State-dependent life-history strategies

A LONG-TERM STUDY ON OYSTERCATCHERS

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PART I

General introduction

Chapter 1

Motivation and outline of thesis

Martijn van de Pol

State-dependent life-history strategies

An individual's life history is the collection of major events during a lifetime. With major events, also called life-history traits, biologists refer to events that affect the fitness of an individual. Survival and reproduction make up the basic components of fitness. Because resources are limited, organisms have to make choices in how to allocate their resources between survival and reproductive tasks. Consequently, several fundamental trade-offs exist, such as the trade off between current reproduction and future success (survival as well as reproduction), and the trade off between the quantity and quality of offspring. Interestingly, different species have found surprisingly many ways to deal with these trade-offs in combining life-history traits to affect fitness. Apparently there are many solutions to the same problem.

Not only has every species evolved its own unique life-history, within species there is also large variation between individuals' life-histories. Individual variation in life-history traits is one of the key-components for Darwinian evolution. Natural selection favors individuals with life-history traits that result in higher fitness. Whether natural selection results in evolutionary change depends on whether the variation in life-history traits has a heritable basis. Consequently, one of the most fundamental goals in biology is to understand what causes life-history traits to vary. Why do some individuals live longer than other individuals? Why do some individuals produce many offspring per reproductive attempt and others few? Why do some individuals start reproducing early in life, while others delay reproduction for years?

Most life-history traits are not fixed during a lifetime, but depend on the condition (state) an individual is in. Historically, most studies addressed how life-history decisions might depend on the age or life-stage of an individual. The age or life-stage of an individual is thought to indirectly represent variation in states. In other words, these variables can be seen as a way to stratify variation in states, without exactly defining or measuring what makes older individuals to survive better than younger individuals. Later, researchers have identified more direct measures of state that might cause some individuals to behave different than others, or individuals to behave different during their lifetime. For example, some individuals might be in a better physical condition, more experienced, mated to a better partner, or live in a more favorable environment than others and adjust their life-history decision to these circumstances.

Life-history decisions are often intricately linked with each other. For example, the decision with whom to breed (mate choice) might directly affect the decision where to reproduce (habitat choice), which are both thought to be important determinants of reproductive performance. Variation in one life-history trait can therefore be associated with variation in other life-history traits, because multiple life-history traits might be part of a complex of strategic decisions. For understanding variation in life-history traits as well as their evolutionary dynamics, it is therefore important to consider how they are linked. In addition, as life-history decisions early in life can affect life-history decisions later in life, it is important to address them from a lifetime perspective.

A long-term study on Oystercatchers on Schiermonnikoog

The research described in this thesis is part of a long-term field study on free-living Oystercatchers (*Haematopus ostralegus*), on the Dutch Wadden Sea island of Schiermonnikoog. The study was started in 1983 by Jan Hulscher, and since then a lineage of PhD-students has investigated life-history decisions in this long-lived bird species. Most of their work has focused on understanding individual variation in settlement decisions, partner choice and reproductive decisions. Their strategy to investigate these life-history decisions has been to combine detailed behavioral observation with a long-term dataset collected over many years, and to conduct critical experiments whenever possible. The research conducted in this thesis is aimed to be a continuation, and it investigates some of the questions which are the direct result of previous work. Furthermore, we will integrate the results from many of these studies to better understand why this breeding population is declining so rapidly in recent years.

Outline of the thesis

This thesis is partitioned into four main parts: (i) a general introductory part, (ii) a section on age-dependent life-history decisions, (iii) a section on state-dependent life-history strategies, and (iv) a concluding part. Each part consists of several chapters, with each chapter discussing one specific research topic. Some of the chapters are followed by a box, which discusses a topic related to the chapter, but in less detail. We end with a general discussion in the final chapter, in which some of the results from individual chapters are brought together. In chapter 2, we continue our General introduction with an introduction to the study system by describing how this population has changed over the last twenty-one years. Breeding numbers of Oystercatchers have declined strongly in recent years on Schiermonnikoog, as well as in most other breeding areas in the Netherlands. We investigate in detail which demographic parameters have changed on Schiermonnikoog and how this relates to changes in food availability and climate change. Subsequently, we discuss what might have caused Oystercatcher breeding numbers to decline rapidly all over the Dutch Wadden Sea.

In the second section on age-dependent life-history decisions we discuss how life-history traits change during a lifetime. In chapter 3, we develop a new statistical model to separate within and between-individual effects. Our model can be useful in many biological situations, and we illustrate our approach by showing that old Oystercatchers can have a higher reproductive performance than young Oystercatchers for two different reasons. Firstly, individuals perform better as they age (within-individual improvement), and secondly Oystercatchers that start breeding late in life perform better than individuals that start breeding early in life (between-individual change). In box A, we give an additional example in which the statistical model developed in chapter 3 can be used. We show that patterns of extra-pair copulation behavior not only change during the duration of a pair bond, but that unfaithful pairs are also more likely to split up the next year. Following up on the role of the pair bond we show in chapter 4 that variation in reproductive performance during a lifetime is more likely to depend on how long a pair had been together, than on the age or breeding experience of pair members. Using observational as well as experimental data, we suggest that mate-familiarity is one of the main determinants of reproductive success in Oystercatchers. In box B, we integrate patterns of age-dependent probabilities of breeding, reproduction and survival into an age-structured population model. We use this model to discuss how the selection for earlier or delayed maturity depends on the population growth rate in Oystercatchers.

In the third section on state-dependent life-history strategies we investigate how life-history strategies depend on the conditions. In chapter 5, we description the main causes of phenotypic variation in life-history traits of Oystercatchers, and what causes life-history traits to co-vary. We show that both reproductive output and survival not only depend on individual quality, but also on the quality of the partner, suggesting that life-history traits in Oystercatchers are not simple sex-linked traits. Furthermore, we discuss how our analyses can be used as a powerful ally to life-history experiments. In chapter 6, we focus on one specific life-history trait, egg size. In Oystercatchers there is substantial variation in egg size, and parents that lay larger eggs produce more offspring. However, it is unclear whether a large egg really constitute an advantage to the chick or that chicks from larger eggs do better because they are also born in a better rearing environment. We performed a cross-foster experiment to disentangle the effect of egg quality and the quality of the rearing conditions on the survival of chicks hatched from small and large eggs. In chapter 7, we investigate the long-term consequences of being reared under favorable conditions. We show that rearing under high quality conditions not only affects life-history traits early in life, but also settlement decisions later in life. Even future offspring benefit. We discuss whether early conditions are likely to have long-term effects in many other species too, and discuss the problems associated with using short-term fitness measures. In box C, we follow up on chapter 7 by discussing why offspring reared under favorable conditions do much better, and what determines offspring quality. In chapter 8, we discuss the relationship between the life-history decisions where and when to reproduce. Oystercatchers strongly vary in the quality of their breeding habitat, as well as in their age at first reproduction. Following up on a previous study by Bruno Ens and colleagues, we further develop the idea that variation in both these traits might be the result of individuals queuing for high quality breeding territories. We improve their original model by incorporating asymmetries in settlement behavior (as suggested by chapter 7), and compare model predictions with observed patterns in the field. Finally, we discuss how queuing behavior might help us understand patterns of population decline in this species.

In the General discussion section, chapter 9 concludes with integrating some of the conclusions from separate chapters. We will specifically return to what we have learned about the main causes of variation in life-history traits. Furthermore, we will discuss how life-history decisions are affected by population composition, and how in turn life-history decisions might affect population dynamics. Finally, we will discuss what might be some of the future challenges for the Oystercatcher population study on Schiermonnikoog.

Chapter 2

What causes the rapid decline in numbers of breeding oystercatchers?

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Kees Oosterbeek, Dik Heg, Marco van der Velde & Simon Verhulst

Abstract

The number of Oystercatchers (*Haematopus ostralegus*) in the Dutch Wadden Sea has declined by approximately 40% during the last two decades, and this is true for both the breeding and the (larger) wintering population. We investigated long term trends (21 years) in life history parameters (reproduction, survival, and emigration) and morphological parameters in an intensively studied population of breeding oystercatchers, and how this relates to changes in food availability and climate change. The number of breeding pairs declined 4.6% annually, most pronounced in low quality habitat. There were no indications that juvenile or adult survival declined systematically over the years. Reproductive output was virtually zero in the last seven years, which was associated with a dramatic decline in summer abundance of ragworm (*Nereis diversicolor*) and possibly Baltic tellin (*Macoma baltica*). The decline in shellfish abundance was associated with a decrease in body condition and a change in bill morphology, from a bill-shape used for eating shellfish to a bill used for eating worms. Frequent flooding of nesting areas in recent years, did not have a large impact on reproductive output, because most nests failed before flooding occurred. Nonetheless, if more nests would survive the egg phase in future years, flooding of nesting areas is likely to become a major problem as extreme water-heights have become much more frequent. Migration also increased strongly during the study period, suggesting Oystercatchers became less site-faithful. In conclusion, the decline in breeding numbers on Schiermonnikoog is likely to have resulted from low reproductive output, causing number of new recruits to decline and making the area less attractive for future breeders. Although, the decline in breeding numbers and reproduction was similar to changes in other breeding areas, we do not think our results can be straightforwardly used to explain patterns on a larger scale as environmental conditions have changed differentially across the Wadden Sea. We discuss several alternative hypotheses that could explain why Oystercatchers are declining rapidly all over the Dutch Wadden Sea area.

Introduction

The Eurasian Oystercatcher (*Haematopus ostralegus* L.), with its strong dependence on the inter-tidal mudflats as a source for food, is considered an indicator species for the status of the Wadden Sea ecosystem. 20% of the total over-wintering Oystercatchers in the Dutch Wadden Sea breeds in the Wadden Sea area, while the remainder of the birds migrates to breeding grounds in Scandinavia or breeds more inland in the Netherlands (Goss-Custard *et al.* 1995). In total, about 30% of the Western-European population lives in the Wadden Sea, at least for a part of the year. During the last two decades the numbers of breeding as well as over-wintering Oystercatchers in the Dutch Wadden Sea estuary have declined strongly (±40%; Ens *et al*, 2003).

Changes in population numbers are the direct result of the combined effects of a variety of demographic parameters: reproduction, survival, immigration and emigration (Fig. 2.1). Detailed knowledge about the changes in demography, and the underlying causes might further help us to identify conservational actions for this species. When the decline in numbers is associated with a decline in survival, the cause of a lower survival might most profitably be sought in changes in the environment of the wintering grounds, because Oystercatchers mortality rate is highest in winter. Alternatively, when the decline in numbers is associated with a decline in reproduction, the cause of a lower reproduction might be sought in changes in the environment of the breeding ground. Additional complexities can arise because environmental conditions can also have delayed effects later in the season through (memory) effects on body condition (Fig. 2.1). For example, bad environmental conditions during winter might result in a low body condition and/or an infection with parasites at the end of the winter which may affect the reproduction of those same individuals in the following summer.

For understanding changes in breeding numbers on a local scale and linking them to population changes on a Wadden Sea wide scale, several additional factors are important (Fig. 2.1). First of all, migration between breeding areas can affect population dynamics in local breeding populations (source-sink dynamics), but for the whole Dutch Wadden Sea population such effects are probably less important. Secondly, the changes in environmental conditions in one population might differ substantially from another population (Fig. 2.1; environment A ≠ environment B). If we are to understand why breeding numbers decline all over the Dutch Wadden Sea, we need to identify which changes in the environment are common to birds breeding in different areas of the Wadden Sea.

Most previous research has focused on relating changes in survival and over-wintering numbers to changes in the over-wintering conditions (Camphuysen *et al.* 1996; Nève & van Noordwijk 1997; Atkinson *et al.* 2000; Le V.dit Durell *et al.* 2001b; Goss-Custard *et al.* 2002; Rappoldt *et al.* 2004b; Ens, Smaal & de Vlas 2004). This focus on changes on the wintering grounds has partially resulted from an interest in the impact of commercial shellfish fisheries (which reduces the winter food stocks) on Oystercatcher numbers (Atkinson *et al.* 2000; Stillman *et al.* 2001; Ens *et al.* 2004; Bell *et al.* 2001; Caldow *et al.* 2004; Goss-Custard *et al.* 2004). But another important reason

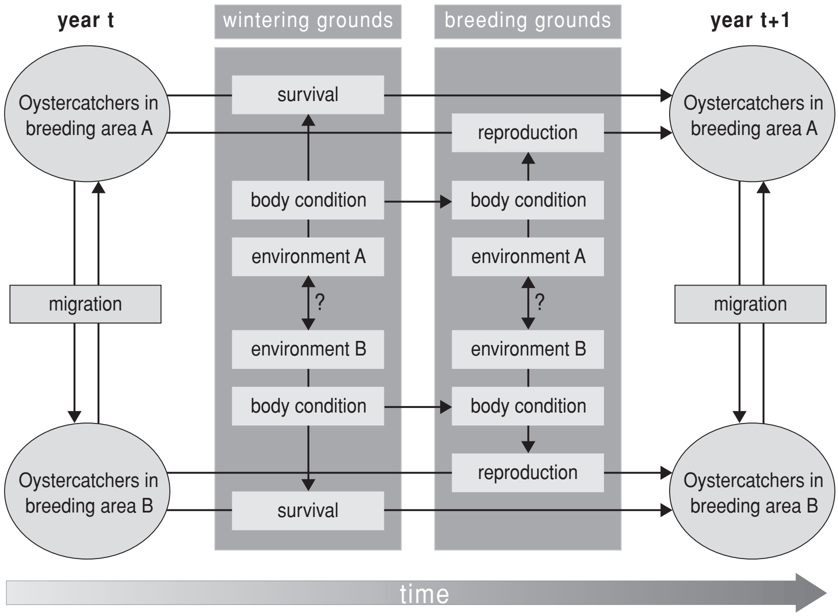


Figure 2.1 Schematic description how demographic parameters (reproduction, survival, and migration) affect the changes in number of Oystercatchers from year to year in different breeding areas (A and B). Furthermore, we describe how environmental conditions in winter and summer might affect reproduction and survival and how effects on body condition might result in memory effects from winter to summer body condition. If the changes in survival are similar between area A and B, it is likely that environmental conditions in winter also changed similarly in both areas. If the changes in reproduction are similar between area A and B, it is likely that environmental conditions in summer also changed similarly in both areas (or alternatively that there is a carry-over effect of winter body condition).

for the focus on the wintering situation was that the environmental conditions, which Oystercatchers from different breeding areas experience, might be more similar in winter than in summer. In summer, Oystercatchers breed both on the coast and far inland, but in winter all Oystercatchers depend on intertidal mudflats. Thus birds from very different breeding areas to some extent use similar winter grounds. Consequently, potential changes in the wintering conditions could therefore have caused breeding numbers to decline all over the Dutch Wadden Sea, while this seems a priori a less likely scenario for environmental changes on the different breeding grounds. Nonetheless, a previous study suggested that the decline in breeding numbers in the province of Friesland was the direct result of a decrease in reproductive output (Hulscher & Verhulst 2003).

As relatively little is known about which demographic parameters have changed and what environmental variables might have caused these potential changes, it is clear that a combined demographic and mechanistic approach, in which both changes in wintering and breeding conditions are addressed, is an important step forward. This study describes the changes in demographic parameters using a 21 year study on a non-migratory breeding population on the Dutch Wadden Sea island of Schiermonnikoog. We investigate in detail how reproduction, survival, migration (and morphology) have changed, differentiating between age-classes, sexes and breeding status. Subsequently, these changes in demography are related to changes in the summer and winter environmental conditions, such as food supply, climate change, and density of conspecifics. We will compare our results with several other breeding populations in the Wadden Sea area, and discuss how our results might help us to identify the potential major causes of population change on the island of Schiermonnikoog, but also on a larger scale of the Dutch Wadden Sea.

Methods

Study area and species

From 1984 until 2004, we followed a breeding population of oystercatchers on the Dutch Wadden Sea island of Schiermonnikoog (32°29’ N 6°14’ W). The study area consisted of a salt marsh area where the oystercatchers bred and inter-tidal mud flats where they fed. In the main study area all breeders and their fledglings were individually marked (in area A from 1984 on; C from 1985, and B and D from 1992; Fig. 2.2). The area surrounding the main study area was followed extensively and not all breeders were color banded there. Oystercatchers are long-lived birds with high site-fidelity, they are socially and genetically monogamous with bi-parental care (Ens *et al*. 1996; Heg *et al*. 1993; Safriel, Ens & Kaiser 1996). All birds were classified into two juvenile age classes (1st and 2nd year) and one adult age-class. Sex of the oystercatchers was determined by DNA analysis and observations of copulations (Heg *et al*. 1993; Heg *et al*. 2000); most birds could only be sexed at the adult stage.

As in most coastal breeding Oystercatcher populations, there is a clear dichotomy in territory quality, mainly based on the nesting location relative to the foraging area (Safriel *et al*. 1996; Ens *et al*. 1992). Some parents, called residents, can take their chicks to the food, because breeding and feeding territory are adjacent. Other parents, called leapfrogs, have to bring the food to their chicks, because the breeding and feeding territory are spatially segregated. Because transporting every food item to the chicks is less efficient, residents consistently produce much more offspring per year than leapfrogs (Ens *et al*. 1992). Throughout the paper we will refer to territories occupied by resident breeders as high quality territories and leapfrog territories as low quality territories. There is a surplus of adult non-breeders that do not defend nesting territories.

The diet of oystercatchers varies during the year, dependent on the availability and profitability of different prey items as well as on the difference in space use during the over-wintering and breeding season. Oystercatchers on Schiermonnikoog are highly dependent on two prey species for raising their young, ragworm (*Nereis diversicolor*) and Baltic tellin (*Macoma baltica*) (Bunskoeke *et al*. 1996). During winter bivalve species become more prominent in the diet, primarily cockles (*Cerastoderma edule*) and mussels (*Mytilus edule*) (Zwarts *et al*. 1996a). Just before the breeding season and in late August,

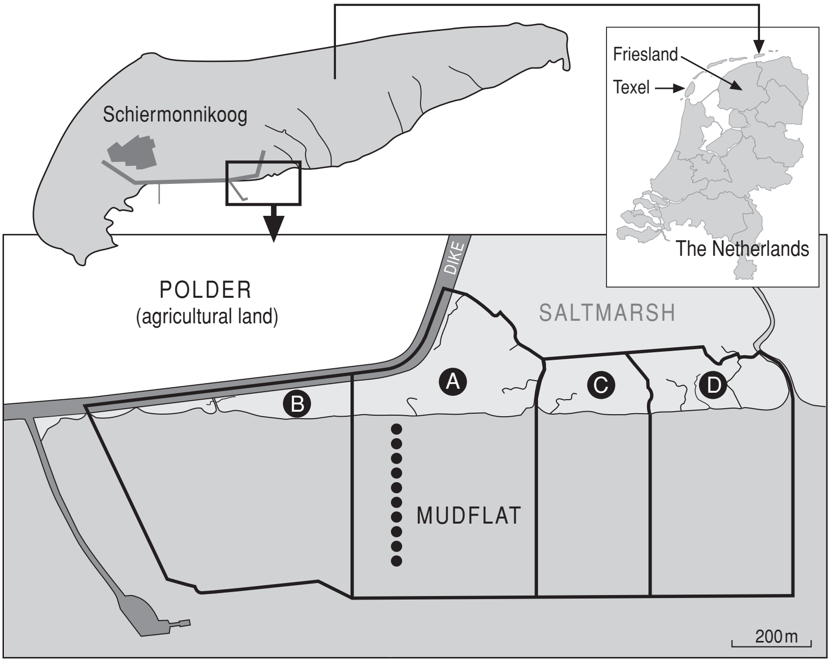


Figure 2.2 The study area on the island of Schiermonnikoog. Subareas A, B, C & D comprised the main study area. The boxed area on the mudflats depicts the area where Oystercatchers feed for 90% of their time in summer. Dots on the mudflat refer to sampling points where summer food supply was determined yearly.

the lug worm (*Arenicola marina*) is also part of an Oystercatcher's diet. Two other bivalve species are also eaten, soft-shelled clam (*Mya arenaria*) and peppery furrow shell (*Scrobicularia plana*), but only constitute a minor part of their diet in most years.

Population counts

Each year we counted the number of high and low quality breeding territories in the main study area, as well as the number of non-breeder pairs that defended feeding territories on the adjacent mudflats. As not all sub-areas of the main study area were systematically followed until 1992 we imputed their values for missing years. The total number of non-breeders was estimated by counts during the breeding season at all high tide roosts on the island (combined with counts by 'Wadvogel-telgroep Schiermonnikoog'). The number of adult non-breeders associated with the study area was assumed to be a fixed percentage (7.7%) of the total island counts. This percentage was based on the proportion of breeders on the island that were breeding in the study area, as such we assumed non-breeders distributed themselves similar to breeders over the island. Annual wintering numbers of oystercatchers (local breeders, non-breeders as well as winter migrants) on the entire island of Schiermonnikoog (SOVON area-code WG31) were counted by SOVON (van Roomen *et al*. 2005).

Survival

In total we collected 172,499 re-sightings of 740 different birds born or breeding in the main study area, which amounts to an average 9079 re-sightings per year and 26 re-sightings per individual per year. Dead recoveries were collected by the Dutch ringing centre. The majority of dead recoveries occurred during winter; recoveries were mainly from the island of Schiermonnikoog and the surrounding Wadden Sea area. During severe winters, frost migration can occur and recoveries were also from more distant estuaries in southern Netherlands and northern France. Most dead recoveries were reported to occur from natural circumstances, although some juveniles were shot in France. In our study population, the reporting rate of dead color ringed oystercatchers was high at 25%, and dependent on winter harshness (van de Pol *et al*. 2006). Juveniles leave the island a few months after fledgling and most are not seen until they return to the study area at the age of 3 years (van de Pol *et al*. 2006).

As juveniles leave the study area, juvenile survival was analyzed using dead recoveries. Adult survival was analyzed combining both dead recoveries and live re-sightings in one model, which allows the estimation of permanent emigration (Burnham 1993; Cooch & White 2004). We also estimated the adult survival of breeders and non-breeders separately using multi-state capture-recapture models, but these survival estimates were confounded by permanent emigration as only local re-sightings could be used. All survival analyses were performed with program MARK (Cooch & White 2004); for details of the analyses see van de Pol *et al*. (2006).

Reproduction

Oystercatchers make a small nest-cup on the ground and they prefer nesting sites in open grass-land, with relatively little coverage. The breeding season commences with egg laying in May and the semi-precocial chicks fledge in July or August. Each year we followed the breeding performance of most pairs in the main study area; for a complete description of the standardized protocol, see Heg *et al*. (2001). For each nest, we determined the laying date of the first egg (n=1395), average egg size (n=1407), the size difference between the largest and smallest egg in a clutch (n=1367), clutch size at the start of incubation (n=1537), number of hatchlings (n=1417) and fledglings (n=1791). All reproductive parameters analyzed are from first clutches only, except annual fledgling production, which is the fledgling production from all clutches in one year from a pair (82% no replacement clutches, 18% one or more replacement clutch).

Morphological characteristics

Each year about 50 Oystercatchers (males and females) were caught on the nest during incubation (n=1126). Body mass was measured to the nearest gram and was statistically corrected for the time elapsed since the start of incubation (birds lose weight during incubation). Wing length was measured to the nearest millimeter. The length and height of the bill as well as the height of the bill-tip were measured to the nearest millimeter (Fig. 2.3). Bill shape, which is known to reflect diet choice in oystercatchers, was classified as either a pointed type, blunt type or the intermediate type (Fig. 2.3).

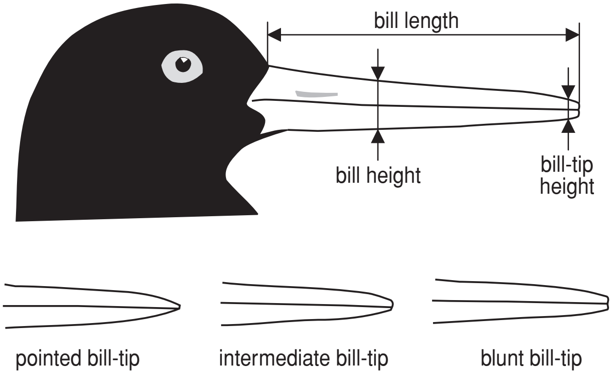


Figure 2.3 Bill morphology of Oystercatchers and its measurements. Figure adapted from Zwarts *et al.* 1996.

This classification is repeatable within as well as between observers, and is known to reflect diet choice (Swennen *et al*. 1983; Hulscher 1985; Le V.dit Durell, Goss-Custard & Caldow 1993; Hulscher & Ens 1991; Hulscher & Ens 1992; Sutherland *et al*. 1996). The tip of the bill erodes as a result of opening bivalves which results in a blunt bill for shellfish-specialists and a pointed bill for worm-specialists. Oystercatchers can change from a pointed into a blunt bill type in about two weeks as a result of a switch in diet (Swennen *et al*. 1983; Hulscher 1985; Hulscher & Ens 1991). A small proportion of individuals (<2%) had different bill shapes (e.g. hammerers) and were omitted from analysis.

Environmental conditions

Many environmental variables changed during the study period that could potentially have affected one or several demographic or morphological parameters. We have quantified several of such variables that are likely to be important, but this list is by no means exhaustive. As such this analyses is explorative of nature, and we cannot exclude other non-measured variables exist that might also be important. For example, Oystercatchers suffer many losses during both the egg and chick phase, but only the egg phase has been studied. The available evidence indicates eggs are most at risk during the laying phase and that herring gulls (*Larus argentatus*) and common gulls (*Larus canus*) are the main predators of these eggs (Verboven, Ens & Dechesne 2001; Harris & Wanless 1997; Ens 1991). Anecdotal observations suggest that Herring gulls are also important predators of chicks (B.J. Ens, pers. obs.). However, little is known what the role of black-headed gulls (*Larus ridibundus*) and rats (*Rattus rattus*) has been. Consequently, we cannot systematically assess the impact of predator abundance, although we have indications their numbers have also changed (see later).

Every year benthic fauna in the local mudflat was sampled on a fixed transect in the first week of July (Fig. 2.2). Ten locations 50m apart were sampled, with four sampling points per location; all points from each year were aggregated. At each sampling point we collected the upper 20cm of the mudflat with a sampling device with a diameter of 17cm. We classified and quantified all bivalve prey species: Baltic tellin, cockles, mussels, soft-shelled clam and peppery furrow shell, as well as ragworm and lugworm. In most years we measured ash free dry mass (AFDM; a measure of caloric value) of every prey species, for other years we used average values to calculate AFDM of each species. Winter food abundances are based on data from RIVO-surveys (1992-2002; Bult *et al.* 2004; Ens *et al.* 2004) on the mudflats surrounding the island of Schiermonnikoog (mudflats surrounding area WG31). The selected scale of sampling for food abundance was larger in winter than in summer as oystercatchers use a larger area of the mudflats in winter. Winter surveys were restricted to the main prey species in winter (cockles, mussels, and Baltic tellin).

Daily weather characteristic were collected at the Schiermonnikoog weather station (Vugts 2002). Winter severity was qualified on the basis of the frequency of cold days between 1 December and 31 March (cf. Camphuysen *et al.* 1996; Neve & van Noordwijk 1997). In this winter-index days with mean temperatures below -10°C count for three units, days with mean temperatures between -10°C and -5°C count for two units, and days with mean temperatures between -5°C and 0°C count for one unit. Similar results were obtained using alternative indices for winter harshness such as the IJnsen index or the Hellmann index (Vugts 2002).

The Wader Energy Balance and Tidal Cycle Simulator (WEBTICS) model was used to calculate a stress index for each winter (Rappoldt *et al.* 2004c). The model simulates the food uptake of Oystercatchers and a distribution of birds over the exposed parts of the mud flats around Schiermonnikoog (area WG31). The mud flats are described on input as a number of spots which have a position, height and surface area. Spots may contain prey items, characterized by type, weight and density. The WEBTICS program simulates tidal cycles and calculates the fraction of time the average and ideal bird has to spend feeding in order to meet its energy requirements. These foraging intensities are combined into a stress index for the winter. Besides historical data on weather, prey distribution, tides, and shell-fisheries, there are bird and prey parameters on foraging, prey growth and energy conversion, based on the extensive literature on Oystercatcher foraging ecology (see e.g. Goss-Custard 1996, or the special issue of Ardea 84A). We will use the stress index as a measure that combines several environmental variables into one measure that quantifies how difficult it was for Oystercatchers to meet their energetic requirements in a specific winter.

Analysis

All measurements on demographic parameters in one year were aggregated into one yearly value. To analyze the effects of environmental variables on demographic parameters we used multiple regression analyses with backward deletion of non-significant terms. Multicollinearity between different environmental variables was often quite strong which may have interfered with model selection, especially because using annual values results in quite low sample sizes (Graham 2003). Therefore we checked the robustness of our models by also using stepwise enter methods. In cases of strong collinearity it remains problematic to correctly identify which covariate explains most of the variance; therefore we will conservatively present multiple scenarios in ambiguous cases.

Results

Changes in numbers and demographic parameters

The total population, comprising breeders and non-breeders, declined on average with 2.6% per year from 1984-2004 (Fig. 2.4A). The number of breeders in low quality habitat declined most strongly since 1995, while the number of high quality habitat breeders declined only slightly (Fig. 2.4B). The population decline in low quality habitat was strongest in the area close to the mudflats; more inland the decline was less pronounced (Fig. 2.5). Paradoxically, the decrease in breeders in low quality habitat occurred in the presence of many adult non-breeders that only occupied some of the newly formed vacancies (Bruinzeel & van de Pol 2003). Counts of the total number of non-breeders varied strongly within years, suggesting measurement error was large, which makes the between year fluctuations difficult to interpret (Fig. 2.4C). However, there was no indication that the total non-breeder numbers declined systematically during the study peri-

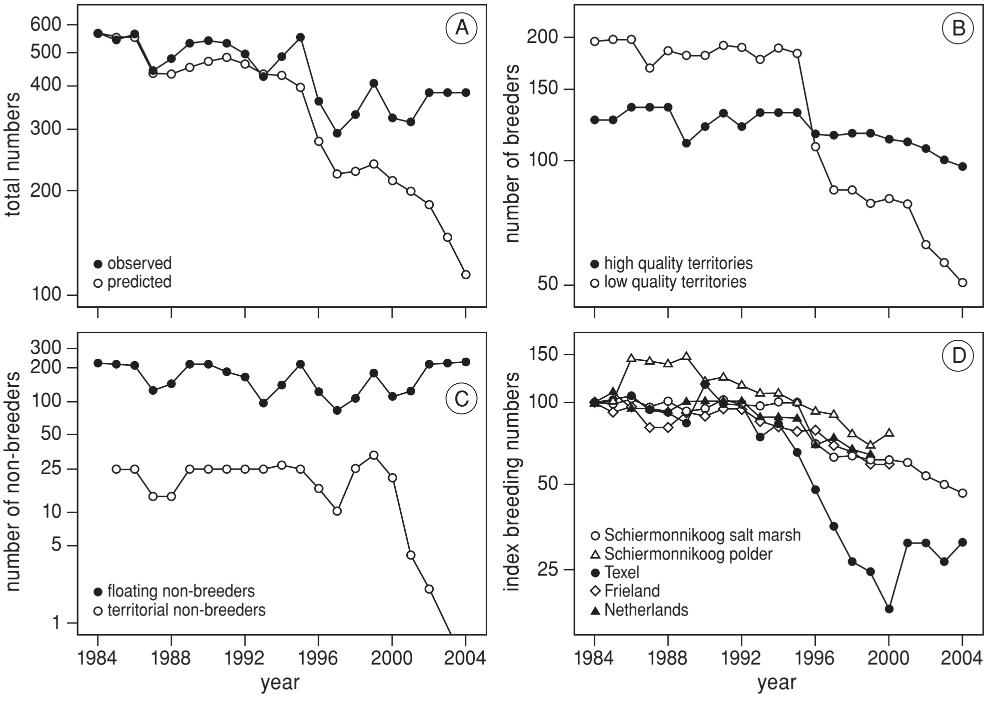


Figure 2.4 Changes in Oystercatcher numbers from 1984-2004 in the main study area. Presented are (A) the total number of Oystercatchers (breeders and non-breeders) observed, and the total numbers predicted by a demographic model (see text), (B) breeders in high quality and low quality territories, (C) non-breeders distinguished by floating non-breeders and territorial non-breeders. In (D) changes in breeding numbers are given for several population; numbers are index on 1984 (=100). Note the logarithmic y-axis in each graph. Data from Schiermonnikoog-polder and Friesland are given in Hulscher & Verhulst (2003) and from Texel in Ens *et al.* (2003).

od (Fig. 2.4C). The number of non-breeders that defended only a feeding territory declined, and this type of non-breeders had disappeared completely at the end of the study period (Fig. 2.4C). Patterns of decline in breeding numbers on the salt marsh on Schiermonnikoog (4.6% annually) were remarkably similar to other areas around the Dutch Wadden Sea and the whole Netherlands (Fig. 2.4D). This synchronous decline over a large scale suggests that the cause of decline should be sought in a common denominator between these areas, although there of course might be additional local causes in each area.

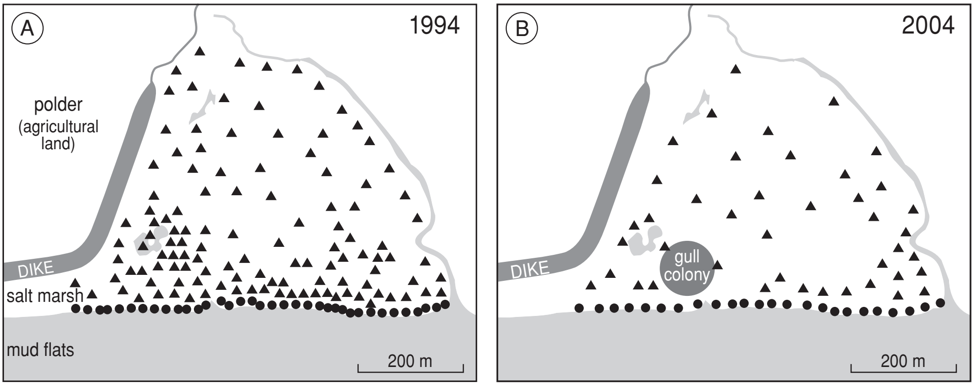


Figure 2.5 Spatial changes in high quality (circles) and low quality (squares) nesting territories from (A) 1994 to (B) 2004 in a cross-section of the main and outer study area (areas A, C, D and OBK). Note the position of a large gull colony (ranging 1,000-10,000 Black-headed gulls and 100 Common gulls between 1997-2004).

First year survival showed a very erratic pattern between years but confidence intervals were large (Fig 2.6A); there was no evidence for a systematic change. We did not have sufficient data to investigate changes in second year survival, and we were not able to estimate juvenile survival from 2002-2004 because too few young fledged in these years. Adult survival was very low in three years (1986, 1995 and 1996) with harsh winter weather (see below) but did not decline systematically during the study period (Fig. 2.6B). Permanent emigration by adults from the study area increased towards the end of the study period (Fig. 2.6C). However, analyses of local re-sightings suggested non-breeders generally had a much lower apparent survival than breeders, which is likely to be caused by permanent emigration of non-breeders from the study area (Fig. 2.6D). Adult survival and emigration rate did not differ systematically between the sexes.

Changes in lay-date showed variable patterns: breeders in low quality territories advanced laying with 0.36±0.10 days per year, while breeders in high quality territories did not change their laying date (delay of 0.08±0.08 days per year; Fig. 2.7A). Consequently, the clear difference in laying date between pairs on high and low quality territories in the early years disappeared in the course of the study. Clutch size at the start of incubation did not change systematically (Fig. 2.7B), but due to frequent egg

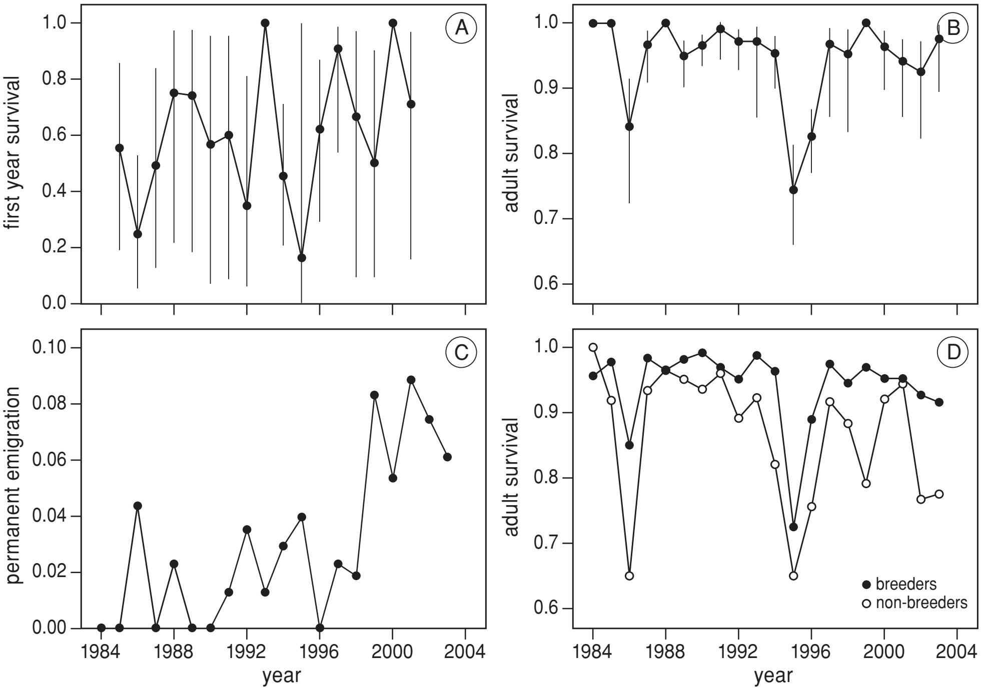


Figure 2.6 Changes in survival and dispersal behavior from 1984-2004. Presented are (a) the first year survival, (B) annual adult survival (including breeders and non-breeders), (C) annual permanent emigration out the study population, and (D) the apparent local survival of breeders and non-breeders, which is confounded with permanent emigration. In (A,B) error bars represent 95% confidence intervals; in (A) values after 2001 are missing because no young fledged in those years.

predation in the egg-laying period we have no good data to investigate whether the actual number of eggs laid or the number of replacement eggs changed during the study period. Egg volume (average per clutch) decreased 0.06cm^3 per year during the study (Fig. 2.7C); while the difference in size between the largest and smallest egg in a clutch increased somewhat (Fig. 2.7D). A large intra-clutch variation in egg-size is thought to increase the asymmetry in competition between siblings and thereby facilitate brood-reduction (Heg & van der Velde 2001).

The probability an egg survived till hatching declined to about one-third of the initial value during the study (Fig. 2.7E). The probability a hatched chick survived till fledging varied substantially over the entire study period but was extremely low during the last few years (Fig. 2.7F). As a consequence of these changes the number of fledglings produced per pair was extremely low in recent years (Fig. 2.7G). The changes in all reproductive parameters were primarily the result of within-individual changes, although there was some additional selective appearance of early laying recruits in low quality habitat (determined using the method described in chapter 3, data not shown).

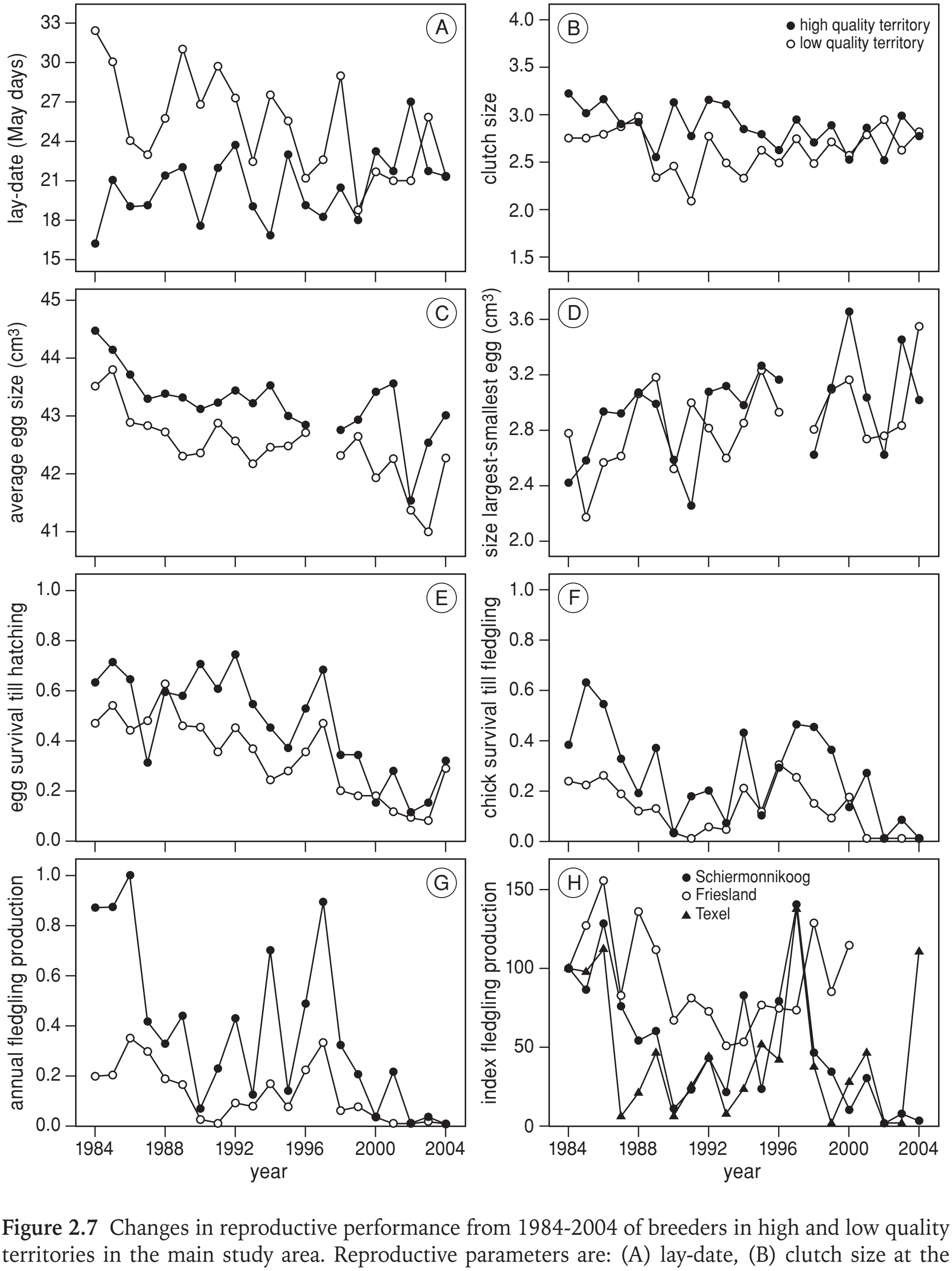


Figure 2.7 Changes in reproductive performance from 1984-2004 of breeders in high and low quality territories in the main study area. Reproductive parameters are: (A) lay-date, (B) clutch size at the start of incubation (C) average egg size in a clutch, (D) difference in egg size between the largest and smallest egg in a clutch, (E) egg survival till hatching, (F) chick survival till fledging, (G) annual fledgling production. In (H) the annual fledgling production on Schiermonnikoog is compared with the number of fledglings per nest on another Wadden Sea island (Texel; Ens *et al.* 2003), and with the number of young ringed in Friesland province corrected for breeder density and ringing intensity (Hulscher & Verhulst, 2003). All measures were indexed on 1984 (=100).

Annual fledgling production on Texel, another Wadden Sea island (Fig. 2.2), varied in parallel with the Schiermonnikoog population ($r=0.63$; Fig. 2.7H). The synchrony in reproductive output between Schiermonnikoog and mainland breeding areas (Friesland; Fig. 2.2) was less strong ($r=0.28$; Fig. 2.7H), and it is unknown whether reproductive output declined in Friesland in the last four years (Hulscher & Verhulst 2003). Nonetheless, the observed synchrony in reproductive output between areas that are up to 100km apart strongly suggests that the cause(s) for a decline in reproductive output might be similar in these areas.

Relating demographic changes to population numbers: immigration

From 1984-2004 breeding numbers on Schiermonnikoog declined on average 4.6% per year. Total population size decline was less strong (2.6% per year), because non-breeder numbers did not decline systematically. The expected change in population numbers from the demographic parameters (survival, reproduction and emigration), calculated using a simple stage-structured population model, was a decline of 6.8% per year (van de Pol *et al*. 2006; although there we equaled immigration to emigration). This predicted decline was much stronger than the observed decline in population size, suggesting there must have been substantial immigration into the Schiermonnikoog population (Fig. 2.4A).

Body condition and diet changes

Body mass of breeders caught on the nest, a proxy for 'condition', declined over the years (Fig. 2.8A). Wing length (Fig. 2.8B), tarsus length and head length (data not shown), which are proxies of body size, did not vary systematically between years. Consequently, the change in body mass did not result from a change in structural body size.

Bill morphology changed dramatically over the years. Bill length and bill height changed in opposite directions for males and females, consequently the sexual dimorphism in bill characteristics completely disappeared during the study (Fig. 2.8C,D). Similarly the bill-tip height of males decreased during the study (Fig. 2.8E), which was consistent with a change from blunt bill types towards more pointy bill types in males, but also in females (Fig. 2.8F). The changes in bill-morphology were mainly the result of within-individual changes (determined using the method described in chapter 3, data not shown). As such the bills of both males and females changed from a bill-shape that is associated with a diet of shellfish towards a bill-shape that is associated with a diet of primarily worms.

The role of environmental change

Variation between years in the main environmental variables is described in Appendix 2A. Adult and juvenile survival were strongly negatively associated with the number of cold days (juvenile survival $R^2=0.39$, $n=17$, $P=0.008$; adult survival: $R^2=0.38$, $n=20$, $P=0.003$), with the absolute effect being most pronounced in juveniles ($\beta_{juveniles}=-0.065\pm0.021$; $\beta_{adults}=-0.018\pm0.005$), but the relative effect being quite similar for juve-

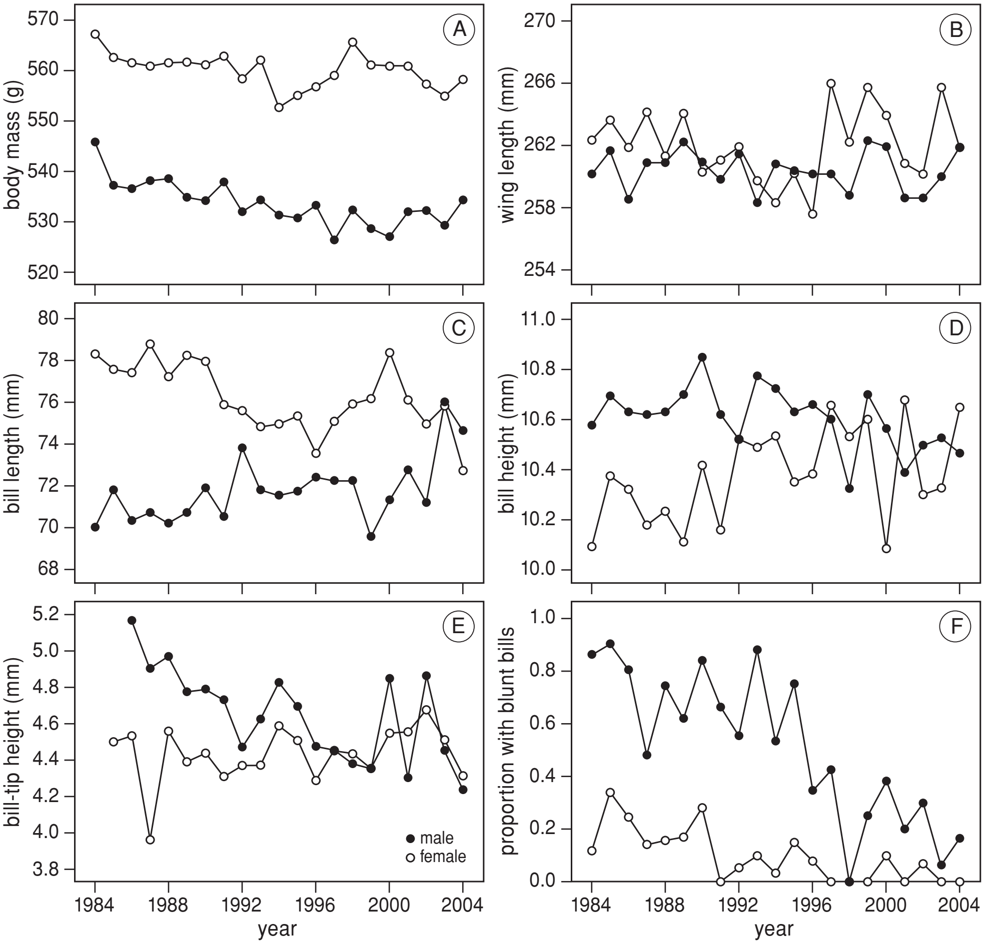


Figure 2.8 Changes in morphological characteristic of male and female breeding birds caught on the nest during the incubation phase 1984-2004. Presented are (A) body mass, (B) wing length, (C) bill length, (D) bill height, (E) bill-tip height, and (F) the proportion of birds with blunt bill types.

niles and adults (Fig. 2.9A). There were no indications that variation in adult and juvenile survival between years covaried with total food availability around Schiermonnikoog (cockles, mussels and Baltic tellin only; Fig. 2.9B), or food availability per bird (Fig. 2.9C). In years with a high stress index, i.e. years in which it was relatively difficult for Oystercatchers to meet their energetic requirements, juvenile survival was also very low (Fig. 2.9D; R^2=0.41, n=10, P=0.045). The effect of stress index disappeared when survival was corrected for the number of cold days (P=0.25, R^2=0.05), which suggests that stress index was only associated with juvenile survival because of the strong collinearity with the number of cold days (r=0.58). The temperature is used in calculating the stress index, so this finding is in itself not surprising, but nevertheless additional effects of food availability, weather, and oystercatcher numbers would have

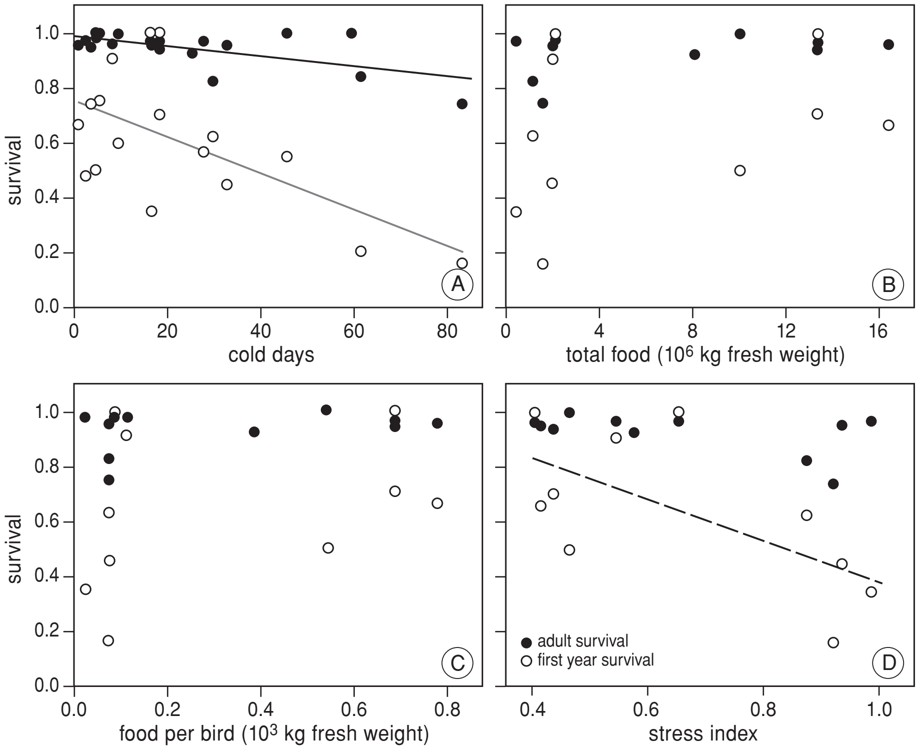


Figure 2.9 Adult survival and first year survival in relation to (A) the number of cold days, and (B) the total food abundance (sum of *Cerastoderma edule, Mytilus edule* and *Macoma baltica*; cockles, mussels, and Baltic tellin), (C) food per bird, and (D) the stress index. Each dot represents one year; sample sizes in (B)-(D) are lower because surveys of winter food abundance were only available from 1992-2002.

been biologically plausible. Adult survival was not associated with stress index (R^2=0.23, n=11, P=0.13); most adult Oystercatchers managed to survive even in years with an extremely high stress index (Fig. 2.9D).

Annual reproductive output was strongly associated with the abundance of ragworm (Fig. 2.10A). The slope of the relationship was substantially steeper for breeders in high quality territories (slope=0.10±0.03, R^2=0.42, n=20, P=0.002) than for low quality territories (slope=0.04±0.01, R^2=0.44, n=20, P=0.002), suggesting breeders in high quality territories more strongly benefit (in absolute terms, not in relative terms) from a high abundance of ragworm. Variation between years in survival during the egg and chick phase was also strongly positively associated with the annual abundance of ragworm (Fig. 2.10C,E). Variation in annual reproductive output covaried less strongly with the abundance of Baltic tellin. Although variation in Batlic tellin explained some of the variation in fledgling production, egg survival and chick survival (Fig 2.9B,D,F), variation in these parameters was better explained by variation in ragworm (as established by multiple regression). Nonetheless, given the strong covariance between the

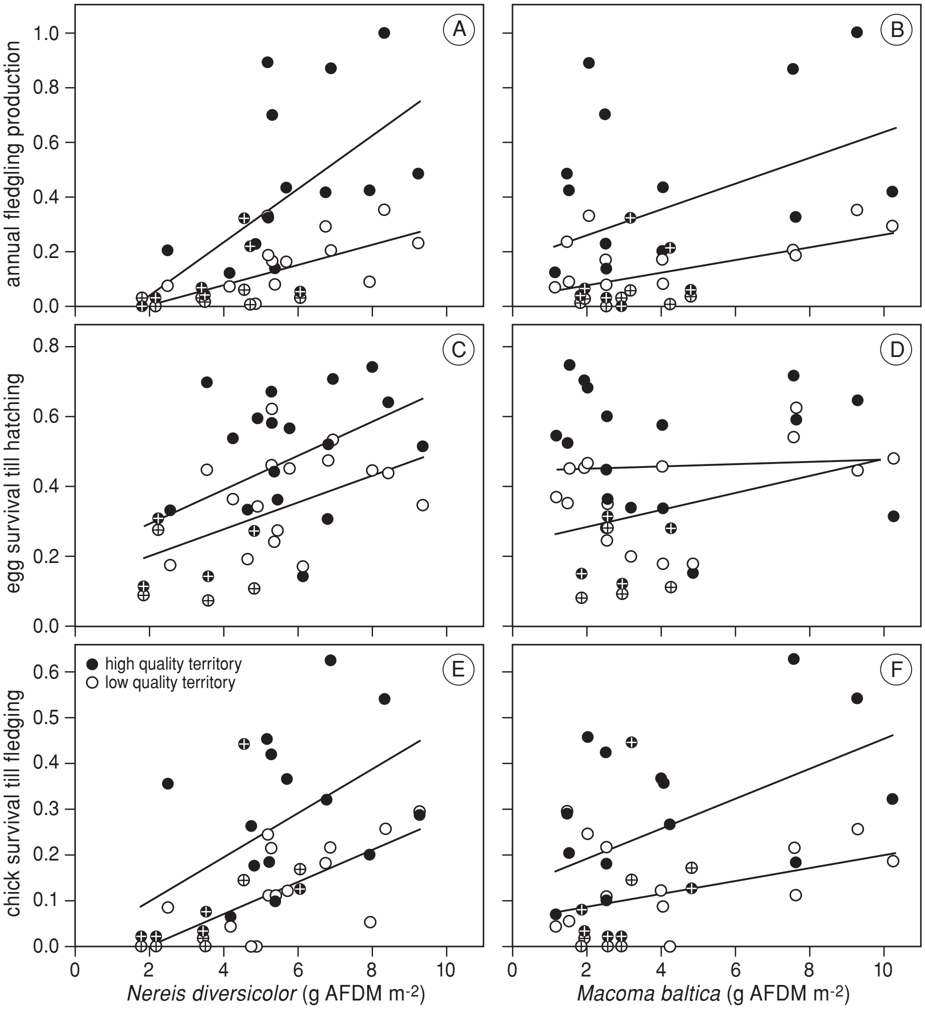


Figure 2.10 Reproductive performance of breeders in high (and low quality territories in relation to the summer food abundance of the two major prey species *Nereis diversicolor* (ragworm; left panel) and *Macoma baltica* (Baltic tellin; right panel). Presented are (A,B) the annual fledgling production, (C,D) the survival from egg till hatchling, and (E,F) the survival from hatched chick till fledging. Each dot represents one year; dots with a cross inside refer to years in which the nesting areas were flooded.

annual abundance of ragworm and Baltic telling (r=0.34), we cannot exclude that Baltic tellin abundance also causes reproductive output to vary between years.

Potentially predation risk also has increased substantially, as since 1997 a large colony of Black-headed gulls established itself in our study area (Fig. 2.5; Fig. 2A3D). It remains unclear whether black-headed gulls actually depredate Oystercatcher eggs, as observing a depredation event is very rare. Herring gulls and Common gulls were observed to depredate Oystercatcher eggs, but their numbers have remained quite stable during the study period (both species <100 individuals; O.Overdijk, pers comm.). Furthermore, a huge colony of black-headed gulls might attract other predators (e.g. rats, birds of prey) which could also have depredated Oystercatcher eggs and chicks. We have insufficient data to assess whether predator pressure increased, but it is striking that the survival from egg till hatchling was low ever since the gull colony established in 1997 (Fig. 2.7E).

Flooding of the nesting areas occurred regularly, especially in recent years (1990, 1998, 2000-2005). A flooding is the result of a spring tide in combination with a strong north-western wind. During such extreme water heights nests are washed away and chicks drown. Nonetheless we do not think flooding had a strong impact on the survival of eggs and chicks in most years, because flooding occurred primarily in the years at the end of the study which were (probably coincidentally) also characterized by low food abundance (Fig. 2.10). Consequently, in most years when the nesting areas flooded, nests had usually already failed. Furthermore, nesting areas that were not flooded also had extremely low reproductive output in those years. Although flooding of the nesting areas did not strongly affect reproductive output in previous years, it is likely to be a potential problem in the future. In most years flooding occurred at a moment when many eggs were about to hatch or chicks were only a few days old (Fig. 2.11A). Especially in this period flooding can have a strong impact, as most eggs and chicks will not survive a flooding at that age, and parents are unlikely to start a new replacement clutch if they lose their clutch so late in the season. If in future years more eggs and chicks would survive, flooding could have an important impact. Frequent flooding of the nesting area in future years is not an unrealistic scenario, as extreme water-levels have become increasingly more common over the last few decades (Fig. 2.11B; Heg *et al.* in prep). This increase in the height of extreme water-levels is probably not directly the result of an overall increase of the water-level in the Wadden Sea, because there was no systematic change in the mean high tide level, but probably related to stronger winds in the last decade (Appendix 2A, Fig. 2A3C).

On an annual level, body mass during the incubation phase was positively correlated with the total abundance of Baltic tellin and cockles (Fig. 2.12A; males $R^2=0.29$, $n=20$, $P=0.014$; females $R^2=0.29$, $n=20$, $P=0.014$). Similarly, in years in which the total abundance of Baltic tellin and cockles was low, few males and females had a blunt bill type, while in years with high bivalve availability the bill-type of birds changed towards a blunt bill-type (Fig. 2.12B). Note that the change from a blunt to a more pointy bill shape during the study period was consistent with a decline in Baltic tellin, but that bill-type also covaried between years with cockle abundance, which did not decline systematically over the years (Appendix 2A, Fig. 2A1). Although the abundance of Baltic tellin and cockles were both separately associated with bill type (multiple regression both $P<0.05$), the sum of these two prey species described the variation more parsimoniously (as established by using Akaike's information criteria). Abundances of other prey-species, such as ragworm and lugworm, were not associated with bill-type; Oystercatcher's bill-type changed towards pointed bills while abundance of worms also declined (Fig 2A1A) .

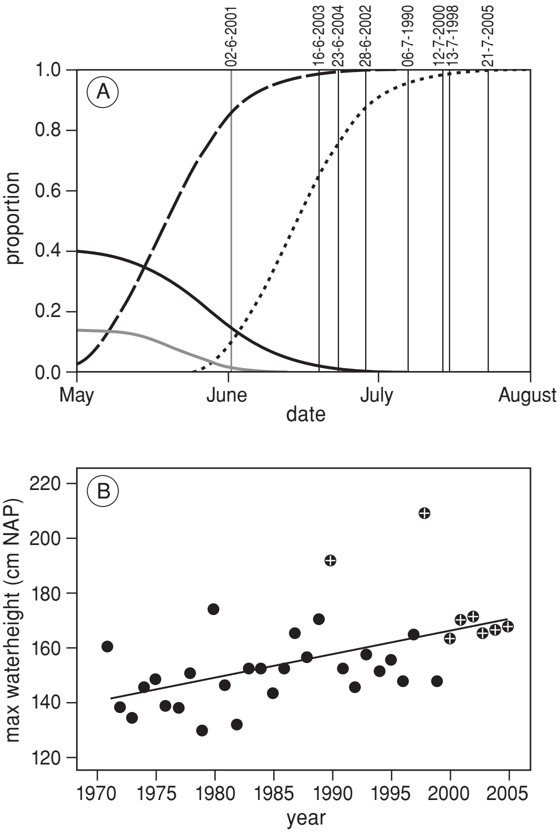


Figure 2.11 Consequences of flooding of the nesting areas. In (A) the occurrence of major flooding in various years (vertical lines) is given relative to the timing of reproductive decisions by Oystercatchers in an average breeding season. Presented are the cumulative proportion of the population that has started egg laying (dashed line), the cumulative proportion of nests that has hatched (dotted line), the proportion of individuals that will initiate a first replacement clutch after the loss of the first clutch (solid line) and the proportion of individuals that will initiate a second replacement clutch after the loss of the second clutch (grey line). In (B) the maximum water-height in the months of June and July is given for the last 34 years. Dots with a cross inside refer to years in which the nesting areas were flooded; we have no information whether flooding occurred before 1984.

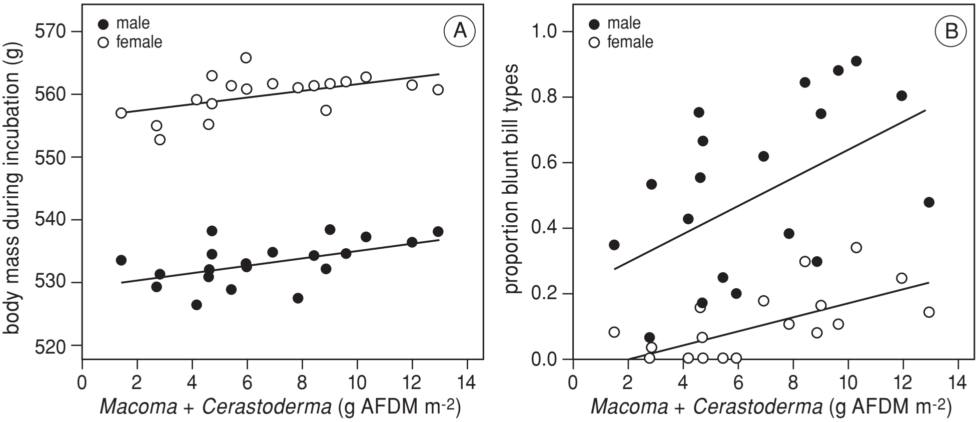


Figure 2.12 (A) Body mass, and (B) bill type of male and female birds during the incubation phase in relation to the summer food abundance of the combined total of the two major bivalve prey species *Macoma baltica* (Baltic tellin) and *Cerastoderma edule* (cockles). Each dot represents one year.

Discussion

Why do breeding numbers decline on Schiermonnikoog?

From 1984-2004 breeding numbers on Schiermonnikoog declined on average 4.6% per year. Our results suggest this decline is the combined result of a decline in reproduction and increased emigration, while survival did not change systematically. Although survival did not decline systematically, years with extreme low survival did have a strong impact on population size in 1995 and 1996, in the sense that population size declined strongly after these winters, while after an earlier winter with high mortality (1986) the vacancies were filled by non-breeders.

In recent years emigration rate of adults (probably non-breeders) has increased manifold (Fig. 2.6C), but at the same time there must have been substantial immigration of non-breeders because the total numbers of non-breeders remained stable (Fig. 2.4C). In other words, Oystercatcher were not more likely to leave the study population in particular, but generally became less philopatric in recent years. Although it would be easy to understand why individuals emigrated from a declining population when this reflects a deteriorating environment, it is not obvious why other individuals would simultaneously immigrate into that population. Possibly, immigrants originated from breeding areas where conditions were even worse. Alternatively, environmental quality has deteriorated on a larger scale, but immigrants require a substantial amount of time to assess the likelihood of acquiring a territory of sufficient quality. Another alternative hypothesis is that non-breeders come to Schiermonnikoog in summer, not to prospect for a breeding site, but to benefit from the recovery of mussel banks in the eastern (but not in the western) part of the Dutch Wadden Sea since 2001 (Bult *et al*. 2004). Non-breeders do not have to defend a territory or nest and can spend much more feeding time on more distant mussel banks than breeding birds can.

Interestingly, the number of occupied low quality territories decreased despite the presence of hundreds of non-breeders. It was not the case that no non-breeders recruited in the breeding population at all after 1995; each year 5-10 non-breeders recruited both into high and low quality territories from 1995-2004. Additionally, experimental removal of either male or female breeders in 1998 and 1999 showed that these territories were re-occupied in both high and low quality habitat (Bruinzeel & van de Pol 2003). Clearly, there were many more low quality territories that could have been occupied by the many non-breeders present in the study area, but apparently they preferred to remain non-breeder. Possibly, the value of the vacated low quality territories that were not re-occupied decreased below the acceptance threshold for non-breeders after 1995. As such, non-breeders preferred to queue for high quality instead of starting reproducing immediately in a low quality territory (see Chapter 8). An alternative hypothesis is that in recent years the size of the feeding territories of breeding birds has increased as a result of the decrease in food abundance. As such, competition for breeding status has shifted from competition over nesting space to competition over feeding space, and consequently breeding population size might now be limited by the size of the feeding area.

What environmental changes caused demographic parameters to change on Schiermonnikoog?

Variation in annual juvenile and adult survival did not change systematically over time, but was mainly associated with variation in winter harshness, as also found by other studies (Camphuysen *et al*. 1996; Nève & van Noordwijk 1997; Le V.dit Durell *et al*. 2001b; Atkinson *et al*. 2003). In contrast to these same studies, we found no association between survival and winter food abundance or Oystercatcher density (total amount of birds or food per bird). Most of these studies showed survival was most strongly dependent on food abundance in years with very cold winters; harsh winters with low food abundance had a much lower survival than harsh winters with high food abundance. In our study, years with harsh weather conditions always coincided with low food abundance. Therefore the absence of an effect of food abundance is not contradictory with previous studies.

The stress index, a new measure of winter severity that integrates information on food availability, weather, Oystercatcher density, and tidal patterns (Rappoldt *et al*. 2004c) also explained a substantial part of the variation in juvenile survival, as expected on the basis of the strong collinearity between the stress index and winter coldness. The stress index was recently used as a measure to predict the effect of bivalve stocks and commercial shellfish fisheries on Oystercatcher numbers in the entire Wadden Sea and the Oosterschelde estuary (Rappoldt *et al*. 2004a; Rappoldt *et al*. 2004b; Ens *et al*. 2004). From our results it remains unclear to what extent the stress index based on data from a small area (as in our study) is a good predictor of juvenile and adult survival, because in years when the stress index was virtually at its maximum most adult Oystercatchers still managed to survive. Possibly, Oystercatchers moved within the Wadden Sea to areas that were richer in food in those years, although the available data suggest that oystercatchers are highly faithful to their wintering site, at least with respect to the location of the tidal roosts (Verhulst *et al*. 2003). A further possibility is that Oystercatchers used alternative food sources or foraged on agricultural land, which were only included as a marginal food source in the model. Furthermore, there is the problem that estimates of winter food abundance on a small scale such as the island of Schiermonnikoog are much less reliable than on the scale of the whole Dutch Wadden Sea. Nonetheless, the absence of a strong correlation between the stress index and survival suggests we need a better understanding of what food sources Oystercatchers use in years of scarcity, how much food there is available, and where they go in order to survive in winter.

We investigated several possible causes why reproductive output declined strongly in recent years. Most importantly, the low availability of ragworm and possibly also Baltic tellin was associated with low reproductive output. Possibly, the low abundance of Baltic tellin has resulted in a shift in Oystercatcher's diet from bivalves to worms (as suggested by the change in bill-shapes), which has made the Oystercatchers on Schiermonnikoog more strongly dependent on ragworm, which also declined strongly. In recent years flooding of the nesting areas was not the main reason why reproductive success was low. Nonetheless, if extreme water-levels remain frequent, as expected on the basis of the long term trend (Fig. 2.11B), flooding is likely to have a strong effect on reproductive output in years when eggs and chicks do not die prematurely. Finally, we cannot rule out the possibility that the number of predators has increased in recent years, but we have insufficient data to evaluate this. Numbers of Common gulls and Herring gulls, which are thought to be the main predators, have not increased in recent years (but some individuals might have specialized on Oystercatcher eggs). And it remains uncertain to what extent black-headed gulls, rats and birds of prey have contributed to the decrease in egg survival. The number of black-headed gulls has increased in recent years, and rats have been known to cause much damage in other breeding colonies on Schiermonnikoog (O.Overdijk, pers. comm.). Therefore identifying the main predators of Oystercatchers eggs and chicks is an important next step. Although we cannot exclude that an increase in predators has caused reproductive success to decline, a more parsimonious explanation is that Oystercatchers had to spend more time feeding and were in worse body condition in recent years, and therefore did not protect their nests very well.

Different environmental causes of low reproductive output might affect breeders in high and low quality territories differentially. Food availability seemed to have the strongest absolute effect on breeders in high quality territories, while breeders in low quality territories were more likely to be affected by flooding, as they breed on the lowest part of the salt marsh (Heg *et al.* in prep). Predators might affect breeders in low quality territories more than in high quality territories. Oystercatchers in high density areas have lower egg predation than low density areas, possibly as a result of cooperative vigilance and mobbing behavior against predators by close neighbors (unpublished data). As density of breeding territories is highest on high quality territories (Fig. 2.5), breeders on low quality territories might be less able to deter additional predators. Furthermore, the decline in breeding numbers might also negatively affect egg survival as density decreases and the distance between neighbors increases.

The long term change in bill shape indicates that breeding Oystercatchers changed their diet from bivalves to worms in the course of the study, which was consistent with a strong decrease in bivalve abundance (mainly Baltic tellin). A decline in bivalve-eaters and an increase in worm-eaters was also apparent in a between species comparison in the Dutch Wadden Sea (van Roomen *et al.* 2005). Interestingly, the sexual dimorphism in bill morphology (and probably also diet choice; Le V.dit Durell *et al.* 2001a) observed at the start of the study disappeared completely during the study period. Consequently, using biometric measurements of bill morphology as a way to determine the sex of Oystercatchers (Zwarts *et al.* 1996b) is no longer reliable, at least for the breeding oystercatchers on Schiermonnikoog. Furthermore, using bill morphology as a measure of structural body size does not seem very useful either, as individuals can change substantially in their bill-morphometrics. The decline in bivalve abundance was also associated with a decrease in body mass during incubation. In this population, body mass during incubation is correlated with the body mass at the end of the winter (Oosterbeek *et al.*, in prep). As such the decrease in breeding body condition during the study period can potentially be, at least in part, a carryover effect of worsened wintering conditions.

Schiermonnikoog in comparison with other breeding populations

The decline in breeding numbers on Schiermonnikoog was strikingly similar to the decline in several other breeding areas and the overall decline in the Netherlands. Likewise, reproductive output was also strikingly similar between the island Schiermonnikoog, the island Texel, and mainland breeding areas in Friesland, which are up to 100km apart. This suggests that there may be a general cause of decline affecting all populations similarly. On Schiermonnikoog, the decline in numbers was mainly the result of a decrease in reproduction. Fewer recruits were produced, more individuals emigrated, but at least as important, many low quality territories did not seem profitable breeding habitat for non-breeders anymore in recent years. In Friesland, breeding numbers are also thought to have declined as a result of low reproductive output over a much longer period, and changes in mowing regime are suggested to have contributed, at least partly, to this decrease in reproductive success (Hulscher & Verhulst 2003). On the saltmarsh of Schiermonnikoog mowing did not occur, and we identified several alternative explanations, one more likely than the other, for the decline in reproductive output. We now discuss to what extent these factors could have affected oystercatcher populations on a larger scale and what additional hypothesis could explain the decline in breeding numbers in the entire Dutch Wadden Sea area.

A lower abundance in summer of ragworm or Baltic tellin is unlikely to serve as a general explanation for a decline in reproductive performance in the Netherlands, as abundance of both species increased in recent years in most intertidal areas of the Dutch Wadden Sea (Rappoldt *et al*. 2004b; Leopold *et al*. 2004). Furthermore, mainland breeders in Friesland had a comparable pattern of reproductive output, while these birds used completely different food sources during the breeding season. On Schiermonnikoog we could not exclude that the low reproductive output resulted from an increase in egg predators, although there was no direct evidence for this. In the entire Dutch Wadden Sea, there are also no clear indications that the number of gull or rats have increased in recent years. Furthermore, it is important to note that frequent extreme water-levels could not have affected reproductive output in Texel and Friesland breeding areas, as these Oystercatchers breed behind a dike. The hypothesis that a lower body condition at the end of winter caused reproduction to decline, is difficult to assess, as we do not know whether body condition decreased in other breeding areas as well. If body condition is dependent on winter food stocks, as suggested by a recent study (Verhulst *et al*. 2004), one would not expect body condition to have declined all over the Wadden Sea as winter food abundance of cockles, mussels and Baltic tellin in the Wadden Sea have recovered somewhat in recent years, at least in the eastern part of the Wadden Sea (Rappoldt *et al*. 2004b). Conversely, the low bivalve stocks during the first part of the 1990s in the Wadden Sea might have strongly favored worm-eaters over bivalve-eaters. Consequently, the current Oystercatcher population in the Wadden Sea might be dominated by worm-eaters which would profit less from increased bivalve stocks, also in winter.

We have not considered yet the role of diseases or parasites, which could also explain why breeding numbers in different areas have declined synchronously. For example, by eating cockles Oystercatchers can become infested with endoparasites, such as helminthes. The occurrence of parasites in prey species has been suggested to directly affect prey selection and intake rate of Oystercatchers (Norris 1999). However, we do not know whether parasites have become more prevalent in recent years, or what the impact of such parasites on reproduction is (van Oers, Heg & Le Drean Quenec'hdu 2002). Similarly, at the moment we have little knowledge to what extent outbreaks of diseases could affect the performance of breeding birds in breeding areas all around the Wadden Sea.

To summarize, this study shows that the decline in breeding numbers on Schiermonnikoog, is likely to be caused by a decrease in reproduction resulting in fewer recruits and making the area less attractive for future breeders. Consequently, fewer breeders settled in low quality habitat and non-breeders more often emigrated. However, using our knowledge about the causes of decline on Schiermonnikoog it is not possible to make strong generalizations to other breeding areas, as environmental circumstances differ substantially between areas. As such, at this moment we do not have good idea why numbers of Oystercatchers have declined rapidly in the Dutch Wadden Sea. Nonetheless, this study does give several important new insights into the likelihood of the various non-exclusive hypotheses. As such we hope this studied helps to identify what future research is necessary to better understand why Oystercatchers are declining so rapidly, and what we could do to stop this decline.

Acknowledgements

We would like to thank Natuurmonumenten for allowing us to conduct our fieldwork in the beautiful Nationaal Park Schiermonnikoog. Many people helped with the fieldwork over the years, of which Jan Hulscher and Marcel Kersten deserve special mention. Joost Tinbergen and Rudi Drent facilitated this research and the use of the field station. Klaas van Dijk and the ‘wadvogeltelgroep Schiermonnikoog’ supplied additional data on Oystercatcher counts. We thank Joost Tinbergen and Rudi Drent for comments on the manuscript. M.V. was responsible for analyzing blood samples to sex the birds. M.P. was supported by a grant from the Breedtestrategie-program ’Dispersal and adaptation’, University of Groningen. L.B., K.O. and S.V. were financed by grants from NWO (respectively ALW-90536124 and STW-GB14804).

Appendix 2.A

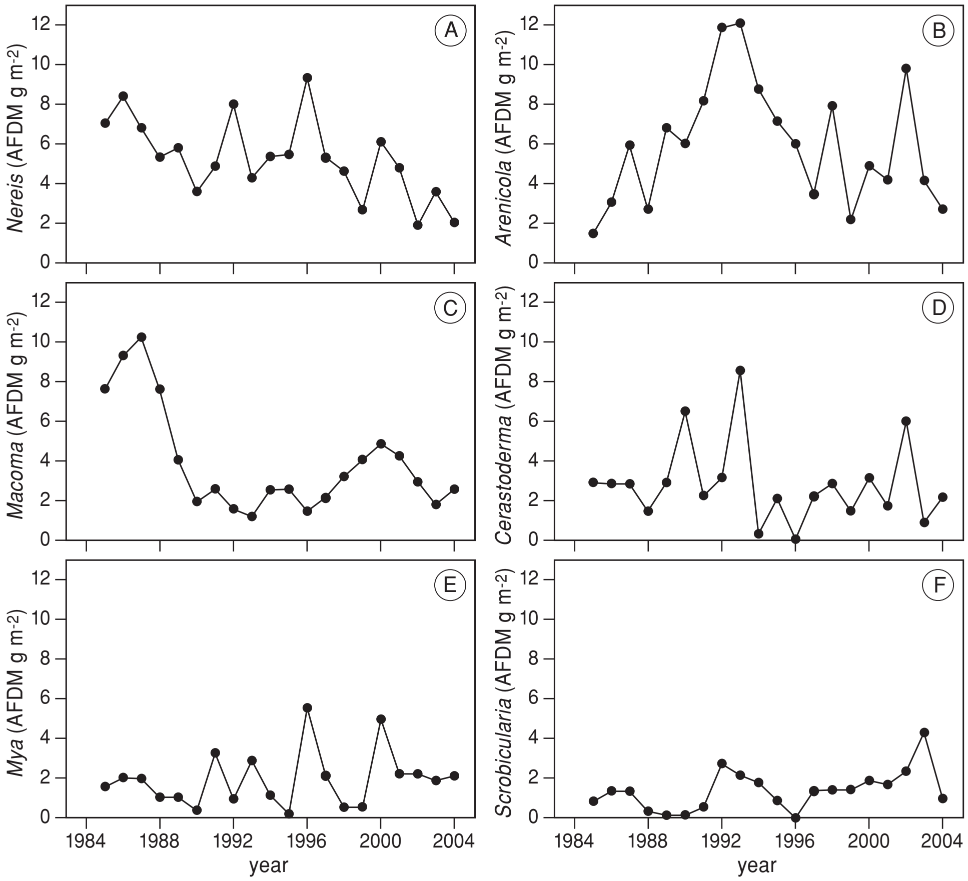


Figure 2.A1 Changes from 1984-2004 in summer food abundance in (A) *Nereis diversicolor*, (B) *Arenicola marina*, (C) *Macoma baltica*, (D) *Cerastoderma edule*, (E) *Mya Arenaria*, (F) *Scrobicularia plana*. *Mytilus edule* were (almost) absent in the area sampled.

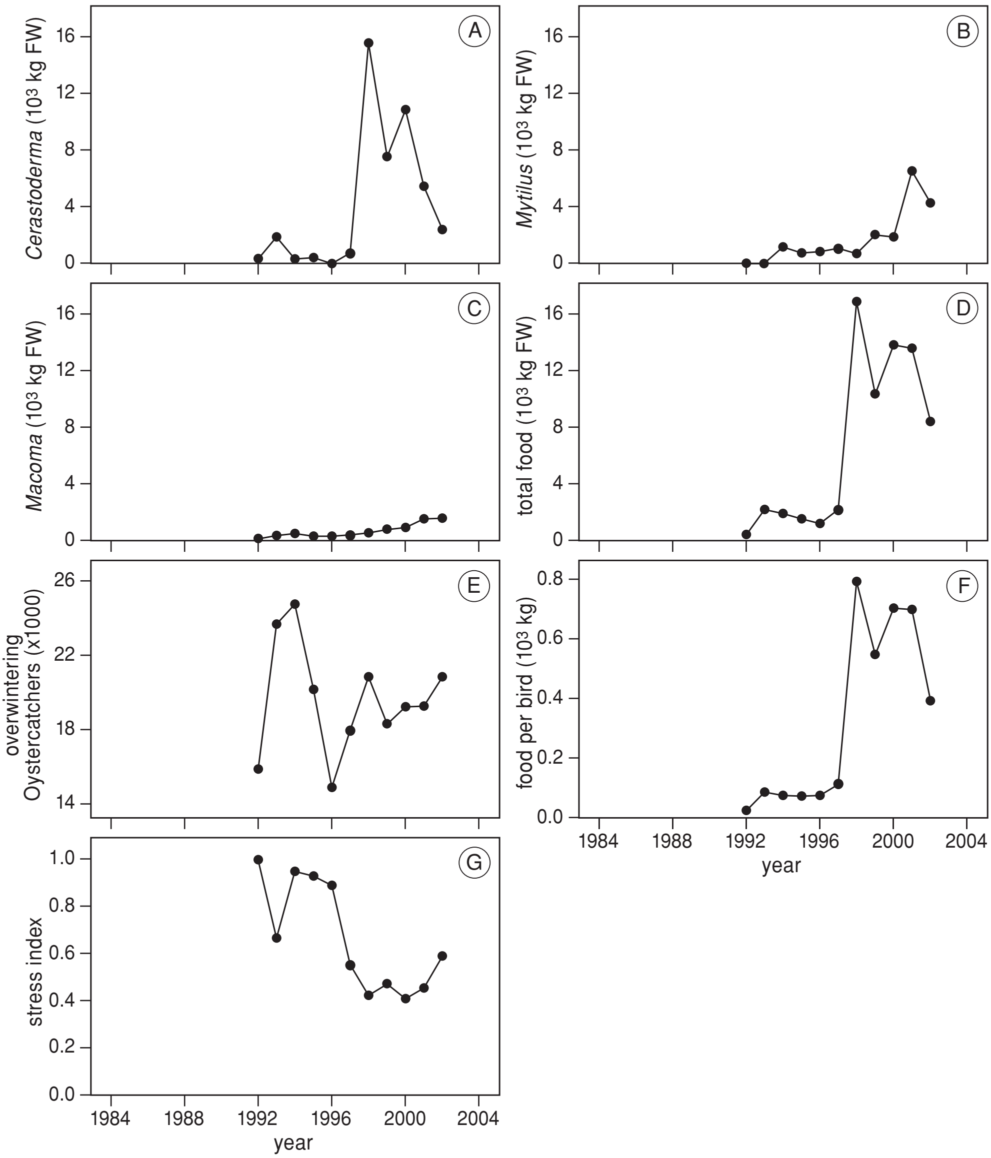


Figure 2.A2 Changes from 1992-2002 in (A) *Cerastoderma edule* abundance, (B) *Mytilus edule* abundance, (C) *Macoma baltica* abundance (D) total winter food abundance (sum of the previous three species), (E) the number of over-wintering Oystercatchers (local birds and migratory birds), (F) the food available in winter per bird, and (G) the stress index.

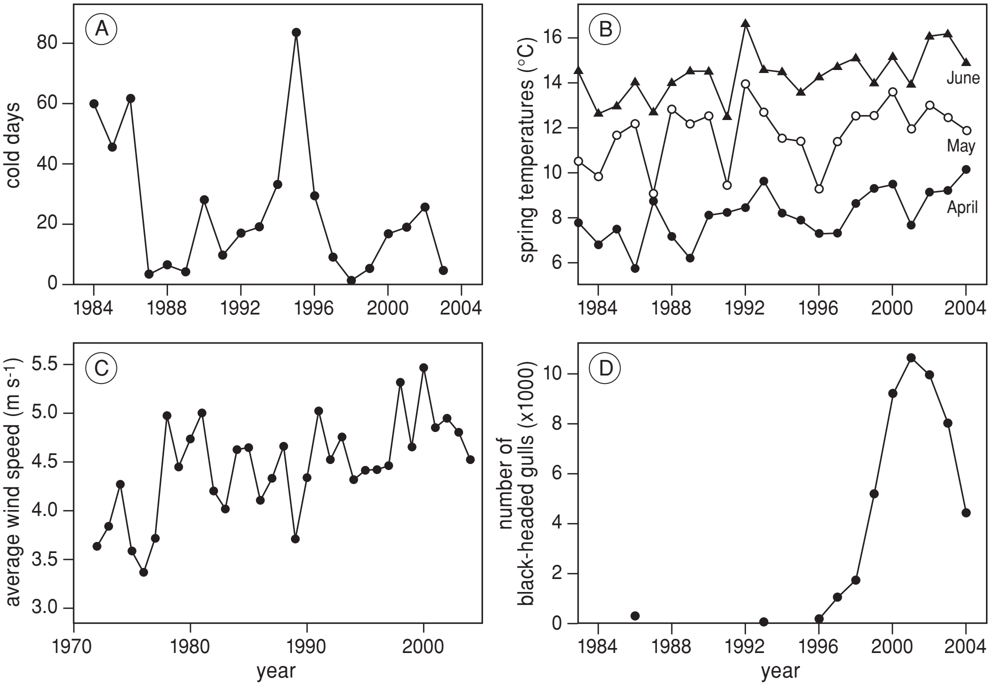
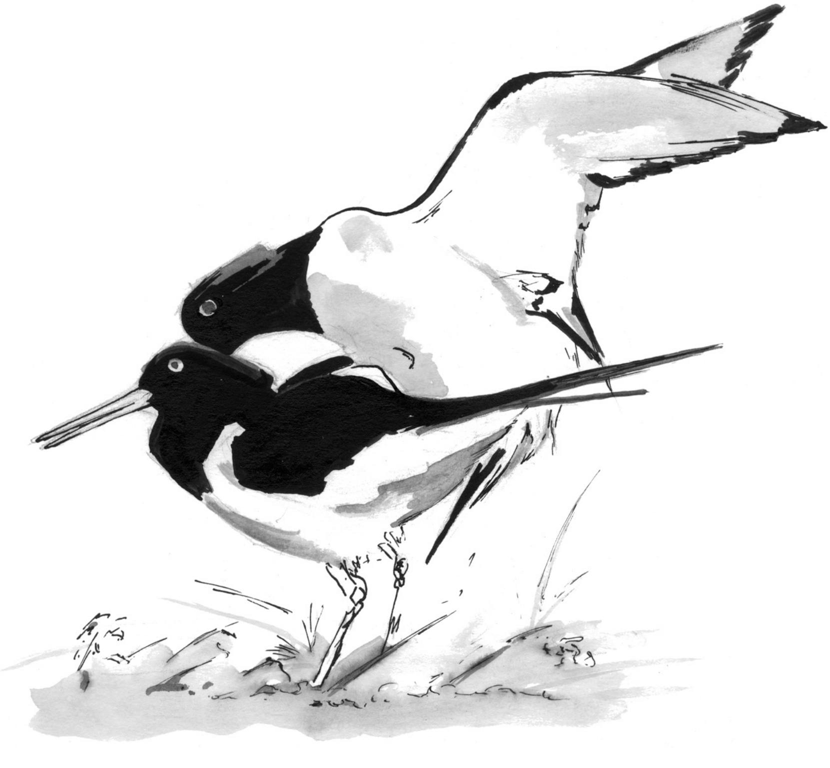


Figure 2.A3 Changes in weather characteristics of (A) winter harshness (expressed as the number of cold days), (B) average spring temperatures in April, May, and June, and (C) the average wind speed in the months of June and July, (D) the number of black-headed gulls in the study area (see Fig. 2.5 for location of colony). Note that from 1984-1995 not in all years the black-headed gulls were counted, but densities were quite constant and low in these years (O.Overdijk, pers. comm.).

PART II

Age-dependent life-history decisions



Chapter 3

Age-dependent traits: a new statistical model to separate within and between-individual effects

Martijn van de Pol & Simon Verhulst

The American Naturalist 167, 764–771

Abstract

Evolutionary questions regarding ageing address patterns of within-individual changes in traits during a lifetime. However, most studies report associations between age and e.g. reproduction based on cross-sectional comparisons, which may be confounded with progressive changes in phenotypic population composition. Unbiased estimation of patterns of age-dependent reproduction (or other traits) requires disentanglement of within-individual change (improvement, senescence) and between-individual change (selective [dis]appearance). We introduce a new statistical model, which allows patterns of variance and covariance to differ between levels of aggregation. Our approach is simpler than alternative methods and can quantify the relative contribution of within and between-individual changes within one framework. We illustrate our model using data on a long-lived bird species, the Oystercatcher (*Haematopus ostralegus*). We show that for different reproductive traits (timing of breeding and egg size) either within-individual improvement or selective appearance can result in a positive association between age and reproductive traits at the population level. Potential applications of our methodology are manifold, since within and between-individual patterns are likely to differ in many biological situations.

Introduction

Phenotypic traits can change due to within-individual changes (phenotypic plasticity) and due to between-individual changes, as selection might favor some individuals over others. When quantifying how population values of phenotypic traits change over time, or differ between groups of individuals, it is therefore important to realize that both within and between-individual processes might be the underlying causal mechanism. The aim of this paper is to introduce a novel statistical method that allows the disentanglement of both the within and between-individual component of phenotypic change in a population. Our paper will focus on differences in phenotypic traits between age-classes, but in principle applies to many biological problems where within and between-individual patterns might differ.

Reproductive performance of iteroparous animals is generally positively associated with age, at least over the first part of animals' lives (Clutton-Brock 1988; Forslund & Pärt 1995). Many studies quantified patterns of age-dependent reproduction and survival, because they allow the construction of age-structured population models. Understanding how mutations and phenotypic changes in age-specific schemes affect population dynamics and individual fitness is crucial for the study of the evolution of ageing, age at maturity, the optimization of reproductive effort during a lifetime and conservation issues. The relationship between age and reproduction is thus at the core of population demography (Caswell 2001), life history evolution (Stearns 1992), and population genetics (Charlesworth 1980).

Evolutionary questions in age-structured populations specifically address patterns of within-individual changes in reproduction during a lifetime (Fig. 3.1A). However, many studies report an association between age and reproduction at the population level (cross-sectional analysis), which does not necessarily imply within-individual change. Correlations at the population level might also result from progressive changes in the phenotypic composition of higher age-classes, either due to the selective appearance or disappearance of certain phenotypes. Selective appearance of good reproducers might occur when individuals queue for high quality breeding position; in such queuing systems a late onset of the reproductive career will be associated with producing many offspring annually (e.g. Ens *et al.* 1995; East & Hofer 2000; Fig. 3.1B). In contrast, selective appearance of poor reproducers might occur when low quality individuals are competitively inferior and start reproducing later in life (Fig. 3.1C). Selective disappearance can also take two forms: (i) when individuals mainly vary in their resource acquisition, poor reproducers might also live shorter and progressively disappear (Fig. 3.1D), conversely (ii) when individuals mainly vary in their resource allocation, reproducing many offspring might be at a cost of a shorter lifespan and good reproducers might progressively disappear (cf. van Noordwijk & de Jong 1986; Fig. 3.1E). Such hypotheses describing patterns of life-history covariation have also been referred to as selection hypothesis (Nol & Smith 1987), bad quality hypothesis (Curio 1983) or delayed breeding hypothesis (Hamann & Cooke 1987). All these effects result in correlations between age and reproduction in cross-sectional analyses, without reflecting within-individual

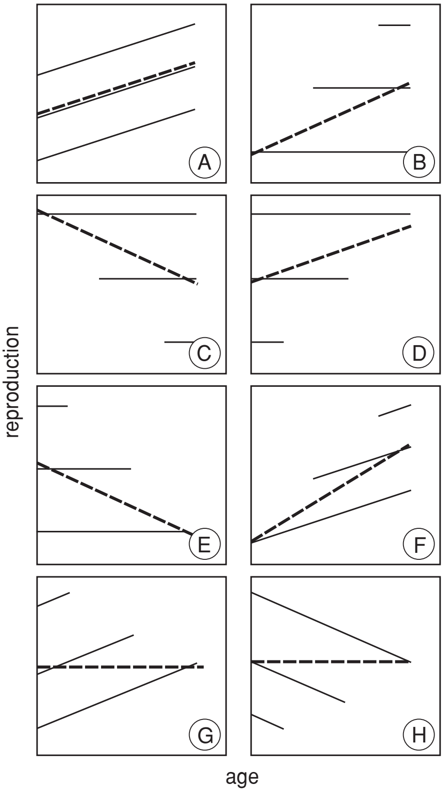


Figure 3.1 Relationship between age and reproduction in a hypothetical population of three individuals (solid lines) of different phenotypic quality, compared with ordinary regression lines (dashed) fitted through all points of all individuals. Possible scenarios are (A) within-individual improvement, (B) selective appearance of good reproducers, (C) selective appearance of poor reproducers, (D) selective disappearance of poor reproducers, (E) selective disappearance of good reproducers, (F) within-individual improvement and selective appearance of good reproducers, (G) within-individual improvement and selective disappearance of good reproducers, and (H) senescence and selective disappearance of poor reproducers.

changes. Within-individual changes can be caused by factors intrinsic to the individual, such as increasing experience (Curio 1983), restraint as part of reproductive tactics (Pianka & Parker 1975) and physiological deterioration (Medawar 1952) or due to extrinsic factors such as changes in habitat quality. Within and between-individual changes are not mutually exclusive. Often within and between-individual changes will affect the relationship between age and reproductive performance at the population level in the same direction (Fig. 3.1F). However, within and between-individual change might work in opposite directions and between-individual change can mask patterns of improvement (Fig. 3.1G) or senescence at the population level (Fig. 3.1H).

The difference between within and between-individual effects on age-dependent reproduction is well recognized in the literature, and when an association between age and reproduction at the population level is found, additional analyses are often performed to test whether within or between-individual changes occurred. Separate longitudinal analyses are used to investigate whether reproductive performance changes within individuals (e.g. Rattiste 2004). Additionally, any selective (dis)appearance is investigated by relating reproductive performance to either longevity (survival) or age at first reproduction (e.g. Berube *et al.* 1999). However, such post-hoc analyses of a correlation between age and reproduction does not allow the quantification of the relative contribution of within and between-individual changes, while this has been named as one of the major challenges in the study of age-dependent reproduction (Forslund & Pärt 1995).

In this paper we introduce and illustrate a new statistical model, that we implement using a random effects approach, to simultaneously test and compare between-individual and within-individual age-effects within one framework. The idea to analyze age-dependent processes with random effects models is in itself not new (e.g. Reid *et al.* 2003; Krüger 2005). Random effects at the individual level can account for variation in reproductive performance between individuals, and in survival analyses this approach is generally known as frailty models (Vaupel *et al.* 1979). However, the selective appearance and disappearance hypotheses suggest that individuals not only vary in their phenotypic quality, but that individual quality covaries with the probability an individual will appear in or disappear from the (breeding) population that is sampled. To our knowledge, Cam *et al.* (2002) were the first to analyze age-dependent reproduction, while specifically modeling an association between an individuals reproductive performance and its survival propensity. They used a multivariate approach to explicitly model a co-variance between reproduction and survival and thereby were able to account for selective disappearance (but not for selective appearance). The multivariate approach they used is quite complex and poses some technical challenges, because survival and reproductive variables generally have different distributions (see also Wintrebert *et al.* 2005 for a time to failure approach). In this study we introduce a novel univariate approach that is much simpler, and able to test for selective appearance as well as disappearance. Moreover, the method we introduce explicitly quantifies the relative effects of within-individual change, selective appearance and disappearance on age-dependent reproduction (or other traits) in one model.

Random effects models

The statistical model that we introduce below is a specific parameterization of a random effects model. Specific applications of such models are also known as mixed models, generalized linear mixed models, hierarchical linear mixed models, or multilevel models. In most biological studies observations are often collected on individuals within the same population or year, or are collected repeatedly on the same individual. Random effects models not only account for heterogeneity between such sources of aggregation, but also allow the partitioning of total variation among these sources (e.g. Goldstein 1995; Verbeke & Molenberghs 1997; Snijders & Bosker 1999; McCulloch & Searle 2000). For example, by modeling individuals and their longitudinal measurements as nested random effects, total variance can be split into a between-individual (σ_u^2) and a within-individual (σ_e^2; residual variance) component. Consequently, this method specifically accounts for the fact that measurements from the same individual might be intercorrelated (i.e. non-independent).

More important for the present purpose is that random effect models also allow patterns of covariance to differ between multiple levels of aggregation, because different hypotheses of age-dependent reproduction deal with co-variation at different levels. Improvement and senescence hypotheses assume a co-variation between age and reproductive performance within individuals. In contrast, selective (dis)appearance hypotheses assume that there is a between-individual covariance between the moment an individual enters (or leaves) the reproductive population and its individual quality. More specifically, the selective appearance hypothesis assumes a correlation between age of first reproduction (α) and individual quality (Fig 3.1B,C), while the selective disappearance hypothesis assumes a correlation between age of last reproduction (ω) and individual quality (Fig 3.1D,E). Note that covariations between age of first or last reproduction and individual quality can potentially be either positive or negative, depending on the underlying mechanisms (see introduction). Individual quality can be measured as an estimate of reproductive performance (r) over a lifetime.

We formalized our approach by the following random effects regression model:

$$r_{ij} = \beta_0 + \beta_W * age_{ij} + \beta_S * \alpha_i + u_{0i} + e_{0ij} \qquad (1)$$

This is a two-level random intercept model, with individual as the highest level *i* and the annual measurement of reproductive performance (r) as the lowest level *j*. The random intercept term u_{0i} and residual error term e_{0ij} are assumed to be drawn from a Gaussian distribution with mean 0 and variance σ_u^2 and σ_e^2, respectively. Subscripts refer to the level at which parameters are variable; age is variable within and between individuals; age of first reproduction (α) only varies between individuals. This model specifically tests for within-individual change ($\beta_W * age_{ij}$) in the presence of a selective appearance effect ($\beta_S * \alpha_i$) and vice versa. It is crucial to test for an effect of selective appearance in the presence of a within-individual effect, because when individuals improve with age, individuals that start reproducing at a later age are expected to do better because they are older. As such the effect of age of first reproduction (β_S) estimates the additional effect of selective appearance, given the estimated within-individual change with age. The independent effect of between-individual differences in age of first reproduction on reproductive performance can be obtained by adding β_W and β_S, giving β_B. Alternatively, the regression equation (1) can also be re-written to the equivalent:

$$r_{ij} = \beta_0 + \beta_W * (age-\alpha)_{ij} + \beta_B * \alpha_i + u_{0i} + e_{0ij} \qquad (2)$$

Using within-group deviation scores (age-α) we obtain a model in which β_B and β_W can be quantified and tested directly (sensu within-group centering; Snijders & Bosker 1999).

Model 1 and 2 investigate selective appearance; effects of selective disappearance can be incorporated in a similar way by adding ω_i (age of last reproduction) to the model. Furthermore, non-linear effects of age can be investigated by using various other non-linear functions of age (or of age of first or last reproduction) in the model, although not all such covariates might be orthogonal. Our approach is robust to intermittent breeding or missing values, as long as they occur at a random age. However, uncertainty about the exact age of first reproduction or last reproduction (e.g. because of dispersal) will reduce the power to correctly identify selective between-individual processes. Although models 1 and 2 are not specific with respect to sex, separate age effects of both sexes can be incorporated by replacing the individual level by a separate female and male level (cross-classified structure).

Two examples on Oystercatchers

To illustrate the use of models 1 and 2 we analyzed data from a 21-year study on Oystercatchers (*Haematopus ostralegus*), a long-lived bird species with large variation in age of first reproduction (3-10 years). See van de Pol *et al*. (2006) for general information on the field work protocol. We analyzed the effect of age on two reproductive parameters: the annual timing of reproduction (laying date) and egg volume (using clutch averages). Both of these parameters are associated with annual reproductive output and strongly inter-correlated within individuals (Heg 1999). Experiments indicated that early laying is causally related to higher reproductive success (Heg 1999), while producing large eggs probably is not causally related to reproductive output, but is associated with another measure of phenotypic quality of individuals (territory quality; van de Pol *et al*. 2006).

A group of 69 individuals was followed, with age varying from 3-19 years. We selected these individuals out of all known breeders because their age and age of first reproduction were known exactly, as they were ringed as juveniles. We succeeded in measuring the reproductive performance of all individuals in most years (N=283 reproductive attempts, on average 4.1 yearly attempts per individual, range 1-11). There were no indications of sex-differences in age effects (results not shown), and therefore sexes were pooled in the analyses. We present analyses of a model for within-individual improvement with age and selective appearance. Analyses of non-linear effects of age and effects of selective disappearance (ω_i) are not presented as these were far from significant. Values were standardized for annual variation in laying date and egg volume by subtracting annual population means from each value. Analyses were performed in MLwiN 2.0 using the restricted iterative generalized least squares algorithm (Rasbash *et al*. 2004).

Laying date was negatively associated with age and egg volume was positively associated with age at the population level, as determined by ordinary cross-sectional regression (β_P; Fig. 3.2A & 3.2D; Table 3.1). At first glance, this result was consistent with expectation as both laying early and producing large eggs are generally thought to increase reproductive output (*i.e.* older individuals did better). However, when we pooled individuals of similar age of first reproduction and plotted longitudinal patterns, this suggested that different mechanisms might be at work (note that the age grouping in Fig. 3.2 is for graphical purposes only ungrouped integer age data were entered in the analysis). Laying date advanced with age within individuals, independent of age of first reproduction (Fig. 3.2B). In contrast, egg volume was independent of age within individuals, but individuals that started breeding late in life (high age of first reproduction) produced larger eggs than individuals that started breeding early in life (low age of first reproduction; Fig. 3.2E).

To quantify the relative effects of within-individual improvement and selective appearance in one model we applied models 1 and 2 to this dataset. As expected, laying date significantly improved within individuals; individuals advanced laying 0.74 days every year they aged (β_W; Fig. 3.2C; Table 3.1). Individuals laid 0.56 days earlier (β_B; Fig. 3.2C; Table 3.1) for each year they delayed age of first reproduction. Although the latter effect bordered on significance (P=0.075), it is important to note the similarity in slope with the within-individual effect (Fig. 3.2C). The difference in slope between the within and between-individual effect in Fig. 3.2C is exactly the effect of selective appearance ($\beta_S=\beta_B-\beta_W$), which was very small for laying date. Thus individuals that started breeding later in life laid earlier because they were older; there was no additional selective appearance of early laying individuals (β_S; Table 3.1). Between-individual differences in laying dates explained 25.4% of total variance (calculated by $\sigma_u^2/[\sigma_u^2 + \sigma_e^2]$ from a model without covariates), indicating laying dates were strongly inter-correlated within individuals. The graphical representation of the final model for laying date (Fig. 3.2C) fit the plotted longitudinal patterns well (Fig. 3.2B). In the case of laying date the selective appearance hypothesis was not supported but within-individual improvement did occur, consistent with the scenario depicted in Fig. 3.1A. As a consequence, a reduced model without an effect of age of first reproduction (the standard random effects approach) would have resulted in the same results (Table 3.1).

Individuals did not increase the size of their eggs during their life (β_W; Fig. 3.2F; Table 3.1). However, individuals laid 0.51 cm^3 larger eggs (1.2%) for each year that they delayed the start of reproduction (β_B; Fig. 3.2C; Table 3.1). Individuals that delayed their first breeding attempt did not lay larger eggs because they were older; but because of selective appearance of individuals that laid large eggs (β_S; Table 3.1). This can be seen by the large difference in slope of the within and between-individual effects (Fig. 3.2C). Between-individual differences explained 45.6% of total variance, indicating egg volume was highly inter-correlated within individuals. A graphical representation of the final model for egg volume (Fig. 3.2F) fitted the plotted longitudinal patterns well (Fig. 3.2E). In the case of egg size there was strong evidence in favor of the selective appearance of good reproducers hypothesis, but no evidence for within-individual change (*cf*. Fig. 3.1B). A reduced model without an effect of age of first reproduction (the standard random effects approach) did not describe the data very well, because it produced an estimate of an age effect (β=0.11) that neither described the within-individual (β_W) nor the between-individual age-effect very well (β_B; Table 3.1). This is because the random effect at the individual level can only account for heterogeneity in phenotypic quality between

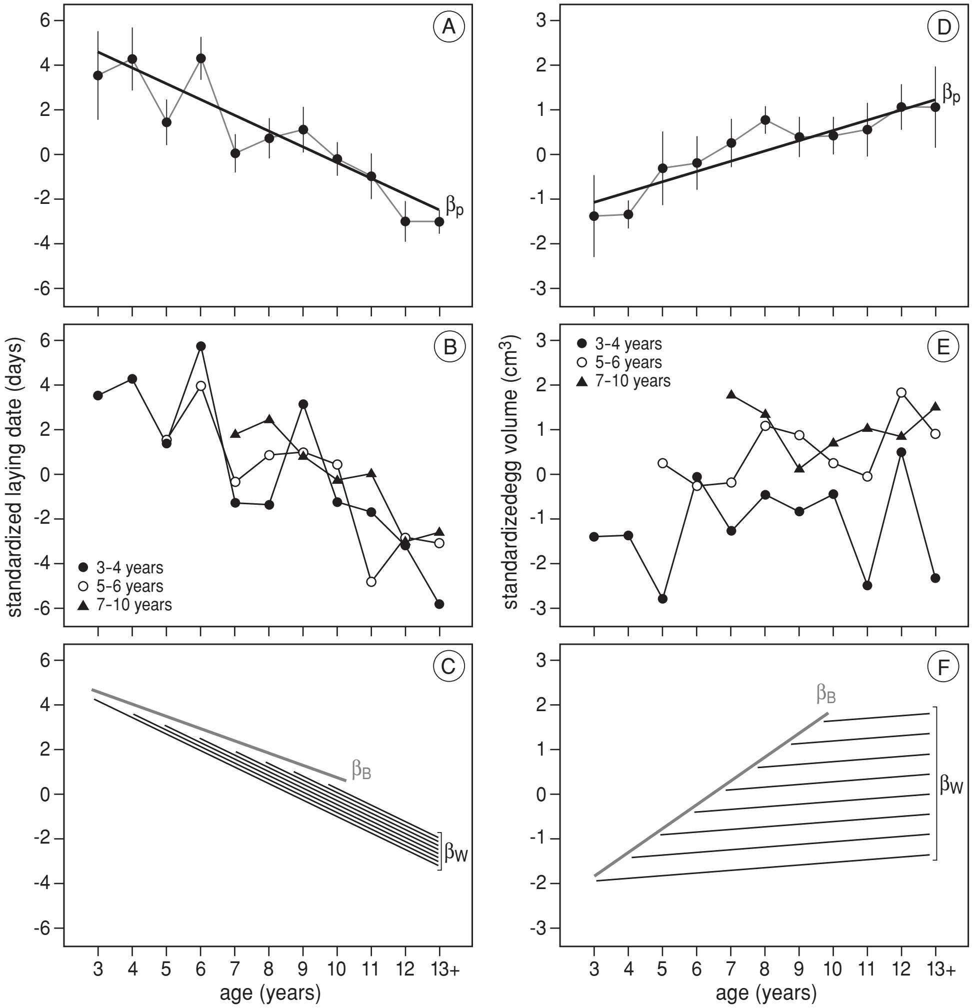


Figure 3.2 The relationship between age and laying date (left panels) and age and egg volume (right panels) in Oystercatchers. For both parameters a significant relationship with age was observed at the population level (A,D). Longitudinal patterns of individuals differing in age of first reproduction were similar to the cross-sectional pattern for laying date (B), but different for egg volume (E). In (B,E) individuals were grouped by age of first reproduction for graphical reasons. The models that best fitted the data (see Table 3.1) are depicted in (C,F). Each solid line gives the average within-individual slope (β_W) of individuals grouped by different age of first reproduction (3-10 year); the dashed line depicts the between-individual slope (β_W; Table 3.1). Note that age-classes 13 years and older were grouped for graphical reasons, because of low sample sizes (ungrouped data was used in analyses).

Table 3.1 Results of the effects of age on standardized laying date and standardized egg volume (deviations from annual mean). The within-individual slope (β_W), between individual slope (β_B), the difference in slope between β_B and β_W (β_S), and the slope at the population level (β_P) are interpreted in the text. The reduced model with only age as a covariate is equivalent to the more standard random effect models used in several other studies.

		Standardized laying date (days)				Standardized egg volume (cm^3)			
Parameter		B	s.e.(B)	$\chi^2_{df=1}$	P	B	s.e.(B)	$\chi^2_{df=1}$	P
Model 1									
intercept	(β_0)	5.9	2.1			-3.44	1.06		
age$_{ij}$	(β_w)	-0.74	0.14	29.9	<0.001	0.06	0.06	0.89	0.34
α_i	(β_S)	0.18	0.35	0.29	0.59	0.45	0.17	7.5	0.006
individual variance	(σ_u^2)	39.8	14.7			3.86	1.06		
residual variance	(σ_e^2)	106.3	13.1			5.58	0.67		
Model 2									
intercept	(β_0)	5.9	2.1			-3.44	1.06		
(age-α)$_{ij}$	(β_W)	-0.74	0.14	29.9	<0.001	0.06	0.06	0.89	0.34
α_i	(β_B)	-0.56	0.31	3.17	0.075	0.51	0.16	11.3	<0.0001
Reduced model									
intercept	(β_0)	6.7	1.3			-0.54	0.63		
age$_{ij}$		-0.70	0.15	25.6	<0.001	0.11	0.06	3.5	0.063
individual variance	(σ_u^2)	43.0	14.8			4.34	1.15		
residual variance	(σ_e^2)	107.4	13.1			5.56	0.678		
Ordinary regression model									
intercept		6.8	1.3			-1.78	0.62		
age$_{ij}$	(β_P)	-0.71	0.12	33.1	<0.001	0.23	0.06	10.0	0.002

individuals, and not for a covariation between age of first reproduction and phenotypic quality. This comparison shows that our method systematically accounts for the effects of selective appearance, which contrasts with previously used random effect approaches.

The slopes at the population level (β_P; Fig. 3.2A & 3.2C; Table 3.1), as obtained using ordinary regression (or the standard random effects approach) are weighted averages of the within and between-individual slopes (β_W and β_B; Fig 3.2C & 3.2F). The contributions of β_W and β_B (or β_S) to β_P depends on several factors. Most importantly, the ratio between the number of individuals and the number of measurements per individual, and the variance within and between individuals. The population slope of laying date on age was quite similar to the within-individual effect; however the population slope of egg volume was much lower than the between-individual effect and much higher than the within-individual effect. This difference is probably caused by the fact that individuals were more consistent in egg size than in laying date; consequently effects of selective appearance (β_S) on egg size have a larger impact on correlations at the population level.

Further extensions

Models 1 and 2 are very simple and allow the testing of most hypotheses of interest, but some simple extensions can be incorporated to further enhance our understanding of underlying processes. For example, some individuals might improve reproductive performance more strongly during their life than others. Random slope models allow slopes of covariates (such as age) to vary between individuals and estimate the total variation in these slopes (e.g. Rasbash *et al.* 2004). In our example, the advancement of laying date with age within-individuals did not vary much between individuals in our data ($\sigma_{\text{slopes}}^2=1.8\pm1.6$), especially compared to the considerable variation in intercepts between individuals ($\sigma_u^2=39.8\pm14.7$). This suggests most oystercatchers advanced laying date at the same rate during their life, which is an interesting result because little is known about individual variation in the improvement of reproductive performance with age.

Several authors have argued reproductive performance does not necessarily increase with age, but correlated increases in breeding or mate experience might be causally responsible for age-dependent reproduction (e.g. Fowler 1995; Forslund & Pärt 1995). By entering the years of breeding experience or pair bond duration to the model, a multiple regression approach can be used to statistically disentangle these inter-correlated parameters. Potentially, only good reproducers are able to become very experienced breeders or pairs. Such effects of selective disappearance can be further investigated by entering the maximum breeding experience or pair bond duration of each individual as a covariate to the model.

Conclusion

The statistical model we introduced provides a simple but powerful tool to disentangle within and between-individual change. The differences with more often used random effects models with age as the only covariate is deceptively small, but nonetheless crucial. Our example on Oystercatchers illustrates that using cross-sectional comparisons in the study of age-dependent reproduction can sometimes be misleading (as illustrated by the analysis on egg size) and that a random effects approach in combination with the parameterization we suggested yields novel insights in the underlying mechanisms.

To our knowledge this is the first study to show that selective appearance of certain phenotypes (individuals that lay large eggs) generates a correlation at the population level between age and a measure of reproductive performance, in the absence of within-individual changes. In contrast, laying date improved with age primarily due to within individual changes. Thus the mechanisms underlying patterns of age-dependent reproduction can vary between different measures of reproductive performance within the same population. Within individual changes in laying date may result from foraging efficiency improving with age and experience (Goss-Custard & Le V.dit Durell 1987), which may affect their condition and timing of breeding (Heg 1999). Conversely, egg size might depend on adult body size (e.g. Nol *et al.* 1984). When large birds start reproducing late in life, for example because they were queuing for high quality territories (Ens *et al.* 1995), the selective appearance of individuals that lay large eggs could be a by-product of this settlement behavior.

It seems likely that the degree to which effects of age on reproductive performance at the population level might be caused by within or between-individual changes is also related to species life-history. For example, for short-lived species, which usually have low variation in age of first reproduction, the reported patterns of age-dependent reproduction are probably little affected by selective appearance of individuals in the population. However, the effects of selective disappearance may potentially be important in both short and long-lived species, because both types of species can have substantial variation in age of last reproduction. Our approach will result in the correct interpretation, independent of the life-history of the species or the various underlying mechanism (as described in Fig. 3.1). We hope our study will further encourage other researchers to compare the effects of within and between-individual change on age-dependent reproduction in a variety of species, enabling a comparative study between different life-history strategies.

We see many other potential applications of the statistical model we present in this paper, because selective (dis)appearance of certain phenotypes is a common phenomenon that can result from temporal as well as spatial processes. Progressive selective changes in phenotypic population composition might be important in the study of any other behavior or trait that is expressed differentially over time. Growth may be a particularly suitable trait, because selective disappearance through death or dispersal typically depends on growth. Similarly, when studying the effects of environmental changes on long-term changes in phenotypic traits, equivalent models can be used to disentangle change as a result of phenotypic plasticity (within-individuals) from selection against certain phenotypes (between-individuals). Alternatively, selective changes in phenotypic composition as a result of spatial processes might occur when the probability of entering or leaving a group of individuals that is measured, is associated with the phenotypic quality of individuals. For example, when examining performance of individuals on leks, migration stop-over sites, or foraging sites, selective (dis)appearance due to movement of individuals in and out of the sampled population is the norm and might strongly affect estimates of time trends of phenotypic traits.

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Box A: Extra-pair copulations during the pair bond and their role in mate change.

Although many species are socially monogamous (especially in birds) their sexual behaviour can be quite promiscuous. Seeking copulations with other partners than your social partner is thought to be an important way of increasing ones individual's fitness. Although extra-pair copulations (EPCs) are quite common in the socially monogamous Oystercatcher *Haematopus ostralegus*, extra-pair fertilizations are very rare (Heg *et al*. 1993). Several lines of evidence suggest that in Oystercatchers extra-pair copulations mainly serve as a social signal in the process of pair-bonding and establishment of social relationships. For example, in several cases of divorce, the switching from partners was preceded by extra-pair copulations with the future partner. In addition, in rare polygynous breeding attempts copulations were also observed between the two females in these ménage a trois (Heg & Van Treuren 1998). Therefore, we think that the EPC behaviour in Oystercatchers might function as an indicator of the strength of social relationships, or conversely of the probability a pair will break up.

In a previous study, Heg *et al*. (1993) showed that newly formed pairs more often engaged in EPCs than already established pairs. However, Heg and colleagues did not investigate whether established pairs had less EPC because pair-members become more faithful to their social partner during the pair bond or whether only the faithful pairs stayed together. In this study we specifically investigate whether EPC frequency is associated with pair bond duration and how patterns vary within and between pairs. As such this study provides an additional example on how to use the technique described in Chapter 3 to a case in which selective disappearance might play an important role.

Methods

A male and a female that together defended a breeding territory and nested were considered social partners; most pairs were socially monogamous within a season. Oystercatchers usually re-mate with the same social partner every year, unless one of the partners dies (5% annual mortality) or the pair divorces (8% annually). The duration of the pair bond was counted as the number of breeding seasons a pair nested together. Cases of polygyny were omitted from analyses (1% annually).

We observed the copulation behaviour of both sexes in breeding pairs from 1984-2004. Oystercatchers have high copulation frequency (±20 times a day), with most copulations occurring in the two months before egg-laying. Following Heg *et al.* (1993), copulations with the nesting partner were defined as within-pair copulations (WPC); copulations with a bird of the opposite sex other than the nesting partner were defined as EPCs. Most EPC were with other breeders, only a small part of the EPCs were with non-breeders. Oystercatchers do not seem to be very secretive about their copulation behaviour (WPC as well as EPC). The excellent visibility and accessibility of the study area facilitated the collection of a large set of observations of the same individuals over many years.

Observations were gathered (partly) in a non-systematic way; consequently the recording of our observations may be biased. As EPC are relatively rare events, we think most observed EPC were actually recorded; however, we think it is quite likely that a much more common behaviour as WPC might not always have been systematically recorded. By comparing our dataset with a smaller systematic study of EPC frequencies in this population, we can estimate how strong this bias was. In our dataset 13.7% of all observed copulations by female breeders and 16.9% of all observed copulations by male breeders were extra-pair, which was much higher than estimated by Heg and colleagues (5.1% for females and 7.0% for males). Thus, in our dataset there apparently was a quite strong reporting bias for EPC (although bias was about equal for males and females); observed EPC frequencies can therefore only be used as an index of the real EPC frequency. Most importantly, in this study we are primarily interested in comparing EPC indices in relation to pair bond duration; we have no reason to assume that the reporting bias towards EPC was different with respect to how long a pair had been together.

Analyses were performed with the statistical method described in Chapter 3, which specifically enables the disentanglement of within and between-pair effects. Our dataset consisted of 253 female breeders, who were observed copulating for 7298 times of which 1000 copulations were EPC. Each female was observed copulating at least once in on average 3.7 years (range 1-14) and during each year on average 8.1 copulations per female were observed (range 1-200). In addition, our dataset consisted of 246 male breeders, which were observed copulating for 7740 times of which 1308 copulations were EPC. Each male was observed copulating at least once in on average 3.5 years (range 1-14) and during each year on average 8.4 copulations per male were observed (range 1-198). Year and pair identity were modelled as cross-classified random effects.

Results

Longitudinal patterns of both males and females suggested that pairs that stayed together for many years had lower EPC indices than pairs that stayed together only shortly (Fig. Box A1). Longitudinal patterns also suggested that the EPC behaviour changed systematically during the pair bond. EPC indices were high during the first few years of the pair bond, but quickly declined during the second and third year of the pair bond, and there was a suggestion that EPC behaviour increased again when pairs were together for very long.

Analyses of the ungrouped data using the statistical model described in Chapter 3 confirmed that both within pair changes as well as between pair differences were important. The estimates of the within-pair changes (β_W) were highly significant and the estimate of selective disappearance (β_S) was also significant for females and bordered significance for males (P=0.10; Table Box A1). The best fitted regression models are shown in the two lowest panels.

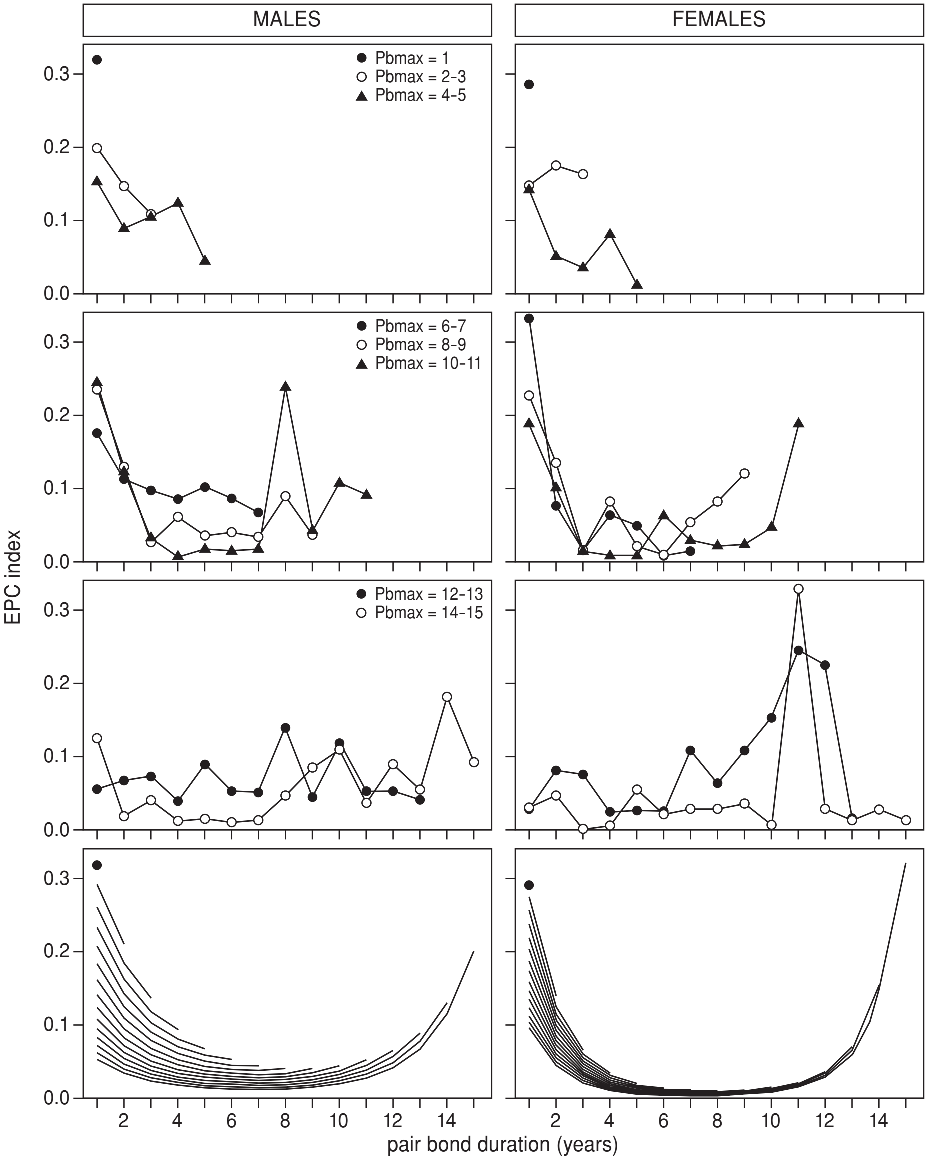

Figure Box A1 Index of extra-pair copulations (EPC) during the pair bond for pairs that vary in how long they stayed together (PbMax). The left panel shows the EPC patterns for males, the right panel for females. Note that individuals were grouped for graphical reasons, and that raw ungrouped data was used in the analyses. The bottom two graphs show the best fitted regression models (see Table Box A1); individuals that stayed together for only one year with the same partner are represented by a solid dot.

Table Box A1 The effects of pair-bond duration on the extra-pair copulation (EPC) index of males (left panel) and females (right panel). The linear and quadratic effects of pair bond duration (pb and pb^2) estimate the changes within-pairs during the pair bond; while the effect of the maximum pair bond duration (PbMax) estimates whether pairs that stayed together for short or for long differed in their overall level of extra-pair copulation index. Analyses were done using a binomial error term and a logit link function, with the number of observations per individual per year as the denominator. Observations were nested within pairs as well as within years (cross-classified). Subscript refer to the level at which covariates were variable (between pairs *i*, or between observations *j*).

Parameter		EPC index males				EPC index females			
		B	s.e.(B)	$\chi^2_{df=1}$	P	B	s.e.(B)	$\chi^2_{df=1}$	P
Model 1									
intercept	(β_0)	-2.472	0.378			-3.55	0.40		
Pb_{ij}	(β_W)	-0.572	0.095	36.2	<0.001	-1.12	0.11	100.8	<0.001
Pb^2_{ij}	(β_W)	0.042	0.007	46.4	<0.001	0.076	0.008	99.8	<0.001
$PbMax_i$	(β_S)	-0.153	0.053	8.31	0.004	-0.099	0.060	2.63	0.10
Pair variance	(σ_u^2)	4.78	0.78			7.63	1.42		
Year variance	(σ_v^2)	0.27	0.17			1.09	0.66		
Residual variance	(σ_e^2)	1				1			
Reduced model									
Intercept		-2.476	0.216			-3.43	0.34		
Pb_{ij}		-0.653	0.087	56.8	<0.001	-1.15	0.11	100.8	<0.001
Pb^2_{ij}		0.056	0.007	67.9	<0.001	0.086	0.009	99.8	<0.001
Pair variance	(σ_u^2)	5.16	0.82			7.73	1.45		
Year variance	(σ_v^2)	0.27	0.17			0.97	0.53		
Residual variance	(σ_e^2)	1				1			

Conclusions

Pairs with high levels of EPC were less likely to stay together for many years than pairs with low levels of EPC. As such EPC behaviour of both the male and the female was a good predictor of whether a pair would be together the next year or not (either due to mortality or divorce). During the pair bond, pairs reduced their extra-pair copulation behaviour substantially, which suggests that both males and females became less interested in other partners during their relationship. A decrease in EPC behaviour during the pair bond coincides with a strong increase in reproductive performance during the pair bond (see chapter 4). Similarly, the suggestion that EPCs increase at high pair bond duration also coincides with a decrease in reproductive performance at high pair bond duration. Because pair bond duration, EPC behaviour and reproductive success are all strongly inter-correlated, at this moment we cannot determine yet the underlying causal structure: Do pairs that are more faithful achieve a higher reproductive success? Or do pairs with a high reproductive success remain more faithful? Or is faithfulness and high reproductive success a result of mate familiarity?

Chapter 4

Experimental evidence for a causal effect of pair bond duration on reproductive performance in Oystercatchers (*Haematopus ostralegus*)

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Abstract

Many studies have suggested that reproductive performance improves during the pair-bond. An important role for the pair-bond sharply contrasts to the general approach to study reproductive performance as an individual trait and it might explain why individuals re-mate with the same partner in many species. However, discussion exists about whether the association between reproductive performance and pair-bond duration reflects a causal relationship. Reproductive performance often also depends on the age or breeding experience of parents, which all co-vary with pair-bond duration. Furthermore, it is usually unclear whether pairs improve during their pair-bond or that a positive association is caused by high-quality pairs staying together for longer. A much needed experimental approach is lacking so far.

We investigated the effect of pair-bond duration on reproductive performance in a long-lived monogamous bird species based on natural as well as experimental variation. The duration of oystercatcher (*Haematopus ostralegus*) pair-bonds, which were followed for 21-years, strongly affected reproductive output, even after controlling for effects of age and breeding experience. Pairs improved during their pair-bond and there were no indications of selective disappearance of low-quality pairs; however, extremely old pairs performed very badly. Experimental removal of one partner showed that the cost of divorce depended on the pair-bond duration with the old partner. In addition, after re-mating, the newly formed pairs strongly improved again, independent of the age and breeding experience of the re-mated pair members. As such, this study provides the first experimental evidence of a causal effect of pair-bond duration on reproductive performance.

Introduction

Reproductive performance of iteroparous animals usually changes systematically during a lifetime (Clutton-Brock 1988; Newton 1989). At least 30 studies, mainly on socially monogamous bird species, have suggested changes in reproductive performance during a lifetime are (partly) caused by pairs improving during their pair bond (reviewed by Fowler 1995). Such an effect is important for our understanding of the evolution of long-term monogamy, as it might explain why in many species individuals re-mate with the same partner every year. Furthermore, it suggests pair-members are more able (or willing) to cooperate during their pair bond. Understanding the mechanism behind improved cooperation might shed light on the evolution of cooperation in repeated social interactions. An important role for the pair bond sharply contrasts to the general approach to study reproductive performance as an individual trait.

Several authors have noted that a correlation between pair bond duration and reproductive performance at the population level does not necessarily imply a causal relationship (e.g. Ens *et al.* 1996; Forslund and Pärt 1995). First of all, reproduction is also often correlated with the age or breeding experience of males and females. Pair-bond duration usually strongly co-varies with age and breeding experience. Therefore, a statistical effect of pair-bond duration on reproductive performance might actually reflect a correlated causal change in one of these other age-related parameters. Several studies have used multiple regression techniques to distinguish between effects of age and pair-bond duration (Fowler 1995); only two studies simultaneously investigated all age-related parameters of both sexes (Bradley *et al.* 1990; Pyle *et al.* 2001). These studies suggest that even after statistically correcting for age effects, pair-bond duration remained important. However, the power of a statistical approach to accurately disentangle strongly inter-correlated effects is often limited. Reliable interpretation of the separate effect of pair-bond duration in a multiple regression approach can be strongly confounded by even low levels of multi-collinearity with age and breeding experience; very large sample sizes are required to overcome this problem (Graham 2003).

A second type of alternative explanations suggests that a correlation at the population level between pair-bond duration and reproductive performance might reflect progressive changes in the phenotypic composition of a population. For example, low quality pairs might divorce more often (or die younger), resulting in pairs with long pair-bonds being of high phenotypic quality. Such selective divorce or widowing results in a correlation at the population level, without any improvement in reproductive performance within pairs.

Because few studies investigated all alternative explanations (but see Bradley *et al.* 1990; Pyle *et al.* 2001), some authors have questioned the overall evidence for an improvement of reproductive performance during the pair-bond (discussed by Cézilly and Nager 1995; Pärt and Forslund 1995). They argued experimental control is crucial, because a statistical approach cannot correct for possible important unmeasured parameters that are correlated with pair-bond duration (e.g. individual quality, breeding site fidelity).

In this study, we investigated whether pairs of the long-lived monogamous oystercatcher (*Haematopus ostralegus*) improved reproductive performance during their pair-bond, using both an observational as well as an experimental approach. We first investigated the effect of pair-bond duration on reproductive performance in a large group of pairs, which were followed over up to 21 years. We statistically controlled for confounding effects of other age-related parameters of the male and female parents. In addition, we investigated whether a correlation between pair-bond duration and reproductive performance was caused by selective divorce (or widowing) of low quality pairs. Subsequently, we experimentally tested whether pair-bond duration affects reproductive performance by removing birds, forcing the remaining partner to re-mate. We investigated whether the reproductive cost of divorce depended on the pair-bond duration with the removed partner. In addition, we investigated whether the newly formed pairs improved their reproductive performance in the four years following re-mating.

Material and methods

From 1983 until 2003, we followed a population of ca. 100 breeding pairs on Schiermonnikoog (32°29' N 6°14' W), an island in the Dutch Wadden Sea. All breeders and their fledglings were colour banded, as well as a large part of the non-breeders. Every year we followed the breeding performance of all pairs (protocol see van de Pol *et al.* 2006). Oystercatchers breed on the salt marsh and feed on the adjacent inter-tidal mud flats. Following earlier studies, we designated territories with adjacent feeding and nesting areas as high-quality territories and territories with spatially separated feeding and nesting areas as low-quality territories (Ens *et al.* 1992). Pairs with high quality territories ('residents') consistently produce two to three times more fledglings each year than pairs in low quality territories ('leapfrogs'). Both male and female oystercatchers contribute about equally to the parental care of their semi-precocial offspring. Birds were sexed using DNA analysis (Heg *et al.* 2000a), biometric measurements (Zwarts *et al.* 1996), and observations of copulations (Heg *et al.* 1993).

Pair-bond duration, age and breeding experience

Oystercatchers are long-lived, socially and genetically monogamous, and have high breeding site fidelity (Heg *et al.* 2003; Heg *et al.* 2000b; Heg *et al.* 1993). Age at first reproduction is extremely variable (range 3-11 years); established breeders display some intermittent breeding (Bruinzeel 2004). Re-sighting rate of breeders in this population is virtually one.

Analyses were restricted to birds with exact known pair-bond duration, i.e. pairs that were ringed at the start of the study were excluded. Only a part of the breeding population was of known age (16%), because only individuals ringed as fledgling or juveniles could be exactly aged on morphological characteristics (Prater *et al.* 1987). The age and breeding experience of known-aged individuals were highly inter-correlated within both sexes (male: r=0.83 female: r=0.82). However, due to frequent divorce

(8% annually) and widowing (7% mortality annually) correlations between pair-bond duration and age (or breeding experience) of males or females were less strong (r=0.4-0.5). Because collinearity between age and breeding experience were extremely high, we decided to include only effects of male and female breeding experience and pair-bond duration in the analyses. We preferred to include effects of breeding experience over age effects because breeding experience could also be estimated for individuals of unknown age. Many breeders were already banded when they were a non-breeder, which allowed exact determination of the amount of breeding experience. In addition we assumed that un-banded birds entering the breeding population had no previous breeding experience, because many breeders in surrounding areas were also colour banded and breeding dispersal is very local (Bruinzeel 2004). To verify that estimated breeding experience was an unbiased estimator of real breeding experience, we calibrated estimation rules on individuals which were ringed as juveniles. Estimated breeding experience predicted exact breeding experience very well (r=0.88). Although age-effects were omitted from analyses, interpretations of effects of breeding experience also encompass age-effects.

Reproductive parameters

We omitted all experimentally manipulated pairs and pairs that could not be assigned to a nest with complete certainty. To quantify the effect of pair-bond duration on annual reproductive output, we used the annual number of fledglings produced by each pair. To investigate effects of pair-bond duration on different stages of the breeding cycle, reproductive performance was further partitioned into laying date, clutch size, egg survival and chick survival (Table 4.1). Note that fledgling production is the result of clutch size egg survival chick survival; laying early is strongly associated with high fledgling production, as in most bird species. Clutch size and fledgling production were known for 1224 pair years; records for other reproductive parameters were less complete (Table 4.1). We analyzed laying date, clutch size, egg survival and chick survival of first clutches only; chick survival could only be determined of nests in which at least one egg hatched. Of all pair-years, 82% had only one clutch per year, 17% had one replacement clutch and 2% had two or more replacement clutches per year.

Table 4.1 Definitions, distributions, sample sizes, means, standard deviations, and ranges of measures of reproductive performance. The dataset comprises 233 females, 230 males, and 370 pairs measured in 21 different years.

Reproductive parameter	Definition	Distribution	N	Mean±s.d.	Range
Laying date	Day first egg was laid (1st April=day 1)	Normal	1006	56.4±13.1	26-100
Clutch size	Maximum number of eggs found in clutch	Normal	1224	2.68±0.88	1–4
Egg survival	Probability egg survived till hatching	Binomial	881	0.54±0.41	0–1
Chick survival	Probability chick survived till fledging	Binomial	612	0.20±0.32	0–1
Annual fledgling production	Annual number of fledglings produced per pair	Poisson	1224	0.23±0.54	0–3

Statistical procedure

We used generalized linear mixed models (GLMMs; Snijders and Bosker 1999) to account for sources of inter-dependency between individual measurements. In this datasets there were many repeated measurements of the same male or female (on average 5.3 cases per individual, range 1-19), which might be inter-correlated; similarly measurement of different individuals in the same year might be inter-correlated due to between year differences. We modeled female identity, male identity and year identity as cross-classified random effects, with individual measurements nested within these random effects. Analyses were performed with MLwiN 2.0 (Rasbash *et al*. 2004).

We entered linear and quadratic effects of pair-bond duration as well as male and female breeding experience as continuous variables into the model. Collinearity between pair-bond duration and the breeding experience of both sexes might make correct model selection problematic (Graham 2003), therefore, we estimated the effect of pair-bond duration in the presence of any effects of breeding experience of the male and the female. Non-significant quadratic terms of age-related parameters were removed from the model, but linear terms were always retained in the model, significant or not.
For the final model, we tested whether other curvi-linear functions of age-related parameters (inverse and logarithmic functions) fitted better than linear and quadratic effects (cf. Sydeman *et al*. 1991). Both a linear, inverse and logarithmic functional response depict a monotonic increase in reproductive performance, but a quadratic functional response might indicate a decline after an initial increase. We compared these non-nested curvi-linear models by using Akaike's Information Criteria (AIC) scores (Akaike 1973). Models within two AIC-units of each other were considered equally well-supported (Burnham and Anderson 2002).

Effects of pair-bond duration in a cross-sectional analyses can be caused by within-pair changes as well as by progressive changes in the phenotypic composition in the population. Therefore, we verified whether individuals or pairs that disappeared from the population (either due to divorce or mortality) were of high or low phenotypic quality. More specifically, by entering the maximum pair-bond duration of a pair as a covariate to the final model, we were able to specifically test for a between-pair co-variation with the reproductive parameter of interest (*sensu* van de Pol & Verhulst 2006). For example, a positive correlation between the maximum pair-bond duration of a pair and its overall fledgling production indicates that high quality pairs stayed together for longer.

Experimental divorce: manipulating pair-bond duration

We manipulated pair-bond duration by permanently removing randomly selected partners (either the male or the female) during the incubation phase, after which the remaining birds re-mated (Bruinzeel and van de Pol 2003). Consequently, the pair-bond duration of the newly mated partners was reset to one. When manipulating pair-bond duration in the field it is not possible to keep all other age-related traits constant. More specifically, by inducing re-mating not only pair-bond duration, but also the age and the breeding experience of the partners was manipulated. In addition, the non-removed individuals increased normally in age and breeding experience, but these changes were small compared to the manipulated age-related parameters. However, by removing both males and females we were able to disentangle effects of manipulated changes in pair-bond duration, age or breeding experience: effects of age or breeding experience are expected to result in a sex-specific response to the experimental manipulation, while effects of manipulating pair bond duration are expected to result in a similar response in both sexes. We followed the change in reproductive performance of the non-removed individual in the four years before and the four years after the removal, and related this to the change in pair-bond duration. Experiments were performed in 1998 and 1999; detailed methods are described in Bruinzeel & van de Pol (2003). The individuals of whom the partners were removed were excluded from the larger data set described in the previous section. Regrettably, in the years after the experiment the salt marsh flooded during the breeding season, which severely reduced sample sizes for most reproductive parameters with exception of laying date. Therefore, only this reproductive parameter could be analyzed. Individuals did not change territories due to the experiment.

Results

Observational patterns

The aim of combined analyses of natural and experimental variation in pair-bond duration and reproductive performance is to compare both patterns. However, experiments were carried out on individuals that did not change between territories, therefore we first analysed the association between pair-bond duration and territory quality. Pair-bond duration did not affect the probability of owning a high quality territory (Table 2a). However, inexperienced males and females had a much lower probability of owning a high quality territory than experienced males and females (Fig 4.1; Table 4.2A). A quadratic functional response of male breeding experience resulted in higher model support (ΔAIC=2.3), than fitting an inverse or logarithmic function of male breeding experience. This suggests that the probability of owning a high quality territory decreased again for males with more than 10 years of breeding experience, while this decline was not apparent in very experienced females. Since we were primarily interested in the occurrence of improvement independent of the environment in which individuals lived, we statistically corrected for territory quality in all other analyses.

Both pair-bond duration and male breeding experience were associated with several reproductive parameters; female breeding experience did not affect any of the reproductive parameters. Lay-date was associated with both pair-bond duration and male breeding experience (Table 4.2B). Pairs with high pair-bond duration laid earlier than newly formed pairs; however, pairs that had been together for over 10 years laid very late (Fig 4.2B). Laying dates were 0.4 days earlier for each year of breeding experience of the male (Fig 4.2A). Clutch size was associated with male breeding experience only (Table 4.2C). Clutch size was slightly higher for experienced males than for first time breeders and seemed to be lower again for very experienced males (Fig 4.2C); however overall

Table 4.2 Final models of analyses of effects of age-related parameters on reproductive performance: (A) probability of owning a high quality territory, (B) laying date, (C) clutch size, (D) egg survival, (E) chick survival, and (F) annual fledgling production. †Note that in models that are use a log or logit function the residual variance is constrained to be 1

Fixed effects	B	s.e.(B)	ΔDeviance	DF	P
(A) Dependent variable: probability owning high quality territory (logit link function)					
Final model			1612	1214	
Intercept	-1.39	0.21		1	
Female breeding experience	0.166	0.049	11.27	1	0.001
Female breeding experience^2	-0.0054	0.0027	4.13	1	0.042
Male breeding experience	0.156	0.053	8.76	1	0.003
Male breeding experience^2	-0.0097	0.0030	10.44	1	0.001
Pair-bond duration	0.163	0.270	0.15	1	0.69
Random effects: $\sigma_{year}^2=0.051\pm0.038$, $\sigma_{residual}^2=1^\dagger$					
(B) Dependent variable: laying date (identity link function)					
Final model			7514	996	
Intercept	61.2	1.4		1	
Territory quality	-2.89	1.13	6.42	1	0.011
Female breeding experience	-0.082	0.140	0.34	1	0.56
Male breeding experience	-0.404	0.134	9.09	1	0.003
Pair-bond duration	-0.823	0.299	6.23	1	0.013
Pair-bond duration^2	0.067	0.022	7.44	1	0.006
Random effects: $\sigma_{year}^2=7.3\pm3.7$, $\sigma_{females}^2=51.3\pm9.0$, $\sigma_{males}^2=8.7\pm6.4$, $\sigma_{residual}^2=102.8\pm5.6$					
(C) Dependent variable: clutch size (identity link function)					
Final model			2904	1214	
Intercept	2.34	0.10		1	
Territory quality	0.16	0.07	5.75	1	0.016
Female breeding experience	0.004	0.009	0.24	1	0.62
Male breeding experience	0.054	0.023	5.44	1	0.020
Male breeding experience^2	-0.0030	0.0013	5.42	1	0.020
Pair-bond duration	0.010	0.013	0.61	1	0.43
Random effects: $\sigma_{year}^2=0.04\pm0.02$, $\sigma_{females}^2=0.07\pm0.03$, $\sigma_{males}^2=0.06\pm0.03$, $\sigma_{residual}^2=0.63\pm0.03$					
(D) Dependent variable: egg survival (logit link function)					
Final model			2652	871	
Intercept	0.30	0.33		1	
Territory quality	0.32	0.13	5.77	1	0.016
Female breeding experience	-0.0004	0.018	0.001	1	0.97
Male breeding experience	-0.0014	0.018	0.007	1	0.93
Pair-bond duration	0.183	0.062	9.42	1	0.002
Pair-bond duration^2	-0.013	0.005	7.61	1	0.006
Random effects: $\sigma_{year}^2=1.59\pm0.61$, $\sigma_{females}^2=0.14\pm0.10$, $\sigma_{males}^2=0.19\pm0.10$, $\sigma_{residual}^2=1^\dagger$					

Table 4.2 Continued

Fixed effects	B	s.e.(B)	ΔDeviance	DF	P
(E) Dependent variable: chick survival (logit link function)					
Final model			1189	607	
Intercept	-1.81	0.32		1	
Territory quality	0.90	0.19	23.4	1	<0.001
Female breeding experience	-0.014	0.028	0.25	1	0.62
Male breeding experience	-0.059	0.034	3.11	1	0.078
Pair-bond duration	-0.016	0.042	0.15	1	0.70
Random effects: σ_{year}^2=0.83±0.45, $\sigma_{females}^2$=0.14±0.15, σ_{males}^2=0.14±0.14, $\sigma_{residual}^2$=1†					
(F) Dependent variable: annual fledgling production (log link function)					
Final model			678	1214	
Intercept	-2.87	0.43		1	
Territory quality	-0.94	0.16	34.5	1	<0.001
Female breeding experience	0.004	0.025	0.02	1	0.89
Male breeding experience	-0.013	0.027	0.23	1	0.63
Pair-bond duration	0.233	0.106	4.77	1	0.029
Pair-bond duration^2	-0.022	0.010	4.48	1	0.034
Random effects: σ_{year}^2=1.63±0.82, $\sigma_{females}^2$=0.22±0.12, σ_{males}^2=0.05±0.06, $\sigma_{residual}^2$=1†					

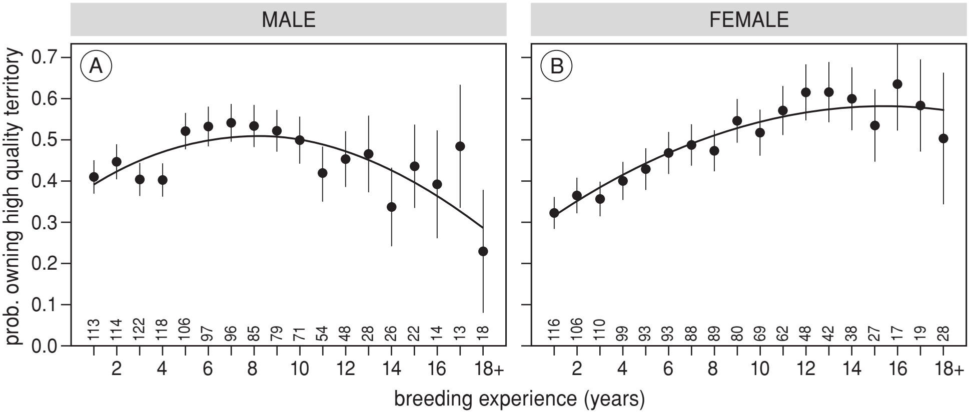

Figure 4.1 Effects of (A) male breeding experience and (B) female breeding experience on the probability of owning a high quality territory, adjusted for all other fixed and random effects in the final models (Table 4.2A). Note that very experienced individuals (18 years and more) were grouped for graphical reasons – analyses were performed on ungrouped values. Sample sizes are above the x-axis.

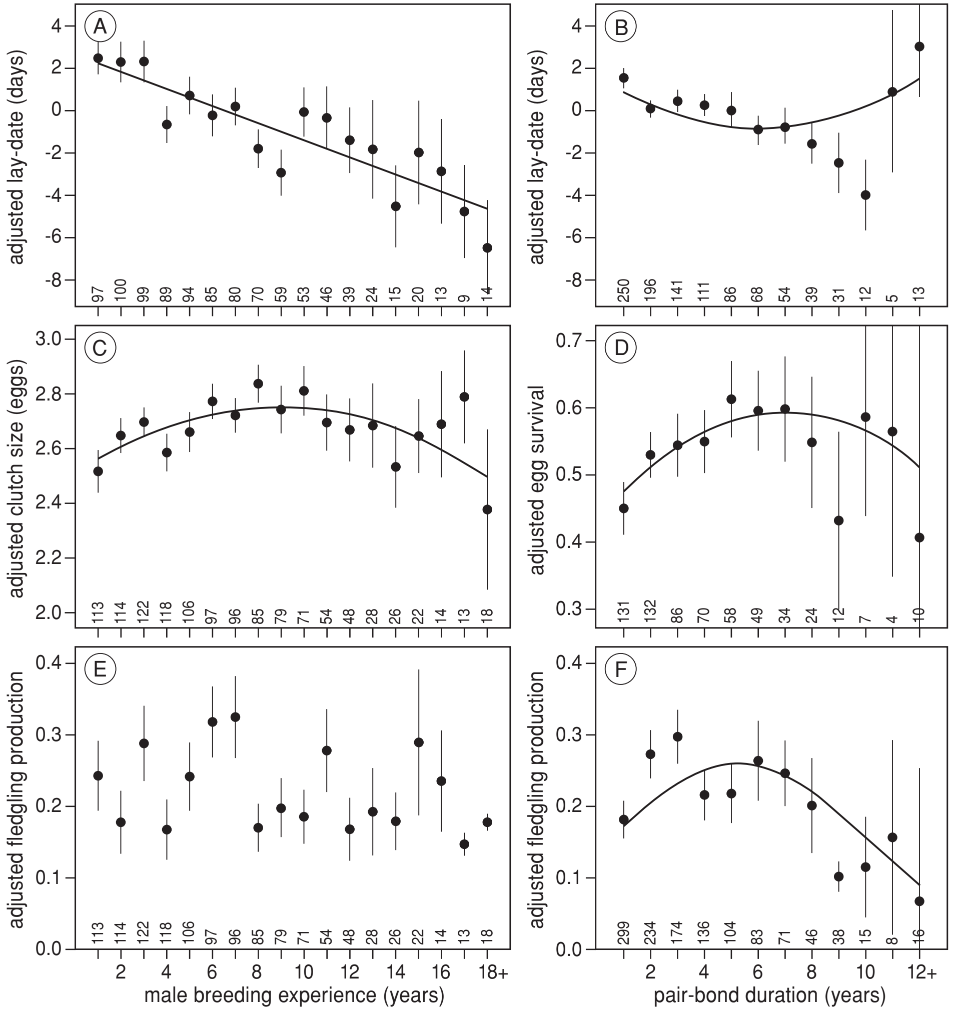

Figure 4.2 Effect of male breeding experience on (A) laying date, (C) clutch size, (E) annual fledgling production and the effect of pair-bond duration on (B) laying date, (D) egg survival, and (F) annual fledgling production. Reproductive parameters were adjusted for all other fixed and random effects in the final models (Table 4.2B-F). Note that very experienced individuals and pairs were grouped for graphical reasons – analyses were performed on ungrouped values. Sample sizes are above the x-axis.

differences were small (0.2 eggs). Egg survival was low for newly formed pairs, highest for pairs that had been together for 5-7 years, but declined again for pairs that had been together for very long (Fig. 4.2D; Table 4.2D). Chick survival was not significantly associated with any of the age-related parameters, although there was a suggestion that chick survival declined with male breeding experience (P=0.078; Table 4.2E). Annual reproductive output was associated only with pair-bond duration. Newly formed pairs produced few fledglings each year, production increased strongly after their first year together and remained high up to the seventh year of the pair-bond; however very old pairs performed extremely bad (Fig 4.2F; Table 4.2F). Annual fledgling production was not associated with male breeding experience (Fig 4.2E; Table 4.2F), probably because the strong positive effects on lay-date was cancelled out by the negative trend with chick survival. Interactive effects of male and female breeding experience (the sum or product of male and female breeding experience) did also not affect final reproductive output (both $P>0.4$).

Quadratic relationships always explained the observed relationships between age-related parameters and reproductive parameters at least as good as inverse or logarithmic relationships. The quadratic effect of pair-bond duration on lay-date, egg survival and annual fledgling production described the data even better than other curvi-linear functional relationships (all $\Delta AIC>2$). This suggests, lay-date, egg survival and fledgling production first increased with pair-bond duration, peaked at intermediate pair-bond duration and subsequently declined (and did not level off) at very high pair-bond duration.

Pairs that broke up early (low maximum pair bond duration) were of similar quality as pairs that stayed together for very long (high maximum pair-bond duration). This result follows from the observation that maximum pair-bond duration did not co-vary with lay-date ($slope=0.32\pm0.22$; $\chi^2=2.4$, $P=0.12$), egg survival ($slope=0.01\pm0.03$; $\chi^2=0.03$, $P=0.86$), or annual fledgling production ($slope=0.02\pm0.03$; $\chi^2=0.48$, $P=0.49$), when evaluated in the final models presented in Table 4.2. As there was no evidence in favour of selective disappearance of high or low quality pairs, older pairs must have performed better because they improved during their pair-bond.

Experimental divorce

We compared the changes in lay-date in the four years before and the four years after the experiment. We calculated the individual change (slopes) in laying dates for the 4 years before and after the divorce separately (Fig. 4.3A). Slopes were similar between the sexes before and after divorce (both $P>0.2$). Slopes before the divorce were not significantly different from zero ($average=1.4\pm1.2$ days/year, $t_{1,12}=1.16$, $P=0.27$). However, slopes after divorce differed significantly from zero ($average=-4.6\pm1.6$ days/year, $t_{1,12}=-2.94$, $P=0.012$) and differed significantly from the same individuals' slopes before the divorce ($\Delta slopes=-6.0\pm2.0$ days/year, paired-$t_{1,12}=-3.06$, $P=0.010$). This indicates that the same non-removed individuals, that had a constant laying date in the four years before the divorce, started advancing their laying dates after they remated with a new partner, independent of the sex of the non-removed bird. The age and breeding experience of the new partners did not differ from the removed old partners (age: paired-$t_{1,12}=-0.05$, $P=0.96$; breeding experience: paired-$t_{1,12}=-0.58$, $P=0.57$). Therefore, the change in slopes before and after the divorce, which was similar in both sexes, cannot easily be explained by a change in age or breeding experience of either males or females. Laying dates were expressed relative to the mean laying date for that year and territory quality, and consequently the experimental effect can also not be explained by a general environmental effect on the whole population.

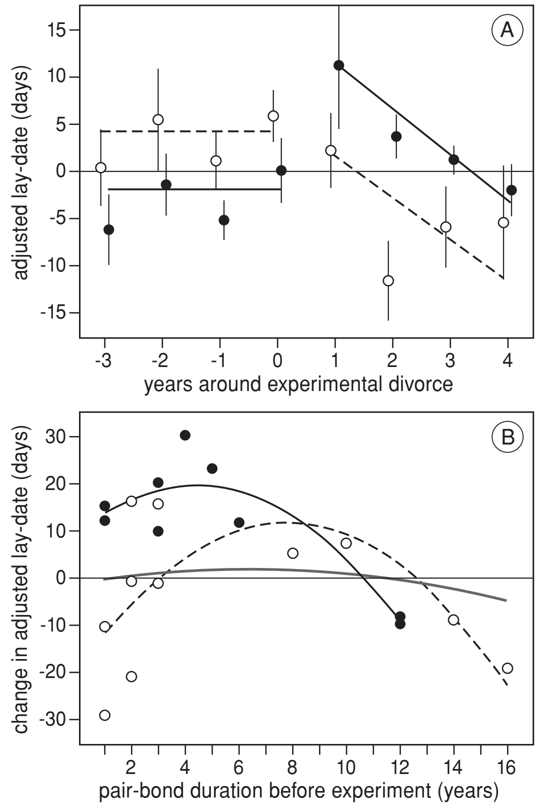

Figure 4.3 Changes in laying date of the re-mated individuals in (A) the four years preceding and in the four years after the experimental divorce, and (B) from the year before to the year after the experimental divorce. In (A) closed dots and continuous lines give values and average slopes of the individual changes in laying dates (before and after removal) for re-mated females (males removed, N=6); open dots and dashed lines are used for males (females removed, N=7). The experimental removal and subsequent re-mating with a different partner occurred in year 0, after egg-laying. In (B) closed dots and continuous line gives values and model fit for re-mated females (males removed, N=9); open dots and dashed lines are used for re-mated males (females removed, N=11). The grey line represents the expected relationship based on the observational data (see Fig. 4.2B). All laying dates are adjusted for year and territory quality effects and we subtracted each individual's overall average laying date. Sample sizes in (B) were higher due to missing values in (A).

The relationship between pair-bond duration and laying date in the observational dataset suggested that divorce should also result in an immediate cost of divorce as divorce results in a loss of mate familiarity (except for newly formed pairs). Therefore, we also calculated the absolute change in laying dates from the year before to the year after the divorce. Based on the observational patterns (Fig. 4.2B), we expected that new pairs would not benefit from divorce (no change in lay-date), pairs that had been together for up to 10 years should suffer a cost of divorce (delayed egg laying), but that very old pairs should even benefit from divorce (advance egg laying). The divorce experiment was qualitatively exactly in agreement with expectation, although the quantitative changes in laying date were much stronger than expected (up to one month delay or advancement; Fig. 4.3B). The change in laying date was quadratically proportional to the change in pair-bond duration (Table 4.3). Note that the change in pair-bond duration is equivalent to the pair-bond duration before the experiment minus one, as all individuals re-mated with new partners. The effect of pair-bond duration before the experiment on changes in laying date differed between the sexes, with male removals more often resulting in delayed laying when young pairs were manipulated. The pair-bond duration before the divorce explained 60% of the variance in both sexes in changes in laying date due to the divorce. Changes in other age-related traits due to the divorce, especially male breeding experience, did not correlate with the change in laying date (Table 4.3). The observed patterns were probably not the result of problems associated with finding a new mate in time for the next breeding season, as most individuals re-mated within a week. Furthermore, a comparison between changes in lay-date between the year before the divorce and two years after the divorce resulted in very similar patters as in Fig. 4.3B (results not shown).

Table 4.3 Effects of experimentally induced changes in age-related parameters on the change in laying date with the old partner in the year of divorce and new partner in the year after divorce. Sex refers to the sex of the removed partner, territory quality refers to the territory quality in which the experiment was performed. Pair bond duration is the pair bond duration before the experiment, which is equivalent to the change in pair bond duration as all remaining individuals started out with a new partner.

Parameter	B	s.e.(B)	DF	F	P
Final model (N=20, R^2=0.60)			4,15	8.0	0.001
Intercept	-18.9	6.4	1	0.6	0.44
Sex	28.8	7.3	1	15.7	0.001
Pair bond duration	7.9	2.4	1	7.9	0.013
Pair bond duration^2	-0.51	0.15	1	12.2	0.003
Sex * pair bond duration	-3.4	1.1	1	9.5	0.008
Rejected from final model					
Δ age old and new partner	0.5	0.6	1	0.1	0.75
Sex*Δ age old and new partner	-0.5	1.2	1	0.2	0.65
Δ breeding experience old and new partner	0.5	0.6	1	0.3	0.58
Sex*Δ breeding experience old and new partner	-0.4	1.1	1	0.1	0.73
Sex * pair bond duration2	-0.04	0.34	1	0.01	0.91
Territory quality	-4.3	5.2	1	0.7	0.42

Discussion

Our study is in agreement with the observation that re-mated pairs outperformed newly formed pairs in another population of oystercatchers (Harris 1987). Reproductive performance improved strongly during the first years of the pair bond, however pairs that had been together for very long performed very bad. These patterns remained after controlling for effects of breeding experience of the male and female. The association between pair-bond duration and reproductive performance in the cross-sectional analyses was not caused by high or low quality pairs splitting up more often, but due to within-pair changes. Annual fledgling production changed during the pair bond because of underlying changes in lay-date and egg survival.

To our knowledge, this is the first study that manipulated pair-bond duration. Because it is impossible to manipulate pair-bond duration and keep the age and breeding experience of the new partners constant in a field situation, it was crucial to remove both males and females. For example, if the difference in male breeding experience between the old and new male had affected the result of the experiment, we would have expected to find only effects of removing a male partner. There are, however, no clear indications of sex differences in re-mating effect, nor did new partners systematically differ from the removed partners in age or breeding experience. Both sexes showed a response to a change in pair-bond duration, only the strength of response differed somewhat between the sexes in Fig. 4.3B. Therefore the combined observational patters and experimental manipulation of pair-bonds provides strong support for a causal relationship between pair-bond duration causally and reproductive performance.

A causal effect of pair-bond duration on reproductive performance implies that a divorce should result in an immediate cost of divorce, as a result of a loss of mate familiarity (except for newly formed pairs). The divorce experiment confirmed that the change in laying date was dependent on the reduction in pair bond duration due to the divorce. Although the result of the experiment qualitatively supported the observational data, the quantitative changes in laying date were much stronger in the experiment. We do not understand why changes after experimental re-mating were much stronger than natural patterns. Nonetheless, both the observational patterns and experimental data suggest it would be beneficial for very old pairs to immediately divorce. However, the probability of divorce was independent of pair-bond duration or any other age-related (Logistic regression, all $P>0.10$, $N=1224$ pair years). Possibly old pairs do not divorce more often because the number of vacancies is limited in a natural situation; consequently initiating divorce could result in becoming a non-breeder.

After the experimentally induced re-mating the newly formed pairs suddenly started advancing their timing of reproduction with two weeks over four years. Long-term gradual improvements are consistent with a mate familiarity effect and were also observed after natural divorce in oystercatchers (Heg *et al*. 2003) and in short-tailed shearwaters (Bradley *et al*. 1990). Studies reporting improvements of reproductive performance associated with age-related traits usually report a strong initial improvement, which is consistent with the idea that individuals or pairs have to become familiar with specific reproductive task, and resembles classical learning curves (Forslund and Pärt 1995). Within-pair improvements in laying date were not confounded to the first few years of the pair bond, but pairs gradually advanced laying up to their 9th year of the pair-bond. Most strikingly, after an initial improvement, pairs deteriorated strongly during the remainder of their pair bond. Pairs that had been together for over 12 years produced three times less offspring each year than young pairs. A decline at high pair-bond duration was not an artifact of the statistical analyses, because also in the experiment a quadratic relationship was observed. Furthermore, a decline at high pair-bond duration does not seem to be an exceptional pattern in studies that report effects of pair-bond duration on reproductive performance (Ens *et al.* 1996). Possibly the decline in reproductive performance is an inescapable cost of the high reproductive performance in the first years of the pair-bond duration and can be interpreted as reproductive senescence.

The underlying behavioral changes that result in a change in reproductive performance during the pair-bond are probably not primarily determined by changes in the individual behavior of the male or the female. More likely, they are the result of synergistic effects between male and female (i.e. how they function as a pair). Possible candidate behaviors must therefore be the result of the actions of both the male and the female (e.g. improved intra-pair coordination or cooperation). The analyses of different measures of reproductive performance offers further insight in the underlying mechanisms of overall improvement of reproductive output. The strong effect of pair-bond duration on annual fledgling production can largely be explained by the combined effects of pair-bond duration on laying date and egg survival. This suggests that the behavioral mechanisms underlying these improvements are acting pre-laying and during egg-incubation. Pre-laying candidate behaviors could include the cooperation in defending a rich feeding territory, as laying date in oystercatchers is affected by access to food (Heg 1999). Egg survival is mainly determined by egg predation (predominantly by gulls and rats). To protect the eggs both the male and the female have to sit on the nest for almost 12h a day each, consequently oystercatchers are time-stressed as they can only use half the usual available time during low tide to feed. Possible candidate behaviors during egg incubation could involve the coordination of incubation bouts and the efficiency of the division of labor between both sexes. Increasing mate familiarity during a pair-bond could help in fine-tuning such cooperative behavior.

So far we assumed, as did most studies, that all individual or pair improvements are due to an accumulation of different types of experience (Curio 1983). An alternative explanation would be that individuals might restrain themselves at a younger age for optimality reasons, when current reproduction is traded off against future reproduction and survival declines with age (Curio 1983; Pianka and Parker 1975). However, we consider this explanation unlikely, because there is no evidence for age dependent mortality among adult oystercatchers (Schnakenwinkel 1970). More importantly, the restraint hypothesis only predicts that individuals should optimize their current reproductive effort in relation to their life expectancy, and therefore the restraint hypothesis cannot explain why reproductive effort should be optimized in relation to pair-bond duration. Nonetheless, reasons for adjusting reproductive effort in relation to pair-bond duration might exist. Roberts and Sherrat (1998) suggested cooperation can evolve in individuals that gradually increase their investments in repeated reciprocal interactions ('raise-the-stakes' strategies), as this strategy is robust against individuals that try to exploit their partners. Several experiments have shown that humans used such strategies to improve cooperation between unrelated partners. (Wedekind & Milinski 1996; Roberts & Renwick 2003). Important to note is that whether pairs were constrained from producing many offspring or might have restrained themselves from producing more offspring, the underlying behavioral changes might not be different.

Studies on divorce and the evolution of monogamy have largely focused on potential costs of divorce (finding a new partner, losing a territory) as an explanation for why long-term mate-fidelity exists (Black 1996). This study suggests that the large fitness benefits of maintaining pair-bonds also provide a good explanation why most oystercatchers re-mate with the same partner. We think that a change of focus from costs of divorce to benefits of mate retention might shed new lights on the evolution of long-term monogamy in many species. For example, a comparison between species shows that studies that did report effects of pair-bond duration on reproductive success were mainly on bird species with low divorce rates (5.8±2.1% annually; N=8), while studies that failed to find an effect of pair-bond duration were on bird species with high divorce rates (18.7±6.7% annually; N=7) (calculated from data in Ens *et al*. 1996).

Finally, the important role of the pair-bond suggests reproductive performance is not purely an individual trait, but is the result of an interaction between phenotypes (Moore *et al*. 1998). Synergistic effects of pair-bond duration in this study were very strong, and such strong effects do not seem to be uncommon (Ens *et al*. 1996). This poses the question how universal such results are and to what extent synergistic effects might interact with natural selection shaping individual life-history patterns. Much more work is needed to answer these types of questions, but given the complex nature of the question, experimental approaches such as this study seem to be crucial.

Acknowledgements

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Box B: Age-dependent reproduction, survival and reproductive values in the Oystercatcher: is delayed maturity favored in a declining population?

Many studies quantified patterns of age-dependent reproduction and survival, because this allows the construction of age-structured population models. These models can be used for sensitivity analysis, which quantifies the strength of phenotypic selection on life history traits. Understanding how mutations and phenotypic changes in age-specific schemes affect population dynamics and individual fitness is crucial for the study of the evolution of ageing, age at maturity, the optimization of reproductive effort during a lifetime and conservation issues. The relationship between age and reproduction is thus at the core of population demography (Caswell 2001), life history evolution (Stearns 1992), and population genetics (Charlesworth 1980).

In this study we quantify the patterns of age-dependent reproduction and survival in a declining population of Oystercatchers *Haematopus ostralegus*, using data on both the breeding and non-breeding part of the population. We will use this to build an age-structured population matrix model to calculate the age-dependent reproductive values, and the selection gradients working on the age-specific fecundity and mortality schemes. Finally, we will address the question whether the negative population growth rate and the age-specific fecundity and mortality schemes of this population can favour individuals that delay their maturation. It is generally assumed that selection should favour earlier reproduction, but Mertz (1971) has suggested that population decline might have selected for delayed maturity in another extremely long-lived bird species, the California Condor (*Gymnogyps californianus*).

Methods

All analyses were performed on individuals of known age, and were estimated for both sexes separately. As this study runs for 21 years we could only estimate age-specific parameters up to the age of 20 years old, while Oystercatchers can live over 30 years old. Age-dependent survival was calculated with the use of mark-recapture analysis (see Chapter 7 for details). For the calculation of age-specific survival and probability of breeding both non-breeders and breeders were included. All values were corrected for differences between years. Age-specific fecundity was calculated as the product of the age specific probability of breeding, the age-specific fledgling production, and the fledgling sex ratio (which was assumed to be 50:50 and age-independent, Heg *et al.* 2000). Age-specific values of survival and fecundity were entered in the Leslie matrix of an age-specific population model. Reproductive values, which weight the contribution of different age-classes to population growth rate, were partitioned into the current reproductive value and the residual reproductive value. The sensitivity of population growth rate (λ) to age-specific fecundity and survival was estimated with the use of the program PopTools (Hood 2005).

Results

As most individuals could be sexed only during the adult life stage, we assumed first and second year survival was equal for males and females. Adult survival was similar for both sexes and seemed to be constant up to the age of 20 years old (Fig Box B1A,B). Although at the moment we cannot determine yet whether survival differed for very old individuals, two other long-term studies on Oystercatchers did not find any evidence for mortality senescence (Schnakenwinkel 1970; Safriel *et al.* 1984). Therefore we assumed individuals over the age of 20 years old had a similar survival as younger adults, but we set a maximum age of 43, as this was the oldest age an Oystercatcher was ever recorded to have died.

The youngest age at which a female was observed to acquire a territory and initiate a breeding attempt was three years old; males took one year longer (Fig Box B1C,D). The probability an individual would breed in a specific year increased strongly with age, and individuals over the age of 15 virtually always bred. We assumed this pattern remained constant for individuals over 20 years old. Young breeders produced relatively few fledglings annually, but this increased strongly in the first few years of life (Fig Box B1E,F). In both males and females, fledgling production peaked around the age of nine years old and declined from that age on. We assumed this negative trend continued for individuals over 20 years old, such that fledgling production reached almost zero around the age of 30.

Reproductive values, which integrate age-specific fecundity and survival values in the total contribution of an age-class, increased up to the age of sexual maturity (Fig. Box B2A,B). Reproductive values declined slowly up to the age of ten years old, after which the decline quickened until reproductive values reached almost zero at the age of 25. Reproductive values of an age-class mainly comprised the residual reproductive values, while the current reproductive values of a brood only contributed marginally to overall reproductive values. Only at very old age current reproductive values and residual reproductive values were of similar magnitude.

Phenotypic selection gradients on age-specific fecundity and survival schemes were estimated by the sensitivity of population growth rate (λ) to age specific fecundity and mortality values (Fig Box B2C,D). Sensitivity of λ to age-specific survival declined strongly up to sexual maturity, after which it slowly further declined for older age-classes. Interestingly, the sensitivity of λ to age-specific fecundity increased from the age of sexual maturity for both sexes. The change in sensitivity of λ to fecundity from one age class to the next is given by the age-specific survival divided by λ (Caswell 2001). As λ was 0.93 for females and 0.91 for males, it was lower than the adult survival probability of all age-classes for both sexes, which resulted in the sensitivity of age-specific survival increasing at a constant rate with age.

We investigated the effect of advanced and delayed maturity on fitness by moving the entire fecundity curve left or rightward (Fig. Box B3A,B). As such we mimicked a mutation that would cause individuals to advance or delay reproduction with one or more years. We assumed a change in the fecundity curve did not affect the age-specific

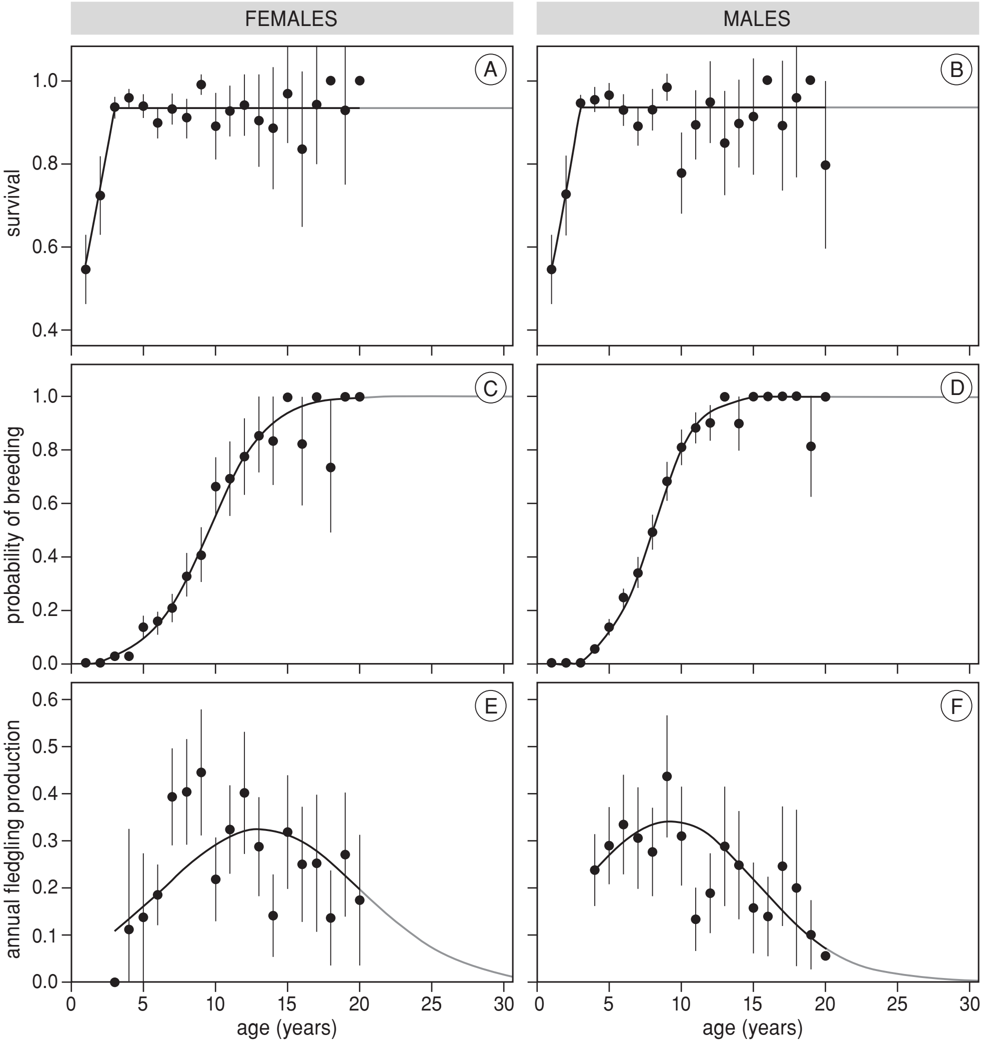


Figure Box B1 Female and male age-specific survival (A,B), probability of breeding (C,D) and annual fledgling production (E,F). The solid line gives the fitted values using regression analyses; the grey lines give the extrapolated values for old age-classes we could not estimate in this dataset. Values are corrected for differences between years and are given with standard error bars.

mortality curve (i.e. no cost of reproduction; no direct survival benefit of delayed reproduction). Individuals that advanced maturity experienced lower fitness, as depicted by the lower λ (Fig. Box B3C,D). However, individuals that delayed maturity have a higher fitness than the resident population. As such selection should favour individuals that would delay their reproduction in this population, even though these individuals would risk dying in the year they delayed reproduction.

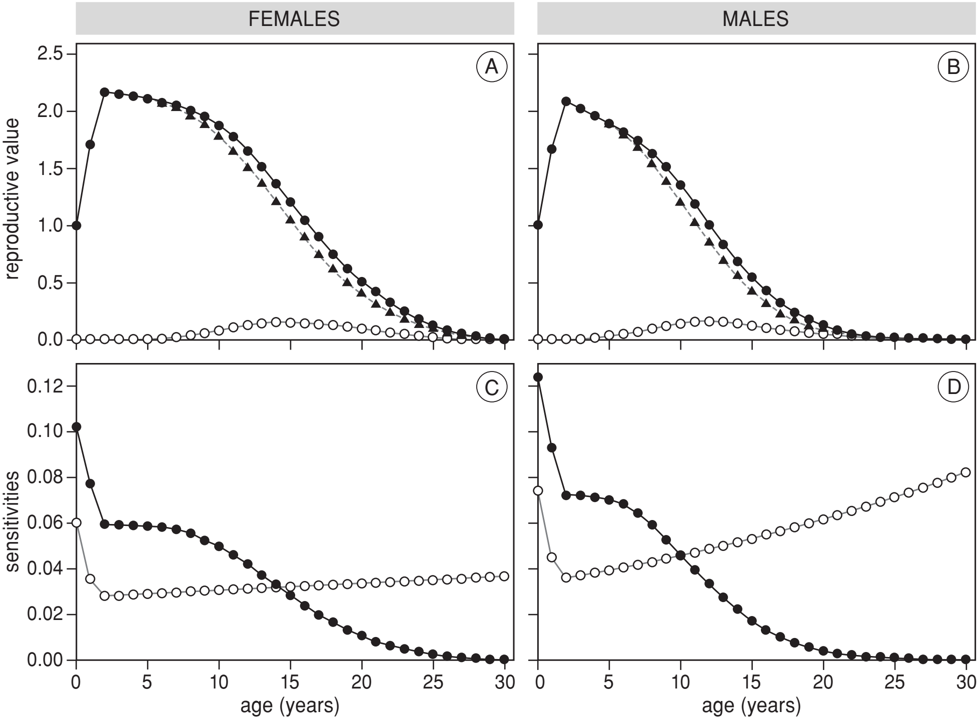


Figure Box B2 Female and male age-specific reproductive values (A,B), sensitivities (C,D). In (A,B) solid dots depict the total reproductive value, which is the sum of the current reproductive value (open dots) and the residual reproductive value (triangles). In (C,D) solid dots depict the sensitivity of λ to age-specific survival and open dots depict the sensitivity of λ to age-specific fecundity. Sensitivities are calculated as $\delta\lambda / \delta a_x$, where a_x is the age-specific parameter of interest.

Conclusions

There were no indications that adult survival varied with respect to age in Oystercatchers, in accordance with two other studies (Schnakenwinkel 1970; Safriel *et al.* 1984). However, breeding probabilities strongly increased with age, as did annual reproductive output up to the age of nine year. There was strong evidence in favour of reproductive senescence, as reproductive output declined with more than 50% from the age of ten to twenty years old. Patterns of current and residual reproductive values were similar to many other studies on long-lived species (e.g. Case 2000; Caswell 2001). Such a pattern suggests that, during most of their life, Oystercatchers are not very likely to increase reproductive investments at the cost of future survival, because the gains do not easily outweigh the costs. However, when Oystercatchers are very old (20+), current reproductive values and residual reproductive values are of similar magnitude, and Oystercatchers might be more inclined to trade off future survival for cur-

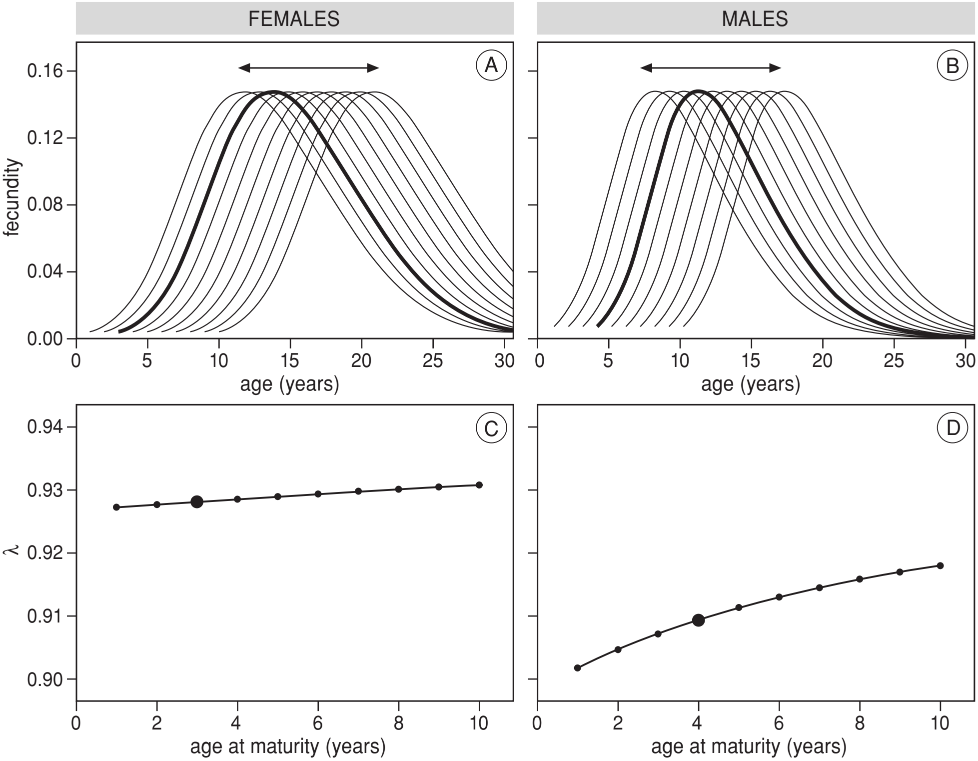


Figure Box B3 The effect of a mutation that would alter the age of maturity in male and female Oystercatchers and its fitness consequences. A change in the age of maturity is simulated by advancing or delaying the complete fecundity curve with one or more years (A,B). The thick solid gives the observed fecundity curve, the thin solid lines depict mutant with a higher or lower age at maturity In (C,D) the selection gradients of age at muturity in this population is presented.

rent reproductive effort. Note that the areas under the reproductive value curves were roughly equal for both sexes, which follows from the fact that the average fitness of males should equal the average fitness of females.

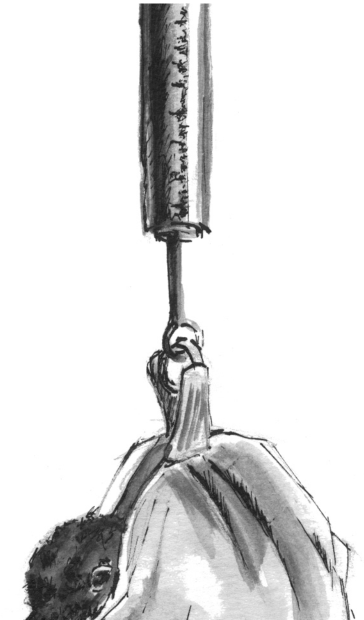
Population growth rate, as determined from the age-structured population matrix, suggested population was declining with about 8% per year (λ_{female}=0.93, λ_{male}=0.91). This decline was stronger than estimated from a stage-structure population model with adult stages defined by breeding status and the breeding habitat quality (λ=0.95; van de Pol *et al.* 2006). The difference in the λ between the age-structured model and the stage-structured model can potentially be caused by several reasons: (i) observations of known age individuals were biased towards the end of the study period, when population declined most strongly, (ii) an age and stage structured population structure constitute two different ways in which the same values can be grouped, which do not necessarily result in the same population average (iii) we assumed individuals could not reach an age over 43 years old (see next section).

Selection gradients of fecundity increased with age, which is quite an exceptional and intriguing pattern. An increase in the sensitivity of λ for fecundity with age can only occur when the adult survival is larger than the population growth rate. Furthermore, the switch point at which either advanced maturity or delayed maturity is favoured by selection also occurs when λ equals the adult mortality (Hoogendyk & Estabrook 1984). The critical question therefore is: in what conditions can annual population decline exceed annual mortality? In populations in which adult mortality is constant (i.e. no mortality senescence) population growth rate can never be lower than the annual adult survival probability, and therefore in such population delayed maturity is never favoured. However, in this population we have assumed that individuals cannot reach infinite age; no individual could live beyond 43 years old. By truncating the age-structure we have assumed that Oystercatchers have a finite lifespan. Because the stable age-distribution of a declining population is skewed towards the highest age-classes, any mortality senescence at high age results in the largest age-classes dying predominantly, and in such situations population decline can exceed average adult mortality. As such the observation that delayed maturity is favoured by selection in this population (at least in the long run), depends strongly on the assumption that annual mortality drops to zero at a certain age. When we would assume individuals have an infinite lifespan (by using the Lefkovitch matrix), we arrive at a population growth rate that exactly equals the adult survival of both sexes (λ_{female}=0.94, λ_{male}=0.94). In this situation there is no selection in favour of both delayed as well as advanced maturity (i.e. the selection gradient is zero).

This study illustrates that there can be a feedback between the population dynamics and the selection pressures acting on life-history traits. Furthermore, predictions about selection pressures on life-history decisions early in life (age at maturity) can strongly dependent on specific assumptions about what happens in the oldest age-classes. Irrespective whether Oystercatchers have an infinite or finite lifespan, it is clear that in the current situation of population decline there is no or almost no selection pressure for advanced maturity. However, given the fact that a population cannot decline with 6% per year for a very long period without going extinct, it is unlikely that evolution of delayed maturity will occur (unless there is an additional survival or future reproductive benefit in of delaying maturity). Should population growth rate increase again for this species, selection would favour earlier reproduction.

PART III

Condition-dependent life-history strategies



Chapter 5

Identifying the main causes of phenotypic variation and covariation in life-history traits in a long-lived species

Martijn van de Pol & Richard A. Pettifor

Abstract

Identifying the main causes of variation and covariation in life-history traits subject to selection is fundamental for understanding the evolution of life-history strategies. Understanding how different sources of phenotypic variance can be partitioned within traits and how important the environmental component of variance is across traits as well as among species allows a much better understanding of the evolution of life-history traits. However, the determination of important sources of (co)variation is often problematic in the wild, as environments vary in time and space and many life-history traits show strong phenotypic covariance. In this paper we investigate patterns of phenotypic variance and covariance between several measures of reproductive performance and parental survival in the Oystercatcher, a long-lived bird species. We use recently developed Bayesian cross-classified multivariate models in order to partition the variance and covariance in these life-history traits within and between different intrinsic and extrinsic sources of variance, such as between years, territories, male parents, female parents, and residual variation. Our main conclusions were that environmental sources of variation were most important, while differences between individuals explained only a relatively small part of the overall variation in life-history traits. This suggests that the selection pressures acting on these traits, might primarily act on the environmental component of phenotypic variation. Interestingly, some combinations of females and males systematically performed better than other pairs, independent of the individual quality of the male and female. Life-history traits in Oystercatchers therefore not only depend on the phenotype of the individual, but also on the phenotype (and possibly the genotype) of the partner. Consequently, in Oystercatchers most life-history traits cannot a priori be regarded as sex-linked traits, which make their evolutionary dynamics much more complex. Covariations between life-history traits at the population level were generally the result of within-individual processes, suggesting they were the result of adaptive adjustments to stochastic events. We illustrate how our analyses might offer alternative perspectives as a means of causal analyses of life-history trait variation by comparing our results with a lay-date manipulation life-history experiment.

Introduction

Variation between individuals in reproduction and survival, and thereby variation in fitness, is a key component of Darwinian evolution. Individuals differ in their phenotype because of differences in their genetic, parental, developmental and environmental background. Identifying the causes (sources) of variation within and between life-history traits is therefore fundamental to understanding the evolution of life-history strategies (Stearns 1992; Roff 1992). Understanding how different sources of phenotypic variation can be partitioned within traits, and how important the environmental component of variance is across traits and among species may help us to better understand the selection pressures acting on these traits under natural conditions. Quantitative geneticists have developed statistical techniques to partition the phenotypic variance in genetic and environmental components, and have performed controlled laboratory experiments to disentangle the components of variance within phenotypic traits (Falconer & Mackay 1996; Lynch & Walsh 1998). However, little is known about the relative importance of different sources of phenotypic variation of life-history traits in the wild. Studying phenotypic variation in the wild is often problematic, as experiments are more difficult to perform than in the laboratory and patterns of natural variation are complex due to variation in time and space.

Another complexity in the study of life-history evolution is that life-history traits also co-vary with other life-history traits (Sæther 1988; Stearns 1992; Roff 1992). Life-history covariations within individuals are the result of several fundamental trade-offs, such as the trade-off between current reproduction and future performance (future survival as well as future reproduction), and the trade-off between the quantity and quality of offspring (e.g. Stearns 1992). Individuals may vary in the way how these trade-offs are resolved due to differences in their genetic, parental, developmental and environmental background. Paradoxically, in the wild, often traits that are expected to be negatively correlated, such as fecundity and survival, are observed to be not or positively correlated at the level of the phenotype in the population (Fig. 5.1A). This might be because natural patterns of covariation might be obscured by covariances that vary between different levels (Reznick *et al.* 2000). For example, whether a positive or negative covariation between life-history traits is observed between individuals strongly depends on the variation in the acquisition and allocation of limiting resources (van Noordwijk & de Jong 1986). For understanding the role of life-history covariations in the evolution of life-history traits it is therefore important to understand whether life-history traits covary as a result of within-individual trade-offs or as a result of environmental effects. Therefore, quantifying the contribution that differing biotic and abiotic sources make to the overall phenotypic variances as well as covariances remains an important challenge in understanding selection and microevolution under natural conditions.

In this study we report on a breeding population of Oystercatchers (*Haematopus ostralegus*). We have studied these long-lived shorebirds over a period of 22 years, in which the breeding performance and fate of most individuals was followed. We con-

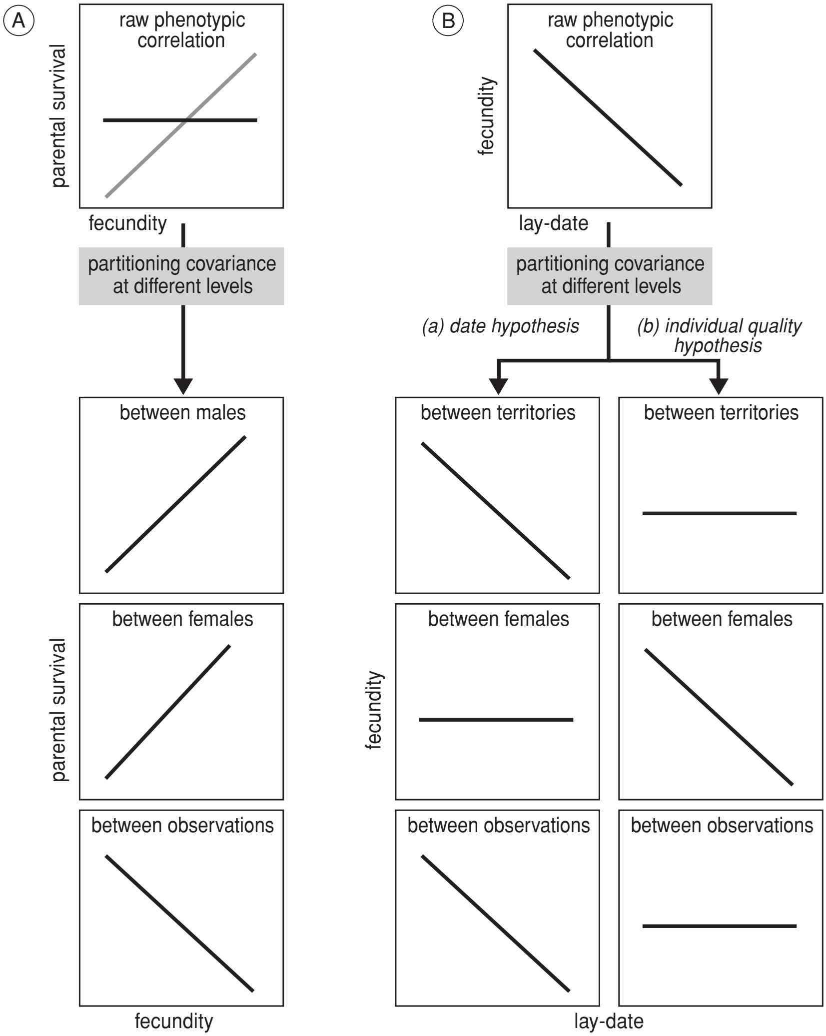


Figure 5.1 Schematic representation of how covariances between two life-history traits can be partitioned within different sources of phenotypic variation. (A) The covariance between current fecundity and future survival. In many species no correlation (or a positive correlation) is observed between these two traits at the population level, while life-history predicts a trade-off to exist between these two traits. The absence of such a relationship can be explained by a positive covariance at the between individual level due to variation in resource acquisition between individuals, while within individuals (between observations) there might actually be a trade-off. (B) The covariance between lay-date and fecundity. When environmental conditions vary this might affect the timing of breeding (e.g. females cannot reach breeding condition in time). The date hypothesis predicts that when environmental conditions vary strongly between territories and causally affect fecundity, we might expect a covariation between lay-date and nest-success between territories; alternatively when environmental conditions strongly vary within territories we might expect a covariation between lay-date and nest-success between observations. On the other hand the individual quality hypothesis predicts that lay-date and nest success mainly covary between females, as high quality females always produce many offspring and also lay early, while low quality females always produce few offspring and also lay late.

structed a list of what we think are some of the main life-history parameters (Table 5.1). Many factors potentially influence the expression of these life-history traits, and many of them have been the topic of specific studies (Table 5.2). However, these studies have not made clear what the relative importance is of different sources of phenotypic variation and covariation. Most studies only investigated one or two factors simultaneously, primarily because of logistic difficulties of performing multi-factorial experiments in natural populations. Recently, newly statistical techniques have been developed to partition the phenotypic variance and covariance in life-history traits in observational data (Pettifor *et al.* 2006; Browne *et al.* 2006). Despite the limitations of observational studies compared to experimental studies, observational studies also offer some important advantages. First, selection gradients on life-history traits are generally rather weak, consequently huge amounts of replicates might be required to detect them (Kingsolver *et al.* 2001). Second, the important environmental sources of variation and covariation may vary between years (e.g. Boyce & Perrins 1987), or even fluctuate systematically over longer periods (e.g. Sinervo & Lively 1996), in which cases a data set collected over many years is required. Thirdly, some sources of variation, such as variation in individual quality and habitat quality, are almost impossible to disentangle experimentally and we have to rely on patterns of natural variation. For example, manipulating individuals to breed in certain habitats or with certain partners is virtually impossible in the field. Luckily, nowadays, more and more observational studies (such as this study) have large datasets available, collected over many years, and newly developed statistical methods can be used to scrutinize these datasets (Pettifor *et al.* 2006; Browne *et al.* 2006).

The potential sources of variation can be roughly classified in five main sources of variation (Table 5.2): variation caused by sources that mainly differ between (i) years, (ii) territories, (iii) males, (iv) females, or (v) observations (e.g. between reproductive attempts). By partitioning the phenotypic variation and covariation in Oystercatchers' life-history traits between these sources several fundamental problems in evolutionary theory of life-histories can be investigated. Nonetheless, for practical reasons we will have to limit the discussion of our results. Besides the more explorative questions, such as, what are the main sources of phenotypic variation in life-history traits, and what are the patterns of life-history covariation and do they differ between levels, our focus will be on the two following two specific problems:

First, reproductive traits are commonly treated as a sex-limited trait, which greatly simplifies the analyses of inheritance and selection. Usually only the effect of females on reproductive traits are taken into account, while in reality in many species, especially in species with biparental care, there are numerous ways in which the male could influence traits such as the number of offspring produced. In situations where life-history traits are the result of the joint phenotype of the male and the female, the evolutionary dynamics produced by such an interacting phenotype can be quite different from selection processes acting on females only (Moore *et al.* 1998; Wolf *et al.* 1999). By partitioning the total phenotypic variance in variation due to differences between females, differences between males, and differences due to spatial and temporal processes, we can quantify the relative importance of the individual quality of the female and the male.

Table 5.1 Description of all life-history traits used in analyses with their mean, variance, coefficient of variation (CV) and sample sizes (N). ^{G}Gaussian error distribution was used in analyses; ^{B}Binomial error distribution was used in analyses.

Life-history trait	Description	Mean	Variance	CV	N
Egg size (cm^3)^G	Average egg volume of all eggs in the first clutch ($V[cm^3]=0.49$*egg-length[cm])egg-width[cm]^2)	43.4	8.92	0.069	1540
Lay-date (days)^G	Day on which the first egg of the each first clutch was laid by a female since 1st May each year	26.2	174.3	0.504	1503
Nest success^B	Whether a pair produced at least one fledged offspring in a given year or not	0.213	0.168	1.922	1732
Recruitment success^B	Whether a pair produced at least one offspring that survived till the age of 3 years old and recruited in the adult non-breeder population in a given year or not	0.076	0.070	3.495	1545
Male survival^B	Survival of each individual male parent from one breeding season to the next	0.920	0.074	0.296	1815
Female survival^B	Survival of each individual female parent from one breeding season to the next	0.926	0.069	0.284	1815
Male breeding^B	Whether each individual male parent survived from one breeding season to the next and bred again or not	0.897	0.093	0.339	1815
Female breeding^B	Whether each individual female parent survived from one breeding season to the next and bred again or not	0.886	0.101	0.359	1815

Second, partitioning the patterns of covariation within different sources of variation need not only be used to explain the absence of covariations at the population level (Fig. 1a), but can also to distinguish between competing hypothesis that try to explain the presence of covariations. For example, in Oystercatchers and most other bird species lay-date and reproductive success are negatively correlated at the population level, and several hypotheses have been proposed to explain this pattern (e.g. Price *et al.* 1988). The date hypothesis suggest that laying early causes high reproductive success, because the offspring from early nests might experience better food conditions or have more time to prepare for the subsequent winter. Alternatively, the individual quality hypothesis suggests that the association between laying early and high reproductive output might be coincidental and laying early is a by-product of individual quality (e.g. female condition). Both hypotheses make different predictions for the covariations between lay-date and reproductive success within different sources of variation (Fig. 5.1B). As such, partitioning phenotypic covariances can provide an alternative or addition to performing lay-date manipulation experiments (as done by Heg 1999 in the Oystercatcher), which have several difficulties of their own (as discussed by Sheldon *et al.* 2003). Several other interesting problems in life-history evolution, such as the relationship between lay-date and clutch size (Pettifor *et al.* 2006), or lay-date and egg size (see later) can be investigated similarly.

Table 5.2 Some sources of variances potentially determining the phenotypic variation in life-history traits in the oystercatcher. This is not an exhaustive list, nor have all the causative effects on the life-history traits been confirmed in this, or other populations, of oystercatchers. Traits are abbreviated to ES– egg size, LD – lay-date, NS – nest success, RS – recruitment success, PS – male/female parental survival to next year, PB –male/female parents bred in next year.

Source of variance	Contributory effects	Life-history traits potentially affected	References
Between years ('year quality')	Winter severity	RS, PS	Camphuysen *et al.* 1996; Nève & van Noordwijk 1997
	Winter food supply	RS, PS	Camphuysen *et al.* 1996; Nève & van Noordwijk 1997
	Predators (gulls, rats, peregrine falcons)	NS, RS, PS	Harris & Wanless 1997; personal observation
	Summer food supply	NS, AD	Heg & van de Velde 2001
Between territories ('territory quality')	Distance between nesting and feeding territory	ES, LD, NS, RS	Ens *et al.* 1992; Heg 1999 van de Pol *et al.* 2006
	Altitude (flooding)	NS, RS	Personal observation
	Habitat	NS, RS	Ens *et al.* 1992
Between male / female parents ('individual quality')	Natal origin	PS, PB	van de Pol *et al.* 2006
	Condition / state	LD, PS	Verhulst *et al.* 2004; Oosterbeek *et al*, in prep
	Age, breeding experience and pair bond duration	ES, LD, NS, RS, PB	van de Pol & Verhulst, 2006; van de Pol *et al.* accepted
Between observations (unquantified residual error, but also an estimate for within source differences e.g. within females)	Age, breeding experience and pair bond duration	LD, NS, RS, PB	van de Pol & Verhulst, 2006; van de Pol *et al.* accepted
	Stochastic events	All traits	
	Unmeasured differences	All traits	
	Measurement error	All traits	

Methods

Study population and study species

Oystercatchers were studied from 1983-2004 on the Dutch Wadden Sea island of Schiermonnikoog (53°29' N 6°14' W). In this population, oystercatchers breed on the salt-marsh and are dependent on inter-tidal mudflats for their food (bivalves and worms). Breeders defend both a nesting and feeding territory; all breeding birds and fledglings were individually colour marked. The size and location of nesting territories are not completely fixed between years, although most territories are in fact quite stable. When a pair changed the position of their nesting territory between years over a distance of more than 50m this was regarded as a territory switch. The location of feeding territories were not systematically determined, however they are generally strongly spatially linked to the location of the nesting territories (see Ens *et al.* 1992 for maps).

Consequently, switches between nesting territories will usually also have resulted in a change of the feeding location.

Re-sighting probability of breeders in the next breeding season, conditional on survival, is virtually one. Fledged young retain their juvenile plumage till the age of three (i.e. adulthood) and virtually all surviving juveniles return to their natal grounds and were re-sighted (van de Pol *et al.* 2006a). Consequently, whether an individual was re-sighted or not is an unbiased estimator of breeder survival as well as recruitment success in the adult non-breeder pool. Individuals that survived to the next year but did not breed were observed at the communal non-breeder roosts. Oystercatchers are long-lived, socially and genetically monogamous with biparental care (Heg *et al.* 1993; Heg *et al.* 2003); rare polygynous breeding attempts were omitted from analyses (1% of pairs). Oystercatchers usually lay only one clutch a year; however replacement clutches do occur (18% of pairs). For a more detailed description of the annual protocol see Heg & van der Velde (2001).

Life-history traits

We partitioned the phenotypic variance and covariances of eight life-history traits (Table 5.1). For the calculation of lay-date and egg size, the replacement clutches were omitted. In total we recorded 1815 unique annual breeding attempts; sample sizes for individual life-history traits were less complete. Male and female probability of surviving and breeding in the next year were known for all cases. Egg size was not always systematically measured (15.2% missing); lay-date could not always be accurately determined because some nests were found too late (17.2% missing); nest success had missing values due to experimental manipulations (4.6% missing); recruitment success could not yet be determined for the last three years of the study (14.9% missing). For the multivariate analyses it was necessary to transform the life-history parameters of nest and recruitment success into a binary variable (see section statistical analyses), thereby omitting some of the information. The frequency distribution of the number of fledglings produced each year by a pair was 78.7% no fledglings, 15.3% one fledgling, 5.2% two fledglings, 0.8% three fledglings, and 0.1% four fledglings. The frequency distribution of the number of juveniles that recruited in the adult non-breeder pool produced by a pair each year was 92.4% no recruits, 6.6% one recruited juvenile, and 1.0% two recruited juveniles.

Classification of sources of variation and covariation

Phenotypic variances and covariances of all life-history traits were partitioned into five sources that were expected to largely determine overall variance, namely the variance attributable to the (i) year of breeding, (ii) nesting territory in which the breeding attempt occurred, (iii) male parent, (iv) female parent, and (v) individual observation (i.e. residual error). The residual error includes the variance associated with the repeated measures within each of the other four classifications. Each chosen classification can represent several ecological contributory sources of variation (Table 5.2). The idea is that the chosen classifications aggregate many of these ecological effects in five specific types of sources of variance. For example, the classification 'year' describes all biotic and abiotic sources of variation that mainly vary at an annual timescale (e.g. winter weather, food abundance). Some parameters can potentially affect multiple sources of variation. For example, age effects can explain variation within individuals (i.e. between observations), but also between individuals as some individuals were followed at different ages during their lifetime (started reproducing earlier or lived longer than others).

The life-history of Oystercatchers makes it a very suitable species to disentangle these different sources of variation. The longevity of oystercatchers and their rigid territorial system ensured that of nearly all males, females and territories, multiple repeated measurements were recorded (Table 5.3). In addition, occasional divorce (8% annually) and mortality (5% annually) ensured that male and female identities were not always intricately linked during a lifetime; both males and females had on average 1.6 different partners. Territory and individual identities were also not completely linked, firstly because individuals switched between territories, and secondly because territories were sequentially taken over by other individuals. On average each female occupied 1.3 different territories, while males only occupied 1.1 different territories; each territory has on average been occupied by 2.0 different females and 1.8 different males.

Table 5.3 Summary statistics of the data structure used in analyses. There were 1815 separate observations; in 1078 cases all variables were measured, these were used in the multivariate analysis (between brackets). The classification of pair as a source of variation, can be seen as a combination of the male and female identity and is used to study the interaction between sources of variation in males and females.

Source	Number of unique i.d.'s	Mean # obs per i.d. ±s.d	Range # obs per i.d.
Year	22 (19)	82.5±25.6 (56.7±29.3)	29-134 (1-110)
Territory	257 (231)	7.1±5.2 (4.7±3.5)	1-20 (1-15)
Pair	523 (397)	3.5±2.8 (2.7±2.1)	1-17 (1-12)
Male parent	321 (274)	5.7±4.0 (3.9±2.8)	1-19 (1-12)
Female parent	324 (278)	5.6±4.3 (3.9±3.0)	1-19 (1-15)

Statistical analyses

Analyses were performed with the use of Bayesian cross-classified generalized linear mixed models (Browne *et al.* 2006). As the data do not follow a simple hierarchical structure, it is crucial a cross-classified structure is mapped into the structure of the statistical model in order to correctly calculate the variances in the response variable(s). Here we will present the general outline of the procedure, a more detailed description of the methods and the technical details can be found in Browne *et al.* 2006 and Pettifor *et al.* 2006. For each life-history trait we initially ran univariate cross-classified models; followed by a multivariate analysis of all life-history traits in one model. Sample sizes in multivariate analyses were lower than in the univariate analyses; in the multivariate analyses we restricted ourselves to breeding attempts with a full complement of all eight life-history traits (N=1078 cases). We used a recently developed Markov Chain

Monte Carlo (MCMC) algorithm to fit multivariate cross-classified mixed models to a set of life-history traits that have differing error structures (Browne *et al.* 2001); these models have all been implemented in the MLwiN software package (Rasbash *et al.* 2004). We follow the standard notation for specifying complex cross-classified random-effects models as introduced by Browne *et al.* (2001).

For computational reasons we restricted the multivariate analyses to six life-history traits at a time (egg size, lay-date, nest success, surviving juveniles, male survival, and female survival). In addition, we constructed a similar model in which male and female survival was replaced by the probability a male or female would breed the next season. In the multivariate analyses, each of the six responses can be thought of as nested within four separate higher classifications (male parent id., female parent id., territory id., and year id.), which do not themselves exhibit any nesting structure. The multivariate model can be described by the following equation:

$$y_i = \beta_{0i} + u^{(2)}_{male(i)} + u^{(3)}_{female(i)} + u^{(4)}_{territory(i)} + u^{(5)}_{year(i)} + e_i$$

where y_i is a vector of six response variables, β_{0i} is a vector of six intercepts. The four higher level random effects ($u^{(2)}....u^{(5)}$) and the residual error term (e_i) are vectors assumed to be drawn from a multivariate normal distribution with zero mean and their respective variance-covariance matrices (${\Omega_u}^{(2)}{}_{(i)}$, ${\Omega_u}^{(3)}{}_{(i)}$, ${\Omega_u}^{(4)}{}_{(i)}$, ${\Omega_u}^{(5)}{}_{(i)}$, $\Omega_{e(i)}$). This model assumes we have six normally distributed y-variables, while this is only (by approximation) the case for the variables egg size and lay-date. Nest success, recruitment success, male survival and female survival are all binary variables and we used a latent variable approach using a probit link to partition the variance in these binary traits (see chapter 18 in Browne 2002 for details).

A MCMC Bayesian approach requires the specification of prior distributions of all unknown parameters. In our analyses, we do not want to express any prior knowledge and therefore we used zero priors for all β_{0i} as well as for all covariances. For the prior estimates of the variance, we distributed the total variance evenly over all five levels (except for the lowest level variances of binary variables, as the latent variable approach constrains these to equal 1).

Interactions between sources of variation

Differences in life-history traits might be expressed depending on the conditions an individual is in. For example, some females might perform better (or worse) when mated to specific males, either due to genetical, immunological, or behavioral (in)compatibility (Delesalle 1986; Foerster *et al.* 2003). Similarly, some individuals might perform better in one habitat than in other habitats. Such effects can be described as interactions between sources of variation, and in this study we will explore the interaction between the identity of females and males (i.e. pair identity). By including the pair identity as a sixth source of variation ($u^{(6)}{}_{pair(i)}$) we quantify how much of the total variation in life-history traits can be attributed to between pair differences, while controlling for variation due to the individual quality of the female and male pair-members.

Identifying biologically measurable sources of variation

The random effects approach presented above is of interest in its own right, but a logical next step is to identify the biotic and abiotic parameters that explain most of the variation within these sources (Table 5.2). Identifying biologically more realistic parameters not only gives more insight in the mechanisms that result into differences between for example territories, but also suggest which traits could be experimentally manipulated (for determining causation, as well as for conservation). Much of the Oystercatcher research has focused on the effects of territory quality on life-history decisions (Ens *et al.* 1995; Heg *et al.* 2000; Bruinzeel & van de Pol 2003; chapter 8). Territory quality is thought to vary mainly due to differences in the distance between nesting and feeding territories. Some pairs have adjacent nesting and feeding territories (‘residents’) and can walk their semi-precocial chicks to the food, while other pairs (‘leapfrogs’) have non-adjacent nesting and feeding territories and parents have to fly in every food item to their chicks (Ens *et al.* 1992; Safriel *et al.* 1996). Consequently, residents consistently produce two to three times more offspring each year than leapfrogs (Ens *et al.* 1992). By adding territory type (resident or leapfrog) as a fixed effect to the model we can identify how much of the total variation between territories is explained by this dichotomy in feeding ecology.

Results

Partitioning the phenotypic variances within life-history traits

We first calculated the total phenotypic variance of all life-history traits and their coefficient of variation, using a multivariate model without any random effects (Table 5.1). With the exception of egg size, reproductive parameters were very variable. Lay-date was especially variable, with the first nests starting the end of April and the last pairs starting at the beginning of July. Parental survival and the probability parents would breed again the next season were much less variable, as expected in a long-lived species. We partitioned the total variance between the five different sources of variation using univariate as well as multivariate analyses, and the results were generally very similar (Fig. 5.2). In the few cases where the variance components differed substantially between the univariate and multivariate analyses, this was not caused by the larger sample sizes that could be used in the univariate analyses. Differences remained when the same reduced dataset was used in both univariate and multivariate analyses. Multivariate analyses are expected to give the more reliable results, because variance components are estimated while accounting for the covariances between all traits within these same sources of variation. Therefore, we discuss only the results from the multivariate analyses.

Within each life-history trait there were large differences in the amount of variation each source explained. Although many variance components were very small (±5%), their 95% confidence intervals usually did not overlap with zero in the multivariate analyses, indicating they were statistically significantly greater than zero (Fig. 5.2; see

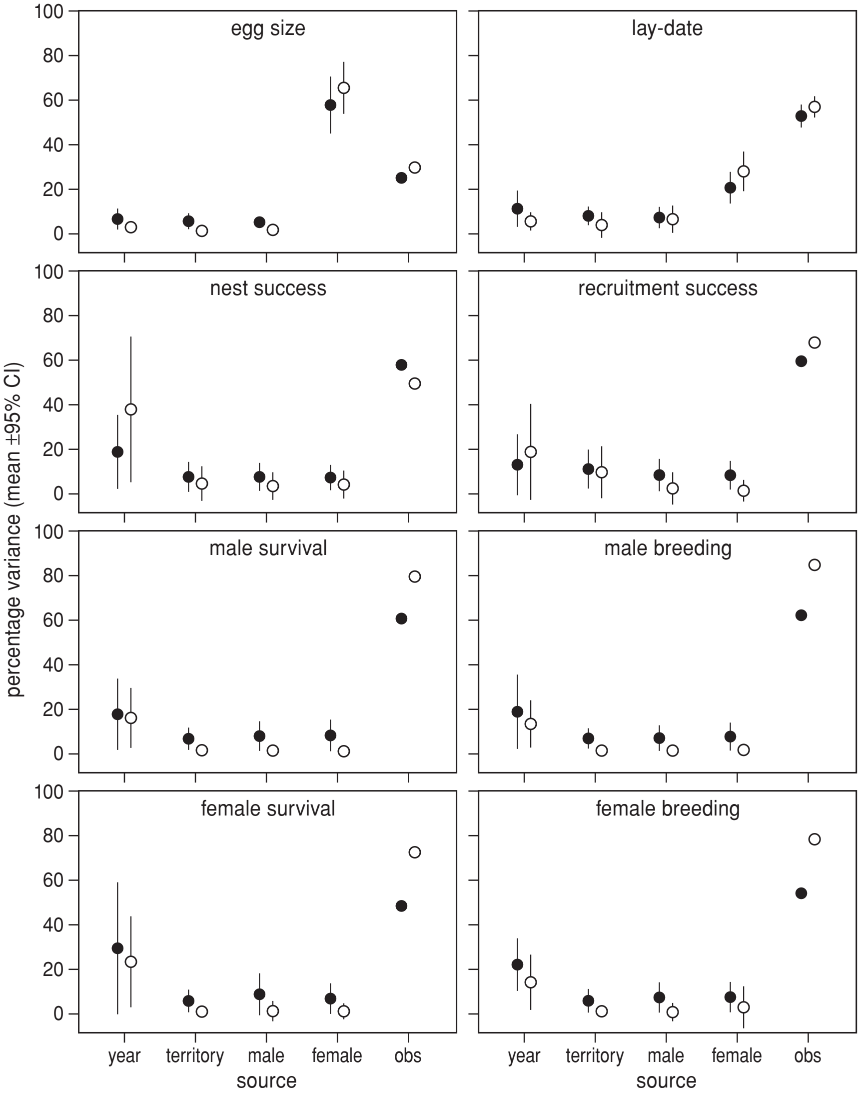


Figure 5.2 Variance components of the five sources of phenotypic variation for the life-history traits: (A) egg size, (B) lay-date, (C) nest-success, (D) recruitment success, (E) survival of the male parent (F) the probability the male parent breeds again next year, (G) survival of the female parent, and (H) the probability the male parent breeds again next year. Variance components (%) and standard error bars are estimated from multivariate analysis (black dots) and univariate analysis (white dots).

Table 5.5 and Table 5A2 for actual values). The relative importance of a specific source of variation varied between the different life-history traits, but nonetheless patterns were quite consistent between traits (Fig. 5.2). Generally most variation in life-history traits was attributable to variation between observations (residual variation). Nonetheless, differences between females explained the largest part of the total variation in egg sizes (58%), and also a substantial part of the total variation in lay-dates (21%). Differences between females only explained minor parts of the variation in reproductive output and parental future performance (all traits 7-8%). Differences between males never explained more than 8% of the total variation of any of the life-history traits. Similarly, differences between territories also never explained more than 8% of the total variation of any of the life-history traits, with the exception that between territory differences explained 11% of the total variation in recruitment success. Differences between years did explain substantial proportions of variations in reproductive parameters (e.g. 19% of total variation in nest success), as well as a large part of the variation in parental survival and the probability the parents would breed again next year (17-29%; Fig. 5.2).

Interactions between sources of phenotypic variation

To test for an interaction between the quality of the male and female, we added a sixth source of variation to the model, the pair identity (male identity female identity). Because some males and females never switched partners during their life, this might reduce the power to accurately partition the overall phenotypic variation between the male, female and pair level. We investigated this potential problem, by conducting the same analyses on a reduced dataset in which all males and females were mated with at least two different partners during their life. The results of the analyses on both datasets were very similar, and therefore only the results of the large dataset will be presented as there seemed to be no problems in accurately partitioning overall variance between sources.

A comparison with the analysis in which only a female and male level were used, suggested that part of the variation in egg size and lay-date that was previously attributed to between female differences, were actually better explained by between pair differences (Fig. 5.3). The addition of a pair level did not reduce the male and female variance component for other life-history traits (Fig. 5.3). Differences between pairs only explained small parts of the total variation in life-history traits, nonetheless 95% confidence intervals of the pair variance components did not overlap with zero in any of the life-history traits (not shown). Although differences between pairs only explained relatively small parts of the total variation, the pair variance components were of similar magnitude as the male and female variance components for most life-history traits. Variation in nest success, recruitment success, parental survival, and in the probability the parents will breed again next year are therefore equally well explained by between female, male and pair differences, and cannot a priori be regarded as sex-linked life-history traits.

The use of territory type as a measure of territory quality

We investigated how much of the variation between territories could be attributed to differences in territory type (whether or not parents could take their chicks directly to the feeding territory: residents *vs*. leapfrogs). Adding territory type as a fixed effect to the model reduced the variance component of the territory level for all reproductive variables, but reductions were generally quite small (not shown). Although residents

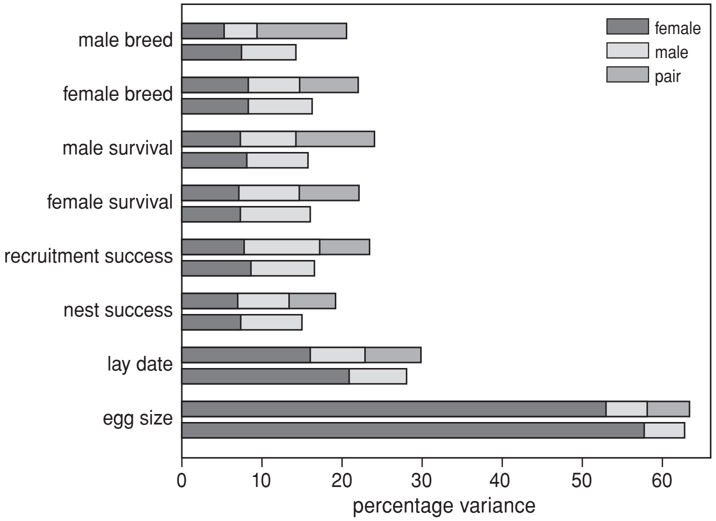


Figure 5.3 Cumulative variance components of the female, male, and pair for all life-history traits. For each life history trait the variance components are shown for the model without a pair level (bottom bars) and for the model with a pair level (top bars). See text for further explanation.

have a three times higher recruitment success, a twice as high nesting success, lay on average five days earlier, and lay 3% larger eggs, territory type only explained a minor part (at most 30%) of the variation between territories in these reproductive variables. Although territory type is an indicator of territory quality, not all resident territories consistently performed better than leapfrog territories and considerable variation in reproductive performance remains between territories of the same territory type (Fig. 5.4). The values presented in Fig. 5.4 are corrected for variation in the quality of the male and female occupants, and as such represent an estimate of territory quality occupied by an average individual in an average year. Therefore even after correcting for differences in individual quality of territory owners (which might be associated with territory quality), resident territories still produce more offspring than leapfrog territories.

Partitioning the phenotypic covariances within life-history traits

We first calculated the overall phenotypic covariations between all life-history traits at the level of the population (Table 5.4). All reproductive variables covaried strongly with each other, and the signs of the covariances were in most cases consistent with the general patterns in most bird species: laying larger eggs was positively, and laying late in the season was negatively associated with nesting and recruitment success. Furthermore, nesting success was strongly positively correlated with recruitment success. Female survival was positively correlated with male survival and the same was true for the correlation between female breeding and male breeding (Table 5.4; Table 5.A1). Most interestingly, recruitment success was positively associated with female and male survival, although only the latter covariation was significant at the 5% level.

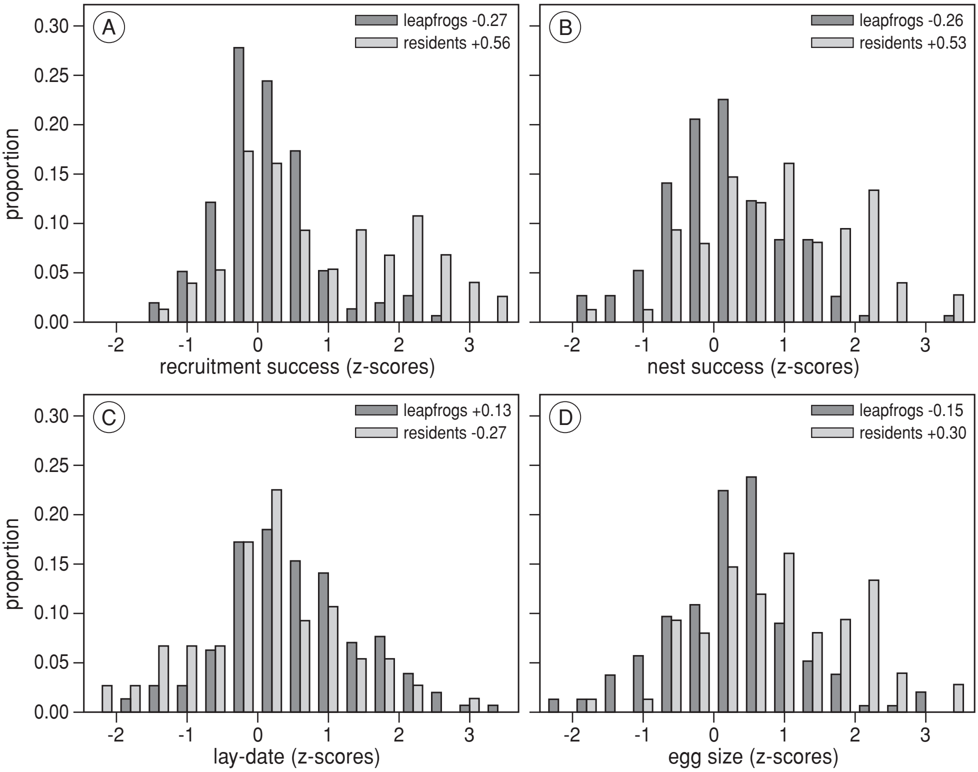


Figure 5.4 Variation between territories in (A) recruitment success. (B) nest success, (C) lay-date, and (D) egg size separated by territory type (resident or leapfrog). Shown is the relative distribution of values per territory (n=231) for each of the four parameters (using z-scores). Resident territories are depicted by light bars and leapfrog territories by dark bars. Group means per territory type are given in the top right corner; proportions sum up to one for each territory type seperately. The value of each territory is corrected for variation in the quality of the male and female occupying it, as well as for variation in the quality of the year in which territories were followed.

Subsequently, we partitioned the overall phenotypic covariations between the life-history traits between the five different sources of variation. Using a multivariate model with six life-history traits reduced the sample sizes considerably due to the omission of breeding attempts with missing values for specific traits (1078 cases per variable were used). Simpler multivariate analyses, for example a tri-variate model with nest success and male and female survival were performed on substantially larger dataset (1732 cases), but resulted in qualitatively similar results and are therefore not presented.

Overall, we found very few covariances between life-history traits within the different sources of variation that were statistically significant at the 5% level, or even at the 10% level (Table 5.5). The statistically significant covariances we did observe were primarily covariances at the between observations level. We found no evidence that covariances between pairs of life-history traits at different levels were of opposite sign.

Table 5.4 Raw covariations in single level multivariate model of the six life history traits. Models run for $2*10^5$ iterations using the data standardised to zero mean and unit variance in the case of egg size and lay-date, and probit errors for nest success, recruitment success and parental survival. Parameter estimates are given alongside the s.e.; covariances that were significant at the 5% level are italicized and underlined.

Trait	Egg size	Lay-date	Nest success	Recruitment success	Female survival	Male survival
Egg size	1					
Lay-date	*-0.149±0.032*	1				
Nest success	*0.108±0.041*	*-0.332±0.044*	1			
Recr. success.	*0.143±0.063*	*-0.293±0.056*	*0.937±0.028*	1		
Female survival	-0.042±0.062	0.031±0.054	-0.037±0.070	0.110±0.125	1	
Male survival	-0.041±0.054	-0.031±0.054	0.041±0.069	*0.178±0.089*	*0.220±0.086*	1

Furthermore, the addition of age of the male and the female to the model did not qualitatively affect the patterns of covariance, suggesting the observed covariances were not caused by similar effects of ageing in different life-history traits.

We did not find any covariances between life-history traits at the between year level, while differences between years did explain substantial parts of the total phenotypic variation in these same life-history traits. This suggests that the biological sources of variation that vary between years might be different for most life-history traits. For example, in some years food availability was high and this resulted in a high nesting success, while adult survival mainly varies as a result of winter harshness (chapter 2). High food availability and winter harshness do not covary. Alternatively, the statistical power to detect covariations at the between year level is probably lowest of all. Although the estimates per year are based on many observations and are probably very reliable, we can only compare the data between the 22 years we followed this population. Two between years covariations were close to statistical significance ($P<0.10$), which were a positive covariance between male and female survival and a positive covariance between male and female breeding (Table 5.A2). In years with a high probability for the female to survive and breed again the next year, the male probability of surviving and breeding again the next year was also high, suggesting that the annual source of variation is probably very similar for all these traits (e.g. winter harshness).

We did not find any significant covariances at the between territories and between males level. The only significant covariation we found at the between females level was a negative covariation between lay-date and nest success. This means that some females consistently laid early and produced many fledglings while other females consistently laid late and produced almost no offspring. This result is consistent with the individual quality hypothesis (Fig. 5.1B). All other covariances were not statistically significant ($P>0.10$; Table 5.5).

Table 5.5 The variances (diagonals in bold) and covariances (below diagonals) of the six life history traits from multivariate cross-classified models run for $2*10^5$ iterations using the data standardized to zero mean and unit variance in the case of egg size and lay-date, and probit errors for nest success, recruitment success, and parental survival. Parameter estimates are given alongside the standard errors. Where 95% CI do not overlap with zero, they are italicized and underlined; where 90% CI do not overlap with zero, they are grey italicized and underlined. †Variances at lowest levels are constrained to equal one for variables with probit errors, see methods.

	Trait	Egg size	Lay-date	Nest success	Recruitment success	Female survival	Male survival
Between years	Egg size	*0.062±0.025*					
	Lay-date	-0.016±0.025	*0.129±0.053*				
	Nest success	0.006±0.040	0.049±0.061	*0.322±0.154*			
	Recr. success	0.003±0.034	0.042±0.054	0.126±0.108	*0.217±0.125*		
	Female survival	0.034±0.056	0.001±0.085	-0.067±0.147	0.105±0.130	*0.602±0.304*	
	Male survival	0.029±0.039	-0.006±0.059	-0.008±0.099	0.076±0.088	*0.294±0.162*	*0.288±0.135*
Between territories	Egg size	*0.056±0.017*					
	Lay-date	-0.019±0.016	*0.087±0.028*				
	Nest success	0.019±0.021	-0.035±0.031	*0.139±0.062*			
	Recr. success	0.022±0.026	-0.034±0.036	0.093±0.064	*0.183±0.092*		
	Female survival	0.005±0.020	0.002±0.029	0.015±0.042	0.020±0.051	*0.120±0.057*	
	Male survival	-0.001±0.019	-0.009±0.026	0.012±0.038	0.020±0.046	-0.007±0.035	*0.108±0.048*
Between males	Egg size	*0.051±0.014*					
	Lay-date	-0.017±0.014	*0.084±0.026*				
	Nest success	0.019±0.019	-0.036±0.029	*0.129±0.054*			
	Recr. success	0.010±0.020	-0.026±0.032	0.062±0.053	*0.135±0.071*		
	Female survival	-0.005±0.022	0.031±0.034	-0.015±0.048	-0.008±0.053	*0.177±0.093*	
	Male survival	-0.001±0.019	-0.004±0.029	0.004±0.040	-0.005±0.042	-0.027±0.052	*0.128±0.063*
Between females	Egg Size	*0.573±0.064*					
	Lay date	-0.011±0.039	*0.238±0.046*				
	Nest success	0.059±0.051	*-0.084±0.040*	*0.125±0.048*			
	Recr. success	0.090±0.066	-0.063±0.048	0.068±0.046	*0.141±0.065*		
	Female survival	-0.070±0.069	-0.012±0.052	-0.003±0.040	-0.017±0.045	*0.148±0.075*	
	Male survival	-0.037±0.061	0.003±0.045	0.001±0.037	0.010±0.041	-0.019±0.048	*0.132±0.062*
Between observations	Egg Size	*0.250±0.013*					
	Lay date	*-0.052±0.012*	*0.610±0.032*				
	Nest success	0.000±0.025	*-0.232±0.041*	1†			
	Recr. success	0.014±0.036	*-0.207±0.054*	*0.967±0.017*	1†		
	Female survival	-0.007±0.043	0.010±0.062	-0.013±0.092	-0.043±0.128	1†	
	Male survival	-0.042±0.036	-0.002±0.057	-0.015±0.110	-0.029±0.130	0.109±0.124	1†

We did find several covariations between pairs of life-history traits within individual observations, which largely mirrored the phenotypic correlations observed at the population level (Table 5.4 vs. Table 5.5). While controlling for variation due to differences between years, territories, males and females, we found negative associations between lay-date on the one hand and egg size, nest success and recruitment success on the other hand. We also observed a strong positive covariation between nest success and recruitment success. All covariations between measures of current reproductive performance and future survival or performance did not approach significance, suggesting that there were no measurable costs of reproduction in terms of mortality or future probability of breeding again in this population. Finally, the probability a female would breed again the next season strongly positively covaried with the probability her male partner would also breed again the next season (Table 5.A2).

Discussion

The recently developed statistical technique we used in this paper (cf. Pettifor *et al.* 2006; Browne *et al.* 2006), allowed us to address questions such as: What are the main sources of variation? Are life-history traits sex-linked traits? What are the patterns of life-history covariation and do they differ between levels? Do oystercatchers have a cost of reproduction? Is the observation that early laying individuals produce more offspring best explained by the date-hypothesis or the individual quality hypothesis, and how does this compare to an experimental approach? Here we will discuss how our results affected our ideas about these questions.

What are the main sources of phenotypic variation: environmental factors

Although the importance of different sources of phenotypic variation differed between life-history traits, differences between observations explained most of the overall variation (as also found in Great tits; Pettifor *et al.* 2006). Differences between observations could arise due to measurement error, age-specific changes during a lifetime, and stochastic events (Table 5.2). We do not think that measurement errors were an important source of variation; especially traits such as nest success could be measured with high accuracy in this species. Although reproductive variables can differ strongly between age-classes (van de Pol & Verhulst 2006; chapter 4; box B), age-differences did not explain much of the variation between observations or between individuals (as also found in Great tits; Pettifor *et al.* 2006). Consequently, although the selective forces that act on age-specific reproductive decisions might be strong, the selective opportunities might actually be rather limited. Stochastic events were likely to be the main source of variation in most life-history traits of Oystercatchers. Such stochastic events might be non-systematic variation in biotic and abiotic conditions within years, within the same territory between years, or within the same male or female between years (e.g. food availability, predators, diseases, human disturbance, hunting).

Another important source of environmental variation in life-history traits was caused by variation between years. Especially the parental survival and probability the parents would breed again differed strongly between years, which is in accordance with the idea that adult survival is mainly driven by variation in winter harshness, which can differ strongly between years (Camphuysen *et al.* 1996; Nève & van Noordwijk 1997; chapter 2). Nest success also strongly varied between years, which is probably caused by fluctuations in the summer food availability (chapter 2).

Surprisingly, differences between territories only explained minor parts of the total variation. Much of the work on this population of Oystercatchers has focused on habitat selection, as territories strongly differ consistently in their reproductive output (Ens *et al.* 1995; Bruinzeel & van de Pol 2003; van de Pol *et al.* 2006b; chapter 8). Territory type (whether or not parents could take their chicks to the feeding territory) is thought to be the main determinant of territory quality (Ens *et al.* 1992) and a driving force behind settlement decisions (Ens *et al.* 1995; chapter 8). Interestingly, territory type only explained a minor part (30%) of the total variation in reproductive performance between territories. Although the use of territory type as a cue for territory quality is informative, these results suggest that there might be other aspects of territories we have not considered yet that might also be very important determinants of territory quality and thereby of settlement strategies in Oystercatchers.

For most traits, the variation due to environmental sources was much more important than phenotypic variation attributable to differences between individuals. Although we have no knowledge of the extent to which individual differences in, for example, lay-date might reflect genetic differences, the phenotypic variation that is under genetic control cannot exceed the total variance explained by the female and male components. Consequently, the genetic component of phenotypic variation is probably rather small for most life-history traits. As such, the phenotypic selection pressure for e.g. laying early is probably quite strong, but might primarily act on the environmental component of phenotypic variation.

The role of the female, male and pair quality

One crucial difference of our approach with most other studies is that all life-history traits are expressed as the phenotype of a pair of individuals, which allows us to disentangle the relative importance of the role of the female as well the male. Furthermore, the addition of a pair level, allowed us to investigate whether some combinations of males and females consistently behaved differently than other pairs, independent of their own individual quality. The fact that females lay the eggs and in the majority of species provide most parental care might be used as an argument to assume that reproductive traits are most dependent on variation in female quality. Nonetheless, male quality can directly affect life-history traits because in many species males do also contribute to parental duties. In addition, male quality can indirectly affect life-history because females might adjust their reproductive effort to the perceived quality of the male (Sheldon 2000), or her compatibility with the male (i.e. pair quality). For example, specific pairs might produce more offspring because they are genetically more compatible (e.g. Foerster *et al.* 2003), or because some male and females cooperate better than other pairs in raising their offspring (e.g. Delesalle 1986).

Between female differences were the main source of variation in the size of Oystercatcher's eggs, which is consistent with the general idea that egg size is a strongly female inherited trait in birds (Christians 2002). Variation in lay-date was for a substantial part explained by differences between females, but an equally large part of the variation was explained by the combined effect of the male quality and the compatibility between the male and female, the pair quality. In the period before egg-laying, Oystercatchers pairs together defend feeding territories, during which the behavior of the male or the intra-pair cooperation might directly influence the food intake and body condition of the female. Laying early is probably constrained by reaching a certain body condition for the initiation of egg production (Heg 1999); males that are good at defending high quality feeding territories could indirectly influence the timing of breeding of their partner. As parental care is not sex-biased in Oystercatchers, it may not be completely surprising that the variation in nesting and recruitment success was equally well explained by variation due to differences between females, males as well as pairs. The variation between pairs in nesting or recruitment success could be explained by genetic compatibility, but this is not a viable explanation for the differences between pairs in lay-date and survival (see next section). Variation in pair quality could also be explained by differences in the pair bond duration between pairs, as pairs that have been together for many years outperformed newly formed pairs (chapter 4).

Surprisingly, for both sexes the variation in annual survival propensity was also affected by differences in the qualities of the partner. This suggests that an individual's survival propensity ('frailty') not only depends on its own quality, but also on the individual one is associated with. The mechanism behind a direct effect of partner and pair quality on the survival of Oystercatchers might again result from the fact that Oystercatcher pairs cooperatively defend feeding territories for at least some parts of the winter (when most mortality occurs). Alternatively, infectious diseases might be another explanation why survival propensities in Oystercatchers strongly depend on the quality of their partners.

In conclusion, with the exception of egg size, life-history traits in Oystercatchers are by no means sex-linked traits. This result is in sharp contrast of how these life-history traits are treated in the literature. When traits are expressed as a function of the phenotype of both the male and the female, and the interaction between these two phenotypes the evolutionary dynamics of these life-history traits are much more complicated (Moore *et al.* 1998; Wolf *et al.* 1999). It remains to be established to what extent socially monogamous Oystercatchers, which operate as a pair for most of the year, are an exceptional species in this respect.

Sources of phenotypic covariation between life-history traits

By partitioning the covariances among different life-history traits to a number of major sources, we identified several important insights in the relationship between these life-history traits in this population. In general, the patterns of raw phenotypic covariance in the population were best reflected by similar covariances at the between observation level, suggesting that these covariances reflected (possibly adaptive) within-individual adjustments to stochastic events. For example, lay-date and egg size most strongly covaried (negatively) at the between observation level. The observation that eggs laid late in the season are smaller is consistent with the time-saving hypothesis, which suggests that laying small eggs is an adaptive way to save time and advance egg laying (Birkhead & Nettleship 1982). There was no evidence that the covariance between egg size and lay-date was a non-adaptive by-product of female quality (e.g. female size), which would have resulted in a covariance at the between female level (Hipfner *et al.* 1997).

Our results sharply contrast to the patterns of covariation found at different levels in Great tits (Pettifor *et al.* 2006), while most of the life-history traits investigated were identical. In Great tits, several phenotypic covariations between life-history traits at the population level were the result of underlying covariances at multiple levels, which were also often of opposing sign. Covariations at the population level in Great tits were quite often caused by good individual/bad individual effects, meaning that some individuals were for example both good reproducers as well as good survivors. Similarly, good territory/bad territory effects, and good year/bad year effects also resulted in covariances at the population level in Great tits, but not in Oystercatchers. Life-history traits in long-lived Oystercatchers seem to be more variable in resource allocation, while Great tits more strongly vary in their resource acquisition.

At least as interesting as the presence of significant covariations between some traits is the absence of covariations between others. For example, the absence of negative covariations between life-history traits that reflect the current reproduction (e.g. nest or recruitment success) and life-history traits that reflect the future success (e.g. parental survival or breeding) are of interest from a ‘cost of reproduction’ perspective. Interestingly the raw phenotypic pattern of covariation suggests that a high recruitment success is positively associated with a high probability the male will survive and breed again the next year. One explanation for such pattern is that the covariations between these pairs of traits differed in sign between different levels (as depicted in Fig. 5.1A and as found by Pettifor *et al.* 2006 in the Great tit), but we did not find any evidence to support this hypothesis. Potentially the positive phenotypic covariation at the population level is in fact a spurious relationship, which might result from neglecting the multilevel structuring of the data. Nonetheless, our results also failed to show a negative covariation between any measure of current performance and future performance, suggesting Oystercatchers do not seem to exhibit a measurable cost of reproduction in terms of future survival or breeding probability.

The absence of a negative covariance between measures of current reproduction and future performance clearly requires some explanation. One possible explanation would be that a (small) cost of reproduction does exist in Oystercatchers, but that our data set is too small to detect it. Stochastic annual events are of considerable importance in determining the variance of life-history traits in Oystercatchers, and these stochastic events might override any signal that is indicative of a cost of reproduction. Secondly, increases in current reproductive investment might have resulted in lower reproductive success in the next breeding season, which we have not analyzed. Thirdly, it might be that Oystercatchers restrain their reproductive effort such that they never face any future costs of their current investments. Reproductive restraint to avoid costs of reproduction might be a very logical thing to do for a long-lived species, because the residual reproductive values usually are an order of magnitude higher than the current reproductive value of a clutch (Box B). Nonetheless, this scenario does not exclude that if one would be able to experimentally increase the reproductive effort of Oystercatchers beyond their normal level of effort, that a cost of reproduction would be detectable.

Comparison with an experimental approach

One of the aims of partitioning the phenotypic covariances between life-history traits among different sources of variation was to assess the validity of different causal models to explain life-history variation. We suggested that by determining the patterns of covariance between lay-date and nest success at different levels it is possible to distinguish between competing hypotheses that differed in their causal pathways (Fig. 5.1B). Our results suggest that both the date hypothesis as well as the individual quality hypothesis were supported. Females that laid consistently early also had a high nest success, while late laying females had a low nest success, which was consistent with the individual quality hypothesis (Fig. 5.1B). At the same time, lay-date and nest success negatively covaried even more strongly within females, suggesting that females that laid late in some years also had a low nest success, but when these same individuals laid early in another year they had a high nesting success. This suggests that laying early is not (only) a simple by-product of female quality, but that lay-date causally affects nest success as suggested by the date-hypothesis (Fig. 5.1B). The phenotypic covariation at the population level was estimated to be -0.33±0.04, the between observation covariation best reflected this relationship (-0.23±0.04), while the between female covariation was much lower (-0.08±0.04). This suggests that although both individual quality and timing were important, most of the seasonal decline in nest success was causally related to the timing of breeding while only a small part was related to quality differences between females. These results were virtually identical to the conclusion reached in a lay-date manipulation experiment performed in the same population, which also aimed to distinguish between these two hypotheses (Heg 1999). By giving late pairs early hatching broods and early pairs late hatching broods, Heg (1999) showed that advanced pairs and delayed pairs had a nest success that was similar to that expected by the natural population trend of hatching dates in Oystercatchers. As such his results also strongly suggested that the date hypothesis was the most important explanation for the decline in nest success during the season. In addition he also recognized that there was an additional effect of female quality, because some females always laid early and had a high nest success.

We suggest that partitioning of covariance between different sources of variation can be used as a powerful ally to experiments to investigate causal pathways. In some cases an observational approach may even be a useful alternative to an experimental approach, as life-history experiments can be intrinsically biased. Researcher aim to manipulate only the life-history trait of interest, but often it is unclear to what extent this is a realistic assumption and whether other biases might occur. For example, when manipulating lay-date by giving some individuals earlier hatching eggs, the incubation period is also shortened. If a shorter incubation period positively affects the condition of the parents, this might also explain why pairs with advanced clutches had an increased nest success.

The results from our analysis can also be used to improve the design of life-history experiments. For example, using the covariations estimated at the between observation level instead of the phenotypic covariations at the population level allows a better prediction of the expected change (i.e. natural trend) in experiments that manipulate life-history traits. In addition, within-individual estimates of covariation can be used to determine appropriate sample sizes for performing experiments, and might warn researchers that certain experimental manipulations of life-history traits may require huge sample sizes (in the order of thousands) in order to be likely to detect an effect of a manipulation.

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Appendix 5.A

Table 5.A1 Raw correlations in single level multivariate model of the six life history traits. Models run for $2*10^5$ iterations using the data standardised to zero mean and unit variance in the case of egg size and lay-date, and probit errors for nest success, recruitment success and parental breeding. Parameter estimates are given alongside the s.e.; covariances that were significant at the 5% level are italicized and underlined.

Trait	Egg size	Lay-date	Nest success	Recruitment success	Female breeding	Male breeding
Egg size	1					
Lay-date	*-0.148±0.031*	1				
Nest success	*0.110±0.043*	*-0.326±0.042*	1			
Recr. success.	*0.144±0.067*	*-0.285±0.055*	*0.942±0.028*	1		
Female breeding	0.006±0.050	-0.011±0.052	0.033±0.067	0.106±0.084	1	
Male breeding	-0.040±0.050	0.013±0.051	0.024±0.065	*0.180±0.082*	*0.527±0.056*	1

Table 5.A2 The variances (diagonals in bold) and covariances (below diagonals) of the six life history traits from multivariate cross-classified models run for $2*10^5$ iterations using the data standardised to zero mean and unit variance in the case of egg size and lay-date, and probit errors for nest success, recruitment success, and parental breeding. Parameter estimates are given alongside the standard errors. Where 95% CI do not overlap with zero, they are italicized and underlined; where 90% CI do not overlap with zero, they are grey italicized and underlined. †Variances at lowest levels are constrained to equal one for variables with probit errors, see methods.

	Trait	Egg size	Lay-date	Nest success	Recruitment success	Female breeding	Male breeding
Between years	Egg size	*0.062±0.025*					
	Lay-date	-0.017±0.025	*0.126±0.051*				
	Nest success	0.004±0.041	0.050±0.062	*0.336±0.164*			
	Recr. success	0.001±0.032	0.037±0.051	0.115±0.101	*0.197±0.112*		
	Female breeding	0.043±0.047	-0.026±0.068	-0.062±0.123	0.054±0.097	*0.399±0.112*	
	Male breeding	0.030±0.036	-0.018±0.053	-0.033±0.095	0.051±0.076	*0.215±0.112*	*0.291±0.137*
Between territories	Egg size	*0.056±0.017*					
	Lay-date	-0.019±0.016	*0.084±0.027*				
	Nest success	0.018±0.021	-0.034±0.030	*0.138±0.060*			
	Recr. success	0.020±0.022	-0.032±0.034	0.085±0.059	*0.167±0.083*		
	Female breeding	0.005±0.020	0.003±0.026	0.021±0.039	0.024±0.046	*0.116±0.050*	
	Male breeding	-0.001±0.018	-0.006±0.023	0.016±0.034	0.020±0.040	-0.015±0.032	*0.098±0.041*
Between males	Egg size	*0.052±0.014*					
	Lay-date	-0.016±0.014	*0.079±0.025*				
	Nest success	0.020±0.019	-0.032±0.028	*0.129±0.056*			
	Recr. success	0.011±0.020	-0.025±0.030	0.060±0.051	*0.127±0.066*		
	Female breeding	0.003±0.021	0.014±0.027	0.012±0.041	0.005±0.043	*0.144±0.067*	
	Male breeding	-0.005±0.018	0.004±0.025	-0.011±0.038	-0.016±0.038	0.006±0.038	*0.112±0.049*
Between females	Egg Size	*0.591±0.066*					
	Lay date	--0.010±0.039	*0.227±0.043*				
	Nest success	0.052±0.051	-*0.086±0.039*	*0.124±0.047*			
	Recr. success	0.091±0.066	-0.056±0.044	0.063±0.041	*0.132±0.056*		
	Female breeding	-0.068±0.060	-0.035±0.045	0.022±0.039	0.004±0.041	*0.149±0.068*	
	Male breeding	-0.038±0.056	0.007±0.040	-0.005±0.033	0.002±0.035	-0.001±0.040	*0.118±0.052*
Between observations	Egg Size	*0.258±0.013*					
	Lay date	-*0.054±0.015*	*0.584±0.031*				
	Nest success	0.012±0.026	-*0.219±0.040*	1†			
	Recr. success	0.024±0.035	-*0.200±0.068*	*0.963±0.020*	1†		
	Female breeding	0.049±0.036	0.009±0.052	0.084±0.092	0.053±0.103	1†	
	Male breeding	-0.027±0.035	0.028±0.049	0.043±0.086	0.110±0.106	*0.547±0.088*	1†

Chapter 6

Rearing conditions determine offspring survival independent of egg quality: a cross-foster experiment with Oystercatchers

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Abstract

Variation in rearing conditions, either due to parental or environmental quality, can result in offspring of different quality (e.g. body condition, immune function). However, evidence is accumulating that egg-size and composition can also affect offspring quality. In Oystercatchers *Haematopus ostralegus* high-quality rearing conditions result in a higher quantity as well as quality of offspring. This is thought to be caused by increased parental food provisioning to the chicks in high-quality environments. However, variation in egg quality between rearing conditions could also affect the quantity and quality of offspring. Determining the mechanism and ontogeny of quality differences is important in unravelling the causes of variation in reproductive success.

To disentangle the effects of egg quality, and quality of the rearing conditions, on the future survival of offspring, we cross-fostered complete clutches between nests. When reared under conditions of similar environmental quality, chicks originating from eggs laid in low-quality environments survived as well as chicks originating from eggs laid in a high-quality environment. However, chicks reared in high-quality environments survived twice as long as chicks reared in low-quality environments, independent of the environmental quality in which the eggs were laid. This suggests that variation in the future survival of offspring is primarily caused by differences in environmental and / or parental quality, with no clear effect of egg quality (size).

Introduction

Variation in rearing conditions, either due to parental or environmental quality, can result in offspring of different quality. Offspring quality can be expressed as offspring mass, structural size and physiological condition. Quality differences, resulting from conditions experienced during early development, can have important long-term fitness consequences (Lindström 1999). Recently, evidence has accumulated that parents can also influence offspring quality by laying eggs of different quality. Egg-size (Williams 1994, Hipfner 2000) and egg composition (nutritional, immunological and hormonal content) (Saino *et al.* 2003, Eising *et al.* 2001) can affect chick immune function, growth or survival. Furthermore, intra-clutch variation in egg-size and composition could result in hatching asynchrony or intra-clutch variability in hatchling mass and as such could affect sibling competition and survival (Slagsvold *et al.* 1984). Determining the exact mechanism (quality of rearing conditions vs. egg quality) and understanding the ontogeny of quality differences are important in assessing the causal effects these life-history traits have on fitness.

In Oystercatchers *Haematopus ostralegus*, rearing conditions are thought to have a strong effect on both the quantity and quality of offspring. Rearing conditions in Oystercatchers mainly vary as a result of the feeding ecology during the chick phase (Ens *et al.* 1992). Some parents (also called ‘residents’) can take their semi-precocial chicks to their adjacent feeding territory and feed them there (high-quality conditions). Other parents (also called ‘leapfrogs’) have to fly to their non-adjacent feeding territory and transport every food item back to their chicks (low-quality conditions). The quality of rearing conditions is therefore mainly thought to be determined by environmental quality (spatial organization of territory), possibly inter-correlated with parental quality. Pairs in high-quality environments consistently produce almost three times more fledglings per year than do pairs in low-quality environments Furthermore, fledglings reared under high-quality conditions are on average 10% heavier than fledglings reared under low-quality conditions (Ens *et al.* 1992, Bruinzeel 2004). However, egg quality might also vary between environments of different quality, either as a result of differences in feeding areas or of differences in female quality. For example, under high-quality rearing conditions egg-size is greater than under low-quality rearing conditions (Heg & van der Velde 2001). Amounts of fat, yolk, carotenoids or androgens deposited in the egg or the genetic quality of the egg might also differ between high and low-quality rearing conditions, but this has not yet been investigated. Furthermore, intra-clutch variation in egg-size is larger under low-quality conditions than under high-quality conditions (Heg & van der Velde 2001).

Both egg-size (and composition) and intra-clutch variability could affect offspring quantity and quality. However all these possible components of egg quality and the quality of offspring co-vary with the quality of rearing conditions. This makes it difficult to disentangle whether egg quality or the rearing condition is responsible for the observed differences in quantity and quality of offspring between high and low-quality environments. Cross-foster experiments are necessary to disentangle any possible effects of egg quality and/or rearing conditions on the future prospects of offspring (e.g. Bolton 1991, Bize *et al.* 2002 and reference therein). Here, we cross-fostered complete clutches of eggs originating from high and low-quality rearing environments to nests in either high or low-quality rearing environments and followed the growth and survival of the chicks.

Reproductive success has declined strongly over the last two decades in this population (Bruinzeel 2004), and during the same period the average egg-size decreased by 3% (chapter 2). Investigating the causal effect of egg-size on reproductive success by conducting a cross-foster experiment allows us to assess whether the decline in reproductive success is (at least partly) caused by a decline in egg-size.

Methods

Study area and nest searches

The study was conducted on the Dutch Wadden Sea island of Schiermonnikoog (32°29’ N 6°14’ W), in the years 2002 and 2003. The study area consisted of a salt marsh area where the colour-ringed Oystercatchers bred and inter-tidal mud flats where they fed. Following earlier studies, we designated territories with adjacent feeding and nesting areas as high-quality rearing conditions and territories with spatially separated feeding and nesting areas as low-quality rearing conditions (Ens *et al.* 1992, 1995). Nest searches were conducted from the end of April until the end of July, and territories were visited every other day to search for new nests and to check existing nests for new eggs. The identity of the parents was noted and the location of the nest was mapped. Oystercatchers lay 1–4 eggs with an interval of 28h, resulting in a modal clutch size of 3 eggs (Strijkstra 1986). All newly-found eggs were individually marked, weighed to the nearest 0.1g using a balance and egg-width and egg-length were measured to the nearest 0.1mm using dial callipers. Egg-size (volume in cm^3) was determined by 0.49*egg-length[cm]*(egg-width[cm])^2 (Jager *et al.* 2000). Intra-clutch variation in egg-size was calculated by the difference in egg-size between the largest and the smallest egg in a clutch.

The clutch-completion date is the laying date of the last-laid egg in a clutch and coincides with the start of incubation. The clutch-completion date could be calculated by two different methods. First, when a nest was newly discovered it usually contained only one or two eggs. During the next nest checks, new eggs were found and the day on which the last egg was laid was taken as the clutch-completion date. Secondly, in some cases we found nests in which no new eggs were laid during any later visits. In these cases, to determine the date of clutch completion, we made use of the fact that eggs lost weight at a constant rate through evaporation of water during incubation. Because Oystercatchers only started incubating after the last egg was laid, the number of days each egg in a clutch was already incubated could be determined by 199.0-183.5*(weight[g]/egg-size[cm^3]) for a one- to three-egg clutch and by 191.1-176.2*(weight[g]/egg-size[cm^3]) for a four-egg clutch. The clutch-completion date could then be determined by subtracting the number of days an egg has been incubated from the date the eggs were measured, taking the egg that had been incubated for the shortest period. This method is based on calibration from data from daily-weighed eggs (Strijkstra, 1986). Both methods gave a clutch-completion date with an error interval of one or two days.

Cross-foster experiment

We selected four nests for each experimental set, comprising two nests under high-quality rearing conditions and two nests under low-quality rearing conditions. We cross-fostered complete clutches as illustrated in Figure 6.1. This way we created clutches under high-quality rearing conditions with eggs originating from either high or low-quality environments and we created clutches under low-quality rearing conditions with eggs originating from either high or low-quality environments. Nests with eggs originating from either high or low-quality environments, but with the same quality of rearing conditions were considered statistically to be a paired unit (comparison ‘E’ in Fig. 6.1). Furthermore, nests with eggs originating from the same type of environmental quality, but with different rearing conditions were also considered as a paired unit (comparison ‘R’ in Fig. 6.1).

All nests in one experimental set were matched on the same clutch-completion date (±1 day), as this date strongly affects fledging success and mass at fledging in Oystercatchers (Heg 1999). In addition, nests were matched on the number of eggs present on the day on which the eggs were experimentally swapped. In a few cases (14%) we induced artificial ‘predation’ to equalize the number of eggs, by removing one or two randomly selected eggs from clutches. Furthermore, the spatial distance between the four nests in one set was never more than 400m, to reduce any possible effects of

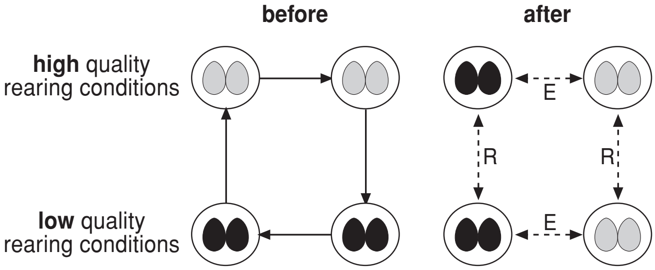

Figure 6.1 Schematic design of the cross-foster experiment. One swap set consisted of four nests (white circles), in which eggs from high-quality rearing environments (grey) and low-quality rearing environments (black) were swapped to other nests following the arrows in the left panel. As a result we created nests in high-quality rearing environments with eggs originating from either high or low-quality environments and nests in low-quality rearing environments with eggs originating from either high or low-quality environments (right panel). ‘E’ refers to the paired nests which enable testing of the effect of different egg origin; ‘R’ refers to the paired nests which enable testing of the effect of different rearing conditions. See text for further explanations.

spatial heterogeneity on the outcome of the experiment. All clutches in an experimental set were swapped (more or less) simultaneously. Eggs were swapped 21 days after the start of incubation, about seven days before hatching. Day 21 of the incubation was chosen for two reasons. First, we wanted to cross-foster the eggs as late as possible in the incubation cycle, because egg predation, which would eliminate nests from the experiment, is frequent in Oystercatchers (Verboven *et al.* 2001). Secondly, Oystercatcher chicks communicate through the egg-shell with their parents for several days before hatching (personal observation): a behaviour which might affect parental behaviour subsequently. We therefore cross-fostered eggs sufficiently early that auditory recognition by 'parents' could not yet have been established.

Chick growth and survival

Every day we checked nests to determine whether the cross-fostered eggs had hatched. Immediately after hatching, chicks were individually marked, by painting different combinations of the lower parts of breast, wing and rump feathers with dye (rhodamine red, picrine yellow or malachite green). After about 4 weeks, chicks were colour-ringed. In the period after hatching we searched for chicks every other day for a standardized period of 10 minutes (Oystercatcher chicks are semi-precocial and leave the nest cup one day after hatching). Furthermore, we recorded whether parents were still alarming (loud calls), as an indicator of the chicks being alive or not. If parents did not alarm during two consecutive visits, we assumed that any chicks were dead, as this is an extremely reliable indicator. Only rarely did we actually find a dead chick, as they are probably eaten by predators or scavengers. During nest checks, parental alarm signalled the chicks to hide in the vegetation and, as a result, chicks were sometimes hard to find. If chicks were not found for two consecutive checks, but parents were still alarming, we combined the searches with observations from a hide nearby until the chicks were found. We searched for chicks in each nest until 50 days after hatching, or until we were certain that all chicks were dead. When chicks were found alive they were weighed to the nearest 0.1g and wing length, tarsus-plus-toe and bill-plus-head were measured to the nearest 0.1mm.

As we did not find all chicks during each nest check and because we sometimes had to rely on the alarming behaviour of parents as an indicator that at least one chick was still alive, we were not able to assess reliably the exact survival duration of each chick individually. However, if parents at some point stopped alarming, and we did not find the chicks, we were able to determine reliably for how long the longest-surviving chick from that brood had survived. Furthermore, we could also reliably determine whether chicks had survived the entire period of 50 days, because chicks should have fledged by the end of this period and so were easy to observe by then.

Data analysis

In total, 25 sets of four nests were cross-fostered, but due to major flooding in both 2002 and 2003 only 12 of these sets were unaffected by the flooding and could be used. Nine nests within these 12 sets were predated after cross-fostering, but before hatching;

these were also omitted from analyses, resulting in a total of 39 nests. As a result we obtained 18 matched pairs of nests with different egg origins, but equal rearing conditions (‘E-comparison, Fig. 6.1). In eleven of these pairs both nests were in high-quality rearing conditions, and seven in low-quality rearing conditions. We also obtained 15 pairs of matched nests differing in rearing quality, but equal in egg origin (‘R-comparison, Fig. 6.1). In eight of these matched pairs both clutches originated from high-quality environments, and in seven matched pairs both clutches originated from low-quality environments.

Chick survival and fledging success in 2002 and 2003 were very poor. Because most chicks died within their first one or two weeks, and only in five nests did a chick survive the entire period of 50 days and fledge, we could not use fledgling success or mass as fitness measures. The longest-surviving chicks of only a small subset of nests survived long enough to obtain sufficient measurements to estimate growth rates reliably (eight pairs of matched nests [‘R-comparison’] had at least four measurements per individual). Therefore, we used the survival duration of the longest-surviving chick as a fitness measure. All durations of survival were log-transformed for use in statistical tests. All tests are two-tailed and means are given with standard errors.

Results

The effect of growth on survival

Chick growth rates were a good predictor of survival duration. Differences in growth rates of body mass, measured over the same number of days and chick stage for two matched nests reared in the same conditions, were positively correlated with the differences in survival duration between those matched nests (Pearson’s $r=0.77$, $n=8$ pairs, $P=0.027$). Similar positive relationships were found between the growth rate of structural features (wing length, tarsus-plus-toe and bill-plus-head) and survival duration (all $P<0.15$). Given the strong correlation between growth and survival time it is reasonable to assume that survival time is a reliable indicator of the fledging success and/or quality that birds would have achieved if environmental conditions had been better. For further analyses we only used survival duration, as we could not measure growth rates for the majority of cross-fostered clutches.

Egg origin versus rearing conditions

In accordance with earlier results in this population (Heg & van der Velde 2001), eggs laid in low-quality environments were smaller (5%) than eggs laid in high-quality environments (low: 40.8 ± 0.57 cm^3 vs. high: 42.8 ± 0.63 cm^3, Paired-$t=2.20$, $df=17$, $P=0.042$), and tended to have larger intra-clutch variation in egg-size (although the latter was not significant in this sample; low: 3.3 ± 0.8 cm^3 vs. high: 2.5 ± 0.3 cm^3, Paired-$t=0.95$, $df=17$, $P=0.35$). Cross-fostered eggs laid in low-quality environments were from similarly-sized clutches as eggs laid in high-quality environments (low: 2.9 ± 0.2 eggs vs. high: 3.0 ± 0.1 eggs, Paired-$t=-0.37$, $df=17$, $P=0.72$).

Egg origin did not affect the survival duration. When reared under similar conditions, the survival duration of chicks hatched from eggs laid in low-quality rearing conditions did not differ from the survival duration of chicks hatched in high-quality rearing conditions (Fig. 6.2A, Paired-t=1.04, df=17, P=0.31). However, rearing quality did strongly affect the survival duration. The survival duration was twice as long in high-quality rearing conditions than in low quality rearing conditions, when comparing eggs originating from the same quality environment (Fig. 6.2B, Paired-t=2.81, df=14, P=0.014).

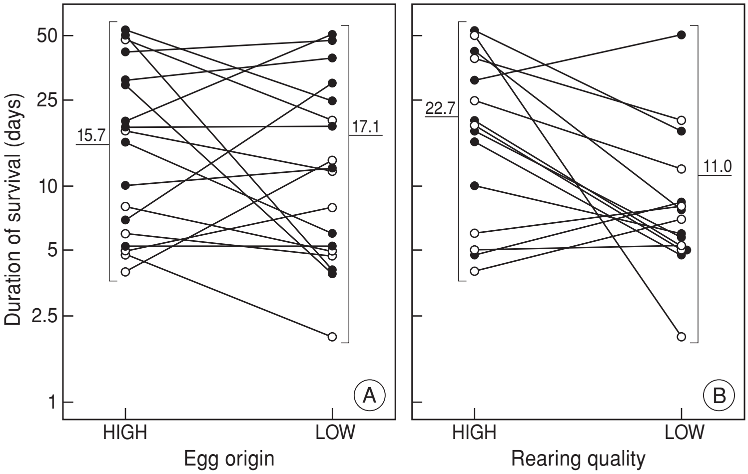

Figure 6.2 Survival duration of the longest-living chick in matched nests with (A) different egg origin, but same quality of rearing conditions ('E-comparison' in Fig. 6.1) and (B) different rearing conditions, but same egg origin ('R-comparison' in Fig 6.1). Averages of groups are shown in figures next to the brackets. In (A), closed dots refer to nests both reared in high-quality conditions, open dots refer to nests both reared in low-quality conditions. In (B), closed dots refer to clutches both originally laid in high-quality environment, open dots refer to clutches both originally laid in low-quality environment. Note the logarithmic Y-axis.

Because clutches laid in low-quality environments contained smaller eggs and showed larger intra-clutch variation in egg-size than clutches laid in high-quality environments, we specifically tested whether the average egg-size of a clutch as well as its intra-clutch variation in egg-size affected survival duration. Under the same quality rearing conditions, neither the egg-size nor the intra-clutch variation in egg-size of foster clutches correlated with survival time (Table 6.1). The size of clutches from which the foster eggs originated did not affect the survival time (Table 6.1). Furthermore, the original egg-size, the original intra-clutch variation in egg-size and the original clutch size of the adoption parents could indicate parental quality. However, none of these traits affected the survival duration. Only the quality of the rearing conditions was significantly related to the survival duration (Table 6.1).

Table 6.1 ANCOVA with survival duration of the longest-living chick as dependent variable (log-transformed). Swap-set was entered as a categorical variable into the model and never removed to account for the paired experimental design. Model selection was done by backward deletion of non-significant terms.

Explanatory variable	B	s.e.(B)	F	df	P
error				26	
corrected model (R^2=0.34)			2.63	12	0.019
inercept			378	1	<0.001
in final model					
swap set			1.89	11	0.089
rearing quality	0.36	0.11	9.93	1	0.004
removed from final model					
rearing quality*egg origin	0.15	0.23	0.44	1	0.52
egg origin	-0.08	0.13	0.40	1	0.53
foster egg size	-0.03	0.03	0.80	1	0.38
foster intra-clutch egg size differences	0.01	0.04	0.02	1	0.88
foster clutch size	0.16	0.15	1.10	1	0.31
origin egg size	-0.02	0.02	0.78	1	0.39
original intra-clutch egg size differences	0.02	0.03	0.03	1	0.62
original clutch size	-0.18	0.12	2.51	1	0.13

Discussion

In this study, egg quality, defined by the environmental quality in which the eggs were laid, did not affect the survival of chicks (in agreement with Blomqvist *et al.* 1997; Meathrel *et al.* 1993, Reid & Boersma 1990, Smith *et al.* 1995, Styrsky *et al.* 1999, Bize *et al.* 2002). However, rearing conditions strongly affected the duration of chick survival. we conclude, therefore, that although parents in high-quality environments laid larger eggs, this did not improve chick survival subsequently. Egg-size appears to be a neutral trait, under no selection pressure (in accordance with Jager *et al.* 2000). Furthermore, the original egg-size and clutch-size of the foster parents, possible correlates of parental quality, also did not affect chick survival, in contrast to some other species (Reid & Boersma 1990, Bolton 1991, Smith *et al.* 1995, Blomqvist *et al.* 1997, Hipfner 2000, Bize *et al.* 2002).

It is somewhat puzzling why an initial advantage of hatching from a larger egg does not constitute a head start for the chick to increase its survival probability. This is especially surprising, given that egg-size is strongly correlated with both hatchling mass (Hatchling mass [g]=1.84+0.68*egg-size[cm^3], R^2=0.68, N=702, P<0.001, Jager *et al.* 2000) and fledgling mass (Fledgling mass [g]=141.8+3.62*egg-size[cm^3], R^2=0.05, N=204, P=0.002 van de Pol, unpublished data) in this population. It has been argued that some studies have been unable to detect effects of egg-size or egg quality on the future survival of offspring because of the absence of adverse conditions and substantial chick mortality (Smith *et al.* 1995, Bize *et al.* 2002). Although we did not investigate directly whether starvation or predation was the principal cause of chick mortality in this experiment, we have strong circumstantial evidence that starvation was most important. First, the availability of the two primary prey species (measured as the combined ash free dry mass of Baltic Tellin *Macoma balthica* and Ragworm *Nereis diversicolor*) was extremely low in the study area during the experiment (2002: 4.8 g/m^2; 2003: 5.4 g/m^2) compared to other years (1985-2001: 9.9±0.9 g/m^2). Secondly, the five chicks that fledged in the experiment were 13% lighter than fledglings reared under the same environmental conditions from 1985–2001 (Δbody mass=-42±21g; measured at day 30). However, even under these extremely adverse conditions we did not find any relationship between egg-size and future survival.

An alternative explanation for the absence of a relationship between egg-size and survival is that the survival duration of the longest-living chick is not an appropriate fitness measure. However, differences in survival duration were strongly related to differences in growth rate, and we found differences in chick survival-duration between adoption parents in high and low-quality environments. Because we think survival duration is an appropriate indirect fitness measure, we conclude egg-size did not affect survival time. Consequently, this suggests that the observed decline in reproductive output in this population is unlikely to be caused by a decrease in egg-size over the same period.

Differences in rearing conditions could either be a result of environmental quality, parental quality or a combination of both as high-quality parents might select high-quality environments (Heg 1999, Verhulst *et al.* 1997). If environmental quality were the principal determinant of reproductive performance, we should expect that individuals that move from low to high-quality environments would improve their reproductive performance to the level of pairs already in high-quality environments. However, a female's average egg-size does not change if she switches between environments of different quality (Fig. 6.3A, paired t=-0.53, df=46, P=0.59): it is constant within females (61% repeatability, Jager *et al.* 2000). Differences in egg-size in our study system therefore seem to be to a large extent determined by female 'quality', and environmental conditions seem to play a lesser role. In contrast, fledging success is probably, to a greater extent, determined by environmental quality, as females that switched between environments changed the fledging success of their chicks accordingly (Fig. 6.3B, paired t=-2.57, df=46, P=0.012), although we cannot exclude the possibility that individuals move to a high-quality environment as a result of an increase in individual quality.

Williams (1994) showed that 42% of studies that investigated the relationship between egg-size and chick survival reported a positive correlation. Most cross-foster experiments (that control for the confounding effects of parental and environmental quality) have provided no evidence for a causal relationship between egg-size and offspring survival (this study, Blomqvist *et al.* 1997; Meathrel *et al.* 1993, Reid & Boersma 1990, Smith *et al.* 1995, Styrsky *et al.* 1999, Bize *et al.* 2002). Only few studies have

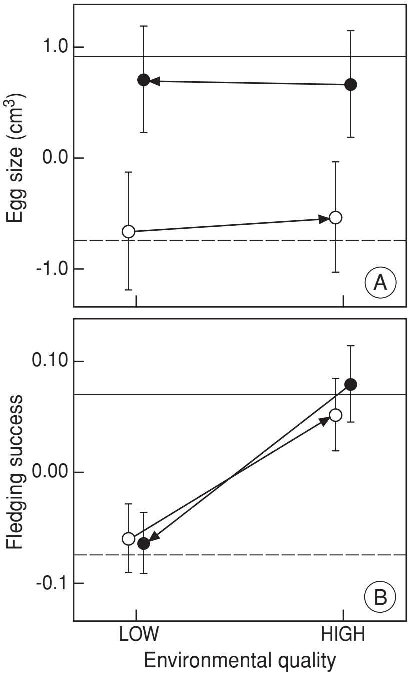

Figure 6.3 Changes in egg-size (A) and fledging success (B) for females switching from low to high-quality environments (white dots, n=25) and for females switching from high to low-quality environments (black dots, n=22). The averages of all individuals breeding in high-quality environments and low-quality environments are given by the continuous and dashed line respectively. Values are corrected for differences between years (1985-2003) and population averages are set to zero.

found that egg-size affects survival (Bolton 1991, Risch & Rohwer 2000), but effects on growth have been reported more often (e.g. Amundsen & Stokland 1990, Hipfner & Gaston 1999, Hipfner 2000). In the non-experimental studies that found a positive correlation between egg-size and chick survival, egg-size only explained a minor part of the variation in chick survival between nests. Therefore, egg-size is probably not a key life history trait that explains much of the variation in reproductive performance between nests. However, the situation might differ completely for within-nest variation in performance, as sibling competition can be manipulated by intra-clutch asymmetries in egg-size (Heg & van der Velde 2001). Furthermore, egg quality is a multidimensional trait, in which many other features besides egg-size might be important determinants for between- (and within-) nest variation in reproductive performance.

If egg-size is a neutral trait in this Oystercatcher population, this does not explain why egg-size is consistently higher in a high-quality environment. One explanation might be that females in high-quality environments lay larger eggs because they are themselves larger. However, other important unmeasured 'female quality'-characteristics (e.g. motivation, size of the reproductive tract), which might be associated with egg-size, might also differ between females breeding in high or low-quality environments. In contrast to the American Oystercatcher (Nol *et al.* 1984), egg-size is neither related to body size or mass in this population (Jager *et al.* 2000), nor does female body size or mass differ between environments of different quality (Ens *et al.* 1995). Another explanation might be that females in low-quality environments lay smaller eggs to obtain the observed larger intra-clutch variation in egg-size. This argument would hold if females cannot increase the size of their largest egg, but can only decrease the size of the smallest egg to increase the intra-clutch variation in egg-size. However, both the largest (42.1±0.1 cm^3) and the smallest eggs (39.1±0.1 cm3) laid in clutches in low-quality environments are smaller than the largest (43.3±0.1 cm^3) and smallest (41.4±0.1 cm^3) eggs laid in clutches in high-quality environments (van de Pol, unpublished data). At this moment we must conclude that we do not understand why consistent differences in egg-size exist: the puzzle remains.

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Chapter 7

A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*)

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Abstract

1. Long-term effects of conditions during early development on fitness are important for life history evolution and population ecology. Using multi-strata mark-recapture models on 20-years of data, we quantified the relation between rearing conditions and lifetime fitness in a long-lived shorebird: the oystercatcher (*Haematopus ostralegus*). We specifically addressed the relative contribution of short and long-term effects of rearing conditions to overall fitness consequences.
2. Rearing conditions were defined by differences in natal habitat quality, in which there is a clear dichotomy in our study population. In the first year of life, fledglings from high quality natal origin had a 1.3 times higher juvenile survival. Later in life (age 3-11), individuals of high quality natal origin had a 1.6 times higher adult pre-breeder survival. The most striking effect of natal habitat quality was that birds that were reared on high quality territories had a higher probability of settling in high quality habitat (44% vs. 6%,). Lifetime reproductive success of individuals born in high quality habitat was 2.2 times higher than that of individuals born in low quality habitat. This difference further increased when fitness was calculated over several generations, due to a correlation between the quality of rearing conditions of parents and their offspring.
3. Long-term effects of early conditions contributed more to overall fitness differences as short-term consequences, contrary to common conceptions on this issue.
4. This study illustrates that investigating only short-term effects of early conditions can lead to large underestimation of fitness consequences. We discuss how long-term consequences of early conditions may affect settlement decisions and source-sink population interactions.

Introduction

The long-term consequences of conditions during early development for fitness are important for life history evolution, population ecology, and the interface between them (Lindström, 1999; Cam, Monnat, & Hines, 2003). Early conditions are likely to influence offspring quality, which is an important factor in main life history trade-offs (Stearns, 1992). For example, long-term effects of early conditions shift the optimal solution of the trade-off between quantity and quality of offspring towards fewer offspring of higher quality. In an ecological context, effects of early conditions may amplify a source-sink population structure when breeders in good habitats produce many offspring that additionally have higher fitness prospects. Effects of early conditions on life history traits can also feedback on population dynamics. For example, early conditions can affect the prospects of entire cohorts, which may have delayed consequences for population dynamics (Albon, Clutton-Brock, & Guinness, 1983; Sæther, 1997); condition dependent dispersal is important for meta-population dynamics (Ims & Hjermann, 2001).

Conditions during early life can vary as a result of differences in parental quality and environmental quality; the latter are partly under parental control. For example, parental habitat selection affects the spatial environment in which offspring are reared; a mother's choice of date of birth affects the temporal environment in which offspring are reared. Parental and environmental quality are therefore intricately linked and probably often positively inter-correlated (e.g. van de Pol *et al*, 2006).

Favourable rearing conditions, *i.e.* being raised with a 'silver spoon' (Grafen, 1988), are often beneficial throughout life, but are thought to be most pronounced during early life stages (Lindström, 1999; Metcalfe & Monaghan, 2001). Two hypotheses may explain why effects of early conditions are most pronounced early in life. First, the environmental stochasticity individuals experience during life accumulates and this decreases the potential for long-term effects of early conditions. Secondly, selection gradients of fitness components usually become less strong in the course of life (Charlesworth, 1980; Caswell, 2001). Consequently, parents can expect a higher fitness payoff by improving conditions that enhance the short-term fitness prospects of offspring, than by investing that same effort in improving early conditions that pay-off later in life.

Many studies report 'silver spoon' effects on juvenile survival (e.g. Tinbergen & Boerlijst, 1990; Magrath, 1991; Green & Cockburn, 2001; Perrins & McCleery, 2001), natal dispersal (e.g. van der Jeugd, 2001) and adult morphology (e.g. Boag, 1987; Gustafsson, Qvarnström, & Sheldon, 1995; de Kogel & Prijs, 1996). In addition, several studies suggest early conditions can also have long-term consequences on fitness components, such as adult survival before recruitment (Harris *et al*, 1994; Cam *et al*, 2003) and recruitment probability (Reid *et al*. 2003). However, less is known about the long-term consequences of early conditions on fitness components during the reproductive stage, such as breeder survival (Perrins & McCleery, 2001), quality of the acquired breeding habitat (Verhulst, Perrins, & Riddington, 1997) and reproductive success (Gustafsson & Sutherland, 1988; Haywood & Perrins, 1992; Visser & Verboven, 1999).

When investigating the ecological and evolutionary consequences of early conditions, cost and benefits should be calculated in terms of fitness. Fitness measures are calculated over (at least) a lifetime (e.g. lifetime reproductive success [LRS], finite population growth rate [λ]) and they are the combined result of many individual fitness components (early as well as late in life). For logistic reasons, most studies only investigate one or a few fitness components. Consequently, little is known about the relative importance of short and long-term consequences of early conditions on fitness. Integrating all fitness components into one fitness measure is also important because early conditions do not always affect all fitness components positively (e.g. Olsson & Shine, 2002; King, 2002).

In this paper we use data from a 20-year study to quantify and compare the contribution of short and long-term effects of early conditions on the fitness of oystercatcher (*Haematopus ostralegus* L.) offspring. In coastal breeding oystercatcher populations, there is usually a clear dichotomy in habitat quality, based on the nesting location relative to the foraging area (Safriel, Ens, & Kaiser, 1996). Some parents can take their chicks to the food, because breeding and feeding territory are adjacent. Other parents have to bring the food to their chicks, because the breeding and feeding territory are spatially segregated. Parents that can escort their chicks to the food consistently produce 2-3 times more fledglings per year, because transporting food to the chicks is costly (Ens *et al*, 1992). Early conditions in oystercatcher are therefore characterized by the habitat type an individual is reared in. However, as natal habit quality is probably intricately linked with parental quality (van de Pol *et al*, 2006), we prefer to use the term natal origin, which encompasses both an environmental and parental (genetic and non-genetic) component of early conditions.

We estimated the fitness consequences associated with the natal origin of offspring by calculating the effects of natal origin on juvenile survival, adult survival, recruitment probability, as well as on their subsequent breeding career (Fig. 7.1). We combined fitness components to estimate fledgling fitness prospects (LRS and λ). Subsequently, using stage-structured population models, we compared the sensitivity of fitness to long-term and short-term effects of early conditions. Finally, we discuss how long-term effects of natal origin affect life history evolution (settlement decisions) as well as population ecology (source-sink population interactions).

Methods

Study population

Oystercatchers were studied from 1985-2004 on the Dutch Wadden Sea island of Schiermonnikoog (53°29' N 6°14' W). In this population, oystercatchers breed on the salt marsh and are dependent on inter-tidal mudflats for their food. Breeding pairs stake out their feeding and nesting territory, facilitating location of territory boundaries (Heg *et al*, 2000b). Following earlier studies, we designated territories with adjacent feeding and nesting areas as high quality (HQ) habitat and territories with spatially separated

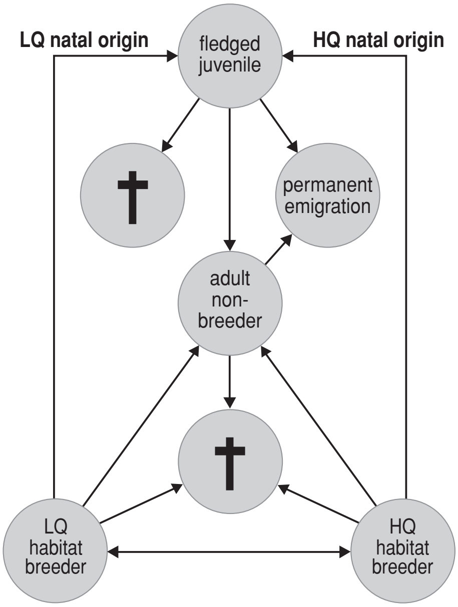

Figure 7.1 Schematic overview of the life cycle stages of an oystercatcher, which are used in the multi-strata mark-recapture analysis as well as the stage-structured population models. LQ is low quality habitat; HQ is high quality habitat.

feeding and nesting areas as low quality (LQ) habitat (Ens, Weissing, & Drent, 1995; Heg & van der Velde, 2001).

All breeding birds and fledglings were individually colour marked in the main study area; a large surrounding area was visited annually to locate new recruits (see Heg *et al*, 2000b for a map). Age of first reproduction is high (median 7, range 3-11 years), therefore we restricted all analysis to fledglings born in 1985-1996, which were followed from 1985-2004. By 2004, all individuals of these cohorts had either settled or had not been seen for several years and were presumed dead. Sex of adult birds was determined on the basis of DNA analysis (Heg *et al*, 2000a) and copulation behaviour (Heg *et al*, 1993); sex of most juvenile birds was unknown till adulthood.

Juvenile survival and dispersal

Young fledge on average 30 days after hatching (Kersten & Brenninkmeijer, 1995). Until the age of 3 years (hereafter called 'adulthood') juveniles retain their juvenile plumage. Information from re-sightings and dead recoveries suggests juveniles have low site fidelity and move around the Wadden Sea. After three years, many juveniles returned to the study area and were repeatedly observed in subsequent years (Kersten & Brenninkmeijer, 1995).

Survival of juveniles born from 1985 till 1996 was analysed using dead recoveries collected by the Dutch Ringing Centre. By comparing the survival till adulthood based on dead recoveries from all over North-western Europe with the number of birds locally re-sighted at adulthood ('local survival') we estimated permanent juvenile emigration (Fig. 7.1). We adopted the same model structure as in a previous study on dead recovered Oystercatchers (Nève & van Noordwijk, 1997), in which it was shown that first and second year survival was lower than adult survival and that adult survival and reporting probability were dependent on winter severity. Reporting rates of dead colour-ringed oystercatchers were high (24%) in most years with mild winters and even higher in years with severe (1986, 1996 and 1997) winters (Camphuysen *et al*, 1996; Nève & van Noordwijk, 1997).

Adult survival, dispersal, recruitment and breeding career

Adult oystercatchers usually occupy the same territory from year-to-year, with the same mate (Heg, Bruinzeel, & Ens, 2003). Non-breeders join communal roosts (Heg *et al*, 2000b). Annual determination of social status (HQ or LQ habitat breeder or non-breeder) was based on observations during the breeding season at the breeding grounds and at roosts (average 30 observations / individual / year). Virtually all surviving breeders and non-breeders were re-sighted each year, with the exception of non-breeders from 1997 till 2004 due to less frequent checking at roosts.

Adult survival and transition probabilities between the state of non-breeder, breeder in LQ habitat, and breeder in HQ habitat (i.e. recruitment, movement between breeding habitat, and territory loss) were all estimated in one combined model, using multi-strata mark-recapture models based on live re-sightings (as in Fig. 7.1). By using live local re-sightings to estimate adult survival, permanent adult emigration will result in an underestimation of survival. In principle this adult dispersal fraction can be quantified by using information from dead recoveries from a larger area. However, given the low number of juveniles that survived till adulthood, the number of dead recovered adults was too few to incorporate this information in the models. Analysis of a larger data-set, including individuals ringed as adults, suggested that a small fraction of adult non-breeders of both sexes emigrated, but breeders did not (van de Pol, unpublished data).

Capture-recapture analyses were carried out using MARK (Cooch & White, 2004). Model selection was done using the Akaike Information Criteria corrected for sample size (AICc; Akaike, 1973). Parameter estimates were calculated using model averaging (Burnham & Anderson, 2002), which combines estimates of all models in one overall estimate using differences in model support (AICc) to determine weight. Estimates from years with mild and severe winters were combined in one weighted parameter estimate. Goodness-of-fit analyses was performed using a median c-hat approach on a reduced model with no differences between years and natal origin (Cooch & White, 2004). There were no indications for lack of fit ($\hat{c}=1.21$).

The local natal dispersal distance (m), was defined as the distance between the centres of the natal territory and the territory in which the individual first recruited. To investigate whether recruits avoided or congregated near their natal territory, the observed settlement pattern was compared with a random settlement pattern generated by taking 5000 bootstrap-replicates (Adams & Anthony, 1996). Breeding dispersal is on the same scale as local natal dispersal (Bruinzeel, 2004).

Stage-structured population models

Stage-structured population matrix models were constructed based on the estimated demographic parameters (Caswell, 2001). These models were used to quantify the finite population growth rate (λ) and thereby allowed the quantification of the strength of phenotypic selection on input parameters (fitness components early and late in life). Such selection gradients (also called sensitivities) are calculated as the partial derivative of a specific parameter to λ (Hamilton, 1966; Caswell, 2001). In addition, stage-structured models were used to quantify the fitness differences of fledglings of LQ or HQ natal origin in terms of reproductive value (RV). RV is a relative measure of the contribution of different groups to λ. RVs account for the fact that timing of reproduction during a lifetime affects fitness when populations change in size, while LRS ignores this.

Results

Juvenile survival and dispersal

Juveniles of HQ natal origin were 1.3 times more likely to survive their first year than juveniles of LQ natal origin (Table 7.1). Since this analysis was based on recoveries of dead birds throughout the Wadden Sea and beyond, it is unlikely that this survival difference can be attributed to differential dispersal. Models with second year (model 2, Table 7.2) or third year (model 3, Table 7.2) survival dependent on natal origin received less support from the data than the model with only first year survival dependent on natal origin (model 1, Table 7.2). Multiplying first year to third year survival we estimated in total 31.9% of fledglings of LQ natal origin and 41.2% of fledglings of HQ natal origin survived till adulthood (Table 7.1). Return rates of juveniles, based on individuals seen alive in the study area at adulthood were remarkably close to these estimates (mean difference 0.6%, Table 7.1). This suggests that practically all surviving fledglings returned to the study area (i.e. no permanent juvenile emigration).

The sex of most individuals could only be determined when they returned as adults; therefore we could not directly test for sex-dependent juvenile survival. However, sex-ratio among adults that returned to the study area was male biased (60% males, binomial test: $N=117$, $P=0.042$). If we assume there is no permanent juvenile emigration and the fledgling sex-ratio is unity (cf. Heg *et al*, 2000a, based on one cohort), this suggests that survival till adulthood was 1.5 times higher in males as compared to females (males: 45.3%; females: 30.4%).

Adult survival, dispersal, recruitment and breeding career

Individuals of HQ natal origin that survived till adulthood were 1.4 times more likely to recruit in the breeding population during the remainder of their life (HQ: 54.8%, LQ:

Table 7.1 Estimates of fitness components and LRS of fledglings born in low quality and high quality territories. †Values between brackets refer to the estimates for the 'emigration scenario' (see text).

Fitness component	Quality natal origin Low (N=107)	 High (N=203)
Survival from fledging till adulthood	31.9%	41.2%
1st year survival	43.7±6.6%	60.5±4.8%
2nd year survival	74.3±9.0%	72.0±7.4%
3rd year survival	98.2±2.2%	94.5±8.9%
Returned to study area at adulthood	30.8% (=33/107)	41.4% (=84/203)
Recruited as breeder	39.4% (=13/33)	54.8% (=46/84)
Recruited in low quality habitat	92.3% (=12/13)	67.4% (=31/46)
Recruited in high quality habitat	7.7% (=1/13)	32.6% (=15/46)
Age of first reproduction (years)	6.4± 0.6	6.8± 0.3
Lifespan of surviving juveniles (years)	13.5 (17.3†)	17.1
Non-breeding lifespan (years)	9.4 (11.6†)	10.5
Breeding lifespan (years)	4.1 (5.7†)	6.6
Breeding lifespan in low quality habitat (years)	2.7 (3.8†)	3.8
Breeding lifespan in high quality habitat (years)	1.4 (1.9†)	2.8
LRS from fledging (# fledged offspring)	0.13 (0.17†)	0.28

Table 7.2 Results of juvenile survival analysis based on dead recoveries. S^1, S^2, S^3, S^A refer to 1st year, 2nd year, 3rd year and adult annual survival, respectively. R refers to the reporting probability, which was equal among all age classes, (n) refers to natal origin, (w) refers to winter severity, and (r) refers to either individuals ringed as fledgling or ringed as adult. Individuals ringed as adults were included to improve parameter estimates.

Model	ΔAICc	AICc Weights	# Par.	Deviance
1. S^1(n),S^2,S^3,S^A(w),R(w)	0.00	0.38	8	140.6
2. S^1(n),S^2(n),S^3,S^A(w),R(w)	0.96	0.23	9	139.5
3. S^1(n),S^2(n),S^3(n),S^A(w),R(w)	2.15	0.13	10	138.7
4. S^1,S^2,S^3,S^A(w),R(w)	2.18	0.13	7	144.9
5. S^1(n),S^2(n),S^3(n),S^A(n*w+r),R(w)	2.88	0.09	14	133.2
6. S^1(n*w),S^2(w),S^3(w),SA(w),R(w)	4.60	0.04	12	137.0

39.4%; Table 7.1). Furthermore, recruits of HQ natal origin were 4.1 times more likely to directly recruit into HQ habitat (15/46=33%) compared to recruits of LQ natal origin (1/13=8%). This difference was not due to low sample sizes, because when recruits born in areas surrounding the main study area were included the quantitative difference remained (HQ natal origin: 27/62=44%, LQ natal origin: 1/18=6%). Thus effects of natal origin persisted many years after fledging, because median age at first recruitment was 7 years. Age at first recruitment was independent of natal origin (HQ: 6.8±0.6, LQ: 6.4±0.3, $F_{1,59}$=1.52, P=0.22) and of sex (male:6.9±0.3, female: 6.3±0.4, $F_{1,59}$=1.30, P=0.26).

Territory loss and territory switches after first recruitment occur regularly, which may involve promotion from LQ to HQ habitat (Fig. 7.1). Therefore we analysed annual transition probabilities between status categories and adult survival probabilities using multi-strata models. This analysis showed that the higher probability for individuals of HQ natal origin to ever recruit resulted from both a higher annual probability of settling in HQ habitat as well as a lower annual mortality as non-breeder (Table 7.3, Fig. 7.2A vs. Fig 7.2B). Non-breeders of HQ natal origin were 2.7 times more likely each year to acquire a territory in HQ habitat (HQ: 4.9%, LQ: 1.8%), but annual settlement probability to LQ habitat was independent of natal origin (HQ: 8.7%, LQ: 8.7%). Non-breeders of HQ natal origin had a 1.6 times lower annual mortality (7.8%) than non-breeders of LQ natal origin (12.2%). Possibly, the high mortality of non-breeders of LQ natal origin partly reflects permanent adult emigration, as we have indications that some adult non-breeders are not completely site-faithful (van de Pol, unpublished data).

Transition probabilities of breeders also tended to depend on natal origin, (Table 7.3, Fig 7.2). Once recruited in LQ habitat, individuals of HQ natal origin rarely moved from LQ to HQ habitat (0.8% annually), indicating a fixed habitat selection strategy (Fig. 7.2A). However, individuals born and settled in LQ habitat had a substantial chance (4.2% annually) of promoting to HQ habitat (Fig. 7.2B). Thus, for individuals of LQ natal origin the recruitment in LQ habitat can potentially serve as a stepping stone for

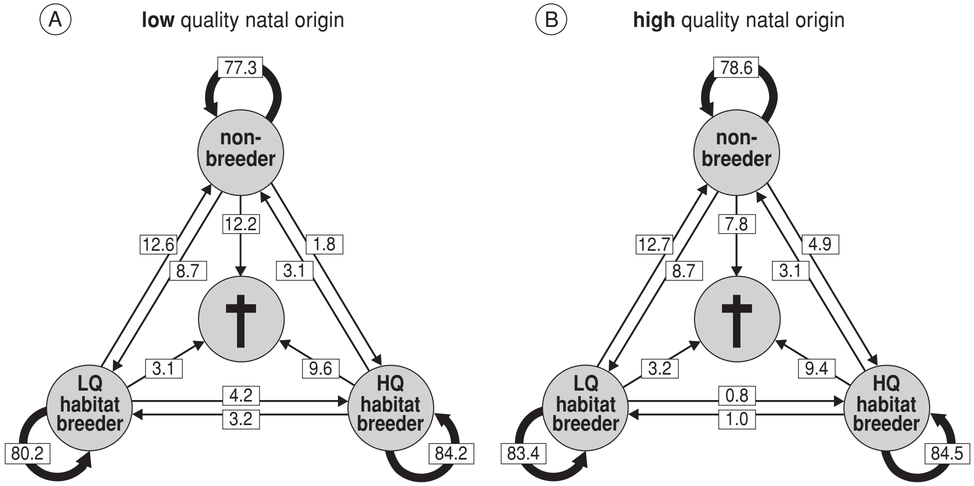

Figure 7.2 Transition probabilities (%) between different life cycle stages of individuals from (A) low quality and (B) high quality natal origin as estimated using multi-strata mark-recapture analysis. Estimates are based on (A) 84 individuals with 635 individual years and on (B) 33 individuals with 201 individual years. Thin arrows represent parameters estimated in the models (Table 7.2); thick arrows represent parameters calculated from the estimated parameters.

Table 7.3 Results of multi-strata analysis based on re-sightings from 1988-2004. S refers to annual adult survival probability; $\Psi^{NB,LQ}$ refers to transitions from non-breeder state (NB) to low quality habitat breeder state (LQ), and so forth. The annual re-sighting probability for all breeders was constant in all years ($P^{LQ}=P^{HQ}=0.99$). †$P^{NB}(y)$ refers to a constant re-sighting probability (0.99) for the years 1988-1996 and variable re-sighting probabilities for the period 1997-2004 (between 0.5 and 0.9). ‡$\Psi^{LQ,HQ}$ did not depend on natal origin (n) in severe winters, therefore we modelled $\Psi^{LQ,HQ}$ to depend on natal origin in mild winters (w_{mild}) only.

Model	ΔAICc	AICc s weight	#Par.	Deviance
1. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	0.00	0.19	33	903.4
2. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(w), \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	0.43	0.15	32	906.0
3. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(n*w)$	0.61	0.14	35	899.6
4. $S^{NB}(w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	0.65	0.14	31	908.4
5. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	0.66	0.14	31	908.4
6. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w), \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	2.17	0.06	34	903.4
7. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(n*w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	2.59	0.05	35	901.6
8. $S^{NB}(n*w), S^{LQ}(n*w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	2.92	0.04	35	901.9
9. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(n*w), \Psi^{HQ,LQ}(w)$	3.65	0.03	35	902.7
10. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(n*w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	3.73	0.03	35	902.8
11. $S^{NB}(n*w), S^{LQ}(w), S^{HQ}(n*w), P^{NB}(y)\dagger, P^{LQ}=P^{HQ}, \Psi^{NB,LQ}(w), \Psi^{NB,HQ}(n*w), \Psi^{LQ,NB}(w), \Psi^{LQ,HQ}(n*w_{mild}+w)\ddagger, \Psi^{HQ,NB}(w), \Psi^{HQ,LQ}(w)$	4.23	0.02	35	903.3

acquiring a HQ habitat. The annual transition probability from HQ to LQ habitat was also lowest for birds of HQ natal origin (HQ: 1.0%, LQ: 3.2%; Fig. 7.2), supporting the idea of a fixed habitat selection strategy. However, modelling movement from HQ to LQ habitat dependent on natal origin does not result in higher model support (model 3 vs. model 1, Table 7.3). The interpretation of the estimated transition probabilities of breeders require caution, as they are based on relatively few individuals, which were repeatedly observed in many years. Nonetheless, given the chosen methodology of model selection and model averaging the estimates presented in Fig. 7.2 represent the most parsimonious description of the data.

Natal origin did not affect the survival of breeders in either HQ (model 11 vs. model 1), or LQ habitat (model 8 vs. model 1). However, independent of natal origin, the annual probability of dying as a breeder in HQ habitat (9%) was much higher than the probability of dying as a breeder in LQ habitat (3%). Territory loss in HQ and LQ habitat was independent of natal origin (Table 7.3, Fig 7.2). Sex of a bird did not affect any of the transition or survival probabilities (results not shown).

Sensitivities of λ to fitness components early and late in life

The population growth rate of the stage structured population matrix model without differences between natal origin was $\lambda=0.954$ (model 1, Appendix 7A). This suggests population size declined 4.6% annually (ignoring possible immigration and emigration), comparable to the decline in breeding numbers actually observed (4.5%; Bruinzeel, 2004). This suggest that our estimates of life-history parameters were quite consistent. Phenotypic selection on fitness components late in life was stronger than on fitness components early in life (Table 7.4). Sensitivities were strongest for settlement probabilities of non-breeders, followed by transition probabilities of breeders, fecundity and juvenile survival. Although sensitivities are used in the calculation of evolutionary scenarios, dimensionless elasticities are more useful for comparing the relative contribution of different demographic parameters to λ, also between species. Fitness components in the breeder stage contributed most (59.8%) to λ, followed by non-breeder transition probabilities (34.2%) and a minor contribution of the fitness components of juvenile survival (6.0%).

Fitness consequences of natal origin

To estimate the fitness consequences associated with natal origin we combined all fitness components (juvenile and adult survival, recruitment probabilities, movement probabilities and reproduction) in one fitness measure (LRS). The expected LRS of a fledgling is given by $LRS=S^J*(T^{HQ}*F^{HQ}+T^{LQ}*F^{LQ})$, in number of fledglings produced. S^J is the survival till adulthood, T is the time an adult is expected to spend breeding in either HQ or LQ habitat and F is the annual fledgling production (counting only female offspring) in either HQ or LQ habitat.

Annual fledgling production was 2.5 times higher in HQ habitat ($F^{HQ}=0.160$) than in LQ habitat ($F^{LQ}=0.065$), averaged over 1985-1996. Natal origin did not affect fledgling production of birds breeding in either HQ or LQ habitat (both analyses GLM, effect

Table 7.4 Sensitivities and elasticities of λ to the input parameters of the population model (model 1, Appendix 7A). Sensitivities reflect the absolute change in λ as a result of a small absolute change in a matrix element (a_{ij}) and are a measure for the strength of phenotypic selection gradients. Elasticities are proportional sensitivities; elasticities sum up to 100% and therefore can be interpreted as relative contributions to λ. Parameter abbreviations follow Table 2-3. †Although S^{NB}, S^{LQ} and S^{HQ} are not matrix elements, their sensitivities can be estimated if we replace $\Psi^{NB,NB}$ by the equivalent $1-\Psi^{NB,LQ}-\Psi^{NB,HQ}-(1-S^{NB})$, and so forth.

Life stage	Parameter a_{ij}	Sensitivity $\delta\lambda / \delta a_{ij}$	Elasticity $(a_{ij} / \lambda)(\delta\lambda / \delta a_{ij})$	
Juvenile	S^1	0.035	2.0%	6.0%
	S^2	0.026	2.0%	
	S^3	0.020	2.0%	
Non-breeder	$\Psi^{NB,NB}$ (S^{NB}†)	0.343 (0.344†)	28.2%	34.2%
	$\Psi^{NB,LQ}$	0.495	4.5%	
	$\Psi^{NB,HQ}$	0.470	1.5%	
Breeder	$\Psi^{LQ,LQ}$ (S^{LQ}†)	0.376 (0.337†)	32.6%	59.8%
	$\Psi^{LQ,NB}$	0.261	3.5%	
	$\Psi^{LQ,HQ}$	0.357	0.8%	
	$\Psi^{HQ,HQ}$ (S^{HQ}†)	0.220 (0.257†)	19.7%	
	$\Psi^{HQ,NB}$	0.160	0.5%	
	$\Psi^{HQ,LQ}$	0.231	0.5%	
	F^{LQ}	0.118	0.8%	
	F^{HQ}	0.073	1.2%	

natal origin: $P>0.4$; $N=205$ breeding attempts; year and individual entered as random effects). Using transition and survival probabilities (Fig. 7.2), we estimated life expectancy from adulthood and how many years a bird would spend breeding in HQ (T^{HQ}) and LQ habitat (T^{LQ}). Individuals from LQ natal origin had a 38% shorter reproductive lifespan (Table 7.1). Consequently, the expected LRS was 2.2 times higher for fledglings of HQ natal origin compared to fledglings of LQ natal origin (Table 7.1). Adults of LQ natal origin spent 34% of their breeding lifespan in HQ habitat (1.4 out of 4.1 years) and consequently produced 56% of their LRS in HQ habitat. This implies recruitment in LQ habitat as a stepping stone to HQ habitat is an important route for individuals of LQ natal origin, because we recorded only one individual of LQ natal origin ever to recruit directly into HQ habitat. Individuals of HQ natal origin spent 42% of their breeding lifespan in HQ habitat (2.8 out of 6.7 years) and consequently produced 64% of their LRS in HQ habitat.

As previously mentioned, the low adult non-breeder survival of individuals of LQ natal origin could (in part) reflect permanent adult emigration. Therefore, we also calculated LRS assuming that the 4.4% mortality difference between non-breeders from LQ and HQ natal origin (LQ: 12.2% HQ: 7.8%; Fig. 7.2) was entirely due to a higher frequency of emigration to the non-breeder state in another population. In the emigration scenario, total lifespan for juveniles that survived till adulthood did not differ, but reproductive lifespan is still 0.9 years shorter for individuals from LQ natal origin, due to less time spent as a HQ habitat breeder (Table 7.1). Consequently, the expected LRS was 1.6 times higher for fledglings of HQ natal origin than for fledglings of LQ natal origin (Table 7.1). In both scenarios LRS was smaller than 1, indicating both LQ and HQ habitat are 'sinks'.

The fitness consequences of natal origin will still be slightly underestimated when fitness is calculated over one generation, because fledglings from HQ habitat are more likely to settle in HQ habitat themselves. Individuals of HQ natal origin produced 64% of their own offspring in HQ habitat, while 56% of the offspring of individuals of LQ natal origin will be of HQ natal origin. Assuming that survival, transition probabilities, and reproductive output are constant in time, the differences in LRS can be extrapolated to many generations. After a few generations the difference in expected number of future offspring between HQ and LQ natal origin levelled off to a 2.4 fold difference (Fig. 7.3).

Although counting the number of offspring alive at some moment in the future allows a comparison between measuring short and long-term fitness consequences, it does not take into account when in life reproduction takes place. As this population was declining, offspring born later in life contribute more to λ than offspring born early in life. Because breeding lifespan is longer for offspring from HQ natal origin and age of first reproduction is independent of natal origin, we would expect that LRS underestimates fitness benefits of HQ natal origin. The RV of a fledgling of HQ natal origin was 3.1 times higher than the RV of fledglings of LQ natal origin (calculated from model 2, Appendix 7A), substantially higher than the 2.4 fold differences in LRS in number of fledged grand-offspring.

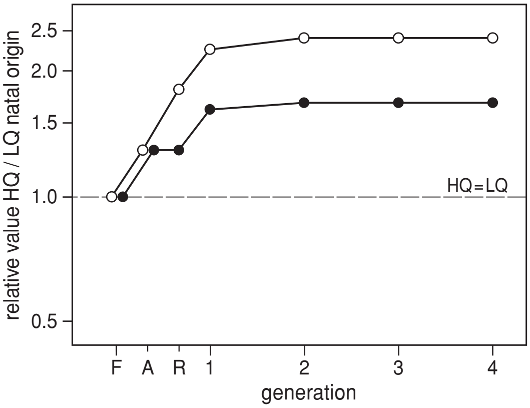

Figure 7.3 Relative output of one fledgling from high quality (HQ) natal origin compared to the output of one fledgling from low quality (LQ) natal origin, in terms of the number of fledglings (F) that survive till adulthood (A), individuals that recruit in the breeding population (R) and fledglings produced after 1, 2, 3 and 4 generations. Open dots are values based on estimates in figure 7.2, closed dots are based on the 'emigration scenario' (see text). Note the logarithmic y-axis.

Natal philopatry

If individuals settled very close to their natal site this alone might explain the association between natal origin and breeding habitat quality. On the scale of the island individuals were highly philopatric, as virtually all individuals returned to the study area. However, within the study area both sexes did not aggregate near, or avoid their natal site compared to a randomly generated settlement pattern (Randomisation test, $N=59$, $P>0.3$). The local natal dispersal distance was on average 444m, much larger than the small distance between HQ and LQ habitat (<100m). Natal dispersal distance was not affected by natal origin (HQ: 441±54m, LQ: 449±95m, $F_{1,59}=0.04$, $P=0.83$) or sex (male: 458±61m, female: 402±37m, $F_{1,59}=0.27$, $P=0.61$).

Discussion

Short and long-term fitness consequences

The fitness prospects of oystercatcher offspring were strongly associated with their natal origin during all life-stages, culminating in a 3.1 fold difference in RV between fledglings from HQ and LQ territories. Early in life, fledglings of HQ natal origin had a higher juvenile survival and later in life a higher adult survival as a non-breeder and a much higher recruitment probability to HQ habitat than individuals of LQ natal origin. Fledglings from LQ territories compensated some of their disadvantage by having a higher probability of promoting from LQ to HQ habitat once they had settled as breeder, though this result was based on few individuals. Because individuals predominantly recruited in the same type of habitat they were born in, there was a positive correlation between natal origin of parents and their offspring. Consequently, effects of early conditions showed carry-over effects to future generations.

Effects of early conditions on fitness components occurred over a very long period and showed mostly positive, but also one negative effect, underlining the importance of integrating all fitness components into one fitness measure. Fitness consequences of natal origin became stronger as birds were followed over more life history stages (Fig. 3). Consequently, the quantification and interpretation of fitness differences between offspring of HQ and LQ natal origin in our study depends on whether only fitness components early in life, fitness components late in life, a fitness measure over a lifetime or a fitness measure over several generations is used.

Many studies have shown that early life fitness components are associated with differences in early conditions (see Introduction). Some studies measured all fitness components necessary to calculate a lifetime fitness measure (Rose, Clutton-Brock, & Guinness, 1998; Kruuk *et al*, 1999; Visser & Verboven, 1999; Reid *et al*, 2003), but did not quantify the relative contribution of short and long-term consequences to fitness. Our study shows that long-term effects of rearing conditions can be at least as strong as short-term effects (compare slopes between life-stages in Fig. 7.3). Sensitivity analysis further showed that fitness components late in life had by far the strongest fitness effects in our population. Consequently, natural selection should favour rearing conditions that result in beneficial long-term effects more strongly than rearing conditions that favour short-term effects. The sensitivity pattern in Oystercatchers seems opposite to the many studies that show that sensitivities of survival and reproduction are highest for youngest age-classes (Charlesworth, 1980; Caswell, 2001). However, in contrast to studies using age-structured population models, we aggregated adult fitness components over many age-classes and consequently their sensitivities were high. As such, we implicitly assumed that long-term consequence of early conditions convey advantages in many more years than a similar effect on juvenile survival. We think this assumption is plausible, because adult survival for example may depend on permanent aspects of phenotypic quality such as body morphology. Potentially, environmental stochasticity experienced during a life could reduce the strength of natural selection acting on long-term effects of early conditions by distorting the strength of the correlation between offspring quality and individual quality later in life. Nevertheless, this study shows that early conditions may affect life-history decisions that take place up to 10 years later. Possibly, developmental pathways to important fitness components are selected for low susceptibility to environmental stochasticity as part of a bet-hedging strategy to reduce variance in fitness (Pfister, 1998; Sæther & Bakke, 2000; Reid *et al*, 2003). Important long-term effects of early conditions may therefore be a characteristic of many long-lived species, but more studies are required to evaluate this.

Potential problems in analyzing long-term effects

Because following individuals over an entire lifetime takes many years, partly incomplete life-histories were used. Right-censoring, in which not all individuals were followed till the end of their lives, could potentially bias the estimates on long-term effects of rearing condition. First of all, because few individuals lived to become a breeder and not all individuals were followed towards the end of their breeding career, estimates of breeder survival and transition probabilities were less reliable than those of non-breeders or juveniles. However, we have no reason to assume that reliability differed with respect to natal origin. Secondly, right-censoring might bias estimates of long-term effects because life-history traits might be age-dependent, and observations were biased towards young ages. However, adult survival is probably age-independent in this species (Schnakenwinkel, 1970; Safriel *et al*, 1984), and recruitment probabilities are only lower for 3 or 4 year olds (Bruinzeel, 2004). Reproduction is strongly age-dependent, but did not differ with respect to natal origin. Therefore, biased sampling of young individuals is unlikely to have affected our main conclusions

Finally, when averaging over all individuals with the same natal origin (cross-sectional comparison) we cannot disentangle whether short and long-term effects of natal origin accurately reflect within-individual changes or that fitness components also varied due to the selective disappearance of certain quality individuals. To address this question we will have to wait until mark-recapture analyses can account for covariances between phenotypic quality and survival propensity (as in Cam *et al*, 2002; Pettifor *et al*, 2006).

Heritability of early conditions

To our knowledge this is the first study that quantified the effects of early conditions on fitness over more than one generation, but results from other studies hinted at the existence of similar effects by demonstrating a positive correlation between natal and breeding habitat quality (e.g. Verhulst *et al*, 1997) or between the quality of your parents and your own parental quality (e.g. Albon *et al*, 1983; Larsson & Forslund, 1992). In such cases, early conditions (*i.e*. natal origin in this study) can be viewed as an inherited trait with a strong social component (Larsson & Forslund, 1992). Differences between offspring of HQ and LQ natal origin could also have a genetic basis, although no genetic differentiation was found using eight polymorphic micro-satellite loci (van Treuren *et al*, 1999) and the large gene flow might counteract any genetic differentiation.

Natal origin and offspring quality

The effect of natal origin on fitness indicates that rearing conditions affected fledgling quality, which in turn mediated the fitness consequences. Fledglings of HQ natal origin were 10% heavier than fledglings of LQ natal origin (body mass corrected for size; $F_{1,294}=11.47$, $P=0.001$), and offspring mass is positively correlated with fitness in many species (e.g. Tinbergen & Boerlijst, 1990; Magrath, 1991; Green & Cockburn, 2001; Perrins & McCleery, 2001). Thus fledging mass constitutes a promising candidate for further investigation. Body size and date of birth are less likely candidates, as neither body size (PC1 of three structural size parameters; $F_{1,294}=1.03$, $P=0.31$) nor date of birth ($F_{1,294}=2.39$, $P=0.12$) depended on natal origin.

Natal philopatry and dispersal

Dispersal at a scale larger than the study site remains a problem for estimating fitness consequences in the wild. In the majority of studies, only local re-sightings of individuals that returned to the study area are available (Bennets *et al*, 2001). Consequently, effects of early conditions on apparent local survival or recruitment are confounded by possible similar effects of early conditions on dispersal behaviour. The oystercatcher is a relatively good study species to account for dispersal, as information from the study area (99% locally re-sighted) can be compared with information from a larger scale (24% dead recovered).

Juvenile oystercatchers leave the study area after fledging, but practically all birds that survived until adulthood returned, and as such juvenile oystercatchers were extremely philopatric (Martin & Hannon, 1987). More males than females returned to their natal area at adulthood, which was probably due to differences in survival rather than philopatry. The cause of this sex difference is not clear, although there is a small sexual dimorphism in bill morphology and associated feeding specialisation that may have played a role (Le V.dit Durell *et al*, 2001). Effects of early conditions did not differ between the sexes in the adult phase, as expected for species with minor sexual dimorphism and comparable sex roles in breeding (Kruuk *et al*, 1999; Lindström, 1999).

Although juveniles did not disperse permanently, some adult non-breeders did subsequently leave the study area before acquiring a territory (van de Pol, unpublished).

However, our finding that natal origin was strongly associated with fitness was robust to specific assumptions about permanent adult emigration. When we assumed that the low non-breeder survival of individuals of LQ natal origin was caused by permanent adult emigration, large fitness differences remained (Fig. 7.3).

Implications for life history decisions and population dynamics

Our results have implications for many oystercatcher life history decisions, but here we will focus on the life history decisions where and when to settle. Ens *et al.* (1995) developed a settlement model to explain why some individuals accept territories in LQ habitat, given the large difference in reproductive success with HQ territories. This model hypothesized that non-breeders selecting a breeding habitat could attain higher fitness by waiting a few years ('queue') till a HQ habitat becomes available, instead of settling immediately in LQ habitat for which competition is low. Their 'queue model' calculates the frequency dependent evolutionary stable settlement strategy, using the expected LRS (in fledglings) as a fitness currency. There were insufficient data to investigate the fitness consequences of natal origin beyond fledging when the model was developed, and Ens *et al.* therefore assumed that fledgling fitness prospects were independent of natal origin. However, with more data available, we can refute the assumption that fledglings from HQ and LQ contribute equally to fitness. Incorporating higher fitness prospects of offspring born in HQ habitat in the queue model should shift the equilibrium to more non-breeders opting for HQ habitat that are also willing to wait for longer, instead of settling immediately in LQ habitat. Furthermore, our results show that individuals of different natal origin have different settlement patterns, with fledglings from LQ territories having much lower probability of settling in HQ habitat than fledglings from HQ territories. The queue model by Ens *et al.* (1995) is not sufficiently detailed to explain why these different settlement strategies exist; this would require the incorporation of condition-dependent settlement strategies.

Finally, this study shows that using short-term or incomplete fitness estimates can lead to incorrect inferences when quantifying source-sink population interactions. Breeders in HQ habitat produced annually 2.5 times more fledglings than breeders in LQ habitat. However, not all fledglings were of the same quality. Consequently, breeders in HQ habitat each year contributed 7.8 times (2.5 fold difference in quantity of fledglings x 3.1 fold difference in RV of one fledgling) more to λ than breeders in LQ habitat. As such, breeders in LQ habitat contributed only marginally to the growth rate of this population of oystercatchers.

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Appendix 7A

The structure of the population matrix models followed Fig. 7.1, with separate 1st and 2nd year stages and no migration. Matrix elements (a_{ij}) refer to parameters estimated in Tables 7.1-3 and Figure 7.2.

Model 1 Stage-structured population model without any differences between natal origins.

$$\begin{bmatrix} N_{FL} \\ N_1 \\ N_2 \\ N_{NB} \\ N_{LQ} \\ N_{HQ} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & 0 & F_{LQ} & F_{HQ} \\ S_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & \Psi_{NB,NB} & \Psi_{LQ,NB} & \Psi_{HQ,NB} \\ 0 & 0 & 0 & \Psi_{NB,LQ} & \Psi_{LQ,LQ} & \Psi_{HQ,LQ} \\ 0 & 0 & 0 & \Psi_{NB,HQ} & \Psi_{LQ,HQ} & \Psi_{HQ,HQ} \end{bmatrix} \begin{bmatrix} N_{FL} \\ N_1 \\ N_2 \\ N_{NB} \\ N_{LQ} \\ N_{HQ} \end{bmatrix}_{t}$$

Model 2 Stage-structured population model with differences between natal origins. Superscripts refer to natal origin. If $a_{ij}{}^{LQ}=a_{ij}{}^{HQ}$, model 2 reduces to model 1.

$$\begin{bmatrix} N_{FL}{}^{LQ} \\ N_1{}^{LQ} \\ N_2{}^{LQ} \\ N_{NB}{}^{LQ} \\ N_{LQ}{}^{LQ} \\ N_{HQ}{}^{LQ} \\ N_{FL}{}^{hQ} \\ N_1{}^{HQ} \\ N_2{}^{HQ} \\ N_{NB}{}^{HQ} \\ N_{LQ}{}^{HQ} \\ N_{HQ}{}^{LQ} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & 0 & F_{LQ}{}^{LQ} & 0 & 0 & 0 & 0 & 0 & F_{LQ}{}^{HQ} & 0 \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & \Psi_{NB,NB}{}^{LQ} & \Psi_{LQ,NB}{}^{LQ} & \Psi_{HQ,NB}{}^{LQ} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \Psi_{NB,LQ}{}^{LQ} & \Psi_{LQ,LQ}{}^{LQ} & \Psi_{HQ,LQ}{}^{LQ} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \Psi_{NB,HQ}{}^{LQ} & \Psi_{LQ,HQ}{}^{LQ} & \Psi_{HQ,HQ}{}^{LQ} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & F_{HQ}{}^{LQ} & 0 & 0 & 0 & 0 & 0 & F_{HQ}{}^{HQ} \\ 0 & 0 & 0 & 0 & 0 & 0 & S_1{}^{HQ} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_2{}^{HQ} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_2{}^{HQ} & \Psi_{NB,NB}{}^{HQ} & \Psi_{LQ,NB}{}^{HQ} & \Psi_{HQ,NB}{}^{HQ} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \Psi_{NB,LQ}{}^{hQ} & \Psi_{LQ,LQ}{}^{HQ} & \Psi_{HQ,LQ}{}^{HQ} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \Psi_{NB,HQ}{}^{HQ} & \Psi_{LQ,HQ}{}^{HQ} & \Psi_{HQ,HQ}{}^{HQ} \end{bmatrix} \begin{bmatrix} N_{FL}{}^{LQ} \\ N_1{}^{LQ} \\ N_2{}^{LQ} \\ N_{NB}{}^{LQ} \\ N_{LQ}{}^{LQ} \\ N_{HQ}{}^{LQ} \\ N_{FL}{}^{HQ} \\ N_1{}^{HQ} \\ N_2{}^{HQ} \\ N_{NB}{}^{HQ} \\ N_{LQ}{}^{HQ} \\ N_{HQ}{}^{HQ} \end{bmatrix}_{t}$$

Box C: Which offspring traits might mediate the effect of natal origin on fitness?

Differences in natal origin are strongly associated with performance later in life in Oystercatchers *Haematopus ostralegus* (Chapter 7). This suggests that offspring from high quality natal origin were of better quality than offspring from low quality natal origin, which enabled them to perform well during their adult life as well. Offspring reared under different conditions might differ in their growth and development (e.g. body size, hormones, immunology), in their social experiences (e.g. sibling competition, competition with conspecifics), or in the temporal environment in which they fledge. Offspring quality is therefore likely to be a multidimensional trait, of which some components are difficult to measure (e.g. differences in social experience might be purely informational), and other components are more easily quantifiable. In this study, we investigate whether offspring reared under high or low quality rearing conditions differed in (i) their date of birth, (ii) the mass at fledging, (iii) the size at fledging, or (iv) whether they grew up with siblings or not. Subsequently, we consider if these offspring characteristics are associated with fitness components later in life and as such might explain why offspring of different natal origin perform differently during their life.

Methods

Each year we systematically searched the study area for nests. All nest were found before hatching, consequently date of birth (hatch date) was determined with high accuracy. Date of birth is an important life history trait in many bird species, because early birds might experience higher food availability and have more time to prepare for the winter. Chicks were caught and individually marked with colour rings just before fledging. Head length (head plus bill length) was measured with sliding callipers. Leg length (length of tarsus plus the longest toe) and wing length were obtained with a ruler with a zero stop (Svensson, 1984). Body mass was measured with pesola spring balances. For each fledgling we recorded whether there were siblings alive at the moment of fledging or not.

Chicks were measured at various ages (90% range; 20-39 days). Measurements were corrected to a standard age of 30-days using a reference growth curve based on individual growth patterns of fledged chicks (Kersten & Brenninkmeijer, 1995). For each fledgling we calculated how many standard deviations its measurement deviated from the mean value of the reference curve at the age it was measured. Subsequently, we calculated the corresponding value at day 30 with the same amount of standard deviations from the mean, again using the reference growth curve. This method was used, because variances around the mean are dependent on the age of the chicks for all biometric measures. All chicks that were measured at an age over 40 days (3% of the total) were omitted from analysis as it is impossible to obtain unbiased reference growth curves for these age-classes (only individuals that grew very slowly had not yet fledged).

A principle component analysis was used to combine the standardized day-30 measurements of head, wing and leg length into one single body size variable. The first principle component (PC1) explained 70% of the variance and this variable, hereafter referred to as body size, was used for further analysis. The loading of all three variables on PC1 was almost equal; Kaiser-Meyer-Olkin measure of sampling adequacy was 0.65, indicating good quality. Residual body mass was calculated by taking the residuals of the quadratic regression of body mass on body size ($R^2=0.53$, $N=310$, $p<0.0001$). Hereafter we will refer to body size and residual body mass at day 30 as 'at fledging'. In all analyses we will use body size at fledging and residual body mass at fledging instead of body size and body mass at fledging, as the first are not inter-correlated and the latter are. Date of birth, body size at fledging and residual body mass at fledging were rescaled to zero and divided by their standard deviation to obtain z-scores. Average body mass at fledging was 307.9g (S.D. 54.2) and the average date of birth was 17.6 June (S.D. 10.3 days); the standard deviation of residual body mass at fledging was 37.8g.

In the analysis we entered all linear and quadratic effects of all offspring characteristics to the model, as well as the random effect of nest and the fixed effects of winter severity, sex, and the main effects of, and interactions between, natal origin, sex and offspring characteristics. Model selection was done by backward deletion of non-significant terms. In the final model containing all significant effects, we re-entered the effect of natal origin to investigate whether it still explained a significant part of the variance.

Results

Fledglings from HQ natal origin were 10% heavier ($t=7.2$, $df=309$, $P<0.001$) and were twice as likely to fledge together with sibs than fledglings from LQ natal origin (Fig. Box C1B,C). However, body size at fledging ($t=1.2$, $df=309$, $P=0.24$) and date of birth ($t=-1.2$, $df=309$, $P=0.22$) of fledglings from HQ or LQ natal origin did not differ (Fig. Box C1A,D).

Fledglings that hatched from early nests were more likely to survive till adulthood than fledglings that hatched from late nests; however this pattern was restricted to individuals from LQ natal origin (Fig. Box C1A; Table Box C1A). Heavier fledglings were more likely to survive till adulthood, independent of natal origin (Fig Box C1B; Table Box C1A). Furthermore, the probability to survive till adulthood was correlated between fledglings from the same nest (Table Box C4A; indicated by significance of 'nest'), suggesting that additional (non-measured) parental or environmental effects affected survival till adulthood, independent of hatch date and residual body mass at fledging.

Among birds that survived till adulthood, those that had fledged with sibs were more likely to recruit than those that fledged alone, independent of natal origin (Fig Box C1C; Table Box C1B). In addition, among the recruits from HQ natal origin, larger recruits had a higher chance to settle in HQ habitat (Fig Box C1D; Table Box C1C). The effect of body size at fledging for individuals from LQ natal origin could not be tested as only one individual from LQ natal origin ever directly recruited in HQ habitat.

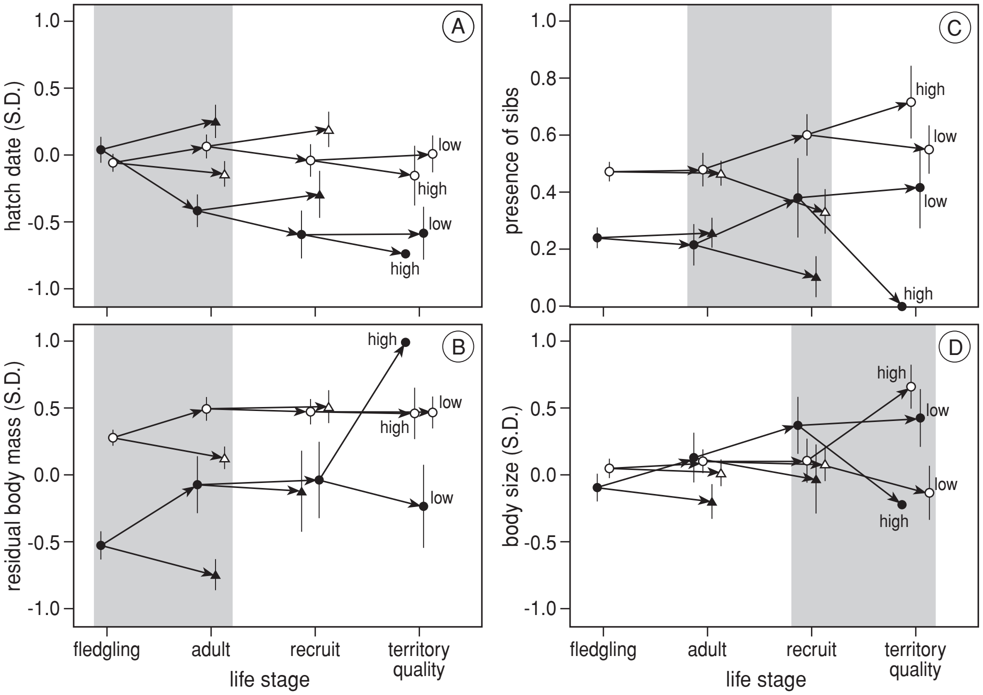

Figure Box C1 Differences in offspring characteristics between individuals that reach a certain life history stage (circles) and individuals that do not reach those life history stages (triangles). The investigated offspring characteristics are (A) date of birth, (B) residual body mass at fledging, (C) the presence of sibs at fledging and (D) the size at fledging. Closed dots refer to fledglings from low quality natal origin, open dots refer to fledglings from high quality natal origin. Shaded areas point to transitions between life history stages that were dependent on certain offspring characteristic (see text and Table Box C1). Error bars are based on standard errors; sample sizes are given in Chapter 7. Note that only one individual from low quality natal origin ever directly recruited in high quality habitat.

Residual body mass and the presence of siblings at fledging differed between fledglings from HQ and LQ natal origin, and these offspring characteristics can therefore potentially explain why offspring from HQ natal origin have better fitness prospects than offspring from LQ natal origin. When we re-entered natal origin to the final models, which included all significant offspring characteristics, natal origin did not explain any of the variation in survival till adulthood (Table Box C1A) and recruitment probability (Table Box C1B) anymore.

Table Box C.1 Analysis of the effects of offspring characteristics on (A) the probability of returning to the study area at adulthood, (B) the probability of recruitment from adulthood, (C) the probability a recruit will settle in high quality habitat. Investigated offspring characteristics were linear and quadratic effects of date of birth, residual body mass at fledging, the presence of sibs at fledging and the size at fledging. Other investigated parameters were natal origin, winter severity, sex (except in [A]) and interactions between sex, natal origin and offspring characteristics. Because some fledglings originated from the same nest, nest was added as a random effect in analysis (A) and (B). Data from 1985-1996 cohorts.

(A) Probability of returning to study area at adulthood (logit link)

Parameter	B	s.e. (B)	deviance	df	P
empty model			425.9	309	
final model (R^2=0.20)			340.1	303	
constant	-0.36	0.16	4.95	1	0.026
nest			8.72	1	0.003
winter severity	-0.80	0.33	5.83	1	0.016
residual body mass	0.67	0.15	21.5	1	<0.001
date of birth	-0.96	0.30	10.5	1	0.001
natal origin * date of birth	1.24	0.35	13.0	1	<0.001
if re-entered to final model					
natal origin	0.04	0.32	0.01	1	0.94

(B) Probability of recruitment from adulthood (logit link)

empty model			169.7	116	
final model (R^2=0.07)			158.0	114	
constant	-0.49	0.25	3.97	1	0.046
nest			0.01	1	0.96
siblings	1.32	0.40	10.6	1	0.001
if re-entered to final model					
natal origin	0.34	0.44	0.60	1	0.44

(C) Probability recruit settled in high quality habitat (logit link)

empty model			71.7	58	
final model (R^2=0.21)			57.4	57	
constant	-2.93	1.09	7.15	1	0.008
body size	0.90	0.45	3.95	1	0.047
if re-entered to final model					
Natal origin	1.92	1.11	2.98	1	0.084

Conclusions

Offspring born in HQ habitat were 10% heavier at fledging and were twice more likely to fledge with siblings than offspring born in LQ habitat. Because both mass at fledging and the presence of sibs was associated with fitness components later in life, these two traits might have mediated the strong effect of natal origin on fitness. This idea was further supported by the observation that natal origin did not explain any of the variation in survival till adulthood and recruitment probability anymore after it was re-entered to the model. Nonetheless, we cannot exclude that other non-measured traits might exist that are inter-correlated with mass at fledging, the presence of sibs, as well as natal origin, that might be causally responsible for the observed silver spoon effects.

Interestingly, date of birth and body size did not differ with respect to natal origin but were strongly associated with variation in survival to adulthood and the quality of the habitat in which these individuals recruited, respectively. This suggests that there was also substantial variation in offspring quality between offspring from the same natal origin; the quality of rearing conditions therefore might also vary substantially within a habitat type. Finally, offspring born early in the season had a higher probability of surviving till adulthood, but this pattern was restricted to offspring of low quality natal origin. As such, offspring quality is likely to be a multidimensional trait, in which some dimensions might only be important under specific conditions. For example, being born late in the season might have only been disadvantageous for individuals of low quality natal origin because they also had a much lower body mass.

Chapter 8

Frequency dependent territory choice and delayed breeding: a quantitative test of the queue hypothesis

Martijn van de Pol, Ido Pen, Dik Heg & Franz J. Weissing

Abstract

When habitat quality is variable, the decisions when and where to start reproducing are intricately linked. Many studies suggest that individuals strategically delay breeding (queue) in order to acquire a better breeding territory or social position. Ens *et al*. (1995) were the first to stress that optimal queuing decisions are frequency dependent, thereby integrating theory about ecological distribution (ideal despotic distribution) and life history evolution (delayed maturity). Little is known how well such simple life-history models can quantitatively predict settlement behavior in the wild. This study aims to compare predictions from optimal queuing models with settlement patterns of free-living Oystercatchers, a long-lived bird species. We first improve the original Ens *et al*. model and derive a different evolutionarily stable queuing strategy. This improved model could not explain why settlement patterns of Oystercatchers depend on natal origin. Therefore, we incorporated conditional queuing strategies into our model by making the decisions to queue for either a high or low-quality territory dependent on where an individual was born. Conditional queuing strategies could no only explain Oystercatchers' settlement patterns remarkably well, but also had important consequences for the variation in queuing strategies both at the individual and population level. We suggest how queuing models help us understand patterns of density regulation and population decline.

Introduction

In many species individuals delay reproduction beyond the age of sexual maturity (Newton 1998). It has been standard practice to invoke life-history theory to explain delayed reproduction, with explanations falling into two major classes or a combination thereof. First, young adults may delay reproduction to later stages in life to maximize lifetime reproductive output, for example because reproducing early in life may be at the cost of reduced lifespan (Stearns 1992; Roff 1992). Second, delayed reproduction is phenotype-dependent, e.g. less adapted phenotypes may need to make the best of a bad job.

Another ubiquitous pattern in nature is that once individuals reproduce, some individuals are apparently willing to do so in inferior breeding positions. Examples include individuals accepting low-quality territories, inferior positions in a colony or lek, or subdominant social positions in a group. Again, two major explanations, or a combination of both, have been put forward to explain these facts. First, breeding in low quality habitat may yield the same lifetime reproductive success as breeding in high quality habitat due to density-dependent effects (the ideal free distribution; Fretwell & Lucas 1970). Second, certain phenotypes may be forced to occupy low-quality breeding opportunities, i.e. they are despotically excluded by others from the best breeding spots (the ideal despotic distribution; Fretwell 1972).

Recently, optimal queuing processes have been suggested as a comprehensive framework to predict how much individuals should be willing to delay reproduction and where or which reproductive opportunity to accept, given a frequency- and density-dependent ‘choice’ between, and competition for, breeding positions of different quality (Ens *et al.* 1995; Kokko & Sutherland 1998; Pen & Weissing 2000; Pen & Weissing 2001; Kokko *et al.* 2001; Kokko & Ekman 2002). Queuing theory predicts that individuals may strategically delay reproduction to queue for high-quality breeding opportunities, instead of immediately accepting a low-quality breeding position. As such, queuing processes can explain variation both in age of first reproduction and in quality of breeding positions, without implicitly assuming that some individuals are phenotypically inferior (i.e. making the best of a bad job); although of course both type of explanations do not necessarily exclude each other.

Originally, ‘queue’ and ‘queuing’ were short-hand terms to describe how individuals might delay reproduction and stay within cooperatively breeding groups to inherit the dominant breeding position as soon as it becomes available (Wiley & Rabenold 1984). In the meantime, queue-like systems have been found in many situations. Descriptions range from queues for mating opportunities (Schwagmeyer & Parker 1987), for social and breeding position in group-living and cooperative breeding species (Wiley & Rabenold 1984; East & Hofer 2000; Mitchell 2005), for positions on the lek (Kokko *et al.* 1998), for access to harems or colonies (Poston 1997; Voigt & Streich 2003), and for high-quality territories (Zack & Stutchbury 1992; Ens *et al.* 1995; Ekman *et al.* 2001). By queuing (waiting) for high-quality breeding positions individuals may increase their social dominance and their chances of acquiring these high-quality resources (e.g. Heg *et al.* 2000).

Although the importance of social queuing has been long recognized, Ens, Weissing & Drent (1995; henceforth EWD) were the first to stress that the payoffs of queuing decisions are frequency-dependent: the success of a queuing strategy depends on how many other individuals are queuing for the same opportunity. The frequency dependent nature of queuing decision has important consequences for the evolution of settlement decisions. Using a game-theoretical approach, EWD showed that in evolutionary equilibrium the competition, and thereby queuing time, for high-quality breeding positions increases to a point at which it pays to accept low-quality breeding positions at a young age. As such, EWD extended the ideal despotic distribution into a life-history framework, and showed that delayed reproduction and habitat selection can be viewed as two sides of the same coin.

Recently, frequency-dependent queuing processes have also been used to explain the logic of territory choice (Kokko & Sutherland 1998; Pen & Weissing 2001; Kokko *et al.* 2001), reproductive skew (Kokko & Johnstone 1999), and the evolution of cooperative breeding (Pen & Weissing 2000; Kokko & Ekman 2002). Nonetheless, little is known about whether optimal queuing models can quantitatively predict behavioral patterns observed in nature, while this is important for assessing the value of such models. Although the model by EWD is a general queuing model for situations with habitat heterogeneity, EWD did use their model to make quantitative predictions about the territory choice and delayed breeding of Oystercatchers (*Haematopus ostralegus*). However, EWD could not yet provide a rigorous quantitative test of the key predictions of their model, because it takes a lot of years to gather sufficient field data on a long-lived bird species such as the Oystercatcher. Ten years later, after 21-years of field study, we are now finally able to perform a quantitative comparison of the key predictions of the model by EWD to the observed settlement behavior of Oystercatchers in the field.

In this paper we first make several important improvements to the original EWD model, for example by incorporating population limitation. We will show that such seemingly small modifications result in substantially different predictions regarding the evolutionarily stable queuing strategy. Furthermore, the original EWD model aimed to explain settlement decisions without assuming any phenotypic differences between individuals. However, we now have strong evidence that settlement decisions do depend on the phenotype of the competitors (via the quality of the natal habitat, see van de Pol *et al.* 2006). By incorporating condition-dependent queuing strategies, i.e. where the queuing strategy depends on the natal habitat, we investigate whether competitive or (non-competitive) informational asymmetries between queuers as a result of different natal conditions can help us understand asymmetries in settlement patterns. Using information on the numbers of high and low-quality breeding opportunities and basic life-history parameters from our long-term population study we make quantitative predictions about the settlement patterns of optimal queuers. By comparing how model predictions fit the settlement patterns of Oystercatchers we assess to what extent different models give a better understanding of the mechanism underlying settlement decisions in Oystercatchers. Finally, we suggest how queuing models might help us understand patterns of population decline and density regulation in this species.

Study population

Life history of Oystercatchers

From 1984-2004 we studied an individually-marked breeding population on the Dutch Wadden Sea island of Schiermonnikoog (53°29' N 6°14' W). Here we describe the basic life history of Oystercatchers; a more detailed description of the social system and methodology is given elsewhere (Ens *et al.* 1992; 1995; Heg *et al.* 2000). Oystercatchers are long-lived (over 30 years) and show large variation in age of first reproduction (range 3-11 years). They are socially and genetically monogamous and exhibit high site-fidelity (Heg *et al.* 1993). In coastal breeding Oystercatcher populations, there is often a clear dichotomy in habitat quality, mainly based on the nesting location relative to the foraging area (Ens *et al.* 1992; Safriel *et al.* 1996). Some parents, called residents (R), can take their chicks to the food, because breeding and feeding territory are adjacent. Other parents, called leapfrogs (L), have to bring the food to their chicks, because the breeding and feeding territory are spatially segregated (Fig. 8.1). Because transporting every food item to the chicks is less efficient, residents consistently produce much more offspring per year than leapfrogs (Ens *et al.* 1992). Most part of the island seems to be occupied by territories and consequently there is a surplus of adult non-breeders (N) that do not defend nesting territories. Juveniles are sexually mature and join the non-breeder pool when they reach the age of three years. Adult mortality mainly occurs in winter, subsequent status change finalizes just before the breeding season (May-August).

Estimation of model parameters from field data

To derive quantitative predictions from optimal queuing models (see next section), it is necessary to estimate the life-history parameters that were used in these models from field data. We re-estimated all parameters used by EWD because we now have more years of data, data from a larger area, and better statistical estimation procedures. Annual census took place at the start of the breeding season, just after the period of status change (see Table 8.A1 in Electronic Appendix A for annual values). The number of high-quality breeding territories (T_R) was about half the number of low-quality breeding territories (T_L) (Fig. 8.2A&B). Counts of non-breeders (T_N) only serve as a rough indication, because estimation error was large and determination of which non-breeders were committed to our study area was difficult (Fig. 8.2C). Annual fecundity was defined as the annual number of female offspring produced by a pair that entered the local adult non-breeder pool (young are philopatric; van de Pol *et al.* 2006). Resident territories consistently had a three times higher annual fecundity (F_R) than leapfrog territories (F_L), except in years with almost no young (Fig. 8.2E). Differences in habitat quality between resident and leapfrogs in terms of annual fecundity are thus highly predictable. As population dynamics changed systematically during the 21 years of study, we distinguished two periods (Fig. 8.2D). In the first period (1984-1994) population numbers were fairly stable and fecundity roughly balanced mortality; during the second period (1995-2004) most of the leapfrog territories were abandoned and fecundity was extremely low (Fig. 8.2).

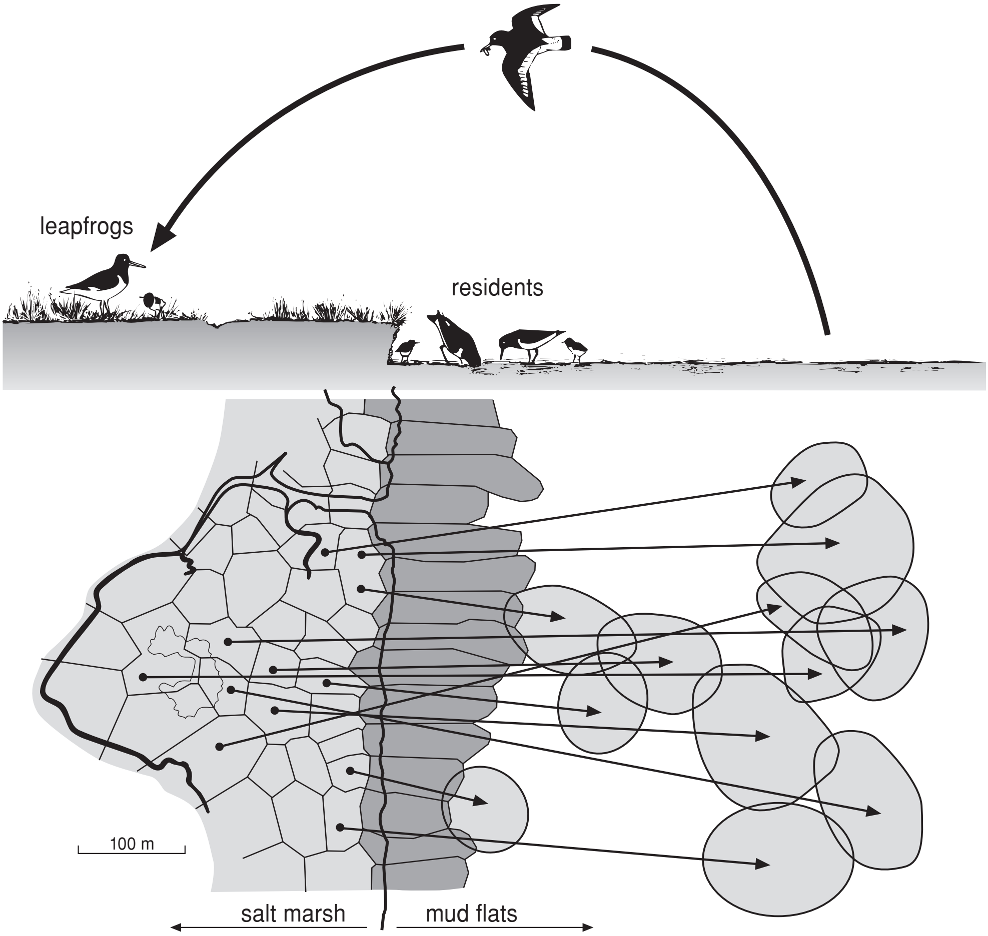

Figure 8.1 Map of part of the study area, showing the location of the nesting territories on the salt marsh and the feeding territories on the inter-tidal mud flats in 1986. Residents (shaded dark) have adjacent nesting and feeding territories, while leapfrogs (shaded light) have spatially separated nesting and feeding territories of leapfrogs (connected with arrows). The diagram at the top depicts how leapfrogs have to transport all food to their chicks, while residents can take their chicks to the feeding ground. Figure adapted from Ens *et al.* (1992), with permission.

The annual probability of changing between states and annual mortality in each state was determined with the use of multi-state capture-recapture models (Fig. 8.3A). These models estimate all transition and mortality parameters in one model and adjust estimates for the fact that we might have missed some individuals (for details of the analyses, see van de Pol *et al.* 2006). Estimates were based on both females and males; estimates did not differ much between the sexes. The population we study is not a closed population; especially non-breeders were probably not completely site-faithful (unpublished data). By comparing patterns of local observations with dead recoveries

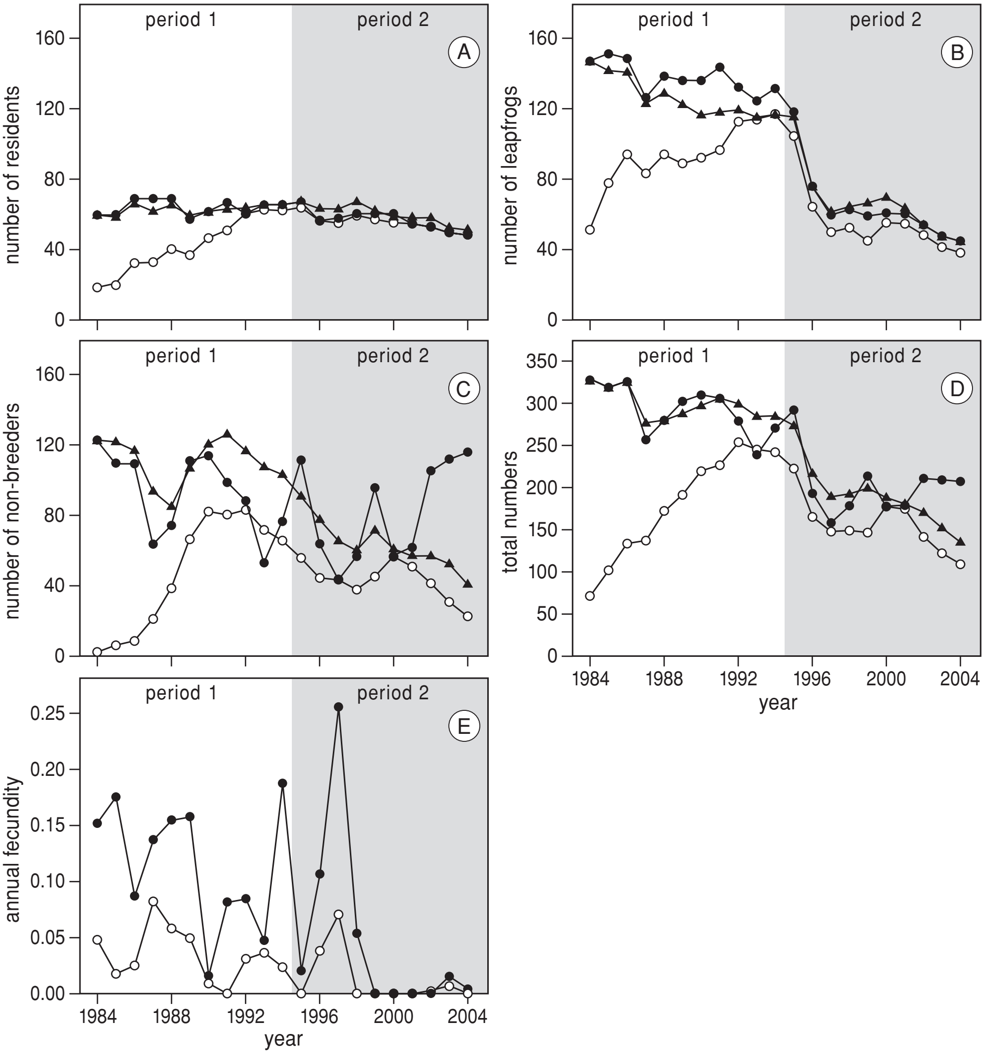

Figure 8.2 Changes in population numbers (A-D) and fecundity (E) from 1984-2004. Number of (A) resident territories, (B) leapfrog territories, (C) non-breeders, and (D) total number of oystercatchers in our population. In (A)-(D), closed circles refer to the counted number of individuals in each state (T_R, T_L, and T_N), open circles refer to the number of ringed individuals, triangles refer to the predicted number of individuals from a population matrix model based on demographic rates (see text). (E) Annual fecundity in resident territories (F_R; closed circles) and in leapfrog territories (F_L; open circles). See Appendix 8B for actual values.

from a larger area (north-western Europe) we estimated that on average 5% of all non-breeders permanently left our study area each year, with dispersal most pronounced in years with high mortality. Annual immigration of non-breeders was difficult to quantify, therefore we assumed immigration matched emigration. Annual values of state transi-

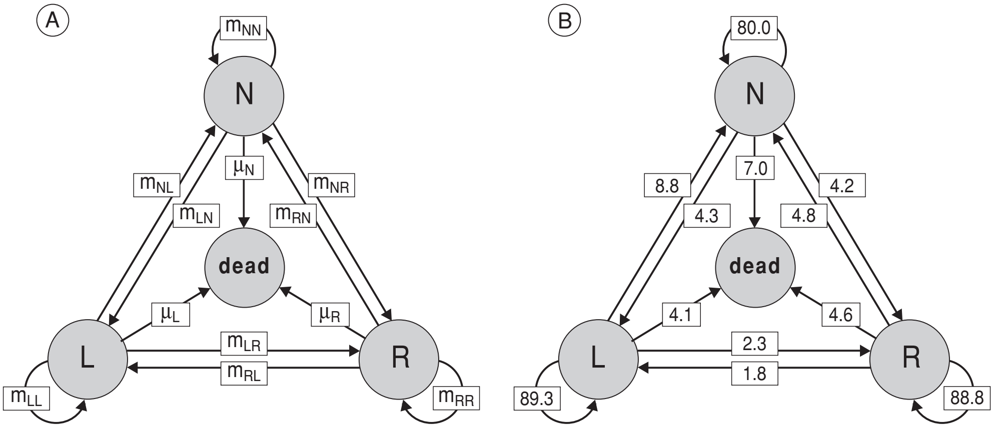

Figure 8.3 Annual state transition (m) and mortality (μ) probabilities (in %) of residents (R), leapfrogs (L) and non-breeders (N) estimated with multi-state mark-recapture models. (A) The structure of the statistical model, and (B) the estimated parameters over period 1 (1984-1994). Note that the sums of the percentages belonging to the arrows originating from each state (N, R, L) sum up to 100% (e.g. $m_{LL}+m_{LN}+m_{LR}+\mu_L=100$). Values per year are given in Appendix 8.B.

tion and mortality probabilities were corrected for migration accordingly (see Table 8.A2 in Appendix 8A). The estimated transition and mortality probabilities used in the queuing models (see next section) are given in Fig. 8.3B, and are with a few exceptions quite similar to EWD.

Counts of the number of non-breeders, resident and leapfrogs and the estimation of life-history parameters were based on separate observations in the field; consequently we can assess their consistency. We constructed a three state (N, R, L) demographic matrix model (see van de Pol *et al.* 2006). Using the numbers per state in 1984 as initial conditions and the estimated life-history parameters of each year (Table 8.A2 in Appendix 8A) we calculated the expected change in numbers from year to year. Despite the fact that we are dealing with an open population, the demographic model predicted the observed annual changes in population numbers quite well (Fig. 8.2), indicating both sources of information were consistent with each other.

The models

We first explain the rationale behind the queue hypothesis before introducing the formal model. The queue hypothesis tries to explain (at least partly) why many oystercatchers start reproducing beyond the age of sexual maturity and why many oystercatchers occupy low-quality habitat. The queue hypothesis suggests that these recruitment patterns can be understood by taking the perspective of non-breeders that face the career decision when and where to settle. Because individuals cannot opt for two options with the same success (due to constraints in time and space), non-breeders have to choose between two different strategies at the start of their adult life. In the first strategy, the hopeful leapfrog (HL) strategy, non-breeders try to settle in low-quality habitat. Hopeful leapfrogs are likely to start reproducing almost immediately and produce few offspring per year for many years. In the second strategy, the hopeful resident (HR) strategy, non-breeders choose to wait (queue) for a high-quality territory to become available. As competition for high-quality territories will probably be fierce, hopeful residents will not be able to reproduce before a much older age than hopeful leapfrogs. Moreover, hopeful residents will have a higher chance of dying before ever reproducing, but if successful they will have a much higher annual reproductive success.

The success of the HR and HL strategy directly depends on the frequency in the population by which non-breeders choose to become either hopeful residents or hopeful leapfrogs, as this determines the strength of competition. Although the HR and HL strategy have different short-term payoff, the key question is whether the different life-history strategies differ in long-term fitness. EWD argue that in evolutionary equilibrium the proportion of non-breeders that plays a HR or HL strategy is such that the expected lifetime reproductive success is equal for both strategies. This makes intuitive sense, because if the fitness of one of the strategies would be higher or lower than the other strategy, non-breeders should switch to the strategy with highest fitness until these fitness differences disappear due to intensified competition.

Some problems with the EWD queue model

Although the idea behind the queue model is attractive, the implementation of the model in EWD has several important shortcomings. Firstly, EWD used a separate population model to derive estimates of expected lifetime reproductive success and subsequently used these values to calculate the evolutionarily stable strategy (ESS) in another model. However, these two models are not fully consistent. In fact, inserting the ESS into the population model yields a stage distribution (percentage N, R and L) that is inconsistent with the data and the analyses on which the first model was based. Therefore, we will here use a life-history approach that incorporates population dynamics and life-history strategies in one coherent model. Secondly, EWD did not include density regulation in their model. In fact, their ESS population increases indefinitely, which is not very realistic. Incorporating density dependence in life-history models is known to strongly affect evolutionary predictions (Mylius & Diekmann 1995; Pen & Weissing 2000). Therefore, we here introduce population limitation in a natural way by setting a maximum on the number of breeding territories. Thirdly, we have recently shown that settlement patterns of Oystercatchers depend strongly on the natal origin of non-breeders, which suggests that settlement strategies are condition (or state) dependent (van de Pol *et al.* 2006). Therefore we will also construct a new model with conditional strategies, in which individuals born in high and low-quality territories can use different queuing strategies.

An improved queue model

Our improved queue model is based on the graphical representation in Fig. 8.4A. Although this model is constructed for Oystercatchers competing for territories of differing quality, the model can also be used as a general description of queuing decisions in situations with habitat heterogeneity. The variable x is the queuing strategy in the population; when $x=1$ all individuals follow a HL strategy; when $x=0$ all individuals follow a HR strategy. For reasons of simplicity, several (implicit) assumptions are made in this model. First, we assume all parameters are time, sex and age independent. Second, we assume the number of resident and leapfrog territories are fixed over time, thereby limiting the population. Consequently, settlement probabilities of HR and HL (a_{HR} and a_{HL}) are density dependent (or more accurately: frequency dependent as they depend on x^*); all other parameters are assumed to be density independent. Third, in the field, it is difficult to qualify all non-breeders as either hopeful resident or hopeful leapfrog. Because we have no reason to assume that the prospecting behavior associated with a HR or HL strategy will result in differential costs, we assumed the annual mortality of both type of non-breeders (HR and HL) was equal ($\mu_{HR}=\mu_{HL}=\mu_N$). Fourth, we assume that non-breeders with breeding experience (breeders that lost their territory) behave similar to non-breeders without breeding experience. Fifth, we assume individuals born in high and low-quality territories make the same strategic queuing decision; this assumption will be relaxed in the next section. Finally, in the model the population size remains stationary and reaches equilibrium where the individuals are asymptotically distributed over the four different states (HR, HL, R and L). As such this model only applies to an equilibrium situation, and we assume this is also the case in the field (see later).

The graphical model in Fig. 8.4A can be described by a system of recurrence equations, from which it is possible to derive the reproductive values (v) and the ESS using standard methods (see Appendix 8B for details). In short, we assess the fitness of a mutant x in a population of individuals playing strategy x^*. The ESS is obtained by finding that value of x^* which cannot be invaded by any alternative mutant strategy ($x \neq x^*$), since the resident population (here meaning the strategy adopted by most members of the population) has a higher fitness than all mutants. It can be shown that an ESS requires that the reproductive values of HR and HL are equal ($v_{HR}^*=v_{HL}^*$), confirming the result by EWD that in the ESS both strategies must yield equal fitness payoffs (see Appendix 8.B). Using this result it follows that in evolutionary equilibrium the ratio of individuals with a HL and HR strategy reflects the ratio of the expected benefits of both types of strategies (see Appendix 8.B):

$$\frac{x^*}{1-x^*}=\frac{m_{NL}(v_L - v_{HL})}{m_{NR}(v_R - v_{HR})} \tag{1}$$

This result was also obtained by EWD (eq. 15 in EWD), although they used expected future reproductive success – a growth rate insensitive fitness measure– instead of reproductive values. EWD subsequently calculated x^* using externally given settlement probabilities of non-breeders (m_{NR} and m_{NL}) derived from field data (Fig. 8.3A).

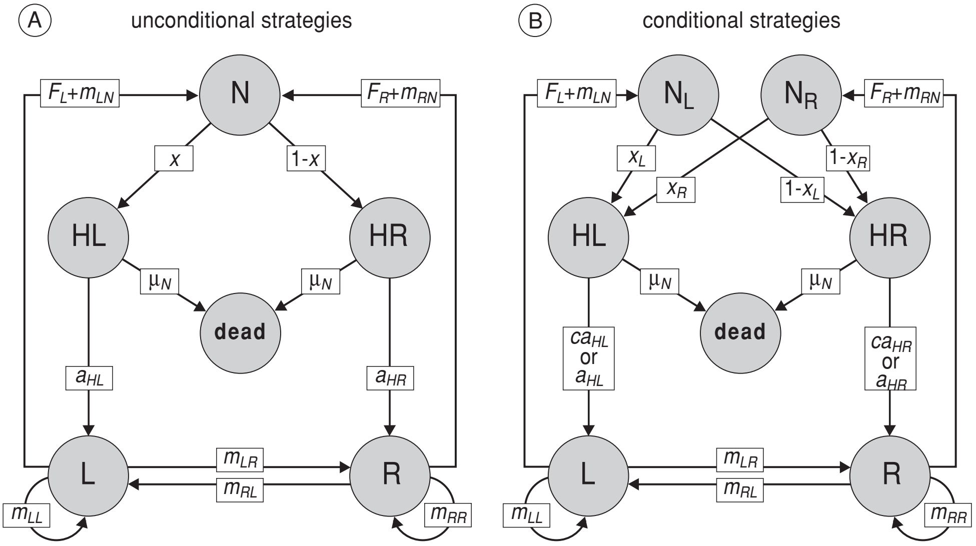

Figure 8.4 Schematic representation of a situation with (A) unconditional queuing strategies and (B) conditional queuing strategies. The parameter x represents the strategic choice individual non-breeders (N) have to make to either follow a hopeful leapfrog (HL) or hopeful resident (HR) strategy. Breeders in leapfrog (L) and resident (R) territories can produce new non-breeders (F_R and F_L) as well as return to the non-breeder state by losing their territory (m_{RN} and m_{LN}). In the conditional model N_R have a_{HR} and a_{HL} annual probability of settling in resident and leapfrog habitat respectively, while N_L have an a_{HR} and a_{HL} probability of settling in resident and leapfrog habitat respectively. Note that only the flows (arrows) between states are given that are necessary for constructing the model (e.g. leapfrogs can die, but this is given by $\mu_L=1-m_{LL}-m_{LN}-m_{LR}$).

However, this approach has three important disadvantages. First, life-history parameters of non-breeders, such as m_{NR} and m_{NL}, are notoriously difficult to reliably estimate in the field, due to the incomplete site-fidelity of non-breeders. Second, the use of estimates of settlement probabilities from field data (m_{NR} and m_{NL}) to calculate the ESS is not ideal as these same parameters are also indirectly used for model validation (i.e. they determine the age of first reproduction and recruitment probabilities). Third, settlement probabilities of non-breeders depend on x^* themselves, as $m_{NR}=(1-x^*)a_{HR}^*$ and $m_{NL}=x^*a_{HL}^*$. Therefore we took a different approach to calculate x^*, which takes full advantage of the fact that we now have incorporated population limitation in our model. Because the total number of territories is fixed, the availability of empty territories for non-breeders (and thereby settlement probabilities) can also be predicted from the behavior of the breeders (see Appendix 8.B). In other words, in our model settlement probabilities are generated by the model itself resulting in an internally consistent model, while this was not the case in the EWD model. When we define the ratio of high and low-quality territories as $q=T_R/T_L$, and the ratio of the total production of new non-breeders by residents and leapfrog territories as $p=(F_R+m_{RN})/(F_L+m_{LN})$, the ESS value for x* in eq. 1 can be rewritten to (see Electronic Appendix 8.B):

$$x^* = \frac{(1 - m_{RR} + m_{LR}p)(1 - m_{LL} + m_{RL}q)}{((1 - m_{RR})(1 - m_{LL}) - m_{RL}m_{LR})(pq+1)} \tag{2}$$

Which shows that the evolutionarily stable queuing strategy x^* is independent of the absolute number of territories as well as independent of the absolute influx of new non-breeders from resident and leapfrog territories. More important, in eq. 2, x^* is expressed as a function of several life-history parameters of breeders, which are much more reliably estimated than life-history parameters of non-breeders (as in eq. 1).

Conditional strategies: asymmetries due to different natal origin

In contrast to EWD, we now know that settlement patterns of Oystercatchers strongly depend on the natal origin of non-breeders (van de Pol *et al.* 2006). Non-breeders born in a resident territory (N_R) settled in both resident and leapfrog territories, however non-breeders born in leapfrog territories (N_L) primarily settled in leapfrog territories (with only one exception). These settlement patterns strongly suggest that settlement strategies are condition (or state) dependent. For example, N_R and N_L might use different settlement rules as a result of their different natal experiences (informational asymmetry). Natal habitat preference induction, in which experience with the natal habitat shapes the habitat preference of individuals, is thought to be an important mechanism for habitat selection (Davis & Stamps 2004). Alternatively, differences in rearing conditions might result in N_R being of higher phenotypic quality than N_L, and as such N_R might be competitively superior to N_L (competitive asymmetry). We extended the previous model to allow both N_R and N_L to make an independent choice of which strategy to follow (x_R and x_L; Fig. 8.4B). The strategic choice N_R have to make can vary between $x_R=0$ when all N_R become HR and we have complete natal habitat preference, and $x_R=1$ when all N_R become HL and we have complete natal habitat avoidance. Similarly, for N_L the choice varies between $x_L=0$, when all individuals leave the habitat type they are born in, and $x_L=1$ when all individuals return to the habitat type they are born in. In addition, we incorporated a new parameter c which reflects differences in competitive abilities between N_R and N_L. When $c=1$ there are no competitive asymmetries; when $c>1$ N_R are competitively superior over N_L, such that they have a c times higher annual probability of acquiring a territory; and the opposite holds for $c<1$. The ESS can be found by simultaneously evaluating the fitness function for x_R^* and x_L^* (see Appendix 8.B for details).

When $c=1$ there is no asymmetry in the model between N_R and N_L, consequently both fitness functions yield the same solution and x_L^* can be expressed as a decreasing function of x_R^*.

$$x_L^* = \frac{(1 - m_{RR} + m_{LR}p)(1 - m_{LL} - m_{RL}q)}{(1 - m_{RR})(1 - m_{LL}) - m_{RL}m_{LR}} - pqx_R^* \tag{3}$$

This expression of a straight line represent a collection of ESSs consisting of many different combinations of x_R^* and x_L^*. We verified whether the two conditional strategies

x_R* and x_L* yield a different queuing strategy at the population level (x*), by describing the population strategy in the conditional model as a weighted average of the conditional strategies:

$$x^* = \frac{x_L^* N_L + x_R^* N_R}{N_L + N_R} = \frac{x_L^* + pqx_R}{pq + 1} \qquad (4)$$

If we insert x_L* from eq. 3 in eq. 4 we return to the same x* from the improved queue model (eq. 2), thereby demonstrating that all different combinations of x_R* and x_L* yield the same population strategy x* as in the improved queue model. From a mathematical perspective there is no reason to assume that one combination of x_R* and x_L* is more likely than any other, or that x_R* should be different from x_L* (i.e $x_R^*=x_L^*=x^*$).

When $c \neq 1$, we introduce competitive asymmetries between N_R and N_L, and the ESS changes substantially. Due to the competitive asymmetries between N_R and N_L, the fitness functions of x_R* and x_L* now have to satisfy two different conditions, which cannot be simultaneously maximized (see Appendix 8.B for details). This means an ESS can only exist when at least one group of individuals plays a pure strategy (Maynard Smith & Parker 1976). Consequently, two candidate ESSs might exist when N_R play a pure strategy ($x_R^*=0$ or $x_R^*=1$), and two candidate ESSs might exist when N_L play a pure strategy ($x_L^*=0$ or $x_L^*=1$). Which of these four solution is evolutionarily stable and what is the optimal strategy of the other group of individuals depends on the actual values of life-history parameters (see next section).

Application of the models

The improved queue model

We limit our quantitative analyses to period 1 as an ESS approach assumes the population is in equilibrium and this is clearly not the case in period 2 (Fig. 8.2). Inserting the parameters estimated averaged over period 1 (Figs. 8.2&8.3) in eq. 2, we quantified x* in this population. To asses the confidence intervals of x*, we simulated 1000 random samples from a multivariate normal distribution of the input parameters used in eq. 2. This distribution was generated from a variance-covariance matrix based on the annual variation and covariation of the life-history parameters used in eq. 2 (see Appendix 8.A, Table 8.A3). We estimated 30% of all non-breeders followed a HR strategy and 70% followed a HL strategy ($x^*=0.70\pm0.08$; 95% CI: [0.59-0.85]). This result is exactly opposite to the result of EWD, who predicted that 70% of all individuals followed a HR strategy ($x^*=0.30$). This difference is not a consequence of differences in estimates of input-parameters, because inserting EWD field estimates of life-history parameters in our model yielded $x^*=0.66$. Similarly, when we insert the parameters estimated in this study in the EWD model we found $x^*=0.26$, again confirming that differences between the studies are primarily caused by differences in modeling approach and not by using different parameter estimates.

Using the ESS we calculated the expected fate of all hopeful residents and hopeful leapfrogs (Fig. 8.5). Although most non-breeders followed a HL strategy, the majority of them are expected to acquire a leapfrog territory immediately as a consequence of the large number of available leapfrog territories. Within three years after sexual maturity virtually all hopeful leapfrogs are expected to have settled, with only a small proportion (9%) dying before ever reproducing. In contrast, most HR have to wait a long time before they can start to reproduce and consequently hopeful resident have a high probability of dying before ever reproducing (39%). Although the model predicts most non-breeders are expected to follow a HL strategy, competition is probably most fierce for the few resident territories. Hopeful residents not only have fewer settlement options, but also have to compete with the many leapfrog territory owners switching to resident territories ($T_L m_{LR} >> T_R m_{RL}$). In equilibrium, the number of hopeful residents that did not settle immediately and were queuing was twice as high as the number of hopeful leapfrogs. Consequently, we expect on average 0.56 hopeful residents queuing per resident territory, while we expect only 0.13 hopeful leapfrogs queuing per leapfrog territory. This leads to the paradoxical result that in the ESS the vast majority of individuals are expected to follow a HL strategy ($x^*=0.70$), while at any given moment 4.3 times more individuals are queuing for resident territories than for leapfrog territories (which can also be seen by comparing the difference in the size of white areas of Fig. 8.5A and 8.5B).

The ESS can be used to predict settlement patterns in resident and leapfrog territories, and to predict how large the difference in age of first settlement between hopeful residents and hopeful leapfrogs should be when Oystercatchers would behave as optimal queuers. These predictions can then be compared to field data. We cannot directly compare the lifetime fitness of hopeful residents and leapfrogs in the field for two rea-

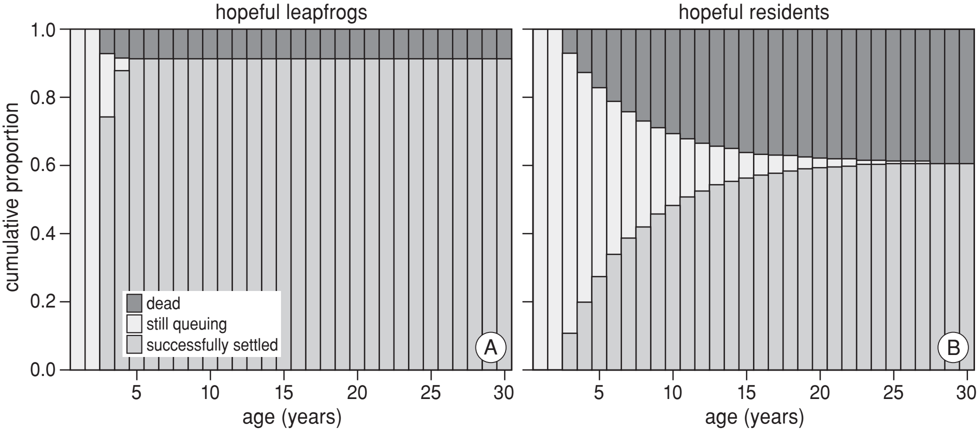

Figure 8.5 Predicted recruitment patterns of (A) hopeful leapfrogs, and (B) hopeful residents in the unconditional model. Plotted are the progressive changes in time of the cumulative proportions of individuals that successfully settled, individuals that are still queuing and individuals that died before ever settling.

sons. First, in the field we cannot qualify all non-breeders unambiguously by their behavior to either a HR or HL strategy. Secondly, our behavioral observations on non-breeders are mainly during the breeding season, after the period in which the majority of status change has already taken place (Heg *et al.* 2000; Bruinzeel & van de Pol 2003). Consequently, the non-breeders we did observe and were able to qualify as either a hopeful resident or hopeful leapfrog, were biased towards unsuccessful non-breeders that did not settle immediately and were still queuing. Because we can qualify all successful hopeful residents and hopeful leapfrogs without any bias (e.g. individuals that settled in resident territories must by definition have followed a HR strategy), we restricted our quantitative comparison between model predictions and field data to these successful individuals.

We calculated the expected proportion of successful hopeful residents and hopeful leapfrogs in the equilibrium situation (Table 8.1). The improved model predicted that 22% of all successful recruits would first settle in a resident territory and 78% in a leapfrog territory. These values were remarkably close to the observed patterns in the field (20% vs. 80%). Predicted age of first settlement for hopeful residents (7.6 years) was 4.3 years higher than for hopeful leapfrogs (3.3 years). In the field, age of first settlement was only 1.1 year higher in resident territories (7.6 years) than in leapfrog territories (6.5 years) Although the observed difference of 1.1 years was statistically significant (ANOVA with settlement territory type: $P=0.044$, sex of bird was not significant), it was much smaller than predicted by the model. This discrepancy between the model predictions and field data was primarily due to the fact that in the field hopeful leapfrogs settled much later than our model predicted (Table 8.1).

The main results were quite robust to small deviations, as determined by sensitivity analyses (see Table 8.C1 in Appendix 8.C). The life-history parameters for which x^* was most sensitive, the ratio of resident and leapfrog territories (q) and the annual transition probability from a leapfrog to a resident territory (m_{LR}), were among the parameters that varied least between years and were probably also quite accurately estimated. However, the difference in age of first settlement between hopeful residents and hopeful leapfrogs was quite sensitive to changes in the mortality of non-breeders (Table 8.C1). Mortality of non-breeders varied substantially between years and could only be roughly adjusted for migration; therefore it probably is one of the least reliable parameters (see also Discussion). The stationary stage distribution of our model described the ratio of non-breeders, residents and leapfrogs in the field well (deviations $<10\%$).

The conditional queue model

We first explore the situation where we have no differences in competitive asymmetries ($c=1$). The collection of ESSs (see eq. 3) is given by the line $x_L^*=1.38-0.98x_R^*$ (Fig. 8.6). This line consists of two extreme cases with one group playing a pure strategy ($x_R^*=1$, $x_L^*=0.40$ and $x_R^*=0.39$, $x_L^*=1$), and many combinations of both N_R and N_L playing a mixed strategy, which also contains the solution of the unconditional model ($x_R^*=x_L^*=x^*=0.70$; see eq. 4). In this model there is no selective force that would explain why conditional strategies would evolve, when starting out with a population

Table 8.1 Comparing settlement patterns and age of first settlement (years) of model predictions with observed values in the field. Values are given for all offspring combined (unconditional queue model), and for offspring separated by their natal origin (conditional queue models). Note that when the predictions from the conditional model with c=1 or c=1.01 are aggregated they equal the predictions of the unconditional model (see text). Field data are calculated for all recruits born in 1984-1994 which all recruited in the period 1984-2004. Observed values are given with ±s.e. and sample sizes between parentheses. Predicted values are given with 95% confidence intervals (between parentheses), calculated with the use of 1000 simulated datasets (see text).

Settlement strategy	Unconditional model	Conditional model with c=1 and x_L*=1 or c=1.01		Conditional model with c=5	
	All offspring (N_R+N_L)	Resident offspring (N_R)	Leapfrog offspring (N_L)	Resident offspring (N_R)	Leapfrog offspring (N_L)
Observed settlement chance					
Successful HR	20.0% (n=11)	18.2% (n=10)	1.8% (n=1)	18.2% (n=10)	1.8% (n=1)
Successful HL	80.0% (n=44)	52.7% (n=29)	27.3% (n=15)	52.7% (n=29)	27.3% (n=15)
Successful N (HL+HR)	100% (n=55)	70.9% (n=39)	29.1% (n=16)	70.9% (n=39)	29.1% (n=16)
Predicted settlement chance					
Successful HR	22.4% (8.0-34.0)	22.4% (8.0-34.0)	0%	24.8% (10.3-36.1)	0%
Successful HL	77.6 (66.0-92.0)	21.8% (11.4-36.2)	55.8% (46.9-61.8)	39.4% (27.2-55.1)	35.8% (29.4-44.4)
Successful N (HL+HR)	100%	44.2% (38.2-53.1)	55.8% (46.9-61.8)	64.2% (55.3-70.1)	35.8% (29.4-44.4)
Observed age of first settlement					
Successful HR	7.6±0.5 (n=11)	7.5±0.3 (n=10)	8.0 (n=1)	7.5±0.3 (n=10)	8.0 (n=1)
Successful HL	6.5±0.3 (n=44)	6.5±0.5 (n=29)	6.5±0.2 (n=15)	6.5±0.5 (n=29)	6.5±0.2 (n=15)
Successful N (HL+HR)	6.8±0.3 (n=55)	6.9±0.3 (n=39)	6.6±0.7 (n=16)	6.9±0.3 (n=39)	6.6±0.7 (n=16)
Predicted age of first settlement					
Successful HR	7.6 (4.3-11.6)	7.6 (4.3-11.6)	-	7.5 (4.2-11.3)	-
Successful HL	3.3 (3.0-6.0)	3.3 (3.0-6.0)	3.3 (3.0-6.0)	3.1 (3.0-5.5)	3.6 (3.0-6.2)
Successful N (HL+HR)	4.3 (3.0-7.0)	5.5 (3.0-8.1)	3.3 (3.0-6.0)	5.3 (3.0-7.9)	3.6 (3.0-6.2)

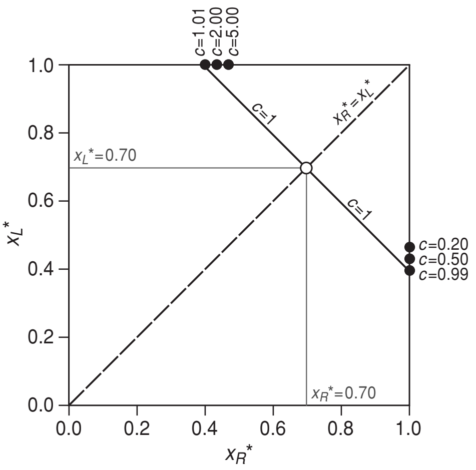

Figure 8.6 ESS values of the strategic queuing variables x_R* and x_L* for varying values of competitive asymmetry (*c*). When $c=1$ there is a line of equilibria (solid line), which also contains the solution of the unconditional model ($x_R^*=x_L^*= x^*=0.70$; open circle). When $c \neq 1$ there always is only one stable ESS (closed circles); either an ESS where x_R* is a pure strategy (for all $c<1$), or an ESS where x_L* is a pure strategy (for all $c>1$). The line where $x_R^*=x_L^*$ is depicted by the dashed line.

where all individuals follow the same strategy ($x_R^*=x_L^*=x^*$). Nonetheless, there might be external biological arguments that might explain why x_R* and x_L* might be different. For example, N_L that use a simple rule as to always return to their natal habitat ($x_L^*=1$) might have to spend less time on prospecting behavior, while a more complex mixed strategy (e.g. when $x_L^*=0.70$) might require more information to be gathered and processed. Note that in the ESS where $x_L^*=1$, N_R also more often return to their natal habitat type ($x_R^*=0.39$), but this preference is not absolute. A situation where N_R always return to their natal habitat ($x_R^*=0$) is never an ESS, at least not in this population (Fig 8.6).

When small asymmetries in competitive abilities are incorporated ($c \neq 1$), the line of equilibria from eq. 3 disappears, even when *c* is close to one (Fig. 8.6). This shows that the conclusions for the situation $c=1$, only hold if there are no competitive asymmetries at all between N_R and N_L. For all $c>1$, i.e. when N_R are competitively superior over N_L, only one ESS exist, namely when all N_L become hopeful leapfrog ($x_L^*=1$; pure strategy) and N_R become both hopeful leapfrog and hopeful resident (mixed strategy). The exact value of x_R* depends on *c*, but did not vary much over all (Fig. 8.6). This weak dependence of x_R* on *c* makes sense because there are so many leapfrog territories, that virtually all hopeful leapfrogs can acquire a territory immediately (Fig. 8.5); increasing competitive asymmetries for a resource that is barely competed for has little effect on the optimal queuing behavior of non-breeders. When $c<1$, the situation of $x_L^*=1$ becomes unstable and an ESS is reached when $x_R^*=1$ and $x_L^*=0.40$, (for $c=0.99$; Fig. 8.6). Therefore, the competitively inferior phenotype always does best to follow a pure strategy in which they all opt for the low-quality resource for which there is almost no direct competition, while the competitively superior phenotype follows a mixed strategy in the ESS. The population strategy in the case of $c \neq 1$ no longer exactly equals the x^* from the unconditional model; the population strategy is always higher than $x^*=0.70$, but this difference was small (<5%) for realistic values of c.

We derived and compared quantitative predictions in the ESS for three scenarios with conditional strategies: (i) with no competitive asymmetry ($c=1$) and complete natal habitat preference for N_L as observed in the field ($x_L{}^*=1$), (ii) with a small competitive asymmetry ($c=1.01$), and (iii) with a large asymmetry ($c=5$) between N_R and N_L. The quantitative predictions from the first and second scenario were virtually similar. When there were no or small competitive asymmetries, the observed settlement patterns of both N_R and N_L in the field deviated substantially from the predicted values from the conditional models (Table 8.1). While the models predicted that most successful hopeful leapfrogs were born in leapfrog territories, in the field most successful hopeful leapfrogs were born in resident territories. However, when competitive asymmetries were large ($c=5$) this discrepancy in settlement patterns between model prediction and observed patterns the field largely disappeared, and the model explained settlement patterns quite well. Quantitative predictions from all models with conditional strategies ($c=1$ to $c=5$) did not explain the patterns of age of first settlement in the field better than the unconditional model. Age of first settlement also did not differ between offspring born in high or low-quality habitat (6.9 vs. 6.6 years), while they were predicted to differ about two years (Table 8.1). In conclusion, the conditional model explained settlement chances and patterns much better than the unconditional model, but only if we assumed that N_R were about five times more likely than N_L to acquire a breeding territory. Furthermore, both the conditional and unconditional models did not predict the difference in age at first reproduction between HR and HL in the field very well. Although the age of first reproduction of successful hopeful residents in the field was exactly as predicted by all models, the age of first reproduction of successful hopeful leapfrogs was much lower in the field than predicted.

Discussion

New insights from our improved queuing models

In this study we first reproduced the main result by EWD: in the evolutionarily equilibrium non-breeders should distribute themselves in such a way over both strategies that the lifetime fitness of both strategies is equal. Delayed breeding and breeding in low-quality habitat can therefore be part of an adaptive strategy and do not necessarily imply phenotypic differences. Subsequently, we have shown that individual variation in phenotypic quality also does not exclude the possibility of queuing; it can even facilitate the evolution of different queuing strategies. For example, in the conditional model where offspring differed in competitive abilities, offspring born in high-quality territories queued for both high as well as low-quality territories, with both strategies yielding similar long-term fitness payoff. When competitive asymmetries exist, inferior phenotypes are forced to make the best of a bad job, but this does not imply that all individuals that occupy low-quality habitat or that have delayed reproduction are necessarily making the best of bad job.

This study shows that behavior at the individual level can strongly depend on whether we assume all individuals make the same queuing decision, or whether queuing decisions are condition dependent. Conditional queuing strategies offer a plausible explanation why some type of individuals played a pure strategy (always settle in low quality habitat) and others played a mixed strategy (settled in both high and low quality habitat). Besides important consequences for the behavior at the individual level, we have shown that conditional strategies can also affect the behavior at the population level. In our model with conditional strategies and competitive asymmetries the population strategy differed from the population strategy in the unconditional model (although the difference was relatively small in this study due to the weak competition for low quality territories). Other biological examples in which the population strategy is different between scenarios with unconditional and conditional strategies include optimal sex allocation strategies under conditional sex expression (Frank & Swingland 1988) and asymmetric contest in owner-intruder conflicts (Maynard Smith & Parker 1976). Incorporating the possibility that individuals might adjust their strategic decision to the conditions they are in, might therefore improve our understanding of individual as well as population level variation in life-history decisions in many situations.

This study also emphasizes an important methodological point for modeling optimal life-history decision. One of the main improvements to the original EWD model was the incorporation of density dependent population limitation. As a result, the ESS strategy in our model was completely opposite from the EWD model; we predicted the majority of individuals were expected to follow a HL strategy instead of a HR strategy. As such this study illustrates the importance of being specific about the mechanism of density dependence, as this can strongly affect evolutionary predictions (see also Mylius & Diekmann 1995; Pen & Weissing 2000).

Model validation: predictions and assumptions

The queuing models we presented serve as simple baseline models to increase our understanding of settlement patterns. In the next section we will discuss the validity of several model assumptions as well as how discrepancies can be used to generate further new hypotheses.

The predicted settlement probabilities seemed to fit the field data quite well. The total number of successful hopeful residents and hopeful leapfrogs was almost exactly as predicted by the models and the observation that non-breeders born in leapfrog territories virtually never settled in residents territories was consistent with N_L playing a pure hopeful leapfrog strategy in the conditional ESS. Even the observation that most successful hopeful leapfrogs in the wild were born in resident territories, could be explained by a model in which hopeful leapfrogs born in resident territories were competitively superior over hopeful leapfrogs born in leapfrog territories. Fledglings born in resident territories are 10% heavier at fledgling than fledglings born in leapfrog territories; as such they might be of higher phenotypic quality (van de Pol *et al.* 2006). However, at this moment we do not have a good understanding what determines differences in competitive ability in adults. Social dominance in Oystercatchers is strongly site-dependent, which makes differences in competitive abilities very difficult to assess in the field (Bruinzeel *et al.* 2006a). Nonetheless, it is clear that a better understanding of qualitative differences between non-breeders is crucial for a better understanding of individual variation in settlement decisions.

In contrast to the good fit of model predictions of settlement probabilities, predicted age at first settlement fitted the field data less well. As predicted by all models, it took more years to acquire a high-quality territory than a low-quality territory. However, the quantitative difference in age of first reproduction between hopeful resident and leapfrogs was about three years less than predicted by these same models, primarily because the age of first reproduction in leapfrog territories was much higher than predicted. Several hypotheses might explain this discrepancy. First, the predicted age of first reproduction by our models is strongly dependent on our estimate of non-breeder mortality. As in many other field studies, dispersal in and out of the study area strongly interfered with the accurate estimation of the mortality of site-unfaithful non-breeders. Second, the high age of first settlement of hopeful leapfrogs in the field might suggest that they reach sexual maturity at a higher age than hopeful residents. Thirdly, except for differences in natal background, we implicitly assumed that all queuing individuals had an equal chance of acquiring the territory they were queuing for (random order service). However, queues of Oystercatchers probably more strongly resemble strict queuing (first in, first out), as social dominance seems to improve gradually while queuing and subsequently facilitate territory acquisition (Heg *et al.* 2000; Bruinzeel & van de Pol 2003). For example, Oystercatchers without breeding experience have a much lower settlement probability than non-breeders with breeding experience (Bruinzeel 2004). Incorporating mechanisms into our models that structure queues into hierarchies based on breeding experience are likely to result in a predicted age of first settlements for hopeful leapfrogs that are closer to those observed in the field.

Our models predicted that on average 0.13 hopeful leapfrogs were actively queuing per leapfrog territory and 0.56 hopeful residents per resident territory. If each queuer would only queue for one single territory this would mean that there would be no-one queuing for the remaining vast majority of leapfrog territories and half of all resident territories. Consequently, hopeful leapfrogs and residents might do better to queue for several territories and thereby hedge their bets. In fact, intrusion patterns of prospecting non-breeders during the breeding season suggest just that: home ranges include around ten to twenty territories and are consistent within individuals between years (Bruinzeel *et al.* 2006b). If queuers queue for multiple territories, this also raises the question on how a population in which 70% is expected to play a HL strategy actually behaves at the individual level. Do 70% of all individuals prospect for leapfrog territories, or do all individuals prospect for 70% of their time for leapfrog territories and for 30% of their time for resident territories? The intrusion patterns seemed to suggest that most individuals played a mixed strategy, as both individual N_R and N_L were seen intruding in both resident and leapfrog territories (Bruinzeel *et al.* 2006b). However, it is unclear why N_L were intruding in resident territories quite often, while they virtually never settled there. By queuing for multiple territories non-breeders hedge their bets, but at the same time enable direct competition among queuers as home ranges overlap between individuals. Individual variation in competitive abilities, also within non-breeders from the same natal habitat, might therefore be very important for understanding more of the variation in settlement patterns.

As in most biological studies, the choice of how to define a population is rather arbitrary. Possibly, important parameters, such as the relative number of high and low-quality breeding opportunities might be different when we would have followed a much larger area. Furthermore, Oystercatchers might use optimal queuing strategies that are not locally adapted to the situation of our study area, but to a much larger area with different environmental conditions. Another simplification was that we assumed that individuals live in an equilibrium situation, which is a compulsory condition for ESS analysis. In the field, it is hard to determine whether a population is in equilibrium, as this depends on the timescale under observation and the year-to-year variability in population numbers. Relatively little is known about the evolution of life-history strategies in non-equilibrium situations (Stearns 2000), while such situations might be of specific interest (see next section).

Queuing strategies and population dynamics

Although we compared the predictions of queuing models only to the equilibrium situation in period 1, the disequilibrium situation in period 2 is very illustrative for understanding how queuing processes might affect population dynamics. During period 2, the number of leapfrog territories declined with 50%; while the number of residents and non-breeders remained fairly stable (Fig. 8.2). This natural pattern of population decline provides support for two important assumptions of queuing. First, non-breeders do seem to be able to discriminate between the qualities of different habitat, because vacancies in resident habitat were re-occupied, while vacancies in leapfrog habitat remained empty. Second, as we have no reason to think that non-breeders were despotically prevented from settling in the many vacated leapfrog territories in period 2 (there were large unoccupied areas), this suggests that most non-breeders preferred to queue for a high-quality territory instead of settling in the vacated leapfrog territories.

If non-breeders preferred to queue for occupied territories in period 2, this implies that the fitness payoff of staying non-breeder was higher than settling immediately in the many vacated leapfrog territories in period 2. In most years the reproductive value of leapfrogs was only slightly (10-15%) higher than the reproductive value of non-breeders, while the reproductive value of residents was on average about 50-60% higher than the reproductive value of non-breeders. When in period 2 the fecundity of leapfrogs was zero in most years, we think the value of many of the vacated leapfrog territories was probably reduced below the threshold value for territory acceptance. Until now we have assumed, for reasons of simplicity, that all leapfrog territories are of the same quality. In reality, leapfrog territories vary consistently in terms of fecundity, but

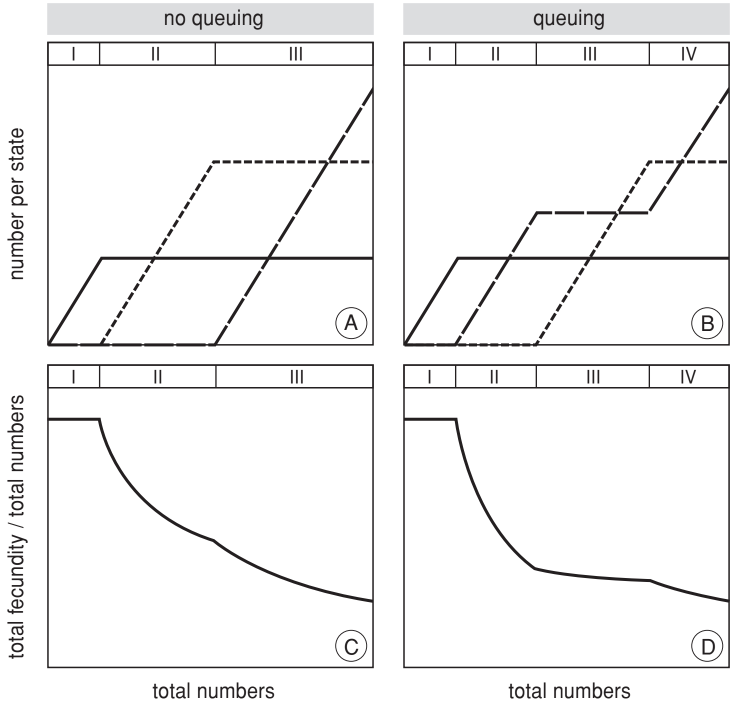

Figure 8.7 Ideal despotic distribution scenarios without queuing (A) and with queuing (B) have a different sequence of habitat occupancy (or abandonment) which is expected to result in different types of density dependent productivity (C) and (D). In situations without queuing the high-quality habitat (solid line) is occupied first, then low-quality habitat (short-dashed line), and when the area is saturated individuals have no other option than to become non-breeder (long-dashed line). In the queuing scenario, once all high-quality habitat is occupied individuals prefer to queue for high-quality habitat instead of settling immediately in low-quality habitat. At some point, competition is so fierce among individuals that queue for high-quality habitat that it is more beneficial to settle in low-quality habitat. Once all low-quality habitat is also saturated, surplus individuals have to become non-breeder and are expected to make a strategic choice to queue for either low-quality or high-quality habitat, as in the case of the Oystercatcher. Both scenarios are presented for a situation with twice as many low-quality territories as high-quality territories and a three-fold difference in annual fecundity per pair, similar tot the case of the Oystercatcher.

most importantly also vary in their distance to resident territories. Owners of leapfrog territories adjacent to resident territories have a much higher chance of acquiring a resident territory each year (8.3±2.2%) than owners of non-adjacent leapfrog territories (1.1±0.6%). Strikingly, the majority of the leapfrog territories that were vacated in period 2 were leapfrog territories that were not adjacent to resident territories. The reproductive values of the leapfrog territories adjacent to resident territories were probably still higher than that of non-breeders, as these leapfrogs had a similar chance as non-breeders of promoting to resident status ($m_{LR} \approx m_{NR}$ in period 2) plus they had some additional (although marginal) reproductive output.

Finally, the models we presented here can be seen as a general model of habitat selection for situations with habitat heterogeneity. When we compare two hypothetical species which both follow an ideal despotic distribution and only differ in their queuing behavior, then their sequence of habitat occupancy (or reversely, habitat abandonment) is quite different. When queuing, the colonization of low-quality habitat occurs at higher population densities than in species that do not queue (Fig. 8.7A,B). Consequently, in situations when not all habitat is saturated, such as in our Oystercatcher population in period 2, queuing behavior results in population productivity to be lower than when not queuing (Fig. 8.7C,D). Optimal queuing decisions therefore directly shape the mechanism of density dependence as well as meta-population dynamics. Consequently, what is an optimal queuing strategy for an individual is not necessarily best for the population. Conservational actions might want to increase the population growth rate by manipulating non-breeders not to queue and settle immediately. One option would be to artificially increase the quality of low-quality habitat above the threshold of territory acceptance (Kokko & Sutherland 1998; Pen & Weissing 2001; Kokko *et al.* 2001). Another option would be to manipulate the cues non-breeders use for making their settlement decisions. Therefore, both for understanding life-history decisions as well as conservational management studying the behavior of individuals that do not (yet) reproduce might be as important as studying the behavior of the reproductive part of the population.

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Appendix 8.A: Annual values of population numbers and life-history parameters.

Table 8.A1 Annual number of high-quality territories (T_R), low-quality territories (T_L), non-breeder counts (T_N), total population size, and offspring per territory that survived till the age of adulthood produced by breeders in high-quality (F_R) and low-quality territories (F_L). [†]F_R and F_L were estimated in 2002-2004 using the mean juvenile survival rate of all previous years as the fate of not all individuals was known yet. [‡]Territory numbers were based on intensive observations in areas A, B, C, D & OBK (see Heg *et al.* 2000 for a map). Territory numbers for B, D & OBK from 1984-1991 were partly imputed, as not all breeders were ringed in those areas until 1992.

	Year	T_R	T_L	T_N	Total	F_R	F_L
period 1	1984	60[‡]	148[‡]	123	331[‡]	0.153	0.048
	1985	60[‡]	151[‡]	110	321[‡]	0.177	0.017
	1986	69[‡]	149[‡]	110	328[‡]	0.088	0.025
	1987	69[‡]	126[‡]	64	259[‡]	0.138	0.084
	1988	69[‡]	139[‡]	75	282[‡]	0.155	0.059
	1989	57[‡]	136[‡]	112	305[‡]	0.159	0.051
	1990	62[‡]	136[‡]	114	312[‡]	0.014	0.009
	1991	67[‡]	144[‡]	99	309[‡]	0.082	0.000
	1992	60	133	88	281	0.085	0.026
	1993	65	124	53	243	0.048	0.037
	1994	65	132	76	273	0.188	0.024
period 2	1995	65	118	112	295	0.020	0.000
	1996	56	76	64	196	0.108	0.038
	1997	57	60	43	160	0.255	0.071
	1998	60	63	58	181	0.054	0.000
	1999	60	59	97	216	0.000	0.000
	2000	59	61	59	179	0.000	0.000
	2001	55	61	62	178	0.000	0.000
	2002	53	54	106	213	0.001[†]	0.002[†]
	2003	50	48	113	211	0.015[†]	0.005[†]
	2004	48	45	117	210	0.003[†]	0.000[†]
mean	Period 1	64	138	93	295	0.117	0.035
	Period 2	56	65	83	204	0.045	0.011
	All years	61	106	87	248	0.084	0.024

Table 8.A2 (next page) Transition and mortality parameters estimated using multi-state capture recapture models and the number of ringed individuals (r) on which estimates were based. All parameters were estimated using one single statistical model which simultaneously estimates the transitions between states, as well as the mortality and re-sighting probabilities per state. In this model estimates are corrected for the fact that we might have overlooked some individuals in certain years (see van de Pol *et al.* 2006 for more details). Re-sighting probabilities of breeders virtually equaled one in all years, annual re-sighting probabilities of non-breeders varied between 0.6 and 1. All parameters in the model were allowed to vary between years (fully time dependent model). Estimates of non-breeder mortality (μ_N) were corrected for 5% annual immigration and emigration (I) of non-breeders as this result in an overestimation of μ_N. Because migration seemed to be most pronounced in years with high mortality we corrected μ_N downward proportional to the mortality in a specific year t ($\mu_N(t)_{\text{corrected}}=\mu_N(t)\text{-}I(\mu_N(t)/\bar{\mu}_N)$). The corrected estimates (given between brackets) were used in all calculations. [†]Non-breeder parameters in 1984-1985 were not included in averages as they were based on too few individuals.

Status year t		Resident (R)					Leapfrog (L)					Non-breeder (N)				
Status year $t+1$			R	L	N	dead		L	R	N	dead		N	L	R	dead
Parameter		r_R	m_{RR}	m_{RL}	m_{RN}	μ_R	r_L	m_{LL}	m_{LR}	m_{LN}	μ_L	r_N	m_{NN}	m_{NL}	m_{NR}	μ_N
period 1	1984-85	37	83.4	2.8	11.1	2.7	103	88.3	2.2	4.3	5.3	4	$100^\dagger$ ($100^\dagger$)	$0^\dagger$	$0^\dagger$	$0^\dagger$ ($0^\dagger$)
	1985-86	39	89.5	0.0	2.8	7.7	156	91.6	2.6	4.6	1.2	12	73.5 (76.5)	9.1	9.1	8.3 (5.3)
	1986-87	63	63.3	5.8	13.5	17.5	189	76.8	6.0	2.7	14.5	17	46.5 (59.0)	9.1	9.1	35.3 (22.8)
	1987-88	65	92.2	1.6	3.2	3.1	168	94.9	1.8	1.8	1.4	43	73.0 (75.5)	12.5	7.5	7.0 (4.5)
	1988-89	80	87.2	2.6	6.5	3.8	189	90.5	1.1	4.5	3.8	78	90.8 (92.3)	5.3	0.0	3.8 (2.4)
	1989-90	73	94.5	1.4	2.8	1.4	179	86.7	2.9	7.6	2.7	134	83.8 (85.5)	8.7	2.4	5.2 (3.4)
	1990-91	93	93.5	2.2	3.3	1.1	185	90.2	3.9	5.0	1.0	165	82.9 (85.4)	9.7	0.6	6.7 (4.3)
	1991-92	101	93.0	1.0	1.0	5.0	193	94.2	1.1	2.1	2.6	162	87.3 (88.8)	5.8	2.6	4.3 (2.8)
	1992-93	120	91.5	0.9	1.8	5.8	226	88.6	1.9	4.7	4.9	167	77.9 (81.8)	6.8	4.1	11.3 (7.3)
	1993-94	124	95.1	0.8	3.3	0.8	226	91.0	0.9	5.9	2.2	145	77.9 (80.7)	11.9	2.2	8.0 (5.2)
	1994-95	123	93.4	0.8	3.4	2.4	234	89.9	1.4	3.7	5.1	133	68.4 (74.8)	9.0	4.5	18.1 (11.7)
period 2	1995-96	127	51.6	2.4	13.0	33.0	209	51.3	12.1	12.2	24.4	113	31.5 (44.0)	17.3	16.0	35.2 (22.7)
	1996-97	112	78.7	2.0	7.1	12.2	130	69.9	9.3	10.1	10.7	90	59.3 (68.1)	8.7	7.3	24.7 (15.9)
	1997-98	109	94.4	1.0	1.0	3.7	100	91.0	4.1	2.5	2.4	89	71.0 (74.1)	11.9	8.6	8.4 (5.4)
	1998-99	117	84.0	1.9	5.7	8.5	105	88.7	4.1	4.1	3.1	77	71.1 (75.4)	12.6	4.2	12.1 (7.8)
	1999-00	113	91.9	0.0	6.4	1.7	90	87.0	2.5	5.0	5.5	92	61.5 (69.1)	17.2	0.0	21.2 (13.7)
	2000-01	110	93.5	0.0	2.0	4.4	111	85.0	2.4	6.8	5.8	115	81.4 (84.5)	7.8	2.3	8.4 (5.4)
	2001-02	110	89.8	2.0	1.2	7.0	109	78.4	5.6	12.2	3.7	109	84.3 (86.5)	5.5	4.1	6.1 (3.9)
	2002-03	105	84.3	1.0	4.1	10.6	96	79.4	3.6	12.4	4.5	85	68.1 (76.5)	5.0	3.3	23.6 (15.2)
	2003-04	100	90.0	3.1	2.0	4.9	82	76.1	3.4	6.7	13.8	64	63.1 (71.2)	10.1	4.0	22.8 (14.7)
Mean	Period 1	918	88.8	1.8	4.8	4.6	2048	89.3	2.3	4.3	4.1	1060	$76.2^\dagger$ ($80.0^\dagger$)	$8.8^\dagger$	$4.2^\dagger$	$10.8^\dagger$ ($7.0^\dagger$)
	Period 2	1003	84.3	1.5	4.7	9.6	1032	78.5	5.2	8.0	8.2	874	65.7 (72.2)	10.7	5.5	18.1 (11.6)
	All years	1921	86.7	1.7	4.7	6.9	3080	84.5	3.6	6.0	5.9	1934	$71.5^\dagger$ ($76.5^\dagger$)	$9.6^\dagger$	$4.8^\dagger$	$14.1^\dagger$ ($9.1^\dagger$)

Table 8.A3 Variance-covariance matrix used to define the multivariate normal distribution for the parameters used in the equation used to calculate x^* (equation 2 in the main text). Variances (diagonal elements) and covariances (below-diagonal elements) are based on between year variation and covariation of life-history parameters. Variances and covariances are calculated using the annual values in period 1 (1984-1994, n=11), which are given in Table 8.A1 and Table 8.A2.

	m_{RR}	m_{RL}	m_{RN}	m_{LL}	m_{LR}	m_{LN}	μ_N	F_R	F_L	T_R	T_L
m_{RR}	0.0083										
m_{RL}	-0.0013	0.0002									
m_{RN}	-0.0032	0.0006	0.0016								
m_{LL}	0.0036	-0.0006	-0.0014	0.0023							
m_{LR}	-0.0010	0.0002	0.0004	-0.0006	0.0002						
m_{LN}	0.0005	-0.0001	-0.0001	-0.0001	0.0000	0.0003					
μ_N	-0.0063	0.0009	0.0018	-0.0035	0.0010	-0.0005	0.0093				
F_R	0.0000	-0.0002	0.0002	0.0002	-0.0002	0.0000	-0.0005	0.0032			
F_L	0.0001	0.0000	0.0002	0.0001	-0.0001	0.0000	-0.0005	0.0006	0.0006		
T_R	-0.1363	0.0274	0.0415	0.0025	-0.0025	-0.0524	0.1511	-0.0297	0.0197	18.7	
T_L	-0.4927	0.0535	0.1822	-0.1747	0.0638	-0.0255	0.1409	0.1219	-0.0885	-5.6	83.6

Appendix 8.B: Derivation of the ESSs.

The improved queue model

The change in density of hopeful residents (n_{HR}), hopeful leapfrogs (n_{HL}), residents (n_R) and leapfrogs (n_L), from year t to year $t+1$ is described by the following system of recurrence equations:

$$\begin{bmatrix} n_{HR} \\ n_{HL} \\ n_R \\ n_L \end{bmatrix}_{t+1} = \begin{bmatrix} 1-\mu_N-a^*_{HR} & 0 & (1-x)(F_R+m_{RN}) & (1-x)(F_L+m_{LN}) \\ 0 & 1-\mu_N-a^*_{HL} & x(F_R+m_{RN}) & x(F_L+m_{LN}) \\ a^*_{HR} & 0 & m_{RR} & m_{LR} \\ 0 & a^*_{HL} & m_{RL} & m_{LL} \end{bmatrix} \begin{bmatrix} n_{HR} \\ n_{HL} \\ n_R \\ n_L \end{bmatrix}_t \qquad \text{(A1)}$$

The matrix elements can easily be derived from the inflow and outflow of each state in Fig. 8.4A. The strategic parameter x reflects the proportion of non-breeders that follow a HL strategy, while 1-x gives the proportion of non-breeders that follow HR. We will assess the performance of a mutant x in a population consisting of individuals playing x^*. Eq. A1 can be written more compactly as $\boldsymbol{n}_t+1=B(x,x^*)\boldsymbol{n}_t$ where the 'resident strategy' x^* (here meaning the strategy adopted by most members of the population) is contained implicitly in the annual settlement probabilities in resident and leapfrog habitat (a_{HR}^* and a_{HL}^* respectively). By setting $\boldsymbol{n}_t+1=\boldsymbol{n}_t$ we assume the population reaches equilibrium, in which the stable stage distribution is given by $\boldsymbol{n}=(n_{HR}, n_{HL}, n_R, n_L)$. In addition, we assume the number of resident and leapfrog territories is fixed over time, by setting $n_R = T_R$ and $n_L = T_L$ respectively. Hereby we introduce density dependent settlement probabilities as breeding territories are a limiting resource and surplus individuals have to become non-breeders. Using the two previously mentioned assumptions we can derive the probabilities that a HR or HL will ever settle from eq. A1:

$$\frac{a^*_{HR}}{a^*_{HR} + \mu_N} = \frac{T_R(1 - m_{RR}) - T_L m_{LR}}{(1 - x^*)(T_R(F_R + m_{RN}) + T_L(F_L + m_{LN}))} \tag{A2a}$$

and

$$\frac{a^*_{HL}}{a^*_{HL} + \mu_N} = \frac{T_L(1 - m_{LL}) - T_R m_{RL}}{x^*(T_R(F_R + m_{RN}) + T_L(F_L + m_{LN}))} \tag{A2b}$$

From the right hand side of eq. A2a it can be seen that the probability a hopeful resident will ever settle directly depends on the number of vacant resident territories divided by the total number of hopeful residents (analogous for eq. A2b). Reproductive values (v) can be found by solving $v^T = v^T B$ (e.g. Taylor 1990), which yields:

$$v_{HR} = (1 - a^*_{HR} - \mu_N)v_{HR} + a^*_{HR} v_R \tag{A3a}$$

$$v_{HL} = (1 - a^*_{HL} - \mu_N)v_{HL} + a^*_{HL} v_L \tag{A3b}$$

$$v_R = (1 - x^*)(F_R + m_{RN})v_{HR} + x^*(F_R + m_{RN})v_{HL} + m_{RR} v_R + m_{RL} v_L \tag{A3c}$$

$$v_L = (1 - x^*)(F_L + m_{LN})v_{HR} + x^*(F_L + m_{LN})v_{HL} + m_{LL} v_L + m_{LR} v_R \tag{A3d}$$

The interpretation of the reproductive values is straightforward. For example, the reproductive values of hopeful resident (v_{HR}) equals the probability of remaining a hopeful resident times the reproductive values of hopeful resident plus the probability of becoming a resident times the reproductive value of residents (v_R). Similarly, the reproductive value of a leapfrog (v_L) is the sum of (i) the number of offspring produced that becomes HR times v_{HR} , (ii) the number of offspring produced that becomes HL times v_{HL}, (iii) the probability of staying a leapfrog times v_L, and (iv) the probability of promoting to resident status times v_R.

Eq. A3a and A3b can be rewritten into a more simple form to show that the reproductive values of hopeful residents and hopeful leapfrogs are also given by the probability of ever settling in resident or leapfrog habitat times the reproductive value in resident and leapfrog habitat, respectively (see also eqs. 11 and 12 in EWD).

$$v_{HR} = \frac{a^*_{HR}}{a^*_{HR} + \mu_N} v_R \tag{A4a}$$

and

$$v_{HL} = \frac{a^*_{HL}}{a^*_{HL} + \mu_N} v_L \tag{A4b}$$

Furthermore, because we are only interested in comparing between groups of individuals we can normalize all reproductive values to the reproductive value of leapfrogs. By setting $p=(F_R+m_{RN})/(F_L+m_{LN})$ we find:

$$\frac{v_R}{v_L} = \frac{(1-m_{LL})p+m_{RL}}{1-m_{RR}+m_{LR}p} \tag{A4c}$$

Calculating the ESS in the improved queue model

We can find the ESS by calculating that value of x where the fitness (λ) of x is maximized in a population playing x^* and cannot be invaded by any alternative strategy. λ here is defined as the relative growth rate of a mutant x in the a resident population x^*, and is given by the dominant Eigen-value of matrix B. In other words $\lambda(x^*, x^*) \geq \lambda(x^*, x^*)$ for any $x=x^*$ and $x \in \langle 0,1 \rangle$, which requires that the selection gradient for x is zero (e.g. Taylor 1990):

$$\left.\frac{\partial\lambda(x, x^*)}{\partial x}\right|_{x=x^*} \propto \sum_{ij}\left(\left.\frac{\partial B_{ij}}{\partial x}\right|_{x=x^*} v_i n_j\right) = 0 \tag{A5}$$

In addition, we checked higher order conditions to verify that we are dealing with a fitness maximum. Applying eq. A4 to the system described in eq. A1 we get the following condition:

$$T_R(F_R+m_{RN})(-v_{HR}+v_{HL}) = 0 \tag{A6}$$

from which it can be seen that at an ESS $v_{HR}{}^* = v_{HL}{}^*$ This result corresponds to the result of EWD that at an ESS both strategies must yield equal fitness payoffs. The condition $v_{HR}{}^* = v_{HL}{}^*$ can be used to find the ESS value for x* (using eq. A2a, A2b and the relationships $(1\text{-}x^*)a_{HR} = m_{NR}$ and $x^* a_{HL} = m_{NL}$):

$$\frac{x^*}{1-x^*} = \frac{(1-x^*)a^*_{HR}(v_L-v_{HL})}{x^* a^*_{HL}(v_R-v_{HR})} = \frac{m_{NL}(v_L-v_{HL})}{m_{NR}(v_R-v_{HR})} \tag{A7}$$

This equation (also given as eq. 1 in the main text) shows that in evolutionary equilibrium the ratio of individuals with a HL and HR strategy reflects the ratio of the expected benefits of both types of strategies. This same result was also obtained by EWD (eq. 15 in EWD), although they used expected future reproductive success – a growth rate insensitive fitness measure– instead of reproductive values. EWD subsequently calculated x^* using externally given settlement probabilities of non-breeders (m_{NR} and m_{NL}) derived from field data. However, this approach has three important disadvantages. First, life-history parameters of non-breeders, such as m_{NR} and m_{NL}, are notoriously difficult to reliably estimate in the field, due to the incomplete site-fidelity of non-breeders. Second, the use of estimates of settlement probabilities from field data (m_{NR} and m_{NL}) to calculate the ESS is not ideal as these same parameters are also indirectly used for model validation (i.e. they determine the age of first reproduction and recruitment probabilities). Third, settlement probabilities of non-breeders depend on x^* themselves, as $m_{NR}=(1\text{-}x^*)a_{HR}{}^*$ and $m_{NL}=x^*a_{HR}{}^*$. Therefore we took a different approach to calculate x^*, which takes full advantage of the fact that we now have incorporated population limitation in our model. Because the total number of territories is fixed, the availability of empty territories for non-breeders and thereby settlement probabilities can also be predicted from the behavior of the breeders (see eq. A2a and A2b). In other words, in our model settlement probabilities are generated by the model itself resulting in an internally consistent model, while this was not the case in the EWD model. By equating eq. A4a to A4b and using eqs. A2a, A2b & A4c, as well as the re-parameterization $q=T_R/T_L$ we find (also given as eq. 2 in the main text):

$$x^* = \frac{(1-m_{RR}+m_{LR}p)(1-m_{LL}-m_{RL}q)}{((1-m_{RR})(1-m_{LL})-m_{LR}m_{RL})(pq+1)} \tag{A8}$$

Which shows that the evolutionarily stable queuing strategy x^* is independent of the absolute number of territories ($q=T_R/T_L$) as well as independent of the absolute influx of new non-breeders from resident and leapfrog territories ($p=(F_R+m_{RN})/(F_L+m_{LN})$). More important, in eq. A8, x^* is expressed as a function of several life-history parameters of breeders, which are much more reliably estimated than life-history parameters of non-breeders (as in eq. A7).

The conditional queue model

We extended the previous model to allow both N_R and N_L to make an independent choice of which strategy to follow (x_R and x_L; Fig. 8.4B). In addition, we incorporated a new parameter c which reflects differences in competitive abilities between N_R and N_L. Incorporating conditional strategies yields the following set of recurrence equations:

$$\begin{bmatrix} n_{HR(R)} \\ n_{HL(R)} \\ n_{HR(L)} \\ n_{HL(L)} \\ n_R \\ n_L \end{bmatrix}_{t+1} = \begin{bmatrix} 1-\mu_N-ca^*_{HR} & 0 & 0 & 0 & (1-x_R)(F_R+m_{RN}) & 0 \\ 0 & 1-\mu_N-ca^*_{HL} & 0 & 0 & x_R(F_R+m_{RN}) & 0 \\ 0 & 0 & 1-\mu_N-a^*_{HR} & 0 & 0 & (1-x_L)(F_L+m_{LN}) \\ 0 & 0 & 0 & 1-\mu_N-a^*_{HL} & 0 & x_L(F_L+m_{LN}) \\ ca^*_{HR} & 0 & a^*_{HR} & 0 & m_{RR} & m_{LR} \\ 0 & ca^*_{HL} & 0 & a^*_{HL} & m_{RL} & m_{LL} \end{bmatrix} \begin{bmatrix} n_{HR(R)} \\ n_{HL(R)} \\ n_{HR(L)} \\ n_{HL(L)} \\ n_R \\ n_L \end{bmatrix}_t \tag{A9}$$

where $n_{HR(R)}$ refers to non-breeders born in resident territories that follow a HR strategy, and so forth. When $c=1$ there are no competitive asymmetries; when $c>1$, N_R are competitively superior over N_L, such that they have a c times higher annual probability of acquiring a R or L territory; the opposite for $c<1$. Reproductive values are given by:

$$v_{HR(R)} = \frac{ca^*_{HR}}{ca^*_{HR}+\mu_N}\, v_R = \frac{q(1-m_{RR})-m_{LR}-(1-x^*_L)\,(F_L+m_{LN})a^*_{HR}/(a^*_{HR}+\mu_N)}{(1-x^*_R)\,(F_R+m_{RN})q}\, v_R \qquad \text{(A10a)}$$

$$v_{HL(R)} = \frac{ca^*_{HL}}{ca^*_{HL}+\mu_N}\, v_L = \frac{1-m_{LL}-m_{RL}q-x^*_L(F_L+m_{LN})a^*_{HL}/(a^*_{HL}+\mu_N)}{x^*_R(F_R+m_{RN})q}\, v_L \qquad \text{(A10b)}$$

$$v_{HR(L)} = \frac{a^*_{HR}}{a^*_{HR}+\mu_N}\, v_R = \frac{q(1-m_{RR})-m_{LR}-(1-x^*_R)\,(F_R+m_{RN})qca^*_{HR}/(ca^*_{HR}+\mu_N)}{(1-x^*_L)\,(F_L+m_{LN})}\, v_R \qquad \text{(A10c)}$$

$$v_{HL(L)} = \frac{a^*_{HL}}{a^*_{HL}+\mu_N}\, v_L = \frac{1-m_{LL}-m_{RL}q-x^*_R(F_L+m_{RN})qca^*_{HL}/(ca^*_{HL}+\mu_N)}{x^*_L(F_L+m_{LN})}\, v_L \qquad \text{(A10d)}$$

$$\frac{v_R}{v_L} = \frac{1-m_{LL}-x^*_L(F_L+m_{LN})a^*_{HL}/(a^*_{HL}+\mu_N)}{m_{LR}+(1-x^*_L)\,(F_L+m_{LN})a^*_{HR}/(a^*_{HR}+\mu_N)} \qquad \text{(A10e)}$$

Note that if competitive asymmetries would affect non-breeder mortality (μ_N/c), for example due to competition over food, this would result in qualitatively the same reproductive values as in the case of competitive asymmetries in terms of settlement probabilities ($ca_{HR}{}^*$ and $ca_{HL}{}^*$); this is a matter of rescaling.

Calculating the ESS in the conditional queue model

In the conditional strategy we have to evaluate the sign of the selection gradients of both strategic parameters x_R and x_L simultaneously (for $x_R \in \langle 0,1\rangle$ and $x_L \in \langle 0,1\rangle$):

$$\left.\frac{\partial\lambda(x_R,\, x^*_R)}{\partial x_R}\right|_{x_R=x^*_R} \propto T_R(F_R+m_{RN})\,(-v_{HR(R)}+v_{HL(R)}) = 0 \qquad \text{(A11a)}$$

and

$$\left.\frac{\partial\lambda(x_L,\, x^*_L)}{\partial x_L}\right|_{x_L=x^*_L} \propto T_L(F_L+m_{LN})\,(-v_{HR(L)}+v_{HL(L)}) = 0 \qquad \text{(A11b)}$$

Thus, in equilibrium two conditions have to be satisfied, namely (i) $v_{HR(R)}=v_{HL(R)}$ and (ii) $v_{HL(R)}=v_{HL(L)}$. The first conditions can be rewritten to (using eq. A10a and A10b):

$$\frac{v_R}{v_L} = \frac{ca^*_{HL}}{ca^*_{HL}+\mu_N}\;\frac{ca^*_{HR}+\mu_N}{ca^*_{HR}} \qquad \text{(A12a)}$$

and the second condition can be rewritten to (using eq. A10c and A10d)

$$\frac{v_R}{v_L} = \frac{a^*_{HL}}{a^*_{HL}+\mu_N}\;\frac{a^*_{HR}+\mu_N}{a^*_{HR}} \qquad \text{(A12b)}$$

When $c=1$ the condition in eq. A12a and A12b are the same, consequently both fitness functions are simultaneously optimized when $v_{HR(R)}{}^*=v_{HL(R)}{}^*=v_{HR(L)}{}^*=v_{HL(L)}{}^*$. This condition yields a line of equilibria consisting of many ESSs with many different combinations of $x_R{}^*$ and $x_L{}^*$ (also given as eq. 3 in the main text).

$$x_L^* = \frac{(1 - m_{RR} + m_{LR}p)(1 - m_{LL} - m_{RL}q)}{(1 - m_{RR})(1 - m_{LL}) - m_{LR}m_{RL})}\, pqx_R^* \tag{A13}$$

We verified whether the two conditional strategies $x_R{}^*$ and $x_L{}^*$ yield a different queuing strategy at the population level (x^*), by describing the population strategy in the conditional model as a weighted average of the conditional strategies (also given as eq. 4 in the main text):

$$x_L^* = \frac{x_L^* N_L + x_R^* N_R}{N_L + N_R} = \frac{x_L^* T_L(F_L + m_{LN}) + x_R^* T_R(F_R + m_{RN})}{T_L(F_L + m_{LN}) + T_R(F_R + m_{RN})} = \frac{x_L^* + pqx_R^*}{pq + 1} \tag{A14}$$

If we insert $x_L{}^*$ from eq. A13 in eq. A14 we return to the same x* from the improved queue model (eq. A8), thereby demonstrating that all different combinations of $x_R{}^*$ and $x_L{}^*$ yield the same population strategy x^* as in the improved queue model. From a mathematical perspective there is no reason to assume that one combination of $x_R{}^*$ and $x_L{}^*$ is more likely than any other, or that $x_R{}^*$ should be different from $x_L{}^*$ (i.e $x_R{}^*=x_L{}^*=x^*$).

When $c \neq 1$, there is an asymmetry in competitive abilities which directly affects the settlement probabilities in both resident and leapfrog habitat. When an asymmetry is included the two conditions required for equilibrium (eq. A12a and A12b) cannot be simultaneously met (at least not with two mixed strategies $x_R \in \langle 0,1 \rangle$ and $x_L \in \langle 0,1 \rangle$). This can be seen by the fact that both eq. A12a and A12b would have to equal eq. A10e, which is very unlikely for virtually all realistic choices of parameter values (if $c \neq 1$). However, an equilibrium could still exist when either $x_R{}^*$ or $x_L{}^*$ plays a pure strategy ($x_R \in [0,1]$ and $x_L \in [0,1]$). The ESS conditions for a pure strategy are different from the ESS conditions with mixed strategies (A11a and A11b), as a pure strategy can also be stable when the selection gradient is not zero. For example, when $x_R{}^*=0$ (or $x_L{}^*=0$) a negative selection gradient means that $x_R{}^*$ (or $x_L{}^*$) is stable, because only mutants with a lower $x_R{}^*$(or $x_L{}^*$) will have a higher fitness, but these cannot exist because $x_R^* \in [0,1]$ (or $x_L^* \in [0,1]$). Similarly, when $x_R{}^*=1$ (or $x_L{}^*=1$) a positive selection gradient means that $x_R{}^*$ is stable, because only mutants with a higher $x_R{}^*$(or $x_L{}^*$) will have a higher fitness, but these cannot exist because $x_R^* \in [0,1]$ (or $x_L^* \in [0,1]$).

Consequently, if we only need to investigate a subset of potential candidate ESSs: two candidate ESSs might exist where N_R plays a pure strategy ($x_R{}^*=0$, $x_R{}^*=1$), and two candidate ESSs might exist where N_L plays a pure strategy ($x_L{}^*=0$, $x_L{}^*=1$). Whether any of these four candidate ESSs actually represents an ESS can be investigated in the following way: When $x_L{}^*=0$, the best response $x_R{}^*$ can be calculated using eq. A11a. Subsequently, the stability of this specific combination of $x_R{}^*$ or $x_L{}^*$ can be evaluated by the sign of the selection gradients of $x_R{}^*$ or $x_L{}^*$. When the best response to $x_L{}^*=0$ is a $x_R{}^* \leq 1$, this combination is evolutionarily stable when

$$\left.\frac{\partial\lambda(x_L, x_L^*)}{\partial x_L}\right|_{x_L=x_L^*} \leq 0 \quad \text{and} \quad \left.\frac{\partial\lambda(x_R, x_R^*)}{\partial x_R}\right|_{x_R=x_R^*} = 0$$

In other words, all mutants with a higher x_L^* will have a lower fitness; mutants with a lower x_L^* cannot exist as . In addition, any mutant with a different x_R^* will have a lower fitness. Alternatively, when the best response to $x_L^*=0$ is $x_R^*=1$, this combination is evolutionarily stable when

$$\left.\frac{\partial\lambda(x_L, x_L^*)}{\partial x_L}\right|_{x_L=x_L^*} \leq 0 \quad \text{and} \quad \left.\frac{\partial\lambda(x_R, x_R^*)}{\partial x_R}\right|_{x_R=x_R^*} \geq 0$$

In other words, all mutants with a higher x_L^* will have a lower fitness; mutants with a lower x_L^* cannot exist as . In addition, any mutants with a lower x_R^* will have a lower fitness; mutants with a lower x_R^* cannot exist as $x_R^* \in [0,1]$. The best response to the three other candidate ESSs and their evolutionarily stability can be determined in a similar way.

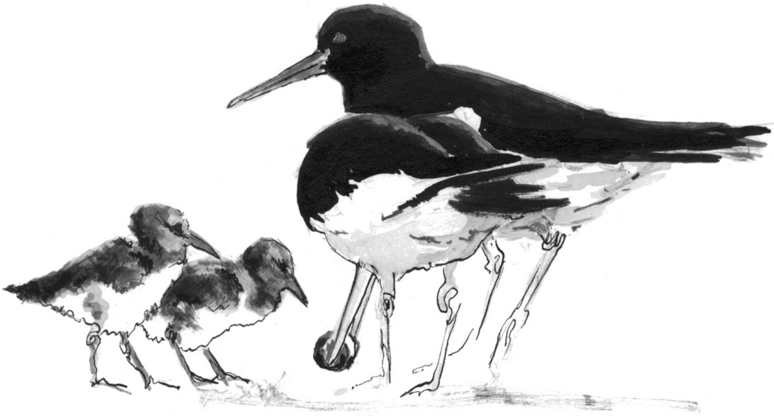
Appendix 8.C: Sensitivity of model predictions to input parameters

Table 8.C1 The effect of small changes in the input parameters on x^*, the difference in age of first settlement between HR and HL ($\Delta\alpha$), and the relative number of queuers per resident territory compared to leapfrog territories ($\frac{n_{HR} / T_R}{n_{HL} / T_L}$). The effects of small changes are expressed as relative sensitivities (elasticities) and are calculated by e.g. $(\partial x^* / \partial m_{RL})(m_{RL} / x^*)$. For example, an increase of 1% in m_{RL} results in a decrease of 0.05% of x^*, a 0.05% smaller difference in age of first reproduction between HR and HL, and a 0.45% higher relative number of queuers per resident territory compared to leapfrog territories. CV_{year} represents the coefficient of variation between years of the parameters over period 1 (1984-1994).

	relative effect of 1% change on			
Parameter	x^*	$\Delta\alpha$	$\frac{n_{HR} / T_R}{n_{HL} / T_L}$	CV_{year}
m_{RL}	-0.05	-0.05	0.45	0.87
m_{RN}	-0.05	-0.16	1.00	0.83
μ_R	-0.14	-0.41	1.32	1.02
m_{LR}	0.35	-0.34	-2.34	0.64
m_{LN}	0.10	0.11	-0.03	0.39
μ_L	0.02	1.17	4.14	0.94
F_R	-0.13	0.62	-0.83	0.48
F_L	0.08	-0.92	-3.37	0.70
$p=(F_R+m_{RN})/(F_L+m_{LN})$	-0.19	1.45	3.31	0.54
$q=T_R/T_L$	-0.58	0	0.92	0.10
μ_N	0	-1.01	0	0.81

PART IV

General discussion



Chapter 9

Synthesis

Martijn van de Pol

In this thesis, my co-authors and I have studied several life-history traits and investigated what has caused these traits to vary. In the final chapter we will discuss how this work has shaped our ideas about (i) the main sources of life-history variation (ii) how studying multiple life-history traits from a lifetime perspective has helped us to understand variation in life-history traits, and (iii) how life-history variation affects population dynamics (Fig. 9.1). We will end with some thoughts about the future of this long-term study on Oystercatchers.

Variation in individual quality

Variation in individual quality is often used to explain why life-history traits vary: some individuals are better than others. When Ens, Weissing & Drent (1995) tried to understand why some Oystercatchers occupy high quality territories and others occupy low quality territories, the first thing they investigated was whether breeders in high quality territories were physically superior or socially dominant over breeders in low quality territories. However, breeders in high quality territories are not bigger or heavier than breeders in low quality territories (Ens, Weissing & Drent 1995). Furthermore, there is no clear global dominance hierarchy, individuals socially dominant at one site can be subdominant at other sites (Heg *et al*. 2000), and also on neutral grounds breeders from high quality territories do not directly dominate breeders from low quality territories (Bruinzeel, van de Pol & Trierweiler 2006). As there were no clear indications that Oystercatchers breeding in high quality territory were superior over Oystercatchers breeding in low quality territories, Bruno Ens and colleagues suggested frequency-dependent queuing behavior might explain why some individuals settle in low quality and others in high quality territories. However, after comparing predictions from a queuing model with field data we were able to show that it is in fact unlikely that queuing behavior can explain the observed settlement behavior in Oystercatchers without assuming quality differences between individuals (chapter 8). Consequently, we returned to the original problem that Oystercatchers do not seem to differ in fighting capabilities, while they do differ strongly in the quality of the territory they occupy. Reassuringly, the results from chapter 7 showed that settlement behavior strongly depends on the natal background of individuals, suggesting that quality differences do exist. Nonetheless, we do not have a good idea yet what behavior or physical attribute makes some individuals more likely to settle than others, and how large competitive asymmetries are in the field. Possibly, future research on the ontogeny of characteristic of chicks born in high and low quality territories (box C) might help us to better understand what makes some Oystercatchers more successful than others.

Variation in mate quality

This thesis shows that the classical view of considering Oystercatcher’s life-history traits (reproductive as well as survival traits) as an individual trait is not really appropriate. The quality of the partner with whom an individual is mated should also be taken into account. However, there is no simple answer to what makes a good partner. At least three different factors might affect the quality of a partner in Oystercatchers (Fig. 8.2).

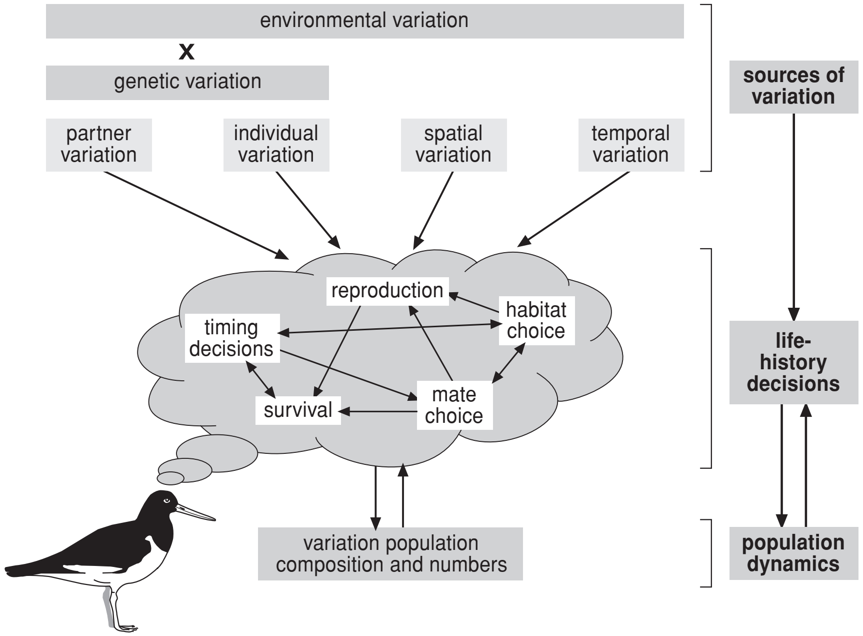


Figure 9.1 Life-history strategies are a nexus of competing goals and complex limitations, with the animal (the Oystercatcher) stuck in the middle to find the optimal solution. Shown is a non-exhaustive schematic representation of the interdependency between life-history decisions, the main causes of variation, and the interaction with population composition and numbers. One of the main challenges for the study of life-history evolution is to understand the relative importance of the different relationships between traits and how this depends on various sources of (environmental and genetic) variation, as well as processes as a result of variation at the population level (density and frequency dependence).

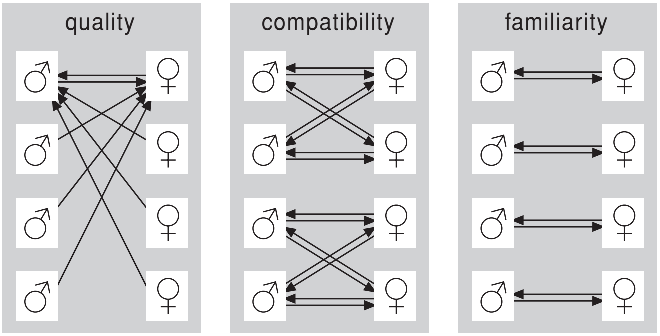


Figure 9.2 What makes a good partner? The preference for a particular mate (arrows), and therefore the intensity of intra-sexual competition, can depend on the intrinsic quality of individuals, the compatibility of certain partners, or a positive effect of mate-familiarity. Figure adapted from Ens *et al*. 1996.

First of all, some partners are of intrinsically higher quality than others, which is a direct result of variation in individual quality. Secondly, some partners are more compatible, because some combinations of partners consistently survived and reproduced better than other pairs of males and females (chapter 5). Compatibility could be a result of genetic compatibility as suggested in several other studies, but as we found compatibility effects on lay-date and survival this does not seem very likely. Behavioral compatibility seems much more likely, but detailed behavioral observations of cooperative incubation behavior and nest defense did not provide much evidence for this so far (Kuijper, MSc thesis). Nonetheless, we did show that some pair-members were consistently unfaithful to their partners, while members from other pairs only copulated with each other (box A), which does suggest that some pair bonds are stronger than others. Thirdly, mate familiarity affected reproductive performance, as pairs that stayed together improved their output strongly (chapter 4). We cannot disentangle which of the three factors, individual quality of the partner, compatibility, or familiarity is most important. For this we would need large scale laboratory experiments, for which the Oystercatcher is not a suitable species. Nonetheless, it is clear that the fitness consequences of an individual's phenotype directly depend on the phenotype of the social partner (i.e. social selection). Social selection is a potent evolutionary force (e.g. West-Eberhard 1979), and is thought to lead to the evolution of traits (such as mate choice) that can mediate social interactions (Moore, Brodie & Wolf 1998; Wolf, Brodie & Moore 1999). Mate choice and thereby the phenotypic quality of the partner are both the agent as well as the target of selection, which can strongly affect how selection would produce an evolutionary response in such traits (Moore *et al*. 1998; Wolf *et al*. 1999). Consequently, variation in mate quality is not only important for understanding the variation in life-history traits, but also for understanding their evolutionary dynamics.

Variation in habitat quality

Variation in habitat quality in Oystercatchers is thought to be primarily determined by the spatial organization of the nesting and feeding territory (Safriel, Ens & Kaiser 1996). In much of the research on this study population, and also in many chapters of this thesis, the Oystercatcher territorial system has been presented as the simplest case of habitat heterogeneity, either high or low quality. This dichotomy, in 'residents' and 'leapfrogs', makes this study system relatively unique, and we have tried to use this to our advantage the best we could. Nonetheless, the simple dichotomy between residents and leapfrogs at most explained only half of the variation between territories in reproductive performance (chapter 5). Clearly there must be additional characteristics of territories that make some leapfrog territories better than other leapfrog territories and some resident territories better than other resident territories. One way to identify such territory characteristics is to look at the spatial patterns of territory quality in terms of reproductive performance as derived in chapter 5 (Fig. 5.3). The values presented in figure 5.3 represent long-term estimates of reproductive parameters that are corrected for variation in male, female and year quality. As such they represent an unbiased estimate of territory quality in terms of reproductive potential for a prospecting non-breeder.

From this figure it is clear that resident territories do differ from leapfrog territories, but also that there is substantial variation within each type. Nonetheless, there does not seem to be an apparent additional spatial pattern (Fig. 9.3): there is no gradient from east to west; and leapfrogs close to the mudflats do not systematically perform better than leapfrogs further inland. Furthermore, if we compare these measures of territory quality to whether a territory was permanently abandoned after two winters of mass mortality, we see no clear association (Fig. 9.3D vs. Fig. 9.3A-C). Within leapfrog territories, territories with low recruitment success, nest success or a late lay-date were not more likely to be abandoned after two severe winters than territories with high success. Possibly, variation in territory quality within leapfrogs is more strongly determined by the quality of the associated feeding territory on the mudflats. Alternatively, non-breeding Oystercatchers might have used other cues for settlement decisions than reproductive measures of territory quality. For example, non-breeders might be more interested in leapfrog territories adjacent to resident territories than in more inland leapfrog territories, because these can serve as a stepping stone to acquire a resident territory (chapter 8). Describing variation in habitat quality as a simple dichotomy between residents and leapfrogs has helped to shape many of our ideas about life-history decision, but it is clear that there is more to a territory than the distance between the nesting and feeding territory in Oystercatchers.

Temporal variation

Most life-history traits not only varied substantially between years, but most traits also changed in a consistent direction over the study period (chapter 2). Although variation in life-history traits between years is sometimes regarded as stochastic noise, temporal variation can systematically affect the evolution of life-history traits in various ways. Firstly, directional changes over time, such as a decrease in fecundity and numbers can directly affect the fitness consequences of life-history decisions. For example, selection for earlier or delayed maturity depends on the population growth rate; in a declining population, such as in this study, selection for earlier breeding is weak or even absent (box B). Or a decrease in the reproductive potential of territories (e.g. due to lower food supplies) can result in the value of a territory dropping below the territory acceptance threshold of non-breeders, causing these territories to be abandoned (as hypothesized in chapter 8). Secondly, individuals might also be driven to reduce the effect of non-systematic annual variation in life-history traits. Selection not only acts on the mean, but also on the variance of fitness (Gillespie 1977). In an environment that varies in time, fitness can be increased by increasing either the mean fitness over a certain period, or by decreasing the variance in fitness over this same period. Consequently, a trade-off between the mean and variance in fitness might exist, which forms the basis for the bet-hedging literature (Slatkin 1974). Caswell (2001) showed how annual variation in life-history traits affects variation in fitness by equating the fitness of an individual to the population growth rate λ. He approximated how the variance in fitness ($\sigma_\lambda{}^2$) depends on the sensitivity of fitness ($\partial\lambda/\partial a_{ij}$) to small changes in life-history traits (a_{ij}) and on the variance in these same traits ($\sigma a_{ij}{}^2$):

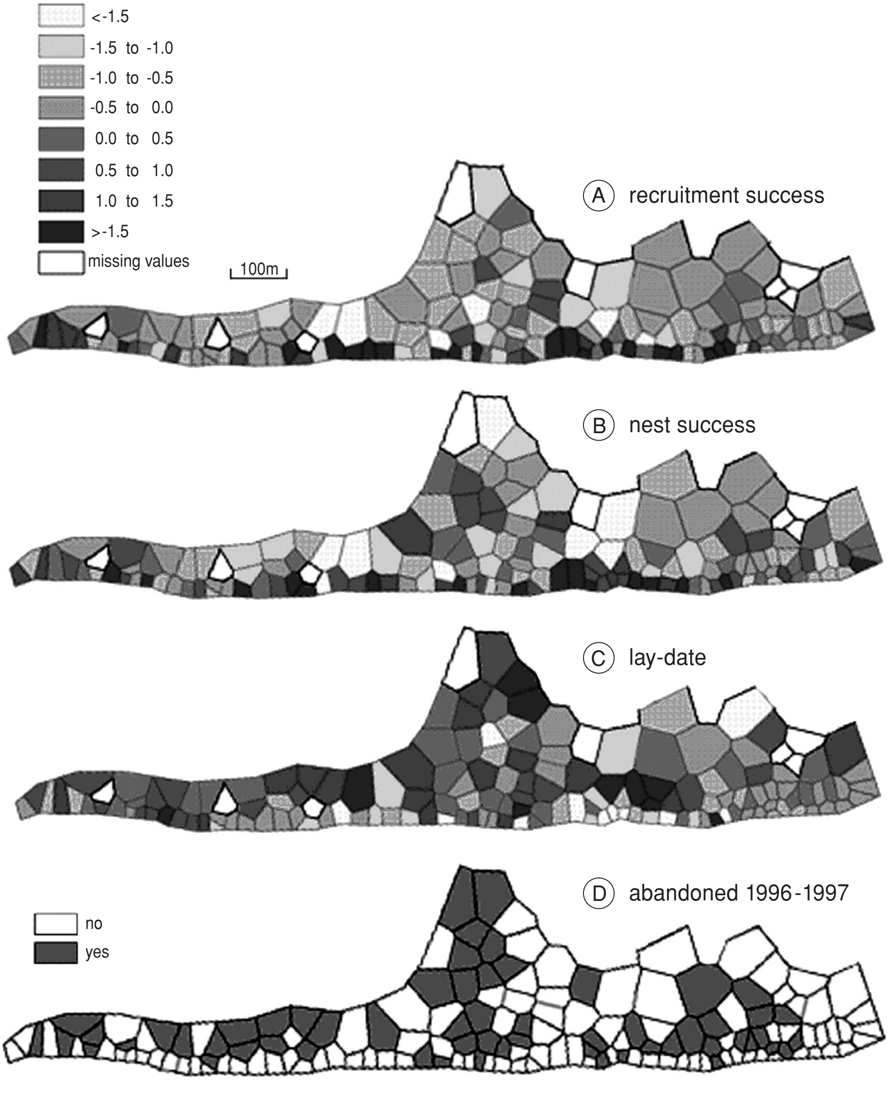


Figure 9.3 Spatial heterogeneity of territory quality in terms of (A) recruitment success, (B) nest success, and (C) lay-date. Shown is the territory maps of areas A, B, C and D in 1995; values are based on data over the period 1985-1995. All values are z-scores, and corrected for variation in the quality of the occupying male and female breeder, as well as variation between years (see chapter 5). In (D) it is shown which territories occupied in 1995 were abandoned and not re-occupied after the harsh winter with mass mortality in 1996 and 1997. Note that the territories are adjacent to the mudflats (lower border of the map) are resident territories, all other territories are leapfrogs. Territory borders were constructed with the use of a Voronoi-tessellation grid based on the centers of territories.

$$\sigma_\lambda^2 \approx \sum_{i,j}((\partial\lambda/\partial a_{ij})^2\, \sigma_{aij}^2))$$

This equation shows that the variance in fitness can be reduced by a decrease in either the sensitivity of fitness to a life-history trait or the variation in that trait. In chapter 7 we described the life-cycle of oystercatchers by a simple stage-structured matrix model in which twelve life-history traits were used (chapter 7: Fig 7.1 & Appendix 7A). If we plot the sensitivity of these twelve traits against the variance of these same life-history traits (calculated in chapter 7: Table 7.4), we indeed find a negative relationship (Fig. 4). There are no life-history traits which are both important determinant of fitness and also vary substantially between years. Interestingly, the relative contribution of each life-history trait to the temporal variation in fitness (σ_λ^2) is rather constant (all points lie close to the curve in Fig. 9.4). As it is unlikely that all points lie close to the curve as a result of chance, this strongly suggests that patterns of sensitivity and temporal variation in life-history traits in Oystercatchers have been shaped by natural selection. In conclusion, all the examples in this paragraph emphasize that temporal variation can be important for understanding life-history variation, and that we can only start to understand the relative importance of temporal variation if we collect data over a very long period.

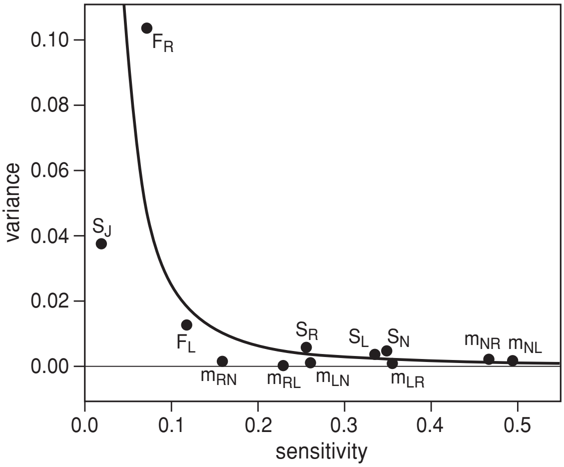


Figure 9.4 The relationship between the sensitivity of λ for twelve life-history traits and the variation in these traits. The curve shows the isoclines where the product between the squared sensitivity and variance is equal to the total variance in λ divided by twelve. In other words if all life-history traits would lie exactly on the isocline, each trait would contribute equally to the total variation in λ. Life history parameters are the annual fledgling production in resident (F_R) or leapfrog (F_L) territories, annual juvenile survival from fledging to adulthood (S_J), annual adult non-breeder (S_N), resident breeder (S_R), or leapfrog breeder survival (S_L), annual settlement probability in resident (m_{NR}) or leapfrog territories (m_{NL}), annual probability of losing a resident (m_{RN}) or leapfrog territory (m_{LN}), annual probability of changing from resident to leapfrog territory (m_{RL}) or vice versa (m_{LR}).

What about the genetics?

Evolutionary adaptation is a genetic process, but fortunately we can often understand it, to a first approximation, without knowing the genetic details. In this thesis we have played such a phenotypic gambit (Grafen 1982): we assumed that traits with the highest fitness tend to be favored. As such we have not bothered whether individual variation in life-history traits was mainly caused by genetic variation or by environmental variation (Fig. 9.1); we just assumed there was a genetic basis. The reason we have ignored genetics has not been because we think it is of no interest; incorporating information about the heritable basis of variation of life-history traits is very important for understanding evolutionary change, or the absence thereof. Regrettably it is very difficult to do meaningful research on genetics in free-living long-lived animals. For example, determining the heritability of life-history traits, either requires cross-fostering experiments or statistical methods ('animal models') to disentangle the effects of the genetic contribution of parents and environmental factors. Both methods require substantial sample sizes, but in Oystercatchers too few offspring survive till adulthood and it takes too many years to gather enough data to accurately determine heritabilities. Clearly, for studying evolutionary change in the wild, the Oystercatcher is not a very suitable species.

Studying life-history traits from a lifetime perspective

Life-history decisions in a long-lived species such as the Oystercatcher are likely to be either directly linked or have delayed consequences on other life-history decisions (e.g. chapter 7 & 8). Consequently, it is important to study fitness consequences of life-history decisions from a lifetime perspective. Using short-term fitness measures can lead to enormous biases in the estimates of fitness consequences, as illustrated by Fig. 9.5. The fitness differences between offspring from high and low quality territories strongly depend on the period over which fitness was calculated. When a fitness measure was defined as the number of hatchlings or fledglings produced, the fitness differences between offspring from high and low quality territories was two to three times lower than when we defined our fitness measure in terms of lifetime reproductive success or the reproductive value of an individual. When making predictions about optimal settlement behavior, about optimal parental effort or about trade-offs between the quantity and quality of offspring, the predictions are likely to be very different when using short-term and long-term fitness measures. In addition, following individuals over a lifetime is also important because the mechanisms that cause life-history traits to vary within-individuals can differ from the mechanisms that result in between individual differences in life-history traits (chapters 3 and 5). Distinguishing between within and between individual processes is crucial for a good understanding of life-history evolution, therefore, studies such as this one, in which longitudinal measurements on a large group of individuals are collected, are very important.

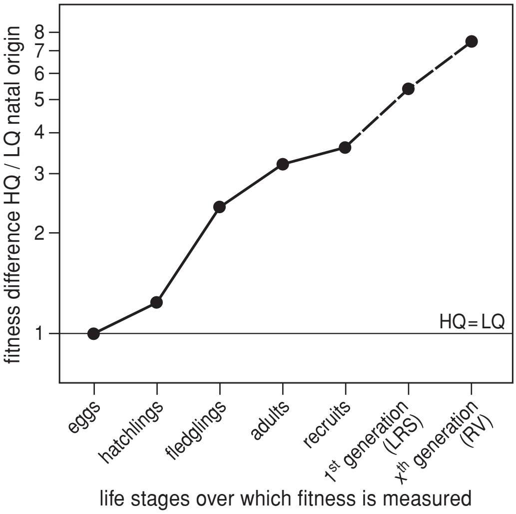


Figure 9.5 The effect of using short-term or long-term fitness measures on inferences about fitness differences between residents and leapfrogs in reproductive output. When both a resident and leapfrog start out with one egg, the fitness differences become stronger when the fitness measure is calculated in terms of the number of hatchling, fledglings, offspring that survives till adulthood, recruits, lifetime number of fledged offspring (LRS) or the reproductive value (RV).

From life-history variation to population processes

Life-history traits such as age or stage-dependent reproduction and survival are linked to population dynamics by the study of demography (e.g. chapters 2, 7, 8, box B). Life-history decisions also give us more insight how population numbers are regulated. In chapter 8 we have shown how queuing behavior affects the shape of density-dependent reproduction for a population. Understanding the density-dependent nature of reproduction and survival is important for understanding the population consequences from changes in reproduction, survival or habitat loss due to environmental change. Several studies have argued that by understanding the adaptive rules individuals use to adjust their behavior to varying circumstances (e.g. density) it is possible to predict how individuals respond to new environments (e.g. Sutherland 1996b; Stillman *et al.* 2000). We also think this is a very important point, and at the end of chapter 8 we have used similar verbal arguments to argue that queuing behavior might explain why many low quality territories were abandoned, while there were many non-breeders present in the study area. Clearly a mechanistic understanding of how density dependence works is much more valuable than a phenomological description derived from changes in demographic parameters at varying population densities. Nonetheless, we think some caution is required in making quantitative predictions and inferences when extrapolating behavioral rules. Extrapolating behavioral rules that are adaptive in equilibrium situations to a novel environment (usually disequilibrium situations) can be misleading, as individuals might adjust their behavioral rules to a novel environment. Furthermore, it is also important to consider feedbacks between behavioral rules. For example, in a stimulating paper, Sutherland (1996a) investigated the effect of habitat loss in winter due to the disappearance of inter-tidal areas (declining with 0.2-0.7% annually in the UK). He argued that habitat loss is likely to result in increased density and competition on the remaining breeding grounds, and thereby an increase in mortality. He suggests that changes in population numbers as a result of over-wintering conditions, such as habitat loss, can be quantitatively predicted by increasing the mortality of Oystercatchers (cf. Fig. 9.6). However, changes in mortality also directly affect the availability of territories as well as the chance non-breeders die before settlement. Consequently, the settlement behavior and density-dependent reproduction curve are also likely to change, however it is a priori unclear in what direction and how strongly this would affect the predictions for changes in population numbers. Furthermore, increased competition for food as a result of habitat loss might also result in a lower body condition of birds at the start of the breeding season. Consequently, loss of over-wintering habitat might not only increase mortality but also decrease reproduction, resulting in an even stronger decline in numbers. In contrast, if increased mortality results from hunting, this might decrease competition over food in winter and increase body condition at the start of the breeding season. In this scenario, the decrease in mortality might be counteracted by an increase in reproduction, resulting in less population decline. Considering simple scenarios in which either the density-dependent mortality or reproduction is varied independently without considering feedbacks between these two processes does not seem very realistic, and more sophisticated models would be needed to incorporate such feedbacks.

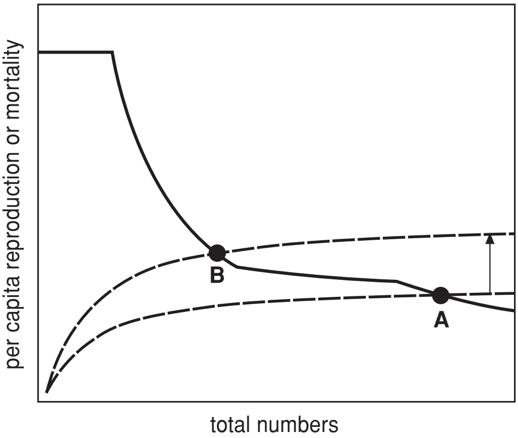


Figure 9.6 The effect of changes in winter mortality on population size when only the mortality curve (dashed lines) is increased (arrow). When mortality is increased population size declines from A to B according to Sutherland. The critical question however is how the density dependent reproduction curve is also affected by what caused mortality to increase in winter. Figure adapted from Sutherland (1996a).

In recent years, awareness is growing that dispersal behavior is an important process in population regulation as well as meta-population processes (Hanski 1999; Clobert *et al*. 2001; Bullock, Kenward & Hails 2002). A major problem is that permanent dispersal out of the study area is usually not noticed as most studies are on a smaller spatial scale than the scale at which individuals move (especially in birds). Consequently, dispersers are often wrongly presumed dead. Ignoring dispersal not only systematically ignores the important role dispersal plays in population dynamics, but can also seriously bias the estimation of fitness consequences of life-history decisions (e.g. Tinbergen 2005). In this study, we could investigate dispersal rates by combining information from local re-sightings with information on dead recovered Oystercatchers from a much larger area (chapter 2 & 7). This resulted in some important insights: e.g. we have seen that emigration rate increased in recent years (chapter 2); if we would have ignored dispersal we would have wrongfully concluded that adult mortality would have increased in recent years. Still we do not know what leads some individuals to disperse and others to stay, and how well these dispersers are doing elsewhere. Attempts to follow juveniles by using radio-transmitters have not been successfully implemented, as there were too few juveniles produced on Schiermonnikoog in recent years. Possibly, re-sightings from intensified color-ringing programs in various other Oystercatcher breeding and overwintering areas will prove to be a more successful avenue for studying dispersal in the future. A better understanding of what causes the high site-fidelity of Oystercatchers in both summer and winter areas is also important for assessing how these birds respond to spatial variation in environmental change as well the use of small protected areas (Verhulst *et al*. 2004).

The future

After 22 years of study a vast amount of data is collected on the Oystercatchers breeding population on Schiermonnikoog. The research in this thesis has relied most strongly on the long-term dataset, in contrast to previous PhD-projects on the same study system. Part of this shift in focus from performing field observations and experiments to database analyses was a direct result of the fact that we now have collected enough data to investigate several important question for which a long-term dataset is required (e.g. chapters 3, 4, 5, 7, 8). On a more practical level, the strong emphasis on the use of the long-term dataset was the result of the problems associated with studying the fitness consequences of life-history variation in a population of Oystercatchers that showed almost no variation in reproductive success in recent years (i.e. almost no chicks fledged). In recent years, we have started several field projects: e.g. a study on the importance of egg size, (chapter 6) and a study on the role of intra-pair cooperation (Kuijper, MSc thesis). However, it has proved difficult to interpret the results of these studies because of this low variation in reproductive success.

Although there are still many unanswered questions in the study of life-history variation in Oystercatchers, at the moment it seems more preferable to focus on a more urgent question: why are breeding numbers in the Dutch Wadden Sea declining so rapidly? The study presented in chapter 2 explored several of the possible explanations why numbers are declining. Many questions remain which need to be answered if we are to understand what causes numbers to decline and what we can do about it. What are the main egg predators? Have the number of predators increased, or do Oystercatchers defend their nests less well because they have to spend more time feeding? Another important step is to investigate whether climate change has also resulted in more frequent flooding of breeding grounds in other salt marsh areas, as this might imply that Oystercatchers are facing the loss of substantial areas of suitable breeding habitat all around the Wadden Sea. Furthermore, are we to understand what has caused breeding numbers to decline in the entire Wadden Sea then we have to identify a common cause that can explain the change in all different areas. Consequently, more research is needed to asses how environmental circumstances have changed in other areas in summer as well as winter. Also it is important to know to what extent Oystercatchers from the western Wadden Sea have moved to the eastern Wadden Sea as bivalve stocks have recovered in recent years in the eastern part of the Wadden Sea. Finally, we need to have a better understanding of how over-wintering conditions might have a carry-over effect on reproductive success. The winter feeding ecology of Oystercatchers is one of the best studied cases in literature, and there is a vast amount of studies on the breeding ecology of Oystercatchers. Strikingly, at the same time very little is known about the relationship between these two periods. Hopefully, the encouraging results from the work by Kees Oosterbeek and colleagues (in prep), which shows that winter body condition and reproductive performance are indeed positively associated, will result in a continued research program to study the relationship between winter conditions and life-history decisions.

In conclusion, we hope this thesis has illustrated that for understanding how environmental factors affect population dynamics it is crucial to have a good understanding how environmental factors affect life-history decisions and how these decisions in turn affect population dynamics (Fig. 9.1). Although many bird species strongly depend on the Wadden Sea for their survival, the Oystercatcher is one of the very few bird species for which it is possibly to study life-history decisions both in winter and summer. As such it would be a loss if the long tradition of Oystercatcher research would stop at a moment at which Oystercatcher breeding numbers are still declining rapidly, and the bird community of the Wadden Sea is changing strongly as a result of changes in the environment (van Roomen *et al*. 2005).

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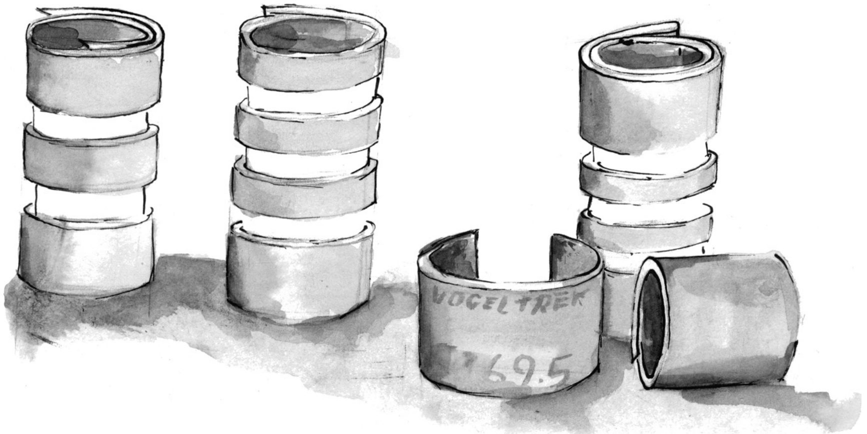

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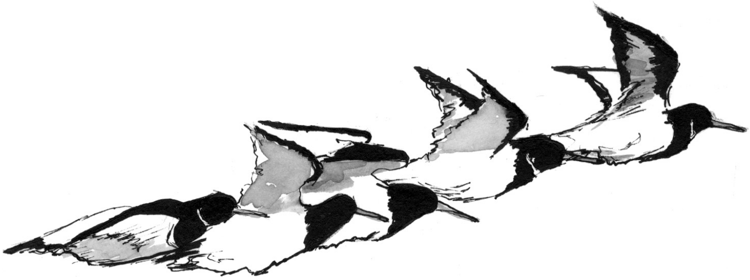

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Nederlandse samenvatting

Opportunistische levensloop strategieeën: Een studie aan de burgerlijke stand van scholeksters

Levensloop beslissingen

De levensgeschiedenis ('life-history') van een individu is de verzameling van belangrijke gebeurtenissen gedurende het leven. Met belangrijke gebeurtenissen bedoelen biologen gebeurtenissen die de fitness van een individu beïnvloeden. Overleving en reproductie zijn de twee basiscomponenten van fitness. Omdat de hoeveelheid energie die een individu tot zijn beschikking heeft gelimiteerd is moeten organismen keuzes maken hoe ze hun energie verdelen tussen de productie van nakomelingen en het veiligstellen van hun eigen overleving, of tussen het aantal en de kwaliteit van hun nakomelingen. Dit soort onontkoombare afwegingen zorgen ervoor dat er verschillende strategieën kunnen bestaan. Zo produceren zalmen eenmalig veel nakomelingen en sterven vervolgens meteen, terwijl albatrossen lang leven maar slechts weinig nakomelingen per jaar produceren. Schildpadden produceren veel nakomelingen waar ze vervolgens niet meer voor zorgen, terwijl mensen weinig nakomelingen produceren maar hier vervolgens wel decennia lang voor zorgen. Kennelijk zijn er in de natuur veel verschillende oplossingen voor hetzelfde probleem.

Niet alleen hebben verschillende soorten hun unieke levensgeschiedenis, binnen soorten zijn er meestal ook grote verschillen tussen individuen in hun levensloop. Individuele variatie in levensloop beslissingen is een van de sleutelvoorwaarden voor het plaatsvinden van evolutie. Stel dat sommige individuen slimmere beslissingen nemen dan andere individuen gedurende hun leven. Het proces van natuurlijke selectie zorgt er dan voor dat de nakomelingen van individuen met een betere levensloop-planning in een volgende generatie meer vertegenwoordigd zijn. Als het nemen van deze slimme levensloop beslissingen een erfelijke basis heeft betekend dit dat in deze nieuwe generatie meer individuen deze slimme levensloop beslissingen zullen nemen. Een van de meest fundamentele doelen van biologen is dan ook het begrijpen waarom er variatie in levensloop beslissingen is. Waarom leven sommige individuen langer dan anderen? Waarom produceren sommigen meer nakomelingen dan anderen? Waarom beginnen sommige individuen al op jonge leeftijd met reproduceren en anderen pas op late leeftijd? Waarom gaan sommige individuen in slechte gebieden broeden en andere in goede gebieden?

Levensloop beslissingen zijn opportunistisch

De meeste levensloop beslissingen zijn niet statisch, maar hangen af van de omstandigheden waar een individu zich in verkeerd. Sommige individuen zijn bijvoorbeeld in een betere fysieke conditie, hebben meer broedervaring, zijn gepaard met een betere partner, of leven in een beter gebied dan anderen en passen daar hun beslissing op aan. Het is voor dieren handig om opportunistisch te zijn en hun beslissingen aan te passen aan de situatie waarin ze zich verkeren omdat dit hun fitness kan verhogen. Zo kan het in slechte jaren gunstig zijn om minder energie in reproductie te investeren dan in goede jaren, bijvoorbeeld omdat ouders meer energie nodig hebben voor hun eigen overleving. Ook gedurende een leven kunnen levensloop beslissingen veranderen omdat de situatie van een individu gedurende een leven verandert. Zo produceren oudere individuen vaak meer nakomelingen per jaar, mogelijk omdat ze meer ervaren zijn in het grootbrengen van jongen. Daarnaast kunnen beslissing vroeg in het leven doorwerken op beslissingen later in het leven. Bij het bestuderen van de fitness consequenties van levensloop beslissingen is het dan ook van belang om deze over het gehele leven van een individu te bepalen.

Dit proefschrift

In dit proefschrift wordt onderzocht waarom levensloop beslissingen van scholeksters (*Haematopus ostralegus*) variëren tussen individuen en hoe dit afhangt van onder andere de leeftijd, de partner, de geboorte- en woonplaats van een individu alsmede het gedrag van zijn soortgenoten. Scholeksters zijn langlevende kustvogels die meerjarige paarbanden vormen en elk jaar in hetzelfde gebied een territorium verdedigen en broeden. Sinds 1983 word elk jaar een grote groep scholeksters bestudeert op het Waddenzee eiland Schiermonnikoog. Door de jaren heen is een burgerlijke stand verzameld met daarin gegevens over welk vrouwtje met welk mannetje, in welk jaar, waar broed, hoeveel jongen ze daar geproduceerd hebben en of ze overleeft hebben tot het volgende jaar. In dit proefschrift proberen we meer inzicht te krijgen in de variatie in levensloopbeslissingen van scholeksters door de gegevens van deze burgerlijke stand te combineren met gedetailleerde gedragsobservaties, veldexperimenten en wiskundige modellen.

De belangrijkste resultaten

Bij scholeksters lijkt het aantal jongen niet alleen af te hangen van individuele kwaliteit, maar ook van de kwaliteit van een partner. De kwaliteit van een partner wordt door drie factoren bepaald. Ten eerste zijn sommige individuen gewoon beter dan andere partners. Als we het broedsucces van vrouwtjes en mannetjes over verschillende jaren heen vergelijken, dan blijken sommige individuen het systematisch beter te doen, ongeacht met wie ze gepaard zijn of in welk territorium ze broeden. Ten tweede, zijn bepaalde combinaties van mannetjes en vrouwtjes meer compatibel dan andere combinaties. Sommige mannen en vrouwen kunnen alleen veel jongen produceren als ze met een specifieke partner gepaard zijn. Ten derde, maakt een onbekende partner onbemind; hoe langer scholekster-partners al bij elkaar zijn, hoe meer jongen ze voortbrengen per jaar. Vooral dit laatste effect is erg belangrijk. Gedurende de duur van een scholeksterhuwelijk kan de jongenproductie wel verdubbelen. Het lijkt er dus op dat scholeksters gedurende hun paarband steeds beter gaan samenwerken of meer durven te investeren in nakomelingen. Het belang van een familiaire partner konden we ook voor het eerst experimenteel aantonen. Doordat we een aantal scholeksters van een nieuwe onbekende partner voorzagen, konden we laten zien dat wanneer je een lang huwelijk opbreekt dit negatievere gevolgen heeft dan bij het opbreken van korte huwelijken. Maar na een aantal jaren met de nieuwe partners doen de meeste scholeksters het weer even goed als vroeger. Dit experiment bevestigd dus dat paren die al lang bij elkaar zijn veel te verliezen hebben bij een scheiding en dat het dus gunstig is om bij elkaar te blijven. Dit is een erg interessant resultaat omdat dit zou kunnen verklaren waarom in veel soorten partners meerdere jaren bij elkaar blijven.

Ook de partnertrouw is afhankelijk van de huwelijksduur. Scholeksterparen die al vele jaren bij elkaar zijn gaan namelijk minder vaak vreemd dan paren die pas kort bij elkaar zijn. Dit komt enerzijds omdat zowel mannetjes als vrouwtjes gedurende hun huwelijk steeds minder vreemd gaan. Daarnaast is het zo dat vooral de trouwe paren bij elkaar blijven en ontrouwe paren sneller scheiden. Vreemdgaan is dus een goede voorspeller voor de kans op scheiding bij scholeksters.

Naast een belangrijke rol van de partner heeft de kwaliteit van de leefomgeving ook een grote invloed op verscheidene levensloopbeslissingen. Dit begint al vroeg in het leven met het belang van een goede omgeving om in op te groeien. Niet alleen bij mensen worden sommige individuen met een zilveren lepel in de mond geboren worden; ook scholeksters die geboren worden in een goed territorium blijken hier gedurende de rest van hun leven voordeel van te hebben. Zo hebben ze een grotere kans om de eerste paar jaren van hun leven te overleven. Verassend genoeg zijn er ook op lange termijn, tot tien jaar later, grote voordelen van gunstige opgroei omstandigheden. Zo blijken scholeksters die geboren worden in een goed territorium een drie tot vier maal grotere kans te hebben om later zelf ook een goed territorium te bemachtigen dan scholeksters geboren in een slecht territorium. Bij scholeksters is de zilveren lepel dus een erfstuk.

Verschillen in habitat kwaliteit spelen ook een belangrijke rol in vestigingsbeslissingen en vooral voor de keuze op welke leeftijd te beginnen met reproduceren. Jonge scholeksters die zich aan het begin van hun reproductieve carrière bevinden staan voor de keuze om te proberen een broedterritorium te bemachtigen in een goed territorium of in een slecht territorium. Natuurlijk hebben goede broedterritoria de voorkeur omdat hierin jaarlijks twee tot drie keer zoveel jongen grootgebracht kunnen worden dan in slechte territoria. Echter de habitat keuze van een individu wordt ook beïnvloed door de keuze van andere individuen. Waarschijnlijk zullen ook veel andere scholeksters in het beperkte aantal goede territoria willen broeden met als gevolg dat scholeksters lang zullen moeten wachten tot ze aan de beurt zijn omdat er een lange wachtrij is. Aan de hand van een wiskundig model heeft een eerdere studie laten zien dat scholeksters zich zo zouden moeten verdelen over de goede en slechte territoria dat het netto over het leven van een individu niet zoveel uitmaakt om op jonge leeftijd te beginnen in een slecht territorium of op latere leeftijd in een goed territorium. In dit proefschrift verbeteren we dit model en laten we zien dat echte scholeksters zich in hun vestigingsgedrag heel vergelijkbaar gedragen als ‘model’-scholeksters. Ook laten we zien dat als de kwaliteit van de slechte territoria genoeg afneemt er een situatie kan ontstaan dat het niet meer uit kan om in slechte territoria te gaan broeden en het beter is om altijd in de wachtrij te gaan staan voor een goed territorium. We denken dat dit kan verklaren waarom in recente jaren veel lage kwaliteit territoria niet meer bezet worden terwijl er tegelijkertijd nog veel individuen op zoek zijn naar een territorium.

Tot slot

Het gaat erg slecht met de scholeksters in Nederland, hun aantallen zijn in de laatste jaren fors afgenomen. De jaarlijkse afname van broedvogels op Schiermonnikoog is van 1983-2004 gemiddeld 4.6%, dit betekent dat de broedpopulatie elke 15 jaar halveert. Deze afname wordt voornamelijk veroorzaakt door een sterke afname in reproductie als gevolg van een lage overlevingskans van eieren tot uitkomst. De afname in ei-overleving valt sterk samen met een afname van de belangrijkste voedselbronnen en conditie van ouders. Daarnaast zien we ook dat het dieet van broedvogels compleet vernadert is van een schelpdierendieet naar een wormendieet, een verandering die samen valt met een sterke afname van schelpdieren in de Waddenzee. Dit patroon suggereert dat ouders meer tijd nodig hebben voor het zoeken van eten voor zichzelf en minder tijd over hebben voor het bewaken van de eieren. Een bijkomend probleem voor de ei-overleving is de verhoogde overstromingskans van nesten, mogelijk als gevolg van klimaatsveranderingen.

Veranderingen in verschillende broedpopulaties rond de Waddenzee (Schiermonnikoog, Texel, Friesland) vertonen opvallend veel parallellen in aantalverloop en jongenproductie, wat suggereert dat er mogelijk één belangrijke omgevingverandering heeft plaatsgevonden die verschillende populaties in de Waddenzee vergelijkbaar heeft getroffen. Verschillende factoren zijn gesuggereerd (voedselaanbod, maai-regime, dichtheid aan predatoren, en overstromingskans) maar geen van deze factoren lijkt een plausibele verklaring voor de Waddenzee-wijde afname. Het meest waarschijnlijk lijkt nog de verklaring dat de verslechterde omstandigheden in de overwinteringgebieden (verdwijnen van mossel en kokkelbanken) negatief doorwerken op de conditie van de vogels tijdens het broedseizoen. Hopelijk kan toekomstig onderzoek hier meer inzicht in geven, en kunnen we meer duidelijkheid verkrijgen over wat voor mogelijkheden er zijn om de achteruitgang van een van de belangrijkste wadvogelsoorten een halt toe te roepen.

Dankwoord

Het schrijven van een proefschrift is een werk dat je niet alleen doet. Gelukkig maar. De ondersteuning, stimulering en samenwerking van, door en met anderen is cruciaal geweest voor het slagen van een meerjarig project als dit. Deze ondersteuning heeft vele vormen gekend en ik wil dan ook graag van de gelegenheid gebruik maken om hier mijn grote waardering uit te spreken voor een aantal mensen in het bijzonder.

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Het doen van onderzoek aan een lange-termijn studie bouwt voort op het werk van vele voorgangers. Naast de meer dan 100 studenten door de jaren heen zijn met name Jan Hulscher, Bruno Ens, Marcel Kersten, Dik Heg, Kees van Oers, Leo Bruinzeel, Simon Verhulst, en Kees Oosterbeek erg belangrijk geweest. Ook in recente jaren heb ik veel input van hen gehad en hun vele bezoeken erg gewaardeerd. De laatste jaren heb ik nauw samengewerkt met Kees Oosterbeek, wat niet alleen het werk in het veld een stuk prettiger maakte, maar ook het verblijf op de Herdershut. Mede door de niet aflatende inzet van Bruno voor het scholekster-project is het onderzoek ook deze zomer weer in de vertrouwde handen van Kees.

Daarnaast hebben nog een flink aantal andere mensen op de een of andere manier hun steentje bijgedragen. Jeroen Creuwels was onontbeerlijk bij het aanleggen van het netwerk van weegschalen. Martijn Salomons heeft enorm veel gegevens ingevoerd in de database. Marco van der Velde heeft mij ingewijd in de wereld van labwerk. Dirk-Jan Saaltink en Bram Kuijper waren uitstekende hulptroepen toen ik mijn schouder brak. De aanwezigheid van Sido Mylius was een belangrijke stimulans in mijn eerste jaar. Henk van der Jeugd was een goede discussiepartner over analyseren. Kees Rappoldt heeft ervoor gezorgd dat de stress-berekeningen voor Schiermonnikoog op orde waren. Ido Pen zijn werk vormde de basis voor het nieuwe queue stuk. And Richard Pettifor invited me to London and introduced me into the world of Bayesian multivariate statistics.

Veel van mijn plezier in onderzoek doen haal ik uit het veldwerk en het samenwerken met andere enthousiaste mensen. De samenwerking met studenten was daarbij erg stimulerend. Mijn doctoraalstudenten, Chris Trierweiler, Trineke Bakker en Bram Kuijper hebben ondanks de moeilijke omstandigheden uitstekend werk afgeleverd en hun aanwezigheid is voor mij erg motiverend geweest. Daarnaast heb ik het geluk gehad elk seizoen te hebben mogen samenwerken en samenleven met een club enthousiaste cursus-studenten (Oscar Vedder, Sandra Bouwhuis, Jeroen Reimerink, Peter van de Brandhof, Camilla Butti, Renske Hekman, Maarten Schrama, en Dirk-Jan Saaltink). Ik blijf het uniek vinden om met mensen samen te werken die het leuk vinden om met -10°C op het wad te gaan staan, die 8 uur lang 5m hoog in een observatiehutje van $2m^3$ willen zitten, die om tien uur ’s-avonds spontaan besluiten om nog even snel wat nestchecks te doen, die vrijwillig meehelpen een paar kilometer datakabel op de kwelder aan te leggen, of die blijven lachen als het werk van twee maanden in een half uurtje wegspoelt.

Het onderzoekstation ‘De Herdershut’ was mijn uitvalsbasis voor het doen van onderzoek. Het belang van een goed functionerend veldstation kan niet worden overschat en deze continuiteit is te danken aan de voortdurende inzet van Jan Bakker, Joost Tinbergen, en Rudi Drent. Vereniging Natuurmonumenten gaf ons toestemming voor het doen van onderzoek in het Nationaal Park Schiermonnikoog, en de hulp van Otto Overdijk en zijn team heeft me zeker en vast een hernia bespaart. Suus Bakker heeft er zorg voor gedragen dat alle adminsitratieve en financiele zaken tip-top in orde waren, en Gudrun Ferber hield me op de hoogte van de gebeurtenissen bij Theoretische Biologie. De vormgeving van dit boekje was in de vertrouwde handen van Dick Visser. Daarnaast was er nog allerlei deskundige ondersteuning door de afdelingen dierverzorging, houtbewerking, mechanica en elektronica.

Naast het goede wetenschappelijke klimaat op het Biologisch Centrum (lunchmeetings, seminars, theoretische clubje, journal club, boek besprekingen, breedtestrategiemeetings, CEES colloquia, en congressen), zorgde vooral de gemoedelijke sfeer onder de AiO’s voor een prettige werksfeer. De borrels, eerst op zondagavond en later op vrijdagmiddag, de etentjes, BBQs, en avondjes stappen waren altijd erg gezellig. Daarnaast bewaar ik erg goede herinneringen aan de trips naar Brazilië, Finland en Hongarije. Ook de sfeer op de Herdershut was altijd erg goed, vooral de vele zomer-avonden met een biertje buiten op het bankje en de oneindig veel potjes Catan, Carcassone en Risk maakten elk veldseizoen een genot. Het is een te lange lijst van mensen om hier iedereen persoonlijk te noemen, maar bedankt allemaal voor deze hoognodige afleiding.

Twee mensen wil ik toch kort persoonlijk bedanken. Roos Veeneklaas heeft er vanaf mijn eerste bezoek aan Groningen zeven jaar geleden voor gezorgd dat ik me hier altijd heb thuis gevoeld. Ze was vele jaren een gezellige huisgenoot en is nog steeds een belangrijke steun en toeverlaat. Ik kan me bijna niet voorstellen hoe mijn tijd in Groningen zou zijn geweest zonder jou. Martijn Salomons zorgde er zowel op het werk als thuis voor dat er altijd wel wat te lachen viel. Zijn relativerende vermogen, flauwe grappen en zijn talent voor het voeren van onzinnige gesprekken heb ik enorm leren waarderen. Roos en Martijn, hopelijk hebben we nog vele gezellige etentjes, LAN-parties, spelletjesavonden en weekendjes weg samen met Martine, Arjen, Machteld en Lyanne.

Heel belangrijk was ook het thuisfront. Mijn school en studie vrienden, Karen, Koos en Lidewij. Helaas is het contact niet meer zo intensief als vroeger in Den Bosch en Utrecht, maar de waardering is er niet minder om. Mijn ouders, zussen, en schoonfamilie waren altijd geïnteresseerd in mijn gekke werk, en het was altijd erg prettig om thuis te komen en me welkom te voelen. Mijn vader en moeder hebben mij van jongs af aan gestimuleerd en mij de kansen geboden die zij zelf niet altijd hebben gehad. De fantastische opvoeding die ik van hen gekregen heb is de basis geweest voor hoe ik in het leven sta, en het is daarom ook erg toepasselijk dat dit boekje opent met een tekening van mijn moeder op de voorkant.

Belangrijkst van allen was en is Lyanne. Gedurende al die jaren heb je me onzettend gesteund, hebben we enorm veel plezier met elkaar beleefd en zijn we ondertussen de hele wereld rond gereisd. En we zijn nog lang niet klaar.

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Stellingen behorende bij het proefschrift

State-dependent life-history strategies
A long term study on Oystercatchers

Martijn van de Pol

1. Het voorbeeld van de scholekster laat zien dat het zelfs voor goed bestudeerde soorten moeilijk is om de oorzaak van hun achteruitgang te duiden[1], laat staan effectieve beschermingsmaatregelen te bedenken[2]. Toch zijn dit soort studies onontbeerlijk om een meer algemene theorie te ontwikkelen om ook minder goed bestudeerde soorten, waaronder het merendeel van de 1210 met uitsterven bedreigde vogelsoorten, effectief te kunnen beschermen.
   [1] Hoofdstuk 2
   [2] Verhulst *et al.* (2004). Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. *Ecology and Society* 9, 9-18.

2. Soms kan natuurbescherming heel simpel zijn: het dragen van een katten-belletje door katten kan in Nederland op jaarbasis miljoenen dierenlevens redden.
   Ruxton *et al.* (2002). Bells reduce predation of wildlife by domestic cats (*Felis catus*). *Journal of Zoology* 256, 81-83.

3. De mens is hard op weg te laten zien dat ‘sustainable growth’ een contradictio in terminis is, de enige ‘sustainable’ optie lijkt dus een evenwicht zonder groei.
   Diamond, J. (2005). *Collapse: how societies choose to fail or succeed*. Penguin, London.

4. Herhaalde interacties tussen ouders als gevolg van langdurige paarbanden maken van ‘parental investment games’ een repeterend ‘prisoners dilemma’ waardoor coöperatie tussen ouders geleidelijk kan toenemen door het opbouwen van een ‘vertrouwensrelatie’.
   Hoofdstuk 4, Roberts & Sherratt (1998). Development of cooperative relationships through increased investment. *Nature* 394, 175-179 en Roberts & Renwick (2003). The development of cooperative relationships: an experiment. *Proceedings of the Royal Society of London: Biological series* 270, 2279-2283.

5. In plaats van studenten te leren dat een correlatie geen causaliteit impliceert, is het nuttiger om te benadrukken dat een correlatie duidt op een onopgeloste causale structuur.
   Hoofdstuk 5 en Shipley (2002). *Cause and correlation in biology: A user’s guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge.

6. Het ontwerpen en interpreteren van life-history experimenten is bijna onmogelijk zonder een gedegen kennis van de natuurlijke (co)variatie van life-history traits.
   Hoofdstuk 5

7. Geboren worden met een zilveren lepel in de mond is bij scholeksters een opmaat voor een gouden toekomst. Omdat de zilveren lepel van scholekster ouder naar jong overerft, zou je ook bij scholeksters kunnen spreken van een sociale cultuur waarin bepaalde families specialiseren in het bereiken van topposities.

   Hoofdstuk 7

8. De keuze van sommige individuen om in slechtere gebieden te gaan broeden dan andere individuen valt goed te begrijpen zonder het bestaan van individuele kwaliteitsverschillen aan te nemen[1]. Zelfs als sommige individuen beter zijn dan anderen, dan betekent dit nog steeds niet dat alle individuen die in slechte gebieden proberen te gaan broeden noodzakelijkerwijs een lagere fitness hebben[2].

   [1] Ens *et al.* (1995). The despotic distribution and deferred maturity: two sides of the same coin. *American Naturalist* 146, 625-650.
   [2] Hoofdstuk 8

9. Onopgemerkte dispersie is een fundamenteel probleem voor het verkrijgen van betrouwbare overlevingschattingen. In veel studies wordt dit probleem omzeilt door te spreken over een effect van factor X op de lokale overlevingskans. Echter omdat diezelfde factor X vaak ook het dispersiegedrag zal beïnvloeden, is de lokale overleving meestal een onzuivere schatter van de echte overlevingskans.

   Doliguez *et al.* (2002). Cost of reproduction: assessing responses to brood size manipulation on life-history and behavioral traits using multi-state recapture models. *Journal of Applied Statistics* 29, 407-423.

10. Effectgroottes in ecologische en evolutionaire studies zijn meestal klein, en de benodigde steekproefgroottes om zulke effecten statistisch aan te kunnen tonen worden zelden verkregen[1,2]. De meeste onderzoeksbevindingen zijn dan ook waarschijnlijk onjuist geformuleerd[3]. Het is dan ook verbazingwekkend dat er weinig bezorgdheid is over het verkeerd interpreteren van onderzoeksresultaten[4].

    [1] Kingsolver *et al.* (2001). The strength of phenotypic selection in natural populations. *American Naturalist* 157, 245-261.
    [2] Møller & Jennions (2002). How much variance can be explained by ecologist and evolutionary biologists? *Oecologia* 132, 492-500.
    [3] Ioannidis (2005). Why most research findings are false. *PLoS Medicine* 2: 696-701.
    [4] Anderson *et al.* (2001). Concerns about finding effects that are actually spurious. *Wildlife Society Bulletin* 29: 311-316.

11. Kort schrijven duurt lang.

42. Het feit dat ultimate vragen ontzettend veel hypothesen genereren is zowel een groot probleem als ook een bron van inspiratie.

    Adams (1995). The *hitch hiker's guide to the galaxy.* William Heinemann, London. en http://en.wikipedia.org/wiki/The_Answer_to_Life,_the_Universe,_and_Everything