



The Study of Career Decisions: Oystercatchers as Social Prisoners

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1. CONCEPTUAL FRAMEWORK

Because resources are limited, animal populations cannot grow forever and the ensuing struggle for existence subjects them to the relentless force of natural selection (Darwin, 1859). Thus, competition among animals for limited resources is a defining property of life. In this chapter, we focus on a case where the access of animals to these limited resources depends on their social position as a member of an animal society.

There are three descriptions of aspects of animal societies in terms of competition, each accompanied by their own body of theory:

1. Distribution theories describe the access of individual animals to limiting resources in space.
2. Life-history theory describes the access of individual animals to limiting resources in the course of their life, and how these resources are allocated to survival and reproduction.
3. Mating systems theory describes the access of individual animals to partners as a resource-limiting reproduction.

According to Wilson (1998), the ultimate goal of science is to unite different fields of knowledge and his term for this enterprise is “consilience.” Our modest contribution to consilience is the attempt to combine adaptive distribution theory to life-history theory and mating systems theory to better understand the social organization of our study species. As Wilson (1975) formulated nearly four decades ago: “The ultimate goal is a stoichiometry of social evolution. When perfected, the stoichiometry will consist of an interlocking set of models that permit the quantitative prediction of the qualities of social organization—group size, age composition, and mode of organization, including communication, division of labor, and time budgets—from a knowledge of the prime movers of social evolution.”

Before we can discuss the three partial descriptions of animal societies in more detail, we must first introduce some definitions. The term *social position* was borrowed by Wiley (1981) from the field of sociology “to refer to

patterns in individuals' social behavior that normally persist over periods of days at least, in order to distinguish these patterns from those that are recognizable over periods of minutes or hours." According to Wiley (1981) all societies are characterized by a "recognizable structure that persists with relative constancy in spite of the passage of succeeding generations of individuals." Thus, any society can be characterized by the proportions of individuals in the population or the absolute numbers of individuals in each social position. To describe the flow of individuals in time through this more or less persistent social structure, Wiley (1981) coined the term *ontogenetic trajectory*, which refers to the age at which individuals reach successive social positions. We adopt this important concept, but prefer to use a different term, *social career*, to emphasize the social context (Ens, 1992). Additionally, we argue that social positions should not only be characterized by specific social behaviors but also by the access they offer to limiting resources. A major complication in this respect arises from the fact that, in many instances, the units that compete for limiting resources do not consist of single individuals, but of groups of individuals with a well-defined social organization. Within the group, many social relationships involve cooperation, not competition. Thus, group members may help each other during contests with other groups and members of a pair may share duties caring for the young. When the unit of competition is a group, the social position must be characterized by the properties of the group and its access to limiting resources, as well as by the properties of the relationship within the group.

Limiting resources vary in quality, be they foraging habitat, breeding territories, or mates. For instance, in the case of pairs defending a breeding territory, the social position of a pair member could be mated to a high-quality (HQ) partner in a HQ territory, mated to a low-quality (LQ) partner in a HQ territory, mated to a HQ partner in a LQ territory, and mated to a LQ partner in a LQ territory. So what is individual quality? Individuals differ in many phenotypic traits, like body size, fighting ability, and breeding experience. The extent to which variation in these traits contributes to variation in individual quality will differ. Accordingly, Wilson and Nussey (2010) suggest that we should equate individual quality to the vector of selection on these traits. This can be determined from the vector of partial regression coefficients of traits on fitness, or more usually a proxy measure of fitness, such as lifetime reproductive success. In short, individual quality is the axis of phenotypic variation that best explains variance in individual fitness. As with social position, we expect individual quality to be persistent and consistent over a sufficiently long time period.

Equipped with definitions of social position, social career, and individual quality, we can return to the three partial descriptions of animal societies.

Distribution theory: At any one time, each animal occupies a particular social position and we can characterize the society in a given locality by the frequency distribution of social positions. In his seminal paper, [Wiley \(1981\)](#) does not consider variation in habitat quality. However, no species can occur everywhere, so it seems inevitable that habitats will differ spatially in quality. Thus, the frequency distribution of social positions will also be linked to the distribution of resources in space, and we would expect the size (or density) and the composition of societies to differ between habitats. When resources fluctuate in time, we expect the animal society to follow suit. Seeking explanations for the numbers and distribution of organisms is a problem as old as ecology itself, but it was not until [Fretwell and Lucas \(1969\)](#) introduced the notions of an ideal free and an ideal despotic distribution that quantitative and testable adaptive distribution theories were developed.

Life-history theory: We can also characterize a society by the flow of individuals through the various social positions over time. This does not imply that each individual will be able to attain every social position. From the point of view of the individual, we can describe these changes in social position as a social career, and therefore necessitating a lifetime perspective ([Wiley, 1981](#)). Individuals can decide to change (or to try to change) their social position. We will refer to such decisions as *career decisions*. By definition, an individual cannot take a career decision in isolation of other individuals, and the costs and benefits of a particular decision will depend on the responses and actions of other animals. In fact, we expect an individual to have rules for deciding which action to perform, depending on its social position, its state, etc. These rules are commonly referred to as strategies ([McNamara & Weissing, 2010](#)). We would also expect the costs and benefits of a *career strategy*, like other behaviors in a social context, to be frequency dependent ([McNamara & Weissing, 2010](#)), that is, the best strategy for an individual to follow will depend on the strategies followed by the individuals with which it is interacting.

If we are to understand the adaptive value of a particular career strategy, these costs and benefits must be expressed in terms of fitness. Many different fitness measures have been used in both empirical and theoretical studies, but theoretical work indicates that the appropriate fitness measure depends on how density dependence limits population growth ([Mylius & Diekman, 1995](#)); in other words, how resources constrain the total size of the animal

society under investigation. Neglecting the mechanism of density regulation can lead to highly misleading conclusions on the optimal strategy (Pen & Weissing, 2000). For example, Pen and Weissing (2000) reached opposite conclusions on the occurrence of helping behavior depending on whether density dependence acted on the survival or fecundity of dispersers. Thus, studying when and where density dependence limits population growth is crucial.

When we describe the social career of an individual, we focus on its access to limiting resources conferred by its social position. The subsequent allocation of acquired resources to survival and reproduction yields the life history, which can also be described as the species-specific adaptive scheme of the distribution of reproductive effort over the life of an animal. Life-history research aims to reveal why this temporal organization varies among species as well as among individuals within a species (Daan & Tinbergen, 1997). Clearly, career decisions precede reproductive decisions, because resources must first be acquired before they can be allocated to either survival or reproduction. However, the reverse is also true. A central concept in life-history theory is the cost of reproduction. This could be due to a loss of social position, including a decreased access to limiting resources, leading to a reduction in survival or a reduction in the options to reproduce in the future. It would seem that we cannot obtain a full understanding of career decisions if we do not take account of reproductive decisions and *vice versa*. Nonetheless, substantial insight can be gained by focusing on the adaptive nature of career decisions and taking the reproductive rates and survival chances associated with a particular social position as fixed. Instead of describing the life history as a sequence of reproductive decisions, we describe it as a sequence of career decisions. Finding the optimal career strategy under both density dependence and frequency dependence is a problem that should be investigated by evolutionary game theory (McNamara & Weissing, 2010).

We do not assume here that reproductive rates and survival probability depend only on the social position of an individual. The phenotypic quality of the individual is also an important variable that is likely to influence reproductive potential and survival probability. Variation in quality between individuals may also mask underlying within-individual negative correlations (i.e., trade-offs) between life-history traits, for example, due to HQ individuals always reproducing and surviving well, while LQ individuals both reproduce and survive poorly (van Noordwijk & de Jong, 1986). The phenotypic quality is also likely to influence the costs and benefits of a particular

career decision, but we do not necessarily expect a precise matching between phenotypic quality and social position. Thus, individuals in a given social position may differ with regard to reproduction and survival chances due to variation among individuals in phenotypic quality.

Textbooks on the evolution of life histories are filled with quantitative mathematical models (Roff, 1992; Stearns, 1992). However, only those models that explicitly incorporate both density and frequency dependence are relevant to our case of animals with a well-defined social organization. Those same textbooks also show the central importance of trade-offs in limiting the scope of variation in life-history traits. Thus, we should seek to identify the trade-offs governing career strategies. According to Lessells (1991), trade-offs result when two traits are limited by the same resources: "time, energy, or any other resource can be spent only once." She also concludes that the many life-history trade-offs that have been identified can be subsumed into two major categories: the trade-off between current and future reproduction and the trade-off between the number and fitness of offspring. In our study of career decisions, we will focus on the trade-off between current and future reproduction.

Mating systems theory: The third body of theory that describes aspects of animal societies is that of mating systems (Davies, 1991; Emlen & Oring, 1977; Orians, 1969), which is closely linked to the topics of sexual selection (Darwin, 1871) and sperm competition (Parker, 1970). For various reasons, mates may be a limiting resource to the opposite sex: (1) if one sex (usually the female) invests more in offspring than the other sex, than we expect competition among members of the sex with little investment for access to the sex with high investment, (2) if both sexes engage in parental care, we may expect intrasexual competition for more mates of the opposite sex, that is, both sexes would benefit from polygamy, (3) if within a sex individuals differ greatly in quality, irrespective of whether quality refers to genotypic or phenotypic traits, we expect intrasexual competition among members of the opposite sex for HQ mates. In many cases, there may be sexual conflict, with the preferred option for the males differing from the preferred option for the females.

There is no shortage of mathematical models on mating systems, sexual selection, and sperm competition, but it is not immediately obvious which models are best suited to link with our distribution and life-history model. What is clear though is that it is important to quantify variation in the quality of males and females and to study how males and females compete for mates.

Our ideal approach would be to combine the three different perspectives on competition for limiting resources into a single mathematical model on career strategies and test the quantitative predictions of the model. So far we have been unable to construct such a model, or set of interlocking models, but the above sketch of our conceptual framework provides guidance to the topics that need to be addressed:

1. Identify the limiting resources that an individual is competing for at the various stages in its social career.
2. Describe the social positions and identify the various career strategies; the costs and benefits of the associated career decisions and the underlying fundamental trade-offs.
3. Describe the processes that generate and maintain variability between individuals and how it affects the probability that individuals will follow a particular career.
4. Explain the structure of a society (i.e., distribution of social positions) from the distribution of limiting resources.
5. Explain the mean and the variability in the age at which particular social positions are reached.
6. As a final step, we should be able to reconstruct the society under investigation, that is, we should be able to provide a description in space (the spatial distribution of social positions) that is fully consistent with a description in time (the flow of individuals through social positions) and with a description of the mating system (the access of individuals of one sex to individuals of the opposite sex).



2. ORGANIZATION OF THE REVIEW

We will apply this conceptual framework to our study species the Oystercatcher *Haematopus ostralegus*. We will describe the social system and the career decisions of Oystercatchers as we currently know them and explain on what grounds we identify different social positions. To illustrate how the conceptual framework can be applied to the case of the Oystercatcher, instead of following the social career from birth to death, our starting point is the career decision that has received most attention: the decision of a nonbreeder to join a queue (i.e., wait) for either a HQ or a LQ territory. Since territories are defended by pairs, this naturally brings us to mate choice and divorce. Before Oystercatchers can start to compete for territories and mates, they must learn to survive the nonbreeding season. Having described career decisions during both seasons, it seems fit to enquire

into the traits that allow for a successful career. We end with a discussion of the progress that we have made and the major challenges that remain.



3. STUDY SPECIES: THE EURASIAN OYSTERCATCHER *HAEMATOPUS OSTRALEGUS*

3.1. Population Studies

The core of this review is based on two long-term studies of populations of individually marked Oystercatchers (Fig. 8.1A and B): the study on Oystercatchers wintering on the estuary of the Exe that was initiated by John Goss-Custard in 1976 and the study on Oystercatchers breeding on the saltmarsh of Schiermonnikoog that was initiated by Jan Hulscher in 1983. While there have been more long-term studies, as on the islands of Skokholm (Harris, 1967; Harris, Safriel, Brooke, & Britton, 1987; Safriel, Harris, Brooke, & Britton, 1984), Mellum (Schnakenwinkel, 1970), and Texel (Oosterbeek, van de Pol, de Jong, Smit, & Ens, 2006), none have been anywhere near as intensive and detailed as either of these two studies.

The study area of the ongoing Oystercatcher population study on the Dutch Wadden Sea island of Schiermonnikoog (32°29' N 6°14' W) consists of a natural salt marsh area, where the Oystercatchers breed and intertidal mud flats where they feed. In the main study area, all breeders and their fledglings are individually marked, as are many (adult) nonbreeders. Oystercatchers are long lived (up to 40 years) and become sexually mature at the age of 3 (Simmons et al., 1983), with two distinguishable juvenile age classes (1st and 2nd year). Sex of the Oystercatchers is determined by DNA analysis and observations of copulations (Heg, Dingemanse, Lessells, & Mateman, 2000; Heg, Ens, Burke, Jenkins, & Kruijt, 1993); most birds can only be sexed at the adult stage. Each year, we determine the number of high- and LQ breeding territories in the main study area (Ens, Kersten, Brenninkmeijer, & Hulscher, 1992). The total number of nonbreeders is estimated by counts during the breeding season at all high-tide roosts on the island. Social status (pair bond, territory quality, breeder, or nonbreeder) of all marked birds is determined through regular observations from elevated hides placed on the saltmarsh. Each year, we follow the breeding performance of all pairs in the main study area; for a complete description of the standardized protocol, see Heg and van der Velde (2001). Every year about 50 Oystercatchers (males and females) are caught on the nest during incubation to collect biometric data, including their bill morphology that reflects their feeding specialization (van de Pol et al., 2009).



Figure 8.1—Cont'd



Figure 8.1 (A) Individually marked adult Oystercatcher carrying a solar-powered UvA-BiTS GPS-tracker (Shamoun-Baranes et al., 2012), as well as a tall ring with one small engraved bar (there can be up to three bars) and a color band. (B) Individually marked immature Oystercatcher during winter, with a typical white neck collar, brownish tip of the bill and brownish eyes, carrying color rings with engraved letters as well as a small color ring. The birds also carry a metal ring with a unique number issued by a national ringing center to which recoveries of dead birds are reported. (C) Four unmarked Oystercatchers in a piping ceremony, almost certainly involving a territorial border dispute between two breeding pairs. (D) Oystercatchers in a *hovering ceremony*, where they perform the aggressive piping display in flight. Such hovering ceremonies only occur during the breeding season and almost always include nonbreeders, who may be claiming local dominance (Heg, Ens, et al., 2000). (A) Photo Jeroen Onrust; (B) photo Tom Voortman; (C) photo Koos Dansen; (D) photo Harvey van Diek.

The Oystercatcher project on the nonbreeding Oystercatchers of the Exe estuary in South-west England began in 1976 and continued until the early 2000s. It was set up at a time when the potential conflict between Oystercatchers and shellfishing was a major issue in the management of the British coast. The study aimed to quantify the reciprocal interaction between the populations of the birds and their shellfish prey to determine the role that each of them played—if any—in determining the population dynamics of the other. But the project also provided an opportunity to test some of the theoretical ideas on individual variation and competition then current in ecological and behavioral science.

The Exe estuary is, on average, about 1 km wide along its 10 km length from the English Channel to the upstream limit of the main intertidal flats. The dominant shellfish is the common mussel, *Mytilus edulis*. The main 10 mussel beds are situated in the downstream half of the estuary and cover an extensive part of the intertidal flats. Some 2000 Oystercatchers spent the

nonbreeding season on the estuary. These birds also fed on other species of prey when the mussel beds were covered by the tide, the most frequent being cockles *Cerastoderma edule*, a clam, *Scrobicularia plana*, a polychaete worm, *Nereis diversicolor*, and earthworms, *Lumbricus* spp., which they found in the grass fields alongside the estuary.

The project included routine surveys of size and distribution of both the mussel and Oystercatcher population, and the collection of survival estimates of the various age classes of Oystercatchers over the nonbreeding season. Intensive observational work was carried out on the foraging behavior of individually marked birds from hides placed on towers. The results of these studies on individuals provided the data with which an individual-based model (IBM) of the Oystercatcher population was built and tested (Stillman, Goss-Custard, West, et al., 2000).

3.2. Social Organization

Oystercatchers are serially socially monogamous (Heg, Bruinzeel, & Ens, 2003; van de Pol, Heg, Bruinzeel, Kuijper, & Verhulst, 2006) and genetically monogamous (Heg et al., 1993). The social system during the nonbreeding season differs from the social system during the breeding season, as a substantial number of individuals leave the breeding area to spend the nonbreeding season elsewhere (Hulscher, Exo, & Clark, 1996). Social relationships are typically not maintained when the birds move from the breeding area to the wintering area and *vice versa*. Birds from a particular breeding area spread out over different wintering areas and birds in a particular wintering area derive from many different breeding areas. Social relationships, and thus social positions, are maintained over the years in both the wintering (Ens & Cayford, 1996) and breeding area (Ens, Briggs, Safriel, & Smit, 1996). Thus, the career of an Oystercatcher actually consists of two interconnected careers and understanding how they impinge upon each other is an outstanding challenge.

The resources that limit Oystercatcher populations have been intensively studied (Goss-Custard, 1996). Although they will be discussed in detail later on, a brief summary is needed here. All evidence indicates that during winter, food is the main limiting resource. Priority of access to this limiting resource is determined by (local) social dominance. However, the rate at which food can be extracted is also determined by the quality of the food supply, individual specialization, and familiarity with the feeding area and/or the local birds.

During the breeding season, the social system is more complex as pairs compete with other pairs for territorial space. Thus, territorial space of high quality is the limiting resource, and social interactions include cooperation with other individuals as part of gaining access to this limiting resource. Furthermore, social and sexual partners of high quality should also be considered a limiting resource.

3.3. Identifying Social Positions

Describing an animal society in terms of social positions (Fig. 8.2) is only possible if we are able to identify, that is, measure, social positions in the field objectively. It involves an iterative process between field observations and theorizing. The suggestion that territories differ in quality was based on field

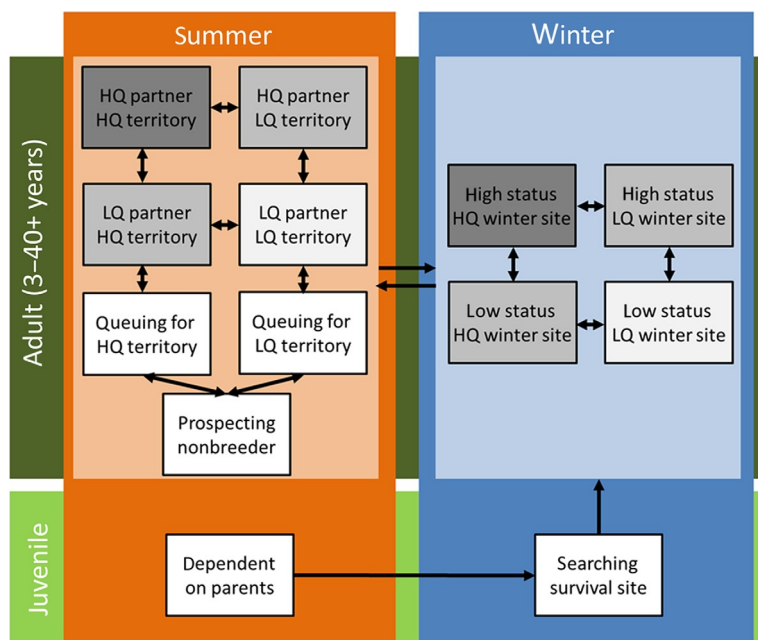


Figure 8.2 Schematic representation of social positions and possible transitions in the Oystercatcher society. Social positions are described in squares, where HQ and LQ stand for high quality and low quality, respectively. The fitness benefits associated with certain social positions are reflected by the intensity of grayness: the darker the gray, the higher the fitness. For simplicity, we have depicted several continuous variables (e.g., mate and site quality) as a dichotomy (high or low quality). For the same reason, we have not depicted all possible transitions and decided not to include some very rare social positions like unmated territorial males, or males and females in a polygynous trio.

observations (Ens et al., 1992). The suggestion that nonbreeders queue for territories differing in quality derived from a modeling exercise (Ens, Weissing, & Drent, 1995). In this enterprise, there are always practical limitations to field observations, which may lead to erroneous conclusions. For instance, in a detailed early study of the social behavior of mostly unmarked Oystercatchers, Makkink (1942) wrongly concluded that Oystercatchers did not defend breeding territories. His description of the various displays remains valid, but his interpretations are wrong. Makkink thought the conspicuous piping display (Fig. 8.1C) had a function in mate choice. However, we now know that during the breeding season piping signals ownership of a breeding territory, with exclusive access to the resources in the territory, and can be performed by both male and female singly as well as jointly (Heppleston, 1970). By contrast, during the nonbreeding season piping signals local dominance (Ens & Goss-Custard, 1986), which means priority of access but not exclusive access.

To aid readability, we will describe the basis for identifying particular social positions when discussing the relevant career decisions connecting them, instead of providing a long and tiresome list now.



4. JOINING THE QUEUE FOR BREEDING TERRITORIES

4.1. The Despotic Distribution and Deferred Maturity

During the breeding season, territory owners restrict their activity to a small exclusive area and chase intruders, perform the piping display against intruders at a distance, and regularly engage in border disputes with neighbors. Such border disputes often involve the piping ceremony (Fig. 8.1C), but this is interspersed with periods where the birds stand still and are bobbing (moving the head up and down) quickly followed by an attack in flight. Usually, breeding territories are defended by a pair, where male and female are equally aggressive against intruders of either sex. A bias to interact with birds of the same sex is only evident in fierce physical fights, which are extremely rare (Ens, 1992). Pair members keep close proximity during feeding and resting before and during egg laying, which can be interpreted as mate-guarding (Ens, 1991).

In most Oystercatcher populations, there is strong variation in habitat quality. Often the variation has a clear dichotomy, due to the (energetic) cost of transporting food to the chicks (Ens et al., 1992; Safriel, Ens, & Kaiser, 1996). In HQ territories, the costs are low because the chicks can follow the parent from the nesting territory to the adjacent feeding territory to

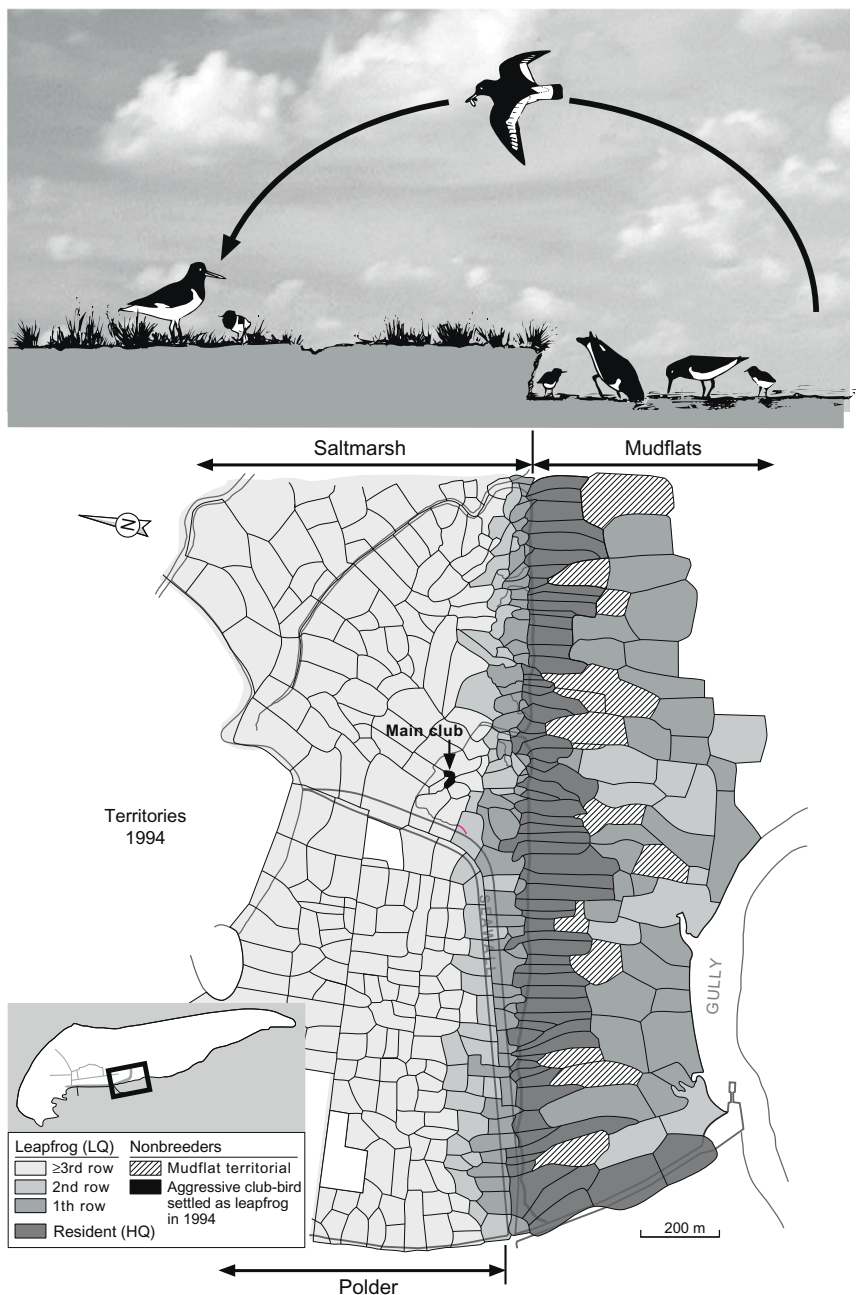


Figure 8.3 Top: scheme of LQ (leapfrog) and HQ (resident) territories during chick feeding, when the birds in the LQ territories have to transport all the food to the chicks on the saltmarsh, whereas the birds in HQ territories can take the chicks to the food on the mudflats. Bottom: territory map of the study area on Schiermonnikoog during the breeding season in 1994 (the inset shows the location of the study area on the island). Based on [Ens et al. \(1992\)](#) and [Heg \(1999\)](#).

be fed (Fig. 8.3). In LQ territories, on the other hand, the feeding and nesting area are separated and the parent has to transport every single prey item to the chicks, until the chicks have reached fledging age and are able to follow the parents on the wing. Parents in LQ territories raise two to three times fewer chicks than parents in HQ territories, because they do not generally transport sufficient food to meet the energy demands of all their chicks (Ens et al., 1992).

Clearly, the limiting resource during the breeding season is territorial space (of high quality). When territory owners are experimentally removed, they are quickly replaced, mostly by nonbreeders (Bruinzeel & van de Pol, 2004; Harris, 1970; Heg, Ens, van der Jeugd, & Bruinzeel, 2000). When population size increased in the Lune Valley (UK) and on Mellum (Germany), an increasing proportion consisted of nonbreeders (Goss-Custard, Clarke, et al., 1995). Wherever they have been studied, during the breeding season Oystercatcher populations are always characterized by substantial numbers of nonbreeding adult birds fully capable of breeding (Harris, 1970; Heg, Ens, et al., 2000; Safriel et al., 1984; Schnakenwinkel, 1970).

Nonbreeders spend time intruding on territories, feeding in undefended areas (or in a group in defended areas), and attending the *club*, which is a small flock at a traditional location where the birds rest and preen. They also engage in aggressive interactions and sexual behaviors there. Most nonbreeders appear to be single, but some nonbreeders establish pair bonds that last over the years. We prefer the term nonbreeder over the commonly used term floater, because the term floater suggests that the birds are without site attachment and purpose, while the opposite is the case for most nonbreeding Oystercatchers.

In fact, it may take more than a decade before a mature Oystercatcher breeds for the first time. From a Darwinian perspective, this apparent “wasting” of breeding years is hard to understand, so in life-history theory it is known as the problem of deferred maturity (Roff, 1992; Stearns, 1992) and from a Darwinian perspective, it is equally hard to understand why Oystercatchers often settle in territories of low quality. The despotic distribution proposes that consistent differences in success between habitats result from settled individuals despotically excluding unsettled individuals from HQ habitats (Fretwell, 1972). It could be that individuals settling in poor quality habitat are poor quality individuals “making the best of a bad job” (Parker, 1982). We developed the alternative hypothesis that the despotic distribution and deferred maturity can be seen as two sides of the same coin (Ens et al., 1995).

The idea that individual nonbreeders, capable of reproducing, might forgo immediate possibilities for poor reproduction and thereby delay reproduction so as to improve the chances of obtaining a position with high reproductive potential was developed by students of cooperatively breeding species (Komdeur, 1992; Stacey & Ligon, 1987; Wiley & Rabenold, 1984). Reviewing the literature on birds, Zack and Stutchbury (1992) concluded that the trade-off between waiting a long time for ownership of a HQ territory or settling immediately in a LQ territory was not restricted to species with helpers at the nest, but might well apply to any species with delayed breeding. In the subsequent literature, “waiting” for a HQ position has been generally referred to as “queuing,” where it was always realized that queues could be structured in many different ways, that is, from very strict to random order service queueing. Wiley and Rabenold (1984) and Zack and Stutchbury (1992) formalized the conditions under which queuing would be selectively advantageous, but they failed to explicitly incorporate that the costs and benefits of queuing will be frequency dependent. Clearly, the success of a queuing strategy depends on how many other individuals are queuing for the same opportunity (Ens et al., 1995). At evolutionary equilibrium, and in the absence of differences between individuals, we would expect competition to make the fitness expectations of a bird settling immediately in a poor quality territory to equal the fitness expectations of a bird queuing for a HQ territory. Of course, once settled, birds in good territories do better than birds in poor territories, but to their success must be added the birds that tried to obtain a HQ territory, but failed.

4.2. Modeling the Queue

The queue model was developed by Ens et al. (1995), and subsequently improved by van de Pol, Pen, Heg, and Weissing (2007), henceforth VPHW, as follows: (1) VPHW integrated the population dynamics and evolutionary dynamics of life-history strategies in one coherent model, (2) VPHW introduced density dependence by setting a maximum on the number of suitable breeding territories.

Furthermore, VPHW extended the model to include individual quality differences conditional on natal origin, thereby allowing queuing strategies to depend on this condition. Figure 8.4 provides a graphical depiction of the model with and without quality differences depending on natal origin; that is, for unconditional queuing strategies (top) and conditional queuing strategies (bottom). In fact, the unconditional model is a special case of the

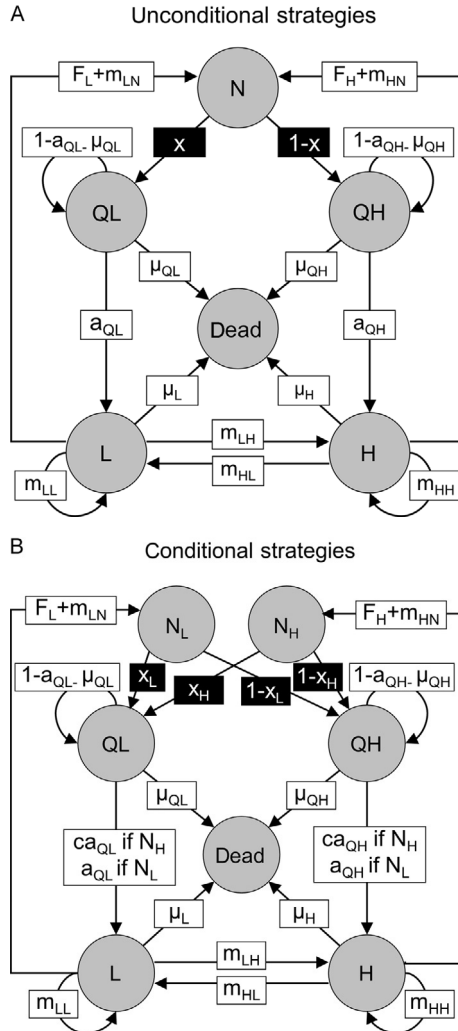


Figure 8.4 Schematic representation of a situation with (A) unconditional queuing strategies and (B) conditional queuing strategies. The parameter x represents the strategic choice individual nonbreeders (N) have to make to queue for either a high- or a low-quality territory (HQ and LQ , respectively). Breeders in high- and low-quality territories (H and L , respectively) can produce new nonbreeders (F_H and F_L) as well as return to the nonbreeder state by losing their territory (m_{HN} and m_{LN}). In the conditional model, nonbreeders originating from high- and low-quality habitats can make a different strategic choice (x_H and x_L , respectively). Furthermore, competitive asymmetries can be included by giving nonbreeders born in high-quality territories (N_H) a c -times-higher annual probability of settling (ca_{QH} and ca_{QL}) than nonbreeders born in low-quality territories (N_L) have (a_{QH} and a_{QL}). Competitive asymmetries (c) reflect differences in, for example, fighting capacity. Note that only the flows between states (arrows) that are necessary for constructing the model are presented (e.g., L can die, but this is given by $\mu_L = 1 - m_{LL} - m_{LN} - m_{LH}$). From *van de Pol et al. (2007)*.

conditional model, where c , the competitive asymmetry between individuals which differ in type of natal territory, equals 1. It is important to realize that F_L and F_H in Fig. 8.4 represent the number of offspring born in LQ and HQ territories that have survived till adulthood and have entered the competition for breeding territories as a nonbreeder. Immature nonbreeders have a clearly recognizable plumage (Fig. 8.1B) and remain on their wintering site during summer (Ens & Cayford, 1996). In our calculations, we have assumed that Oystercatchers reach sexual maturity when 3-years old.

The model also allows quantitative predictions when the necessary demographic parameters and transition probabilities have been measured. Collecting demographic data has been a major part of our activities on Schiermonnikoog since the study was initiated in 1984. In nearly all years, birds in HQ territories fledged more chicks than birds in LQ territories, but success has varied widely between years, although on average success is lower in recent years (Fig. 8.5A). The breeding population was relatively stable until 1995, but started to decline thereafter, with most of the decline taking place in the number of LQ territories (Fig. 8.5B). The decline in breeder numbers occurred in the presence of a substantial number of nonbreeders (Fig. 8.5C). Nonbreeder numbers strongly fluctuated over time, in part due to sampling error, but did not show a strong systematic decline.

To find the optimal queuing strategy, the queue model made the simplifying assumption that all demographic parameters are independent of time, sex, and age (within a stage). Demographic data from the stable period were used by VPHW to derive three quantitative predictions from the optimal queuing strategy. The first prediction is for the age at which birds successfully recruited in HQ and LQ territories. On average, new recruits in HQ territories were aged 7.6 years, which was very close to the predictions, which ranged from 7.5 to 8.0 years. In contrast, the observed age of successful recruitment in LQ territories was 6.5 years, whereas the predictions ranged from 3.1 to 3.6 years, that is, were much lower than observed. Increasing the competitive advantage of birds born in HQ territories over birds born in LQ territories, hardly affected the predictions.

The second prediction that could be tested related to the distribution of new recruits over territories of different quality. Of 55 recruits of known natal origin, 20% recruited in HQ territories, and 80% in LQ territories. The match was very close (22% of recruits predicted to settle in HQ territories) to the predictions of the unconditional model, but for the conditional model, there was only a good match when the competitive advantage of birds born in HQ territories was high.

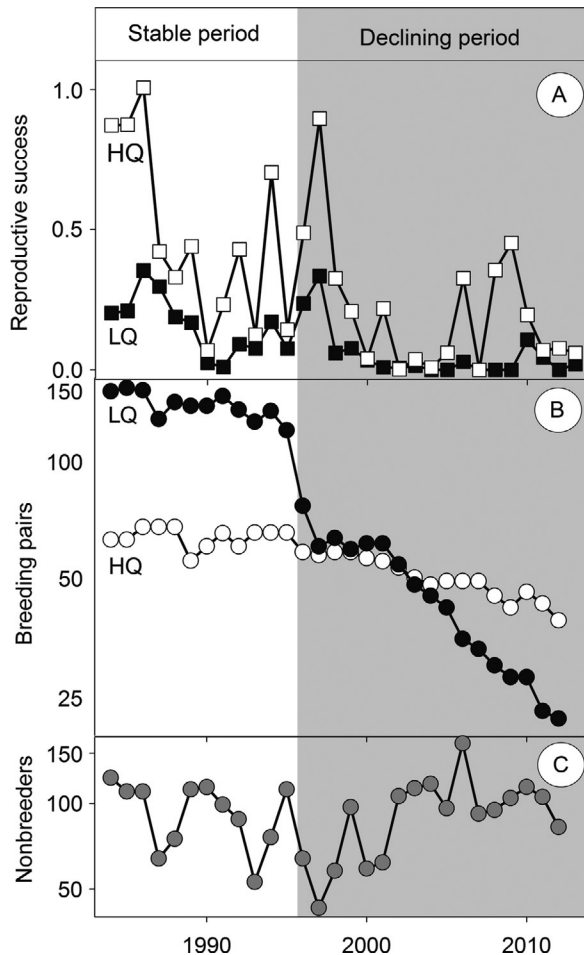


Figure 8.5 Reproductive success and composition of the study population on Schiermonnikoog from 1984 to 2012: (A) reproductive success comparing pairs in HQ and LQ territories, (B) number of HQ territories (open dots) and number of LQ territories (closed dots). The study area was extended in 1992. Numbers for areas not followed during the entire period were imputed based on trends in areas that were censused in those years, (C) Number of nonbreeders (estimated from counts at high-tide roost during the breeding season). Note the logarithmic scale in (B) and (C).

Thus, for predictions on the age of first breeding and the distribution of new recruits over the two types of territory, the conditional and unconditional models perform equally well. One might therefore argue that adding a competitive asymmetry between birds of different natal origin does not add much insight. However, there is one additional insight that only the

conditional model makes. As soon as birds from an HQ territory have a competitive advantage, however slight, over birds born in a LQ territory, the model predicts a pure strategy for birds originating from a LQ territory, and that is to queue only for LQ territories. In contrast, the model predicts a mixed strategy for birds originating from an HQ territory which is to queue with a certain probability for either type of territory. So far, 94% of fledglings from a LQ territory have indeed recruited into a LQ territory, suggestively close to a pure strategy. In contrast, fledglings from a HQ territory settled both in HQ and LQ territories (44% vs. 56%, respectively) consistent with a mixed strategy (van de Pol, Bruinzeel, Heg, Van der Jeugd, & Verhulst, 2006).

Although the conditional queue model explains important aspects of settlement patterns in the wild, there are clear limitations. Evidence for site dominance of nonbreeders (see later) is used as an argument for the assumption that nonbreeders must decide to either queue for a HQ or an LQ territory. However, we expect site dominance to build up over the years, so that the annual probability of settling should increase with the number of years the individual was queuing. Yet, the queues are modeled as lotteries, where the chances of settling do not increase with the number of waiting years but only depend on the ratio between vacancies and competitors.

To investigate how the relationship between waiting years and probability of settling affects predictions on settlement patterns, we introduced a correlation between age and rank in the queue, which could vary from 0 (the original lottery independent of age) to 1 (older birds always settle before younger birds). Figure 8.6 compares the distribution of the predicted age at first breeding to the observed age at first breeding for birds recruiting in LQ and HQ territories. When queues are modeled as a lottery both the predicted mean age at first breeding in LQ territories and the distribution of the recruitment ages for HQ and LQ territories are far off (Fig. 8.6A). As we would expect under a lottery, the predicted distributions are highly skewed, whereas the observed distributions are much more symmetrical (Fig. 8.6A). When we allow the hierarchy in the queue to be strictly age dependent, the predicted mean age of first breeding in LQ territories increases considerably, and the predicted distribution becomes less skewed, but much narrower than the observed variation in age at first breeding (Fig. 8.6B). Only when we model queues that are weakly structured by age-dependent priority do we find similar amounts of individual variation in age of first reproduction as observed in the wild in HQ territories, but not in LQ territories (Fig. 8.6C). However, at the same time the predicted

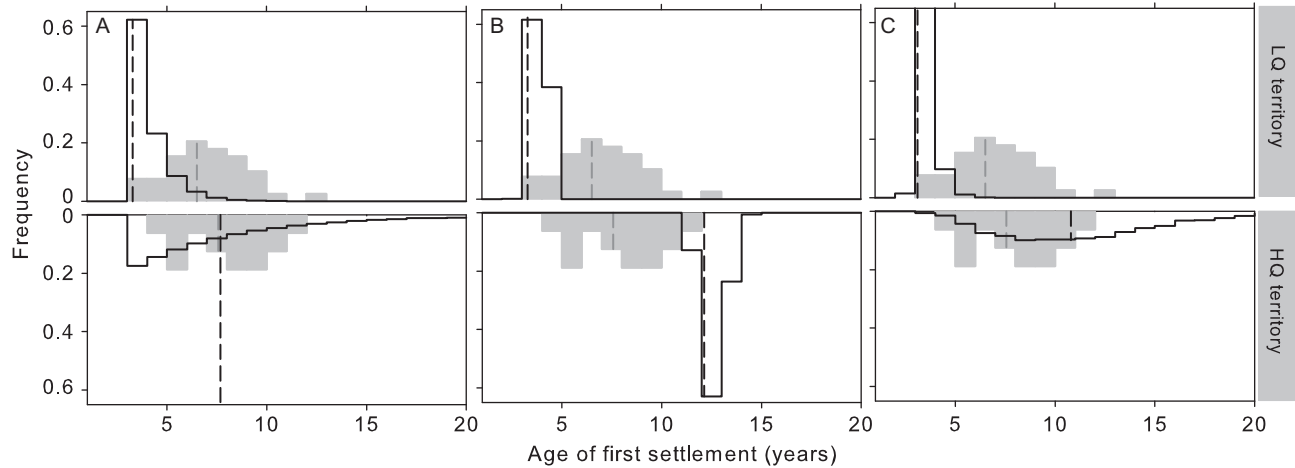


Figure 8.6 Comparison of the frequency distribution of the observed age of first breeding (gray bars) with predicted age of first breeding (open bars) according to: (A) queue model with random order service (lottery), (B) queue model with strict age-dependent queuing (first-in first-out), and (C) queue model with weak age-dependent queuing (correlation between age and rank in queue was 0.5). Dashed lines indicate mean values.

mean ages at first breeding are still far from the observed values. Potentially the predicted distribution in age at first breeding in LQ territories is too narrow because we ignored any additional variation within LQ territories. Furthermore, age-dependency is just one mechanism by which queues might be structured. Breeding experience might also be important, as birds that lost a breeding territory have a much higher settlement probability than inexperienced birds (Bruinzeel, 2007). Finally, we may need to incorporate the site dependency of social interactions more explicitly into account. In all our models, nonbreeders now queue for either all HQ or all LQ territories in the study area. However, each individual probably only competes for a subset of territories (see later). Similarly, breeders occupying LQ territories may move to HQ territories in later years, but this probability quickly decreases the further their territories are removed from the HQ territories (Heg, 1999); see also Fig. 8.3.

4.3. Site Dominance and Familiarity

Queue models assume that nonbreeding Oystercatchers can tell the difference between HQ and LQ territories, which seems vindicated by the observation that intrusion rates in HQ territories greatly exceed intrusion rates in LQ territories (Heg, Ens, et al., 2000). Queue models also assume that nonbreeders must decide to either queue for a HQ or a LQ territory, that is, that they cannot successfully compete for territories if they do not commit themselves to a specific geographical location. This is the kind of fundamental trade-off that we hypothesize to underlie career decisions.

Here, we will address three questions:

1. What is the evidence for such commitment?
2. What is the precise nature of this commitment?
3. Why is commitment necessary?

Detailed study of natural recruitment on Schiermonnikoog showed that nonbreeders that successfully recruited were either members of a pair of nonbreeders that had previously defended a nearby mudflat territory (Fig. 8.3), or had been very aggressive on the club nearby, or had intruded frequently (including displaying aggressively) as a single individual at or near the area where they were eventually successful at obtaining a territory (Heg, Ens, et al., 2000). Sometimes, breeders were ousted from their territory and spent between 1 and 9 years (average 2.4 years) before they could settle again (Bruinzeel, 2007). Importantly, resettlement occurred close to the former breeding territory. Additional insights were obtained by inducing

recruitment through the experimental removal of territory owners (Bruinzeel & van de Pol, 2004). Before removal of either a male or a female from either a HQ or a LQ territory, the intrusion behavior of marked nonbreeders was studied, including the precise location of each intrusion. Nonbreeders that acquired an experimental vacancy were seen intruding significantly closer to that vacancy prior to its creation, compared with a set of alternative candidates of the same sex that did not occupy the vacancy but were also regularly intruding in the study area. This shows that local site attachment is needed to fill a vacancy.

According to Heg, Ens, et al. (2000), attachment to one site is needed to build up local dominance, since a single bird cannot be dominant at all sites. For instance, the dominance of territory owners on the club decreased with distance to their territory. Bruinzeel and van de Pol (2004) suggested that opportunistic nonbreeders mainly acquire site familiarity through intrusion behavior and that this site familiarity (getting to know the territory owners and the neighbors), not local dominance, provides them with a competitive edge over nonbreeders with lower site familiarity.

The primary difference of opinion is whether explicit dominance relationships exist among nonbreeders intruding in an area or whether such relationships only develop once one of the nonbreeders has settled there. The main arguments of Bruinzeel and van de Pol (2004) are that they almost never observed aggressive behavior of intruding nonbreeders and that intruding nonbreeders were hardly ever together in a territory. Thus, in their view, intruding nonbreeders do not meet regularly enough to build up a dominance relationship at a given site. Although most intruders let themselves be chased quickly away, aggressive behavior among intruders not defending a territory on the mudflats and away from the club was regularly observed by Heg, Ens, et al. (2000). This included hovering ceremonies (Fig. 8.1D), where the piping display (Fig. 8.1C) is performed in flight by a small group of Oystercatchers. Heg, Ens, et al. (2000) provide evidence that such hovering ceremonies are ritualized contests over local dominance, above areas that are defended by territory owners not taking part in the hovering ceremony. The nonbreeders are “claiming” as it were who will take the territorial space below, when it becomes available. Such hovering ceremonies were not scored by Bruinzeel and van de Pol (2004). Furthermore, even though Bruinzeel and van de Pol (2004) collected over 1000 h of observation, this represents approximately 15% of the total time available for intrusions. Thus, short but important interactions among nonbreeders may have been missed.

Irrespective of whether or not local intruders derive their competitive edge over distant intruders from site familiarity only, or whether they have already established dominance relationships before settling, we regard this result as evidence for the despotic distribution. This contrasts with a recent review of habitat selection by [Piper \(2011\)](#), who concludes that both the ideal free and the ideal despotic distribution suffer from “familiarity blindness,” that is, they implicitly assume that animals settle on and switch territories regardless of past residency or the duration of that residency. Whereas this criticism is valid for the ideal free distribution, in our opinion it does not apply to the underlying concept of the ideal despotic distribution. The basic assumption in the ideal despotic distribution is that unsettled individuals have a lower fitness in a given habitat compared to settled individuals ([Fretwell & Lucas, 1969](#)). We interpret this fitness difference as resulting from settled individuals being highly familiar with a particular area (including the social neighborhood) and unsettled individuals being less familiar. This provides the territory owner with a competitive advantage over intruders, that is, residents win in contests against intruders because of an asymmetry in payoff rather than an asymmetry in resource-holding potential or an arbitrary convention, as shown in Great Tis *Parus major* ([Krebs, 1982](#)). In Oystercatchers, when 16 territory owners were temporarily removed for at most 2 days, they all regained their territory, albeit sometimes only after vicious fighting ([Heg, Ens, et al., 2000](#)). When 14 territory owners were held in captivity for 1–3 months, only two birds regained their territory after release ([Harris, 1970](#)).

So far, we have completely ignored a very basic aspect of Oystercatcher society, namely, that male and female of a breeding pair jointly defend territorial space ([Fig. 8.1C](#)). Settling may be preceded by the formation of a pair bond, or it may go hand in hand with pair-bond formation. The first is probably the case when a pair of nonbreeders conquers space from established breeders. In contrast, the second occurs when a nonbreeder either fills a vacancy—because a territory owner is without a mate as a result of death or desertion—or evicts the territory owner of its own sex ([Heg, Ens, et al., 2000](#)). Although it does not show (yet) in our queue models, the topics of mate choice and divorce are closely linked to the recruitment process. Basically, competition for territorial space and competition for mates is expected to go hand in hand, but how strongly so may depend on how much variation there is in the quality in mates compared to the quality in territorial space (e.g., if the competition for getting a territory is very high, animals might initially settle with a partner of any quality).



5. MATE CHOICE AND DIVORCE: COMPETING FOR MATES

What is the evidence that Oystercatchers compete for mates in addition to competing for territories of high quality? Oystercatchers are socially monogamous as well as sexually monogamous, so if there is competition, it should be over the genetic or phenotypic quality of the mate. In this, individuals might value partners in the same way, or it might depend on familiarity or compatibility with the partner (Ens, Choudhury, & Black, 1996). Van de Pol and Pettifor applied hierarchical variance component models to quantify patterns of phenotypic variance and covariance between several measures of reproductive performance and parental survival (van de Pol, 2006). They found that environmental sources of variation were most important, while differences between individuals explained only a relatively small part of the overall variation in these life-history traits. Adding a pair level to the analysis showed that differences between pairs explained a similar small part of the variation, but it was additional to individual components. Thus, there is evidence that individuals as well as pairs vary in quality. Below, we will investigate if these quality differences are sufficiently large to lead to active competition for particular mates.

We now know that social monogamy need not imply sexual monogamy, for example, Griffith, Owens, and Thuman (2002). Sexual behavior is easily observed in Oystercatchers and it is estimated that established pairs copulate about 700 times annually before the first eggs are laid (Heg et al., 1993). Only 5% of successful copulations by females that were observed were extra-pair copulations (EPCs). The proportion of EPCs dropped to even lower levels around the time of egg laying. Although Oystercatchers in their open habitat have nowhere to hide when they copulate, EPC rate may have been underestimated if such copulations occurred more secretly outside the territory, for which there is some evidence (Heg et al., 1993). However, DNA fingerprinting proved that extra-pair paternity was as rare as the behavioral observations suggest (Heg et al., 1993). In that study, only 1 out of 65 chicks was identified as having resulted from extra-pair paternity. The one extra-pair chick was from a female that in a later year switched to the putative father, suggesting that EPCs serve to locate or establish a bond with potential new mates (Heg et al., 1993). The sample size is admittedly small and it would certainly be worthwhile studying extra-pair paternity in more populations. However, the Oystercatcher fits the general pattern

among birds that extra-pair paternity is very low in long-lived species and in species where male contribution to parental care is necessary for successful reproduction (Griffith et al., 2002). Neither behavioral observations, nor the genetic analysis, provide any indication that egg dumping may occur (Heg et al., 1993).

Since males and females both provide parental care, we might expect them to profit from polygyny and polyandry, respectively (Davies, 1989). Whereas polyandry has been reported only once in Oystercatchers (Harris et al., 1987), polygyny is known to occur regularly, albeit at very low frequency (Briggs, 1984; Harris, 1967; Heg & Van Treuren, 1998). On average, 1.9% of the male bonds and 2.7% of female bonds were polygynous on Schiermonnikoog (Heg & Van Treuren, 1998). As expected, polygynous females experienced a significantly reduced reproductive success compared to monogamous females. Surprisingly, those males that mated polygynously also experienced a reduced reproductive success compared with monogamous males.

How can this be? Two types of polygyny occur in Oystercatchers with roughly equal frequency (Heg & Van Treuren, 1998). In *aggressive polygyny*, the two females are aggressive toward each other and each defends their part of the territory together with the male. It is a very common form of polygyny in many bird species (Slagsvold & Lifjeld, 1994). In *cooperative polygyny*, the two females are not aggressive to each other and the two females and the male defend the territory as a trio. In such cases, the females regularly copulate with the male and with each other, adopting both the male and the female position. The two females lay their eggs in a single nest. The three birds share the incubation and the brooding and feeding of the chicks. Irrespective of the type of polygyny, both male and female Oystercatchers have reduced reproductive success compared with monogamously mated birds. In aggressive polygyny, females continued to behave aggressively toward each other, and as the male only helped the first female to lay with incubating and defending the clutch, the clutch of the second female was often left unguarded and suffered from an increased risk of predation. In cooperative polygyny, the females successfully synchronized egg laying and all three birds incubated the eggs. But the combined clutch size usually exceeded the maximum clutch size of four eggs for monogamous pairs, and the birds in a trio had difficulty properly incubating the large clutches (Fig. 8.7). As a result, hatching success was significantly reduced.

Why does polygyny occur if neither male nor females profit in terms of reproductive success? Heg and Van Treuren (1998) tested several

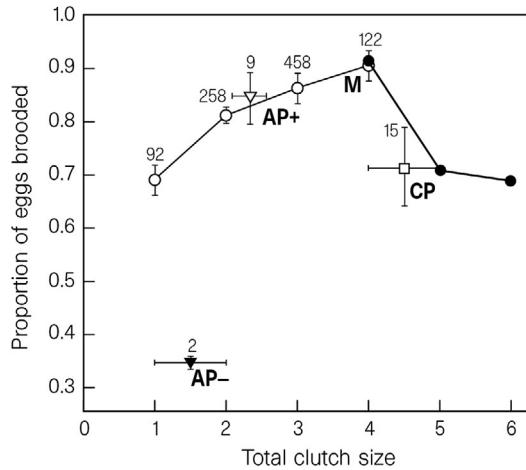


Figure 8.7 Mean proportion of brooded eggs for different clutch sizes, separated for different types of pairs and trios: monogamous pairs (M, open circles), aggressive polygynous trios with male assistance (AP+, open triangle) and without male assistance (AP–, filled triangle), cooperative polygynous trios (CP, open square; clutches of both females were combined, because they were brooded in one nest), and experimental monogamous nests containing copper eggs (filled circles), providing independent evidence that Oystercatchers have difficulty incubating clutches exceeding four eggs. Sample sizes (number of nests) are indicated in the graph. From [Heg and Van Treuren \(1998\)](#)—reproduced with permission.

hypotheses. There was no evidence that polygynous females were more closely related than randomly paired females, so kin selection does not seem to play a role. There was no evidence either that polygynous females survived better or that polygyny was more likely in HQ territories compared to LQ territories. The most likely explanation is that the females benefited through the increased probability of obtaining a monogamous breeding position in later years. Their chances were certainly much better compared to the average nonbreeder. Nearly always, polygyny resulted from a “failed” attempt at usurpation, that is, instead of one female successfully evicting the other female from the territory, a stalemate was reached. Stalemates have also been described for the Dunnock *Prunella modularis* when the alpha male is unable to drive the beta male off to claim polygyny, and neither female can evict the other to claim polyandry, so that polygynandry is the end result ([Davies, 1992](#)). However, stalemate is a description, not an explanation. In the case of Oystercatchers, the main question is why the male did not take sides with one of the females, helping her to chase off the other female. This brings us to the topic of divorce.

Usually, Oystercatchers return to the same territory and pair up with the old mate following the intervening winter. Sometimes, a *divorce* occurs, that is, both partners are alive, yet do not breed together. The average annual divorce rate is $\sim 8\%$ (Harris et al., 1987; Heg et al., 2003).

A large number of hypotheses have been proposed to account for divorce in birds (Black, 1996; Choudhury, 1995). These can be grouped into four distinct hypotheses on the ultimate causation (Heg et al., 2003): (1) the *incompatibility hypothesis* (Coulson, 1966) proposes that pairs consisting of incompatible partners have reduced reproductive success and both members may initiate divorce and benefit from it, (2) the *better option hypothesis* (Ens, Safriel, & Harris, 1993) proposes that a pair member should initiate divorce (and profit) at the expense of the mate, when the expected benefits of breeding with the new mate outweigh the costs of changing mate, (3) the *forced divorce hypothesis* proposes that a new bird usurps the breeding position of one of the pair members, in which case neither pair member may benefit (Taborsky & Taborsky, 1999), (4) the *bad luck hypothesis* proposes that an external event other than usurpation destroys the basis of the partnership leading to divorce, like partners losing track of each other on migration (Owen, Black, & Liber, 1988), or the destruction of a nesting burrow through a land slide.

Reviews of divorce show that the phenomenon is very often studied without observing the behavior of the divorcing birds in great detail (Ens, Choudhury, et al., 1996; Rowley, 1983). However, without such behavioral observations, it is very difficult to arrive at meaningful interpretations. In Oystercatchers, divorce occurs through (1) desertion, where one of the pair leaves the territory and mate, often pairing up with a neighboring territory owner, or (2) usurpation, where one of the pair is aggressively driven off the territory by a usurper. Thus, there are (1) individuals that initiate a divorce by deserting their mate and (2) individuals that are clearly victims, being either deserted or evicted. There are also (3) individuals whose role is not completely clear and appear just to be “bystanders.” Desertions were usually initiated by females: 79% of 56 cases observed by Heg et al. (2003). Similarly, females were also the most likely victim of usurpation (by another female): again 79% of 56 cases observed (Heg et al., 2003).

We would expect initiators to benefit and victims to suffer from a divorce in terms of fitness (Ens et al., 1993) and the evidence suggests that this is indeed the case (Heg et al., 2003). The fitness prospects of victims of divorce are reduced compared to the fitness prospects of individuals that initiated a divorce. However, if we compare the fitness prospects of divorced birds to

the prospects of birds that did not divorce, we only find an improvement for the birds that deserted from a LQ territory. This is due to the birds that succeeded in moving from a LQ territory to a HQ territory. In contrast, birds that desert from a HQ territory do worse than birds in HQ territories that do not change mate. Only 10 females deserted from a HQ territory during the study period: five moved to another HQ territory, four moved to a LQ territory, and one even became a nonbreeder. We believe that the explanation for the apparent lack of improvement of females deserting from HQ territories lies in the fact that these calculations are based on average fitness associated with the three social positions. They do not take account of the quality of the mate that is deserted and the quality of the new mate. Two anecdotal observations lead us to hypothesize that females in HQ territories that desert their mate, may sometimes be leaving a “sinking ship” (Heg et al., 1993). In both cases, the territory declined in size over a series of years, suggesting, though not proving, poor performance of the male. Over the years, both females started to copulate more and more with alternative mates, which we interpret as searching for a new mate, and in one case the female actually switched to that mate in a later year.

Compared to birds that did not divorce, bystanders seemed neither to benefit nor to suffer from their mate being expelled from the territory. The role of the bystander seems passive, but repeated intrusions are common in Oystercatchers and a cooperative pair can easily displace a single intruder. Very often, males will chase intruding females from the territory, even when these solicit copulations (Ens, 1992; Heg et al., 1993). When the usurper successfully evicted a pair member, the bystander decided not to assist its mate in a joint effort to deter the intruder. In this sense, bystanders have a decisive role. The benefits to the bystander are not clear to us. Allowing your mate to be harassed by an aggressive intruder may also lead to a stalemate and polygyny, as we described above. So far, we have not been able to identify any benefits of polygyny to a bystanding male.

Divorce is clearly a minority strategy. Following winter, when male and female are generally separated and away from the territory, most Oystercatchers reunite in spring with their mate of the previous year on their territory. Many studies on long-term pair bonds report that the performance of breeding pairs improves with the number of years they have been together—see reviews by Fowler (1995) and Black (1996). Lumping data on many breeding pairs, these studies show a positive correlation between reproductive performance and pair-bond duration. However, such a correlation could also be due to an improvement of reproduction with age or

breeding experience of males and/or females, or to poorly performing pairs being short-lived and not necessarily to the lengthening pair-bond *per se* (Ens, Choudhury, et al., 1996).

Data from Oystercatchers are available to explore these possibilities. Van de Pol, Heg, et al. (2006) analyzed a data set on 233 females, 230 males, and 370 pairs measured in 21 different years on Schiermonnikoog. They took great care in statistically correcting for all the confounding factors mentioned above and found a significant effect of pair-bond duration on laying date, egg survival, and fledgling production (Fig. 8.8), but not on the probability of owning a HQ territory, clutch size, or chick survival. Remarkably, the relationship was quadratic in all cases, that is, performance first increased and then declined. Evidence that this is indeed a causal relationship was obtained through a removal experiment, forcing the remaining male or female to take a new mate and resetting the duration of the pair bond for the experimentally widowed bird to 1. Regrettably, only the impact on laying date could be analyzed, because in the years after the experiment, the saltmarsh flooded during the incubation phase, severely reducing the already small sample sizes for the other reproductive parameters. The results confirmed the prediction that birds from pairs with intermediate pair duration, when performance of pairs was highest, suffered the greatest setback from changing mate. It must be admitted, though, that the observed effect was much greater than predicted from the statistical analysis of natural pair durations and differed

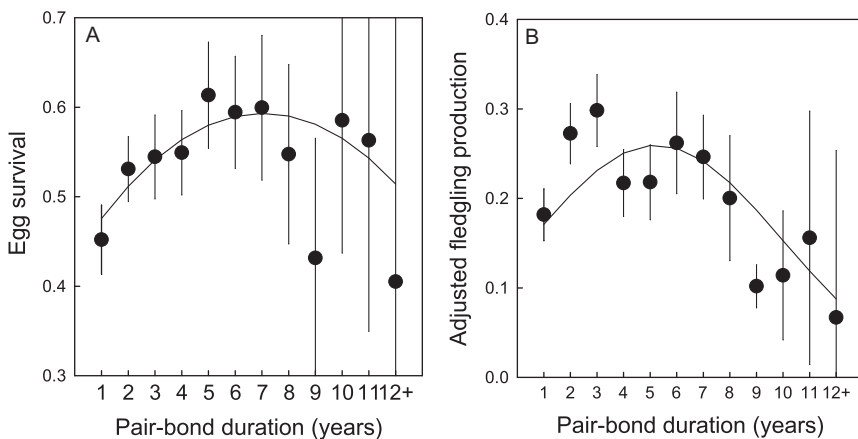


Figure 8.8 (A) Egg survival and (B) fledgling production (adjusted for territory quality, breeding experience of both birds, and random effects due to year, male and female) as a function of pair-bond duration. From van de Pol, Heg, et al. (2006).

between males and females. Although labor intensive, it would be clearly worthwhile to repeat the experiment.

At present, we can only speculate on the causes of the initial improvement of performance and subsequent decline with the duration of the pair bond. One explanation is that the birds must learn how to cooperate effectively in various behaviors, like reducing the duration of prelaying activities (Chardine, 1987), more synchronous initiation of nest-building (Griggio & Hoi, 2011), proper coordination in taking incubation turns (Brooke, 1978), jointly attending the eggs at hatching (Cooke, Bousfield, & Sadura, 1981), sharing brooding and feeding the chicks more equally (Fowler, 1995), or establishing a competitively successful behavioral routine as a pair in the flock (Black, 2001). However, such learning cannot explain the subsequent decline in reproductive performance.

An alternative explanation starts from the expected conflict of interest between male and female on how much each should invest in cooperative enterprises, such as territory defense and parental care (Chase, 1980). It has been suggested that an evolutionarily stable strategy in such cases consists of gradually over the years raising the stakes, that is, increasing investment (in feeding the chicks for instance) if the partner has equalled or bettered investment (Roberts & Sherratt, 1998). Again, it is not clear how this would lead to a decline in performance in later years.

A third explanation for the low success in the early years of the pair bond is that one or both mates are not fully committed to reproduction, but are also engaged in mate searching. We interpret EPCs as mate searching (see above), and it is indeed the case that EPC rates were higher for short-lived pair bonds and in the early years of long-lived pair bonds for both male and female (Fig. 8.9). Furthermore, EPC rates increased again for long pair-bond durations, which fits with the decline in reproductive success (Fig. 8.8). Thus, only changes in mate searching with pair-bond duration can explain both the increase and subsequent decline in reproductive success with pair-bond duration.

We can only speculate why partners that have been together for 10 years or even longer would suddenly start searching for a new mate. Perhaps, a difference in quality develops between the mates that at some point reaches a level where searching a new mate becomes profitable for either male and/or female. We previously described anecdotal observations that suggest that females may sometimes attempt to leave a “sinking ship.” Furthermore, whereas the probability of owning a HQ territory is not linked to pair-bond duration, it is linked to breeding experience in both males and females (van

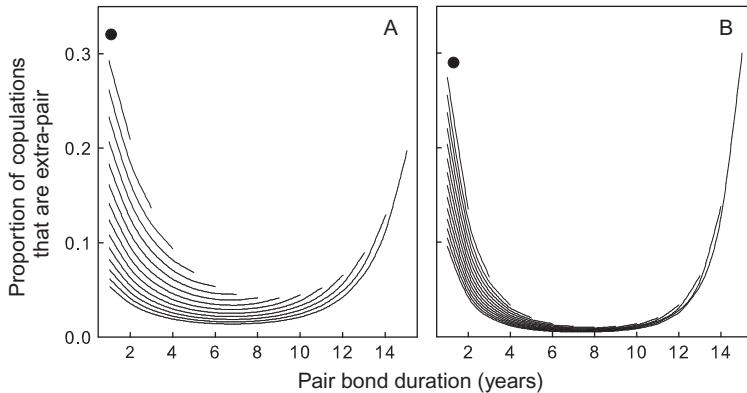


Figure 8.9 Index of extra-pair copulations (EPCs) during the pair bond for pairs that vary in how long they stayed together, for (A) males and (B) females. Depicted are the best-fitting regression models, using the methodology developed by [van de Pol and Verhulst \(2006\)](#) to separate within-pair from between-pair effects. From [van de Pol \(2006\)](#).

[de Pol, Heg, et al., 2006](#)). The probability initially increases with breeding experience for both sexes ([Fig. 8.10](#)). Whereas the probability peaks for males at around 8 years of breeding experience and strongly declines thereafter, it peaks for females at around 15 years of breeding experience and the evidence for a subsequent decline is weak.

On the basis of the above, we hypothesize the following:

1. Mate searching (through EPCs) is incompatible with effective cooperation in territory defense and reproduction, leading to a fundamental trade-off governing career decisions as suggested by [Heg, Ens, et al. \(2000\)](#).
2. The costs and benefits of this trade-off may differ between males and females, leading to different career strategies. This includes a greater propensity on the part of females, compared to males, to desert their mate and move territory ([Ens et al., 1993; Heg et al., 2003](#)).
3. The career strategy of young nonbreeding females may involve the decision to settle at a relatively early age in a poor quality territory and/or with a poor quality mate and/or as part of a polygynous trio, because a position as a settled breeder is a good vantage point for improvement.



6. SURVIVING THE NONBREEDING SEASON

To discuss career decisions during the nonbreeding season, we must first identify the resources that Oystercatchers are competing for at that time

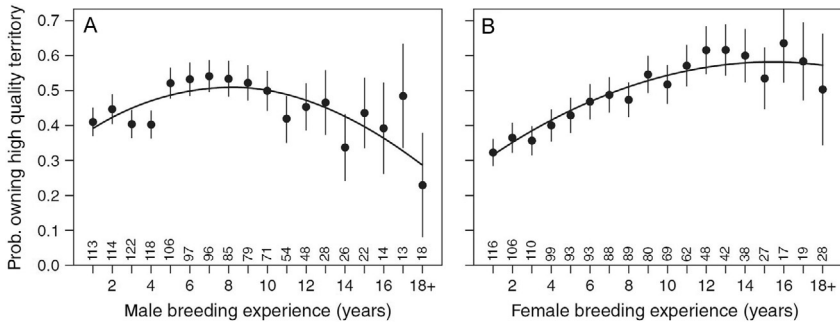


Figure 8.10 Probability of owning a high-quality territory as a function of pair-bond duration for (A) males and (B) females. From [van de Pol, Heg, et al. \(2006\)](#).

of year. We then describe how Oystercatchers compete for these resources and what it takes to become a successful competitor.

6.1. What are Oystercatchers Competing for During Winter?

In many bird species, competition during the nonbreeding season is for food ([Newton, 1998](#)) and Oystercatchers are no exception. There is good evidence that Oystercatchers sometimes have difficulty in meeting their energy requirements during the nonbreeding season ([Goss-Custard, 1996](#)). On the Wash, for example, as many as 20% of adult Oystercatchers starved to death in winters when their shellfish food stocks were extremely low, whereas 99% of birds survived in winters with abundant shellfish stocks ([Atkinson et al., 2003](#)). On the Exe estuary, mortality increased among wintering mussel-eating adult Oystercatchers when feeding density on the mussel beds increased, with the mortality rate being particularly high in winters with inclement weather ([Durell, Goss-Custard, Clarke, & McGrorty, 2000](#); [Durell, Goss-Custard, Stillman, & West, 2001](#)).

Oystercatchers compete singly for this limiting resource, as pair bonds are not maintained outside the breeding season, and young birds winter independently of their parents. During low tide, the birds feed on exposed intertidal mud flats, mainly preying on shellfish ([Hulscher, 1996](#)). During high tide, the birds may roost in flocks in the vicinity of the feeding grounds or continue feeding in terrestrial habitats where, for example, they eat earthworms. It may appear as if, at low tide, the birds also roam around in flocks, but this is not the case. Instead, high densities occur because the birds aggregate on good feeding areas, most often shellfish beds where prey occurs in extremely high densities ([Ens & Cayford, 1996](#)).

Predictability of the food supply between seasons depends on growth, survival, and recruitment of the shellfish. Although the life span of Oystercatchers exceeds the life span of their shellfish prey, the life span of the shellfish prey is usually sufficiently long for shellfish beds to persist for several years. Persistence is increased when new shellfish recruit into existing beds during summer. This process allows mussel beds to persist for decades, that is, the life span of mussel beds may far exceed the average life span of Oystercatchers. This stability of the food supply may explain why adult Oystercatchers are extremely faithful to their wintering area, to which they return year after year.

6.2. Competition for Food: Depletion and/or Interference

It is important to know how Oystercatchers compete for food during the winter. Two main mechanisms have been proposed: *depletion* and *interference* (Goss-Custard, 1980). Under depletion, which can also be referred to as exploitation competition, the food supply is reduced through consumption by Oystercatchers to such an extent that the Oystercatchers have difficulty finding food at the end of winter at a sufficient rate to match their rate of expenditure of energy. In Oystercatchers, this is a long-term process because, not only does it take months for the food supply to be depleted, but the restoration of the food supply requires a summer period during which the shellfish grow and new recruits settle. Under interference competition, on the other hand, the intake rate of food is reduced due to the immediate presence of conspecifics. The negative effect of interference is reversible over a very short time scale: when the conspecifics move away, intake rate increases again. And, of course interference-prone individuals can reduce its impact by moving away themselves.

Interference and depletion are not mutually exclusive mechanisms of competition. Oystercatchers measurably deplete shellfish beds over the winter, with prey depletion ranging widely, the amount actually removed by the birds being likely to depend on the size of the initial stocks when the birds arrive in autumn. On the Wash, for example, Oystercatchers probably removed up to 58% of the available shellfish stocks in winters when shellfish were scarce but only up to 14% in winters when shellfish were abundant (Stillman et al., 2003). In the Exe estuary, Oystercatchers feeding on mussel beds removed over the winter 12% of mussels in the size range from which they obtained most of their consumption (Goss-Custard et al., 2001). However, the functional response, describing the relationship between capture

rate and prey density, of Oystercatchers feeding on mussels is very flat over a wide range of mussel densities and only drops to low levels at very low mussel densities (Goss-Custard et al., 2006). As a result, the reduction in intake rate leading to starvation of some individuals at the end of winter is primarily due to the loss of condition of the mussels and interference (Goss-Custard et al., 2001). As the population size increases, the contribution that depletion makes to the rate of starvation increases, but only contributes 15% even when the population size is over five times that which has ever been recorded on the estuary. In contrast, the loss of mussel flesh over the winter makes a major contribution to Oystercatcher mortality over the whole range of population sizes (Fig. 8.11). The evidence therefore indicates that it is interference and loss of mussel flesh, and not depletion that is the main reason why Oystercatchers starve on the Exe.

There is ample evidence for interference among Oystercatchers feeding on mussels in the estuary of the Exe and elsewhere (Ens & Cayford, 1996). In contrast, the majority of field studies on Oystercatchers feeding on cockle beds failed to find evidence for interference (Ens, Merck, Smit, & Bunscooke, 1996; Goss-Custard, 1977; Norris & Johnstone, 1998; Sutherland & Koene, 1982), the exception being a study in the Baie de Somme (Triplet, Stillman, & Goss-Custard, 1999).

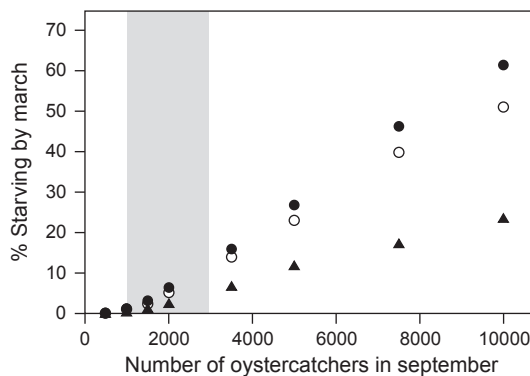


Figure 8.11 The density-dependent function obtained from the behavior-based individual's model of the Exe estuary for an Oystercatcher population with depletion allowed (closed circle) or not allowed (open circle) to occur. The closed triangles show the function obtained when mussels do not lose flesh content over the winter and depletion is allowed. The means of three simulations are shown. The gray area indicates the present-day range in population size. *Reproduced with permission from Goss-Custard et al. (2001).*

The frequent absence in field studies of a negative correlation between the intake rate of food and the density of conspecifics in Oystercatchers eating cockles does not mean, however, that interference seldom occurs among cockle-feeding Oystercatchers (Triplet et al., 1999). It is likely though that Oystercatchers on mussel beds suffer more from interference (making it more easy to detect) than Oystercatchers on cockle beds. This is because, usually, the time taken by an Oystercatcher to open a mussel and to extract its flesh is much greater than the time taken to handle and consume a cockle. The duration of this “handling time” is one of the main factors determining whether interference competition mediated by prey-stealing occurs and how strong the interference will be (Stillman, Goss-Custard, & Caldow, 1997, Stillman et al., 2002).

Thus, we have evidence for interference and a body of theory predicting interference competition, but how good are our quantitative estimates of interference parameters? With a few exceptions, shorebird studies have relied on nonexperimental field data to quantify interference (Vahl, 2007). As in all studies based on correlation, negative correlations between intake rate and forager density may not reflect interference, but instead result wholly or partly from an unidentified third factor that covaried with intake rate and bird density. In studies on Oystercatchers, variation in Oystercatcher density is almost always obtained through the influence of the tidal cycle; with higher bird densities occurring at higher water levels (Ens & Cayford, 1996). Many factors covary with stage of the tide (Rutten, Oosterbeek, van der Meer, Verhulst, & Ens, 2010). One solution to this perennial problem in field studies has been to employ statistical models to control for confounding factors that are known or suspected to influence intake rate, for example, Goss-Custard, Clarke, and Durell (1984) and Goss-Custard and Durell (1987a).

The best way to manipulate the density of foragers is to do so in a controlled experiment. So far, two such studies have been carried out on Oystercatchers. Rutten, Oosterbeek, Verhulst, and Ens (2010) experimentally studied interference in the wild on two cockle beds that differed in quality. They increased forager density by chasing birds from one cockle bed, leaving the other cockle bed as the only nearby alternative. The density increase was most pronounced on the cockle bed with the poorer food stocks and where the initial feeding densities had been lower compared to the rich cockle bed. Oystercatchers that were normally present on this poor mussel bed suffered a significant decline in intake rate when bird density was experimentally increased, providing evidence of interference. The

incoming birds that had been displaced from their home bed experienced an even stronger reduction in intake rate compared to the residents and compared to their intake rate on their “home bed,” probably partly due to their unfamiliarity with the poorer cockle bed.

In the field experiment, the Oystercatchers that were disturbed from their cockle bed had the opportunity to leave the study area, instead of moving to the other cockle bed to increase bird density there. Many did, so that Oystercatcher densities were not increased as much as hoped for. This was especially the case on the rich bed (Rutten, Oosterbeek, Verhulst, et al., 2010). Cages are the only means to prevent birds from moving elsewhere. In the second experimental study, Rutten, Oosterbeek, van der Meer, et al. (2010) manipulated the feeding density of captive Oystercatchers foraging on cockles in a facility that mimicked natural feeding conditions as closely as possible. In the high-density experiment, the intake rate was on average reduced by 36% compared to the interference-free intake rate (IFIR) (Fig. 8.12). As had been found among mussel feeders on the Exe estuary, and as would be predicted on theoretical grounds, the intake rate of subordinates was more strongly reduced than the intake rate of dominants (45% vs. 25%). It was clear that birds actively avoided each other, possibly to avoid kleptoparasitism, that is, food stealing. Very likely, it was the subdominant avoiding the dominant, but a more detailed description of the search path would be needed to confirm this.

Thus, the results of the experiments are consistent with the idea that interference does occur among cockle-feeding Oystercatchers, but in both experimental studies interference was stronger than was predicted by the IBM developed by Stillman et al. (2002). For the cage experiment, we could compare predictions to observations for the dominant and the subdominant. In the case of the field experiment, we could not distinguish between dominant and subdominant birds and used the analytical approximation derived for the “average” Oystercatcher by Rappoldt, Stillman, and Ens (2010) to arrive at a prediction. There are several possible explanations for this discrepancy. Under natural conditions, birds may have more options to avoid the negative consequences of interference. They can stop feeding (Ens & Cayford, 1996; Zwarts & Drent, 1981) or move elsewhere. Indeed, chasing Oystercatchers to an undisturbed cockle bed to increase feeding density was much less successful than anticipated. At the end of a tidal cycle with disturbance, for example, densities on the undisturbed bed had returned to normal, even though the experimental disturbance continued throughout the entire low-water period (Rutten, Oosterbeek, Verhulst, et al., 2010).

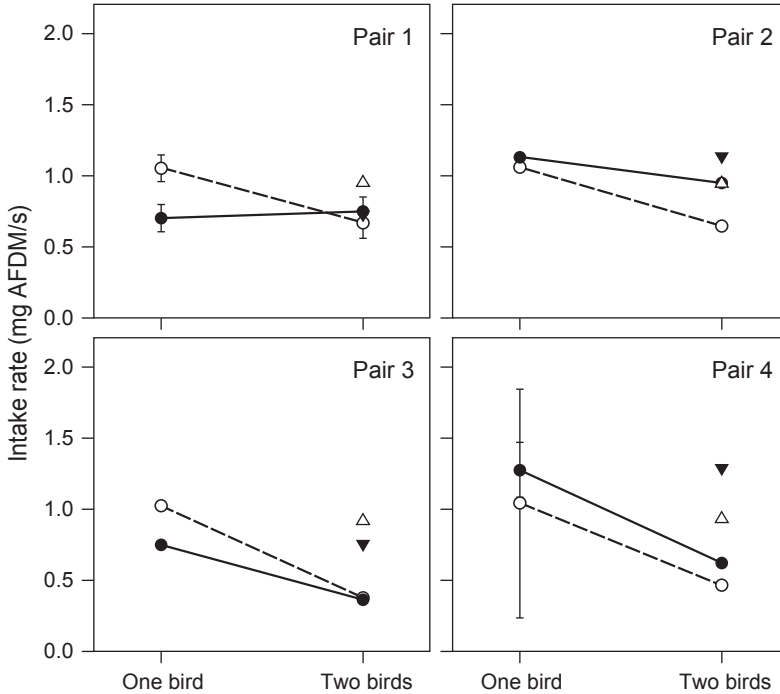


Figure 8.12 Experimental evidence for interference in captive Oystercatchers, showing intake rate (mg AFDM/s \pm SE) of birds under different feeding densities. Dominants are represented by solid lines and solid markers. Subordinates are represented by dashed lines and open markers. Dots represent observed data while triangles indicate predictions according to the model described in [Stillman et al. \(2002\)](#). From [Rutten, Oosterbeek, van der Meer, et al. \(2010\)](#).

Taken together, the findings of the observational studies on the Exe estuary and elsewhere and the experimental studies in both the field and in cages do suggest that interference occurs in both mussel-feeding and cockle-feeding Oystercatchers. No single observation or experiment in any sense decisively proves its existence but most of the findings point in that direction, as do the studies on the mechanism of interference discussed below.

6.3. The Mechanism(s) of Interference

Interference may be caused by a variety of mechanisms: (1) by high densities of foragers attracting interspecific kleptoparasites which steal an increasing number of prey items ([Swennen, 1990](#); [Zwarts & Drent, 1981](#)), (2) by more prey being lost to intraspecific kleptoparasitism as forager density rises ([Ens & Goss-Custard, 1984](#)), (3) by an increase in the amount of time lost in

aggressive encounters as the density of competitors increases (Ruxton, Guerney, & de Roos, 1992), (4) by a decrease in searching efficiency through avoidance behavior or disturbance of the search path, recently referred to as “cryptic interference” (Bijleveld, Folmer, & Piersma, 2012; Gyimesi, Stillman, & Nolet, 2010), (5) by displacement from good feeding spots within the feeding area at large (Leopold, Swennen, & de Bruijn, 1989; Vahl, van der Meer, Weissing, van Dulleman, & Piersma, 2005), (6) by depletion of a small attackable fraction of the prey (Goss-Custard, 1980), (7) by prey depression (Charnov, Orians, & Hyatt, 1976; Goss-Custard, 1970; Stillman, Goss-Custard, & Alexander, 2000). These mechanisms are not mutually exclusive, so the challenge consists of identifying the extent to which the various mechanisms contribute to interference among foraging Oystercatchers.

Though Oystercatchers sometimes lose a considerable portion of their food to robbing gulls and crows, this loss does not increase with an increase in Oystercatcher density, so interspecific kleptoparasitism as a cause of interference can be ruled out (Ens & Cayford, 1996).

Oystercatchers regularly steal food from each other (Goss-Custard, Durell, & Ens, 1982) and it is the dominants that steal from the subdominants (Ens & Goss-Custard, 1984). Food stealing also increases with the density of conspecifics and clearly depresses the intake rate of the subdominant birds (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1988). However, dominants gain the food, so it is conceivable that on average, intake rate does not change with Oystercatcher density. The fact that it does decline is due to (1) some kleptoparasitized mussels being lost in the process, that is, the subdominant losing the mussel, but the dominant failing to locate or open it, (2) more time lost in overt aggression, and especially (3) a strong decline in capture rate of prey (Ens & Goss-Custard, 1984). The most likely explanation for the decline in capture rate is avoidance behavior, for which there is clear evidence in the spacing behavior of foraging Oystercatchers (Moody, Thompson, DeBruijn, Houston, & Goss-Custard, 1997; Rutten, Oosterbeek, van der Meer, et al., 2010; Vines, 1980). Subdominants with a mussel also increase their scanning behavior during handling and are more likely to pick it up and move to a safe place to continue handling as forager density rises, indicating their increasing wariness (Boates, 1988; Cayford, 1988).

At present, it is not possible to rule out the possibility that prey depression contributes to interference in Oystercatchers (Rutten, Oosterbeek, van der Meer, et al., 2010), but the primary mechanism seems to be the stealing of food (and possibly good feeding spots) and associated adaptive

behaviors like avoidance, in a situation where dominance relationships are clearly defined. This calls for models that consider the adaptive value of attacking a conspecific for prey (or feeding spot) and the adaptive value of avoidance behavior.

For species that feed in flocks, it has been postulated that the strategies of “producing” (i.e., finding food) and “scrounging” (i.e., food stealing) were incompatible, so that the profitability of adopting a particular strategy depended on the relative frequency of their occurrence in the population, making game theory the appropriate tool for theoretical analysis (Barnard & Sibly, 1981; Barta & Giraldeau, 1998; Broom & Ruxton, 1998; Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991). There is no doubt that game theory must be invoked, but according to Ens, Esselink, and Zwartz (1990), game theory should address the question of how stable dominance hierarchies can evolve where dominants steal food from subdominants. In a review of social dominance in birds, Piper (1997) lists several hypotheses why subordinates tolerate their low status instead of fighting to improve it. Within the context of a stable dominance hierarchy, robbing can be treated as a problem of prey choice (Charnov, 1976), where dominants should initiate a kleptoparasitic attack against a subdominant with prey if they can expect to increase their intake rate by doing so (Dunbrack, 1979; Ens et al., 1990; Stillman et al., 1997; Thompson, 1986).

The probability that it will be profitable for a dominant to initiate a kleptoparasitic attack against a subdominant handling prey will increase with (1) decreasing distance to the victim handling prey, as it will increase the probability of a surprise attack, (2) increasing size of the prey, (3) increasing handling time of the prey, (4) decreasing possibilities of the victim to transport the prey, and (5) decreasing capture rate of the dominant while searching its own food. A behavior-based simulation model incorporating several of these relationships correctly predicted the occurrence of kleptoparasitism (and hence interference) in 11 of 13 shorebird-prey systems (Stillman et al., 1997). The model proved highly sensitive to the encounter distance, that is, the distance within which individuals initiated an attack for prey or initiated avoidance behavior (Stillman et al., 1997, 2002, Stillman, Caldow, Goss-Custard, & Alexander, 2000). This inspired Rappoldt et al. (2010) to construct a simple model containing three parameters: attack distance, the density of foraging animals, and the behavioral aspects of interference through kleptoparasitism. The model predicts that the average intake rate will decrease exponentially with animal density and that a measure of the strength of interference depends on attack distance squared.

Is there a minimum density below which no interference occurs? According to [Stillman, Goss-Custard, Clarke, and Durell \(1996\)](#), the threshold density is not related to dominance, but is related to feeding method. A behavior-based simulation model does not predict a sharp cut-off point below which interference does not occur, but shows that for Oystercatchers the impact on intake rate is generally negligible below 150 competitors/ha ([Stillman et al., 1997, 2002, Stillman, Caldow, Goss-Custard, & Alexander, 2000](#)).

6.4. Feeding Specialization and Competition

So far, we have ignored the well-known fact that individual Oystercatchers differ in feeding specialization ([Sutherland, Ens, Goss-Custard, & Hulscher, 1996](#)). Yet, feeding specialization undoubtedly influences competition for food (and *vice versa*). Individuals that feed on different prey do not reduce each other's food supply. Furthermore, susceptibility to interference may depend on feeding specialization as well.

[Partridge and Green \(1985\)](#) and [Durell \(2000\)](#) distinguish three main mechanisms leading to specialization: (1) different prey may occur in different patches, (2) individuals may differ in phenotype (morphological differences, individually acquired skills, differences in social status), and (3) frequency-dependent selection. We agree with the assessment of the first mechanism that “an obvious and almost trivial explanation for differences between individuals in the prey species they take and the feeding techniques they use is that they occupy different habitats” ([Sutherland et al., 1996](#)). But clearly this begs the question as to which comes first—the habitat choice or the specialization. Furthermore, these mechanisms refer to different levels of explanation. We therefore follow [Araujo, Bolnick, and Layman \(2011\)](#), who derive three general scenarios from foraging theory ([Stephens & Krebs, 1986](#)) why co-occurring individuals might consume different resources:

The first scenario suggests that individuals may have different optimal diets due to different rank preferences, that is, they rank prey differently. This could be linked to phenotypic variation (genetic or environmental) in ability to detect, capture, handle, or digest alternative prey. In Oystercatchers, there is a clear difference between the sexes ([Fig. 8.13](#)). Females have longer and thinner bills on average, so they can probe for prey that is buried deeper. The bill of the male is better suited to exert force and therefore to open hard-shelled prey ([Hulscher & Ens, 1992](#)). Indeed, males more often feed on thick-shelled bivalves, which entails a real risk of bill damage

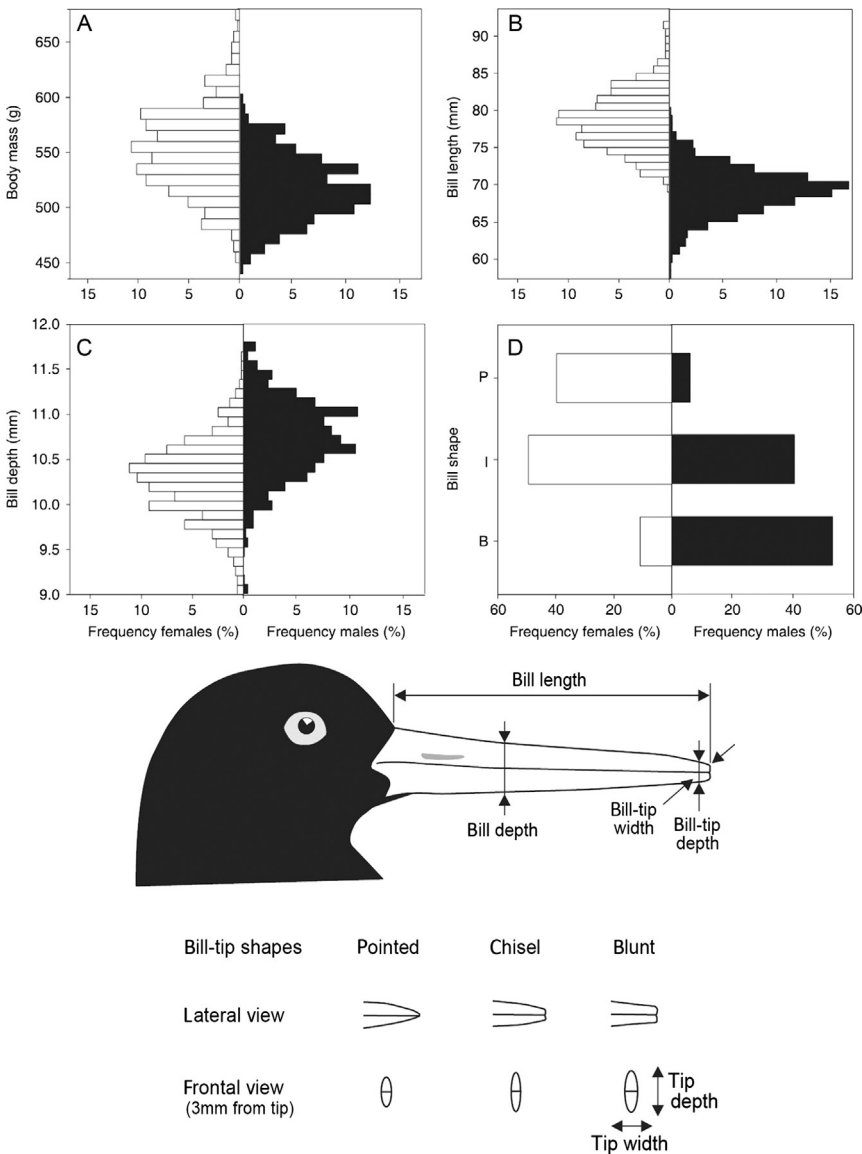


Figure 8.13 Frequency distributions of biometric measurements of females (white) and males (black) that were used for sex determination: (A) body mass, (B) bill length, (C) bill depth, and (D) bill shape (P, pointed; I, intermediate; B, blunt). Measurement and qualification of bill morphology are indicated on the right. Data from birds caught on Schiermonnikoog in the months of March–August from 1983 to 2006 (N = 1487). From *van de Pol et al. (2008, 2009)*.

when prey are large (Rutten, Oosterbeek, Ens, & Verhulst, 2006), while females more often feed on worms and buried bivalves (Durell, Goss-Custard, & Caldow, 1993; Hulscher & Ens, 1992). Furthermore, females are more likely to stab or open prey *in situ*, whereas males are more likely to hammer prey (Durell et al., 1993; Hulscher, Alting, Bunscoke, Ens, & Heg, 1996).

Phenotypes are also known to vary in the short term. Oystercatcher bills experience heavy wear on the tip of the bill, so that the shape of the bill tip adapts to prey type and the way it is handled (Hulscher, 1985; Swennen, de Bruijn, Duiven, Leopold, & Marteijn, 1983). Males more often have a blunt bill, because they hammer shellfish, whereas females more often have a pointed bill, because they probe for deep prey (Fig. 8.13). Because the bill becomes adapted to the particular way of searching and handling prey, this leads to a cost of switching (Hulscher & Ens, 1991; Swennen et al., 1983). The fact that different prey types occur in different habitats need not lead to different rank preferences among individuals, but it will reinforce emerging differences in rank preferences related to bill tip shape. Prey may also occur in the same habitat, but differences in crypticity may make it impossible to search for both prey types simultaneously (Ens, Bunscoke, et al., 1996). Again, this need not lead to different rank preferences among individuals, but it will reinforce emerging differences in rank preferences related to bill tip shape.

The second scenario suggests that individuals may have different optimal diets because they use different optimization criteria. These could be related to differences in physiological requirements or the state of the individual. For instance, adults preparing for migration in late winter might use different optimization criteria compared to nonmigratory young birds, but nothing is known to this effect.

The third scenario suggests that individuals may differ in their ability to attain their optimal diet. This clearly applies to young Oystercatchers which are generally subdominant to old Oystercatchers (Ens & Cayford, 1996). Juveniles are displaced from mussel beds by adults in autumn (Goss-Custard, Durell, McGrorty, & Reading, 1982). The displaced birds moved to less-preferred mussel beds or started feeding on mudflats and/or in the fields (Goss-Custard & Durell, 1983). This subdominance, along with their softer bills, may explain why juveniles feed more often on worms (Goss-Custard & Durell, 1983; Triplet, 1989) compared to adults. As a result, juveniles have higher parasite loads (Goater, Goss-Custard, & Kennedy, 1995), as they are more likely to attract parasites in upshore areas and in

the fields (Goss-Custard et al., 1996a). To avoid being robbed, juveniles take smaller prey size classes in autumn of mussels (Goss-Custard & Durell, 1987a) and ragworm *Hediste diversicolor* (Durell, Goss-Custard, & PerezHurtado, 1996) and, when feeding on mussels, juveniles do not use the hammering technique (Goss-Custard & Durell, 1987a). There is clear evidence that Oystercatchers of equal dominance suffer more from interference when they hammer mussels than when they stab mussels (Goss-Custard & Durell, 1988): at low densities, hammerers have on average higher intake rates than stabbers, but this difference is reduced as bird density increases.

Frequency dependence is a plausible mechanism to contribute to the maintenance of feeding specializations in the population (Partridge & Green, 1985) but there is no evidence for this. The different feeding strategies do not have equal payoffs, irrespective of whether the payoff is measured in terms of intake rate, ability to maintain energy balance, or survival over the winter (Sutherland et al., 1996). A synthesis combining many different data sets collected over the years 1976–1991 in the estuary of the Exe confirmed that mussel hammerers outperformed mussel stabbers, which outperformed birds specializing on clams and worms with regard to condition, tendency to engage in supplemental feeding, and survival (Durell, Goss-Custard, Caldow, Malcolm, & Osborn, 2001); see Table 8.1. Remarkably, a follow-up study in the Exe from 2002–2006 found no significant differences in summer, winter, or annual survival between birds of different feeding specialization (Durell, 2007). This was due to an increase in the survival of clam and worm feeders and mussel stabbers during winter, possibly

Table 8.1 Body Condition (the Log of the Ratio of the Body Weight Observed to the Body Weight Predicted from Wing Length, Age, Month, and Time Since Capture), the Propensity to Engage in Supplementary Feeding, and Annual Winter Mortality for Adult Oystercatchers of Different Feeding Specialization in the Exe Estuary

Feeding Specialization	Index Body Condition	Supplementary Feeding on One or More Occasions (%)	Winter Mortality (1988–1991) (%)	Winter Mortality (2002–2006) (%)
Worm/clam feeder	−0.029	100.0	3.1	5.3
Mussel stabber	0.012	80.8	2.3	2.7
Mussel hammerer	0.053	58.7	1.2	3.3

Data from Durell, Goss-Custard, Caldow, et al. (2001) and Durell (2007).

as a result of milder winters (Durell, 2007). These contradictory results fit with an analysis of phenotypic selection on diet specialization (as derived from bill tip shape) in Oystercatchers breeding on Schiermonnikoog (van de Pol, Brouwer, Ens, Oosterbeek, & Tinbergen, 2010). Over 25 years viability selection fluctuated strongly: slightly favoring generalists in most years, but strongly disfavoring generalists in rare harsh winters.

6.5. Feeding Distribution

We are now in a position to describe the Oystercatcher society during the nonbreeding season which largely means addressing how social positions are distributed over limiting resources, that is, the food supply. The majority of models start from the ideal free distribution model of habitat selection, which assumes that habitat suitability decreases with density of competitors and that individuals settle in the most suitable habitat, are omniscient, and are free to move (Fretwell & Lucas, 1969). According to Fretwell, habitat suitability “may be thought of as the average success rate in the context of evolution (and/or “adaptedness”) of adults resident in the habitat.” In other words, some measure of fitness.

This very simple and general model was subsequently applied to the feeding distributions of birds during the nonbreeding season, assuming that foragers maximized food intake rate, in line with optimal foraging theory (Krebs, Stephens, & Sutherland, 1983), and that they suffered from interference (Sutherland, 1983). The observation that individuals differed in aggressiveness and susceptibility to interference (Ens & Goss-Custard, 1984; Goss-Custard, Durell, & Ens, 1982) fuelled ideal free distribution models of foragers differing in competitive ability (Parker & Sutherland, 1986; Sutherland & Parker, 1985), building on the concept of phenotype-limited evolutionarily stable strategies (Parker, 1982). Whereas the ideal free distribution model predicts equal success rates in all occupied habitats, these models generally predict higher success in HQ habitat. A plethora of models was subsequently developed, adding or relaxing assumptions and increasing realism and detail, and put to the test (Kacelnik, Krebs, & Bernstein, 1992; Tregenza, 1995). Analyzing the properties of these models, it was shown that the shape of the aggregative response, that is, the distribution of foragers over limiting resources, depended strongly on the shape of the interference function (van der Meer & Ens, 1997). The aggregative response also proved very sensitive to variation in competitiveness among individuals and to the average level of interference (Sutherland, 1992).

Since the predictions of the distribution models that were tried for the Oystercatchers of the Exe proved to depend so strongly on details of the model, it was decided to spend much effort on good parameter estimation in the field and to construct a more realistic, though initially situation-specific, model (Goss-Custard et al., 1996b). Three versions of an IBM of Exe estuary Oystercatchers were published. These models assumed that animals maximize fitness, but this is implemented via a behavioral decision rule assuming to lead to maximization of fitness, that is, a fixed decision rule not derived via state-dependent modeling (Houston & McNamara, 1999; Mangel & Clark, 1988). In the case of the Exe estuary Oystercatcher model, the behavioral rule is to feed where intake rate is highest (Stillman & Goss-Custard, 2010). This assumption was made because it seemed reasonable that the birds would maximize their intake rate at those times in the winter when the risk of starvation was highest. No doubt this meant that the birds in these models consumed food faster than they need to do at other times of the winter when there was very little chance of them starving. But this did not matter for the purposes of the model. The key thing was that, at the times of the winter when the birds were hard-pressed, the decision rules used in the model were likely to be appropriate. Simulations with a subsequent model of Humber estuary shorebirds confirmed that this was a justifiable assumption to have made on the Exe estuary (Stillman et al., 2005). Thus, the IBMs of the Exe estuary Oystercatcher population assumed simply that fitness is maximized at times of food stress by the birds maximizing their intake rate, this being the current best estimates of the decision rules that the starving individuals would use.

In the IBMs, each individual is characterized by its susceptibility to interference (measured as the slope of the intake rate against the logarithm of conspecific density) and its IFIR (based on an empirically determined functional response, relating intake rate to prey characteristics). Susceptibility to interference depends on feeding method and local dominance, which itself depends on the *global dominance* of the bird, relative to the global dominance of the other birds in the patch. Global dominance is a hypothetical construct as it proved unfeasible to measure in the field, despite some attempts being made. It is assumed that global dominance is a fixed property of the individual, irrespective of where it feeds, that is, it could be fighting ability or *resource-holding potential* (Ens & Cayford, 1996). Local dominance could be readily measured in the field as the proportion of encounters won by the focal individual at a given location. In the models, local dominance is calculated as the percentage of individuals in the patch with lower global

dominance. An individual chooses to feed in the patch where it can achieve the highest intake rate, which at any one time depends on the food supply, its own feeding method, foraging efficiency, local dominance, and the density of conspecifics.

The first version did not include many aspects of the animals' natural history and was limited to predicting the distribution in late summer (Goss-Custard, Caldow, Clarke, Durell, & Sutherland, 1995; Goss-Custard, Caldow, Clarke, & West, 1995). The second version deals with the autumn and entire winter period, so keeps track of the shellfish population (including loss of condition) and the body condition of the individual Oystercatchers throughout winter. But as it only included mussels as food supply, it could not predict the observed mortality rates very accurately (Clarke & Goss-Custard, 1996). The third version incorporated all major feeding areas, that is, upshore areas and fields, as well as many other additional aspects of the system and much-refined parameter estimates (Stillman, Goss-Custard, West, et al., 2000). This version was successful at predicting the mortality rates that had been recorded on the Exe.

The aim during the development of the three versions of the model had been gradually to minimize the difference between predicted and observed overwinter starvation rates of juveniles, immatures, and adults during the model calibration years of 1976–1980. The model successfully predicted the density-dependent starvation on the Exe in the years 1980–1991, when Oystercatcher densities had increased considerably, even though at the time the predictions were made, it was not yet known that mortality was indeed density dependent (Stillman, Goss-Custard, West, et al., 2000). The model also correctly identified 3 years with mass mortality in the Wash due to overfishing of the shellfish beds (Atkinson et al., 2003), and years with low mortality; but quantitative estimates of mortality depended on the assumed intake rate on upshore flats, which was unknown (Stillman, Goss-Custard, West, et al., 2000). A sensitivity analysis showed that the model's predictive ability depended on nearly all of its many parameters. However, variation in gross energetic parameters had a greater influence on predictions than variations in behavioral parameters (Stillman, Goss-Custard, West, et al., 2000).

It is assumed in the model that individuals consistently vary in feeding efficiency or IFIR and that this variation is independent of global dominance. Because field studies indicate that there is no correlation between IFIR and *local* dominance (Caldow et al., 1999; Goss-Custard & Durell, 1988), it was assumed that there also is no correlation between IFIR and

global dominance. We would expect the most dominant individuals to have the least difficulty in meeting their daily energy needs and this is indeed predicted by the model (Stillman, Goss-Custard, West, et al., 2000). The most (globally) dominant individuals should engage least often in supplementary feeding in upshore areas and in the fields (Fig. 8.14). However, there was no clear relationship between local dominance and the relative use of fields. In contrast, the model predicted, and field data confirmed that individuals of a high feeding efficiency engaged least often in supplementary feeding (Fig. 8.14). These findings have led to the suggestion that in investigations on individual variation in competitive ability, too much emphasis has been placed on dominance as a way of gaining access to limiting resources and too little on feeding efficiency as a way of efficiently exploiting resources (Caldow et al., 1999; Stillman, Caldow, Goss-Custard, & Alexander, 2000).

At first sight, the suggestion that feeding efficiency is more important than interference in competition for food seems at odds with the conclusion that in the Exe density-dependent mortality is due to interference, not depletion (Goss-Custard et al., 2001). However, this is not so and the

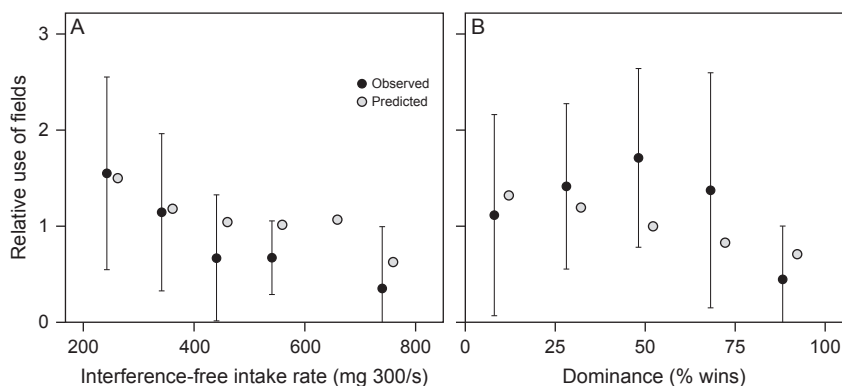


Figure 8.14 Predicted and observed use of fields for supplementary feeding by birds of different (A) foraging efficiency and (B) global dominance. The predicted use for each bird was the proportion of high tides (on full neaps during daylight between September and March) on which it used the fields for supplementary feeding. The observed use for each bird was the proportion of observer visits to the fields (mostly on neap tides, during daylight between September and March) on which it was seen. The use for both model and real birds is expressed relative to the average use of birds of that type because the observed data underestimated field use as birds could not always be identified in the fields even if they were present. The average use of fields is shown (95% confidence limits for observed data) within ranges of foraging efficiency and dominance. From Stillman, Goss-Custard, West, et al. (2000).

finding can be understood as follows. On the Exe estuary, the difference between the water level at low and high tide—the tidal range—varies from under 2 m on neap tides to well over 4 m on spring tides. As mussel beds on the Exe mostly lie between mid-shore and extreme low-water mark on Spring tides, the proportion of the mussel beds that are exposed and so accessible to Oystercatchers varies through each tidal cycle and through the fortnightly neap-spring cycle too. The largest area of mussels is accessible to Oystercatchers over low tide. Accordingly, over low water on most spring and mid-tides, the birds can spread out so that their density is very low over most of the low tide period, as is shown by the density profiles in [Goss-Custard and Durell \(1987c, 1988\)](#). In fact, for much of the exposure period, the densities of Oystercatchers on the mussel beds are well below the threshold density at which interference begins to occur and interference will not affect the intake of many, if any, of the birds, even the least dominant. How well a bird forages at these low densities will depend, by definition, on its efficiency. It is likely that the most efficient birds will be able to obtain most of their food requirement over this part of the tidal cycle and that it is only the least efficient individuals that will have to feed on the mussel beds as the tide recedes and advances at the end of the exposure period. These are the stages of the exposure period when bird densities are regularly high enough for interference to depress the intake rate of the subdominants. Although it is their subdominance that causes their intake rate to be depressed by interference at these stages of the exposure period, it is their low foraging efficiency that, in the first place, causes them to be subjected to it. Hence, a bird's foraging efficiency is the pre-determinant of whether it will be at risk of interference, and it is their dominance that then determines how strong the effect of that interference will be on their rate of consumption at the more competitive stages of the tidal cycle. The situation in Neap tides is similar but, because so much of the mussel beds do not expose even at low tide, interference will affect the intake rate of subdominants for a greater proportion of the exposure period. Nonetheless, it is the most efficient individuals that will still be most likely to be able to avoid feeding at the beginning and end of the exposure period when competitor densities are particularly high. Although this explanation has yet to be tested in the field, it does explain satisfactorily why the foraging efficiency of an individual has so much influence on its use of supplementary upshore and terrestrial feeding sites and why the mortality rate—which only affects a small minority of the population—is nonetheless density dependent.

An alternative explanation for feeding efficiency being more important than interference in competition for food revolves around the fact that both dominance and feeding efficiency were necessarily measured where the birds were feeding. Individual feeding areas differ greatly and may show little overlap (Goss-Custard, Durell, & Ens, 1982). We expect a bird's local dominance to vary between mussels beds according to the quality of the competitors present. Similarly, IFIR as measured will not only depend on how efficiently a bird can feed but also on the food supply where it is feeding. Thus, a bird with a high local dominance and a poor feeding efficiency could be a bird in a poor quality feeding area evading a HQ feeding area crowded with more dominant competitors. This would mean that the impact of interference competition is underestimated.

In the various distribution models of individuals differing in competitive ability, including the IBMs tailored to the Oystercatchers studied in the estuary of the Exe, individuals are basically free to move, that is, there is no cost to moving. Yet, adult Oystercatchers are extremely faithful to their wintering site, inhabiting small home ranges year after year, especially the very dominant individuals (Ens & Goss-Custard, 1986; Goss-Custard, Durell, & Ens, 1982). Some individuals can be very aggressive in very small areas (Goss-Custard, Durell, & Ens, 1982), but such birds do not defend feeding territories where they have exclusive access to the food. Instead, they assert their dominance (Ens & Goss-Custard, 1986), so that they have priority of access to the food in their "pseudo-territories" (Ens & Cayford, 1996).

Recently, theoretical models of habitat selection, like the ideal free and the ideal despotic distribution model, have been criticized for their failure to take site familiarity into account (Piper, 2011). According to Piper (2011), the ideal models suffer from "familiarity blindness," that is, they implicitly assume that animals settle on and switch territories regardless of past residency or the duration of that residency. Whereas this criticism is valid for the ideal free distribution, it may apply to the name of the ideal despotic distribution, which suggests despotic exclusion, but not to the underlying concept. The basic assumption is that unsettled individuals have a lower fitness in a given habitat compared to settled individuals. It seems possible to interpret this fitness difference as resulting from settled individuals being familiar with a particular area and unsettled individuals being unfamiliar. Of the many benefits of familiarity reviewed by Piper (2011), two are likely to apply to Oystercatchers: success in dominance interactions (the

“resident advantage”) and the capacity to learn locations of food, that is, increased feeding efficiency. In Oystercatchers, there is evidence that intake rate is lower when individuals are forced to feed in an unfamiliar area (Rutten, Oosterbeek, Verhulst, et al., 2010). It has also been suggested that dominance is at least partly site dependent (Ens & Cayford, 1996), that is, that it not only depends on fighting ability but also on prior residence, like in wintering White-throated Sparrows (Piper & Wiley, 1989).

6.6. Career Decisions During the Nonbreeding Season

Now that we have described the limiting resources of time and food supply and the social organization during the nonbreeding season, we can ask ourselves what career strategy young Oystercatchers should follow to maximize fitness after reaching independence from their parents. From the point of view of the bird, the challenge consists of finding a good area to survive the winter when energy demands are high and feeding conditions are poor. In later years, it should also allow the bird to accumulate sufficient reserves to migrate successfully to the breeding grounds, arrive there in good condition and with sufficient reserves remaining to survive if the feeding conditions are poor upon arrival.

Contrary to geese, which travel as a family to the wintering area, Oystercatchers travel to their wintering grounds on a solitary basis. The exact age at which the young bird sets out on its quest is not known, and may well vary between individuals. Before the young bird can depart, it must learn to find and handle a sufficient number of prey. In territories where the parents feed on heavily armored prey, like shellfish, chicks may depend on their parents for food up to 2 months after fledging, but chicks fed on worms may be independent within a month after fledging (Safriel et al., 1996). This difference may be related to the fact that it probably takes an adult-sized bill to crack the defenses of cockles and mussels, and that the chick has not reached adult dimensions at the time of fledging. The exact age at which the young bird can be considered full-grown is not known, but bill dimensions vary little between yearlings, immatures, and adults (Zwarts, Hulscher, Koopman, & Zegers, 1996), suggesting adult size is reached within the first year of life. However, it may take some more time for the bill to become tough enough to crack open a mollusc.

At present, we lack strict criteria for distinguishing between searching and settled birds, because the searching birds have not really been

systematically studied yet. Thanks to the employment of GPS trackers (Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013; Shamoun-Baranes et al., 2012), we now have data on the whereabouts of an individual during its second year of life (Ens et al., 2014), an age at which the birds generally do not visit the breeding grounds and are clearly recognizable as immature birds from their plumage. The bird spent several months in a particular area, but then moved on several times (Fig. 8.15). Since settled birds return year after year to the same site (Ens & Cayford, 1996), we are inclined to interpret the entire behavioral sequence as searching for a survival site, consisting of periods of sampling a site interspersed with movement periods to a different site. Sometimes, settled birds may also switch to searching for another site during winter. This happens during exceptionally rare cold winters, when the mudflats freeze over. Under these conditions, large numbers

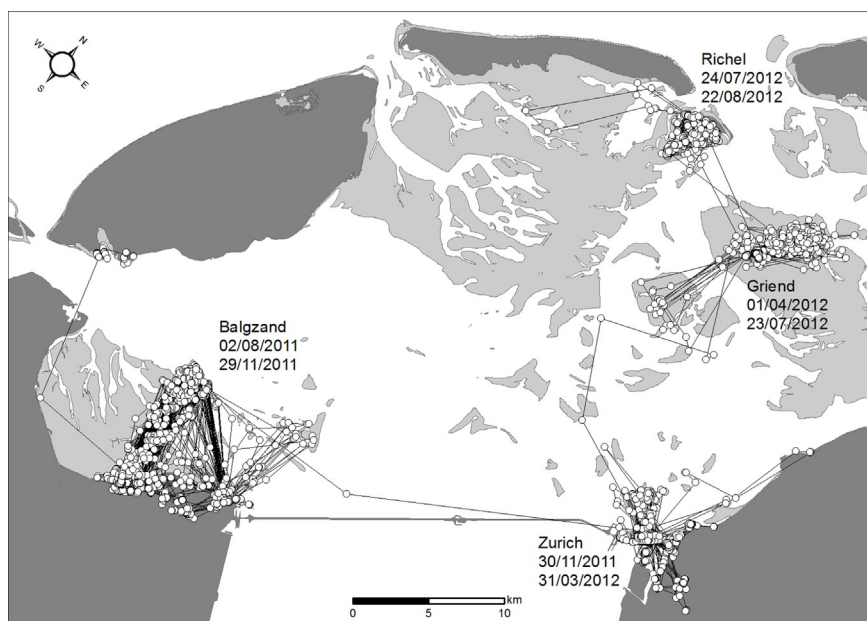


Figure 8.15 Movements of a bird (LB-LAGC) that would classify as “searching for a survival site” registered with UvA-BiTS GPS-tracker. Land is indicated dark gray, intertidal mud flats as light gray, and water as white. LB-LAGC was caught and marked on Aug 2, 2011 and determined to have fledged in 2010. It never returned to the low-tide feeding area where it was caught (the closest it came was 3 km), but initially remained to feed and roost on the eastern part of the Balgzand, but subsequently moved to a sequence of different sites.

of Oystercatchers are known to leave their traditional wintering area in search of more benign areas, which often lie further south and west (Duriez et al., 2009; Hulscher, 1989; Hulscher, Exo, et al., 1996).

Once the young bird has settled, it is likely to remain in the area throughout the breeding season in its second and third calendar year, and a few even do so in their fourth calendar year (Fig. 8.16). There is abundant evidence that during these early years of its life, the bird must learn to survive in a society that revolves around competition for food. We will first review the evidence that (1) young birds have higher mortality, (2) that this is related to the failure to meet their food needs, because (3) young birds lose out in the competition for food.

With one exception (Atkinson et al., 2003), it has been found that juveniles have high mortality rates, immatures have intermediate mortality rates, and adults have low mortality rates, for example (Duriez, Ens, Choquet, Pradel, & Klaassen, 2012; Goss-Custard, Durell, Sitters, & Swinfen, 1982; van de Pol, Vindenes, et al., 2010). This is especially clear during winters with severe weather conditions when individuals find it difficult to meet their energetic needs (Heppleston, 1971; Swennen & Duiven, 1983; van de Pol, Vindenes, et al., 2010).

Young birds have greater difficulty in meeting their energetic needs for two reasons. Juveniles have lower intake rates than adults at the start of winter (Goss-Custard & Durell, 1987a) and suffer more from interference in later winter, when interference is more intense anyway (Goss-Custard & Durell, 1987a). They are also more likely to feed on inferior prey in inferior habitats (Goss-Custard & Durell, 1983). Immatures are displaced from preferred mussel beds when adults return from the breeding grounds and the proportion of immatures is lowest on beds with the highest densities of adults in winter (Goss-Custard, Durell, McGrorty, et al., 1982).

Young Oystercatchers increase their survival chances as they age by increasing feeding efficiency (Goss-Custard & Durell, 1987a) and social status (Goss-Custard & Durell, 1987b), which reduces the negative impact of interference (Goss-Custard & Durell, 1987c). As a result, the probability of being seen on preferred mussel bed increases with age (Goss-Custard, Durell, McGrorty, et al., 1982), while the probability of feeding on inferior prey in inferior habitats decreases with age (Goss-Custard & Durell, 1983). This is summarized in Fig. 8.16.

Ens and Cayford (1996) suggested that the queue hypothesis developed for territorial animals (Ens et al., 1995) also applied to Oystercatchers during

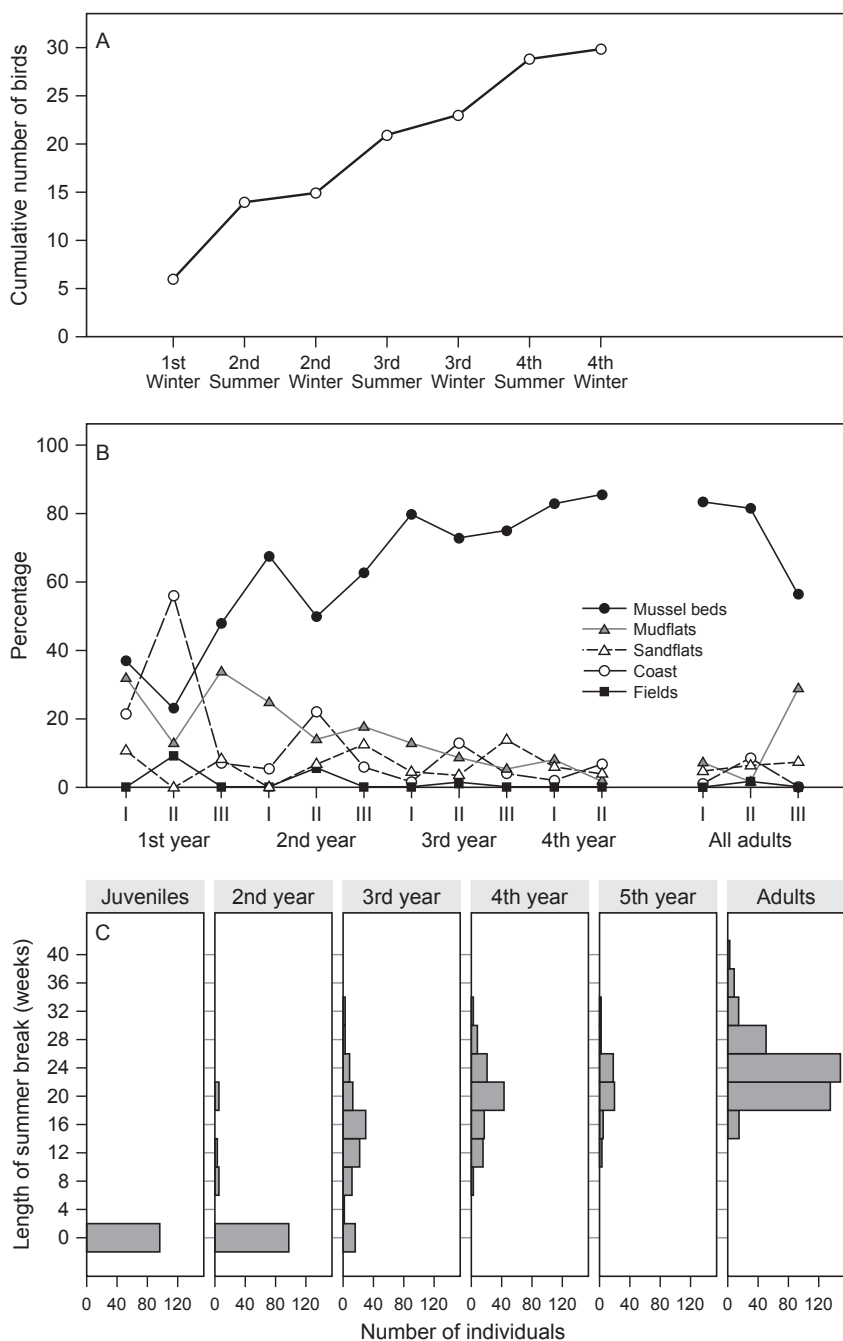


Figure 8.16 Composite figure of important changes with age taking place in the wintering area. (A) Prey choice: the age at which 30 Oystercatchers were first seen to consistently eat mussels. Winter is October to March inclusive. (B) Habitat choice. The proportion of all the sightings of color-marked Oystercatchers within a year class recorded in each habitat during three periods of the year. (I) 15 July–31 October, (II) 1 November–31 March, and (III) 1 April–14 July. (C) The number of weeks that birds of a different age class were absent from the Exe during summer. (A) and (B) From Goss-Custard and Durell (1983); (C) from Ens and Cayford (1996).

the nonbreeding season. Piper (1997) calls this the “hopeful dominant” hypothesis explaining why young birds tolerate low dominance initially, because it will lead to higher dominating ability later in life. The idea is that wintering birds of lower dominance that regularly feed in an area can be thought of as queuing, albeit competitively with individuals of adjacent rank, to take the position of more dominant birds when these disappear. This hypothesis implies stable dominance ranking in the short term, which was indeed observed: the dominance ranking of 10 birds studied in 1980 was the same as in 1979 (Goss-Custard, Durell, & Ens, 1982). The hypothesis also implies a slow increase in rank with age, which has been observed as well: Caldow and Goss-Custard (1996) followed 25 color-marked individuals between 2 and 12 years and found that dominance rarely increased by more than 10% per year, except for two low-ranking individuals whose dominance increased by 30% (Fig. 8.17). Based on these data, it can be calculated that it takes between 5 and 15 years to reach a high dominance rank (Fig. 8.17), which is in the order of magnitude of the average life expectancy of an adult Oystercatcher. However, several low-ranking individuals remained low ranking for many years, including individuals that had been followed for 12 years. Morphological measurements suggested that females predominated among these consistently low-ranking birds, whereas males predominated among the high-ranking and upwardly moving birds (Caldow & Goss-Custard, 1996). We do not know if it is generally true that males dominate females. To date, the only published data concerns eight color-marked individuals studied in late summer along the Frisian coast: the five most dominant birds were male, and the three least dominant were female (Zwarts, Hulscher, Koopman, Piersma, & Zegers, 1996).

Queuing for the position of top-dominant in a HQ feeding area makes sense if the environment is very stable and indeed mussel beds can be extremely stable. However, the high site fidelity needed to maintain high social status is expected to come with a cost. When sudden bonanzas appear, they may not be so quickly discovered by the dominant birds. Indeed, an exceptionally good spatfall of cockles in the Ribble estuary caused an influx of mainly young and presumably less site-faithful Oystercatchers (Sutherland, 1982). And in a world increasingly impacted by humans, site-faithful Oystercatchers may be confronted by the unexpected disappearance of their shellfish prey due to mechanized shellfish fishery, leading to high mortality (Atkinson et al., 2003; Camphuysen et al., 1996; Verhulst, Oosterbeek, Rutten, & Ens, 2004).

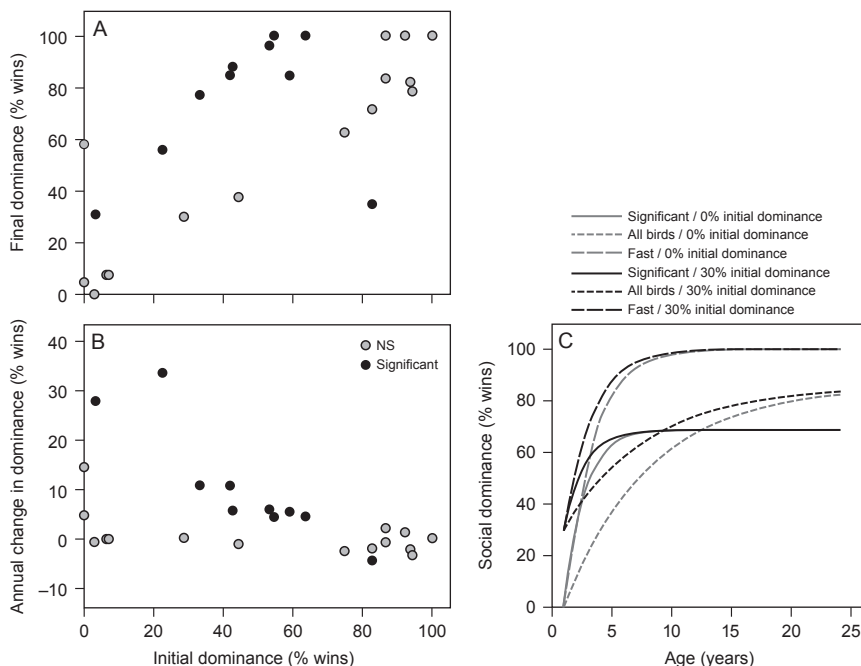


Figure 8.17 Reconstruction of the social career of Oystercatchers wintering in the estuary of the Exe, based on data published by [Caldow and Goss-Custard \(1996\)](#). Only data on color-marked individuals are included. (A) Dominance in the last year of observation plotted against dominance in the first year of observation, separated for birds whose dominance changed significantly, or not significantly. (B) Annual change in dominance as a function of dominance in the first year of observation, separated for birds whose dominance changed significantly, or not significantly. (C) Social dominance as a function of age based on different relationships between change in dominance and initial dominance (all birds, only birds with a significant change, only birds that quickly increase) and different initial dominance values (0% and 30%).



7. RETURNING TO THE BREEDING AREA

An important career decision facing a young Oystercatcher that has successfully settled in a nonbreeding area is at what age to return to the breeding area. The available data suggest that this happens when they are between 2 and 4-years old ([Fig. 8.16](#)). We would expect that it would depend on the proficiency that the individual has achieved in balancing its energy budget, but no correlates are known that relate to the variation in the age of first return.

The young bird must also decide where to go. In the breeding area, such “prospecting” birds are classified as uncommitted nonbreeders (Heg, Ens, et al., 2000). They do not behave aggressively on either club or mudflats and are not known to regularly intrude in a restricted area. If they do intrude, it can occur anywhere. Often it occurs as part of a *gathering*, a sudden influx of Oystercatchers which temporarily swamps the territory owner. Such gatherings are most likely to occur around the time that many pairs are feeding chicks.

To what extent is it simply a return to the area where it was born? Calculations for the Oystercatchers on Schiermonnikoog suggest that all locally born Oystercatchers that survive to this age return to the natal area, qualifying the Oystercatchers as a highly philopatric species (van de Pol, 2006). However, the lack of population structure on Schiermonnikoog, as well as across larger geographical distances, is thought to be due to high levels of gene flow through dispersal of juveniles (Van Treuren, Bijlsma, Tinbergen, Heg, & Van de Zande, 1999). Thus, at least some juveniles should disperse away from the natal area. What seems to occur is that all surviving juveniles return to the breeding area to become nonbreeder but that some then leave the study area before acquiring a territory (van de Pol, 2006). Between 1984 and 1996, the annual permanent emigration rate from the study area on Schiermonnikoog was estimated to vary between 0% and 4%, and it increased to between 2% and 9% after 1996, when the population started to decrease (van de Pol, 2006). How far these emigrating nonbreeders subsequently settled from their natal origin is not known. Within the study area, neither sex aggregated near nor avoided their natal site (Bruinzeel, 2004) and both sexes settled on average ~425 m from their natal territory (van de Pol, Bruinzeel, et al., 2006).



8. THE IMPACT OF NATAL CONDITIONS ON SOCIAL CAREERS

Oystercatchers are special among birds in that the fully precocial young leave the nest upon hatching, but are fed by the parents until well after fledging (Safriel et al., 1996). The period that the chicks are still being fed varies from a few weeks after fledging, as is generally the case for migratory inland-breeding birds, up to several months after fledging, as may happen in sedentary coastal breeding birds (Kersten & Brenninkmeijer, 1995; Norton-Griffiths, 1969).

Thus, the first social position that an Oystercatcher occupies is that of a chick depending on its parents for food, as well as brooding and protection. For the large majority of chicks, this is also their last social position. An estimated 90% (Heg & van der Velde, 2001) perish due to predation, starvation, disease, flooding, trampling, agricultural activities, and road accidents. The conditions that the surviving 10% of chicks experience before fledging can vary dramatically from one chick to the next and potentially have a decisive impact on their subsequent career.

The processes that create variation in rearing conditions of the chicks are an inherent part of the social system, with breeding pairs defending territories varying in quality against other breeding pairs (Fig. 8.3). Even pairs in HQ territories often fail to provide sufficient food for all of the chicks. In broods with two or more chicks, a dominance hierarchy develops with the dominant chick receiving most of the food (Safriel, 1981). Disease may impact the social hierarchy (Safriel, 1982). For various reasons, mechanisms for brood reduction, like hatching asynchrony, are only partially successful (Heg & van der Velde, 2001). Thus, many chicks experience periods of food shortage before and around fledging, leading to a considerable spread in fledging weight (190–400 g) and fledging age (27–52 days), with slow-growing chicks fledging with a lower mass at a later age (Kersten & Brenninkmeijer, 1995). In the population study on Schiermonnikoog, fledging mass was influenced by territory quality, general food abundance (rich year or poor year), hatching order, and brood size at fledging (Heg & van der Velde, 2001).

Do differences in fledging mass and other aspects of fledging phenotype influenced by rearing conditions have an impact on the birds' subsequent success? An early study concluded that a slow growth rate severely reduced a chick's chance of fledging, but that, once fledged, it probably did not result in irreversible damage that resulted in an increased risk of mortality during the first few years after fledging (Kersten & Brenninkmeijer, 1995). The latter suggestion was subsequently proven wrong in a paper aptly titled "a silver spoon for a golden future" (van de Pol, Bruinzeel, et al., 2006). As described above, chicks generally grow well in HQ territories (Ens et al., 1992), and fledglings from HQ territories had a 1.3 times higher juvenile survival, a 1.6 times higher survival as adult prebreeder (age 3–11 years), a higher probability of recruitment and a much higher probability of settling in HQ habitat (44% for fledglings from HQ territories vs. 6% for fledglings from LQ territories) (van de Pol, Bruinzeel, et al., 2006). This silver-spoon effect (Grafen, 1988) has a long-term impact on fitness that increases over

generations due to a correlation between the quality of rearing conditions of parents and their offspring (Fig. 8.18). As a result, the reproductive value of an egg in a HQ territory is almost eight times the reproductive value of an egg in a LQ territory. This calculation assumes that all offspring return to the natal area, for which there is indirect evidence (van de Pol, Bruinzeel, et al., 2006). If the difference in local survival between nonbreeders of different natal origin is due to emigration instead of mortality, this reduces the long-term fitness difference, which remains nonetheless very substantial.

What do we know of the phenotypic or genotypic correlates that make fledglings from HQ territories successful later in life? There is no evidence for a genetic subdivision between occupants of HQ and LQ territories (Van Treuren et al., 1999), so systematic differences between fledglings from HQ and LQ territories may primarily be due differences in rearing conditions. Four measurements were available to describe rearing conditions: hatch date, residual body mass (i.e., corrected for body size) at age 30 days, body size at age 30 days, and the presence of siblings (Fig. 8.19). Fledglings from HQ and LQ territories did not strongly differ with regard to hatch date and body size. However, fledglings from HQ natal origin were 10% heavier, which positively affected the probability of returning to the study area at adulthood, and they were twice as likely to fledge together with siblings, which positively affected the probability of recruitment at adulthood (Fig. 8.19). These two traits alone might have mediated the strong effect of natal origin on fitness. However, HQ chicks that were large at fledging had a higher probability of recruiting into a HQ territory than HQ chicks that were small (Fig. 8.19). Thus, a main contributor to the high success of chicks born in HQ territories, namely, the probability to recruit into a HQ territory, is linked to a trait (body size at fledging) that may not depend on natal territory! Large body size was also important for successful recruitment of LQ fledglings in LQ territories. Thus, LQ territories were occupied by small-bodied HQ fledglings and large-bodied LQ fledglings. At present, we do not know if or how body size at fledging is related to adult body size. However, comparing adult territory owners we found no evidence of a difference in wing length, bill length, or body mass between occupants of HQ and LQ territories in both sexes (Ens et al., 1995). Whereas hatch date did not affect the probability that HQ fledglings recruited, only early hatched fledglings from LQ territories successfully recruited (in LQ territories).

Oystercatcher parents could potentially also influence the subsequent success of their chicks through cultural transmission. In a famous study, Norton-Griffiths (1968) showed that chicks adopted the feeding specialization of their

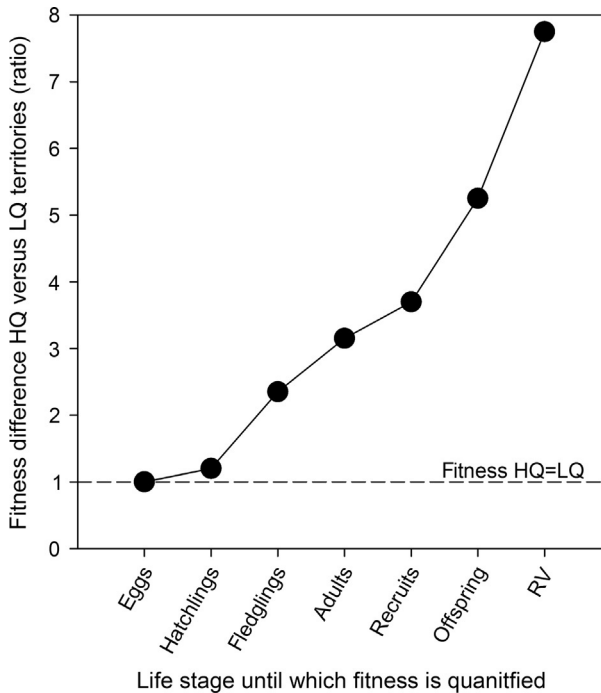


Figure 8.18 The effect of using short-term or long-term fitness measures to infer fitness differences between birds from high-quality (HQ) or low-quality (LQ) territories. When both start out with a single egg, the fitness difference (expressed as the ratio of the fitness value for HQ natal origin divided by the fitness value for LQ natal origin) increases with the length of time over which the fitness measure is calculated, from the number of hatchlings, to fledglings, offspring reaching adulthood, offspring recruiting as a breeder, and grand offspring produced. The reproductive value (RV) estimates the contribution of an individual to the long-term population growth rate. From [van de Pol \(2006\)](#).

parents. To prove that this was due to cultural transmission, he performed a cross-foster experiment and showed that the chicks adopted the feeding specialization of their foster parents, instead of their biological parents. While the experiment shows that feeding specialization was not genetically transmitted, it cannot exclude the possibility that the feeding specialization was optimal for the particular foraging habitat in the territory.

At present, we have no information on the link between feeding specialization in summer and feeding specialization in the subsequent winter or even later in life, but the studies in the Exe at least provide clear evidence of a link between feeding specializations and competitive processes. This goes some way to deepening our understanding of how rearing conditions

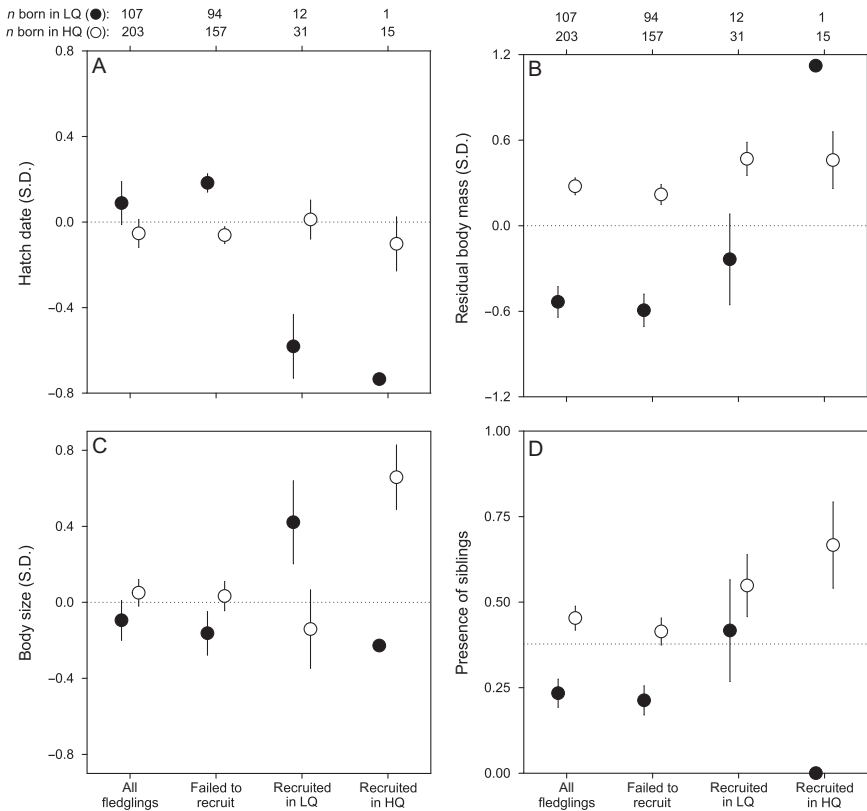


Figure 8.19 Comparison of the differences between offspring from HQ and LQ territories that reached a certain life stage with respect to (A) hatch date (expressed as z-score), (B) body mass at age 30 days corrected for body size (expressed as z-score), (C) body size at age 30 days (expressed as z-score), and (D) the presence of siblings. In each panel, average values (\pm SE) are indicated for all fledglings, fledglings that failed to recruit, fledglings that recruited in LQ territories, and fledglings that recruited in HQ territories, respectively. Sample sizes are indicated above panel (A). *Based on van de Pol (2006).*

affect subsequent success. In contrast, we can only speculate how a large body size at fledgling or being reared with a sibling would benefit an individual during competitive interactions in either winter or summer. Body size might be related to fighting ability, and therefore competitive ability. Having had a sibling might mean that birds have learned to compete for food at a very early age. Alternatively, there may not be a direct effect of having had the social experience of a sibling; it might just be a proxy for parental quality or territory quality that is not accounted for by the HQ/LQ dichotomy.



9. REMAINING CHALLENGES

This review shows that we have not yet reached our goal for the Oystercatcher society of providing a description in space (i.e., the spatial distribution of social positions) that is fully consistent with a description in time (i.e., the flow of individuals through social positions) and with a description of the mating system (i.e., the access of individuals of one sex to individuals of the opposite sex). Below, we will discuss the progress that we made and the major challenges that remain.

9.1. Limiting Resources and Trade-Offs

We have extensive knowledge on the limiting resources that Oystercatchers are competing for at the various stages in their career and the details of the competitive process, including queuing.

From the perspective of our conceptual framework, it is clear that the queue models potentially meet an important goal, namely, the ability to predict the mean and the variability in the age at which particular social positions are reached. They also go some way to predict the structure of the Oystercatcher society (i.e., the distribution of social positions) from the distribution of limiting resources. However, they take the maximal number and minimum size of HQ territories as fixed, instead of deriving these from measurements of the limiting resources.

We suspect that this requires development of models that incorporate the fundamental trade-offs governing the behavior of individuals more explicitly. In this review, we identified the following trade-offs: (1) prospecting (i.e., searching a site to survive the winter or searching a site to settle as a breeder) is incompatible with settling, (2) ranging over a large area is incompatible with building up or defending local dominance, and (3) mate searching is incompatible with successful reproduction.

9.2. Social Positions and Career Strategies

We have successfully described the social positions making up Oystercatcher society in both summer and winter (Fig. 8.2). Wiley (1981) proposes two hypotheses to account for the stable structure of societies, despite the continual turnover of individuals: homeostasis and steady state.

A steady state will occur if demographic rates, including the probabilities of moving from one social position to another, are constant. It is true that

under these conditions a stable distribution over social positions will be reached, but populations with constant demographic rates either go extinct or become infinitely large. Thus, while it may be true that the transition between some social positions occurs at a fixed rate and is not subject to feedback from individuals already occupying that position, this cannot be true for all demographic rates. A likely example of a career decision that perhaps only depends on age or experience is the decision of young birds to return to the breeding area and become a prospecting nonbreeder. At the time this decision is taken, the individual has no information on the number of other prospecting nonbreeders it will encounter in the breeding area, and so it cannot be influenced by that number.

Under homeostasis, the recruitment of individuals to particular social positions is constrained by the number of individuals already occupying those positions. In Oystercatchers, this is clearly the case with changes in social position during the breeding season. The probability of moving from a breeding territory in LQ habitat to a breeding territory in HQ habitat on Schiermonnikoog depended strongly on the number of breeding vacancies per competitor (van de Pol, Vindenes, et al., 2010). Similarly, the number of remaining vacancies per surviving nonbreeder was a good predictor of the probability that a nonbreeder would settle in both LQ and HQ habitat (van de Pol, Vindenes, et al., 2010). Removal experiments prove the causal nature of these relationships (Bruinzeel & van de Pol, 2004; Harris, 1970; Heg, Ens, et al., 2000). For the nonbreeding season, we know that summering immatures, which are generally subdominant to adults, leave HQ mussel beds, when adults return from the breeding grounds (Goss-Custard, Durell, McGorty, et al., 1982) and that many adults increase in dominance rank over the years (Caldow & Goss-Custard, 1996); see also Fig. 8.17. However, we have no experiments to show that removal of dominants accelerates the rise in rank of subdominants, and such an experiment would be very difficult to carry out.

Our aim is to explain the transitional probabilities from the career strategies followed by the individuals. Our queue model on the decision to queue for either a HQ or a LQ territory shows the advantages and problems associated with thinking in terms of career strategies. In the model, birds that settled in good territories do better than birds in poor territories, but to their success must be added all the birds that tried to obtain a HQ territory, but failed. This crucial perspective is absent from many studies that investigate the age of first breeding and compare only individuals that successfully established a territory (Kruger, 2005; Pyle, Nur, Sydeman, & Emslie,

1997) or ignore the possibility that birds that delay breeding may queue for HQ habitat (Orell & Belda, 2002). The problem is that it is easy to get information, such as the age of first breeding, on the individuals that successfully establish a territory, but it is often very difficult to identify the strategy of the individuals that perished before they could settle. Yet, if we cannot classify the unsuccessful individuals, we cannot directly measure the costs and benefits of a particular career strategy in the field. Putting GPS tags on a large number of nonbreeders may provide a way forward.

Although it does not show yet in our queue models, the topics of mate choice and divorce are closely linked to the habitat selection process, because competition for territorial space and competition for mates go hand in hand. However, it is possible that for nonbreeders the value of obtaining a territory is so high that it pays to settle with any partner, and try to improve upon this later. This might not be unthinkable, since the fitness gain from gaining a territory or not is so high that a poor quality partner may not alter the costs and benefits much in addition. The costs and benefits might be different for established breeders that have already built up a strong local dominance position and for them mate choice might be an important reason to divorce and change territories.

9.3. Do Males and Females Follow Different Careers?

Males and females look and behave very similarly and this is one reason why we made no distinction in the analysis of recruitment and the queue model. However, there is evidence that males and females follow a different career strategy with females being more likely than males to take the initiative for a change of mate to improve their reproductive prospects. Differences between the sexes in longevity and abundance are likely to alter the cost and benefits of career decisions such as mate choice and the life-history decision of delayed reproduction.

There could be a sex difference in longevity linked to a difference in success in food competition during winter. Males and females specialize on different foods and, perhaps, females have lower social dominance. Durell (2006) reported that in five major overwintering sites in the United Kingdom, females predominated among juveniles and males predominated among adults. In one of these sites survival of adult females was measured and found to be substantially lower than survival of males: 82% versus 91%. This led Durell to suggest that Oystercatchers preferentially rear female young in response to a male bias in the adult population as whole. However, Heg,

Dingemanse, et al. (2000) found a sex ratio in hatchlings and fledglings that did not differ from unity. Furthermore, there was no difference in survival among males and females breeding on Skokholm (Safriel et al., 1984).

It is very clear that future studies should put more effort into distinguishing males and females. Despite clear and consistent differences in biometric measurements between the sexes, the only reliable way to distinguish them is on the basis of genetics (van de Pol et al., 2008).

9.4. Individual Variation, Personality, and Social Careers

To what extent do we understand the processes that generate and maintain variability between individuals and how it affects the probability that individuals will follow a particular career?

The importance of individual variation in behavior was recognized early on in Oystercatcher studies, for example, Norton-Griffiths (1967). As this review shows, understanding the causes and consequences of individual variation in feeding specialization, feeding efficiency, social dominance, territorial settlement, age of first breeding, and other life-history traits has been at the heart of many Oystercatcher studies. It has among other things culminated in the claim that only population models that incorporate individual variation in adaptive behavior are able to reliably predict the population consequences of environmental change (Stillman & Goss-Custard, 2010), in line with the tenets of individual-based ecology, in general (Grimm & Railsback, 2005).

At the same time, it has proven very difficult to identify the traits that make an individual into a HQ or a LQ individual. Individual chicks experience very different feeding regimes when raised by their parents due to differences in territory quality and imperfect brood reduction. This could be an important process generating variation in quality between individuals. Yet, we cannot translate these rearing conditions to traits later in life that determine individual quality during either the breeding season or the non-breeding season.

Recently, the study of individual variation was transformed with the introduction of the concept of “animal personality” (Dingemanse & Reale, 2005; Wilson, Clark, Coleman, & Dearstyne, 1994), also referred to as “animal temperament” (Reale, Reader, Sol, McDougall, & Dingemanse, 2007) or “behavioral syndrome” (Sih, Bell, Johnson, & Ziemba, 2004). The idea is that individual behavioral differences are repeatable over time and across situations and that different behaviors are correlated within individuals. To date, no studies of Oystercatchers have

explicitly addressed the possibility of variation in personality. However, several results are highly relevant:

1. There is a very clear “silver-spoon” effect. Young raised in HQ territories are much more likely to settle in HQ territories later in life than are young from LQ territories (van de Pol, Bruinzeel, et al., 2006), leading to long-term fitness differences (Fig. 8.18). Bruinzeel, van de Pol, and Trierweiler (2006) captured occupants of both types of territory and staged encounters in captivity. There was no evidence that occupants of HQ territories were more likely to win, although sample size was admittedly small. In a less convincing field test, individuals were observed in late winter/early spring feeding on the mud flats near the breeding grounds (Bruinzeel et al., 2006). The dominance score ranged from 0% to 100% for both occupants of HQ territories and occupants of LQ territories, but it appeared that the dominance of occupants of HQ territories exceeded the dominance of occupants of LQ territories: on average 45% versus 30%. Perhaps the observed variation in dominance was related to variation in a personality trait like “boldness,” but this remains to be investigated.
2. On the wintering grounds, there is clear evidence that some birds move up in rank and eventually reach high status, whereas others remain low-ranking throughout their life (Caldow et al., 1999; see also Fig. 8.17). This difference in social career could well reflect differences in personality, including the suggestion that it is mainly females that remain low-ranking throughout their life.

Of course, there is no shortage of studies on Oystercatchers that show consistent differences in individual behavior. However, the intriguing suggestion from the quickly expanding literature on animal personality is that behavioral traits do not vary independently. Translated to Oystercatchers, this could mean that feeding specialization might be linked to aggressiveness, dispersal behavior, etc. This would have important implications for the study of career decisions, both for modeling the development of career decisions, and for empirical studies. Oystercatchers are easily captured, especially during the breeding season. Furthermore, it is easy to raise chicks by hand and subject them to tests of their personality, as long as contact with wild-caught animals is avoided.

9.5. Interlinked Career Decisions and Carry-Over Effects

Each Oystercatcher has two social careers: one during the breeding season and one during the nonbreeding season. For most individuals, the societies

in which these careers take place are completely independent, because the probability that a focal bird will meet a particular individual in both seasons is extremely small. Resident coastal populations are the exception. However, even on Schiermonnikoog, not all birds remain for the winter, but some migrate tens of kilometers each year to different parts of the Wadden Sea (Ens et al., 2014). Furthermore, the remaining birds spread out over a much larger area than they use during the breeding season (Ens et al., 2014) and there is an influx of large numbers of inland-breeding birds and birds breeding further north in Scandinavia. Thus, the resident population is greatly diluted by immigration.

Although for most individuals the two careers take place in two very different social and physical environments, they are connected via the individual and its state. This may lead to carry-over effects, processes in one season that influence the success of an individual in the following season. For example, an individual may survive the transition between seasons, but due to its changed state, some component of its fitness may be affected the following season. It has been hypothesized that these carry-over effects are much more important than generally appreciated (Harrison, Blount, Inger, Norris, & Bearhop, 2011).

The most commonly described carry-over effect is that conditions during winter affect breeding success in the subsequent season. This could also be the case in Oystercatchers and is the subject of current investigation. Furthermore, an analysis of recoveries of Oystercatchers ringed between 1975 and 2000 in continental Europe indicated that severe winters with high mortality were often followed by increased mortality during the subsequent breeding season (Duriez et al., 2012). Perhaps this carry-over effect is mediated by the social unrest caused by the many territorial vacancies following a high mortality in winter. Divorce rate is greatly increased in years following high winter mortality (Heg et al., 2003).

We have learned much about the processes governing career decisions in both winter and summer, but long-term studies of marked individuals have either focused on the breeding season or on the nonbreeding season. Hence, we know very little about the connections between the two careers. Studying these connections (using new technology like UvA-BiTS) stands out as a major challenge for the future.



10. CONCLUSION

Animals that build up social relationships do so because they typically benefit from those relationships. However, at the same time, they become

prisoners as it were of those relationships, and the Oystercatcher is no exception. Nothing prevents a nonbreeder queuing for a HQ territory on the saltmarsh of Schiermonnikoog from moving to a different island, except that the bird would throw away its familiarity with the local neighborhood and site dominance acquired over the years. Elsewhere, it would have to start from scratch. For the same reason, a bird that has reached high local dominance on a particular mussel bed in the estuary of the Exe will be very reluctant to move to a different estuary. Potentially, it is this social imprisonment that makes the Oystercatcher very vulnerable to rapid anthropogenic environmental change, such as local overexploitation of food stocks (Verhulst et al., 2004) or increased flooding risk of nesting habitat (van de Pol, Ens et al., 2010).

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