

Variation in Habitat Choice and Delayed Reproduction: Adaptive Queuing Strategies or Individual Quality Differences?

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ABSTRACT: In most species, some individuals delay reproduction or occupy inferior breeding positions. The queue hypothesis tries to explain both patterns by proposing that individuals strategically delay breeding (queue) to acquire better breeding or social positions. In 1995, Ens, Weissing, and Drent addressed evolutionarily stable queuing strategies in situations with habitat heterogeneity. However, their model did not consider the non-mutually exclusive individual quality hypothesis, which suggests that some individuals delay breeding or occupy inferior breeding positions because they are poor competitors. Here we extend their model with individual differences in competitive abilities, which are probably plentiful in nature. We show that including even the smallest competitive asymmetries will result in individuals using queuing strategies completely different from those in models that assume equal competitors. Subsequently, we investigate how well our models can explain settlement patterns in the wild, using a long-term study on oystercatchers. This long-lived shorebird exhibits strong variation in age of first reproduction and territory quality. We show that only models that include competitive asymmetries can explain why oystercatchers' settlement patterns depend on natal origin. We conclude that predictions from queuing models are very sensitive to assumptions about competitive asym-

metries, while detecting such differences in the wild is often problematic.

Keywords: age of first reproduction, conditional strategies, evolutionarily stable strategy, habitat selection, *Haematopus ostralegus*, natal habitat preference.

In many species, individuals delay reproduction beyond the age of sexual maturity (e.g., Charnov 1991; Newton 1998). Life-history theory tries to explain delayed reproduction, with explanations falling into two major classes or a combination thereof (e.g., Stearns 1992). First, young adults may delay reproduction until later stages in life to maximize lifetime reproductive output, for example, because reproducing early in life may be at the cost of reduced life span, future reproduction, or somatic growth (e.g., Oli et al. 2002; Krüger 2005). Second, delayed reproduction may be phenotype dependent, for example, because low-quality individuals may need to make the best of a bad job and are forced to delay their onset of reproduction.

Another ubiquitous pattern in nature is that once individuals reproduce, some individuals are apparently willing to do so in inferior breeding positions, such as low-quality territories, inferior positions in a colony or lek, or subordinate positions in a group. Again, two major explanations, or a combination of both, have been put forward to explain these facts (e.g., Fretwell 1972). First, occupying an inferior breeding position may maximize lifetime reproductive success when it is counterbalanced by a longer life span. Second, certain phenotypes may be forced to occupy low-quality breeding opportunities; that is, they are despotically excluded by others from the best breeding spots.

Recently, an alternative hypothesis has been put forward that tries to simultaneously explain both variation in age of first reproduction and variation in settlement decisions. The queue hypothesis suggests that individuals maximize lifetime fitness by strategically waiting (queuing) for high-

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quality breeding opportunities to become available, instead of immediately accepting a low-quality breeding position (Zack and Stutchbury 1992; Ens et al. 1995). Moreover, the queue hypothesis does not necessarily invoke the existence of individual quality differences (i.e., some individuals are competitively inferior and therefore have to make the best of a bad job), although, of course, the queue hypothesis and the individual quality hypothesis do not necessarily exclude each other.

Originally, queuing was a shorthand term to describe how individuals delay reproduction and stay within cooperatively breeding groups to inherit the dominant breeding position (Wiley and Rabenold 1984). Nowadays, it is realized that queuelike systems range from queues for mating opportunities (Schwagmeyer and Parker 1987), social and breeding position in group-living and cooperative-breeding species (Wiley and Rabenold 1984; East and Hofer 2000; Heg et al. 2005; Mitchell 2005), positions on the lek (Kokko et al. 1998), or access to harems or colonies (Poston 1997; Voigt and Streich 2003) to queues for high-quality territories (Zack and Stutchbury 1992; Ens et al. 1995; Ekman et al. 2001). Moreover, queuing processes seem to occur in a wide variety of taxa (birds, fish, mammals, and invertebrates) and life histories.

Adaptive queuing models try to predict how much individuals should be willing to delay reproduction and which reproductive opportunity to accept (Ens et al. 1995; Kokko et al. 1998, 2001; Pen and Weissing 2000, 2001; Kokko and Ekman 2002). An important feature of queuing decisions is their frequency-dependent nature. Ens, Weissing, and Drent (Ens et al. 1995; henceforth EWD) were the first to stress—and mathematically formalize—that the success of a queuing strategy depends on how many other individuals are queuing for the same opportunity. They showed that in evolutionary equilibrium, the competition, and thereby queuing time, for high-quality breeding positions increases up to a point at which it pays to accept low-quality breeding positions at a young age. Thereby, EWD extended the ideal despotic distribution into a life-history framework and showed how delayed reproduction and habitat selection can be viewed as two sides of the same coin. Frequency-dependent queuing processes now have been used to explain the logic of delayed breeding (EWD), territory choice (Kokko and Sutherland 1998; Kokko et al. 2001; Pen and Weissing 2001), reproductive skew (Kokko and Johnstone 1999), and cooperative breeding (Pen and Weissing 2000; Kokko and Ekman 2002).

Although EWD developed a general queuing model, their model was also used to study territory choice and delayed reproduction in a population of free-living oystercatchers (*Haematopus ostralegus*), a long-lived shorebird. Oystercatchers are an interesting test case because some individuals clearly occupy better territories than oth-

ers and some individuals delay breeding up to 8 years longer than others (van de Pol et al. 2006). Strikingly, in this species there seem to be no clear indications that individuals occupying high- or low-quality territories or individuals that delay or do not delay reproduction differ in their competitive abilities (EWD; also Bruinzeel et al. 2006). This puzzling observation prompted EWD to investigate whether adaptive queuing decisions could explain the large variation in territory choice and delayed reproduction in oystercatchers without invoking differences in individual quality. However, EWD could not yet provide a rigorous test of the quantitative predictions of their queue model, because it takes many years to gather sufficient field data on long-lived oystercatchers.

The aim of this article is threefold. First, we improve the original EWD model by removing an important inconsistency from the model and incorporating population limitation. These modifications result in a substantially different evolutionarily stable queuing strategy. Second, the original EWD model did not incorporate individual quality differences. However, differences in competitive abilities are probably plentiful in many species, although they sometimes may be hard to detect. To investigate the relative importance of the queue hypothesis and the individual quality hypothesis, we extend the original model to allow queuing strategies to differ between individuals and also incorporate differences in competitive abilities. Third, after 21 years of study, we are now able to perform a quantitative comparison between the predictions of these queuing models and the observed settlement behavior of oystercatchers in the field. To our knowledge, no other studies have compared predictions from adaptive queuing models with settlement patterns and variation of age of first reproduction in the wild, although such a quantitative comparison is crucial for our understanding of the importance of queuing processes in nature.

The Queuing Models

The Rationale

The EWD model addressed habitat choice and delayed reproduction in the simplest case of habitat heterogeneity, in which a surplus of nonbreeders (N) compete for a limited number of high- (H) and low-quality (L) territories. The queue hypothesis suggests that variation in habitat choice and delayed reproduction can be understood by taking the perspective of nonbreeders facing the “career decision” of when and where to settle. Because individuals cannot opt for two options with the same success (because of constraints in time and space), nonbreeders do best to choose between two strategies. In the first strategy, which we call the “QL strategy,” nonbreeders queue for low-

quality habitat and try to settle there. Individuals queuing for low-quality territories are likely to start reproducing at an early age and produce few offspring per year. In the second strategy, which we call the "QH strategy," nonbreeders wait (queue) for a high-quality territory to become available. Because competition for high-quality territories will be fierce, individuals queuing for high-quality territories (QHs) will not reproduce before a much older age than individuals queuing for low-quality territories (QLs). Moreover, individuals queuing for high-quality territories will have a high chance of dying before ever reproducing but, if successful, will produce many offspring per year. Although the two strategies have different short-term payoffs, the key question is whether they differ in long-term fitness. Furthermore, the success of both strategies directly depends on the frequency in the population at which nonbreeders choose to queue for either high- or low-quality territories, as this determines the strength of competition. Ens et al. (1995) argued that in evolutionary equilibrium, the proportion of nonbreeders that follows a QH or a QL strategy is such that the expected lifetime reproductive success is equal for both strategies. This makes intuitive sense, because if the fitness of one strategy is higher than the other, nonbreeders should switch to the strategy with higher payoff until fitness differences disappear because of intensified competition. It is important to note that the queue hypothesis takes a perspective fundamentally different from that of most other studies on delayed breeding (e.g., Oli et al. 2002; Krüger 2005 and references therein). In understanding the fitness consequences of delayed reproduction, the queue hypothesis takes into account the fate of both successful (i.e., recruited) and unsuccessful individuals (i.e., died before recruitment), while most other studies compare only the fitness of successful individuals that vary in age of first reproduction.

Shortcomings of the EWD Model

Although the general idea behind the queue hypothesis is attractive, the implementation of the model in EWD has three important shortcomings. First, EWD used a demographic model to calculate the expected lifetime reproductive success of queuers and subsequently used these results to calculate the evolutionarily stable strategy (ESS) in a separate model. However, these two models are not fully consistent. In fact, inserting the ESS into the demographic model yields a stage distribution that is inconsistent with the data and analyses on which the demographic model was based (ESS: N = 60%, H = 21%, L = 19%; demographic model: N = 31%, H = 28%, L = 41%). Therefore, we here use an approach that integrates the population dynamics and evolutionary dy-

namics of life-history strategies in one coherent model. Second, EWD did not include density regulation in their model. In fact, their ESS population increases indefinitely, which is not very realistic. Therefore, we here introduce population limitation in a natural way by setting a maximum on the number of suitable breeding territories. Third, the EWD model does not allow the investigation of the individual quality hypothesis. Ens et al. (1995) did not include individual differences in competitive abilities because there were no clear indications for such differences in oystercatchers. However, differences in competitive abilities are probably very common in many species (e.g., Stearns 1992), and it therefore seems important to incorporate them to generalize the applicability of the model. In fact, even in the population of oystercatchers described in the EWD study, we have recently shown that settlement patterns differ strongly between nonbreeders born in high- and low-quality habitats (van de Pol et al. 2006). Although this is not direct evidence for the existence of differences in competitive abilities, it does suggest that queuing strategies depend on natal origin. Therefore, we extend the original model to allow for conditional queuing strategies to evolve in which individuals born in high- and low-quality territories can use different queuing strategies. In this model, we assess how competitive asymmetries (i.e., individual quality differences) between nonbreeders born in high- and low-quality territories affect adaptive queuing decisions.

New Model with Unconditional Queuing Strategies

To address the first two shortcomings, we constructed a new version of the EWD model that combines the population dynamics and life-history strategies in one coherent model and also incorporates population regulation. We refer to this model as the unconditional model (i.e., not conditional on natal origin); the role of conditional queuing strategies is investigated in the next section. Our unconditional model is based on the graphical representation in figure 1A. The corresponding mathematical model and ESS can be analyzed using standard methods (e.g., Taylor 1990; Caswell 2001) and are described in full technical detail in appendix A in the online edition of the *American Naturalist*; below, we describe the major steps and main results.

The variable x represents the queuing strategy in the population; when $x = 0$, all individuals queue for high-quality territories; when $x = 1$, all individuals queue for low-quality territories. The changes in numbers of individuals queuing for high- and low-quality territories and the numbers of high- and low-quality territory owners can be described by a system of recurrence equations based on the flows between states in figure 1A. For reasons of

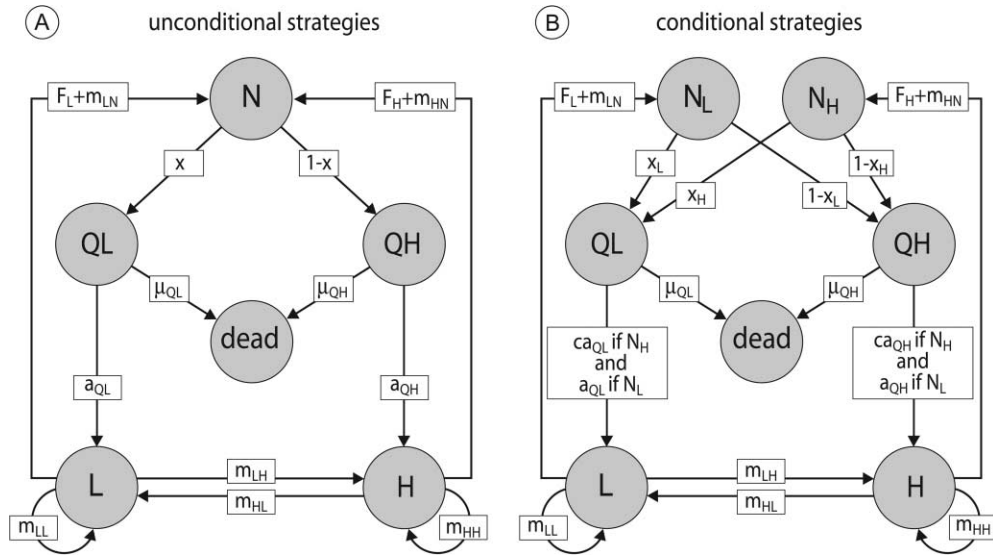


Figure 1: Schematic representation of a situation with (A) unconditional queuing strategies and (B) conditional queuing strategies. The parameter x represents the strategic choice individual nonbreeders (N) have to make to queue for either a high- or a low-quality territory (QH and QL, respectively). 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, are assumed to be externally given, and usually cannot be directly estimated in the field. 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 $\mu_L = 1 - m_{LL} - m_{LN} - m_{LH}$).

simplicity, several (implicit) assumptions are made in this model. First, we assume that all parameters are time, sex, and age independent. Second, we assume that the numbers of suitable high- and low-quality territories are fixed over time, thereby limiting the population (see “Discussion”). Because breeding opportunities are limited and there is a surplus of nonbreeders, the annual settlement probabilities of QHs and QLs (a_{QH} and a_{QL} , respectively) directly depend on the number of competitors, which is determined by the frequency of x in the population. All other parameters are assumed to be density and frequency independent. Third, we assume that the behavior of nonbreeders with breeding experience (breeders that have lost their territory) is similar to that of nonbreeders without breeding experience (see “Discussion”).

From our system of recurrence equations, we can derive the state-dependent reproductive values v , the relative contribution of different types of individuals to the population growth rate, which are the standard fitness measure in evolutionary cost-benefit analysis (e.g., Taylor 1990; Caswell 2001). To derive the ESS, we assessed the fitness of a mutant strategy x in an established population of individuals playing strategy x^* . The ESS is obtained by finding the value of x^* that cannot be invaded by any alternative

mutant strategy, since the established population has a higher fitness than all mutants. The queuing strategy of the established population (x^*) is implicitly contained in the annual settlement probabilities (a_{QH}^* and a_{QL}^*). It can be shown that coexistence of the QH and QL strategies at evolutionary equilibrium requires that their reproductive values be equal ($v_{QH}^* = v_{QL}^*$), confirming the result of EWD that at the ESS, both strategies must yield equal long-term fitness payoffs. From this condition, it follows that in evolutionary equilibrium, the ratio of QHs to QLs reflects the ratio of the expected benefits of the two types of strategies (app. A):

$$\frac{x^*}{1-x^*} = \frac{m_{NL}(v_L^* - v_{QL}^*)}{m_{NH}(v_H^* - v_{QH}^*)}. \quad (1)$$

This result was also obtained by EWD (their eq. [15]), although they used expected future reproductive success instead of reproductive values. They subsequently calculated x^* using realized settlement probabilities of nonbreeders (m_{NH} and m_{NL}). However, this approach has two important disadvantages. First, life-history parameters of nonbreeders, such as m_{NH} and m_{NL} , are notoriously difficult to reliably estimate in the field because of the incomplete

site fidelity of nonbreeders in many species. Second, the use of estimates of realized settlement probabilities from field data (m_{NH} and m_{NL}) to calculate the ESS is rather begging the question, as these same parameters are also used for model validation (i.e., they determine the age of first reproduction and recruitment patterns). Therefore, we took a different approach to calculating x^* that takes full advantage of the fact that we now have incorporated population limitation in our model. Because the total number of suitable territories is assumed to be fixed, the availability of empty territories for nonbreeders (and thereby settlement probabilities) can be predicted from the behavior of the breeders (breeder mortality, territory loss, and switching between habitats). In other words, in our model, settlement probabilities are generated by the model itself, resulting in an internally consistent model, while this was not the case in the EWD model. When we define q as the ratio of high- to low-quality territories and p as the ratio of the total production of new nonbreeders by high-quality territory owners to that of low-quality territory owners, the ESS value for x^* in equation (1) can be rewritten as (app. A)

$$x^* = \frac{(1 - m_{HH} + m_{LH}p)(1 - m_{LL} - m_{HL}q)}{[(1 - m_{HH})(1 - m_{LL}) - m_{HL}m_{LH}](1 + pq)}. \quad (2)$$

In equation (2), x^* is expressed as a function of several life-history parameters of breeders, which can be more reliably estimated than life-history parameters of nonbreeders (as in eq. [1]).

Conditional Queuing Strategies and Competitive Asymmetries

We extended the previous model to allow nonbreeders born in both high- and low-quality habitats (N_H and N_L) to make an independent choice of which strategy to follow (x_H and x_L , respectively; figure 1B). The strategic choice that N_H have to make can vary between $x_H = 0$, when all N_H become QHs and we have complete natal habitat preference, and $x_H = 1$, when all N_H become QLs and we have complete natal habitat avoidance. Similarly, for N_L , the choice varies between $x_L = 0$, when all individuals leave the habitat type they were born in, and $x_L = 1$, when all individuals return to the habitat type they were born in. In addition, we incorporated a new parameter, c , that reflects differences in competitive abilities between N_H and N_L . When $c = 1$, there are no competitive asymmetries; when $c > 1$, N_H are competitively superior over N_L , so that they have a c times higher annual probability of acquiring a territory; and the opposite holds for $c < 1$.

If there are no competitive asymmetries between N_H and N_L ($c = 1$), the ESS condition results in a neutral line

of equilibrium conditional strategies (x_H^* , x_L^*) given by (app. A)

$$x_L^* = \frac{(1 - m_{HH} + m_{LH}p)(1 - m_{LL} - m_{HL}q)}{(1 - m_{HH})(1 - m_{LL}) - m_{LH}m_{HL}} - pqx_H^*. \quad (3)$$

At the population level, the conditional strategies x_H^* and x_L^* yield an average strategy x^* that is identical to the population strategy in the unconditional model (eq. [2]). When $c = 1$, there is no selection pressure that results in one combination of x_H^* and x_L^* being favored over any other. Therefore, starting out with a population using unconditional queuing strategies ($x_H^* = x_L^* = x^*$), it is unlikely that conditional queuing strategies evolve.

When there are competitive asymmetries between N_H and N_L ($c \neq 1$), the ESS changes substantially (see app. A for details). Asymmetric conflicts generally do not allow for a completely mixed ESS (Maynard Smith and Parker 1976). Consequently, an ESS can exist only when at least one group of individuals plays a pure strategy. There are two candidate ESSs where N_H play a pure strategy, $x_H^* = 0$ and $x_H^* = 1$, and two candidate ESSs where N_L play a pure strategy, $x_L^* = 0$ and $x_L^* = 1$. Which of these four candidate equilibria is evolutionarily stable depends on the actual values of life-history parameters. Furthermore, the conditional equilibrium strategies x_H^* and x_L^* yield an average population strategy x^* that is no longer identical to the population strategy in the unconditional model.

Application of Models to Oystercatchers

Territory Quality and Delayed Reproduction in Oystercatchers

From 1984 to 2004, we studied an individually marked breeding population on the Dutch Wadden Sea island of Schiermonnikoog (53°29'N, 6°14'W). Oystercatchers are long-lived (>30 years) and socially and genetically monogamous and exhibit high site fidelity (Heg et al. 1993, 2003). In many oystercatcher populations, there is a clear dichotomy in habitat quality caused by permanent differences in the spatial organization of territories (Ens et al. 1992; Safriel et al. 1996). Some parents—called residents—have adjacent nesting and feeding territories, which allows them to take their chicks to the food. Other parents—called leapfrogs—have spatially separated nesting and feeding territories and are forced to bring the food to their chicks (see fig. 1 in Ens et al. 1992). Because transporting every food item to the chicks is less efficient, leapfrogs produce consistently fewer offspring per year than residents. Thus, we categorized leapfrog territories as low-quality territories and resident territories as high-quality

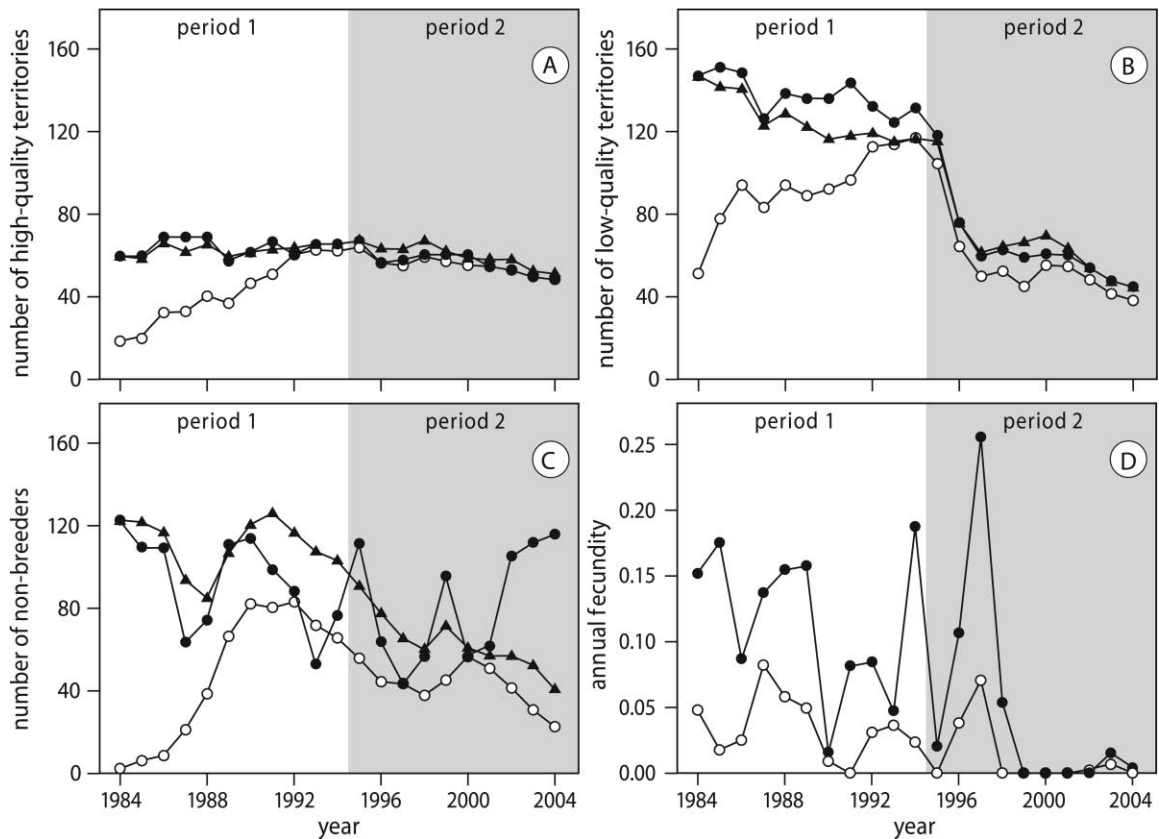


Figure 2: Changes in population numbers and fecundity from 1984 to 2004. Presented are the number of (A) high-quality territories, (B) low-quality territories, and (C) nonbreeders. In A–C, filled circles refer to the counted number of individuals in each state (T_H , T_L , and T_N), open circles refer to the number of color-ringed individuals, and triangles refer to the number of individuals predicted by a demographic model based on estimated life-history parameters (see text). D, Annual fecundity in high-quality territories (F_H ; filled circles) and in low-quality territories (F_L ; open circles). Period 1 (1984–1994) represents a situation where the population was in equilibrium and numbers were fairly stable, while in period 2 (1995–2004), the population was declining strongly.

territories. There is a surplus of adult nonbreeders that do not defend nesting territories. Juveniles differ in plumage from adults in their first 2 years of life; therefore, we assume that oystercatchers become sexually mature and join the adult nonbreeder pool when they reach the age of 3 years. Oystercatchers show large variation in age of first reproduction (range 3–11 years). Mortality occurs mainly in winter; subsequent status changes finalize before the breeding season.

Estimation of Model Parameters from Field Data

To make quantitative model predictions, we estimated the relevant model parameters from field data. We reestimated all parameters used by EWD because we now have more years of data, data from a larger area, and better statistical estimation procedures. For technical details of estimation procedures, annual values, and a comparison with EWD

estimates, see appendix B in the online edition of the *American Naturalist*. The number of high-quality territories (T_H ; fig. 2A) was half the number of occupied low-quality territories (T_L ; fig. 2B). There were substantial numbers of nonbreeders (T_N ; fig. 2C), but annual counts serve only as a rough indication because sampling error was large. Annual fecundity was defined as the annual number of female offspring produced by a pair that survived until adulthood and entered the local nonbreeder pool (young are philopatric; van de Pol et al. 2006). High-quality territories consistently had three times higher annual fecundity (F_H) than low-quality territories (F_L), except in years with no young (fig. 2D). Differences in territory quality in terms of annual fecundity are thus highly predictable. Annual probabilities of status change and state-dependent mortality were estimated using a multistate capture-recapture model (fig. 3). This model estimates all transition and mortality parameters simultaneously and

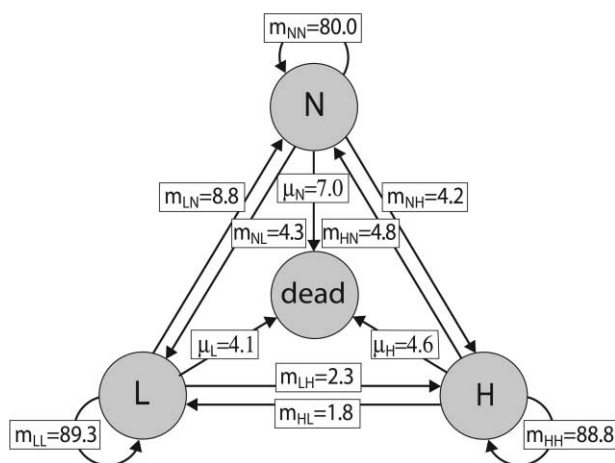


Figure 3: Annual state transition (m) and mortality (μ) probabilities (%) of owners of high- (H) and low-quality territories (L) and of nonbreeders (N). Values were estimated using a multistate mark-recapture model and are averages for period 1 (1984–1994).

accounts for the fact that not all individuals were always resighted. Furthermore, by comparing information from local resightings with recoveries of dead individuals from a much larger area, we could adjust estimates for permanent migration.

To assess the consistency of our estimates of life-history parameters with population counts, we constructed a demographic model (see van de Pol et al. 2006). We calculated the expected change in numbers over the study period by using the numbers per state in the first year of study as initial conditions and demographic rates of each year as projection matrices. Despite the fact that we were dealing with an open population, the demographic model described the counted population numbers well, indicating that both types of model parameters are consistent with each other (fig. 2). Because population dynamics changed systematically during the 21 years of study, we distinguished two periods. In the first period (1984–1994), numbers were fairly stable, and fecundity roughly balanced mortality; during the second period (1995–2004), most low-quality territories were abandoned, and fecundity was below replacement level (fig. 2). Furthermore, life-history parameters (co-)varied between years. Therefore, besides estimating mean values over the years, we also estimated their temporal variation and covariation (table B3 in the online edition of the *American Naturalist*). Using mean values and (co)variances of all life-history and population parameters, we constructed a multivariate normal distribution of all parameters that are used in the queuing models. From this distribution, we randomly drew 1,000 sets

of model input parameters, which were used to calculate confidence intervals around model predictions.

Application of the Unconditional Queue Model to Oystercatchers

We restricted the application of the queuing models to oystercatchers to period 1 (fig. 2). Using life-history parameters from period 2 in an equilibrium approach results in a situation where there are not enough new nonbreeders produced to queue for low-quality territories ($x^* = 0$). In addition, we assumed that there are no differential costs to the QH and QL strategies because prospecting behavior in oystercatchers is highly ritualized and fights are rare (Heg et al. 2000). The reason we were forced to assume that the two types of nonbreeders have similar annual mortality ($\mu_{QH} = \mu_{QL} = \mu_N$) is that in the field, it is difficult to attribute all nonbreeding oystercatchers to either the QH or the QL strategy.

By inserting parameter estimates averaged over period 1 in equation (2), we predict that 30% of all nonbreeders follow a QH strategy and 70% follow a QL strategy ($x^* = 0.70$; 95% confidence interval: 0.59–0.85). This result is exactly opposite to that of EWD, who predicted that 70% of all individuals followed a QH strategy ($x^* = 0.30$). This difference is not a consequence of differences in estimation of model parameters, because using EWD's field estimates in our model yielded $x^* = 0.66$. Conversely, when we insert the parameters estimated in this study in the EWD model, we found $x^* = 0.26$, confirming that differences between studies are caused by differences in modeling approach. Our results were quite robust to small deviations in mean values of model parameters (see sensitivity analysis in app. C in the online edition of the *American Naturalist*). Moreover, in contrast to the EWD model, the equilibrium stage distribution of our model fitted the proportions of nonbreeders and high- and low-quality territory owners in the field well (model: $N = 25\% \pm 4\%$, $H = 24\% \pm 3\%$, $L = 51\% \pm 3\%$; field: $N = 31\%$, $H = 22\%$, $L = 47\%$).

We calculated the expected life histories of individuals that queue for either a high- or a low-quality territory at evolutionary equilibrium (fig. 4). Within 3 years after sexual maturity, virtually all QLs are expected to have settled, with only a small proportion dying before ever reproducing (9%). In contrast, most queuers for high-quality territories have to wait a long time before they can start to reproduce, and consequently QHs have a high probability of dying before ever reproducing (39%). Although the model predicts that 70% of nonbreeders follow a QL strategy, competition is expected to be most fierce for the few high-quality territories. Individuals queuing for high-quality territories not only have fewer settlement options

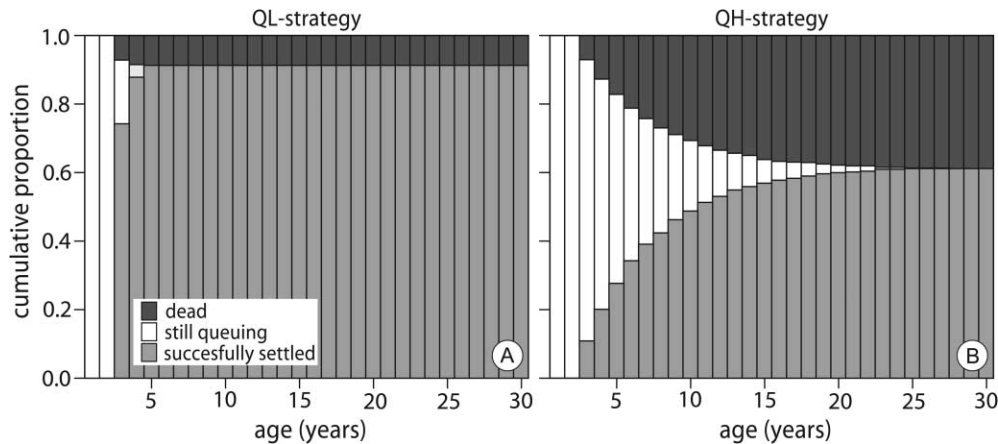


Figure 4: Predicted recruitment patterns of individuals that follow a strategy to queue for either (A) low-quality territories or (B) high-quality territories (unconditional model). Plotted are the changes in a cohort followed over time (i.e., age) of the proportions of (1) individuals that successfully settled, (2) individuals that are still queuing, and (3) individuals that died before ever settling. Note that we assume that oystercatchers become sexually mature when they reach the age of 3 years.

($T_L \gg T_H$) but also have to compete with the many low-quality territory owners switching to high-quality territories ($T_L m_{LH} \gg T_H m_{HL}$). Consequently, we expect, on average, 0.56 nonbreeders actively queuing per high-quality territory, while we expect only 0.13 nonbreeders queuing per low-quality territory.

The unconditional model predicted that in equilibrium, 22% of all successful recruits first settle in a high-quality territory and 78% in a low-quality territory, which is remarkably close to observed patterns in the field (20% and 80%, respectively; table 1, top). The unconditional model cannot explain why settlement patterns depend on natal origin in oystercatchers because it does not allow for conditional queuing strategies (see next section). Predicted age of first settlement was 4.3 years higher for QHs than for QLs (7.6 vs. 3.3 years; table 1, bottom). In the field, age of first settlement was only 1.1 year higher in high-quality territories than in low-quality territories (7.6 vs. 6.5 years; table 1, bottom). Although the observed difference of 1.1 years was statistically significant (ANOVA, settlement territory type: $P = .044$; sex: $P > .40$), it was considerably smaller than that predicted by the model. This discrepancy between model predictions and field data was due to the fact that in the field, QLs settled later than our model predicted.

Application of the Conditional Queue Model to Oystercatchers

When we assumed that there was no competitive asymmetry between nonbreeders of different natal origin ($c = 1$), the neutral line of equilibria (eq. [3]) was given by $x_L^* =$

$1.38 - 0.98x_H^*$, which includes the solution of the unconditional model (fig. 5). When we assumed that there were asymmetries in competitive abilities ($c \neq 1$), this line of equilibria disappeared, even for infinitesimally small asymmetries. This result shows that the assumption of no competitive asymmetries is rather specific and gives nonrobust results. For all scenarios where N_H are competitively superior over N_L ($c > 1$), only one ESS exists where all N_L become QLs ($x_L^* = 1$; pure strategy) and N_H become both QHs and QLs ($0 < x_H^* < 1$; mixed strategy). The exact value of x_H^* depends on how strong the competitive asymmetry is, but only weakly so (fig. 5). This weak dependence makes sense because there are so many low-quality territories that virtually all QLs can acquire a territory immediately; further increasing competitive asymmetries for a resource that is barely competed for has little additional effect. When $c < 1$, the situation of $x_L^* = 1$ is unstable, and an ESS is reached when $x_H^* = 1$ and $x_L^* = 0.40$ (for $c = 0.99$; fig. 5). Therefore, inferior competitors always do best to follow a pure strategy of opting for the resource for which there is least competition. When competitive asymmetries exist ($c \neq 1$), the average queuing strategy in the population x^* is always higher than that in the unconditional model, but this difference is small (<5%) for a wide range of c values.

Conditional strategies, in combination with even very small differences in competitive abilities, can explain a striking feature of settlement patterns in oystercatchers. Namely, the observation that oystercatchers born in low-quality territories virtually always settled in low-quality territories (cf. pure strategy), while oystercatchers born in high-quality territories settled in both type of territories (cf. mixed strategy), is qualitatively in agreement with the

Table 1: Comparing settlement patterns and age of first reproduction (years) of model predictions with observed values in the field

Settlement strategy	Unconditional model		Conditional model					
	All offspring ($N_H + N_L$)		Offspring born in high-quality habitat (N_H)			Offspring born in low-quality habitat (N_L)		
	Observed	Predicted	Observed	Predicted, $c = 1.01$	Predicted, $c = 5$	Observed	Predicted, $c = 1.01$	Predicted, $c = 5$
Settlement pattern (%):								
Successful QH	20.0	22.4 ± 7.5	18.2	22.4 ± 7.5	24.8 ± 7.5	1.8	0	0
Successful QL	80.0	77.6 ± 7.5	52.7	21.8 ± 7.7	39.4 ± 7.6	27.3	55.8 ± 4.2	35.8 ± 4.6
Successful N (QH + QL)	100	100	70.9	44.2 ± 4.2	64.2 ± 4.1	29.1	55.8 ± 4.2	35.8 ± 4.6
Age of first reproduction (years):								
Successful QH	7.6 ± .5 (11)	7.6 ± 1.6	7.5 ± .3 (10)	7.6 ± 1.6	7.5 ± 1.6	8.0 (1)
Successful QL	6.5 ± .3 (44)	3.3 ± 1.3	6.5 ± .5 (29)	3.3 ± 1.3	3.1 ± 1.2	6.5 ± .2 (15)	3.3 ± 1.3	3.6 ± 1.3
Successful N (QH + QL)	6.8 ± .3 (55)	4.3 ± 1.7	6.9 ± .3 (39)	5.5 ± 1.3	5.3 ± 1.3	6.6 ± .7 (16)	3.3 ± 1.3	3.6 ± 1.3

Note: Values are given for all offspring combined (unconditional queue model) and for offspring separated by their natal origin (conditional queue model with competitive asymmetries $c = 1.01$ or 5). Field data were calculated using all recruits born in 1984–1994 that recruited in the period 1984–2004 ($n = 55$; detection probability of first-time breeders is virtually 1). Observed values are given ±SE, and sample sizes are given in parentheses for age of first reproduction. Predicted values are given ±SE and were calculated with the use of 1,000 bootstrapped data sets (see text).

predictions from conditional queuing models that assume that N_H are competitively superior over N_L ($c = 1.01$; table 1, top). The quantitative agreement between settlement patterns in the field and model predictions improved even more when we assumed large competitive asymmetries ($c = 5$; table 1, top). Conditional queuing models did not explain patterns of age of first settlement in the field better than the unconditional model. Age of first settlement in the field also did not differ between offspring born in high- and low-quality habitats (6.9 vs. 6.6 years), whereas they were predicted to differ by about 2 years under conditional queuing strategies (table 1, bottom).

Discussion

General Insights from Queuing Models

In this study, we first reproduced the main result of EWD: in evolutionary equilibrium, nonbreeders should distribute themselves in such a way over both strategies that the lifetime fitness of both strategies is equal. Delayed reproduction and breeding in low-quality habitat can therefore be part of an adaptive strategy. However, the ESS we derived was substantially different from the ESS in EWD. We think that our evolutionarily stable queuing strategy is more accurate because it is based on a model that combines population dynamics and evolutionary dynamics of life-history strategies in one internally consistent model and also incorporates population regulation. Several other studies have emphasized that evolutionary predictions can strongly depend on assumptions about how populations are regulated (e.g., Mylius and Diekmann 1995; Pen and Weissing 2000). At the same time, our understanding is rather limited as to how populations are regulated and

which demographic rates are density dependent in the wild. In this study, we have incorporated population limitation in a simple—but, we think, also biologically plausible—way by fixing the number of suitable territories. Thereby, we do not imply that there is no empty habitat available for additional territories (or that territories cannot split up). However, we do assume that any nonoccupied habitat is of such low quality that it is below the acceptance threshold of nonbreeders; otherwise, it would have been occupied by surplus nonbreeders. The idea of the existence of an acceptance threshold is supported by results from queuing models that investigated the logic of territory choice, which predict a fixed evolutionarily stable threshold quality above which territories are acceptable for nonbreeders (Kokko and Sutherland 1998; Kokko et al. 2001; Pen and Weissing 2001).

We extended the original queue model to allow conditional queuing strategies to evolve (i.e., dependent on natal origin). Thereby, we investigated whether the queue hypothesis can also explain individual variation in settlement strategies. We show that if no competitive asymmetries exist, conditional strategies are unlikely to evolve. However, even very small competitive asymmetries between individuals, which are probably plentiful in nature, will facilitate the evolution of conditional strategies. Thus, individual quality differences in the form of competitive asymmetries strongly affect adaptive queuing decisions at the individual level, emphasizing the importance of investigating the adaptive queuing hypothesis and individual quality hypothesis together instead of separately. This poses the question of to what extent the incorporation of conditional strategies and individual quality differences might also affect predictions from other queuing models

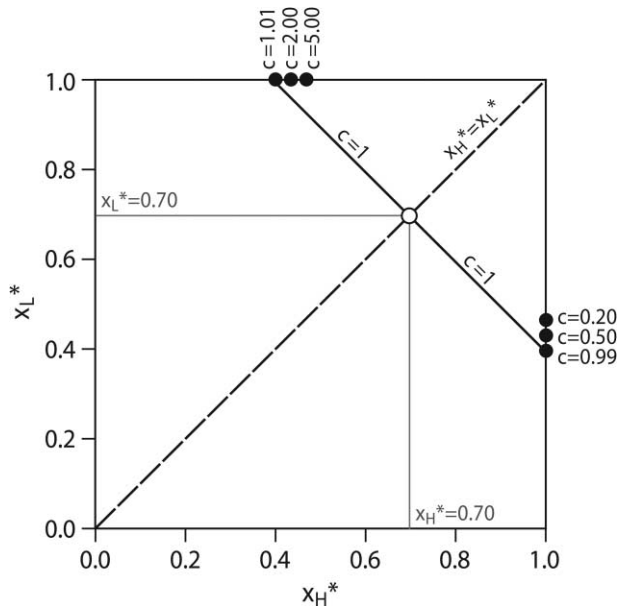


Figure 5: Evolutionarily stable strategy (ESS) values of the strategic queuing variables $x_{H_i}^*$ and $x_{L_i}^*$ for various degrees of competitive asymmetry (c). When $c = 1$ (no competitive asymmetry), there is a line of equilibria (solid line) that contains the ESS of the unconditional model ($x_{H_i}^* = x_{L_i}^* = x^* = 0.70$; open circle). When $c \neq 1$, there always is only one ESS (filled circles), either an ESS where $x_{L_i}^*$ is a pure strategy (for all $c > 1$) or an ESS where $x_{H_i}^*$ is a pure strategy (for all $c < 1$).

that have ignored such differences for reasons of simplicity. In this study, we incorporated individual quality differences as a function of natal origin. Although effects of early conditions are thought to be very important in nature (Lindström 1999), queuing strategies and competitive asymmetries could also depend on other factors, such as breeding experience. We suspect that other sources of variation in individual quality will also strongly affect adaptive queuing strategies at the individual level but not necessarily at the population level.

Oystercatcher Settlement Patterns: Adaptive Queuing and/or Quality Differences?

The oystercatcher is an interesting test case of the queue hypothesis because oystercatchers exhibit strong variation in both age of first reproduction and territory quality. Our queuing models were able to predict several striking features of settlement patterns in oystercatchers: (1) age of first reproduction was higher in high-quality habitat than in low-quality habitat; (2) the proportion of first-time recruits that settled in either high- or low-quality habitat was exactly as predicted; and (3) nonbreeders born in low-quality territories virtually never settled in high-quality

territories, which is consistent with individuals born in low-quality territories playing a pure QL strategy. These results strongly suggest that oystercatchers make adaptive queuing decisions.

The degree to which individual quality differences affect settlement decisions in oystercatchers is less clear. The agreement between model predictions and oystercatchers' settlement pattern strongly improved when we assumed small differences in competitive abilities. The quantitative agreement between model predictions and field data became even better when we assumed very large differences in competitive abilities. Although it does not seem implausible that very small differences in competitive abilities were overlooked, these results seem to be in sharp contrast with the lack of evidence for strong differences in competitive abilities in oystercatchers (EWD; Bruinzeel et al. 2006). Possibly, the discrepancy is not as strong as we think but might be (partially) caused by the difficulty of measuring differences in competitive abilities between nonbreeders in the field. Observation of physical fights between nonbreeders are rare, and outcomes of ritualized fights are strongly site dependent in oystercatchers (Heg et al. 2000). Consequently, both studies had to rely on indirect measures of competitive abilities over breeding territories, such as morphology and fights on feeding grounds or in captivity. Clearly, evidence from more direct measures of differences in competitive abilities over breeding territories between nonbreeders is crucial. In fact, given that individuals born in high-quality habitat are 10% heavier at fledging than individuals born in low-quality habitat (van de Pol et al. 2006), we would not be surprised if future research indicates that natal origin does indeed influence competitive abilities in oystercatchers. Although, at the moment, this part of the puzzle remains unsolved, it does point out a more general problem. Our queuing models are very sensitive to assumptions about competitive asymmetries, while detecting such differences in the wild is likely to be difficult in many species (i.e., how to measure parameter c).

Although the observation that age of first reproduction is higher in high-quality habitat than in low-quality habitat was qualitatively in agreement with the queuing models, the difference in age of first reproduction in the wild was 3 years less than predicted. This discrepancy was because age of first reproduction of oystercatchers in low-quality territories was higher than predicted. Two alternative individual quality hypotheses might explain this discrepancy. First, the high age of first settlement in low-quality habitat in the field might suggest that nonbreeders that queue for low-quality habitat reach sexual maturity later in life than others. Similarly, if queuing for low-quality territories is less costly than queuing for high-quality territories ($\mu_{QL} < \mu_{QH}$), this would also increase the predicted age of

first settlement in low-quality habitat. Second, except for differences in natal background, we implicitly assumed that all queuing individuals had an equal chance of acquiring the territory they were queuing for (“random-order service”). However, queues of oystercatchers probably more strongly resemble strict queuing (“first in, first out”), because social dominance seems to improve gradually during queuing and subsequently facilitates territory acquisition (Heg et al. 2000; Bruinzeel and van de Pol 2004). For example, oystercatchers with breeding experience have a higher annual settlement probability than inexperienced nonbreeders (Bruinzeel 2007). Incorporating mechanisms into our models that structure queues into hierarchies based on breeding experience is likely to result in a predicted age of first settlements in low-quality habitat that is closer to those in the field.

Population Consequences of Queuing Strategies

Although we applied our queuing models to period 1 only, period 2 provides some useful insights into the consequences of queuing processes at the population level. During period 2, the number of low-quality territories halved, while the number of high-quality territories and, most interesting, also the number of nonbreeding oystercatchers remained fairly stable (fig. 2). This pattern of population decline supports the idea that nonbreeders can discriminate between the quality of different habitats because vacancies in high-quality habitat were reoccupied, while many vacancies in low-quality habitat remained empty in period 2. Furthermore, the abandonment of low-quality territories in the presence of many nonbreeders strongly suggests that these nonbreeders preferred to queue for a high-quality territory instead of settling in vacated low-quality territories. But why would surplus nonbreeders choose not to occupy vacant low-quality territories in period 2, while they were willing to do so in period 1? We think that this change in queuing behavior results from a general decline in environmental quality from period 1 to period 2, caused by a drop in food supplies (Bruinzeel and van de Pol 2003). In period 1, the reproductive value of breeding in a low-quality territory was still slightly higher (10%) than the reproductive value of nonbreeders. When in period 2 fecundity dropped as a result of low hatching success, nonbreeders probably perceived the value of many low-quality territories to be reduced below the threshold value for territory acceptance and therefore stopped queuing for them ($v_L < v_N$; see Kokko and Sutherland 1998; Pen and Weissing 2001). This idea is further supported by recent observations of pairs that abandoned their low-quality territory to become nonbreeders, while there were no indications for widowing, divorce, or takeovers (M. van de Pol, personal observation). Consequently,

population productivity in period 2 was probably lower than it would have been had nonbreeders reoccupied all empty low-quality habitat. Thus, although queuing behavior might be optimal for individuals, it generally is not for the population (e.g., Kokko et al. 2001). Therefore, for understanding both life-history decisions and population dynamics, studying the behavior of individuals that do not (yet) reproduce might be as important as studying the behavior of the reproductive part of the population.

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Appendix A from M. van de Pol et al., “Variation in Habitat Choice and Delayed Reproduction: Adaptive Queuing Strategies or Individual Quality Differences?”

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Models and Derivation of the Evolutionarily Stable Strategies

The Unconditional Queue Model

The Model

Ens et al. (1995) used a separate demographic and game-theoretical model to quantify the evolutionarily stable queuing strategy. Here we integrate both types of analysis into one coherent model, which—as we show below—has several crucial advantages. The structure of our model is based on the life-cycle plot in figure 1A. The change in density from year t to year $t + 1$ of queuers for high- and low-quality territories (n_{QH} and n_{QL} , respectively) and of high- and low-quality territory owners (n_H and n_L , respectively), is described by the following system of recurrence equations (e.g., Caswell 2001):

$$\begin{pmatrix} n_{QH} \\ n_{QL} \\ n_H \\ n_L \end{pmatrix}_{t+1} = \begin{pmatrix} 1 - \mu_{QH} - a_{QH}^* & 0 & (1-x)(F_H + m_{HN}) & (1-x)(F_L + m_{LN}) \\ 0 & 1 - \mu_{QL} - a_{QL}^* & x(F_H + m_{HN}) & x(F_L + m_{LN}) \\ a_{QH}^* & 0 & m_{HH} & m_{LH} \\ 0 & a_{QL}^* & m_{HL} & m_{LL} \end{pmatrix} \begin{pmatrix} n_{QH} \\ n_{QL} \\ n_H \\ n_L \end{pmatrix}_t. \quad (A1)$$

The matrix elements correspond to the parameters of the life-cycle plot in figure 1A. The strategic parameter x reflects the proportion of nonbreeders following the strategy of queuing for a low-quality territory (QLs), while $1 - x$ corresponds to the proportion of nonbreeders that follows the strategy of queuing for a high-quality territory (QHs). We assess here the performance of a mutant strategy x in a population consisting of individuals playing strategy x^* . The established strategy x^* is indirectly reflected by the annual settlement probabilities in high- and low-quality habitat (a_{QH}^* and a_{QL}^* , respectively). Equation (A1) corresponds to a system of the form $\mathbf{n}_{t+1} = \mathbf{A}(x, x^*)\mathbf{n}_t$, where \mathbf{n} is a vector of the numbers of individuals in each state and $\mathbf{A}(x, x^*)$ is the projection matrix of the population for strategy x in an established population of x^* . In the long term, the population projection reaches an equilibrium with a stable stage distribution given by $\mathbf{n} = (n_{QH}, n_{QL}, n_H, n_L)$ and a growth rate λ . We assume that the numbers of suitable high- and low-quality territories are fixed over time by setting $n_H^* = T_H$ and $n_L^* = T_L$, respectively, which results in a stationary population ($\lambda^* = 1$). Thereby, we introduce density-dependent settlement probabilities because breeding territories are a limiting resource and surplus individuals have to become nonbreeders. By fixing the state variables n_H and n_L , equation (A1) reduces to a system with only two state variables, and we can derive the equilibrium probabilities that a QH or a QL will ever settle (by setting $\mathbf{n}_{t+1} = \mathbf{n}_t$):

$$\frac{a_{QH}^*}{a_{QH}^* + \mu_{QH}} = \frac{T_H(1 - m_{HH}) - T_L m_{LH}}{(1 - x^*)[T_H(F_H + m_{HN}) + T_L(F_L + m_{LN})]} \quad (A2a)$$

and

$$\frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} = \frac{T_L(1 - m_{LL}) - T_H m_{HL}}{x^*[T_H(F_H + m_{HN}) + T_L(F_L + m_{LN})]}. \quad (A2b)$$

These equations have a clear-cut interpretation: for example, the probability a QH will ever settle (left-hand

side of eq. [A2a]) depends on the number of vacant high-quality territories divided by the total number of individuals following the QH strategy (right-hand side of eq. [A2a]). To perform an evolutionary cost-benefit analysis, we calculated the reproductive values (v), which can be found by solving $\mathbf{v}^T = \mathbf{v}^T \mathbf{A}$ (e.g., Taylor 1990):

$$v_{\text{QH}}^* = (1 - a_{\text{QH}}^* - \mu_{\text{QH}})v_{\text{QH}}^* + a_{\text{QH}}^*v_{\text{H}}^*, \quad (\text{A3a})$$

$$v_{\text{QL}}^* = (1 - a_{\text{QL}}^* - \mu_{\text{QL}})v_{\text{QL}}^* + a_{\text{QL}}^*v_{\text{L}}^*, \quad (\text{A3b})$$

$$v_{\text{H}}^* = (1 - x^*)(F_{\text{H}} + m_{\text{HN}})v_{\text{QH}}^* + x^*(F_{\text{H}} + m_{\text{HN}})v_{\text{QL}}^* + m_{\text{HH}}v_{\text{H}}^* + m_{\text{HL}}v_{\text{L}}^*, \quad (\text{A3c})$$

$$v_{\text{L}}^* = (1 - x^*)(F_{\text{L}} + m_{\text{LN}})v_{\text{QH}}^* + x^*(F_{\text{L}} + m_{\text{LN}})v_{\text{HL}}^* + m_{\text{LH}}v_{\text{H}}^* + m_{\text{LL}}v_{\text{L}}^*. \quad (\text{A3d})$$

The interpretation of the reproductive values is straightforward. For example, the reproductive value of an individual queuing for a high-quality territory (v_{QH}) equals the probability of remaining a QH times the reproductive value of a QH plus the probability of becoming a high-quality territory owner times the reproductive value of high-quality territory owners (v_{H}). Similarly, the reproductive value of a high-quality territory owner (v_{H}) is the sum of (1) the number of offspring produced that become QHs times v_{QH} , (2) the number of offspring produced that become QLs times v_{QL} , (3) the probability of staying a high-quality territory owner times v_{H} , and (4) the probability of moving to a low-quality territory times v_{L} . Equations (A3a) and (A3b) can be expressed in simpler form:

$$v_{\text{QH}}^* = \frac{a_{\text{QH}}^*}{a_{\text{QH}}^* + \mu_{\text{QH}}} v_{\text{H}}^* \quad (\text{A4a})$$

and

$$v_{\text{QL}}^* = \frac{a_{\text{QL}}^*}{a_{\text{QL}}^* + \mu_{\text{QL}}} v_{\text{L}}^*. \quad (\text{A4b})$$

Again, these equations have an intuitive meaning: the reproductive values of individuals queuing for high- or low-quality territories equal the probability of ever settling in high- or low-quality habitat times the reproductive value in high- or low-quality habitat, respectively (see also eqq. [11], [12] in EWD). Furthermore, because we are interested only in comparisons between groups of individuals, we can normalize all reproductive values to the reproductive value of low-quality territory owners. By inserting equations (A4a) and (A4b) into equations (A3c) and (A3d), respectively, solving for v_{H} and v_{L} and dividing the resulting equations, we find

$$\frac{v_{\text{H}}^*}{v_{\text{L}}^*} = \frac{(1 - m_{\text{LL}})p + m_{\text{HL}}}{1 - m_{\text{HH}} + m_{\text{LH}}p}, \quad (\text{A4c})$$

where $p = (F_{\text{H}} + m_{\text{HN}})/(F_{\text{L}} + m_{\text{LN}})$.

Calculating the Evolutionarily Stable Strategy

We can find the evolutionarily stable strategy (ESS) by calculating the value of x^* where no mutant strategy $x \neq x^*$ can invade. At an ESS, the fitness $\lambda(x, x^*)$ of each mutant is smaller than the fitness $\lambda(x^*, x^*)$ of the predominant strategy. Here, $\lambda(x, x^*)$ is defined as the relative growth rate of a mutant x in the established population x^* and is given by the dominant eigenvalue of \mathbf{A} . At an ESS, the selection gradient has to be 0 (e.g., Taylor 1990). This equilibrium condition can be expressed in terms of reproductive values and the deviations of the elements of matrix $\mathbf{A}(x, x^*)$ with respect to the strategic variable x :

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

To check the stability of such an equilibrium, higher-order conditions have to be checked as well, which we

skip here to avoid technical detail. In our case, all but four terms in equation (A5) vanish, and in view of $n_H^* = T_H$ and $n_L^* = T_L$, we obtain

$$(v_{QL}^* - v_{QH}^*)[T_H(F_H + m_{HN}) + T_L(F_L + m_{LN})] = 0, \quad (A6)$$

from which it can be seen that at an ESS, $v_{QH}^* = v_{QL}^*$; in other words, individuals that decide to queue for high- and low-quality habitat can coexist at equilibrium only if they have the same reproductive value. This corresponds to the result of EWD that at an ESS, both strategies must yield equal fitness payoffs. The ESS x^* can be found by finding the value of x^* where the condition $v_{QH}^* = v_{QL}^*$ is satisfied. For comparison reasons, we first express this equality condition in a form similar to EWD’s. By equating equation (A3a) with equation (A3b), we find

$$\frac{x^*}{1 - x^*} = \frac{m_{NL}(v_L^* - v_{QL}^*)}{m_{NH}(v_H^* - v_{QH}^*)}, \quad (A7)$$

where $m_{NH} = (1 - x^*)a_{QH}^*$ and $m_{NL} = x^*a_{QL}^*$, which is equivalent to equation (15) in EWD (although EWD used expected future reproductive success instead of reproductive values). Equation (A7) (also given as eq. [1]) shows that in evolutionary equilibrium, the ratio of QH individuals to QLs reflects the ratio of the expected benefits of the two types of strategies. Ens et al. (1995) subsequently calculated x^* using settlement probabilities of nonbreeders derived from field data (m_{NH} and m_{NL}). However, this approach has two important disadvantages. First, life-history parameters of nonbreeders, such as m_{NH} and m_{NL} , are notoriously difficult to reliably estimate in the field because of the incomplete site fidelity of nonbreeders in many species. Second, the use of estimates of settlement probabilities from field data to calculate the ESS is not ideal because these same parameters are also indirectly used for model validation (i.e., they determine the age of first reproduction and recruitment probabilities). Therefore, we took a different approach to calculating x^* , one that takes full advantage of the fact that we have incorporated population limitation in our model. Because the total number of suitable territories is fixed, the availability of empty suitable territories for nonbreeders and thereby settlement probabilities can also be predicted from the behavior of the breeders (see eqq. [A2]). In other words, in our model, settlement probabilities are generated by the model itself, resulting in an internally consistent model, while this was not the case in the EWD model. By equating equation (A4a) to equation (A4b) and using equations (A2a), (A2b), and (A4c), as well as the reparameterization $q = T_H/T_L$, we find

$$x^* = \frac{(1 - m_{HH} + m_{LH}p)(1 - m_{LL} - m_{HL}q)}{[(1 - m_{HH})(1 - m_{LL}) - m_{HL}m_{LH}](1 + pq)}, \quad (A8)$$

(also given as eq. [2]), which shows that the evolutionarily stable queuing strategy x^* is dependent on the relative—rather than absolute—number of territories ($q = T_H/T_L$) as well as on the relative—rather than absolute—influx of new nonbreeders from high- and low-quality territories ($p = (F_H + m_{HN})/(F_L + m_{LN})$). More importantly, x^* is expressed as a function of several life-history parameters of breeders, which can be more reliably estimated than those of nonbreeders (as in eq. [A7]). The average time it takes a successful QH to acquire a high-quality territory is given by $1/(a_{QH}^* + \mu_{QH})$ (EWD). From this, we can calculate the predicted age at first reproduction of successful QHs by adding the age of sexual maturity to this value (similar for QLs).

The Conditional Queue Model

The Model

We extend the previous model by allowing nonbreeders born in high- (N_H) or low-quality territories (N_L) to make an independent choice of which strategy to follow (x_H or x_L ; see fig. 1B). In addition, we incorporate a new parameter, c , that represents differences in competitive abilities between N_H and N_L . We now get the following set of recurrence equations:

$$\begin{pmatrix} n_{QH(H)} \\ n_{QL(H)} \\ n_{QH(L)} \\ n_{QL(L)} \\ n_H \\ n_L \end{pmatrix}_{t+1} = \begin{pmatrix} 1 - \mu_{QH} - ca_{QH}^* & 0 & 0 & 0 & (1 - x_H)(F_H + m_{HN}) & 0 \\ 0 & 1 - \mu_{QL} - ca_{QL}^* & 0 & 0 & x_H(F_H + m_{HN}) & 0 \\ 0 & 0 & 1 - \mu_{QH} - a_{QH}^* & 0 & 0 & (1 - x_L)(F_L + m_{LN}) \\ 0 & 0 & 0 & 1 - \mu_{QL} - a_{QL}^* & 0 & x_L(F_L + m_{LN}) \\ ca_{QH}^* & 0 & a_{QH}^* & 0 & m_{HH} & m_{LH} \\ 0 & ca_{QL}^* & 0 & a_{QL}^* & m_{HL} & m_{LL} \end{pmatrix} \begin{pmatrix} n_{QH(H)} \\ n_{QL(H)} \\ n_{QH(L)} \\ n_{QL(L)} \\ n_H \\ n_L \end{pmatrix}, \quad (A9)$$

where $n_{QH(H)}$ refers to nonbreeders born in high-quality territories that follow a QH strategy, and so forth. When $c = 1$, there are no competitive asymmetries; when $c > 1$, N_H are competitively superior to N_L , so that they have a c times higher annual probability of acquiring a high- or low-quality territory; the opposite holds when $c < 1$. Reproductive values are now given by

$$v_{QH(H)}^* = \frac{ca_{QH}^*}{ca_{QH}^* + \mu_{QH}} v_H^* = \frac{q(1 - m_{HH}) - m_{LH} - (1 - x_L^*)(F_L + m_{LN})a_{QH}^*/(a_{QH}^* + \mu_{QH})}{(1 - x_H^*)(F_H + m_{HN})q} v_H^*, \quad (A10a)$$

$$v_{QL(H)}^* = \frac{ca_{QL}^*}{ca_{QL}^* + \mu_{QL}} v_L^* = \frac{1 - m_{LL} - m_{HL}q - x_L^*(F_L + m_{LN})a_{QL}^*/(a_{QL}^* + \mu_{QL})}{x_H^*(F_H + m_{HN})q} v_L^*, \quad (A10b)$$

$$v_{QH(L)}^* = \frac{a_{QH}^*}{a_{QH}^* + \mu_{QH}} v_H^* = \frac{q(1 - m_{HH}) - m_{LH} - (1 - x_H^*)(F_H + m_{HN})qca_{QH}^*/(ca_{QH}^* + \mu_{QH})}{(1 - x_L^*)(F_L + m_{LN})} v_H^*, \quad (A10c)$$

$$v_{QL(L)}^* = \frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} v_L^* = \frac{1 - m_{LL} - m_{HL}q - x_H^*(F_H + m_{HN})qca_{QL}^*/(ca_{QL}^* + \mu_{QL})}{x_L^*(F_L + m_{LN})} v_L^*, \quad (A10d)$$

$$\frac{v_H^*}{v_L^*} = \frac{1 - m_{LL} - x_L^*(F_L + m_{LN})a_{QL}^*/(a_{QL}^* + \mu_{QL})}{m_{LH} + (1 - x_L^*)(F_L + m_{LN})a_{QH}^*/(a_{QH}^* + \mu_{QH})}. \quad (A10e)$$

Note that if competitive asymmetries affected nonbreeder mortality (μ_{QH}/c'), for example, because of competition over food, this would result in qualitatively the same reproductive values as in the case of competitive asymmetries in settlement probabilities (ca_{QH}^* and ca_{QL}^*); this is a matter of rescaling.

Calculating the Evolutionarily Stable Strategy

We now have to evaluate the selection gradients for both strategic parameters, x_H and x_L , simultaneously:

$$\left. \frac{\partial \lambda(x_H, x_H^*)}{\partial x_H} \right|_{x_H = x_H^*} \propto (v_{QL(H)} - v_{QH(H)})T_H(F_H + m_{HN}) = 0 \quad (A11a)$$

and

$$\left. \frac{\partial \lambda(x_L, x_L^*)}{\partial x_L} \right|_{x_L = x_L^*} \propto (v_{QL(L)} - v_{QH(L)})T_L(F_L + m_{LN}) = 0. \quad (A11b)$$

At an interior equilibrium ($0 < x_H^* < 1$, $0 < x_L^* < 1$), both conditions have to be satisfied, yielding $v_{QH(H)} = v_{QL(H)}$ and $v_{QH(L)} = v_{QL(L)}$. These conditions can be rewritten using equation (A10):

$$\frac{v_H}{v_L} = \frac{ca_{QL}^*}{ca_{QL}^* + \mu_{QL}} \frac{ca_{QH}^* + \mu_{QH}}{ca_{QH}^*} \quad (A12a)$$

and

$$\frac{v_H}{v_L} = \frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} \frac{a_{QH}^* + \mu_{QH}}{a_{QH}^*}. \quad (\text{A12b})$$

When $c = 1$, these conditions are identical; consequently, both fitness functions are simultaneously optimized. Proceeding as before, we can show that both equation (A12a) and equation (A12b) imply that

$$x_L^* = \frac{(1 - m_{HH} + m_{LH}p)(1 - m_{LL} - m_{HL}q)}{(1 - m_{HH})(1 - m_{LL}) - m_{LH}m_{HL}} - pqx_H^* \quad (\text{A13})$$

(also given as eq. [3]). When $c = 1$, there is no asymmetry in the model parameters between N_H and N_L ; hence, the strategy space is overparameterized, which results in a line of neutral equilibria of many different combinations of x_H^* and x_L^* . We verified whether the two conditional strategies x_H^* and x_L^* yield the same queuing strategy at the population level as the unconditional model (x^*) by describing the population strategy in the conditional model as a weighted average of the conditional strategies:

$$x^* = \frac{x_L^*N_L + x_H^*N_H}{N_L + N_H} = \frac{x_L^* + pqx_H^*}{1 + pq}. \quad (\text{A14})$$

If we insert x_L^* from equation (A13) in equation (A14), we return to the x^* from the unconditional queue model (eq. [A8]), thereby demonstrating that all different combinations of x_H^* and x_L^* in the conditional model yield the same population strategy x^* as in the unconditional model. In the absence of competitive differences, there is no mathematical reason to assume that one combination of x_H^* and x_L^* is more likely than any other. However, starting out with a monomorphic population that plays strategy x^* , there is no selection pressure that results in x_H^* being different from x_L^* in the unconditional model without competitive asymmetries (i.e., $x_H^* = x_L^* = x^*$).

When $c \neq 1$, there is an asymmetry in competitive abilities that directly affects the settlement probabilities in both types of habitat. When an asymmetry is included, the two conditions required for an interior equilibrium (eqq. [A12a], [A12b]) cannot be simultaneously met, and their solutions will be generically different if $c \neq 1$. Hence, we recover the principle that asymmetric conflicts do not allow a completely mixed ESS (Maynard Smith and Parker 1976). At an ESS, either x_H^* have to play a pure strategy (i.e., $x_H^* = 0$ or $x_H^* = 1$) or x_L^* have to play a pure strategy (i.e., $x_L^* = 0$ or $x_L^* = 1$), resulting in four candidate ESSs. If x_H^* plays a pure strategy, the selection gradient $[\partial\lambda(x_H, x_H^*)/\partial x_H]_{x_H=x_H^*}$ is not required to be 0. Instead, $x_H^* = 0$ will be stable if $[\partial\lambda(x_H, x_H^*)/\partial x_H]_{x_H=0} < 0$ (i.e., selection favors smaller values of x_H); the corresponding ESS x_L^* can be found by solving $[\partial\lambda(x_L, x_L^*)/\partial x_L]_{x_L=x_L^*, x_H^*=0} = 0$. Similarly, $x_H^* = 1$ will be stable if $[\partial\lambda(x_H, x_H^*)/\partial x_H]_{x_H=1} > 0$ (i.e., selection favors larger values of x_H); the corresponding ESS x_L^* can be found by solving $[\partial\lambda(x_L, x_L^*)/\partial x_L]_{x_L=x_L^*, x_H^*=1} = 0$. The ESS conditions for $x_L^* = 0$ and $x_L^* = 1$ are analogous.

Appendix B from M. van de Pol et al., “Variation in Habitat Choice and Delayed Reproduction: Adaptive Queuing Strategies or Individual Quality Differences?”

(Am. Nat., vol. 170, no. 4, p. 000)

Estimation of Annual Values of Population and Life-History Parameters

Table B1

Annual counts of high- and low-quality territories (T_H and T_L), nonbreeder counts (T_N), total population size, and annual fecundity in high- and low-quality territories (F_H and F_L)

Year	Population numbers				Fecundity	
	T_H	T_L	T_N	Total	F_H	F_L
Period 1:						
1984	60 ^a	148 ^a	123	331 ^a	.153	.048
1985	60 ^a	151 ^a	110	321 ^a	.177	.017
1986	69 ^a	149 ^a	110	328 ^a	.088	.025
1987	69 ^a	126 ^a	64	259 ^a	.138	.084
1988	69 ^a	139 ^a	75	282 ^a	.155	.059
1989	57 ^a	136 ^a	112	305 ^a	.159	.051
1990	62 ^a	136 ^a	114	312 ^a	.014	.009
1991	67 ^a	144 ^a	99	309 ^a	.082	.000
1992	60	133	88	281	.085	.026
1993	65	124	53	243	.048	.037
1994	65	132	76	273	.188	.024
Period 2:						
1995	65	118	112	295	.020	.000
1996	56	76	64	196	.108	.038
1997	57	60	43	160	.255	.071
1998	60	63	58	181	.054	.000
1999	60	59	97	216	.000	.000
2000	59	61	59	179	.000	.000
2001	55	61	62	178	.000	.000
2002	53	54	106	213	.001 ^b	.002 ^b
2003	50	48	113	211	.015 ^b	.005 ^b
2004	48	45	117	210	.003 ^b	.000 ^b
Means:						
Period 1	64	138	93	295	.117	.035
Period 2	56	65	83	204	.045	.011
All years	61	106	87	248	.084	.024
EWD	26	56	37	119	.670 ^c	.190 ^c

Note: Estimates are based on areas A, B, C, D, and O (see Heg et al. 2000 for a map) and are derived from the annual census of population numbers at the start of each breeding season and intensive monitoring during the whole breeding season. Annual fecundity was defined as the annual number of offspring per territory that survived until adulthood. EWD refers to the values used by Ens et al. (1995) based on areas A and C from 1984 to 1992. The number of nonbreeders represents half the number of counted individuals because we are interested in tracking only females in our models (we assumed an adult sex ratio of 50 : 50).

^a Territory numbers for areas B, D, and OBK from 1984 to 1991 were imputed because not all breeders were color ringed in those areas until 1992.

^b Values of F_H and F_L in 2002–2004 could not be determined exactly because we do not know yet how many offspring survived until adulthood. Reported are the annual number of fledglings per territory times the probability that they survived until adulthood based on average survivorship from 1984 to 2001.

^c Fecundity values in EWD were too high because they (1) did not account for the fact that not all offspring survive from fledging to adulthood and (2) used the total number of fledglings produced, while population models account for only female offspring.

Table B2

Annual state transition and mortality probabilities (%) estimated using multistate capture-recapture models and the number of color-ringed individuals on which estimates were based

	High-quality territory owner (H)					Low-quality territory owner (L)					Nonbreeder (N)				
	Ringed	m_{HH}	m_{HL}	m_{HN}	μ_H	Ringed	m_{LL}	m_{LH}	m_{LN}	μ_L	Ringed	m_{NN} (m_{NN}^*)	m_{NL}	m_{NH}	μ_N (μ_N^*)
Period 1:															
1984–1985	37	83.4	2.8	11.1	2.7	103	88.3	2.2	4.3	5.3	4	100 (100) ^a	0 ^a	0 ^a	0 (0) ^a
1985–1986	39	89.5	.0	2.8	7.7	156	91.6	2.6	4.6	1.2	12	73.5 (76.5)	9.1	9.1	8.3 (5.3)
1986–1987	63	63.3	5.8	13.5	17.5	189	76.8	6.0	2.7	14.5	17	46.5 (59.0)	9.1	9.1	35.3 (22.8)
1987–1988	65	92.2	1.6	3.2	3.1	168	94.9	1.8	1.8	1.4	43	73.0 (75.5)	12.5	7.5	7.0 (4.5)
1988–1989	80	87.2	2.6	6.5	3.8	189	90.5	1.1	4.5	3.8	78	90.8 (92.3)	5.3	.0	3.8 (2.4)
1989–1990	73	94.5	1.4	2.8	1.4	179	86.7	2.9	7.6	2.7	134	83.8 (85.5)	8.7	2.4	5.2 (3.4)
1990–1991	93	93.5	2.2	3.3	1.1	185	90.2	3.9	5.0	1.0	165	82.9 (85.4)	9.7	.6	6.7 (4.3)
1991–1992	101	93.0	1.0	1.0	5.0	193	94.2	1.1	2.1	2.6	162	87.3 (88.8)	5.8	2.6	4.3 (2.8)
1992–1993	120	91.5	.9	1.8	5.8	226	88.6	1.9	4.7	4.9	167	77.9 (81.8)	6.8	4.1	11.3 (7.3)
1993–1994	124	95.1	.8	3.3	.8	226	91.0	.9	5.9	2.2	145	77.9 (80.7)	11.9	2.2	8.0 (5.2)
1994–1995	123	93.4	.8	3.4	2.4	234	89.9	1.4	3.7	5.1	133	68.4 (74.8)	9.0	4.5	18.1 (11.7)
Period 2:															
1995–1996	127	51.6	2.4	13.0	33.0	209	51.3	12.1	12.2	24.4	113	31.5 (44.0)	17.3	16.0	35.2 (22.7)
1996–1997	112	78.7	2.0	7.1	12.2	130	69.9	9.3	10.1	10.7	90	59.3 (68.1)	8.7	7.3	24.7 (15.9)
1997–1998	109	94.4	1.0	1.0	3.7	100	91.0	4.1	2.5	2.4	89	71.0 (74.1)	11.9	8.6	8.4 (5.4)
1998–1999	117	84.0	1.9	5.7	8.5	105	88.7	4.1	4.1	3.1	77	71.1 (75.4)	12.6	4.2	12.1 (7.8)
1999–2000	113	91.9	.0	6.4	1.7	90	87.0	2.5	5.0	5.5	92	61.5 (69.1)	17.2	.0	21.2 (13.7)
2000–2001	110	93.5	.0	2.0	4.4	111	85.0	2.4	6.8	5.8	115	81.4 (84.5)	7.8	2.3	8.4 (5.4)
2001–2002	110	89.8	2.0	1.2	7.0	109	78.4	5.6	12.2	3.7	109	84.3 (86.5)	5.5	4.1	6.1 (3.9)
2002–2003	105	84.3	1.0	4.1	10.6	96	79.4	3.6	12.4	4.5	85	68.1 (76.5)	5.0	3.3	23.6 (15.2)
2003–2004	100	90.0	3.1	2.0	4.9	82	76.1	3.4	6.7	13.8	64	63.1 (71.2)	10.1	4.0	22.8 (14.7)
Means:															
Period 1	83	88.8	1.8	4.8	4.6	186	89.3	2.3	4.3	4.1	96	76.2 (80.0) ^a	8.8 ^a	4.2 ^a	10.8 (7.0) ^a
Period 2	111	84.3	1.5	4.7	9.6	115	78.5	5.2	8.0	8.2	97	65.7 (72.2)	10.7	5.5	18.1 (11.6)
All years	96	86.7	1.7	4.7	6.9	154	84.5	3.6	6.0	5.9	97	71.5 (76.5) ^a	9.6 ^a	4.8 ^a	14.1 (9.1) ^a
EWD	46	90.2	1.9	3.1	4.9	82	88.4	2.6	3.9	5.1	47	72.4	13.8	5.4	8.4

Note: Column headings indicate status in year t . Estimates were derived from intensive observations in areas A, B, C, D, and O and nearby roosts (see Heg et al. 2000 for a map). Parameters were estimated using one statistical model that simultaneously estimates transitions between states, mortality, and resighting probabilities per state (fig. 3). This model makes corrections for the fact that we have overlooked some individuals in certain years. The resighting probability of breeders was >0.99 in all years; annual resighting probabilities of nonbreeders varied between 0.6 and 1. Estimates did not differ between the sexes and were therefore combined. All model parameters were allowed to vary between years (fully time-dependent model; for more details on the analysis, see van de Pol et al. 2006). We studied a nonclosed population; in particular, nonbreeders were not completely site faithful. By comparing patterns of local observations with dead recoveries from a larger area (northwestern Europe), we estimated that annual emigration (E_N) of nonbreeders was on average 5%, with emigration most pronounced in years with high mortality (M. van de Pol, unpublished data). Furthermore, annual immigration of nonbreeders was difficult to quantify; therefore, we assumed that immigration equaled emigration. Because emigration of nonbreeders out of the study area results in an overestimation of (local) nonbreeder mortality (μ_N), we corrected μ_N in a specific year t downward proportionally by $\mu_N^*(t) = (1 - E_N/\bar{\mu}_N)\mu_N(t)$. Consequently, m_{NN} was also adjusted by $m_{NN}^*(t) = 1 - m_{NH}(t) - m_{NL}(t) - \mu_N^*(t)$. Corrected estimates (in parentheses) were used in all calculations. EWD refers to values used by Ens et al. (1995) based on areas A and C from 1984 to 1992 for breeders and from 1987 to 1992 for nonbreeders.

^a Nonbreeder parameters in 1984–1985 were not included in means because they were based on few individuals.

Table B3

Variance-covariance matrix of the model parameters used in the calculation of the confidence intervals around point estimates of model predictions

	m_{HH}	m_{HL}	m_{HN}	m_{LL}	m_{LH}	m_{LN}	μ_N	F_H	F_L	T_H	T_L
m_{HH}	<u>.0083</u>										
m_{HL}	-.0013	<u>.0002</u>									
m_{HN}	-.0032	.0006	<u>.0016</u>								
m_{LL}	.0036	-.0006	-.0014	<u>.0023</u>							
m_{LH}	-.0010	.0002	.0004	-.0006	<u>.0002</u>						
m_{LN}	.0005	-.0001	-.0001	-.0001	.0000	<u>.0003</u>					
μ_N	-.0063	.0009	.0018	-.0035	.0010	-.0005	<u>.0093</u>				
F_H	.0000	-.0002	.0002	.0002	-.0002	.0000	-.0005	<u>.0032</u>			
F_L	.0001	.0000	.0002	.0001	-.0001	.0000	-.0005	.0006	<u>.0006</u>		
T_H	-.1363	.0274	.0415	.0025	-.0025	-.0524	.1511	-.0297	.0197	<u>18.7</u>	
T_L	-.4927	.0535	.1822	-.1747	.0638	-.0255	.1409	.1219	-.0885	-5.6	<u>83.6</u>

Note: Variances (underscored diagonal elements) are based on between-year variation in life-history parameters or number of breeders. Covariances (below-diagonal elements) are based on between-year covariations between all combinations of number of breeders and life-history parameters. Variances and covariances are calculated using the annual values in period 1 (1984–1994; $n = 11$), which are given in tables B1 and B2, along with the parameter definitions. The variance-covariance matrix was used to generate a multivariate-normal distribution of all parameters, from which 1,000 random samples were taken. These 1,000 random samples were used as input parameters of the queue models and were used to generate confidence intervals and standard errors around model predictions to assess their reliability.

Appendix C from M. van de Pol et al., “Variation in Habitat Choice and Delayed Reproduction: Adaptive Queuing Strategies or Individual Quality Differences?”
(Am. Nat., vol. 170, no. 4, p. 000)

Sensitivity of Model Predictions to Input Parameters

Table C1

Effect of small changes in the input parameters on the evolutionarily stable strategy (x^*), the difference in age of first settlement between successful QHs and QLs ($\Delta\alpha$), and the relative number of queuers per high-quality territory compared to low-quality territories (P)

Parameter	Effect of 1% change in parameter (%)			CV _{year}
	x^*	$\Delta\alpha$	P^a	
m_{HL}	-.05	-.05	.45	.87
m_{HN}	-.05	-.16	1.00	.83
μ_H	-.14	-.41	1.32	1.02
m_{LH}	.35	-.34	-2.34	.64
m_{LN}	.10	.11	-.03	.39
μ_L	.02	1.17	4.14	.94
F_H	-.13	.62	-.83	.48
F_L	.08	-.92	-3.37	.70
p^b	-.19	1.45	3.31	.54
q^c	-.58	0 ^d	.92	.10
μ_N	0 ^d	-1.01	0 ^d	.81

Note: QH = individual following the QH strategy; QL = individual following the QL strategy. The effects of small changes are expressed as relative sensitivities (elasticities) and are calculated by, for example, $(\partial x^*/\partial m_{HL})(m_{HL}/x^*)$ (Caswell 2001). For example, an increase in m_{HL} of 1% results in a decrease of 0.05% of x^* , a 0.05% smaller difference in age of first reproduction between QHs and QLs, and a 0.45% higher relative number of queuers per high-quality territory compared to low-quality territories. Here, CV_{year} represents the coefficient of variation between years of the parameters over period 1 (1984–1994) and is a measure of the temporal variability of parameters. See tables B1, B2 for definitions of parameters.

^a $P = (n_{QH}/T_H)/(n_{QL}/T_L)$.

^b $p = (F_H + m_{HN})/(F_L + m_{LN})$.

^c $q = T_H/T_L$.

^d Note that some parameters do not affect x^* , $\Delta\alpha$, or P at all.