained by variations in individual quality, i.e. differences between individuals in performance levels related to reproduction and survival that are consistent throughout life. For example, variation in individual quality in relation to resource acquisition (i.e. foraging skills) may strongly affect the age at first reproduction. As a consequence, low quality individuals may recruit at old age, and some may not recruit at all as indicated by the observation of lower survival and recruitment probability for the oldest immature age-class (Aubry et al. 2009). Once sexually mature, an individual must not only choose a suitable time, but also a suitable place to start his reproductive career. Ideally, individuals should select sites where they will experience the greatest reproductive success. To optimize their future reproductive success it is believed that pre-breeders prospect potential breeding sites towards the end of the breeding season to gather information on their quality (Becker and Bradley 2007). Conspecific attraction and conspecific reproductive success are two possible cues in this selection process (Frederiksen and Bregnballe 2001). Accordingly, recruitment is most likely at sites following years with high breeding population densities and high local reproductive success. If all sites happen to be unattractive, an individual will choose to postpone its first breeding attempt rather than recruit at any of the available sites. Obviously, the age of first breeding may also be affected by constraints. More specifically, if nest sites or mates are in short supply, some individuals will not be able to attempt to breed in the year or at the site that would otherwise be optimal for them (Frederiksen and Bregnballe 2001).

### Variability in movement patterns: timing and extent

Birds show a striking variety in inter- and intraspecific movement patterns. During the breeding stage of the annual cycle, the nesting site is the fixed center of activity and from here parents move around from one feeding place to another as part of their day-to-day routine. Movements are in all directions, but are restricted to a home range extending over distances of meters in small passerines to hundreds of kilometers in pelagic seabirds (Newton 2010, Chapman et al. 2011, Newton 2011). Movements of sedentary species remain limited within this home range during their entire adult life. In contrast, migratory birds will make seasonal return movements in a more fixed direction between breeding and wintering areas ranging over hundreds to thousands of kilometers (Alerstam et al. 1990), with the transpolar journeys of Arctic terns (*Sterna paradiseae*) often featured as the quintessential example. Members of the same species can also differ in their migratory tendency. For example, European robins (*Erithacus rubecula*) show a longitudinal gradient of migratory tendency, where populations from the north of the species range are migratory and southern populations are sedentary (Newton et al. 2008). Furthermore, individuals within populations may show differences in migratory behavior as well, with some individuals migrating whilst others remain resident (Dingle 1995). This migratory dimorphism is known as ‘partial migration’ and is widespread among birds. Even when all individuals within a population migrate, the distances they travel may vary according to sex and/or age. These differences can be linked to body size and dominance status which also differ between sex and age groups. The phenomenon is referred to as differential migration and is equally ubiquitous in birds (Ketterson and Nolan 1983).

The young of both sedentary and migratory parents, after they have become independent, will undertake their first journey. Sedentary individuals will wander off in all directions, and surviving young will eventually settle to breed at a distance of a few meters to tens of kilometers from their hatch sites, i.e. natal dispersal (Newton 2010). About the same time, migratory individuals embark on their first autumn migration to the wintering areas. Juveniles leave the breeding areas earlier or later than the adults depending on whether they molt before or after autumn migration. The time pressures are somewhat different between the two age groups because, whereas the juveniles have a short body molt (or in some species no molt), the adults have a longer complete post-breeding molt, including all flight feathers (Newton 2010). If the molt is completed after migration, adults will leave before the juveniles and vice versa. Such age-related differences in migration timing occur in a wide range of species. In some species, the juveniles also progress more slowly on migration, taking longer and more frequent stops, or less direct migration routes (Evans and Davidson 1990). The effects of relaxation on time constraints on timing of migration are also apparent among the immatures of species which do not breed in their first year of life, freeing them to migrate at different times than adults. In such species, individuals migrate from the breeding grounds in their first autumn, and do not return from the wintering grounds in the next spring, but only in a later one, when they are two or more years old. These immatures either remain in their non-breeding areas year-round over one or more years, or they may only return part ways towards the breeding areas. Alternatively, they may prospect the breeding areas later in the breeding season (see previous paragraph). Unconstrained by the needs of breeding, they can follow a slower migration schedule allowing for more stop-overs and explorative detours. Eventually they will start to breed in their natal or another breeding site and even then, young breeders usually arrive later than older, more experienced breeders (Forslund and Pärt 1995). Timing of migration will also often differ between the sexes as a consequence of the different roles they fulfill in breeding. In most bird species, males arrive first on the breeding areas to establish and defend territories, where they are later joined by the females. Not being involved in territory establishment, females are under less pressure than males, and can arrive later. Albeit females are not completely unconstrained as there is substantial competition for the most desirable territory-holding males. This need for the territory-holding sex to arrive early is supported by the fact that, in species with reversed sexual roles like the three phalarope species, females arrive before the males (Newton 2011).

## 1.3. STUDY SPECIES

I studied variation in life-history traits within and between Herring Gulls *Larus argentatus* and Lesser Black-Backed Gulls *Larus fuscus*, two phylogenetically and ecologically closely related species that occur in sympatry in NW Europe (Wernham et al. 2002). It might be argued that because a large proportion of the variation in each life-history variable is located at high taxonomic levels, differences in ecology and behavior between closely related species must have little effect on life-history variation (Bennett and Owens 2002). Nevertheless, fine-grained differences between closely related taxa are also likely to be adaptive and using a comparative approach will help to pinpoint important factors associated with variation in particular suites of life-history traits (Linden and Moller 1989). Moreover, in order to investigate how life-histories vary, you need to collect a sufficient amount of data on a number of key variables pertaining to measures of size, rates of development, survival and reproduction. As both species breed in mixed colonies along the coasts and some inland sites, this concentration of breeding pairs in one place allows one to collect life-history data on a large number of individuals with relative ease. Last, but not least, the Herring Gulls and Lesser Black-backed Gulls have been part of a color-ringing scheme since 1999 and subject to additional field work that yielded a wealth of information on the individual life-history trajectories.

The Bulk of the Belgian breeding population could be found on newly created land at the port of Zeebrugge. In 1987 the first Herring Gulls started to breed there, followed a year later by the first breeding records of Lesser Black-backed Gulls. From 1995 onwards, number of breeding pairs increased exponentially and maxima of 2336 Herring Gull pairs and 4760 Lesser Black-backed gull pairs were counted. From 2011 onwards, predation by foxes, disturbance and habitat loss through ongoing industrial development were largely responsible for a decline in breeding numbers. In the period 2000–2010, Zeebrugge hosted on average 91% of all large gulls in Belgium. This proportion decreased to 33% in 2015. In 2015, only 549 Herring Gull pairs and 1149 Lesser Black-backed Gull pairs continue to breed in the port of Zeebrugge.  In the colony of Ostend, breeding started in 1993. Here the the numbers of breeding pairs are still increasing with a maximum of 505 pairs of HG and 551 pairs of LBBG in 2015. In Ostend most gulls breed on rooftops both in industrial areas and in the town itself (Stienen et al. 2016).

Both species show a comparable degree of sexual size dimorphism with males larger than females and mature after 3–7 years (Snow et al. 1998). Besides breeding side by side in mixed colonies, they show striking similarities in their breeding biology. In the colony at Zeebrugge, egg-laying starts as early as mid-April, but has a marked synchronized peak mid-May when most pairs start laying. Eggs of both species are identical in size, shape and color pattern, although those of Herring Gull might be slightly larger in mean size. Incubation takes 28-30 days. The semi-precocial young are cared for by both parents and leave nest within 2–3 days, but stay within territory. Offspring fledges after ± 45 days.

Herring Gulls were believed to predominantly feed in the intertidal zone on mollusks, crustaceans and other invertebrates, while Lesser Black-backed Gulls were believed to chiefly feed at the open sea and generally avoid the nearshore area (Bosman 2009 and references therein). However,  Stienen et al. (2016) identified a more divers use of foraging areas in both species using GPS-loggers. Lesser Black-backed Bulls (and to a lesser extent Herring Gulls) do frequently feed in agricultural areas, while both species do frequently use urban environments and industrial areas for foraging. In fact, both species were found to predominately feed inland.

### Herring Gull

Herring Gull has two subspecies: *L. a. argentatus* and *L. a. argenteus*. It is one of our most common gulls and a familiar sight, particularly in coastal areas, where it outnumbers al other gull species throughout the year (Bosman 2009). Belgian breeding birds belong to the race *argenteus* (Fig. 1.1).

**Figure 1.1.** Adult breeding Herring Gull (*Larus argentatus argenteus*) in the outer port of Zeebrugge, May 2010. Peter Adriaens.

Already in October the first Herring Gulls return to the breeding colony in Zeebrugge, but numbers stay low until February (Van Waeyenberghe et al. 2002). The breeding season runs roughly from mid-April to the end of July. From August onwards, Belgian Herring gulls disperse within a variable, but mostly limited, predominantly coastal radius, resulting in seasonal movements towards nonbreeding areas and convergence towards breeding areas at the population level. Dispersal is in all directions towards the Netherlands, northern France, the North Sea, and the English Channel, but there is a marked tendency for south-westward movements (Van Waeyenberghe et al. 2002). Some individuals move such short distances that they can be regarded as residents.

### Lesser Black-backed Gull

In Lesser Black-backed Gull, three subspecies are recognized: *L. f. graellsii*, *L. f. intermedius* and *L. f. fuscus*. Lesser Black-backed Gulls migrate over greater distances and spend more time at sea than Herring Gulls. Birds breeding Belgium belong to the race *graellsii* (Fig.1.2).

**Figure 1.2.** Adult breeding Lesser Black-backed Gull (*Larus fuscus graellsii*) in the outer port of Zeebrugge, July 2013. Simon Feys.

Lesser Black-backed gulls can be considered true migratory birds with the breeding and wintering grounds clearly separated from each other. Belgian Lesser Black-backed Gulls migrate south in winter, mainly hibernating in the south of Spain, Portugal, and North Africa (Stienen et al. 2016). The first adults return to the breeding grounds already in December, but numbers stay low until March (Van Waeyenberghe et al. 2002). Most sexually immature Lesser Black-backed Gulls stay on the wintering grounds in their second and third calendar-year. From April till July adults are breeding. From August onwards they start the migration back to the wintering grounds and in October hardly any adults and their offspring are still present in the colony. In the post-breeding season Lesser Black-backed gulls mainly head southwards to the coast of Southwest Europe and Northwest Africa in accordance with the main wintering grounds of the western population of this species (i.e. *intermedius* and *graellsii*; Wernham et al. 2002).

## 1.4. STUDY METHODS AND MATERIALS

My approach to study the life-history variation within and between Herring Gulls (HG) and Lesser Black-backed Gulls (LBBG) was twofold: (a) measuring life-history traits in the offspring of both species from egg till fledging during the breeding season and (b) analyzing the data on individual life-history trajectories contained within the color-ring database managed by the Research Institute for Nature and Forest, Belgium.

### Fieldwork

Field work was carried out during three successive breeding seasons (2010–2012) in the mixed breeding colonies in the outer ports of Zeebrugge (51°21’N, 03°11’E) and Oostende (51°14’N, 02°56’E, Belgium). Each year, from mid-April until the end of May, I searched these colonies daily for new nests. In total, 960 nests (HG: 191, 171 and 140; LLBG: 102, 174 and 182 in 2010, 2011 and 2012 respectively) were marked with an individually coded stick and visited every day to record laying order. For each new egg, I recorded the laying date (earliest recorded laying date, HG: 26th April in 2010 and 2012, LBBG: 27th April in 2010). Eggs were measured with calipers (± 0.01 mm; maximum length and width) and marked with a non-toxic, water-resistant marker in relation to their laying order. I calculated egg volume (hereafter, absolute egg size) using the formula V (in cm3) = 0.000485×length×width2 (Oro et al. 1996, Soldatini et al. 2008). To facilitate location of nestlings, a selection of 210 nests (HG: 65, 42 and 37; LLBG: none, 39 and 27 in 2010, 2011 and 2012 respectively) were surrounded with a 50-cm-high chicken-wire enclosure (± 3–4 m in diameter) a week before expected hatching. Enclosures were provided with wooden shelters (roughly large enough to fit three near-grown fledglings) where chicks could hide from predators or inclement weather. From the end of May until mid-June, enclosed nests were visited daily to record hatching dates (earliest recorded hatching date, HG: 19th May in 2010, LBBG: 25th May in 2011). To assign each chick to its egg of origin, egg teeth of chicks were marked with nontoxic ink during the pipping stage. The level of hatching asynchrony of a chick was calculated as the time (in days) elapsed since the hatching of the first chick of the same brood and was set to 0.5 days for eggs that hatched on the same day if there was an unambiguous difference in timing of hatching (i.e., assessed by dry versus still-wet plumage). Once hatched, 581 chicks (HG: 190, 116 and 98; LLBG: none, 107 and 70 in 2010, 2011 and 2012 respectively) were marked with individually coded insulation tape around the tarsus, weighed with a digital balance, and measured every third day during the first 3 weeks of linear growth. I measured tarsus length, head length, bill length, and bill depth of each chick with calipers (± 0.01mm). Growing wings were measured with a ruler (± 1mm). At the time of fledging, a total of 338 surviving chicks (HG: 123, 66 and 67; LLBG: none, 47 and 35 in 2010, 2011 and 2012 respectively) were equipped with uniquely coded color-rings so that their life-history trajectories could be traced after fledging. A few body feathers were also sampled. To determine sex, DNA was extracted from these feathers using the Nucleospin® Tissue method and amplified using CDH1-linked primers P2/P8 (Griffiths et al. 1998) and 2550F/ 2718R (Fridolfsson and Ellegren 1999).

### Color-ring database

In 1999, a color-ring project on Herring Gull and Lesser-blacked Gull was launched at the Flemish coast. Every individual equipped with a color-ring was entered in the database managed by the Research Institute for Nature and Forest, Belgium. Most birds were ringed either as pullus or as breeding adult in the colonies of Zeebrugge and Oostende. Besides 104942 resightings from as many as 1465 ring-reading volunteers up to May 2015 and counting, additional field work at the colony of Zeebrugge yielded a wealth of information on the individual life-history trajectories of color-ringed Herring Gulls and Lesser Black-backed Gulls. For each color-ringed gull, the earliest sighting in the colony (arrival date) was written down based on meticulous observations conducted from morning to evening every second weekday between mid-winter until the start of egg-laying. Every year, the activity of all breeding birds was followed up throughout the breeding season, taking GPS coordinates of each nest during early nest-building and marking all nests with an individually coded stick. Gulls display a high degree of nest site fidelity which facilitated early detection of known breeders in the colony and allowed ample time to search for new recruits. For new recruits ringed as pullus and, hence, of known age, age of first breeding was recorded. Breeding birds were sexed on the basis of direct size comparison of paired individuals, complemented by observations of copulation and courtship behavior at the colony during subsequent breeding seasons. For the analysis of variation in life-history traits, I compiled sub-datasets and made extensive use of linear mixed-effects models in which individual identity was always included as a random factor to account for between-individual variation.

## 1.5. OBJECTIVES OF THE THESIS

The objective of this doctoral thesis is to deepen our conceptual knowledge of life-history variation using Herring Gulls and Lesser Black-backed Gulls as study species.

In Chapters 2 and 3, I studied the effects of pre-fledging characteristics on both pre- and post-fledging survival in Herring Gulls. Being less sensitive to manipulations during the nestling stage than Lesser Black-backed Gulls, Herring Gulls were chosen as study species for these studies.

In **Chapter 2**, my objective was to examine the significance of egg size variation within clutches, while simultaneously considering the effect of hatching asynchrony on pre-fledging survival because both might operate concomitantly, either directly or indirectly through effects on relative body condition. Is egg size variation solely the result of constraints acting on the laying female or does it have adaptive value. If the latter is true, patterns of variation must be associated with patterns of chick mortality in a consistent manner. Because most pre-fledging mortality in Herring Gulls occurs before 10 days post-hatching, particularly for c-chicks, I also examined whether this period coincides with the brood-reduction period, that is, the period post-hatching where offspring survival most strongly varies with laying order.

Although life-history theory predicts that adult survival will be the key parameter driving population trajectories in long-lived species, post-fledging survival has recently been acknowledged as an important source of variability in population growth rates (Sergio et al. 2011, Payo-Payo et al. 2016). Therefore, improving the accuracy of age-specific survival estimates and the factors the influence them will improve our understanding of the population dynamics of long-lived species. However, knowledge about post-fledging development in long-lived species is usually limited due to a lengthy immature stage coinciding with natal dispersal during which individuals are generally not observable (Nevoux et al. 2010, Souchay et al. 2013, Saunders et al. 2014). Therefore, pre-fledging characteristics are often used to predict the survival of young birds because they are relatively easy to monitor and, hence, carry-over effects of breeding season events on post-fledging survival have been found in long-lived species (Cooke et al. 1984, Harris et al. 1994, Weimerskirch et al. 2000, Ludwig and Beckers 2006, Cam and Aubry 2011). In **Chapter 3**, I therefore examined the possible carry-over effects of nestling growth and other pre-fledging characteristics (hatching date, hatching asynchrony, and brood size and rank after brood reduction) on post-fledging survival.

In **Chapter 4**, I investigated the mechanisms underlying temporal variation in timing of arrival among and within individual Lesser Black-backed Gulls in the context of age-related life-history variation. Are they the result of the progressive (dis)appearance of phenotypes, age-related improvements of competence and/or optimization of reproductive effort. We opted for the Lesser Black Backed Gull as study species, because this species is much more time constrained during spring migration compared to Herring Gull due to the longer distances it migrates. I addressed the following questions: (i) To what extent does timing of arrival constitute a dynamic trait (i.e. resulting from changes within individuals over time) or a fixed, consistent individual trait (i.e. resulting from phenotypic variation among individuals)? (ii) What is the role of experience gained from earlier prospecting or breeding?; (iii) Is there a correlation between variation in age of first breeding ($\alpha$) or age of last breeding ($\omega$) and age-related variation in timing of arrival?; (iv) To what extent is survival probability affected by early arrival and/or prospecting behavior at early age?

In **Chapter 5**, I assessed the extent to which sex-specific constraints related to structural size and/or reproduction may shape variation in migratory behavior of sexually mature male and female Herring Gulls and Lesser Black-Backed Gulls. Herring gulls and Lesser Black-backed gulls represent an ideal study system for a comparative approach, because both species display a similar sexual size dimorphism and breeding biology, but widely differ in their migratory behavior.

# 2

# Effects of intraclutch variation in egg size and hatching asynchrony on nestling development and survival in semi-precocial Herring Gulls

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## SUMMARY

Intraclutch egg size variation may non-adaptively result from nutritional/energetic constraints acting on laying females or may reflect adaptive differential investment in offspring in relation to laying/hatching order. This variation may contribute to size hierarchies among siblings already established due to hatching asynchrony, and resultant competitive asymmetries often lead to starvation of the weakest nestling within a brood. The costs in terms of chick mortality can be high. However, the extent to which this mortality is egg size-mediated remains unclear, especially in relation to hatching asynchrony which may operate concomitantly. I assessed effects of egg size and hatching asynchrony on nestling development and survival of Herring Gulls (*Larus argentatus*), where the smaller size and later hatching of c-eggs may represent a brood-reduction strategy. To analyze variation in egg size, I recorded the laying order and laying date of 870 eggs in 290 three-egg clutches over a 3-year period (2010–2012). I measured hatchlings and monitored growth and survival of 130 chicks from enclosed nests in 2011 and 2012. The negative effect of laying date ($\beta = -0.18 \pm$ SE 0.06, $P = 0.002$) on c-egg size possibly reflected the fact that late breeders were either low quality or inexperienced females. The mass, size, and condition of hatchling Herring Gulls were positively related to egg size (all $P < 0.0001$). C-chicks suffered from increased mortality risk during the first 12 days, identified as the brood-reduction period in my study population. Although intraclutch variation in egg size was not directly related to patterns of chick mortality, I found that smaller relative egg size interactively increased differences in relative body condition of nestlings, primarily brought about by the degree of hatching asynchrony during this brood-reduction period. Thus, the value of relatively small c-eggs in Herring Gulls may lie in reinforcing brood reduction through effects on nestling body condition. A reproductive strategy Herring Gulls might have adopted to maintain a three-egg clutch, but that also enables them to adjust the number of chicks they rear relative to the prevailing environmental conditions and to their own condition during the nestling stage.

## INTRODUCTION

Among birds, egg size varies both among and within clutches. Egg size may be positively correlated with hatchling size, mass, condition, and nestling growth rate and survival and, hence, could have important fitness consequences (Christians 2002, Risch and Rohwer 2000, Krist 2011). Although egg size variation between clutches accounts for most observed variation (Christians 2002), intraclutch variation may affect fitness more than the former because smaller chicks that hatch from smaller eggs must compete with larger siblings during early development (Aparicio 1999, Maddox and Weatherhead 2008). Although the relative size of the egg from which a nestling hatches is known to affect its probability of fledging, the causes of intraclutch variation in egg size and the nature of the relationships with offspring survival remain unclear (Amat et al. 2001, Hargitai et al. 2005, Whittingham et al. 2007, Maddox and Weatherhead 2008, Forbes and Wiebe 2010, Svagelj and Quintana 2011, Parejo et al. 2012). For instance, intraclutch variation in egg size could either reflect an adaptive maternal strategy to improve reproductive success or, alternatively, be a non-adaptive consequence of maternal constraints.

If intraclutch variation in egg size has adaptive value, this variation may be related to laying order and ultimately to the hatching order of offspring (Slagsvold et al. 1984). In this context, parents often start incubating before clutch completion and eggs laid first will then be among the first to hatch (i.e., hatching asynchrony) and, consequently, have a head start on their siblings (Stenning 1996). The resulting size and strength advantage creates a hierarchy among siblings, and the ensuing competitive asymmetries can often initially lead to a poorer relative body condition and ultimately cause the death of the weakest, last-hatched chick(s) in a brood (Kim et al. 2010, Gilby et al. 2011, Merkling et al. 2014). Regardless of the adaptive value of asynchronous hatching (Kim et al. 2010), female birds may adaptively vary egg size to modify the effects of hatching asynchrony (Slagsvold et al. 1984). For instance, an increase in egg size with laying order would counteract competitive asymmetries imposed by hatching asynchrony (brood survival hypothesis, Howe 1978), whereas a decrease in egg size would accentuate competitive differences established by asynchronous hatching (brood reduction hypothesis, Parsons 1970). However because the ability of females to affect chick survival by varying egg size is dependent on the degree of hatching asynchrony, Maddox and Weatherhead (2008) argued that researchers should consider their effects simultaneously when trying to identify the relative contribution of egg size to chick survival.

Like most species in the genus *Larus* (Reid 1987), Herring Gulls (*Larus argentatus*) have a truncated clutch-size frequency distribution centered at three eggs, and last-laid (c) eggs are considerably smaller than the first (a) and second (b) eggs. Individual Herring Gulls also show considerable variation in when they begin incubation and, as a consequence, c-eggs generally hatch 1–4.5 days after the other two eggs (Parsons 1972, Kim et al. 2010).

Asynchronous hatching and the smaller size of the c-egg of gulls have potential adaptive value because, during periods with unfavorable environmental conditions (e.g., food scarcity), being able to reduce brood size and allocate available resources to fewer young by preferentially provisioning larger, high-quality young may be beneficial (Slagsvold et al. 1984, Stenning 1996, Hilström et al. 2000). However, the results of previous studies of Larids have been contradictory. Comparing synchronous and asynchronous broods, Hébert and McNeil (1999) found reduced survival of c-chicks in asynchronous broods, whereas other investigators have reported either reduced survival of c-chicks in synchronous broods (Sydeman and Emslie 1992, Hillström et al. 2000) or no difference in c-chick survival between synchronous and asynchronous broods (Royle and Hamer 1998, Bradbury and Griffiths 1999). In addition, the results of several studies have revealed a positive relationship between small c-egg size and increased mortality rate in c-chicks (Parsons 1970, Hébert and Barclay 1986, Risch and Rohwer 2000), whereas other investigators have reported that small terminal egg size did not influence c-chick survival (Nager et al. 2000, Kim et al. 2010). Nevertheless, c-chick mortality can be very high and the extent to which this mortality is egg size-mediated, especially in relation to hatching asynchrony, remains unclear.

My objective was to examine the importance of egg size variation in clutches of a coastal population of Herring Gulls, while simultaneously considering the effect of hatching asynchrony on chick survival because both might operate concomitantly (Maddox and Weatherhead 2008). Of previous studies of Larids, only Kim et al. (2010) modeled the effects of hatching asynchrony and egg size on chick survival simultaneously, but only did so for Herring Gull chicks up to 10 days old. Because most chick mortality in Herring Gulls (Kilpi et al. 1996) occurs before this age, particularly for c-chicks (Hillström et al. 2000), I also examined whether this period coincides with the brood-reduction period, that is, the period post-hatching where offspring mortality most strongly varies with laying order (Mock 1994).

Within a constraints-adaptation conceptual framework, I also examined the extent to which absolute egg size was negatively affected by laying date. In my study population, inexperienced and lesser-quality birds start breeding later in the season (Van Waeyenberghe et al. 2002, D. S. Bosman, unpubl. data). Risch and Rohwer (2000) found that parental quality of Herring Gulls was reflected in the capacity to lay large eggs, and Davis (1975) found that older birds laid larger eggs. Additional objectives were to determine if (1) absolute egg size is positively correlated with one or more absolute measures of individual offspring development (i.e., mass, size, and condition at hatching and nestling growth rate), (2) patterns of intraclutch variation in egg size and hatching asynchrony are directly associated with patterns of chick mortality, (3) intraclutch variation in egg size and hatching asynchrony are indirectly related to nestling survival through effects on relative body condition, and (4) the effect of intraclutch variation in egg size (direct or indirect) encompasses the whole chick-rearing period or is restricted to the brood-reduction period.

## METHODS AND MATERIALS

Field work was carried out during the breeding seasons of 2010–2012 in a mixed breeding colony of Herring Gulls and Lesser Black-backed Gulls (*L. fuscus graellsii*) at the outer port of Zeebrugge (Belgium, 51°21′N, 03°11′E). Each year, from mid-April until the end of May, I searched selected sub-colonies daily for new nests. New nests were marked with an individually coded stick and visited daily to record laying order. For each new egg, I recorded the laying date, expressed as the number of days after 1 December of the previous year (i.e., the earliest recorded arrival date of a breeding bird in my study population; Bosman et al. 2013). Eggs were measured with calipers (± 0.01 mm; maximum length and width) and marked with a non-toxic, water-resistant marker in relation to their laying order. I calculated egg volume (hereafter, absolute egg size) using the formula $V$ (in $cm^3$) = $0.000485 \times \text{length} \times \text{width}^2$ (Oro et al. 1996, Soldatini et al. 2008). Because I was mainly interested in effects of intraclutch variation in egg size on survival and the relative body condition of chicks, I converted absolute egg size measures to relative differences in egg size (hereafter, relative egg size) as the difference between the volume of each egg of a clutch and the clutch mean (Maddox and Weatherhead 2008).

To facilitate location of nestlings in 2011 and 2012, some nests (2011: 53 nests; 2012: 48 nests) were surrounded with a 50-cm-high chicken-wire enclosure (~3–4 m in diameter) a week before expected hatching. Enclosures were provided with wooden shelters (variable size, but large enough for three near-grown fledglings) where chicks could hide from predators or inclement weather. I assumed that providing shelter did not improve the survival of enclosed versus non-enclosed chicks because the colony was located in a developing harbor with many places for chicks to hide (e.g., abandoned construction material, rabbit holes, and vegetation within a radius of 10 meters around each nest). The placement of enclosures differed between years and because of high nest-site fidelity by Herring Gulls, nests of different adults were likely studied in each year.

From the end of May until mid-June, enclosed nests were visited daily to record hatching dates. To assign each chick to its egg of origin, egg teeth of chicks were marked with nontoxic ink during the pipping stage. The level of hatching asynchrony of a chick was calculated as the time (in days) elapsed since the hatching of the first chick of the same brood and was set to 0.5 days for eggs that hatched on the same day if there was an unambiguous difference in timing of hatching (i.e., assessed by dry versus still-wet plumage). Because chicks generally hatched in the same order eggs were laid (see results), laying order and hatching order were treated as synonymous. Using laying order in statistical analyses allowed me to differentiate between chicks with a hatching spread of less than half a day.

Once hatched, all chicks were marked with individually coded insulation tape around the tarsus, weighed with a digital balance, and measured every third day. Only individuals measured on the first day of hatching were included in the analyses. Because single trait measures were earlier shown to provide poor proxies of overall body size in gulls (Bosman et al. 2012), I measured tarsus length, head length, bill length, and bill depth of each chick with calipers (±0.01 mm), and quantified body size as the first axis of a principal component analysis (PC1) in SPSS statistics Ver. 21 (IBM Corporation, Armonk, NY). PC1 explained 98% of the body size variation in nestlings and had high positive loadings for tarsus length (0.97), head length (0.99), bill length (0.98), and bill depth (0.98). Chick growth rates were calculated for the period of linear growth as the slope of the linear regression of body size on age (in days) performed in SPSS statistics (Bolton 1991). When calculating growth rates, only chicks that survived until 23 days old and where I had at least four measurements between day 3 and 23 post-hatching were included (Bogdanova and Nager 2008, Hauber and Moskat 2008). Body mass was regressed on body size, and the standardized residuals were used as a measure of body condition (GLM, $r = 0.29$, $P < 0.0001$; Green 2001). Relative body condition was calculated as the deviance from the average body condition of siblings measured on the same day.

To analyze variation in egg size, I only used three-egg clutches because it was impossible to determine if eggs in clutches of one or two eggs had been lost to predation or cannibalism. One four-egg clutch was also excluded from further analysis, resulting in a sample size of 870 eggs from 290 nests for which both laying date and egg size were measured. In addition, hatching order was recorded for 93 nests (Table 2.1). Because multiple eggs from a single nest are not statistically independent, I fitted a series of linear mixed-effects models (LMM; Littell et al. 1996) in SAS 9.3 (SAS Institute Inc., Cary, NC) with nest-specific (i.e., random) intercepts and slopes and with nest nested in year (Schielzeth and Forstmeier 2009). Absolute egg size was modeled as the dependent variable, laying order (treated as a continuous variable) and laying date and their interaction as fixed effects, and year as random factor. Levels of significance of all fixed variables and their two-way interactions were tested in a stepwise backward selection procedure, and the Kenward–Roger method was applied for estimating the degrees of freedom (not necessarily integers; Kenward and Roger 1997). When laying order significantly interacted with laying date, analyses were split by laying order. To compare group means, *post-hoc* tests were carried out with Tukey's tests. To explain variation in hatchling size, mass, and condition, I analyzed the effect of laying order, laying date, absolute egg size and their two-way interactions on these traits for 115 hatchlings. I also tested the relationships of these independent variables with growth rates of 75 nestlings.

**Table 2.1.** Within-clutch variation in timing of egg laying and hatching, and related variation in egg size in a Herring Gull colony. The a-egg is the first-laid, the b-egg the second-laid, and the c-egg the last-laid egg in a clutch. Values of laying and hatching are mean ± SE relative to the laying day of the a-egg (day 0). Values for egg size are mean ± SE.

| Variable | a-egg(1) | b-egg(2) | c-egg(3) | *N* (clutches) |
|---|---|---|---|---|
| Laying (days) | NA | 2.16 ± 0.04 | 4.48 ± 0.06 | 295 |
| Hatching (days) | 0.01 ± 0.01 | 0.63 ± 0.09 | 2.06 ± 0.12 | 93 |
| Hatching first | 92/93 | 1/93 | 0/93 | |
| Hatching last | 0/93 | 0/93 | 93/93 | |
| Egg size | 81.46 ± 0.39 | 79.66 ± 0.41 | 73.66 ± 0.35 | 290 |
| Largest egg size | 184/290 | 103/290 | 3/290 | |
| Smallest egg size | 11/290 | 21/290 | 258/290 | |

To analyze how patterns of chick survival (*N* = 130 chicks) were directly affected by relative egg size and hatching asynchrony, I fitted a mixed-effects Cox regression in R Ver. 2.15.3 (package coxme; Therneau 2012, R Core Team 2014) with laying date, laying order, hatching asynchrony, relative egg size, and all two-way interactions as fixed factors. Levels of significance of all fixed variables and two-way interactions were tested by a stepwise backward selection procedure. Year and nest nested in year were included as random factors in this and all subsequent mixed-effects Cox regressions. To test how patterns of chick survival were indirectly influenced by relative egg size and hatching asynchrony, I applied a three-step procedure. First, I determined the brood-reduction period, defined as the period during which offspring mortality most strongly varied with laying order (Mock 1994). To determine this period, I fitted a series of mixed-effects Cox regressions with a change point (Pons 2003). Such models divide data into two discrete time steps, which allowed me to test the effect of laying order on chick mortality during discrete time periods before and after this change point. Because chick survival was monitored daily from hatching to fledging, I shifted the setting of this change point from one Cox regression to the next on a daily basis as well. If brood reduction is restricted to the early period of the nestling stage, I would expect a time step that divides the brood-reduction period (i.e., significant effect of laying order) from the non-brood-reduction period (i.e., no significant effect of laying order; Shizuka and Lyon 2013). Second, I modeled two additional mixed-effects Cox regressions with the change point set at the dividing time step (see Results) to test for relationships between relative body condition and chick survival. In the first model, I tested whether chick survival varied with relative body condition during the brood-reduction period (*N* = 78 chicks with an average age of 5.4 ± 2.5 SD days). In the second model, I tested whether chick survival after the dividing time step/change point varied with relative body condition of the survivors during the non-brood reduction period (*N* = 60 chicks with an average age of 21.8 ± 6.9 SD days). Finally, I ran two LMMs (SAS 9.3) to determine relationships of hatching asynchrony, relative egg size, and the two-way interaction with relative body condition during the brood reduction and the non-brood reduction periods, respectively. In these analyses, I modeled hatching asynchrony and relative egg size as fixed effects (independent of their levels of statistical significance) and laying order as a covariate. Because hatching asynchrony, relative egg size and laying order may be highly correlated, modeling these variables simultaneously might produce problems with collinearity. To determine the severity of the latter among independent variables in my dataset, I used the COLLIN, VIF, and TOL Options (SAS 9.3) to obtain condition indices, variance inflation factors, and tolerance values, respectively, that is, collinearity diagnostics (see Results). Values are presented as means ± SE.

## RESULTS

I recorded the laying order and laying date of 870 eggs in 290 three-egg clutches (2010: 122 nests, 2011: 103 nests, 2012: 65 nests). Egg-laying started on 26 April in 2010, 2 May in 2011, and 1 May in 2012. For 93 three-egg clutches (2010: 41 nests, 2011: 36 nests, 2012: 16 nests), I also recorded the hatching date for all eggs. The last egg hatched on 19 June in 2010, 18 June in 2011, and 19 June in 2012. In 2011 and 2012, I monitored survival until fledging (i.e., the latter half of July) for 130 chicks (2011: 86 chicks, 2012: 44 chicks) in enclosed nests (*N* = 75 nests) where all three eggs hatched. Most chicks that did not survive simply disappeared and were probably predated. In 2011, an unknown proportion of chicks (including near-grown fledglings) died from an unidentified infection. Although I cannot formally analyze it, I have no reason to believe that either predation or disease rates differed between enclosed and non-enclosed nests (pers. obs.). Few chicks died of starvation.

**Table 2.2.** Results of a mixed-effects Cox regression with change point on survival rates of Herring Gull nestlings. For each model, I tested the effect of laying/hatching order on chick survival before and after the change point. Day 12 is the earliest point at which I detected a switch between laying/hatching-order-based survival to laying/hatching-order-independent survival. Only the results for the period from 8 to 14 days post-hatching are shown. Bold data indicate significant p-values.

| | Before Change point | | After Change point | |
|---|---|---|---|---|
| Change point | *Z* | *P* | *Z* | *P* |
| Day 8 | 2.24 | **0.03** | 2.66 | **0.008** |
| Day 9 | 2.42 | **0.02** | 2.53 | **0.01** |
| Day 10 | 2.72 | **0.006** | 1.96 | **0.05** |
| Day 11 | 2.72 | **0.006** | 1.96 | **0.05** |
| Day 12 | 3.04 | **0.002** | 1.18 | 0.24 |
| Day 13 | 3.06 | **0.002** | 1.12 | 0.26 |
| Day 14 | 3.06 | **0.002** | 1.12 | 0.26 |

### Variation in egg traits

Eggs were laid every second day on average, although both shorter and longer laying intervals regularly occurred (mean = 2.24 ± 0.03 d, range = 0–7 d). Eggs generally hatched in the order they were laid (Table 2.1), and hatching asynchrony was significantly related to laying order (LMM, $F_{1,185} = 346.4$, $P < 0.0001$). Although the timing of hatching differed significantly for a-, b-, and c-chicks (Tukey, $P < 0.0001$), a- and b-chicks often hatched on the same day (56.9%, $N = 93$) and the hatching asynchrony between them was lower than expected from the laying interval (0.63 ± 0.09 d). The laying span between a- and c-eggs averaged 4.48 ± 0.06 d, but the hatching span of 2.06 ± 0.12 days was significantly shorter (paired *t*-test: $t_{90} = 16.7$, $P < 0.0001$). Absolute egg size decreased with laying order (LMM, laying order, $\beta = 3.9 \pm 0.2$, $F_{1,584} = 566$, $P < 0.0001$; Table 2.1) and a-, b-, and c-eggs differed significantly in size (Tukey, $P < 0.0001$).

When jointly modeling the effects of laying date and laying order on absolute egg size, the two-way interaction was significant (LMM, $\beta = -0.09 \pm 0.03$, $F_{2,582} = 12.3$, $P = 0.0005$). Splitting the data by laying order revealed a significant negative relationship between laying date and the absolute size of c-eggs ($\beta = -0.18 \pm 0.06$, $F_{1,286} = 9.7$, $P = 0.002$), but not a-eggs ($\beta = -0.06 \pm 0.07$, $F_{1,154} = 1.0$, $P = 0.33$) and b-eggs ($\beta = -0.05 \pm 0.07$, $F_{1,288} = 0.5$, $P = 0.49$).

Relative egg size of c-eggs was negatively related to mean egg size of a clutch (GLM, $r = -0.28$, $P = 0.02$).

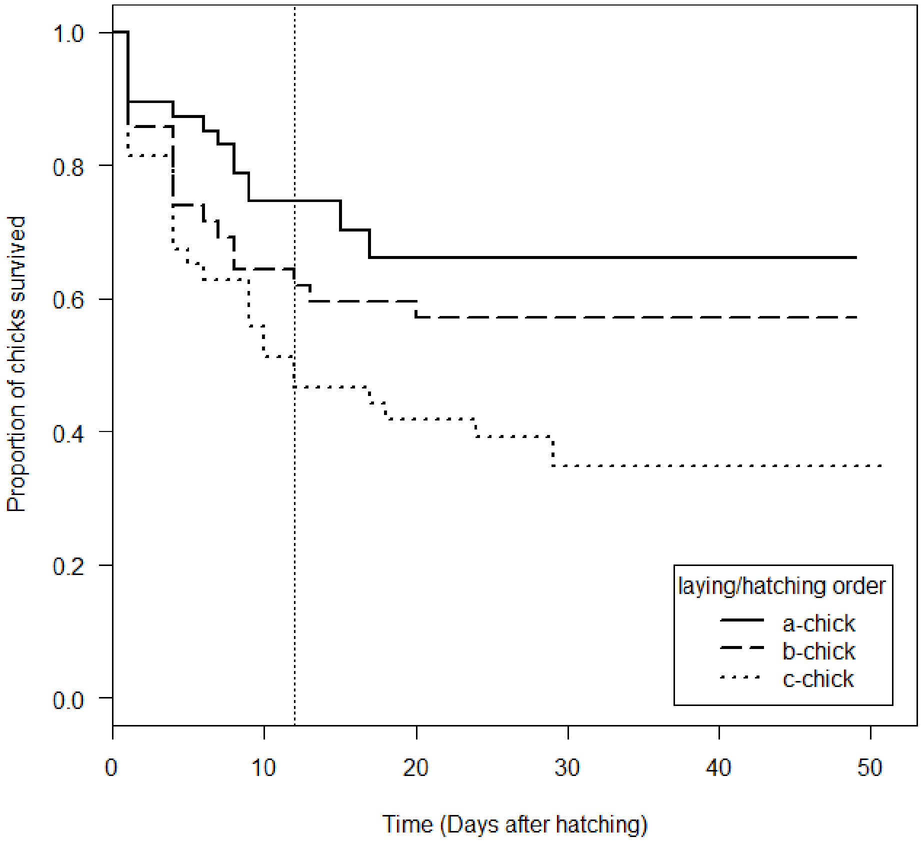

**Figure 2.1.** Laying/hatching order effect on chick survival over time in a Herring Gull colony ($N = 130$ chicks). Kaplan–Meier curves demonstrate that chick survival varied with the laying/hatching order, with b- and (especially) c-chicks showing lower survival probabilities. Although this effect was evident before day 12, chicks that survived the brood-reduction period (first 12 days post-hatching as indicated by the dashed line) had equal probability of survival afterward.

### Variation in offspring development.

Hatchling mass was positively correlated with absolute egg size (LMM, $\beta = 0.81 \pm 0.09$, $F_{1,7.55} = 68.9$, $P < 0.0001$). The positive sign of the laying date*laying order interaction ($\beta = 0.34 \pm 0.11$, $F_{1,109} = 9.3$, $P = 0.003$) indicated that the loss in mass with laying date decreased later in the laying sequence. Interactions of absolute egg size with both laying order and laying date were not significant and were therefore removed from the final model (all $P \geq 0.67$).

Hatchling size increased with absolute egg size (LMM, $\beta = 0.005 \pm 0.001$, $F_{1,109} = 22.9$, $P < 0.0001$) and decreased with laying order ($\beta = -0.02 \pm 0.008$, $F_{1,85.2} = 7.1$, $P = 0.009$), but was not related to laying date ($\beta = -0.001 \pm 0.001$, $F_{1,88.8} = 1.0$, $P = 0.32$). None of the two-way interactions between absolute egg size, laying order, and laying date were significant (all $P \geq 0.39$).

Hatchling condition increased with absolute egg size (LMM, β = 0.07 ± 0.01, $F_{1,67.9}$ = 28.7, $P$ < 0.0001). The positive sign of the laying date*laying order interaction (β = 0.04 ± 0.02, $F_{1,103}$ = 5.9, $P$ = 0.02) indicated that the negative relationship with late laying date decreased with increasing laying order. Two-way interactions of absolute egg size with laying order and laying date were not significant (all $P \geq 0.83$).

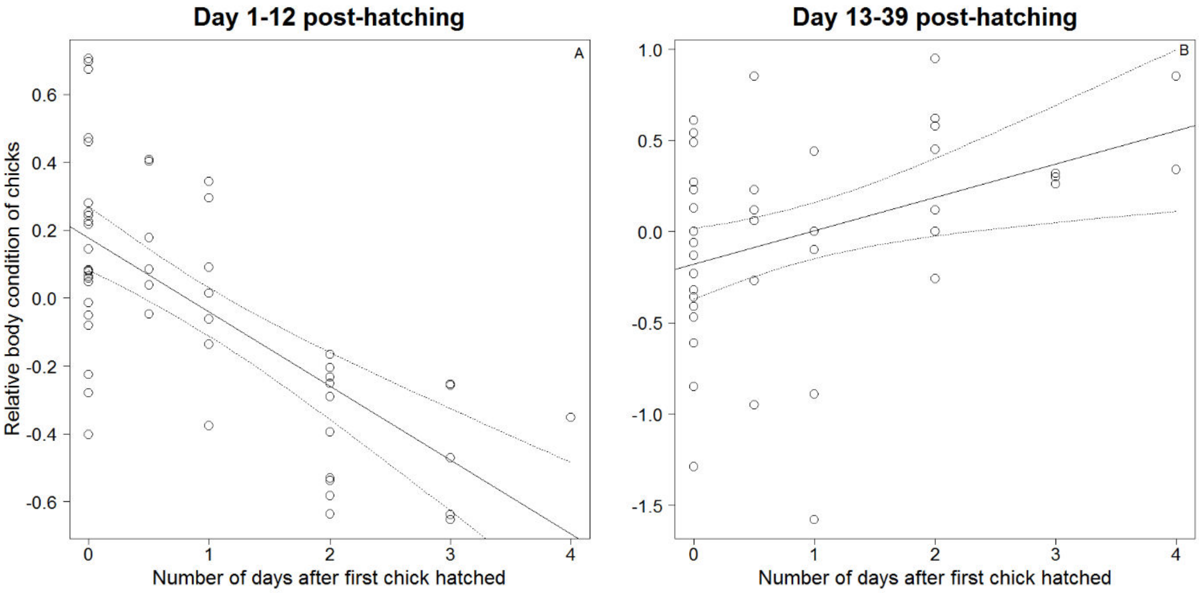

**Figure 2.2.** Changes in competitive asymmetries within broods as reflected by the relative body condition of Herring Gull nestlings (A) during and (B) after the brood-reduction period (78 and 60 chicks, respectively). Plots show individual body conditions as deviance from mean body conditions in a brood on a given day. Chicks from any given brood are measured on the same day. Trendlines with 95% confidence bands are shown, but statistical analyses incorporated nest as a random effect. (A) During the brood-reduction period, relative body condition declined with increasing hatching spread/asynchrony. (B) After the brood-reduction period, relative body condition improved with increasing hatching spread/asynchrony.

Hatchling growth was inversely related to laying date (LMM; β = −0.0008 ± 0.0004, $F_{1,43.4}$ = 4.0, $P$ = 0.05), but was not influenced by either absolute egg size (β = 0.0002 ± 0.0004, $F_{1,66.2}$ = 0.2, $P$ = 0.7) or laying order (β = 0.003 ± 0.003, $F_{1,51.5}$ = 0.7, $P$ = 0.39). Two-way interactions were not significant (all $P \geq 0.10$).

### Variation in offspring survival and relative body condition.

I assessed the degree of correlation between the predictor variables in the following models using a collinearity analysis. However, there is no formal criterion for determining a threshold value for the condition index (CI), the tolerance value (TOL), or the variance inflation factor (VIF). Conventionally, a CI greater than 30, a TOL less than 0.1, or VIF greater than 10 roughly indicates significant and high multi-collinearity (Jeeshim and KUCC625 2003). Collinearity diagnostics revealed no severe symptoms of collinearity among independent variables in my dataset (all CI ≤ 9.6, all TOL ≥ 0.4, all VIF ≤ 2.9).

Nestling mortality increased with laying order (mixed-effects Cox regression; $Z$ = 3.3, $P$ = 0.0008), but I found no effect of laying date ($Z$ = 1.6, $P$ = 0.10), hatching asynchrony ($Z$ =

−0.1, $P = 0.91$), or relative egg size ($Z = -0.03$, $P = 0.98$) on nestling mortality. None of the two-way interactions were significant (all $P \geq 0.24$). When fitting mixed-effects Cox regressions with a change point (Table 2.2), laying order predicted chick survival during the first 12 days after hatching (to the left of the dashed line in Fig. 2.1; $Z = 3.0$, $P = 0.003$), but no such relationship occurred during the period between 12 days post-hatching and fledging ($Z = 1.2$, $P = 0.23$; Fig. 2.1).

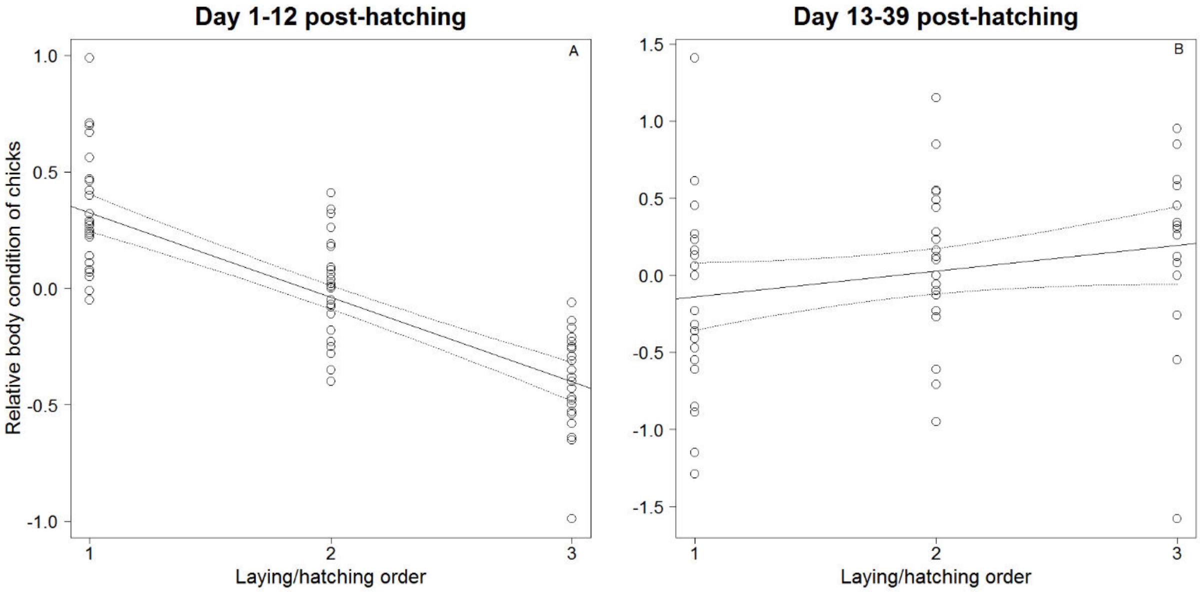

**Figure 2.3.** Changes in competitive asymmetries within broods as reflected by the relative body condition of Herring Gull nestlings (A) during and (B) after the brood-reduction period (78 and 60 chicks, respectively). Plots show individual body conditions as deviance from mean body conditions in a brood on a given day. Chicks from any given brood are measured on the same day. Trendlines with 95% confidence bands are shown, but statistical analyses incorporated nest as a random effect. (A) During the brood-reduction period, relative body condition declined with increasing position in the laying/hatching order. (B) After the brood-reduction period, relative body condition was independent of laying/hatching order.

During the brood-reduction period (first 12 days post-hatching), chick mortality tended to be negatively related with relative body condition ($Z = -1.9$, $P = 0.06$). A significant positive interaction between hatching asynchrony and relative egg size (LMM, $\beta = 0.03 \pm 0.01$, $F_{1,47} = 7.5$, $P = 0.009$) on relative body condition further indicated that the negative effect of increasing hatching asynchrony (Fig. 2.2A) was strengthened by a smaller relative egg size. Relative body condition decreased with laying order ($\beta = -0.25 \pm 0.08$, $F_{1,47} = 11.5$, $P = 0.001$; Fig 2.3A).

After the brood-reduction period (first 12 days post-hatching), chick mortality was not affected by relative body condition ($Z = 0.8$, $P = 0.43$). Relative body condition improved with increasing hatching asynchrony ($\beta = 0.18 \pm 0.07$, $F_{1,43} = 8.4$, $P = 0.008$; Fig 2.2B), whereas relative egg size ($\beta = 0.03 \pm 0.02$, $F_{1,42} = 1.6$, $P = 0.22$) and the interaction between hatching asynchrony and relative egg size did not explain additional variation ($\beta = 0.0007 \pm 0.0234$, $F_{1,40} = 0.01$, $P = 0.98$). In addition, relative body condition did not vary with laying order ($\beta = 0.28 \pm 0.19$, $F_{1,41} = 2.3$, $P = 0.14$; Fig. 2.3B).

## DISCUSSION

My results revealed consistent intraclutch variation in egg size with laying order in Herring Gulls, with c-eggs being smallest in most (89%) clutches. B-eggs were similar in size to a-eggs in many clutches, and were the largest eggs in 35% of all clutches. The negative effect of laying date on absolute size of c-eggs in my study suggests that many late breeders may have been low quality or inexperienced females more limited in their breeding effort. Laying smaller eggs is assumed to reflect lower individual quality in gulls, that is, reduced foraging efficiency due to limited competitive abilities (Bolton 1991, Risch and Rohwer 2000). Likewise, reduced foraging efficiency due to a learning curve effect and lack of previous breeding experience of younger birds (not necessarily of lower quality) might also negatively influence their body condition (nutritional and energetic reserves) and reduce their reproductive investment (Sydeman and Emslie 1992). In gull species in particular, nutritional and energetic demands of egg formation are believed to be relatively high because egg size is about 15.6% of adult body size and energy requirements of egg laying reach 170% of their basic metabolic rates (Ricklefs 1974).

Female Herring Gull use stored lipids for egg production to a large extent (Hario et al. 1991). For late breeders that may be more energy-limited due to inexperience or poor body condition, these reserves probably cannot be replenished in time for production of the c-egg because delayed laying has costs related to a seasonal decline in reproductive success (Brouwer et al. 1995). Furthermore, intraclutch egg size variation, and particularly the relative size of the c-egg, has previously been shown to reflect energetic and nutritional constraints in other species of gulls (Pierotti and Bellrose 1986, Bolton et al. 1992, Sydeman and Elsmie 1992, Kilpi et al. 1996).

My results provide additional empirical evidence that the mass, size, and condition of hatchling Herring Gulls are positively related to egg size. Egg size has previously been shown to be an important measure of egg "quality" in Herring Gulls and other bird species, probably because larger eggs contain more nutrient reserves for chicks during embryonic development (Parsons 1972, Hébert and Barclay 1986, Risch and Rohwer 2000, Krist 2011). In contrast, I found no significant relationships between egg size and growth rates of nestlings. Significant positive correlations are often found between egg size and nestling growth rates (Williams 1994, Krist 2011). However, Viñuela (1997) found no such relationship in nestling Black Kites, and argued that the effect of egg size on nestling growth could have been masked by other factors such as hatching order, feeding rate, type of food, or laying date.

Hatchling growth rates were inversely related to laying date in my study. Growth rates of young Herring Gulls have previously been shown to reflect parental quality through variation in the amount or quality of food provisioned (Risch and Rohwer 2000), possibly related to laying date because inexperienced or low-quality individuals may initiate clutches later (Bogdanova et al. 2007).

### Is intraclutch variation in egg size adaptive in Herring Gulls?

Despite the negative relationship between laying date and c-egg size, the small relative size of the last-laid egg in my study was likely not the sole result of energetic and nutritional constraints on late-laying inexperienced or lesser-quality female Herring Gulls because small terminal egg size should then have been more marked in females laying smaller eggs, reflecting their more limited reserves available for reproduction (see above; Pierotti and Bellrose 1986, Kilpi et al. 1996, Viñuela 1997). To the contrary, I found an inverse relationship between a clutch's mean egg size and the relative size of c-eggs in my study population. This was unexpected because Parsons (1976) reported that female Herring Gulls that laid larger eggs also laid the most similarly sized eggs. However, Parsons (1970, 1972, 1976) also noted that Herring Gulls apparently have a lower size limit for eggs, below which hatchability abruptly drops, so very small eggs are not laid. In addition, Kim et al. (2010) argued that smaller eggs might be more vulnerable to suboptimal conditions such as exposure to cold temperature during periods of neglect. If so, c-eggs may need to exceed a minimum size threshold to be viable, and this may explain why females laying smaller-sized three-egg clutches might have been more limited in the degree to which they could reduce the relative size of their small terminal egg.

The relative body condition of c-chicks in my study was negatively impacted by an interaction between hatching asynchrony and relative egg size. Increasing hatching asynchrony reduced the relative body condition of c-chicks, particularly for c-chicks that hatched from smaller eggs. Furthermore, the relative body condition of nestlings in my study was positively related to their probability of survival during the first 12 days post-hatching and c-chicks had the highest mortality rates. Similarly, Hillström et al. (2000) reported a lower survival rate of c-chicks in Herring Gulls during the first 10-d post-hatching (see also Kilpi et al. 1996, Kim et al. 2010). This pattern is highly consistent with a brood-reduction strategy, that is, reduction of the survival probability of last-hatched chicks by laying relatively small final eggs (Slagsvold et al. 1984). After this brood-reduction period, however, relative body condition was no longer related to egg size, but was still related to hatching asynchrony, suggesting a longer-lasting effect of the latter.

My results suggest that the three-egg clutches of Herring Gulls, with smaller c-eggs, allow parents to adjust the number of chicks reared during the nestling stage (Slagsvold et al. 1984). Given some variation based on laying date, female Herring Gulls could, when sufficient food is available, reduce the degree of hatching asynchrony by delaying the onset of effective incubation (Kim et al. 2010) and, by doing so, increase the likelihood of the c-chick surviving the first 12 days post-hatching. However, when food is scarce, initiating effective incubation sooner likely increases the likelihood that c-chicks will die, allowing parents to direct more food to the surviving chicks and maximize their reproductive success relative to prevailing environmental conditions and to their own breeding condition (Slagsvold et al. 1984).

I found that the relative body condition of chicks only influenced nestling survival during the brood-reduction period whereas the degree of hatching asynchrony appeared to affect relative body condition throughout the nestling period. Although increased hatching asynchrony had a strong negative effect on relative body condition during the brood-reduction period, it affected relative body condition positively afterwards, albeit less strongly, but still to an extent that c-chicks were in the same or slightly better condition than a- or b-chicks. Although the latter result sounds counterintuitive, parents may allocate more food to c-chicks after they have survived the brood-reduction period, as recently observed in American Coots (*Fulica americana*) where late-hatched survivors equaled or exceeded their older siblings in size prior to independence because they received more food from parents (Shizuka and Lyon 2013).

## ACKNOWLEDGEMENTS

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# 3

# Sex, growth rate, rank order after brood reduction, and hatching date affect first-year survival of long-lived Herring Gulls

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## SUMMARY

Among most species of birds, survival from hatching throughout the first year of life is generally lower than subsequent survival rates. Survival of young birds during their first year may depend on a combination of selection, learning, unpredictable resources, and environmental events (i.e. post-fledging factors). However, knowledge about post-fledging development in long-lived species is usually limited due to a lengthy immature stage when individuals are generally unobservable. Therefore, pre-fledging characteristics are often used to predict the survival of young birds. We assessed effects of nestling growth rates, hatching date, hatching asynchrony, brood size and rank order after brood reduction, and sex on first-year survival of 137 fledglings using a mark-resighting analysis. We found that the survival probability ($F_{1y} = 0.39$) of first-year Herring Gulls (*Larus argentatus*) in our study colony located at the outer port of Zeebrugge (Belgium) was lower than that of older individuals ($F_{>1y} = 0.75$). All 10 models best supported by our data included nestling growth rate, suggesting that variability in first-year survival may be linked primarily to individual variation in growth. First-year survival was negatively correlated with hatching date and rank order after brood reduction. Hence, carry-over effects of breeding season events such as timing of breeding, early development, and social status had an influence on survival of Herring Gulls after fledging. Furthermore, we found sex-biased mortality in first-year Herring Gulls, with females ($F_{1y} = 0.45$) surviving better than males ($F_{1y} = 0.38$). Although adult survival is generally regarded as the key parameter driving population trajectories in long-lived species, juvenile survival has recently been acknowledged as an important source of variability in population growth rates. Therefore, increasing our knowledge of factors affecting age-specific survival rates is necessary to improve our understanding of population dynamics and ultimately life-history variation.

## INTRODUCTION

Age-related survival rates are key parameters in determining population dynamics (Lack 1954, Ricklefs 1973, Martin 1994). The results of a number of studies suggest that the effect of adult survival on the size and age composition of avian populations is the most important trait affecting population trajectories of long-lived species consistent with high annual survival probabilities (Croxall and Rothery 1991, Russell 1999, Sæther and Bakke 2000, Crone 2001). However, unusually high or low survival rates due to exceptionally benign (e.g., high food availability) or adverse (e.g., disease or cold spells) environmental conditions during this period can impact population dynamics as well, especially when adult survival is relatively constant (Croxall and Rothery 1991, Morris and Doak 2002). Consequently, estimation of this demographic parameter is of equal importance for assessing population dynamics and ultimately understanding life-history variation.

First-year survival includes both nestling survival (from hatching to fledging) and post-fledging survival (once chicks fledge and leave the nesting site; first-year survival sensu stricto). Variation in conditions experienced during the nestling period may affect survival rates before and after fledging (Lindström 1999, Cam and Aubry 2011). Nestlings reared under poor conditions may grow at a slower rate and, hence, may exhibit smaller structural size and lower body condition (Souchay et al. 2013). Simultaneously, chicks in enlarged broods usually reach a lower body mass than those in smaller broods due to increased sibling competition (Nisbet and Drury 1972). Sexes can differ in their sensitivity to conditions experienced during the growth period (Lindström 1999). For instance, sexual size dimorphism can affect survival because of different energy requirements in males and females. Moreover, the larger sex usually grows faster than the smaller sex, leaving them more vulnerable to food deprivation or other environmental changes (Griffiths 1992, Lindström 1999). Given the importance of growth and acquiring sufficient body size and condition at independence, adverse rearing conditions are manifested through lower survival chances, whereas good conditions may positively influence both offspring growth and survival rates (Martin 1994, Clutton-Brock et al. 1985, Sedinger et al. 1995). In species where asynchronous hatching seems to be an adaptation to a stochastic rearing environment (brood reduction hypothesis, Lack 1968), the youngest nestling usually has a higher mortality risk due to starvation and sibling aggression.

The influence of early conditions may be particularly important in survival before fledging (Cam et al. 2003), yet many bird species also suffer a comparably high mortality during their first year of life after fledging. For example, an estimated 38% of Western Gulls (*Larus occidentalis*) die before becoming independent, and 37% die in the first nine months after reaching independence (Spear et al. 1987). Whether a young and inexperienced bird survives the first year of life may depend on a combination of selection, learning, unpredictable resources, and environmental events (i.e., post-fledging factors) (Nevoux et al. 2010). However, knowledge about post-fledging development in long-lived species is usually limited due to a lengthy immature stage coinciding with natal dispersal during which individuals are generally not observable (Nevoux et al. 2010, Souchay et al. 2013, Saunders et al. 2014). Therefore, pre-fledging characteristics are often used to predict the survival of young birds because they are relatively easy to monitor and, hence, carry-over effects of breeding season events on post-fledging survival have been found in long-lived species (Cooke et al. 1984, Harris et al. 1994, Weimerskirch et al. 2000, Ludwig and Beckers 2006, Cam and Aubry 2011). For example, first-year survival has been found to be negatively correlated with hatching date (Nisbet and Drury 1972, Saunders et al. 2014) and hatching order (Cam et al. 2003).

Herring Gulls (*Larus argentatus*) are long-lived and sexually dimorphic, with males larger than females, and a number of investigators have studied adult survival (Harris 1970, Chabrzyk and Coulson 1976, Coulson and Butterfield 1986, Pons and Migot 1995, Camphuysen and Gronert 2012). However, little is known about first-year survival of Herring Gulls (e.g., Parsons et al. 1976). In a previous study, we reported the direct and indirect effects of reproductive parameters on nestling survival in Herring Gulls and identified a 12-day brood-reduction period (Bosman 2014). Here we present estimates of age- and sex-related survival of Herring Gulls after fledging using capture-mark-resighting (recapture) analysis (CMR), and also examine the possible carry-over effects of nestling growth and other pre-fledging characteristics (hatching date, hatching asynchrony, and brood size and rank after brood reduction) on first-year survival. Because it is widely accepted that reduced development will manifest itself through reduced survival, we expected a positive relationship between nestling growth rate and first-year survival. Given this expected association, we investigated the effect of pre-fledging traits on nestling growth rates only if they were also found to influence first-year survival rates.

## METHODS AND MATERIALS

Pre-fledging data were collected during three breeding seasons (2010–2012) at a mixed breeding colony of Herring Gulls and Lesser Black-backed Gulls (*L. fuscus graellsii*) at the outer port of Zeebrugge (Belgium, 51°21’N, 03°11’E). The outer port was constructed on land reclaimed from the sea and is protected and enclosed by two breakwaters stretching more than 4 km into the sea. Each year from mid-April until the end of May, we searched sub-colonies daily for new nests. New nests were marked with an individually coded stick and visited daily to record laying order. Marked nests were visited daily and chicks were measured every third day from the hatching of the first chicks until the end of July when the last surviving chicks had fledged (see below and also Bosman 2014). To facilitate monitoring of nestlings, nests were surrounded with a 50-cm-high chicken-wire enclosure (± 3–4 m in diameter) a week before expected hatching. Enclosures were provided with wooden shelters just large enough to fit three near-grown fledglings where chicks could hide from predators and inclement weather. We assumed that providing shelter did not improve the survival of enclosed compared to non-enclosed chicks because the colony was located in an area with many places for chicks to hide (e.g., abandoned construction materials, rabbit holes, and vegetation within a radius of 10 meters around each nest), and therefore both had equal opportunity to find shelter and protection. Placement of enclosures differed between years and, because of high nest-site fidelity by Herring Gulls and the fact that some individuals were color-banded, nests of different adults were studied each year. At the time of fledging, surviving chicks were equipped with uniquely coded color-bands and entered in the capture-resighting database managed by the Research Institute for Nature and Forest (Belgium).

### Individual covariates and interactions

We recorded hatching date, sex, hatching asynchrony growth rate, laying order, brood size, and rank order after brood reduction for 137 chicks that fledged (68 in 2010, 38 in 2011, and 31 in 2012) in 88 enclosed nests (43 in 2010, 25 in 2011, and 20 in 2012). Successful fledging was inferred when an individual was seen alive either by us or one of the band-reading volunteers at least once outside the breeding colony (i.e., the well-defined perimeter of the outer part of Zeebrugge) after the nest plot was vacated.

Herring Gulls have a clutch-size frequency distribution truncated at three eggs (Parsons 1970). Natal clutch size does not necessarily reflect the brood size a bird is reared in, given the loss of eggs and nestlings and the fact that some eggs do not hatch. Brood size, measured as the number of young surviving to day 12 (BS12) (identified as the brood-reduction period in our study population; Bosman 2014), better reflects rearing conditions. This brood-reduction period is defined as the period during which offspring survival varies most strongly with laying order (Mock 1994). Bosman (2014) determined that offspring survival varied most strongly with laying order during the first 12 days after hatching in our study population, and the oldest chicks more likely to survive. However, after brood reduction, laying order (LO) no longer affected offspring survival so LO may also have no effect on first-year survival. Therefore, we also tested rank order after brood reduction (RO12) when some b- and c-chicks were promoted to first or second rank after older chicks had died. We further felt this rank order would better reflect rearing conditions because it is upheld during the larger part of the nestling period (± 45 days in Herring Gulls). Because LO and RO12 were correlated, we could not model both simultaneously so we ran separate, but identical, statistical procedures including either LO or RO12 as described below to test their effect on first-year survival. From the end of May until mid-June, enclosed nests were visited daily to record hatching dates (HATCH), expressed as the number of days after 1 December of the previous year (i.e., the earliest recorded arrival date of a breeding bird in our study population; Bosman et al. 2013). The level of hatching asynchrony (HAS) of a chick was calculated as the time (in days) elapsed since the hatching of the first chick of the same brood and was set to 0.5 d for eggs that hatched on the same day if there was an unambiguous difference in timing of hatching (i.e., assessed by dry versus still-wet plumage). Once hatched, all chicks were marked with individually coded insulation tape around the tarsus, and measured every third day. Only individuals measured on the first day of hatching were included in the analyses. Because single-trait measures were earlier shown to provide poor proxies of overall body size in gulls (Bosman et al. 2012), we measured tarsus length and bill length (from the tip to the anterior edge of the nostrils) of each chick with calipers (± 0.01 mm), and quantified body size as the first axis of a principal component analysis (PC1) in SPSS statistics Ver. 21 (IBM Corporation, Armonk, NY). PC1 explained 98% of the body size variation in nestlings and had high positive loadings for tarsus length (0.99) and bill length (0.99). Chick growth rates (GROW) were calculated for the period of linear growth as the slope of the linear regression of body size on age (in days) performed in SPSS statistics (Bolton 1991).When calculating growth rates, only chicks where we collected at least four measurements between days 3 and 23 post-hatching were included (Bogdanova and Nager 2008, Hauber and Moskat 2008). To determine sex, DNA was extracted from down feathers using the Nucleospin® Tissue method and amplified using CDH1-linked primers P2/P8 (Griffiths et al. 1998) and 2550F/ 2718R (Fridolfsson and Ellegren 1999). SEX was coded as a binominal variable (female = 0, male = 1). We also modelled biologically plausible interactions. Mothers may influence variation in survival by preferably assigning one sex a higher rank order (SEX*RO12). Such interactions between offspring sex and rank order could have exaggerated effects in asynchronous hatching species, especially if one sex particularly benefits from good rearing conditions (Lack 1954, Kathryn and Griffiths 2003). Seasonal variation in rearing conditions may affect the survival prospects of the sex that is more vulnerable to starvation, especially in sexual size dimorphic species due to the increased resource requirements of the larger sex (SEX*HATCH; Nager et al. 2000). When parents are not able to feed their young sufficiently, the more vulnerable sex is usually less likely to grow normally and this may, in turn, affect its survival prospects (GROW*SEX; Nager et al. 2000). Likewise, survival probabilities of late-hatched offspring may be affected because they are less likely to grow normally due to a seasonal decline in food supply (GROW*HATCH). Rank order and the resulting competitive asymmetry may similarly inhibit normal growth and in turn influence offspring survival rates (GROW*RO12). To test the shape of the relationship between nestling growth rates and first-year survival, we also modelled a quadratic term ($GROW^2$). A quadratic effect of growth rates on first-year survival would provide evidence of a non-linear relationship indicating that survival would be maximized at a certain growth rate.

### Analysis of variation in growth rates

To analyze variation in nestling growth rates, we fit a linear mixed-effects model in SAS 9.4 (SAS Institute Inc., Cary, NC) with nest modeled as a random effect (LMM; Littell et al. 1996). Growth rate (GROW) was modeled as the dependent variable, rank order after brood reduction (RO12), hatching date (HATCH), and SEX were modelled as fixed effects, while controlling for YEAR as a random factor. Levels of significance of all fixed variables were tested and the Satterthwaite approximation was applied for estimating the degrees of freedom. To compare group means, *post-hoc* tests were carried out with Tukey's tests.

### Survival analysis

We compiled five-occasion encounter histories for 137 individual Herring Gulls from July 2010 - June 2011 to July 2014 – June 2015 (e.g., 01110 for an individual that hatched in 2011). All cohorts (i.e. 2010, 2011, and 2012) had at least three years of resighting time. Herring Gulls of our study population (i.e. regardless of sex and age) that are not resighted for at least three consecutive years in the breeding colony, or in other well-studied neighboring colonies in the southern part of the North Sea, at gull-attracting rubbish tips, and during dispersal movements to and from their well-watched 'wintering grounds' (Nord-Pas de Calais, Normandy, the Flemish coast and Zeeland), are without exception never reported as 'seen alive' again in our database and are likely dead. All these areas and even areas beyond their known dispersal range, i.e. from Normandy south to the Moroccan coastline where Lesser

Black-backed Gulls (*Larus fuscus*) from our study population have been reported, are regularly inspected by band-reading volunteers for the presence of color-banded gulls. In total, 1465 volunteers have participated in our color-banding project since 1999.

In the first step of our survival analysis (live-recapture framework, CJS-models), we determined the best starting model for comparison with subsequent models constrained by our individual covariates. We started by fitting the data to the most general approximating model in our model set. Using the notation recommended by Lebreton and Pradel (2002), this model was: $\Phi$(3a-t/t/t)p(t), where '$\Phi$' and 'p' are survival and resighting probabilities, respectively, 't/t/t' indicates time-dependence in each age class, 'a' an age effect with '3a' for three age classes (i.e., first-years, immatures, and [sub]adults). To avoid overparameterization, we did not allow for age-dependence in resighting probabilities. After model selection using an AIC-approach, the most parsimonious model that best fit our data was chosen as the starting model.

In the second step of our survival analysis, we sequentially fitted models with constrained parameterization for first-year survival only. First, we fitted a constrained model containing all individual covariates and biologically relevant two-way interactions. Next, we evaluated their importance in first-year survival by running and comparing a series of models with a different variable or interaction missing in turn, except for variables still involved in an interaction. The variable absent from the best supported model was deemed least important in affecting first-year survival and was omitted from further analysis (see web-based manual to MARK, chapter 5). This process was repeated until we ended up with the top models best supported by our data. The ability of the initial models to describe the data was assessed using a goodness-of-fit (GOF) median-$\hat{c}$ test (see web-based manual to MARK, chapter 5).Model selection relied on Akaike's information criterion (AIC) and candidate models were ranked by second-order AIC differences ($\Delta AIC_c$). Only models that deviated less than 2 $AIC_c$ units from the most parsimonious model ($\Delta AIC_c = 0$) were considered to have approximately equal weight (Burnham and Anderson 2002). To be conservative, models that deviated more than 2 $AIC_c$ units from the most parsimonious model were considered unsupported by our data (see web-based manual to MARK, chapter 4). Model selection and parameter estimation were performed using the program MARK 8.0 (Colorado State University, USA). The model averaging procedure was used to compute the average estimates for first-year ($F_{1y}$) and subsequent ($F_{>1y}$) survival and based on weighted $AIC_c$-values for each model and thus accounts for model uncertainty in these estimates.

### Collinearity diagnostics

Because growth rate (GROW), rank order after brood reduction (RO12), and SEX may be highly correlated, modeling these variables simultaneously might produce problems with collinearity. To determine the severity of the latter among independent variables in our dataset, we used the COLLIN, VIF, and TOL Options (SAS 9.4) to obtain condition indices (CI), variance inflation factors (VIF), and tolerance values (TOL), respectively (i.e., collinearity diagnostics). However, there is no formal criterion for determining a threshold value for CI, VIF, and TOL. Conventionally, a CI greater than 30, a TOL less than 0.1, or VIF greater than

10 roughly indicates significant and high multi-collinearity (Jeeshim and KUCC625 2003). Values are presented as means ± SE.

## RESULTS

### Pre-fledging development

Nestling growth rates were correlated with rank order after brood reduction (LMM, RO12, $F_{2,66.8} = 3.6$, $P = 0.03$) and differed between the sexes (LMM, SEX, $F_{1,112} = 23.3$, $P < 0.0001$; Fig.3.1). Third-ranked chicks ($\beta = 0.10 \pm 0.01$, Tukey, $P = 0.03$) grew on average slower than first- and second-ranked chicks, with the latter two having similar growth rates ($\beta = 0.11 \pm 0.01$, Tukey, $P = 0.99$; Fig.3.1). As the larger sex in Herring Gulls, males ($\beta = 0.12 \pm 0.01$) had faster growth rates than females ($\beta = 0.10 \pm 0.01$; Tukey, $P < 0.0001$). Hatching date had no significant effect on chick growth rate (LMM, HATCH, $F_{1,90.2} = 1.1$, $P = 0.29$).

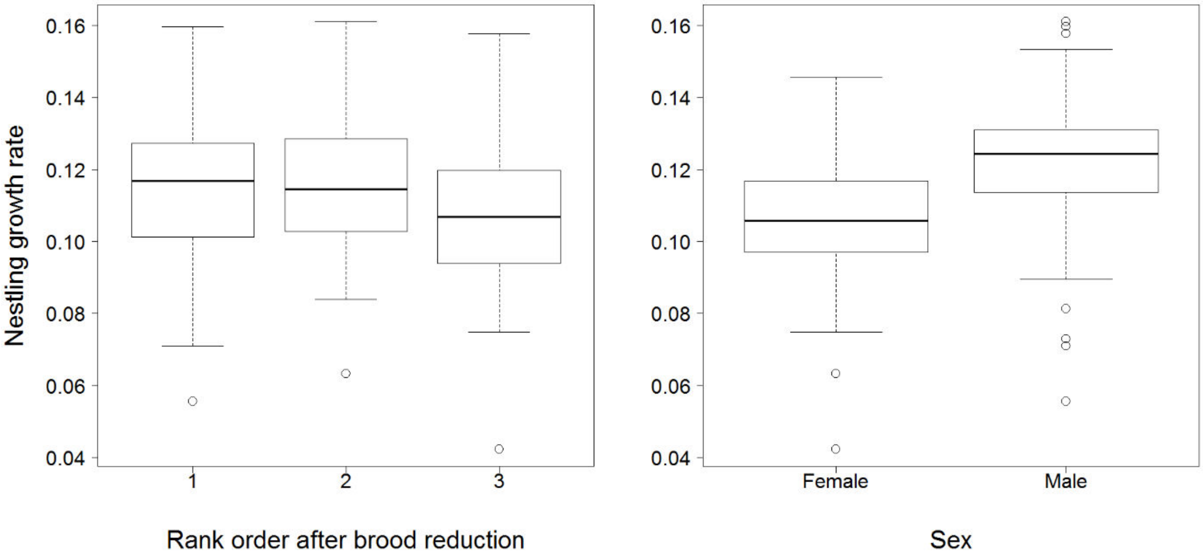

**Figure 3.1.** Relationship between nestling growth rates (GROW) and rank order after brood reduction (RO12; left panel) or SEX (right panel) for 137 Herring Gulls at a Belgian colony situated at the outer port of Zeebrugge. The box and whiskers plots represent the distribution for each group, with means (solid lines), 10% and 90% (whiskers), and 25% and 75% (box) quartiles.

### Post-fledging survival

After initial model selection to evaluate the number of age classes, the most parsimonious survival model only distinguished between first-year (1y) and older individuals (>1y). This model was Φ(2a-./.)p(.), where 'Φ' and 'p' are survival and resighting probabilities, respectively, './.' indicates constant survival probability in each age class, and 'a' is an age effect with '2a' for two age classes (1y and >1y) (Table 3.1). Modelling different survival probabilities for first-years, immatures, and (sub)adults did not provide a better fit for our data. The lack of significance between modelling either two or three age classes on variation in survival rates was further confirmed by a likelihood ratio test (LRT, $P = 0.32$). Following the

GOF median-$\hat{c}$ test to assess the ability of our starting model to describe the data, the results were corrected for slight over-dispersion using the value of the GOF parameter $\hat{c} = 1.10 \pm 0.02$ (lower bound =1.0, upper bound = 2.0, and 10 design points with 100 replicates at each point).

Starting from this initial model, we sequentially fitted models with constrained parameterization for first-year survival only. In all, 52 models were fitted to the data (Model results). After a stepward model selection procedure by AIC, the model that additively constrained variation in first-year survival to growth rate (GROW) and SEX best fit our data (Table 3.2). Nine models that also related variation in first-year survival to rank order after 12 days (RO12), hatching date (HATCH), and the interactions GROW*SEX and SEX*HATCH had $\Delta QAIC_c$ values < 2 (Table 3.1) and were therefore considered equally informative as our most parsimonious model. All models that included constraints on variation in first-year survival to brood size after 12 days (BS12), hatching asynchrony (HAS), and the interactions GROW*RO12, GROW*HATCH, and SEX*RO12 deviated considerably from this most parsimonious model ($\Delta QAICc > 2$) and were therefore considered unsupported by our data. In addition, the notion of normalizing selection on growth rate (GROW$^2$) was not supported by our survival data. In an identical stepward model selection procedure, but with RO12 replaced, no model containing laying order (LO) ranked among the 10 most parsimonious models (results not shown). In a direct comparison of two models with first-year survival exclusively constrained by either LO or RO12, the one modelling RO12 and the starting model had a slightly better fit (Table 3.2).

First-year survival ($F_{1y} = 0.39 \pm 0.05$; weighted average) was considerably lower than subsequent survival ($F_{>1y} = 0.75 \pm 0.05$; weighted average). First-year survival was positively related to growth rate ($\beta = 18.95 \pm 10.46$; Fig. 3.2). In contrast, hatching date ($\beta = -0.03 \pm 0.03$; Fig. 3.2) and rank order after brood reduction ($\beta = -0.44 \pm 0.29$) were inversely related to first-year survival (Ranked first: $F_{1y} = 0.47 \pm 0.06$, Ranked second: $F_{1y} = 0.36 \pm 0.06$, Ranked third: $F_{1y} = 0.27 \pm 0.09$). Males ($F_{1y} = 0.38 \pm 0.06$) had a lower first-year survival probability than females ($F_{1y} = 0.45 \pm 0.07$). The estimated resighting probability appeared to be high ($p(.) = 0.83 \pm 0.05$) (Fig. 3.2). There was a positive effect of GROW*SEX ($\beta = 32.31 \pm 26.46$) and a negative effect of SEX*HATCH ($\beta = -0.10 \pm 0.07$).

### Collinearity diagnostics

We found that GROW, SEX, and RO12 affected first-year survival, and SEX and RO12 were found to affect GROW. Hence, these three individual covariates might be correlated, which could have biased the estimated effect on survival. Therefore, we assessed the degree of correlation between these individual covariates using a collinearity analysis. Collinearity diagnostics revealed no severe symptoms of collinearity among these individual covariates in our dataset (all $CI \leq 16.85$, all $TOL \geq 0.83$, and all $VIF \leq 1.21$).

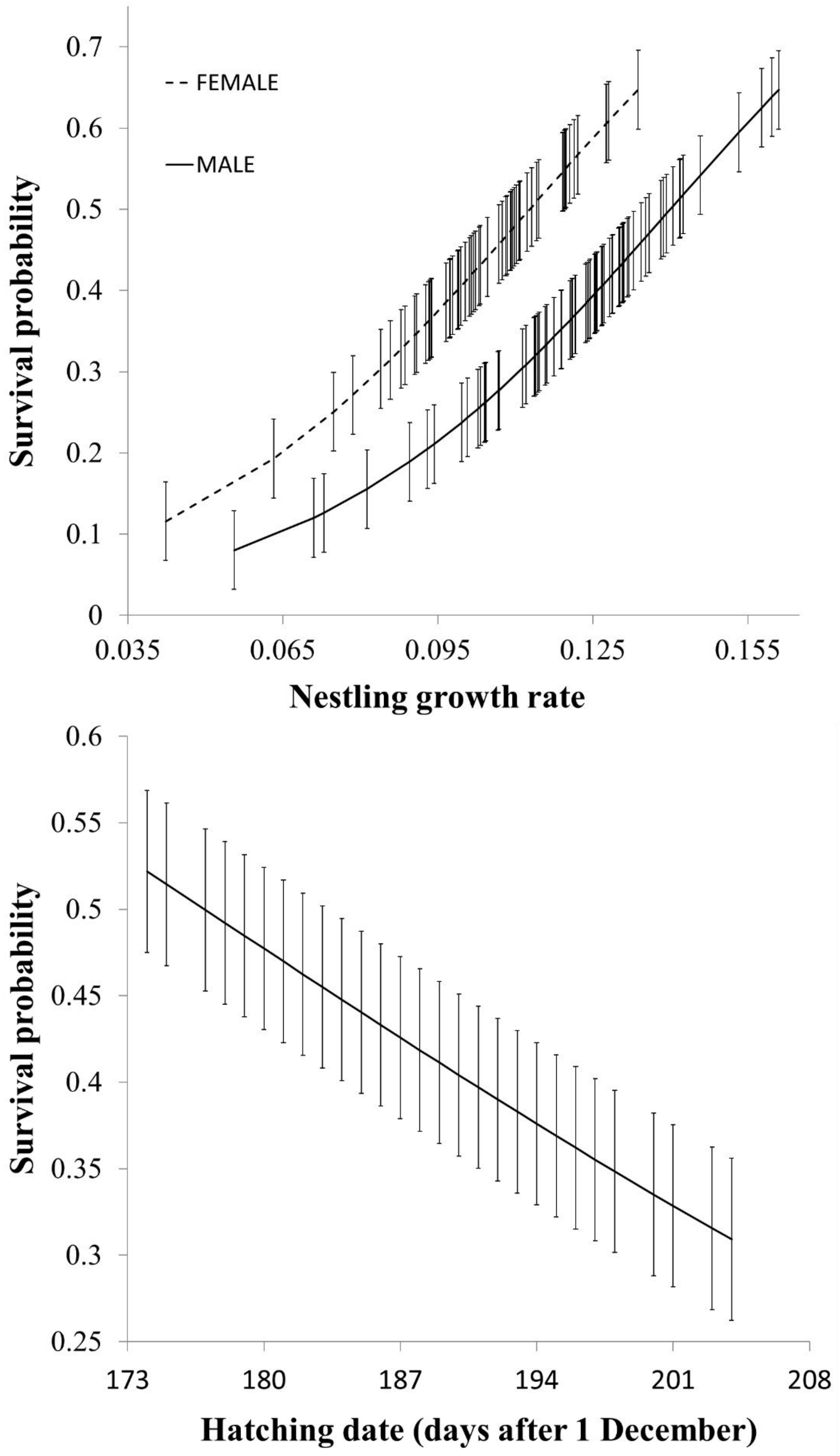

**Figure 3.2.** Relationships between first-year survival probabilities (± SE) and nestling growth rates of males and females (upper panel), and hatching date (lower panel) for 137 Herring Gulls at a Belgian colony located at the outer port of Zeebrugge.

## DISCUSSION

Survival of first-year ($\Phi_{1y}$ = 0.39) Herring Gulls in our study population was lower than that of individuals in the older age class ($\Phi_{>1y}$ = 0.75), and this survival probability remained constant throughout our study. In contrast, studies of other bird species have revealed that first-year survival is often highly variable among years (Frederiksen and Bregnballe 2000, Harris et al. 2007, Monticelli and Ramos 2012). There are no other published estimates of first-year survival of Herring Gulls using modern CMR-analysis. However, based on recoveries of dead birds, Harris (1970) and Chabrzyk and Coulson (1976) calculated much higher first-year survival rates (0.82 and 0.67-0.83, respectively) for Herring Gulls. Likewise, Parsons et al. (1976) reported recovery rates of birds found dead during their first winter. However, their low recovery rates (range = 0.012 to 0.026 for three cohorts) did not reflect true mortality at all, but instead were used to compare post-fledging survival of young hatching at different times in the season, on the assumption that birds suffering greater mortality during their first winter would yield proportionately more recoveries. Although Kadlec and Drury (1968) estimated juvenile survival rates of the American Herring Gull (*Larus argentatus smithsonianus*) within the range of 0.68-0.70, Paynter (1966) found survival rates of 0.38, comparable to our estimate. Spear and Nur (1994) examined age-related survival in Western Gulls (*Larus occidentalis*) and reported a relatively high juvenile survival rate (0.54) in the 1979 cohort, but survival rates of the 1978 and 1980 cohorts (0.38 and 0.40) were similar to our estimated first-year survival probability for Herring Gulls. Arizaga et al. (2015) found that first-year survival rates of Yellow-legged Gulls (*Larus michahellis*) ranged from 0.40 to 0.80. Although estimates of first-year survival of gulls (*Larus* spp.) vary among years and studies, survival rates of first-year birds are generally lower than that of older birds.

Our estimate of post-juvenile annual survival probability is consistent with a K-selected strategy of a long-lived species (deferred maturity, low fecundity, and high life expectancy), with annual values normally ranging between 0.75 and > 0.95 (Croxall and Rothery 1991). Our estimate of post-juvenile survival was on the lower end of this range, probably because our study cohorts (2010, 2011 and 2012) were largely subadults that have slightly lower survival probabilities than adult Herring Gulls (Vercruijsse 1999).

All 10 models best supported by our data included nestling growth rate (GROW). Hence, our results suggest that variability in first-year survival could be linked primarily to individual variation in nestling growth rates. Although larger fledglings may be more likely to survive because they are better able to compete for limited resources (Parsons et al. 1976), good feeding conditions experienced during early growth may fix some physiological or structural traits that enhance an individual's performance levels related to components of fitness, i.e., individual quality (Lindström 1999, Cam et al. 2003, Sedinger et al. 2004, Nevoux et al. 2010). For example, variation in the slope of the learning curve in relation to resource acquisition (i.e., foraging skills) may strongly affect first-year survival.

A methodological issue may explain why we found no evidence of a quadratic effect of growth ($GROW^2$) on first-year survival. Nestling growth rates were calculated for the period of linear growth during the first three weeks post-hatching and thus provide estimates of peak growth. Therefore, these estimates do not reflect sustained growth over the entire length of the rearing period (Martin 2015). In the latter case, a quadratic effect might be expected on first-year survival because otherwise the development of other (e.g. physiological) traits positively influencing survival might be impeded, e.g., investment in growth at the cost of the immune system (cf. Souchay et al. 2013).

**Table 3.1.** Results of the initial CMR model selection on survival and recapture probabilities of Herring Gulls. These models were compared to evaluate the number of age classes that should be included in the starting model of the constrained model selection.

| Model | $QAIC_c$ | $\Delta QAIC_c$ | $QAIC_c$ Weights | Model Likelihood | NP | QDeviance |
|---|---|---|---|---|---|---|
| Φ(a2- ./.)p(.) | 196.40 | 0.00 | 0.31 | 1.00 | 3 | 12.95 |
| Φ(a2- ./t)p(.) | 197.34 | 0.94 | 0.20 | 0.63 | 5 | 9.72 |
| Φ(a3-././.)p(.) | 197.47 | 1.06 | 0.18 | 0.59 | 4 | 11.94 |
| Φ(a3- ././t)p(.) | 198.73 | 2.32 | 0.10 | 0.31 | 5 | 11.11 |
| Φ(a2- ./.)p(t) | 199.93 | 3.53 | 0.05 | 0.17 | 6 | 10.21 |
| Φ(a2- t/.)p(.) | 200.83 | 4.43 | 0.03 | 0.11 | 6 | 11.11 |
| Φ(a3- ./t/t)p(.) | 201.52 | 5.12 | 0.02 | 0.08 | 7 | 9.67 |
| Φ(a3- ././.)p(t) | 201.65 | 5.25 | 0.02 | 0.07 | 7 | 9.80 |
| Φ(a2- t/t)p(.) | 201.94 | 5.54 | 0.02 | 0.06 | 8 | 7.94 |
| Φ(a3- t/./.)p(.) | 201.95 | 5.55 | 0.02 | 0.06 | 7 | 10.10 |
| Φ(a2- ./t)p(t) | 203.69 | 7.29 | 0.01 | 0.03 | 8 | 9.69 |
| Φ(a3- ././t)p(t) | 203.78 | 7.37 | 0.01 | 0.03 | 8 | 9.78 |
| Φ(a2- t/.)p(t) | 204.45 | 8.04 | 0.01 | 0.02 | 9 | 8.28 |
| Φ(.)p(.) | 205.51 | 9.11 | 0.00 | 0.01 | 2 | 24.11 |
| Φ(a3- t/t/t)p(.) | 206.19 | 9.78 | 0.00 | 0.01 | 10 | 7.84 |
| Φ(a3- t/./.)p(t) | 206.26 | 9.85 | 0.00 | 0.01 | 10 | 7.91 |
| Φ(a3- ./t/t)p(t) | 207.99 | 11.59 | 0.00 | 0.00 | 10 | 9.64 |
| Φ(a2- t/t)p(t) | 208.49 | 12.09 | 0.00 | 0.00 | 11 | 7.94 |
| Φ(t)p(.) | 210.45 | 14.05 | 0.00 | 0.00 | 5 | 22.83 |
| Φ(.)p(t) | 210.82 | 14.42 | 0.00 | 0.00 | 5 | 23.20 |
| **Φ(a3- t/t/t)p(t)** | **212.85** | **16.45** | **0.00** | **0.00** | **13** | **7.83** |
| Φ(t)p(t) | 216.54 | 20.14 | 0.00 | 0.00 | 8 | 22.55 |

Goodness-of-fit of the most general model (bold) was assessed by a median-ĉ GOF test and the relative fit of subsequent models was assessed by Akaike's Information Criterion. The number of parameters in each model is indicated by NP.

The results of previous studies have demonstrated that first-year survival is negatively correlated with hatching date (HATCH) in many species (e.g., Nisbet and Drury 1972, Cooke et al. 1984, Harris et al. 1994, Saunders et al. 2014) and this was also the case for Herring Gulls in our study. Because immature gulls are probably less effective foragers than adults (Maclean 1986), we would expect later-hatched chicks to have less time to develop and improve their foraging skills before the onset of winter, potentially compromising post-fledging survival. Likewise, decreased survival of late-hatching chicks may be explained by less experienced or lower-quality parents breeding later in our study population (Bosman 2014) and, hence, parental quality may have confounded the effect of hatching date on post-fledging survival (Coulson and Porter 1985, Spear and Nur 1994). Alternatively, parents may reduce investment in late-season young because they have lower reproductive value or higher costs (Daan et al. 1990, Tinbergen and Daan 1990, Verhulst and Nilsson 2008).

In the latter context of reduced investment in later-hatched chicks, we found an unambiguously negative influence of rank order after brood reduction (RO12) on both growth rates and first-year survival. Interestingly, we found that later-hatched young grew slower than their siblings, and significantly slower for c-chicks that remained third in rank after brood reduction. This suggests that parents do not attempt to balance the amount of food delivered to chicks (Cam et al. 2003). Bosman (2014) hypothesized that parents may allocate more food to c-chicks after they have survived the brood-reduction period to the extent that they were in the same or slightly better condition than a- or b-chicks. However, our results suggest that this improved development only involved c-chicks that increased in rank after brood reduction and, hence, profited from the death of their older siblings. Reasonably, older chicks are dominant in competition with younger siblings for food, leading to reduced development of surviving juniors at independence (Slagsvold et al. 1984, Sydeman and Emslie 1992, Bosman 2014). Accordingly, it is fair to hypothesize that individuals dominant in competition for food within broods, or individuals without siblings, are in a better condition at independence and have lower mortality rates during the first year of life (Cam et al. 2003).

We detected no influence of brood size after brood reduction (BS12) on first-year survival in our study population. Previous studies of the effect of brood size on post-fledging survival have produced conflicting results. For example, post-fledging survival has been found to be higher in American Herring Gulls from smaller broods (Nisbet and Drury 1972). In contrast, Newton and Moss (1986) found no effect of brood size on post-fledging survival of Sparrowhawks (*Accipiter nisus*), whereas chicks in larger broods of Kittiwakes (*Rissa tridactyla*), Shags (*Phalacrocorax aristotelis*), and Western Gulls (*Larus occidentalis*) survived better than those from smaller broods (Coulson and Porter 1985, Harris et al. 1994, Spear and Nur 1994). However, observational studies of the effect of brood size on post-fledging survival are necessarily confounded by a number of factors (e.g., parental quality, food availability, and weather), so experimental manipulations would be needed to really evaluate the effect of brood size.

Likewise, we found no effect of hatching asynchrony (HAS) on first-year survival. In asynchronous-hatching species, the youngest nestlings usually have higher mortality rates due to a combination of reduced body condition and competitive ability (Kim et al. 2010). Hatching asynchrony proved to be a considerable source of offspring mortality during the nestling stage in Herring Gulls (Bosman 2014), but was seemingly unimportant in survival after fledging.

Male Herring Gulls in our study experienced lower first-year survival and faster growth rates than the smaller females. Higher post-fledging mortality rates of the larger sex have previously been reported in other size-dimorphic species (e.g., Martín et al. 2007), but not all (e.g., Husby and Slagsvold 1992). The usual explanation for such bias toward the larger sex in juvenile mortality is that reduced food availability has a greater effect on the survival of the sex with higher nutritional requirements associated with their larger size and faster growth rates (Martín et al. 2007). This results in greater vulnerability of males to poor parental investment or unfavorable rearing conditions. Because of the positive interaction between nestling growth rates and sex (GROW*SEX) on post-fledging survival, our results seem to suggest that faster-growing males indeed survive their first year better. If male Herring Gulls do have higher nutritional requirements, a seasonal decline in rearing conditions is likely to further lower their survival prospects. Accordingly, a negative interaction of hatching date with offspring sex (HATCH*SEX) indicated reduced survival of later-hatched males.

In conclusion, we found that first-year Herring Gulls had a lower probability of survival than individuals older than one year, and similar results have been reported in many other long-lived species of birds (Martin 1994, Monticelli and Ramos 2012).  First-year mortality is often related to the negative influence of stochastic environmental events, inexperience, and selection pressures operating outside the breeding season, i.e., post-fledging factors (Spendelow 1991, Lindström 1999, Lebreton et al. 2003,Ludwigs and Becker 2006, Meathrel and Carey 2007). However, reproductive parameters potentially covary with survival as well (Ludwigs and Becker 2006, Cam and Aubry 2011). We have presented evidence of carry-over effects of breeding season events on first-year survival of Herring Gulls. Pre-fledging characteristics such as timing of breeding (hatching date), early development (nestling growth rates), and rank order within broods were shown to influence survival after fledging. Furthermore, we found sex-biased mortality of first-year Herring Gulls, with females more likely to survive than males.

Although life-history theory predicts that adult survival will be the key parameter driving population trajectories in long-lived species, juvenile survival has recently been acknowledged as an important source of variability in population growth rates (Sergio et al. 2011, Payo-Payo et al. 2016). Therefore, improving the accuracy of age-specific survival estimates will improve our understanding of the population dynamics of long-lived species. Furthermore, increased knowledge of the factors affecting age-specific survival rates will provide insight into interspecific variation in life-history traits and the trade-offs that exist between them.

**Table 3.2.** Results of CMR model selection with constraint parameterization of first-year survival probability for Herring Gulls.

| Model | QAIC$_c$ | ΔQAIC$_c$ | QAIC$_c$ Weights | Model Likelihood | NP | QDeviance |
|---|---|---|---|---|---|---|
| Φ (a2-./.)p(.) GROW SEX | 339.07 | 0.00 | 0.09 | 1.00 | 5 | 328.80 |
| Φ (a2-./.)p(.) RO12 GROW SEX | 339.12 | 0.05 | 0.09 | 0.97 | 6 | 326.75 |
| Φ (a2-./.)p(.) GROW | 340.08 | 1.01 | 0.06 | 0.60 | 4 | 331.91 |
| Φ (a2-./.)p(.) GROW HATCH SEX | 340.28 | 1.21 | 0.05 | 0.55 | 6 | 327.91 |
| Φ (a2-./.)p(.) RO12 GROW | 340.29 | 1.22 | 0.05 | 0.54 | 5 | 330.03 |
| Φ (a2-./.)p(.) RO12 GROW HATCH SEX | 340.33 | 1.26 | 0.05 | 0.53 | 7 | 325.83 |
| Φ (a2-./.)p(.) RO12 GROW HATCH SEX SEX*HATCH | 340.36 | 1.29 | 0.05 | 0.52 | 8 | 323.72 |
| Φ (a2-./.)p(.) GROW HATCH SEX SEX*HATCH | 340.65 | 1.58 | 0.04 | 0.45 | 7 | 326.15 |
| Φ (a2-./.)p(.) RO12 GROW HATCH SEX GROW*SEX | 340.96 | 1.89 | 0.04 | 0.39 | 8 | 324.31 |
| Φ (a2-./.)p(.) RO12 GROW HATCH SEX GROW*SEX SEX*HATCH | 340.99 | 1.92 | 0.04 | 0.38 | 9 | 322.18 |
| | | | | | | |
| Φ (a2-./.)p(.) RO12 | 341.35 | 2.28 | 0.03 | 0.32 | 4 | 333.17 |
| **Φ (a2-./.)p(.)** | **341.54** | **2.47** | **0.03** | **0.29** | **3** | **335.43** |
| Φ (a2-./.)p(.) LO | 342.72 | 3.65 | 0.05 | 0.16 | 4 | 334.55 |

Top models best supported by our data are shown in the upper half. The model results of the starting model (bold) and a model either including laying order (LO) or rank order after brood reduction (RO12) are shown in the lower half. Goodness-of-fit of the starting model (bold) was assessed by a median-ĉ GOF test and the relative fit of alternative models was assessed by Akaike's Information Criterion. The number of parameters in each model is indicated by NP.

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# 4

# Age of first breeding interacts with pre- and post-recruitment experience in shaping breeding phenology in a long-lived gull

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Modified from Bosman (2013) PLoS ONE 8: e82093.

## SUMMARY

Individual variation in timing of breeding is a key factor affecting adaptation to environmental change, yet our basic understanding of the causes of such individual variation is incomplete. This study tests several hypotheses for age-related variation in the breeding timing of Lesser Black-backed Gulls, based on a 13 year longitudinal data set that allows to decouple effects of age, previous prospecting behavior, and years of breeding experience on arrival timing at the colony. At the population level, age of first breeding was significantly associated with timing of arrival and survival, i.e. individuals tended to arrive later if they postponed their recruitment, and individuals recruiting at the age of 4 years survived best. However, up to 81% of the temporal variation in arrival dates was explained by within-individual effects. When excluding the pre-recruitment period, the effect of increasing age on advanced arrival was estimated at 11 days, with prior breeding experience accounting for a 7 days advance and postponed breeding for a 4 days delay. Overall, results of this study show that delayed age of first breeding can serve to advance arrival date (days after 1 December) in successive breeding seasons throughout an individual's lifetime, in large part due to the benefits of learning or experience gained during prospecting. However, prospecting and the associated delay in breeding also bear a survival cost, possibly because prospectors have been forced to delay through competition with breeders. More generally, results of this study set the stage for exploring integrated temporal shifts in phenology, resource allocation and reproductive strategies during individual lifecycles of long-lived migratory species.

## INTRODUCTION

Individual variation in reproductive performance is an omnipresent feature of the demography of natural populations (Froy et al. 2013). As evolutionary change is generated by variation in individual performance, understanding the processes driving this variation is fundamental to gain insight into individual behavioral strategies, life-history evolution and population dynamics (Coulson et al. 2006, Hammers et al. 2013). The influence of age on reproductive performance is widely recognized and patterns of improved performance in early life, an asymptote at middle age, and evidence of senescence in older individuals, have been described in many long-lived mammals and birds (Wiebe and Martin 1998, Low and Forslund 2007, Nussey et al. 2006, Blas et al. 2009, Limmer and Becker 2010, Rebke et al. 2010, Dugdale et al. 2011, Martin and Festa-Bianchet 2011).

In migratory species, a key life-history trait associated with reproductive performance is the timing of individual appearance on the breeding grounds (Becker et al. 2008). In seasonally reproducing animals, the timing of reproduction is very important and subject to intense selection pressures because parents are expected to time their reproduction such that maximum offspring food requirements coincide with maximum food availability to ensure offspring survival (Schroeder et al. 2012). Hence, a timely arrival on the breeding grounds constitutes an important precondition of successful reproduction because it affects the length of the period available for breeding and can buffer yearly variation in peak food availability that determines the optimal onset of breeding. In migratory birds, early arrival at the breeding grounds has also been shown to result in priority access to high quality territories and nesting sites (Becker et al. 2008). Moreover, the evidence that early nesting confers advantage in terms of reproductive success (e.g. highest survival of nestlings) is overwhelming (reviewed in Drent 2006). Although early arrival may thus improve reproductive success, it may also lead to considerable survival costs, e.g. as a result of inclement weather (Kokko 1999). It is generally believed that the timing of arrival on the breeding grounds has important fitness consequences and, hence, is considered to constitute a key fitness parameter (Hötker 2002, Saino et al. 2004).

While age is commonly regarded as a key parameter in explaining temporal variation in arrival at the breeding grounds, with older individuals usually arriving before younger ones (Hötker 2002, Smith and Moore 2005, Cooper et al. 2009), age-related variation in timing of arrival has almost exclusively been studied from a between-individual (population) perspective. Hence, little is known about within-individual patterns of age-related variation. Two major hypotheses, not mutually exclusive, have been suggested to explain improvements in reproductive performance with age at the individual level and age-related competence and resource allocation (Forslund and Pärt 1995, Mauck et al. 2012). The experience or improvement of competence hypothesis (Froy et al. 2013, Limmer and Becker 2010, Mauck et al. 2012) states that reproductive performance may improve with age as a result of increasing experience, but only if experience enhances competency. This makes intuitive sense, as long-lived animals may take several years to acquire the skills necessary to forage efficiently, to obtain and defend good-quality territories or mates, which may have consequences for their arrival timing. This hypothesis is sometimes also referred to as the ‘constraint hypothesis’, suggesting that the lack of accumulated skill constrains the reproductive performance of young individuals (Mauck et al. 2012). By contrast, the trade-off or effort hypothesis argues that age-related improvement in reproductive performance is driven by increasing an individual’s level of reproductive investment owing to changes in reproductive costs or residual reproductive value, and implies a trade-off between current reproductive effort and future survival and fecundity (Froy et al. 2013, Limmer and Becker 2010, Mauck et al. 2012). This hypothesis is sometimes also referred to as the ‘restraint hypothesis’, suggesting that reproductive effort should be withheld early in life, if it has a disproportionately negative effect on future survival and breeding probabilities (Mauck et al. 2012).

Another important factor underlying an improvement in reproductive performance with age might be the age of first breeding (Limmer and Becker 2008). In long-lived migrants, the pre-reproductive period varies in length among individuals. Intraspecific variation in recruitment age may reflect quality of individuals (Becker et al. 2008) with lower-quality individuals experiencing higher costs and higher mortality associated with early arrival on the breeding grounds (Lescroël et al. 2009). For some species there is indeed evidence that high-quality individuals are the first to arrive (Forstmeier 2002 and references herein). The delayed breeding or recruitment hypothesis (Pianka and Parker 1975, Curio 1983) proposes that these high-quality individuals delay their first breeding and recruit into the population at a later age (e.g. awaiting the opportunity to select a high-quality breeding territory) because early acquisition of a low-quality territory may lead to life-long low reproductive success due to high breeding site fidelity (Cooper et al. 9000). This progressive appearance of early arrivers into the breeding population may result in an advancement of arrival timing with age at the population level, even though no change is apparent at the individual level.

Delayed maturity is also often associated with the occurrence of a high proportion of pre-breeders at the breeding grounds, also known as prospectors (Becker et al. 2008, Jenouvrier et al. 2008). During prospecting, individuals are believed to gather knowledge about potential breeding partners, territories, foraging sites and food supply, which may allow for a better integration into the breeding population afterwards. In support of this, several studies showed direct or indirect fitness benefits from prospecting behavior prior to the first breeding attempt, (Schjørring et al. 1999, Dittmann and Becker 2003, Doligez et al. 2004, Dittmann et al. 2007, Pärt et al. 2011, Veiga et al. 2012), also in relation to arrival timing. For instance, in Common tern (*Sterna hirundo*), former prospectors arrived significantly earlier in the breeding colony during their reproductive life (Dittmann and Becker 2003).

Finally, the selection hypothesis holds that if individuals that tend to arrive later also tend to die at a younger age, they will be underrepresented in the older age classes. As a consequence of these unobserved differences in survival abilities across individuals (commonly called frailty; (Aubry et al. 2011)), arrival timing will advance with age at the population level, but again no change must have taken place at the individual level.

**Table 4.1.** Linear mixed models testing the linear and quadratic effects of age, age of first breeding ($\alpha$) and age of last reproduction ($\omega$) on arrival date including and excluding pre-recruitment arrivals.

| | breeders (**incl.** prospecting years) | | | | | breeders (**excl.** prospecting years) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Variable | Estimate | SE | d.f. | *F* | *P* | Estimate | SE | d.f. | *F* | *P* |
| Intercept | 195.06 | 3.61 | — | — | — | 172.10 | 5.99 | — | — | — |
| Age | -14.78 | 1.12 | 497 | 175.45 | **<0.0001** | -8.66 | 1.67 | 478 | 26.97 | **<0.0001** |
| Age$^2$ | 0.77 | 0.08 | 351 | 97.49 | **<0.0001** | 0.41 | 0.11 | 350 | 14.76 | **0.0001** |
| Random variance (Year) | -0.23 | 0.37 | — | — | — | -0.64 | 0.43 | — | — | — |
| Individual (nested in pair) variance (intercept) | 83.19 | 48.77 | — | — | — | 118.58 | 76.92 | — | — | — |
| Individual (nested in pair) variance (slope) | 0.94 | 1.36 | — | — | — | 0.92 | 1.76 | — | — | — |
| Autogressive covariance | 0.08 | 0.05 | — | — | — | 0.08 | 0.06 | — | — | — |
| Residual variance | 558.41 | 28.57 | — | — | — | 540.01 | 32.81 | — | — | — |
| Intercept | 201.20 | 10.10 | — | — | — | 164.47 | 13.73 | — | — | — |
| Age | -23.64 | 2.12 | 120 | 124.94 | **<0.0001** | -13.25 | 3.92 | 83.2 | 11.44 | **0.001** |
| Age$^2$ | 1.46 | 0.18 | 62 | 64.73 | **<0.0001** | 0.74 | 0.28 | 50.1 | 6.83 | **0.01** |
| $\alpha$ | 5.08 | 2.21 | 63.4 | 5.28 | **0.02** | 5.72 | 2.83 | 58.8 | 4.07 | **0.04** |
| $\omega$ | -1.22 | 0.87 | 53.9 | 1.96 | 0.17 | -1.25 | 1.12 | 69.7 | 1.24 | 0.27 |
| Random variance (Year) | 0.02 | 1.51 | — | — | — | -0.31 | 2.69 | — | — | — |
| Individual variance (intercept) | 23.24 | 51.31 | — | — | — | 78.40 | 106.73 | — | — | — |
| Individual variance (slope) | 3.74 | 2.69 | — | — | — | 2.41 | 3.76 | — | — | — |
| Autogressive covariance | 0.05 | 0.09 | — | — | — | 0.12 | 0.12 | — | — | — |
| Residual variance | 342.86 | 32.96 | — | — | — | 297.28 | 42.88 | — | — | — |

**Table 4.2.** Linear mixed models testing the linear and quadratic effects of breeding experience (EXP) and age of first breeding ($\alpha$) on arrival date including and excluding pre-recruitment arrivals.

| | breeders (**incl.** prospecting years) | | | | | breeders (**excl.** prospecting years) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Variable | Estimate | SE | d.f. | *F* | *P* | Estimate | SE | d.f. | *F* | *P* |
| Intercept | 181.75 | 5.86 | — | — | — | 159.79 | 6.70 | — | — | — |
| Age | -18.37 | 1.09 | 379 | 285.56 | **<0.0001** | -11.12 | 1.61 | 320 | 47.44 | **<0.0001** |
| Age$^2$ | 1.01 | 0.08 | 268 | 165.66 | **<0.0001** | 0.58 | 0.10 | 302 | 31.68 | **<0.0001** |
| $\alpha$ | 4.79 | 1.27 | 201 | 14.13 | **0.0002** | 3.72 | 1.44 | 191 | 6.65 | **0.01** |
| Random variance (Year) | -0.32 | 0.29 | — | — | — | -0.24 | 0.38 | — | — | — |
| Individual variance (intercept) | 99.19 | 37.73 | — | — | — | 103.10 | 60.99 | — | — | — |
| Individual variance (slope) | -0.62 | 1.15 | — | — | — | -0.37 | 1.50 | — | — | — |
| Autoregressive covariance | 0.15 | 0.05 | — | — | — | 0.15 | 0.06 | — | — | — |
| Residual variance | 414.02 | 23.96 | — | — | — | 331.34 | 24.72 | — | — | — |
| residual variance | 148.66 | 5.25 | — | — | — | 140.59 | 5.40 | — | — | — |
| EXP | -11.68 | 1.03 | 361 | 128.47 | **<0.0001** | -7.18 | 0.94 | 396 | 57.92 | **<0.0001** |
| EXP$^2$ | 1.05 | 0.14 | 89.6 | 56.15 | **<0.0001** | 0.70 | 0.12 | 86 | 31.69 | **<0.0001** |
| $\alpha$ | 0.27 | 1.24 | 201 | 0.05 | 0.83 | -0.15 | 1.29 | 182 | 0.01 | 0.91 |
| Random variance (Year) | -0.48 | 0.32 | — | — | — | -0.12 | 0.38 | — | — | — |
| Individual variance (intercept) | 58.80 | 33.43 | — | — | — | 81.43 | 38.23 | — | — | — |
| Individual variance (slope) | 4.95 | 2.68 | — | — | — | 3.89 | 2.59 | — | — | — |
| Autoregressive covariance | 0.25 | 0.05 | — | — | — | 0.18 | 0.07 | — | — | — |
| Residual variance | 532.40 | 32.78 | — | — | — | 337.32 | 26.07 | — | — | — |

**Table 4.3.** Linear mixed models testing the linear and quadratic effects of breeding experience (EXP) and the effects of prospecting behavior excluding pre-recruitment arrivals and maturation including pre-recruitment arrivals on arrival dates.

| breeders (excl. prospecting years) | | | | | | breeders (incl. prospecting years) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | Estimate | SE | d.f. | *F* | *P* | Variable | Estimate | SE | d.f. | *F* | *P* |
| Intercept | 145.07 | 2.09 | — | — | — | Intercept | 161.87 | 1.59 | — | — | — |
| EXP | -7.08 | 0.93 | 392 | 58.56 | **<0.0001** | EXP | -5.13 | 1.63 | 295 | 9.92 | **0.001** |
| $EXP^2$ | 0.70 | 0.12 | 91 | 32.63 | **<0.0001** | $EXP^2$ | 0.46 | 0.19 | 63.9 | 6.18 | **0.02** |
| Prospect | -7.33 | 2.30 | 194 | 10.15 | **0.002** | Maturation | — | — | 743 | 65.86 | **<0.0001** |
| | | | | | | Prospects | 0 | — | — | — | — |
| | | | | | | First-time breeders | -20.60 | 1.98 | — | — | — |
| | | | | | | Experienced | -25.63 | 3.03 | — | — | — |
| Random variance (Year) | -0.10 | 0.35 | — | — | — | Random variance (Year) | -0.27 | 0.31 | — | — | — |
| Individual variance (intercept) | 78.07 | 34.11 | — | — | — | Individual variance (intercept) | 89.85 | 33.11 | — | — | — |
| Individual variance (slope) | 3.90 | 2.56 | | | | Individual variance (slope) | 4.15 | 2.50 | | | |
| Autogressive covariance | 0.14 | 0.06 | — | — | — | Autogressive covariance | 0.14 | 0.05 | — | — | — |
| Residual variance | 326.81 | 23.82 | — | — | — | Residual variance | 429.94 | 25.21 | — | — | — |

**Table 4.4.** Results of multi-state CMR model selection on survival and recapture probabilities in *Larus fuscus*.

| Model | $QAIC_c$ | Δ $QAIC_c$ | $QAIC_c$ Weight | Model Likelihood | NP | Qdeviance |
|---|---|---|---|---|---|---|
| $S^m$(.) $p^m$ (.) $\Psi^{i\to m}$ (age) | 641.7845 | 0.0000 | 0.2531 | 1.0000 | 11 | 619.4782 |
| $S^m$(.) **$\alpha$ $\alpha^2$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 642.7719 | 0.9874 | 0.1545 | 0.6104 | 13 | 616.3487 |
| $S^m$(.) **PROS** $p^m$ (.) $\Psi^{i\to m}$ (age) | 643.2420 | 1.4575 | 0.1221 | 0.4825 | 12 | 618.8797 |
| $S^m$(.) **PROS $\alpha$ $\alpha^2$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 643.3955 | 1.6110 | 0.1131 | 0.4469 | 14 | 614.9066 |
| $S^m$(.) **$\alpha$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 643.7775 | 1.9930 | 0.0934 | 0.3692 | 12 | 619.4151 |
| $S^m$(.) **AIFY $\alpha$ $\alpha^2$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 644.4558 | 2.6713 | 0.0666 | 0.2630 | 14 | 615.9668 |
| $S^m$(.) **AIFY PROS** $p^m$ (.) $\Psi^{i\to m}$ (age) | 645.2409 | 3.4564 | 0.0450 | 0.1776 | 13 | 618.8176 |
| $S^m$(.) **PROS $\alpha$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 645.2560 | 3.4715 | 0.0446 | 0.1763 | 13 | 618.8327 |
| $S^m$(.) **AIFY PROS $\alpha$ $\alpha^2$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 645.3464 | 3.5619 | 0.0427 | 0.1685 | 15 | 614.7869 |
| $S^m$(.) **AIFY $\alpha$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 645.6632 | 3.8787 | 0.0364 | 0.1438 | 13 | 619.2399 |
| $S^m$(.) **AIFY PROS $\alpha$** $p^m$ (.) $\Psi^{i\to m}$ (age) | 647.2519 | 5.4674 | 0.0165 | 0.0650 | 14 | 618.7629 |
| $S^m$(.) **AIFY** $p^m$ (.) $\Psi^{i\to m}$ (age) | 647.9150 | 6.1305 | 0.0118 | 0.0467 | 12 | 623.5526 |
| $S^m$(.) $p^m$ (t) $\Psi^{i\to m}$ (age) | 655.5974 | 13.8129 | 0.0003 | 0.0010 | 26 | 601.9398 |
| $S^m$(t) $p^m$ (.) $\Psi^{i\to m}$ (age) | 664.7807 | 22.9962 | 0.0000 | 0.0000 | 26 | 611.1231 |
| $S^m$(t) $p^m$ (t) $\Psi^{i\to m}$ (age) | 677.5672 | 35.7827 | 0.0000 | 0.0000 | 41 | 591.4278 |

Goodness-of-fit of the starting model was assessed by a median-ĉ GOF test and the relative fit of alternative models was assessed by Akaike's Information Criterion. The number of parameters in each model is indicated by NP. The following parameters were fixed in all models : $S^i = 1$, $p^i = 0$, $\Psi^{m\to i} = 0$ and for $\Psi^{i\to m}$ (age): $a_1 = 0$ and $a_6 = 1$ (see Methods for details and rationale).

Here we study mechanisms underlying temporal variation in timing of arrival among and within individuals of the iteroparous Lesser Black-backed Gull (*Larus fuscus*), based on the analysis of a longitudinal dataset of phenological records from prospecting and breeding individuals in a coastal colony in NW Belgium spanning 13 annual cycles. Earlier studies in this colony showed that the yearly per capita number of fledglings is inversely related to laying date (Bosman unpublished data), while immature birds return later to the breeding grounds than breeding adults (Van Waeyenberge et al. 2002). By taking advantage of the fact that age and age of first breeding are known from a large number of individually-marked birds, we here aim to investigate and disentangle effects of age, previous prospecting behavior, and years of breeding experience on arrival timing at the breeding colony. Within the framework of the non-mutually exclusive hypotheses outlined above, we address the following questions: (i) To what extent does timing of arrival constitute a dynamic trait (i.e. resulting from changes within individuals over time) or a fixed, consistent individual trait (i.e. resulting from phenotypic variation among individuals)? To disentangle within- from between-individual sources of variation in arrival dates and quantify their relative contribution, we used linear mixed-effects models. Modeling individuals and their longitudinal measurements as nested random effects thereby allows us to split total variance into a between-individual ($\sigma^2_u$) and a within-individual ($\sigma^2_e$; residual variance) component (van de Pol and Verhulst 2006); (ii) What is the role of experience gained from earlier prospecting or breeding?; (iii) Is there a correlation between variation in age of first breeding ($\alpha$) or age of last breeding ($\omega$) and age-related variation in timing of arrival?; (iv) To what extent is survival probability affected by early arrival and/or prospecting behavior at early age?

## METHODS AND MATERIALS

### Study species, field procedures and data collection

*Larus fuscus* of the subspecies *graellsii* are long-distance migrants between their main wintering areas in Iberia and western North Africa and their breeding grounds in NW Europe (Rock 2002), where they breed in mixed colonies with Herring Gull (*Larus argentatus*). Our study colony is located in the outer port of Zeebrugge (Belgium, 51°21'N, 03°11'E) and hosts up to ± 4500 pairs of *Larus fuscus* annually. In this study, we analyzed phenology data collected between 1999 and 2012, a timeframe spanning 13 annual cycles (database managed by the Research Institute of Nature and Forest, Belgium). Only established breeding birds that were individually marked as nestlings and therefore of known age, were considered for analysis. On a total ringing effort of 1664 nestlings up to 2009, 310 individuals of different birth cohorts for which arrival data were collected, survived to breeding age and established themselves in our study colony. Breeding adults were sexed on the basis of direct size comparison of paired individuals, complemented by observations of copulation and courtship behavior at the breeding colony. The repeatability of sex assessment of individuals recorded during subsequent breeding seasons equaled 100%. The transition from migration to breeding was defined as the earliest sighting in the colony each year, based on meticulous observations conducted from morning till evening every second day between mid-winter till the start of egg-laying. For each sexually mature *Larus fuscus* of known age, individual arrival dates were subsequently calculated as the number of days since 1 December of the previous year (the nominal starting point in our population; see also Bosman et al. 2012). Up to 2012, we obtained comprehensive data on the breeding experience of 211 individuals, calculated as the number of reproductive years accumulated before the current breeding season. Each year, highly experienced observers recorded the activity of all individually-ringed birds throughout the breeding season, taking GPS coordinates of each nest during early nest-building and marking all nests with an individually coded stick. Throughout the study, individuals showed a high degree of nest site fidelity which facilitated their early detection in the colony and allowed ample time to search for new recruits. Given the high level of nest site fidelity, the high search effort by multiple experienced observers from nest-building till fledging, and the high and constant resighting probability during the study period (see Results), we believe that our breeding data were both highly accurate and complete. Realized age of first breeding (α), defined as the age when an individual was first recorded breeding, ranged between 3 to 7 years (μ = 4.09 years ± 0.05 years). To be conservative, we assumed that only individuals that were not resighted in the breeding colony during at least three consecutive years and that had not been resighted during migration, at their wintering grounds, or in other well-studied neighboring colonies in the southern part of the North Sea: Nord, Pas-de-Calais (France); Zeeland, Noord-Brabant, Zuid- and Noord-Holland (the Netherlands); Suffolk (United Kingdom); Schleswig-Holstein (Germany), were dead. In very rare occasions birds were observed to loose uniquely-coded rings, however this was actively countered by targeted re-ringing campaigns during each breeding season. Applying these criteria, realized age of last breeding (ω) was known for 66 individuals, of which six were actually reported dead. Data on prospecting behavior before recruitment, inferred from the earliest sighting in number of days for each year (see above), were available for 150 breeding individuals.

### Statistical analysis and hypothesis testing

Within- and between-individual variation in timing of arrival was analyzed by linear mixed-effects models (LMM; Littell et al. 1996) in SAS 9.3 (SAS Institute Inc., Cary, NC, USA). In all models, random intercepts and slopes were included to account for variance among individuals and for non-independency of repeated measures from the same individual, respectively. By modeling individuals and their longitudinal measurements as random effects, we accounted for between-individual variation in strength of relationships (i.e. slope of response) with other variables (e.g. advanced arrival with age) (Schielzeth and Forstmeier 2009). In addition, individual identity was modeled as a repeated effect with autoregressive covariance structure to control for covariance between pairs of observations, given that repeated measures closer in time are likely to be more strongly correlated (Dugdale et al. 2011, Littell et al. 1996). We used the Kenward-Roger denominator degrees of freedom method to correct for downward bias in standard error estimates in the covariance matrix. As year and age are likely correlated in studies of individually-marked animals unless they continue over decades, we included year as a random factor in all models. To test for age-related variation in timing of arrival, age was modeled both as linear and quadratic (age*age) effect with arrival date as dependent variable. As age effects are predicted to be more pronounced when non-breeding individuals are included (Forslund and Pärt 1995), we additionally modeled pre-recruitment (prospecting) arrival dates of subsequent breeders to compare age effect sizes on timing of arrival between analyses that either included or excluded these data. As factor sex did not significantly explain variation in timing of arrival in any of the models including survival analysis (data not shown), data from males (*N* = 179), females (*N* = 53) and unsexed individuals (*N* = 78) were subsequently pooled.

Age-related variation in arrival timing was first examined at the population level. We analyzed all arrival dates, i.e. including those related to prospecting behavior (*N* = 1364), while in a second model we only included arrivals directly related to reproduction (*N* = 1134). However because 12 of these pooled individuals were mates (i.e. belonging to six breeding pairs), they were nested (Table 4.1, upper panels) to avoid pseudoreplication at the level of the breeding pair.

To test predictions stemming from the selection and recruitment hypotheses, we built a LMM including parameters age of first breeding (α) and age of last reproduction (ω) as explanatory variables (pre-recruitment arrivals included: *N* = 352 dates; pre-recruitment arrivals excluded: *N* = 254 dates; Table 4.1, lower panels) and a third model with age of first breeding (α) only (*N* =1048 and *N* = 818, respectively; Table 2, upper panels). As curvilinear relationships with fitness performances were documented in vertebrates before (Dugdale et al. 2001, Reid et al. 2003), we initially tested for quadratic relationships with α and ω. However, as these effects were not significant at the 5% probability level (data not shown), they were not withheld in our final models. If early individuals survive better, we expect a negative relationship between arrival date and ω in accordance with the selection hypothesis. If early individuals delay recruitment into the breeding population until a later age, we expect a negative relationship between arrival date and α as predicted by the recruitment hypothesis. A positive relationship between arrival date and α, in contrast, would be consistent with a more advanced arrival with accumulating breeding experience in individuals of similar age (Forlund and Pärt 1995).

To test whether sexual maturation and experience gained from earlier prospecting or breeding explain average within-individual variation in timing of arrival as predicted by the experience hypothesis, we first performed two additional LLMs modeling breeding experience (EXP) while controlling for the effect of α (*N* = 1048 and *N* = 818 arrival dates when including and excluding pre-recruitment arrivals, respectively; Table 4.2, lower panels). In a subsequent LMM (Table 4.3, left panel), we tested whether or not prospection before recruitment (0 or 1) was significantly related to individual timing of arrival during reproduction (*N* = 818 arrival dates). In a final LMM (Table 4.3, right panel), we constricted individual life-histories of breeding individuals to a three-level fixed factor (pre-recruitment/prospecting, first-time breeding or experienced breeding) as a measure of degree of sexual maturation, and tested whether the timing of arrival spanning the entire lifetime significantly varied among these life-stages (*N* = 1048 arrival dates). In these last two models, we initially controlled for α, but removed this factor after backward selection (results not shown). Because age and breeding experience are highly correlated, we substituted linear and quadratic covariates of age by breeding experience (EXP and EXP$^2$) when testing the constraint hypothesis (cf. Dugdale et al. 2011). Because of the occurrence of prospecting behavior before recruitment and/or instances of intermittent breeding after recruitment, age was modeled as a categorical variable in the repeated statement to specify the order of each observation within each individual. First-order interactions with EXP and $EXP^2$ were not significant in all analyses and were sequentially removed in a backward selection procedure.

### Survival analysis

To test whether early investment in reproductive performance has a negative effect on survival as predicted by the trade-off hypothesis, we performed two survival analyses. In these analyses, we investigated the survival cost of early arrival during the year of first reproduction, rather than during the year of first arrival in the colony because not all individuals prospected and different processes might drive the arrival timing of prospectors and first-time breeders. Additionally, we examined if the absence or presence of prospecting behavior affected survival chances. We also included age of first breeding and its quadratic effect because stabilizing selection on recruitment age through differential survival has previously been found in gulls (Pyle et al. 1997).

First, we performed a multi-state CMR-analysis in MARK 7.0 (Colorado State University, USA). Within the framework of this study, birds of known age were initially marked as immatures (STATE A) and matured when recruiting into the breeding population (STATE B). Hence, realized age of first breeding was defined as the maturation point. Next, we imposed a series of logical constraints based on a priori knowledge of the realized life-histories of the individuals under study here. Since only individuals that survived to maturity were included, the parameter for immature survival was fixed to $S^i = 1$. Next, variation in realized age of first breeding was known to be age-related (3 to 7 years old). Therefore, we modeled an age-dependent transition probability to maturity ($\Psi^{i \to m}$) with six age steps ($\leqslant 2,3,4,5,6,\geqslant 7$), without recruitment probability before the age of 3 ($a1 = 0$), and with a recruitment probability of 1 for individuals of age 7 years or older ($a6 = 1$; i.e. knowing that all individuals still alive at this age had recruited). Once an individual matured, it remains so and maturity, hence, constitutes an absorbing state ($\Psi^{m \to i} = 0$). Since we primarily aimed to model variation in mature survival after recruitment (Sm), immaturity was regarded an unobservable state with zero resighting probability ($p^i = 0$). Individual resighting histories were restricted to 198 individuals for which (i) initial release data as pullus (age = 0), (ii) arrival dates in the first year of reproduction, and (iii) resightings as mature breeding bird within the colony in subsequent years after recruitment were available. The dataset also contained three individual-level covariates, i.e. the timing of arrival during the first year of reproduction (AIFY), the absence or presence of prospecting behavior during pre-recruitment (PROS = 0 or 1) and age of first breeding ($\alpha$ and its quadratic effect coded as power($\alpha$,2) in the design matrix). As few birds recruited at age 6 and 7 ($N$ =9 individuals), we restricted $\alpha$ to three levels (3 years; 4 years; 5 years or older) in order to obtain reliable estimates of the mature survival parameters as a function of $\alpha$ (see Results). We used a starting model with time variation in mature survival and resighting probabilities, i.e. $S^m(t)\ p^m\ (t)\ \Psi^{i \to m}$ (age). Being a reduced parameter general model, we applied a median-$\hat{c}$ GOF test to assess the goodness-of-fit (GOF) of this starting model (see web-based manual to MARK, chapter 8). Subsequently, the results were corrected for slight over-dispersion of the data using the value of the GOF parameter $\hat{c} = 1.67 \pm 0.08$ (lower bound =1.0, upper bound = 5.0, 10 design points with 100 replicates at each point). Next, a series of candidate models were fitted that differed in the extent to which mature survival and resighting rates were held constant (indicated with $S^m(.)$ and $p^m$ (.) respectively) or whether $S^m$ was considered to be a function of AIFY, PROS, α and/or α². Model selection methods were based on Akaike Information Criterion (AIC; Anderson et al. 1998) and candidate models were ranked by second-order AIC differences ($\Delta$ $AIC_c$). Only models that deviated less than 2 $AIC_c$ units from the most parsimonious model (ΔAICc = 0) were considered to have approximately equal weight in the data in accordance with model weights and evidence ratios presented by (Burnham and Anderson 2002). To be conservative, models that deviated >2 $AIC_c$ units from the most parsimonious model were considered to be unsupported by our data (see web-based manual to MARK, chapter 5). The model averaging procedure was used to compute the average estimates for mature survival and resighting probabilities based on weighted $AIC_c$-values for each model and thus accounts for model uncertainty in these estimates.

Second, we built a backward stepwise Cox proportional hazards Model (Proc PHREG) in SAS 9.3 (SAS Institute Inc., Cary, NC, USA) to relate the risk of death after recruitment (i.e. hazard) to (i) the timing of arrival during the first year of reproduction (AIFY), (ii) the absence or presence of prospecting behavior during pre-recruitment (PROS = 0 or 1), and (iii) the age of first breeding (α) and its quadratic effect ($N$ = 198 individuals, ties = breslow). TIME*STATUS was modeled as the response variable, where TIME refers to the follow-up time (in years) after recruitment and STATUS is the event indicator with value 1 for death time and value 0 for censored time. When performing the Cox regression, α was modeled as a continuous variable.

## RESULTS

### Age-specific phenology, selection and recruitment hypotheses

Timing of arrival at the breeding colony showed linear and quadratic relationships with age (Tables 4.1 and 4.2, Fig. 4.1), and the positive quadratic effect indicated that the advance of arrival date with age decreased when individuals grew older. Contrary to the selection hypothesis, the age when individuals disappeared (ω) did not significantly explain variation in timing of arrival (Table 4.1). The effect of age of first breeding (α) on arrival date was significant, however, the relationship was positive whereas a negative relationship was predicted by the recruitment hypothesis. When controlling for the significant effect of α, individual identity accounted for and 19% and 24% of the total variance (calculated as the sum of the individual variance component and the residual variance) in arrival dates when including or excluding pre-recruitment arrival dates, respectively (Table 4.2 upper panel). These percentages reflect a common measure of repeatability (R) and, hence, quantify the constancy of phenotypes, while 1-R can be considered a measure of phenotypic plasticity, cf., (Nakagawa and Schielzeth 2010). Hence, within-individual effects explained 81% and 76% of the total variation in arrival dates when including or excluding pre-recruitment arrival dates, respectively. Overall, effect sizes of relationships with age were stronger when pre-recruitment arrival dates were included (Tables 4.1 and 4.2).

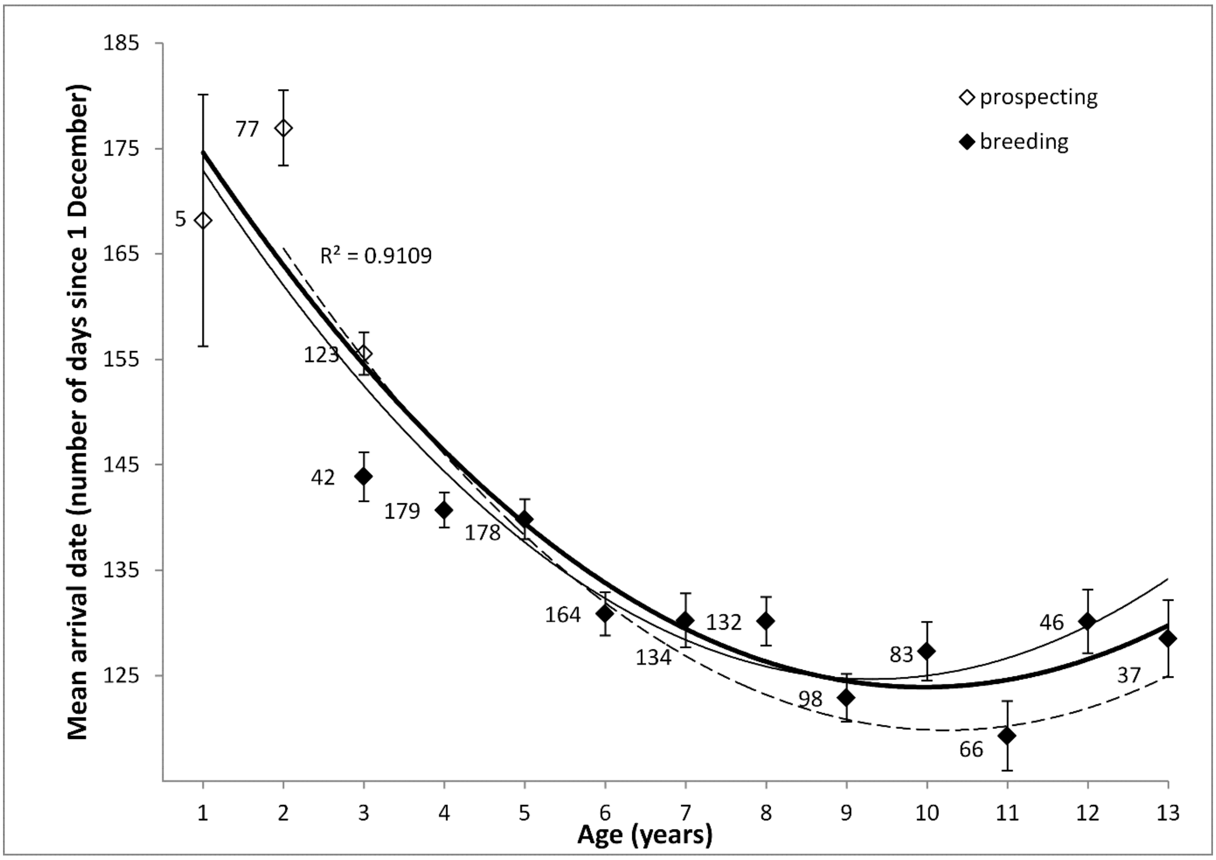

**Figure 4.1.** Progressive advancement in mean arrival date (± SE) with age at the population level. For 310 *Larus fuscus* from a Belgian breeding colony spanning 13 annual cycles (solid bold trendline). Numbers refer to sample sizes. Male (n = 179) and female (n = 53) trendlines are depicted by solid and dashed thin lines respectively. Pre- and post-recruitment arrival data are depicted by open and filled symbols, respectively.

### Experience hypothesis

Individuals that delayed their first breeding tended to arrive consistently later at the colony throughout their lifetime, but nevertheless advanced their arrival with increasing age. This pattern, and the fact that the effect of α on arrival date was strongly reduced when accounting for breeding experience (Table 4.2), is consistent with the hypothesis that breeding experience may underlie the positive relationship between α and timing of arrival (Table 4.2). Individuals indeed showed linear and quadratic advances in arrival date with accumulating levels of EXP (Table 4.2 and 4.3). Additionally, sexual maturation and experience drawn from prospecting behavior both explained variation in arrival dates while accounting for EXP, i.e. resulting in a further advancement of timing of arrival with age (Table 4.3, Fig. 4.2).

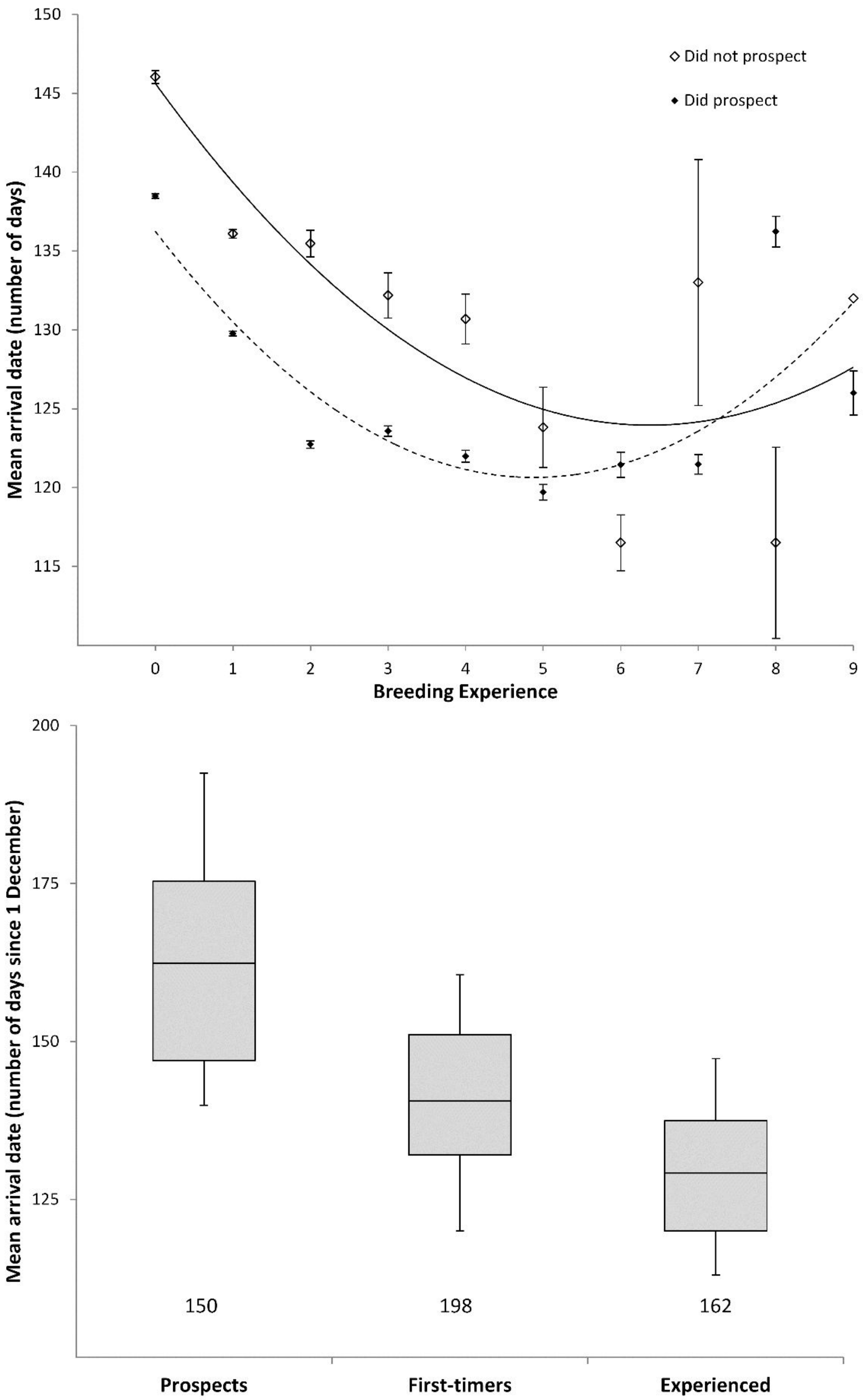

**Figure 4.2.** Relationship between breeding experience and mean arrival date (± SE). 211 *Larus fuscus* from a Belgian breeding colony spanning 10 breeding cycles were grouped by whether they prospected (n = 150) or not (n = 61) and depicted by filled and open symbols, and dashed and solid trendlines, respectively (upper panel). The lower panel shows the same individuals grouped by successive stages of sexual maturity. The box and whiskers plots represent the distribution of arrival dates for each group, with means (solid lines), 10% and 90% (whiskers), and 25% and 75% (box) quartiles Numbers refer to sample.

### Trade-off hypothesis

Both survival analyses yielded highly comparable results (probabilities ± SE). Of the candidate set of CMR models, the one with a constant probability of mature survival ($S^m(.) = 0.91 \pm 0.02$; weighted average) and a constant resighting probability ($p^m(.) = 0.97 \pm 0.01$; weighted average) fitted best to our data (Table 4.4). All models that related variation in mature survival to timing of arrival in the first year of reproduction (AIFY), deviated considerably from this most parsimonious model ($2 < \Delta QAIC_c > 7$; Table 4.4) and were therefore considered unsupported by our data. In contrast, four models that related variation in mature survival to the effect of age of first breeding (α), prospecting behavior (PROS) or both, had $\Delta QAIC_c$ values of less than two (Table 4.4) and were therefore considered equally informative as the most parsimonious model. Prospecting behavior during pre-recruitment was inversely related to mature survival ($S^m = 2.53 - 0.35(PROS)$) with a slightly lower survival probability for prospectors ($S^m = 0.89 \pm 0.02$) compared to non-prospectors ($S^m = 0.93 \pm 0.03$). As adult survival was highest in individuals that recruited at the age of 4 ($S^m = 0.92 \pm 0.02$) and lower in both early (age of 3: $S^m = 0.86 \pm 0.04$) and late (age of 5 or older: $S^m = 0.88 \pm 0.03$) recruiters, our survival data support the notion of normalizing selection acting on age of first breeding ($S^m = -7.27 + 4.81(\alpha) - 0.59(\alpha^2)$). Likewise, mature survival was inversely related to the occurrence of prospecting behavior before recruitment in a Cox proportional hazards model ($\beta = 1.34 \pm 0.54$, $\chi^2 = 6.18$, $P = 0.01$; -2 log likelihood = 480.393, Global Score $\chi^2 = 8.91$, $p = 0.03$), with a fourfold increase in mortality risk after recruitment (Hazard ratio = 3.83). While mature survival was also significantly related to both α ($\beta = -2.83 \pm 1.17$, $\chi^2 = 5.76$, $P = 0.02$) and $\alpha^2$ ($\beta = 0.33 \pm 0.54$, $\chi^2 = 5.98$, $P = 0.02$) with minimal mortality risk when recruiting at the age of 4 (data not shown), no significant relationship was apparent between AIFY and mortality risk following recruitment into the breeding population ($\chi^2 = 2.10$, $P = 0.99$).

## DISCUSSION

In our study population of *Larus fuscus*, age of an individual has a significant effect on its phenology, with older age classes arriving progressively earlier at the breeding grounds (Fig. 4.1). After statistical deconstruction of the within- and between-individual processes underpinning this pattern, we found support for age-related variation in arrival timing at both the population and individual levels. In particular, variation in *Larus fuscus* phenology was related to recruitment age and experience gained from earlier prospecting or breeding.

### Arrival timing and recruitment age

At the population level, age of first breeding (α) was significantly associated with both survival and arrival timing in *Larus fuscus*. Individuals tended to arrive significantly later if they postponed their recruitment, which countered the overall trend of advanced arrival with increasing age and opposes the predictions of the recruitment hypothesis. As we suspect that early recruits might possess inherent reproductive, competitive and cognitive abilities that could allow them to arrive earlier than individuals that delay recruitment (cf. Becker et al.

2008, Aubry et al. 2001), recruitment at young age might be an indicator of higher quality in *Larus fuscus*. Our study further showed that individuals recruiting at the age of 4 years had the highest survival probability. Reduced survival chances for later recruits ($\alpha > 4$ years old) suggest that these birds may be of lower phenotypic quality and therefore less able to cope with costs associated with early arrival (Kokko 1999). Such conclusion supports those of other studies that showed lower reproductive performance in more strongly delayed breeders, e.g., (Blas et al. 2009, Dugdale et al. 2011, Forslund and Larsson 1992, Pärt 1995). Nevertheless, recruiting at the earliest possible age may not be the best strategy either. According to life-history theory, individuals should begin to reproduce at an age when the net benefits are greater than delaying reproduction (Stearns 1992). Earlier recruits ($\alpha < 4$ years old) may consistently arrive too early throughout their lifetime and as a consequence pay the elevated cost of reduced survival probability. Hence, progressive appearance of late arriving *Larus fuscus* at the population level may jointly reflect the disappearance of phenotypes that consistently arrive too early and the appearance of low-quality phenotypes that consistently arrive later than average recruits ($\alpha = 4$ years old) of the same age during subsequent years. This supports the idea that timing of arrival in *L. fuscus* is at least to some degree a consistent individual trait, and evidence for (partial) individual consistency in timing of arrival and migration was earlier shown in other species of birds, e.g., Common Tern (*Sterna hirundo*), (Becker et al. 2008); Pied Avocet (*Recurvirostra avosetta*), (Hötker 2002); Snow Goose (*Anser caerulescens*), Bêty et al. 2004); and Marsh Harrier (*Circus aeruginosus*) (Vardanis et al. 2011), and fishes; Roach (*Rutilus rutilus*), (Brodersen et al. 2012).

### Arrival timing and breeding experience

Despite indications for consistent variation in timing of arrival among individuals belonging to different recruitment age groups, up to 81% of the temporal variation in arrival dates in our population was explained by within-individual effects. Similarly, 87% of the variation in reproductive performance in a longitudinal study on *Sterna hirundo* was explained by within-individual changes (Rebke et al. 2010). Although it is tempting to argue that this is primarily related to progressive gain in breeding experience with age (experience hypothesis; table 4.2), the confounded nature of both variables renders it difficult, if not impossible, to study their independent effects on arrival date. Nevertheless, over the entire reproductive lifetime of *Larus fuscus* (i.e. when excluding the pre-recruitment period), the effect of growing age on advanced arrival was estimated at 11 days, with prior breeding experience accounting for a 7 days advance and postponed breeding for a 4 days delay (Table 4.2, right panel). This suggests that accumulating breeding experience may be at least one important factor explaining advanced arrival over an individual's reproductive lifetime. Likewise, the role of breeding experience was considered strong in the long-lived Greater Flamingo (*Phoenicopterus roseus*) where breeding propensity was largely determined by increasing levels of experience (Pradel et al. 2012). When including the pre-recruitment years in our study, however, arrival advanced with 18 and 12 days in relation to age and breeding experience respectively, while the delay related to postponed breeding remained comparable (Table 4.2, left panel). This discrepancy suggests that additional factors may trigger variation in timing of arrival during immature (pre-recruitment) life-stages.

### Arrival timing and previous prospecting behavior

One additional trigger of variation in timing of arrival during pre-recruitment may be that non-recruited individuals, and to lesser extent first-time breeders, are still subject to maturation of (sexual) function, which may constrain their navigational skills, foraging or breeding abilities. While post-recruitment experience can improve reproductive performance through previous breeding opportunities (see above), pre-recruitment experience may help to achieve higher levels of reproductive performance through prospection. During prospection, immature and subadult birds may improve these skills and thereby facilitate a timely, stepwise transition from migration to breeding (Becker et al. 2008). In support of this (Jorge et al. 2011), showed a strong reduction in annual distribution range of *Larus fuscus* as maturing individuals progressively remained closer to the breeding grounds year-round. Furthermore, prospectors arrived on average seven days earlier at the breeding colony throughout the larger part of their reproductive life, compared to individuals that did not show such behavior (Table 4.3; Fig. 4.2, left panel). However, in *Larus fuscus*, prospecting behavior also comes with a considerable survival cost, which may explain why half of the breeders that indulged in prospecting prior to recruitment, restricted this behavior to a single season at the age of three years or older. Prospecting is presumably costly owing to higher competition for food resources around colonies, more abundant parasites and higher risk of aggressive encounters with conspecifics (Schjørring et al. 1999), while time and energy spent during prospection may also be traded off against other activities, such as foraging and resting (Ponchon et al. 2013).

### Selection and trade-off hypotheses

We did not find evidence that selective disappearance contributed to the observed population-level arrival trajectory. The absence of a significant effect of age of last reproduction (ω) on timing of arrival renders it unlikely that age-related variation in arrival dates resulted from a selective disappearance of late arrivers with increasing age, as predicted by the selection hypothesis. While 66 individuals with known or inferred realized age of last breeding may appear low in terms of sample size when testing for selective disappearance, our results are strongly in line with the weak evidence for differential survival commonly reported from other long-lived species in which low annual mortality (ca. 10% for *Larus fuscus*; (Camphuysen and Gronert 2012), this study) may only cause minor changes in the distribution of early and late individuals among age classes (Forslund and Pärt 1995), but see (Blas et al. 2009). Additionally, survival probabilities did not increase with more advanced arrival early in reproductive life which further disproved the selection hypothesis (cf. Blas et al. 2009).

Likewise, and contrary to the predictions from the trade-off hypothesis, we did not find direct evidence for the existence of a trade-off between current reproductive effort and future survival. Specifically, more advanced arrival dates early in reproductive life did not reduce survival chances later on. Although lowered adult survival probabilities through survival costs related to prospecting behavior and through very early recruitment when only 3 years old (see above)—both in turn related to a more advanced arrival timing—may indirectly affect an individual's timing effort with increasing age.

Overall, our findings demonstrate that age, recruitment age and individual experience may interact in shaping patterns of variation in timing of arrival in *Larus fuscus*. The advancement of arrival date occurred primarily at the individual level and can be explained mainly by a gain in individual experience with increasing age, although we did not succeed in fully disentangling the roles of the latter two factors. As previously shown in Black-legged Kittiwake (*Rissa tridactyla*), delaying recruitment up to intermediate ages may be associated with fitness advantages that offset the costs of delayed maturity (Aubry et al. 2009). In *Larus fuscus*, individuals recruiting at the age of 4 balanced pre- and post-recruitment experience in an advantageous way, advanced their arrival timing with age accordingly and achieved the highest survival probability through stabilizing selection acting on age of first breeding.

While in many species, arrival dates at breeding sites significantly vary between sexes (Cooper et al. 2009, Morbey and Ydenberg 2001)], an earlier study in the same *L. fuscus* colony showed highly synchronized arrival dates of male and female breeders (Bosman et al. 2012). We currently lack sufficient data to directly relate timing of arrival to individual laying dates. However, if present, such relationship might still be obscured by age-related variation in breeding and resource allocation strategies. For example, late individuals might make disproportional use of capital (rather than income) resources to advance their laying date in the face of a seasonal decline in reproductive success, e.g., Snow Goose (*Caerulescens caerulescens*) (Gauthier and Hobson 2003). Hence, to assess to what extent age-specific strategies in timing of arrival affect lifetime reproductive success in long-lived migrant species, future studies need to explore integrated temporal shifts in phenology, resource allocation and reproductive strategies during individual lifecycles (cf. Rebke et al. 2010). We thereby predict ageing individuals to shift along the income-capital allocation continuum, relative to parallel shifts in migratory and reproductive strategies.

In conclusion, this study has shown that a complex interplay between a fixed trait (age of first breeding) and the balancing of pre- and post-recruitment experience can shape a dynamic trait, i.e. age-related advancement in timing of arrival.

## ACKNOWLEDGEMENTS

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# 5

# Effects of body size on sex-related migration vary between two closely related gull species with similar size dimorphism

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## SUMMARY

Studies of migration have revealed multiple trade-offs with other life-history traits that may underlie observed variation in migratory properties among ages and sexes. To assess whether, and to what extent, body size and / or sex-specific differences in competition for resources (e.g. breeding territories or winter food) may shape variation in migration distance and timing of arrival in ecologically and phylogenetically related species, we combined over 30 000 sightings of individually marked, sexually mature males and females of Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*Larus fuscus*) with biometric measurements and phenological observations at a mixed breeding colony. In Herring Gulls, larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females. In Lesser Black-backed Gulls, no relationship between body size and migration distance was apparent in either sex. Mean arrival dates at the breeding colony did not vary with migration distances but differed between males and females of Herring Gulls (but not Lesser Black-backed Gulls). As allometry at least partly explains sexual segregation in migration behavior in Herring Gulls, but not in Lesser Black-backed Gulls, we conclude that the effect of body size on sex-related migratory strategies may vary between closely related, sympatric species despite similar size dimorphism.

## INTRODUCTION

Migratory behavior has evolved independently among many animal groups, such as birds, fish, mammals, reptiles, amphibians, insects and marine invertebrates (Alerstam et al. 2003), and is expressed through a wide range of movement-related behaviors (Dingle 1995, Quinn & Myers 2004, Bolger et al. 2008). As migration is predicted to be favored when benefits gained from moving between habitats outweighs fitness risks and energetic costs of the journey (Calvert et al. 2009), seasonal and spatial variation in environmental conditions comprise primary forces in its evolution (Alerstam & Enckell 1979). Over the past decades, studies on the proximate and ultimate causes of migration have elucidated the role of migration in the annual life cycle of migratory species. Studies on differential migration, defined as 'the situation in which migration in some distinguishable classes (ages, sexes, races) differs with respect to distance, timing or both' (Terrill & Able 1988), in particular, have revealed how migratory behavior may trade-off against other costly activities such as breeding (Dingle 1995, Saino et al. 2004, Boyle 2008, McNamara & Houston 2008, Marques et al. 2010).

Life-history trade-offs, which are a key assumption underlying optimality models of life-history evolution (Roff 1992, Stearns 1992), also play a prominent role in the interpretation of life-history variation within populations, i.e. between ages or sexes. In many vertebrate species, males and females show a marked sexual size dimorphism and/or suffer from different levels of competition for breeding resources that may directly or indirectly affect fitness costs and benefits associated with migration (Catry *et al.* 2005). As a result, various properties of their migratory behavior, such as migration distance, timing of departure or arrival, or habitat use outside the breeding season, have been predicted to differ between sexes (e.g. Cristol 1995, Cristol *et al.* 1999, Kissner *et al.* 2003, Catry *et al.* 2005, O'Hara *et al.* 2006, Palacin *et al.* 2009). Optimal life-history variation in migratory behavior between sexes translates into three hypotheses, each of which focuses on a particular component of ecological specialization in relation to body size or other sex-related variation. The social dominance hypothesis (Gauthreaux 1982) puts forward competitive exclusion of the smaller subordinate sex from preferred habitats or habitats closer to the breeding grounds by larger and dominant conspecifics. The body size (or physiological) hypothesis (Ketterson & Nolan 1976) explains latitudinal (clinal) sexual segregation in wintering sites in relation to body size and cold resistance, with the smaller sex predicted to migrate to lower latitudes. Finally, the arrival time hypothesis (Myers 1981) explains sexual segregation in timing and distance of migration as a function of competition for breeding resources with the sex experiencing higher levels of competition for breeding opportunities predicted to arrive earlier on the breeding grounds and, with this goal, to stay closer and/or return sooner. Despite the different ecological mechanisms underlying these non-exclusive hypotheses, their predictions substantially overlap (Belthoff & Gauthreaux 1991, Jenkins & Cristol 2002) and within-sex variation needs to be taken into account to test or refute them properly (Smith & Nilsson 1987, O'Hara *et al.* 2006, Guillemain *et al.* 2009).

Comparison of life-history traits between closely related species is considered a strong approach for studying the nature of trade-offs underlying life-history variation between and within species (Cristol *et al.* 1999). Following this approach, we assessed variation in migratory behavior of sexually mature male and female Herring Gulls (*Larus argentatus*) and Lesser Black-Backed Gulls (*Larus fuscus*), two phylogenetically and ecologically closely related species that occur in sympatry in NW Europe. Although both species breed in mixed colonies, show a comparable degree of sexual size dimorphism and mature after 3–7 years (Snow *et al.* 1998), they differ in their annual migration pattern along the western coastline of continental Europe. Western populations of Lesser Black-backed Gulls are considered long-distance migrants between their northwestern breeding colonies and main wintering grounds in Iberia and western North Africa (Wernham *et al.* 2002). Individuals of Herring Gulls, in contrast, migrate across a much more variable, but mostly limited, predominantly coastal, radius, resulting in seasonal movements towards non-breeding areas and convergence towards breeding areas at the population level (Dingle 1995, Wernham *et al.* 2002, Roshier & Reid 2003). To assess the extent to which sex-specific constraints related to structural size and/or reproduction may shape variation in migratory behavior within and between both species, we analyze over 30 000 sightings of individually marked adults of both species during breeding, migration and wintering, and model variation in migration distances and arrival dates in a mixed breeding colony at species, sex and individual levels.

## METHODS AND MATERIALS

### Study area and species

We analyzed 31 256 sightings of 153 adult male and 167 adult female Herring Gulls and 288 adult male and 270 adult female Lesser Black-backed Gulls within a time frame spanning 11 annual cycles (May 1999–July 2010; database managed by the Research Institute for Nature and Forest, Belgium). All individuals were color-ringed as pulli or breeding adults in a mixed colony at the outer port of Zeebrugge (Belgium, 51°21′N, 03°11′E). For the former, only sightings made during establishment as adult breeder (3½ years or older) in the colony were considered for this study (hereafter referred to as ‘adults’). The breeding colony hosted peak numbers of 1986 pairs of Herring Gulls (spring 2004) and 4573 pairs of Lesser Black-backed Gulls (spring 2005). Outside the breeding season, adult Herring Gulls were resighted as far north as IJmuiden (The Netherlands), southwest as far as Calvados (France) and inland as far as Tilburg (The Netherlands). Adult Lesser Black-backed Gulls were resighted as far southwest as Banc d’Arguin (Mauritania), north as far as Texel (The Netherlands) and inland as far as Madrid (Spain). The majority of resightings of individuals from both species were made near the coastline and at inland refuse tips.

Because univariate proxies of body size, such as tarsus length, have been shown to provide poor measures of overall size in birds (Rising & Somers 1989, Freeman & Jackson 1990, Blas *et al.* 2009), we measured tarsus length, head length, bill length and gonys width of 97 breeding Herring Gulls (45 males, 52 females) and 284 breeding Lesser Black-backed Gulls (134 males, 150 females) to the nearest 0.1 mm using slide calipers. Using these metrics, body size was estimated as the first axis of a principal component analysis (PC1, hereafter ‘body size’) conducted in PASW statistics 18 (SPSS Inc., Chicago, IL, USA). PC1 explained 80% of the body size variation in both species and had high positive loadings for tarsus length

(Herring Gulls/Lesser Black-backed Gulls: 0.84/0.86), head length (0.95/0.95), bill length (0.88/0.90) and gonys width (0.90/0.88). Only individuals color-ringed and measured as adult breeders were considered for the size analysis. These individuals had been captured over several years since the beginning of the study (some had already been metal-ringed as pulli) and were, hence, considered representative for the different cohorts/ages. Birds color-ringed as pulli were measured at different stages of their structural growth and, if not recaptured as breeding adult, lack of measurements of fully grown traits prevented us from including these individuals in the analysis. Breeding adults were sexed by HJPV on the basis of direct size comparison of paired individuals, complemented by observations of copulation and courtship behavior at the breeding colony. The repeatability of sex assessment of individuals recorded during subsequent breeding seasons equaled 1.00, whereas a discriminant analysis showed that males of both species were significantly larger than females, when based both on each of the univariate biometrics (see above) separately (all $P < 0.001$) and on the multivariate analysis: Herring Gulls: ($\lambda = 0.276$, $\chi^2$ ($df = 4$, $N = 97$) = 119.6, $P < 0.001$; $R^2$-canonical = 0.85, 93% correct reclassification); Lesser Black-backed Gulls: ($\lambda = 0.221$, $\chi^2$ ($df = 4$, $N = 284$) = 422.1, $P < 0.001$; $R^2$-canonical = 0.88, 98% correct reclassification). Birds for which sex identification based on direct observations (five male and two female Herring Gulls and six male Lesser Black-backed Gulls) disagreed with sex identification based on biometrics were excluded from analysis.

### Migration distance and arrival date

For each individual Herring Gull (total: 12 994 sightings) and Lesser Black-backed Gull (total: 18 262 sightings) breeding in the colony, we calculated the median of all distances (km) recorded away from the breeding colony in each month of the year over a time frame spanning 11 annual cycles ('monthly migration distance') (Great circle distance method, http://www.movable-type.co.uk/scripts/latlong.html). Although estimating individuals' maximum recorded migration distances following this method yielded similar migration patterns, using an extreme value in this way increases the risk of strong influences from errors in color-ring reporting. Biases in resighting effort are unlikely to have influenced our results, as the breeding population was large and well represented by marked individuals of known sex, whose migration and wintering sites are well known and extensively visited by a large number of ring-reading volunteers. For 71 breeding Herring Gulls and 94 breeding Lesser Black-backed Gull*s* with known sex and body size, relationships between the median migration distance recorded while on the non-breeding grounds (Herring Gulls: 627 sightings in October; Lesser Black-backed Gulls: 757 sightings in November–January) and body size were assessed. For each adult Herring Gulls and Lesser Black-backed Gulls of known sex, the earliest sighting in the colony (arrival date) was recorded during each year an individual was observed breeding, based on meticulous observations conducted from morning to evening every second weekday between mid-winter until the start of egg-laying. Individual arrival dates were expressed as the number of days since 1 December of the previous year (earliest arrival date recorded). For 200 breeding Herring Gulls and 119 breeding Lesser Black-backed Gulls, arrival date (*Herring Gulls*: 1287 arrival dates, Lesser Black-backed Gulls: 2477 arrival dates) and the median migration distance during the previous year (Herring Gulls: 627

sightings in October; Lesser Black-backed Gulls: 757 sightings in November–January) were related during each year in which both estimates were available.

### Statistical analysis

Monthly variation in migration distance averaged over 11 annual cycles was analyzed for both species separately with a general linear mixed model (ANOVA) with Gaussian error structure (Proc MIXED in sas 9.2 (SAS Institute Inc., Cary, NC, USA); SAS institute 2008). Categorical variables MONTH, SEX and the two-factor interaction were modelled as fixed effects. To account for statistical dependence, INDIVIDUAL was included as a random factor (Littell *et al.* 1996). Inter- and intraspecific variation in the median recorded migration distance and relationships with body size were analyzed with a general linear model (ANCOVA) with Gaussian error structure. To account for size differences between species and sexes, body SIZE was expressed as standardized residuals, i.e. within each species and sex, mean body size was subtracted from individual measurements and values were divided by the standard deviation. Categorical variables SPECIES, SEX (fixed effects), SIZE (covariate) and all two- and three-way interactions were modelled as independent variables. As the SPECIES × SEX × SIZE interaction was statistically significant, SEX × SIZE interactions were tested for each species separately. Inter- and intraspecific variation in mean arrival date was also analysed with ANCOVA with Gaussian error structure. Variables SPECIES, SEX (fixed effects), median migration DISTANCE (covariate) and all two- and three-way interactions were modelled as independent variables, and INDIVIDUAL and YEAR were included as random factors. The effect of body size on arrival date could not be tested reliably due to the small number of individuals for which all data (median migration distance, arrival time, sex and body size) were known (*Herring Gulls*: $N = 24$; Lesser Black-backed Gulls: $N = 18$).

In each model, levels of significance of all fixed variables were tested in a stepwise backward selection procedure, and the corresponding degrees of freedom were corrected by Satterthwaite formulas (Littell *et al.*1996). *Post-hoc* tests were carried out with Tukey tests (Proc LSMEANS in sas 9.2). All mixed models properly dealt with putative deviations of the underlying statistical assumptions as inferred from mixed_dx (Bell *et al.* 2010). Statistical results of all models were confirmed by non-parametric Kruskal–Wallis one-way ANOVAs (Proc NPAR1WAY in sas 9.2) (data not shown).

## RESULTS

### Variation in migration distance

In Herring Gulls, adult females remained closer to the breeding colony than adult males during September and October (SEX × MONTH: $F_{11,2668} = 5.76$, $P < 0.0001$; Tukey $P < 0.0001$; Fig. 5.1, upper panel). In Lesser Black-backed Gulls, a similar pattern of sexual segregation in monthly migration distance was observed between October and December (SEX × MONTH: $F_{11,3457} = 6.23$, $P < 0.0001$; Tukey $P < 0.0001$; Fig. 5.1, lower panel).

Migration distances differentially varied with body size in males and females of both species (SPECIES × SEX × SIZE: $F_{1,158} = 4.34$, $P = 0.04$; Fig. 5.2). In Herring Gulls, larger males migrated further than smaller males ($F_{1,29} = 4.46$, $P = 0.04$; $\beta = 31.15 \pm 14.76$); however, migration distances were independent of body size in females ($F_{1,38} = 0.28$, $P = 0.59$; $\beta = -2.89 \pm 5.46$; SEX × SIZE: $F_{1,67} = 5.64$, $P = 0.02$) (Fig. 5.2, upper panel). In Lesser Black-backed Gulls, migration distances were independent of body size in males ($F_{1.52} = 0.82$, $P = 0.37$; $\beta = -57.04 \pm 63.05$) or females ($F_{1,37} = 0.35$, $P = 0.56$; $\beta = 52.37 \pm 88.07$; SEX × SIZE: $F_{1,90} = 1.06$, $P = 0.31$) (Fig. 5.2, lower panel).

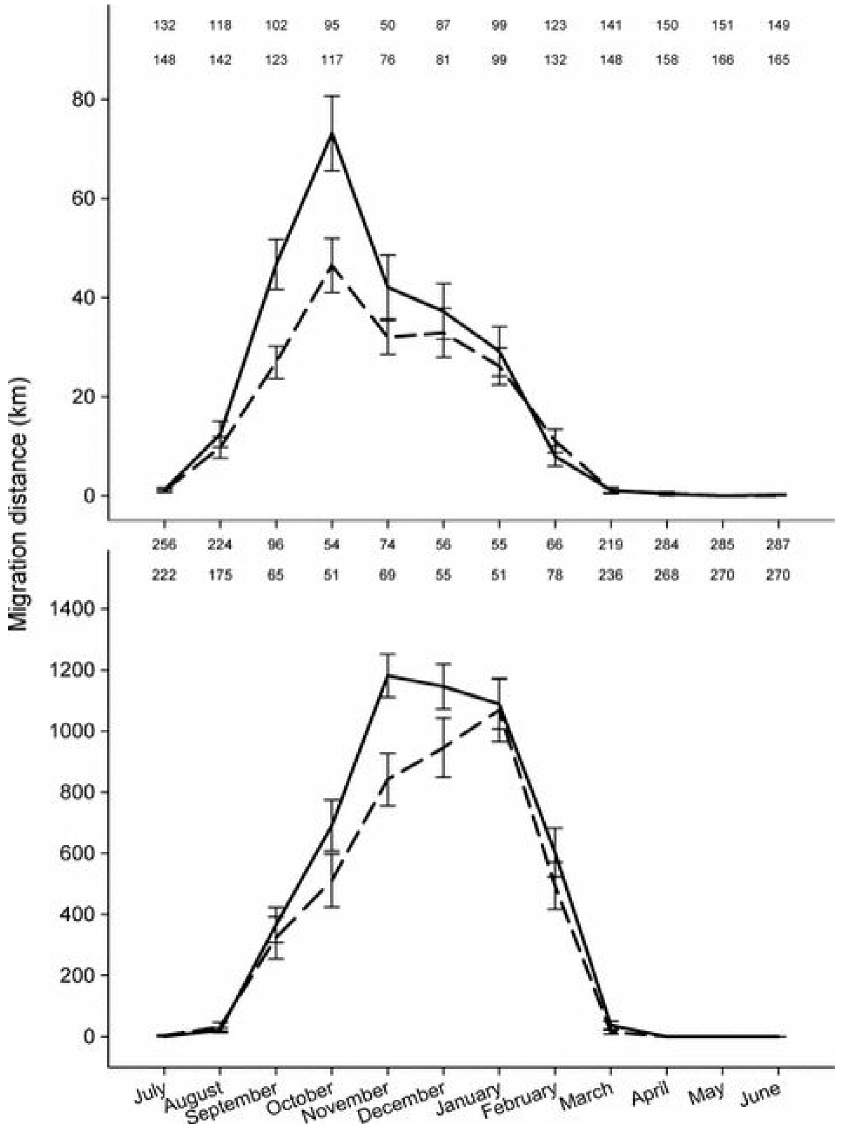

**Figure 5.1.** Monthly median migration distances (± se) away from a mixed Belgian breeding colony (km) averaged over 11 annual cycles, for 320 adult Herring Gulls (upper panel) and 558 adult Lesser Black-backed Gulls (lower panel). Males are depicted by solid lines, females by dashed lines. Numbers refer to male (top row) and female (bottom row) sample sizes.

### Variation in arrival date

Both species differed in the timing of arrival of males and females at the breeding colony (SPECIES × SEX: $F_{1,347} = 5.1$, $P = 0.03$). In Herring Gulls, males arrived significantly earlier than females (males: μ = 67.39 ± 4.08 days; females μ = 80.83 ± 4.05 days; $F_{1,189} = 9.10$, $P = 0.003$; Fig. 5.3, upper panel), whereas in Lesser Black-backed Gulls, both sexes arrived at nearly the same time (males: μ = 116.4 ± 2.9 days; females: μ = 115.6 ± 3.1 days; $F_{1,123} = 0.06$, $P = 0.81$; Fig. 5.3, lower panel). Arrival times did not vary with migration distance in Herring Gulls ($F_{1,352} = 0.08$, $P = 0.77$), whereas in Lesser Black-backed Gulls, individuals that migrated further tended to arrive later, albeit not significantly so ($F_{1,143} = 2.25$, $P = 0.13$). The effect of migration distance on arrival time did not differ significantly between species (SPECIES × DISTANCE: $F_{1,506} = 0.25$, $P = 0.61$) or between sexes (SEX × DISTANCE: $F_{1,448} = 0.32$, $P = 0.58$).

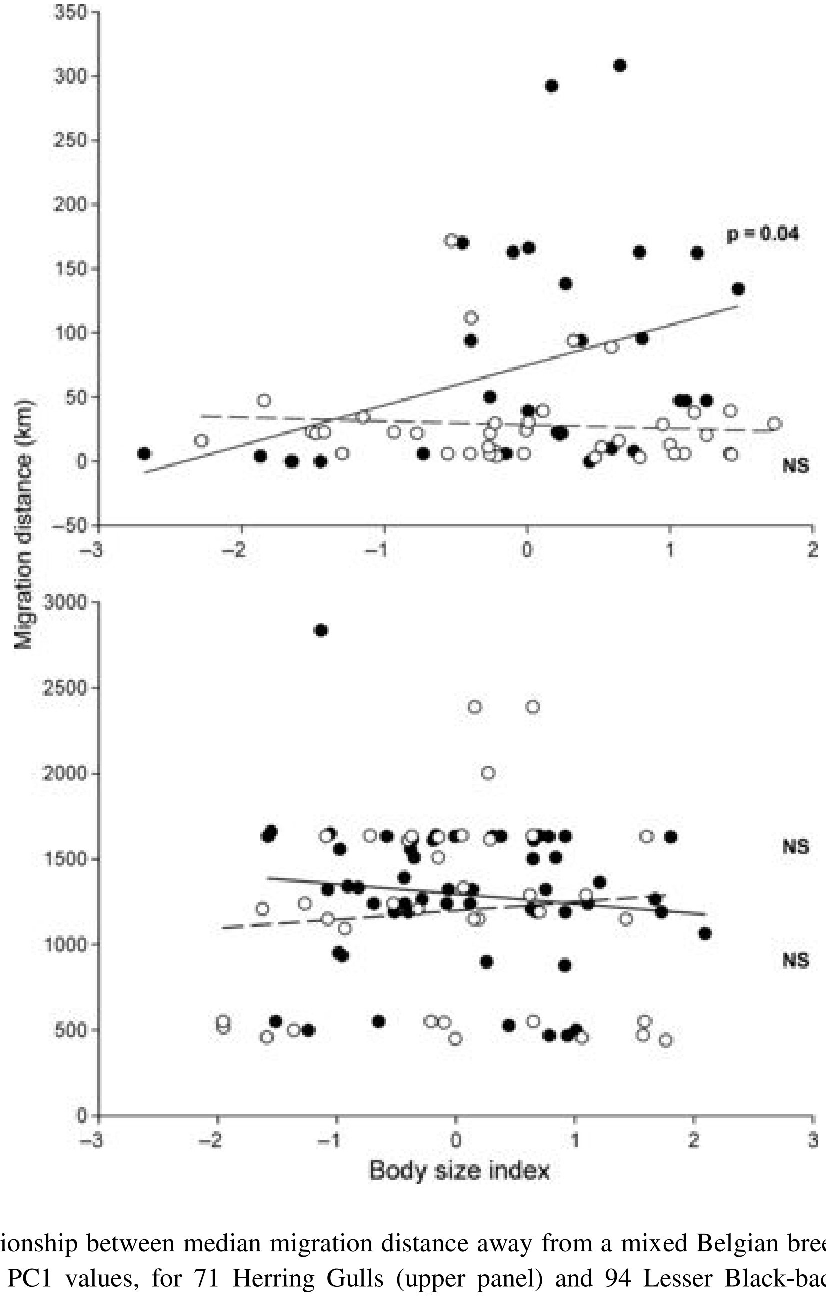

**Figure 5.2.** Relationship between median migration distance away from a mixed Belgian breeding colony (km) and standardized PC1 values, for 71 Herring Gulls (upper panel) and 94 Lesser Black-backed Gulls (lower panel). Males are depicted by closed circles and solid trend lines; females are depicted by open circles and dashed trend lines.

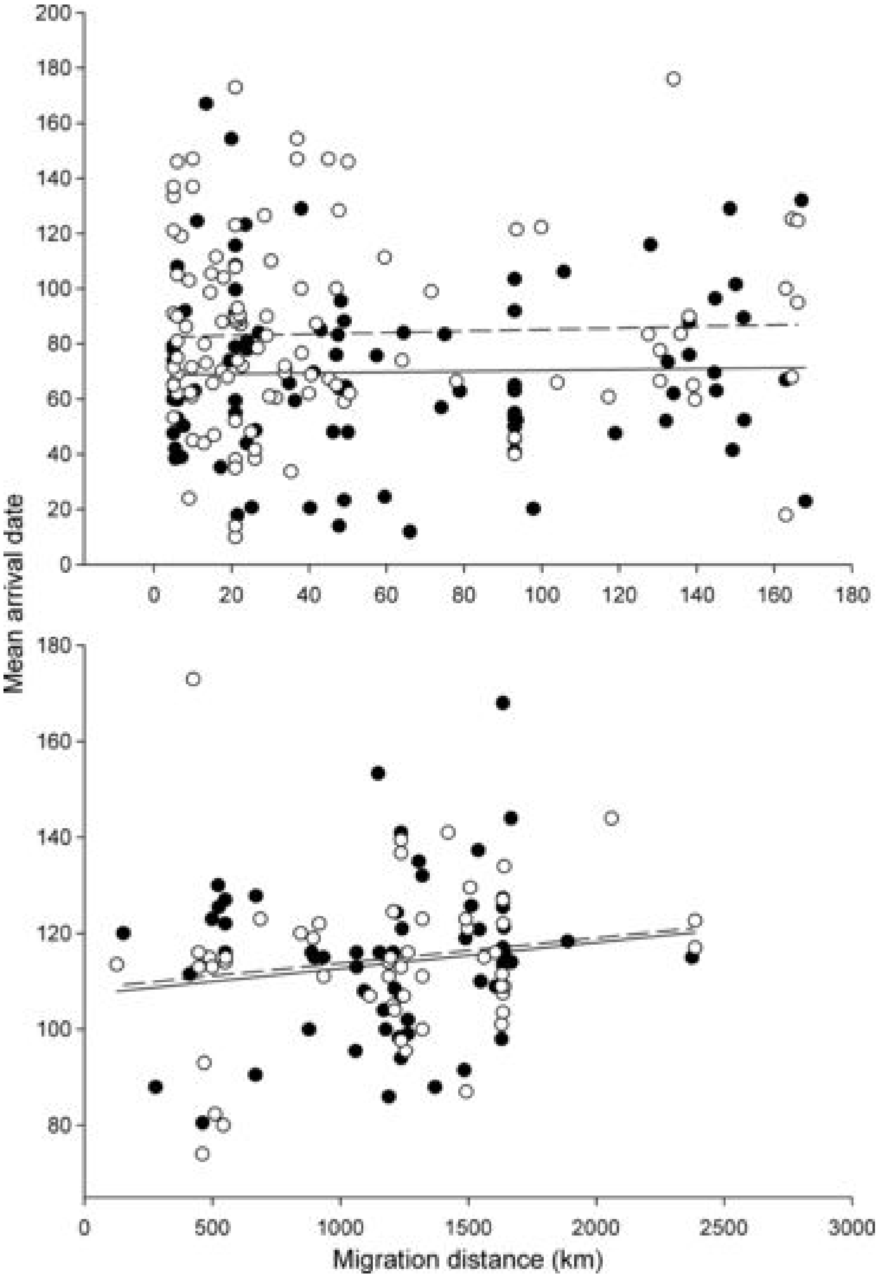

**Figure 5.3.** Relationship between median migration distance away from a mixed Belgian breeding colony (km) and mean arrival time at the colony (number of days after 1 December), for 200 Herring Gulls (upper panel) and 119 Lesser Black-backed Gulls (lower panel). Males are depicted by closed circles and solid trend lines; females are depicted by open circles and dashed trend lines.

## DISCUSSION

A large number of migratory species segregate at least partly by sex and body size on the non-breeding grounds (Cristol *et al.* 1999, Newton 2010), and variation in migration distance has been regarded as a by-product of variation in sexual size dimorphism (cf. Bennett & Owens 2002, Catry *et al.* 2005). Two hypotheses that consider allometric relationships as the biological basis of sex-related variation in migratory behavior (i.e. body size and social dominance hypothesis) predict that individuals of the smaller sex should migrate further southward along a north–south axis. Our finding of a reversed pattern in two closely related Larid species was therefore unexpected, yet consistent with empirical data on sexual segregation in other migratory species (e.g. Western Sandpiper *Calidris mauri*, O'Hara *et al.* 2006; Teal *Anas crecca*, Guillemain *et al.* 2009). Mean arrival dates at the breeding colony differed between male and female Herring Gulls in the direction predicted by the arrival time hypothesis (Ketterson & Nolan 1983), i.e. earlier arrival of the sex that is most strongly involved in breeding resource competition. In Lesser Black-backed Gulls, however, males and females arrived synchronously, despite the same level of sexual size dimorphism and the much longer migration route compared with Herring Gulls (Kissner *et al.* 2003). Possibly, a narrower time window between the end of migration and the start of the breeding activities compared with Herring Gulls constrains the evolution of sex-differential timing of arrival in Lesser Black-backed Gulls (cf. Ketterson & Nolan 1983). Within each species, median migration distances did not significantly correlate with arrival time between or within sexes. This result was unexpected given the inverse relationship between migration distance and arrival time predicted by the arrival time hypothesis (Ketterson & Nolan 1983).

Because of the sexual size dimorphism and predominantly north–south migration in Herring Gulls and Lesser Black-backed Gulls, variation in average migration distances between males and females directly corresponded to a latitudinal segregation in body size, with the larger sex (males) wintering further south than the smaller sex (females). Patterns of latitudinal segregation in body size are usually interpreted within the framework of Bergmann's rule, which predicts larger individuals will winter at higher latitudes because of their better ability to withstand low temperatures and food shortage (Cristol *et al.* 1999, Katti & Price 2003, Newton 2010). Results from this study, i.e. larger males wintering at lower latitudes, do not support the pattern of sex segregation predicted by the body size hypothesis, possibly because distances between male and female wintering sites were too small to result in differential climatic conditions, a basic assumption underlying Bergmann's rule (Stouffer & Dwyer 2003). Variation in migration distances has further been linked to social rank, with subordinate individuals predicted to be competitively excluded from preferred habitats or habitats closer to the breeding grounds by dominant conspecifics (Cristol *et al.* 1999). As Herring Gull and Lesser Black-backed Gull males are larger and socially dominant over females (Snow *et al.* 1998), yet wintered further from the breeding colony than the subordinate females, the results of this study do not support the pattern of sex segregation generally predicted by the social dominance hypothesis either.

For allometry and its relationship with stress tolerance and dominance to drive sexual segregation in migration distance in the direction expected, gradients of proximity to the breeding ground should covary with gradients in habitat and ambient quality (Ketterson & Nolan 1983), i.e. *nearer* should be *better* for the predictions of the social dominance hypothesis to hold. However, this is unlikely to be the case for Herring Gull populations breeding in the southern North Sea area. During autumn, this species migrates southward through a heterogeneous coastal landscape, with habitats further south thought to offer better foraging opportunities and greater prey densities. Males are more often reported from the

French department Somme (Fig. 5.4), where beaches between the Baie d'Authie and Baie de Somme provide high-quality winter habitat for Herring Gulls. First and most importantly, large, contiguous mussel beds stretch over a distance of many kilometers. Secondly, vast cockle banks stretch near the non-protected area of the nature reserve Baie de Somme, especially near the town of Le Crotoy. Thirdly, after periods of strong winds, there are often mass strandings of bivalves (mainly *Ensis* and the large, nutritious *Lutraria lutraria*). Similar food concentrations are not encountered elsewhere within the wintering range of this species (Harry J. P. Vercruijsse pers. obs). Females, in contrast, are mainly reported from sandy beaches in the Belgian province of West-Vlaanderen and the French department of Nord (Fig. 5.4) where structures such as breakwaters provide ample feeding opportunities, albeit of lesser quality (Davy S. Bosman pers. obs.). Given this configuration of habitat, the pattern of sex segregation observed in our study might still fit a greater resource holding power of larger males and size-mediated competitive exclusion of females (and possibly smaller males, Fig. 5.2, upper panel) from high-quality habitat further south. Under such an assumption, the results of this study are in agreement with the social dominance hypothesis but disagree with the condition it sets that better resources are nearer. Likewise, in the Greenish Warbler (*Phylloscopus trochiloides*) species complex, a cline of increasing body size toward lower (not higher) latitudes was explained by a corresponding spatial distribution of critical resources, mediated by competitive interactions (Katti & Price 2003). Alternatively, the observed latitudinal segregation between wintering males and females of Herring Gulls may reflect sex-specific niche specialization. Although Greig *et al.* (1985) found differences in feeding efficiency and foraging behavior between males and females on the shared use of landfill areas by Herring Gulls, they also reported that individuals of both sexes regularly feed in mixed-sex flocks at a variety of feeding sites. However, to the best of our knowledge, sex-related differences in foraging habitat preference on a larger spatial scale have not yet been described in Herring Gulls. How social dominance, optimal foraging and sexual segregation are interrelated in Herring Gulls, and to what extent body size mediates these relationships, remains a topic of further research (Catry *et al.* 2005). In the longer-distance migrant Lesser Black-backed Gulls, no relationship between body size and migration distance was apparent in males or females.

The results of this study do not support the overall hypothesis that allometric relationships drive variation in migration behavior within and between Herring Gulls and Lesser Black-backed Gulls. Although allometry partly explains sex-related relationships in migration distance in Herring Gulls, data from the closely related Lesser Black-backed Gulls do not seem to fit such a pattern. As longer migration routes did not result in a significantly later return at the breeding grounds in either species, presumed sex differences in the intensity of selection for early arrival cannot explain patterns of latitudinal sexual segregation in Herring Gulls and Lesser Black-backed Gulls either. The results of this study therefore show that the effect of body size on sex-specific life-history strategies related to migration may vary between closely related, sympatric species despite a similar size dimorphism. Future comparative research of related species pairs that are very similar in many aspects of their ecology but strongly differ in their use of space may help to identify important life-history distinctions (Cristol *et al.* 1999). In conclusion, it seems likely that a complex life-history trait like migration did not evolve in relation to any one selection pressure, but that multifactorial explanations will be required (Catry *et al.* 2005).

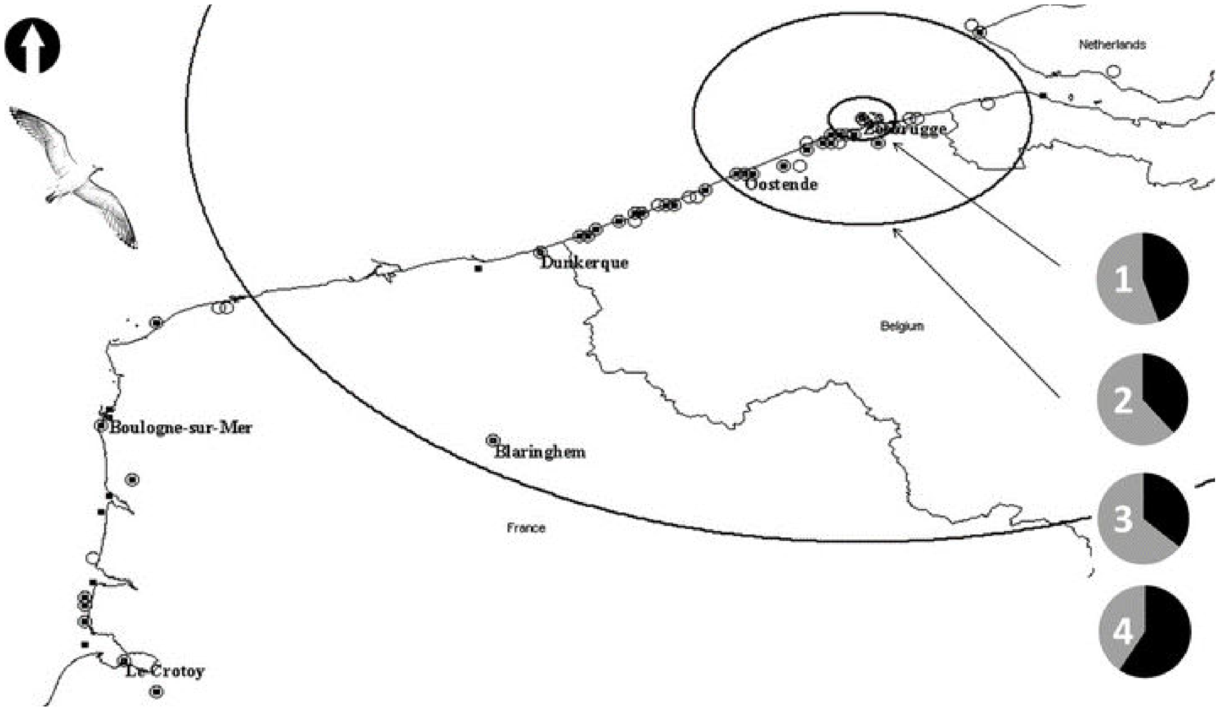

**Figure 5.4.** Variation in sex ratio of color-ringed adult Herring Gulls resighted during October (1999–2010) at progressive distances from their Belgian breeding colony. Closed squares, male resightings only; open circles, female resightings only; closed squares in open circles, resightings of both sexes. Sex ratios are calculated for four zones (males: black, females: grey): (1) ≤ 5 km (19 males, 24 females); (2) ≤ 25 km (19 males, 31 females); (3) ≤ 100 km (21 males, 38 females); (4) > 100 km (38 males, 26 females).

## ACKNOWLEDGEMENTS

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# 6

# General Discussion

The main aim of this thesis was to gain insight into the life-history variation using two phylogenetically and ecologically closely related study species: Herring Gulls and Lesser Black-backed Gulls. In the concluding chapter, I will summarize the main results and discuss them within the context of budget constraints individuals undergo throughout their annual cycle. I will end by making some minor suggestions for future research.

## 6.1. OVERVIEW OF THE MAIN RESULTS

### Pre- and post-fledging survival of Herring Gulls

Variation in conditions experienced during the nestling period affected survival rates of Herring Gulls before and after fledging (Chapter 2-3).

With respect to pre-fledging survival (Chapter 2), offspring mortality varied most strongly with laying order during the first 12 days after hatching (Fig 2.1, p. 22). Last-born (c)-chicks, especially, suffered from increased mortality risk during this period. Furthermore, the relative body condition of c-chicks was negatively impacted by an interaction between hatching asynchrony and relative egg size (Fig 2.2, p. 23; Fig2.3, p. 24). More specifically, increasing hatching asynchrony reduced the relative body condition of c-chicks, particularly for c-chicks that hatched from smaller eggs. Importantly, the probability of survival during the first 12 days post-hatching was positively related to the relative body condition of chicks. After this time, however, relative body condition was no longer related to egg size, but was still related to hatching asynchrony, suggesting a longer-lasting effect of the latter during the nestling stage.

With respect to post-fledging survival (Chapter 3), certain pre-fledging characteristics were found to influence survival after fledging. Variability in first-year survival could be linked primarily to individual variation in nestling growth rates (Table 3.2, upper half, p. 41; Fig 3.2, upper panel, p. 36). After brood reduction, laying order no longer affected pre-fledging survival and it also did not affect post-fledging survival (Table 3.2, lower half, p. 41) . However, rank order after brood reduction, – when some second-born (b)- and last-born (c)-chicks were promoted to first or second rank after older chicks had died –, were believed to better reflect rearing conditions because it is upheld during the larger part of the nestling period (± 45 days in Herring Gulls). In fact, an unambiguously negative influence of rank order after brood reduction was found on post-fledging survival. Post-fledging survival was also negatively correlated with hatching date. Male Herring Gulls in our study experienced lower first-year survival and faster growth rates than the smaller females (Fig 3.1, right panel, p.34; Fig 3.2, upper panel, p.36). The positive interaction between nestling growth rates and sex on post-fledging survival indicated that faster-growing males survived their first year better. A negative interaction of hatching date with offspring sex indicated reduced survival of later-hatched males.

### Age-related variation in the breeding timing of Lesser Black-backed Gulls

The age of a Lesser Black-backed Gull had a significant effect on its phenology regardless of sex, with older age classes arriving progressively earlier at the breeding grounds (Chapter 4, Fig.4.1, p. 55). Age-related variation in breeding timing was found at both the population and individual levels.

At the population level, age of first breeding was significantly associated with both survival and arrival timing in Lesser Black-backed Gulls. Individuals tended to arrive significantly later if they postponed their recruitment, which countered the overall trend of advanced arrival with increasing age. Moreover, individuals recruiting at the age of 4 years had the highest survival probability. Earlier recruits (< 4 years old) may consistently have arrived too early throughout their lifetime and as a consequence paid the elevated cost of reduced survival probability. Reduced survival chances for later recruits (> 4 years old) suggested that these birds may have been of lower phenotypic quality and therefore less able to cope with costs associated with timely arrival for breeding. Hence, progressive appearance of late arriving individuals at the population level may jointly reflect the disappearance of phenotypes that consistently arrived too early and the appearance of low-quality phenotypes that consistently arrived later than optimal recruits (= 4 years old) during subsequent years. This supports the idea that timing of arrival in Lesser Black-backed Gulls fuscus was at least to some degree a consistent individual trait, and evidence for (partial) individual consistency in timing of arrival.

Despite this consistent variation in timing of arrival between individuals belonging to different recruitment age groups, up to 81% of the temporal variation in arrival dates in our population was explained by within-individual variation. Over the entire reproductive lifetime of Lesser Black-backed Gulls (i.e. when excluding the pre-recruitment period), the effect of growing age on advanced arrival was estimated at 11 days, with prior breeding experience accounting for a 7 days advance and postponed breeding for a 4 days delay (Table 4.2, right panel, p. 47). This suggests that accumulating breeding experience may have been at least one important factor explaining advanced arrival over an individual’s reproductive lifetime. When including the pre-recruitment years, however, arrival advanced with 18 and 12 days in relation to age and breeding experience respectively, while the delay related to postponed breeding remained comparable (Table 4.2, left panel, p.47). This discrepancy suggests that additional factors may have triggered variation in timing of arrival during immature (pre-recruitment) life-stages. While post-recruitment experience can improve reproductive performance through previous breeding opportunities, pre-recruitment experience may have helped to achieve higher levels of reproductive performance through prospection. Indeed, prospectors arrived on average seven days earlier at the breeding colony throughout the larger part of their reproductive life, compared to individuals that did not show such behavior (Table 4.3, p.48; Fig. 4.2, left panel, p. 56). However, in Lesser Black-backed Gulls, prospecting behavior also came with a considerable survival cost.

### Sex-specific differences in migratory behavior of adults in both species

In adult Herring Gulls, larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females (Chapter 5, Fig. 5.2, p. 67). In adult Lesser Black-backed Gulls, no relationship between body size and migration distance was apparent in either sex. Mean arrival dates at the breeding colony did not vary with migration distances but differed between males and females of Herring Gulls (but not in Lesser Black-backed Gulls, Fig. 5.3, p.68).

## 6.2. ENERGY CONSTRAINTS VERSUS ADAPTATION

Breeding is a crucial stage in the annual cycle of animals and in terms of energy requirements probably the most demanding. Hence, many reproductive traits may be constrained by energy demands (Drent and Daan 1980, Clutton-Brock 1991). One of these traits is egg size, which typically varies with laying order in many bird species (Slagsvold et al. 1984). Herring Gulls have a clutch-size frequency distribution truncated at three eggs (Parsons 1972). Consistent intraclutch variation in egg size with laying order was also found in Herring Gulls at the colony in Zeebrugge, with c-eggs being smallest in most clutches. B-eggs were similar in size to a-eggs in many clutches. The negative effect of laying date on absolute size of c-eggs suggests that many late breeders may have been more limited in their breeding effort as low quality or inexperienced females start breeding later at the colony of Zeebrugge (Van Waeyenberghe et al. 2002, Verhulst and Nilsson 2008). The concepts of trade-offs and constraints are often closely related because trade-offs are also the result of an organism's finite energy budget (Stearns 1992). Hence, these late-laying females may have ‘opted’ for a smaller terminal egg size as part of the trade-off between current reproduction and future survival in long-lived species. Despite this negative relationship between laying date and c-egg size, the small relative size of the last-laid egg was likely not the sole result of energetic constraints on late-laying female Herring Gulls because small terminal egg size should then have been more marked in females laying smaller eggs, reflecting their more limited energy reserves available for reproduction (Pierotti and Bellrose 1986, Kilpi et al. 1996). To the contrary, I found an inverse relationship between a clutch’s mean egg size and the relative size of c-eggs. This was unexpected because Parsons (1976) reported that female Herring Gulls that laid larger eggs also laid the most similarly sized eggs. However, Parsons (1970, 1972, 1976) also noted that Herring Gulls apparently have a lower size limit for eggs, below which hatchability abruptly drops, so very small eggs are not laid. In addition, Kim et al. (2010) argued that smaller eggs might be more vulnerable to suboptimal conditions such as exposure to cold temperature during periods of neglect. If so, c-eggs may need to exceed a minimum size threshold to be viable, and this may explain why females laying smaller-sized three-egg clutches might have been more limited in the degree to which they could reduce the relative size of their small terminal egg.

Alternatively, reproductive traits could also be affected by selective pressures which would induce the appearance of adaptive patterns. If variation in egg size is to be adaptive, patterns of variation must be associated with patterns of chick mortality in a consistent manner (Viñuela 1197). In asynchronous hatching Herring Gulls, small terminal egg size could then be adaptive if c-chicks suffered from increased mortality risk as a result of a competitive disadvantage compared to older chicks. During the first 12 days post hatching, chick mortality in Herring Gulls varied most strongly with laying order, subsequently identified as the brood-reduction period as defined by Mock (1994). Although intraclutch variation in egg size was not directly related to patterns of chick mortality during this brood reduction period, smaller relative egg size increased differences in relative body condition of nestlings, primarily brought about by the degree of hatching asynchrony. At the same time, the relative body condition of c-chicks was positively related to their probability of survival. Thus, the adaptive value of relatively small c-eggs in Herring Gulls may lie in reducing the survival probability of last-hatched chicks in interaction with hatching asynchrony through effects on nestling body condition. This pattern is highly consistent with a brood-reduction strategy of female Herring Gulls to facultatively reduce brood size to align with prevailing resource availability so that the remaining offspring has higher probabilities of survival and recruitment into the breeding population (Stenning 1996).

On top of being a non-adaptive consequence of energetic constraints on late-laying females, small terminal egg size in Herring Gulls seems to reflect an adaptive maternal strategy to improve lifetime reproductive success by means of brood reduction. The results of several others studies on Gulls have revealed a positive relationship between small c-egg size and increased mortality rate in c-chicks (Parsons 1970, Hébert and Barclay 1986, Risch and Rohwer 2000), whereas other investigators have reported that small terminal egg size did not influence c-chick survival (Nager et al. 2000, Kim et al. 2010). Likewise, in other bird species, the extent to which this offspring mortality is egg size-mediated , especially in relation to hatching asynchrony, remains unclear, but it is widely accepted that chicks hatching from larger eggs are heavier and structurally larger, and have greater energy reserves (Slagsvold et al. 1984). Our study reveals that these conflicting results on egg size-mediated offspring mortality might ensue because large egg size might affect subsequent offspring survival neither directly, nor independently. Instead, large eggs may enhance the survival probability of offspring in interaction with hatching asynchrony through indirect effects on nestling body condition

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## 6.3. TTME CONSTRAINTS AND AGE

Possibly the best time in the annual cycle to study time constraints in birds is the final part of the spring migration when the transition to breeding takes place. In this period, the birds are often time-pressed (Alerstam 2006). In seasonally reproducing birds, the timing of reproduction is very important and subject to intense selection pressures because parents are expected to time their reproduction such that maximum offspring food requirements coincide with maximum food availability to ensure offspring survival (Schroeder et al. 2012). Hence, a timely arrival on the breeding grounds constitutes an important precondition of successful reproduction because it affects the length of the period available for breeding and can buffer yearly variation in peak food availability that determines the optimal onset of breeding. In migratory birds, early arrival at the breeding grounds has also been shown to result in priority access to high quality territories and nesting sites (Becker et al. 2008). Moreover, the evidence that early nesting confers advantage in terms of reproductive success (e.g. highest survival of nestlings) is overwhelming (reviewed in Drent 2006). It is generally believed that the timing of arrival on the breeding grounds has important fitness consequences (Hötker 2002, Saino et al. 2004).

Age is commonly regarded as a key parameter in explaining temporal variation in arrival at the breeding grounds, with older individuals usually arriving before younger ones (Hötker 2002, Smith and moore 2005, Cooper et al. 2009). Lesser Black-backed Gull also arrived progressively earlier at the breeding grounds with increasing age regardless of sex. During the adult life stage, increasing breeding experience was identified as an important factor explaining this age-related pattern suggesting that the lack of accumulated competence and skills constrained the timing of arrival of younger adults. An additional trigger of variation in timing of arrival before recruitment may be that immature individuals are still subject to maturation of (sexual) function and, hence, unconstrained by the needs of breeding, they are in less of hurry to arrive on the breeding grounds. These immatures either remain in their non-breeding areas year-round over one or more years, or they may only return part ways towards the breeding areas. Alternatively, they may prospect the breeding areas later in the breeding season (Newton 2011). During prospection, immatures may improve knowledge of prime breeding sites, navigational and foraging skills facilitating a timely, stepwise transition from migration to breeding (Becker et al. 2008). Adult Lesser Black-backed Gulls that prospected before recruitment arrived on average earlier at the breeding colony over the larger part of their reproductive life than those that did not prospect before age of first breeding. However, in Lesser Black-backed Gulls, prospecting behavior also came with a considerable survival cost, which may explain why half of the breeders that indulged in prospecting prior to recruitment, restricted this behavior to a single season at the age of three years or older.

## 6.4. SEX-SPECIFIC CONSTRAINTS

Sex-specific constraints related to breeding season events and/or body size may lead to sexual segregation in migration timing and distances travelled during the migratory and non-breeding stages of the annual cycle.

Relating to sex-specific time constraints, the sex that is most strongly involved in breeding resource competition (e.g. the need to establish and defend a territory) arrives earlier on the breeding grounds in spring than the less time-pressed sex. Accordingly, male Herring Gulls arrived significantly earlier than females at the colony in Zeebrugge. In Lesser Black-backed Gulls, however, males and females arrived synchronously despite a greater migration distance. Possibly, a narrower time window between the end of migration and the start of the breeding activities compared with Herring Gulls constrained the evolution of sex-differential timing of arrival in Lesser Black-backed Gulls.

Relating to sex-specific energy constraints, large number of migratory species segregate at least partly by sex and body size on the non-breeding grounds (Cristol et al. 1999, Newton 2010), and variation in migration distance has been regarded as a by-product of variation in sexual size dimorphism. Patterns of latitudinal segregation in body size are usually interpreted within the framework of Bergmann's rule, which predicts larger individuals will winter at higher latitudes because of their better ability to withstand low temperatures and food shortage (Cristol et al. 1999, Katti & Price 2003, Newton 2010). However, in Herring Gulls, larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females. Results from this study therefore do not support the pattern of sex segregation predicted by differences in body size, possibly because distances between male and female wintering sites were too small to result in differential climatic conditions, a basic assumption underlying Bergmann's rule (Stouffer & Dwyer 2003). In Lesser Black-backed Gulls, no relationship between body size and migration distance was apparent in either sex. Hence, despite a similar sexual size dimorphism, the effect of body size on differences in migratory behavior were found to differ within and between sexes of both species.

Furthermore, and still relating to energy constraints, a sex-biased mortality of first-year Herring Gulls was found, with smaller females more likely to survive than males. The usual explanation for such bias toward the larger sex in juvenile mortality is that reduced food availability has a greater effect on the survival of the sex with higher energy requirements associated with their larger size and faster growth rates (Martín et al. 2007). This results in greater vulnerability of males to poor parental investment or unfavorable rearing conditions. If male Herring Gulls do have higher energy demands, a seasonal decline in rearing conditions is likely to further lower their survival prospects. Accordingly, earlier-hatched and faster-growing males were shown to survive their first year better.

## 6.5. CONSTRAINTS AND CARRY-OVER EFFECTS

In a life-history context, carry-over effects may occur in any stage of the life-cycle in which an individual's history and experience explains their current performance levels in components related to fitness (O'Connor et al. 2014). Against this background, carry-over effects of breeding season events were found on first-year survival of Herring Gulls. Pre-fledging characteristics such as timing of breeding (hatching date), early development (nestling growth rates), and rank order within broods were shown to influence survival after fledging.

With respect to energy constraints, variability in first-year survival of Herring Gulls could be linked positively to individual variation in nestling growth rates. Although larger fledglings may be more likely to survive because they are better able to compete for limited resources (Parsons et al. 1976), good feeding conditions experienced during early growth may fix some physiological or structural traits that enhance an individual's performance levels (Lindström 1999, Cam et al. 2003, Sedinger et al. 2004, Nevoux et al. 2010). For example, variation in the slope of the learning curve in relation to resource acquisition (i.e., foraging skills) may strongly affect first-year survival. Furthermore, an unambiguously negative influence of rank order after brood reduction was found on first-year survival. Reasonably, older chicks are dominant in competition with younger siblings for food, leading to reduced development of surviving juniors at independence (Slagsvold et al. 1984, Sydeman and Emslie 1992, Bosman 2014). Accordingly, it is fair to hypothesize that individuals dominant in competition for food within broods, or individuals without siblings, are in a better condition at independence and have lower mortality rates during the first year of life (Cam et al. 2003).

With respect to time constraints, first-year survival of Herring Gulls was found negatively correlated with hatching date. Because immature gulls are probably less effective foragers than adults (Maclean 1986), later-hatched chicks may have less time to develop and improve their foraging skills before the onset of winter, potentially compromising post-fledging survival.

## 6.6. SUGGESTIONS FOR FUTURE RESEARCH

It might be argued that because a large proportion of the variation in each life-history variable is located at high taxonomic levels, differences in ecology and behavior between closely related species must have little effect on life-history variation (Bennett and Owens 2002). Nevertheless, fine-grained differences between closely related taxa are also likely to be adaptive and using a comparative approach will help to pinpoint important factors associated with variation in particular suites of life-history traits (Linden and Moller 1989). Despite similar sexual size dimorphism, the effects of body size on differences in migratory behavior were found to differ within and between sexes of closely related Herring Gulls and Lesser Black-backed Gulls. In addition, Lesser Black-backed Gulls appeared to be more pressed for time during the transition to breeding as a result of a longer migration distance compared to Herring Gulls. Illustrating that variation in a complex life-history trait like migration did not evolve in relation to any one selection pressure, but that multifactorial explanations will be required. Future comparative research of this species pair that are very similar in many aspects of their ecology, but strongly differ in their use of space, may further help to identify important life-history distinctions.

Due to the rarity of relevant datasets, too few studies have addressed the consequences of conditions during early development on fitness components later in life. Whether these conditions have long-term fitness consequences is still ambiguous (Cam and Aubry 2011). In this context, I built a dataset containing measurements of early life-history traits of individual Herring Gulls and Lesser Black-backed Gulls from egg till fledging. Surviving chicks were color-ringed so that they could be followed up after fledging. At present, carry-over effects of breeding season events were found on pre- and post-fledging survival of Herring Gulls. As the lives of these color-ringed individuals progress, timely future analyses of their advancing life-history trajectories may shed light on the long-term effects of conditions experienced early in live. For example, it will be interesting to explore if the influence of natal conditions on survival will persist into adulthood or that it is levelled out by variation in age of first breeding as part of the trade-off between early reproduction and adult survival in long-lived species.

Although field experiments have proven their worth in the past, in my opinion, there is a limit in the way the natural world can be used as a laboratory. Egg-removal and cross-fostering experiments immediately spring to mind. Removing or replacing an egg is so much more than manipulating one variable. Most of the experimental designs control for egg size and laying date because those are widely accepted to be correlated with parental quality, but all fail to control for all confounding variables. Which is to be expected when many are unknown. It is impossible to infer a causal relationship from correlative studies, but what can anybody deduce from an experimental study when nobody really knows what has been manipulated to begin with. Not surprisingly, many of these kind of studies have yielded conflicting results. Furthermore, many individuals that have been the subject of a non-lethal experiment live on, but there is no way of knowing to what extent these manipulations will affect their future life-history trajectories. This can be problematic when you are conducting research on variation in life-history traits in the same population. Ideally, you should be able to exclude these individuals by color-ring them and keeping an administration. In practice, this quickly becomes an impossible task. In conclusion, think twice before setting up an experimental study in the wild. An even then, only do it when you have a good idea what is possible in your population through extensive monitoring and observational studies.

# Summary

Animal species differentially invest in growth, reproduction and survival throughout their lifetime and the balance between these conflicting demands in terms of time and energy is what we refer to as ‘life-history’. The life-history of an individual, includes all of the stages from birth to death, i.e. from early development and maturation, over the adult life-stage to senescence. Many long-lived species inhabit areas with strong seasonality where environmental conditions such as resource availability and temperature may change in a predictable manner within the year, and consistently from year to year within the period of a single lifespan. To cope with such temporal variability, individuals are likely to experience selection pressures to carry out different activities related to reproduction and survival at favorable times of the year, i.e. an optimal annual routine or cycle. These routines vary according to the annual pattern of environmental conditions individuals experience and show great variation in the timing, duration and sequence of major activities through the year. Breeding is a crucial stage in the annual cycle and in terms of energy requirements probably the most demanding. Logically, the timing of breeding takes precedence over other activities of the annual cycle that are then scheduled around it.

Birds are remarkably consistent in their basic life-cycle. However, at all stages of this basic life-cycle, birds display a great deal of variation in the way these stages are realized and organized. Age- and sex-differences commonly explain a large part of the life-history variation between and within individuals. Understanding this variation requires examining the performance of individuals and changes in performance over life.

Here, I studied life-history variation in Herring Gulls and Lesser Black-backed Gulls on an individual basis.

In Chapter 2, my objective was to examine the importance of egg size variation within clutches, while simultaneously considering the effect of hatching asynchrony on pre-fledging survival because both might operate concomitantly, either directly or indirectly through effects on relative body condition. Because most pre-fledging mortality in Herring Gulls occurs before 10 days post-hatching, particularly for c-chicks, I also examined whether this period coincides with the brood-reduction period, that is, the period post-hatching where offspring survival most strongly varies with laying order.

Consistent intraclutch variation in egg size with laying order was found in Herring Gulls at the colony in Zeebrugge, with c-eggs being smallest in most clutches. B-eggs were similar in size to a-eggs in many clutches. The negative effect of laying date on absolute size of c-eggs suggests that many late breeders may have been more limited in their breeding effort as low quality or inexperienced females start breeding later at the colony of Zeebrugge. Despite this negative relationship between laying date and c-egg size, the small relative size of the last-laid egg was likely not the sole result of energetic constraints on late-laying female Herring Gulls because patterns of egg size variation were found to be consistently associated with patterns

of chick mortality. During the first 12 days post hatching, chick mortality in Herring Gulls varied most strongly with laying order, subsequently identified as the brood-reduction period. Although intraclutch variation in egg size was not directly related to patterns of chick mortality during this brood reduction period, smaller relative egg size increased differences in relative body condition of nestlings, primarily brought about by the degree of hatching asynchrony. At the same time, the relative body condition of c-chicks was positively related to their probability of survival. Thus, the adaptive value of relatively small c-eggs in Herring Gulls may lie in reducing the survival probability of last-hatched chicks in interaction with hatching asynchrony through effects on nestling body condition. This pattern is highly consistent with a brood-reduction strategy of female Herring Gulls to facultatively reduce brood size to align with prevailing resource availability

In Chapter 3, I examined the possible carry-over effects of nestling growth and other pre-fledging characteristics (hatching date, hatching asynchrony, and brood size and rank after brood reduction) on post-fledging survival.

Variability in first-year survival could be linked primarily to individual variation in nestling growth rates. After brood reduction, laying order no longer affected pre-fledging survival and it also did not affect post-fledging survival. However, rank order after brood reduction, – when some b- and c-chicks were promoted to first or second rank after older chicks had died –, were believed to better reflect rearing conditions because it is upheld during the larger part of the nestling period (± 45 days in Herring Gulls). In fact, an unambiguously negative influence of rank order after brood reduction was found on post-fledging survival. Post-fledging survival was also negatively correlated with hatching date.

In Chapter 4, I investigated the mechanisms underlying temporal variation in timing of arrival among and within individual Lesser Black-backed Gulls. I investigated to what extent does timing of arrival constitute a dynamic trait (i.e. resulting from changes within individuals over time) or a fixed, consistent individual trait (i.e. resulting from phenotypic variation among individuals)? I also examined the importance of experience gained from earlier prospecting or breeding?.

Lesser Black-backed Gull also arrived progressively earlier at the breeding grounds with increasing age regardless of sex. Despite consistent variation in timing of arrival between individuals with regard to age of first breeding, up to 81% of the temporal variation in arrival dates in our population was explained by within-individual variation. During the adult life stage, increasing breeding experience was identified as an important factor explaining this age-related pattern suggesting that that the lack of accumulated competence and skills constrained the timing of arrival of younger adults. An additional trigger of variation in timing of arrival before recruitment may be that immature individuals are still subject to maturation of (sexual) function and, hence, unconstrained by the needs of breeding, they are in less of hurry to arrive on the breeding grounds. These immatures either remain in their non-breeding areas year-round over one or more years, or they may only return part ways towards the breeding areas. Alternatively, they may prospect the breeding areas later in the breeding season. During prospection, immatures may improve knowledge of prime breeding sites, navigational and foraging skills facilitating a timely, stepwise transition from migration to breeding. Adult Lesser Black-backed Gulls that prospected before recruitment arrived on average earlier at the breeding colony over the larger part of their reproductive life than those that did not prospect before age of first breeding. However, in Lesser Black-backed Gulls, prospecting behavior also came with a considerable survival cost, which may explain why half of the breeders that indulged in prospecting prior to recruitment, restricted this behavior to a single season at the age of three years or older.

In Chapter 5, I assessed the extent to which sex-specific constraints related to structural size and/or reproduction may shape variation in migratory behavior of sexually mature male and female Herring Gulls and Lesser Black-Backed Gulls.

In adult Herring Gulls, larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females. In adult Lesser Black-backed Gulls, no relationship between body size and migration distance was apparent in either sex. Mean arrival dates at the breeding colony did not vary with migration distances but differed between males and females of Herring Gulls (but not in Lesser Black-backed Gulls).

In summary, this study revealed considerable life-history variation within and between two closely related species, expecially in relation to age- and sex-specific constraints.

# Samenvatting

Diersoorten investeren op verschillende wijze in groei, reproductie en overleving in de loop van hun leven en het evenwicht tussen deze tegenstrijdige belangen aangaande tijd en energie is wat wij als 'levensgeschiedenis' aanduiden. De levensloop van een individu, omvat alle levensfasen, van geboorte tot de dood, vanaf de vroege ontwikkeling en maturatie, over volwassenheid naar veroudering. Veel langlevende soorten bewonen gebieden met een sterke seizoenaliteit, waar omgevingsomstandigheden, zoals voedselvoorziening en temperatuur kunnen veranderen op een voorspelbare wijze gedurende het jaar, en consequent van jaar tot jaar binnen de duur van één leven. Om te kunnen omgaan met zulke temporele variabiliteit, ervaren individuen selectiedruk om verschillende activiteiten met betrekking tot reproductie en overleving uit te voeren op een gunstig tijdstip tijdens het jaar, d.i. een optimale jaarlijkse routine of cyclus. Deze jaarlijkse routines zijn afhankelijk van de omgevingsomstandigheden die individuen ervaren en vertonen een grote individuele variatie in het tijdstip, duur en de volgorde van belangrijke activiteiten tijdens het jaar. Voortplanting is een cruciale fase in de jaarlijkse cyclus en inzake energie-vereisten waarschijnlijk de meest veeleisende. Het is dan ook de logica zelve dat de timing van de reproductie voorrang neemt boven andere activiteiten van de jaarlijkse cyclus, die er vervolgens omheen worden gepland.

Vogels zijn consistent in hun fundamentele levenscyclus. Echter, binnen de verschillende fasen van deze levenscyclus, vertonen vogels een grote mate van variatie in de manier waarop deze worden gerealiseerd en georganiseerd. Leeftijds- en sekseverschillen verklaren vaak een groot deel van de variatie in levensgeschiedenissen tussen en binnen individuen. Inzicht in deze variatie vereist onderzoek naar de levensgeschiedeniskenmerken van individuen en veranderingen in deze kenmerken in de loop van hun leven.

In deze studie bestudeerde ik variatie in de levensgeschiedenissen van Zilvermeeuwen en Kleine Mantelmeeuwen op individuele basis.

In hoofdstuk 2, onderzocht ik tegelijkertijd het belang van variatie in eigrootte en 'hatching asynchrony' binnen broedparen op de overleving van kuikens voor het uitvliegen, aangezien beide gelijktijdig een effect kunnen hebben, hetzij direct, hetzij indirect via effecten op relatieve lichaamsconditie. Omdat de meeste sterfte voor het uitvliegen in Zilvermeeuwen plaatsvindt vóór de eerste tien dagen na het uitkomen, in het bijzonder voor c-kuikens, onderzocht ik ook of deze periode samenvalt met de periode van broedreductie, d.i. de periode na het uitkomen wanneer de overleving van kuikens het sterkst varieert met de legorde.

Consistente variatie binnen legsels in eigrootte met de legorde werd aangetoond in Zilvermeeuwen in de kolonie van Zeebrugge, waar c-eieren het kleinst bleken in de meeste broedparen. b-eieren waren vergelijkbaar in grootte met a-eieren. Het negatieve effect van de eilegdatum op de absolute omvang van c-eieren suggereerde dat veel late broeders beperkt waren in hun reproductieve inspanning doordat vrouwtjes van lage kwaliteit of onervaren vrouwtjes later beginnen te broeden in de kolonie van Zeebrugge. Ondanks deze negatieve relatie tussen de legdatum en c-ei grootte, was de kleine relatieve omvang van het laatst gelegde ei waarschijnlijk niet enkel het resultaat van energetische beperkingen op laat leggende Zilvermeeuwvrouwtjes, omdat patronen van variatie in eigrootte consequent geassocieerd bleken te zijn met patronen van mortaliteit bij kuikens. Gedurende de eerste 12 dagen na het uitkomen, varieerde de sterfte in Zilvermeeuwkuikens het sterkst met de legorde en deze tijdspanne werd vervolgens geïdentificeerd als de periode van broedreductie. Hoewel variatie in eigrootte binnen legsels niet op directe wijze gerelateerd was aan de patronen van kuikensterfte tijdens deze periode, verhoogde een kleiner relatieve eigrootte de verschillen in relatieve lichamelijke conditie van nestjongen, voornamelijk veroorzaakt door de mate van ‘hatching asynchrony’. Tegelijkertijd beïnvloedde de relatieve lichaamsconditie van c-kuikens op positieve wijze hun kans op overleving. Aldus kan de adaptieve waarde van relatief kleine c-eieren in Zilvermeeuwen liggen in het verkleinen van de overlevingskansen van laatst uitgekomen kuikens in interactie met ‘hatching asynchrony’ door middel van effecten op hun lichaamsconditie. Dit patroon is zeer consistent met een broedreductie strategie van Zilvermeeuwvrouwtjes om facultatief de omvang van het broedsel te reduceren in overeenstemming met de heersende voedselbeschikbaarheid.

In hoofdstuk 3 heb ik gezocht naar mogelijke ‘carry-over effecten’ van groei en andere levensgeschiedeniskenmerken voor het uitvliegen (uitkomdatum, ‘hatching asynchrony, grootte van het broedsel en rangorde na broedreductie) op de overleving na het uitvliegen.

Variabiliteit in overleving van eerstejaars kon in de eerste plaats worden gekoppeld aan de individuele variatie in de groeiratio van kuikens. Na broedreductie, had legorde geen invloed meer op de overleving van kuikens voor het uitvliegen en ook op de overleving na het uitvliegen had het geen effect. Echter, rangorde na broedreductie, - wanneer sommige b- en c-kuikens waren gepromoveerd tot eerste of tweede rang nadat oudere kuikens waren gestorven -, werd verondersteld om beter de omstandigheden tijdens het opgroeien weer te geven, omdat het werd gehandhaafd gedurende het grootste deel van het verblijf in het nest (± 45 dagen in Zilvermeeuwen). In overeenstemming werd een ondubbelzinnig negatieve invloed van de rangorde na broedreductie gevonden op de overleving na het uitvliegen. Overleving na het uitvliegen was ook negatief gecorreleerd met de uitkomdatum.

In hoofdstuk 4 heb ik onderzoek gedaan naar de mechanismen die ten grondslag liggen aan temporele variatie in de timing van aankomst in de kolonie tussen en binnen individuele Kleine Mantelmeeuwen. Ik onderzocht in hoeverre het tijdstip van aankomst een dynamische eigenschap (d.i. als gevolg van veranderingen binnen individuen in de tijd) of een vaste, consistente individuele eigenschap (d.i. als gevolg van fenotypische variatie tussen individuen) vertegenwoordigde. Ik onderzocht ook het belang van opgedane ervaring door prospectie of eerdere reproductie.

Kleine mantelmeeuwen kwamen geleidelijk eerder op de broedplaatsen aan met toenemende leeftijd, ongeacht van hun geslacht. Ondanks consistente variatie in de timing van aankomst tussen individuen in relatie tot hun leeftijd van eerste reproductie, kon tot 81% van de temporele variatie in aankomstdata in onze populatie worden verklaard door variatie binnen individuen. Tijdens de volwassen levensfase, kon een stijgende ervaring door eerdere reproductie worden geïdentificeerd als een belangrijke factor voor het verklaren van dit leeftijdsgerelateerde patroon. Het suggereerde bovendien dat een gebrek aan opgebouwde deskundigheid en vaardigheden het tijdstip van aankomst beperkt in onvolwassen individuen. Een extra oorzaak van variatie in het tijdstip van aankomst voor rekrutering in de broedpopulatie kon zijn dat onvolwassen individuen nog niet geslachtsrijp zijn en dus zonder enige druk om zich voort te planten minder haast moesten maken om tijdig op de broedplaatsen aan te komen. Deze onvolwassenen blijven ofwel het hele jaar door in hun overwinteringsgebieden over één of meerdere jaren, ofwel kunnen ze slechts voor een deel van de weg naar de broedgebieden terugkeren. Als alternatief kunnen zij de broedgebieden later in het broedseizoen verkennen. Tijdens deze verkenning en leerperiode, kunnen onvolwassen individuen kennis opdoen van mogelijk geschikte toekomstige broedplaatsen of hun vaardigheden in relatie tot navigatie en foerageren verbeteren om zodoende een tijdige, stapsgewijze overgang van de migratie naar reproductie te faciliteren. Volwassen Kleine Mantelmeeuwen die verkenningstochten uitvoerden alvorens te rekruteren, kwamen gemiddeld eerder aan in de broedkolonie gedurende het grootste deel van hun reproductieve leven dan degenen die dat niet deden. Echter, in Kleine Mantelmeeuwen, kwam dit verkenningsgedrag ook met een aanzienlijke overlevingskost, wat kan verklaren waarom de helft van de broedvogels die zich voor rekrutering aan verkenningstochten waagden, dit gedrag beperkten tot één seizoen op de leeftijd van drie jaar of ouder .

In hoofdstuk 5 onderzocht ik de mate waarin geslachtsspecifieke beperkingen met betrekking tot structurele omvang en/of de voortplanting vorm kunnen geven aan de variatie in het trekgedrag van geslachtsrijpe mannelijke en vrouwelijke Zilvermeeuwen en Kleine Mantelmeeuwen.

Bij volwassen Zilvermeeuwen, trokken grotere mannetjes verder weg van de kolonie, terwijl trekafstand onafhankelijk was van de lichaamsgrootte bij volwassen vrouwtjes. Bij volwassen Kleine Mantelmeeuwen, kon geen verband tussen lichaamslengte en trekafstand in beide geslachten gevonden worden. Gemiddelde aankomstdata in de broedkolonie varieerden niet met trekafstanden, maar verschilde wel tussen mannetjes en vrouwtjes van Zilvermeeuwen (maar niet van Klein Mantelmeeuwen).

Kortom, onthulde deze studie aanzienlijke variatie in levensgeschiedenissen binnen en tussen twee nauw verwante soorten, vooral in relatie tot leeftijds- en geslachtsgerelateerde beperkingen.

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