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THE DESPOTIC DISTRIBUTION AND DEFERRED MATURITY: TWO SIDES OF THE SAME COIN

BRUNO J. ENS,[1,*] FRANZ J. WEISSING,[2] AND RUDOLF H. DRENT[1]

[1]Zoological Laboratory, University of Groningen, Postbox 14, 9750 AA Haren, The Netherlands;
[2]Department of Genetics, University of Groningen, Postbox 14, 9750 AA Haren, The Netherlands

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Abstract.—For an individual, the decision on when to settle (i.e., at what age) cannot be separated from the decision on where to settle (i.e., in which habitat). We tackle both problems simultaneously by treating territory settlement in the long-lived oystercatcher *Haematopus ostralegus* (in which territories differ strikingly in quality and many individuals delay settlement) as a *career decision* with long-term fitness consequences through its effect on social status. We reject the hypothesis that oystercatchers are not able to judge territory quality or that short-term advantages of a high-quality territory are offset by long-term costs. We estimate the expected future reproductive success (EFRS) of birds of different social status on the basis of a Markov model. A simple contest model shows that owners of high-quality territories must have a considerable advantage that allows them to despotically exclude other birds. We find no evidence for a phenotypic superiority of owners of high-quality territories. Also, the act of breeding, even in a poor territory, does not enhance the probability of subsequently settling in a good territory. The available data support the *queue hypothesis* that unsettled individuals must develop site dominance in order to overcome the owner advantage. By queuing for a specific territory, an individual reduces its chances of becoming established elsewhere. At evolutionary equilibrium, the local queues for high-quality territories are longer, which implies longer waiting times and a higher probability of premature death. This trade-off between territory quality and waiting time links the despotic distribution to deferred maturity and provides a partial explanation for both.

In many species individuals have to settle on a territory before they can commence reproduction. The decisions that lead to successful territory establishment are rather complex and involve several aspects, such as habitat quality and the age at first settlement. The literature tends to treat these aspects as independent. In our opinion, deeper insights might be gained by an integrative approach.

To illustrate our point, we will consider recruitment decisions in the oystercatcher *Haematopus ostralegus,* whose breeding populations have two puzzling features. First, breeding pairs occupy territories which differ strikingly in quality (Safriel 1985; Ens et al. 1992). Second, a substantial number of birds, fully mature and quite capable of breeding, are present in the breeding area, yet these birds do not breed (Harris 1970; Safriel et al. 1984). Why do so many oystercatchers reside in territories of poor quality? And why does it take so long

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[*] To whom correspondence should be addressed at present address: Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 167, 1790 AD Den Burg (Texel), The Netherlands; E-mail: b.j.ens@ibn.agro.nl.

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before oystercatchers breed for the first time? In this article, we argue that the solution to the first, ecological problem provides an answer to the second, life-history problem.

The question of how organisms should distribute themselves over habitats of different quality has been addressed by Fretwell (1972), who presented a polished version of ideas introduced by Fretwell and Lucas (1970). They considered two models, which are both based on the assumption that the reproductive success of an individual in a habitat is negatively affected by the density of conspecific competitors in this habitat. If the organisms are free to move between habitats, an "ideal free" distribution is expected to result. In this distribution, the average success at equilibrium is the same in all habitats since crowding will occur in the better habitats. In contrast, if settled individuals tend to exclude unsettled individuals, an "ideal despotic" distribution should result in which reproductive success is positively related to habitat quality, as is the case in our study of oystercatchers (Ens et al. 1992).

In both models the animals are ideal in the sense that their choices maximize fitness and that they have perfect knowledge of habitat quality and competitor density. Thus, these models cannot be applied if unsettled oystercatchers are not able to judge the quality of a territory properly. Different lines of evidence suggest that oystercatchers are able to discriminate quite well between good and poor territories. The differences in territory quality are consistent among years and can be simply predicted from topographical features (Ens et al. 1992). Given the large number of intrusions preceding the act of territory establishment (Ens et al., in press) it is also unlikely that birds would misjudge territory quality due to limited experience. However, although we dismiss this *poor discrimination hypothesis,* potential recruits almost certainly face a sampling problem (see Bernstein et al. 1988; Slagsvold et al. 1988).

The despotic distribution assumes that settled individuals can despotically exclude unsettled individuals. However, it is not clear why territory owners are successful despots. In order to gain a deeper understanding of the despotic distribution, we will show that it is profitable to take the perspective of the excluded birds. At least four hypotheses explain why it might be adaptive for such birds to let themselves be excluded and settle in a poor habitat:

1. The *low benefit–low cost hypothesis,* which proposes that the short-term disadvantages of a low-quality territory are compensated by long-term advantages such as a reduced mortality
2. The *inferior phenotype hypothesis,* which maintains that individuals in poor territories are of poor quality and are thus forced to make the best of a bad job
3. The *breeding skill hypothesis,* which assumes that the best way to get into a good territory is to settle first in a poor territory to acquire breeding skills
4. The *queue hypothesis,* which suggests that unsettled individuals have to develop site-specific dominance relationships in order to overcome the owner advantage

The ideal despotic distribution as proposed by Fretwell (1972) is an equilibrium consideration independent of time. In contrast, some of the above hypotheses on the mechanism of despotic exclusion explicitly incorporate time; that is, they explicitly represent an important aspect of the life history of the individual. Inspired by Wiley (1981), we propose that the settlement decision should be treated as a *career decision* with long-term consequences for lifetime reproductive success through its effects on social status.

Since at least three of the four hypotheses consider these long-term consequences of recruitment decisions, the short-term reproductive success associated with a behavioral alternative is insufficient to judge its evolutionary significance. In long-lived species such as the oystercatcher, this situation presents a serious problem because the lifetime reproductive success associated with a behavioral decision can often not be measured directly. Oystercatchers may live up to 35 yr (Cramp and Simmons 1982), and our 10-yr study was far too short to cover this period. In order to overcome this problem, we developed a Markov model that allows the estimation of expected future reproductive success (EFRS; Grafen 1987) on the basis of mortality rates and the annual transition rates between different behavioral categories. This method is quite general and may also prove useful for estimating lifetime reproductive success in other long-lived species.

SHORT-TERM REPRODUCTIVE SUCCESS

The Study Population

Since 1983 oystercatchers have been caught and color-marked on Schiermonnikoog, an island in the Wadden Sea in the Netherlands. The study area and the methods used to measure reproductive success are described elsewhere (Ens et al. 1992). The birds nest on the salt marsh but depend on the adjacent mudflats for their food supply. Outside the breeding season, most feeding is concentrated on vast expanses of tidal mudflats farther down shore. During the breeding season (March–August), breeders spend much time close to the shore. Figure 1 provides a territory map and schematic representation of the social organization during this time of year. Three classes of adult birds can be distinguished. *Nonbreeders* are all individuals not defending a nesting territory. Pairs of nonbreeders may defend feeding territories on the mudflats (see Ens et al., in press, for a detailed description of the social organization of the nonbreeders). Pairs that defend a nesting territory some distance inland and a feeding territory some distance down shore are called *leapfrogs,* because they have to spend some time in flight traveling back and forth between their two territories, flying over the intervening territories to do so. Pairs that defend a nesting territory on the edge of the salt marsh and a contiguous feeding territory on the mudflats are called *residents.* Throughout this article we shall refer to the *status* of a bird when we want to indicate whether it is a nonbreeder, a breeder defending a leapfrog territory, or a breeder defending a resident territory. Most mortality occurs in winter, while most subsequent status changes finalize in early spring, before the first eggs are laid (Ens et al., in press).

Status-Dependent Reproductive Success

It should be clear from figure 1 that the structure of the breeding habitat in combination with the ecological requirements of the oystercatcher, especially the

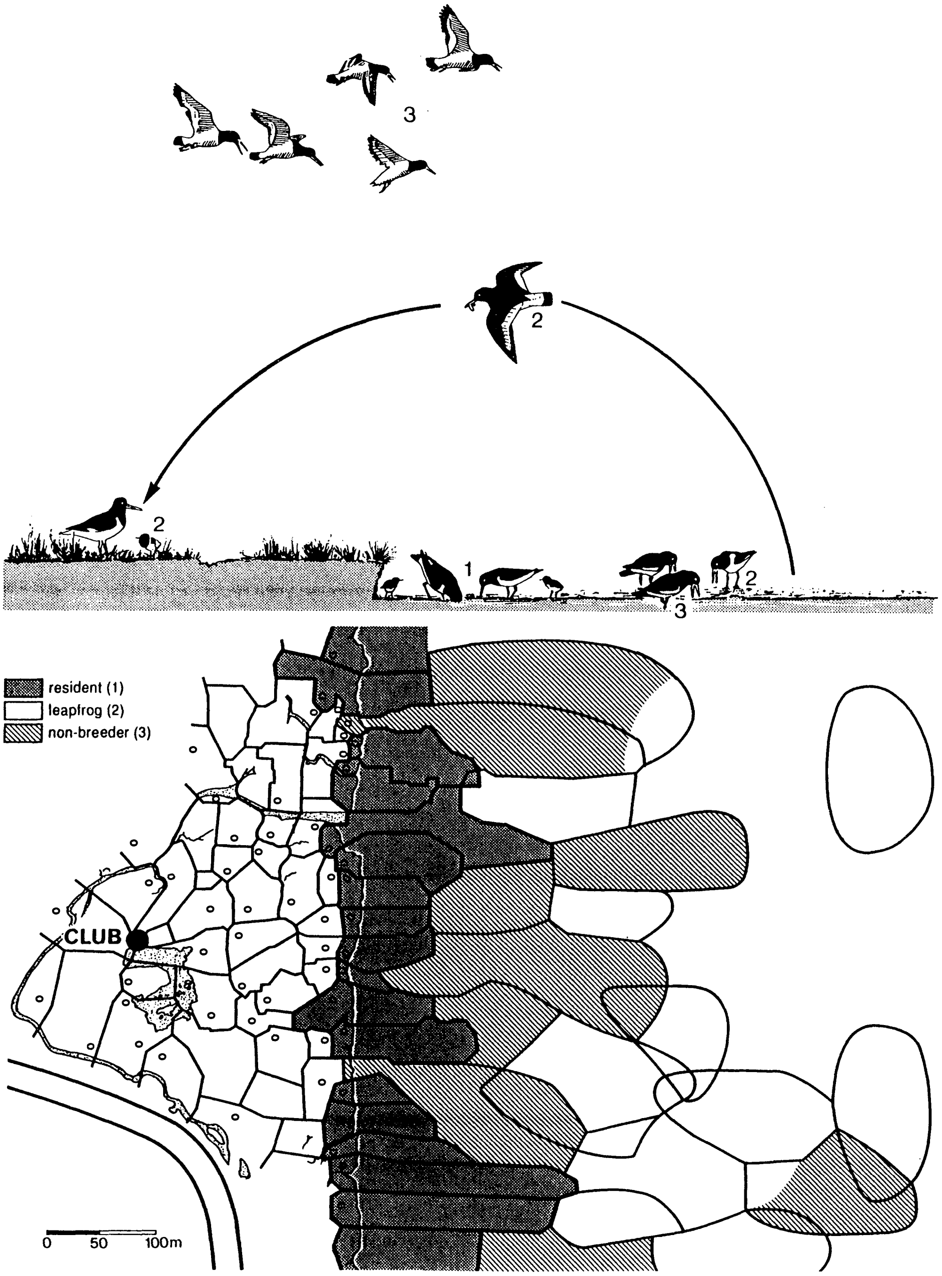

FIG. 1.—Territory boundaries in the main study area in June 1990. Territories of residents are shaded dark, while nesting and feeding territories of leapfrogs are both white. Feeding territories defended by pairs that classified as nonbreeding in April are shaded light (two pairs gained access to the salt marsh in the course of that spring; one of the pairs even nested). Open dots are nests, while the large black dot shows the center of the club, where the nonbreeders aggregate during high tide. Above the map is a schematic representation of this social organization. Apart from a pair of resident breeders taking their chicks to the mudflats to feed them there and a pair of leapfrog parents having to transport all food to the chicks, a pair of nonbreeders is shown defending their feeding territory. Furthermore, it is shown how nonbreeders engage in hovering ceremonies (aggressive displays with other nonbreeders and, on occasion, with breeders that occur most often above the resident territories).

TABLE 1

FLEDGLING PRODUCTION OF RESIDENTS AND LEAPFROGS 1984–1992

YEAR	RESIDENTS			LEAPFROGS		
	Mean	SD	*N*	Mean	SD	*N*
1984	1.20	.63	10	.33	.49	15
1985	1.31	.63	13	.29	.46	24
1986	1.12	1.09	25	.40	.54	45
1987	.55	.74	22	.19	.46	37
1988	.43	.66	23	.23	.43	30
1989	.55	.51	22	.20	.47	35
1990	.00	.00	26	.02	.15	43
1991	.33	.48	27	.00	.00	53
1992	.52	.75	27	.08	.27	52
Average	.67			.19		

NOTE.—Elsewhere we (Ens et al. 1992) provide a detailed description of the methods used to study fledgling production. In this table, the category leapfrogs includes leapfrogs whose nesting territory contained a creek, in contrast to our earlier study (Ens et al. 1992), in which such pairs were excluded from the analysis. Sample sizes should not be interpreted as total population sizes as many pairs were unmarked in 1984, the study area was increased in 1986, and in some years some pairs were excluded because they had been used in experiments potentially affecting reproductive success.

habit of feeding the young with food from the intertidal, result in leapfrog parents having to spend much more time in flight when they want to provision their chicks with a similar amount of food, compared with resident parents (Ens et al. 1992). Because of this, residents always fledged more chicks than leapfrogs, except for 1 yr of nearly complete breeding failure (table 1). The reproductive lows and highs, which may be due to annual variation in the food supply, coincided for the two types of territory owners ($r_s = 0.81$, $N = 9$, $P < .01$). Thus, there can be little doubt that leapfrog territories are of consistently poorer quality than resident territories, and it comes as no surprise that competition seems most intense for the best territories. Though there are no obvious differences in vegetation characteristics, the size of the nesting territories on the salt marsh decreases the closer the nesting territory is situated to the edge of the salt marsh (fig. 2). Furthermore, feeding territories of residents extend much farther from the edge of the salt marsh than they are wide, which suggests intense competition for space at the edge of the salt marsh (fig. 1; Ens et al. 1992).

ESTIMATES OF LONG-TERM REPRODUCTIVE SUCCESS

A Markov Model for Status Change

The settlement decision of an individual does not affect only the short-term reproductive success in the season in which settlement takes place. In oystercatchers, the present status of an individual is a good predictor of its status in future seasons. In fact, annual mortality is low, and the majority of individuals return to the same territory and mate with the same partner (Harris et al. 1987;

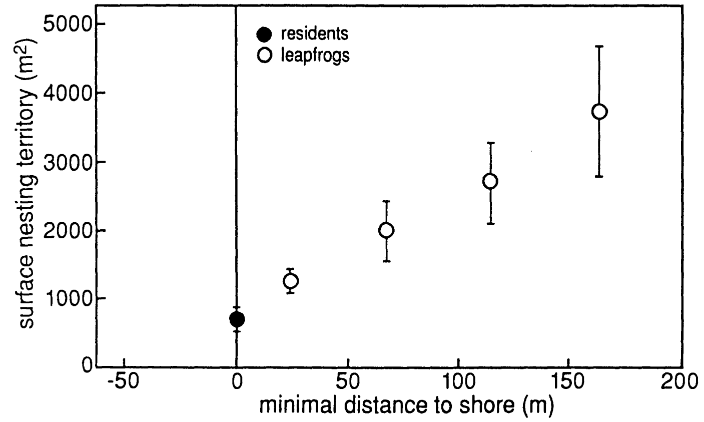

FIG. 2.—Size of the nesting territory vs. distance from the edge of the salt marsh; based on the territory map in fig. 1. Bars represent SEs.

TABLE 2

TRANSITION MATRICES THAT DESCRIBE THE ANNUAL PROBABILITY OF CHANGING STATUS

	NEW STATUS			
INITIAL STATUS	Resident	Leapfrog	Nonbreeder	Dead
Resident	90.2 (3.4)	1.9 (.7)	3.1 (.9)	4.9 (2.7)
Leapfrog	2.6 (.9)	88.4 (3.1)	3.9 (1.4)	5.1 (2.1)
Nonbreeder	5.7 (4.2)	11.1 (3.3)	74.8 (8.3)	8.4 (2.4)
Nonbreeder*	5.4	13.8	72.4	8.4

NOTE.—Average probability of changing status between years (expressed in percentage with SE in parentheses) is separated for nonbreeders, leapfrogs, and residents but not separated for sex. Data for residents and leapfrogs are for the years 1984/1985–1991/1992; for nonbreeders, for the years 1987/1988–1991/1992. Per-year status change was observed for, on the average, 46 residents, 82 leapfrogs, and 47 nonbreeders.

* Average probabilities (expressed in percentage) of changing status between years are reestimated for nonbreeders using information on the origin of recruits (table 3) and the distribution of status types in the population (table 4) using eq. (2) (see text).

Ens et al. 1993). Accordingly, the present status of an individual has important consequences for the expected reproductive success in the future. To estimate the long-term consequences of a settlement decision, the probabilities of maintaining or changing status have to be taken into account.

Each year we determined the status of all marked individuals in the study population (see Ens et al., in press). From this we calculated the annual probability of changing status, including death. For each pair of seasons t and $t + 1$ where data are available, we get an estimate $\hat{m}_{ij}(t)$ for the probability that an individual changes from status i to status j. The average annual transition probability m_{ij} from status i to status j was estimated by taking the arithmetic mean of $\hat{m}_{ij}(t)$ for those years t when data were available (see table 2). For each initial

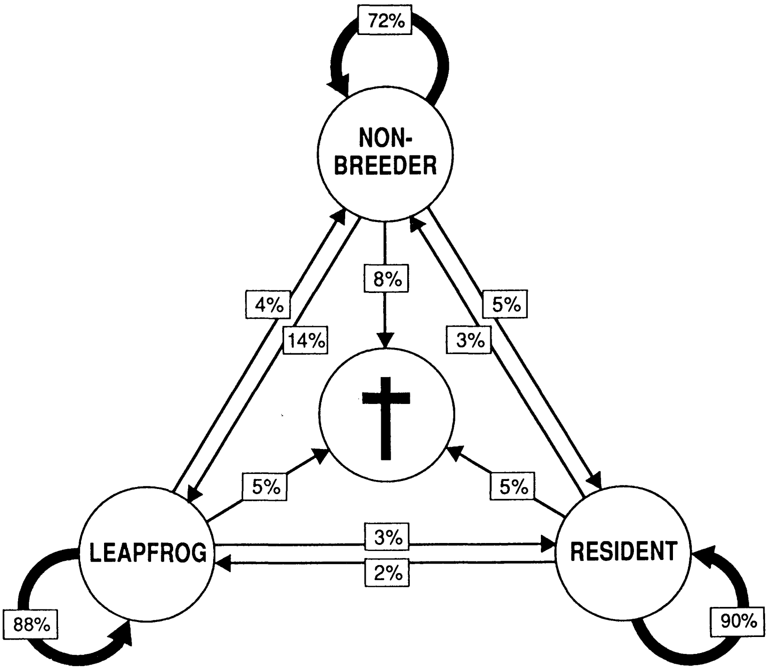

FIG. 3.—Graphical depiction of the Markov model of status change; transition probabilities (expressed as percentages) are those of the matrix in table 2.

status, the most likely outcome is to have the same status in the following year (fig. 3). The long-term consequences of status change can be estimated if we assume that the annual transition probabilities estimated in table 2 are constant in time and the same for all individuals. Under this assumption, status change is a Markov process characterized by the matrix $\mathbf{M} = (m_{ij})$, where $i = 1$ for residents, $i = 2$ for leapfrogs, $i = 3$ for nonbreeders, and $i = 4$ means death.

Reliability of the Estimates

Not all entries in table 2 have the same degree of reliability. The estimates of switching probabilities for breeders are fairly reliable since they are based on a period of 10 yr (1983–1992) and a reasonable number of birds. For nonbreeders, the situation is different. The first successful catch of nonbreeders roosting on the club was in 1987. Therefore, the estimates of the state transition probabilities for nonbreeders are based on the data of the 6 yr when a sufficient number of marked individuals were available.

Fortunately, the reliability of the estimates for nonbreeders can be checked from data on the origin of recruits and the distribution of the different types in the population. Let N_{ij} denote the total number of status transitions from i to j during the study period. For transitions to the resident ($j = 1$) or the leapfrog ($j = 2$) status, N_{ij} can be estimated by tracing back the previous status of those individuals that recruited into resident or leapfrog territories, respectively (table

TABLE 3

ORIGIN OF MALES AND FEMALES THAT RECRUITED INTO RESIDENT OR LEAPFROG TERRITORIES BETWEEN 1985 AND 1992

	New Status	
Old Status	Resident	Leapfrog
Resident	. . .	6
Leapfrog	16	. . .
Nonbreeder	22	55

NOTE.—The old status of all unmarked settlers is assumed to be nonbreeder. Individuals that shifted territory but did not change territory type are not included.

TABLE 4

THE DISTRIBUTION OF STATUS TYPES IN THE STUDY POPULATION

	Counts* (%)	Markov Model† (%)
Resident	24.2	27.8
Leapfrog	45.3	41.2
Nonbreeder	30.5	31.0

* Estimated from territory counts and counts of roosts (see Ens et al., in press).

† Limit distribution of the Markov model under the assumption of a stable population size.

3). Let p_i denote the relative frequency of status i in the population. The frequency distribution p is easily derived from estimates of the total numbers of breeders, nonbreeders, residents, and leapfrogs in the study area (table 4). In view of the interpretation of m_{ij}, the total number of status transitions from i to j, N_{ij}, should be proportional to $p_i \cdot m_{ij}$. As a consequence, we get the relation

$$\frac{N_{ij}}{N_{kj}} = \frac{p_{\mathrm{i}} \cdot m_{ij}}{p_k \cdot m_{kj}}, \tag{1}$$

which yields m_{kj} as a function of m_{ij}:

$$m_{kj} = \frac{p_i \cdot N_{kj}}{p_k \cdot N_{ij}} \cdot m_{ij} \,. \tag{2}$$

Equation (2) can be used to reestimate the transition probabilities m_{kj} for nonbreeders ($k = 3$) in terms of the transition probabilities m_{ij} for residents ($i = 1$) and leapfrogs ($i = 2$). Table 2 shows that the reestimated values of the transition probabilities m_{31} and m_{32} are rather close to the original estimates. All calculations

TABLE 5

Calculation of EFRS and Its Components on the Basis of the Markov Model (see app. b) for Birds of Different Initial Status

Initial Status	Expected Years in Status of Resident	Leapfrog	Nonbreeder	Future Life Span	EFRS
Resident	12.5	4.5	2.0	19.0	9.2
Leapfrog	4.4	11.8	2.2	18.4	5.2
Nonbreeder	4.6	6.8	5.1	16.5	4.4

will be based on the new estimates since we consider them more reliable than the original values.

Population Consequences of the Markov Model

Let $p_i(t)$ denote the frequency of birds of status i in year t. Remember that m_{ij} denotes the probability that a bird in status i will switch to status j in the following season $t + 1$. Therefore, the frequency of birds of status j in year $t + 1$ is given by

$$p_j(t + 1) = \sum_i p_i(t) \cdot m_{ij} . \tag{3}$$

These recurrence equations characterize the expected change of the status frequency distribution in the course of time. It can be shown (see app. A) that the process converges rapidly to a stable limit distribution p^* that is independent of the starting conditions and characterized by the equation

$$p_j^* = \sum_i p_i^* \cdot m_{ij} . \tag{4}$$

If the Markov model is appropriate (and if the population had enough time to approach the limit distribution), p^* should coincide with p, the independent estimate of the status frequency distribution based on territory counts and counts of roosts (Ens et al., in press). For our data, there is no reason for doubting that this consistency requirement is met (table 4). The discrepancy between p^* and p is larger if the original matrix is used instead of the reestimated matrix.

Estimation of Expected Future Reproductive Success

The Markov model sketched above can be used to predict the dependence of life-history characteristics on the initial status of an individual. For each initial status, the expected number of years spent in the different status categories can readily be calculated (see app. B). The EFRS for each initial status is obtained by multiplying the mean number of years spent on resident and leapfrog territories with the mean annual chick production in either type of territory (see table 1). The results of these calculations are presented in table 5. Markov theory also

TABLE 6

EXPECTED FATE OF NONBREEDERS ACCORDING TO THE MARKOV MODEL

Fate	Percentage
Will never breed	30.4
Will directly recruit as resident	19.6
Will directly recruit as leapfrog	50.0
Will breed as leapfrog, never as resident	32.5
Will breed first as leapfrog, later as resident	17.5

allows more detailed investigation of the expected life history of an individual starting as a nonbreeder (table 6).

We checked our calculations by means of computer simulations tracking the fate of three cohorts of 10,000 individuals that started as resident, leapfrog, and nonbreeder, respectively. The simulation approach gave the same results (tables 5 and 6) as the analytical calculations. Simulations and calculations were both based on the reestimated transition probabilities for nonbreeders (see table 2). However, EFRS is hardly affected if the original values of m_{31} and m_{32} are used instead. For each initial status, the estimates of EFRS differed by less than 1%.

Robustness of the Model Predictions

The Markov model is based on a number of simplifying assumptions. First, it assumes that the annual state transition frequencies observed in the population give a reasonable estimate for the state transition probabilities of each individual. In particular, the transition probabilities of males and females are considered identical. Second, our model assumes that the state transition probabilities do not change during the lifetime of an individual. In other words, aging effects are neglected, and, in particular, mortality is considered to be independent of age. Third, annual variations in the transition probabilities are not taken into account (see Hulscher 1989 for the effects of cold vs. mild winters on oystercatchers). Fourth, we have ignored local and temporal variations in the fledgling production on resident and leapfrog territories, respectively (see table 1 for the annual variation). Fifth, we have ignored possible quality differences between chicks fledged in different types of territory. Though leapfrog chicks fledged, on the average, 4 d later than residents and their body mass at fledging was 58 g lower (Ens et al. 1992), there is no evidence that this affected postfledging survival (Kersten and Brenninkmeijer 1995), possibly because of the extended parental care in this species.

Aging as well as demographic and environmental stochasticity might affect the relation between present and future reproductive success. Therefore, these factors might influence the conclusions of our model. To check the robustness of our life-history estimates, we modified the model in a number of ways: (1) the Markov matrices for males and females were considered separately, (2) aging was simulated by including a maximal life span in our models, and (3) a Monte Carlo simulation model was constructed that includes annual stochasticity in fledgling production, mortality, and status transition probabilities. All modifica-

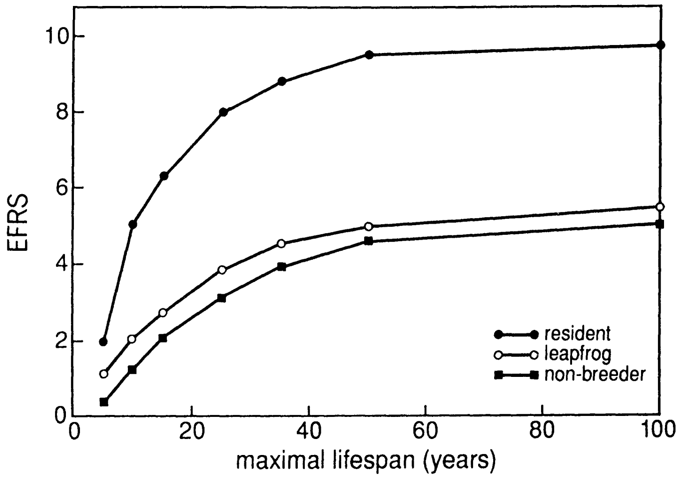

FIG. 4.—The EFRS plotted against maximum life span for birds initially nonbreeder, initially leapfrog, and initially resident (10,000 runs per initial status).

tions of our basic models gave qualitatively and quantitatively similar results. The inclusion of a maximal life span, for example, has no effect on EFRS if a realistic value (± 40 yr) is used (see fig. 4).

DESPOTIC DISTRIBUTION OVER TERRITORIES

The Low Benefit–Low Cost Hypothesis

Clearly, in oystercatchers low benefits are not offset by low costs: mortality rates of leapfrogs and residents are almost identical (fig. 3). In fact, the EFRS of individuals that recruit into a resident territory is almost twice the EFRS of individuals that recruit into a leapfrog territory (table 5). There can be no doubt that, once settled, individuals in a poor territory experience a lower EFRS, compared with individuals in a good territory. Since, in addition, experiments have shown that nonbreeding oystercatchers will settle in a high-quality habitat if the territory owners are removed (Harris 1970; Ens et al., in press), the conclusion that the distribution is despotic seems inescapable.

A Cost-Benefit Analysis of Fighting

But why should residents be able to exclude other birds? Why do nonbreeders and leapfrogs not fight for better reproductive opportunities? We shall now address these questions by means of a simple model.

Let $F(\mathrm{R})$, $F(\mathrm{LF})$, and $F(\mathrm{NB})$ denote the EFRS of a resident, a leapfrog, and a nonbreeder, respectively. Let $F(\mathrm{C})$ denote the expected future reproductive success of an individual that is ready to engage in escalated fighting for a resident territory. Fighting behavior will spread in the population if it is profitable for the challenger—that is, if $F(\mathrm{C})$ exceeds the EFRS of the challenger's present status.

In our simple model, we assume that a fight has three possible outcomes for a challenger: (1) with probability β, it gets successfully established as a resident, (2) with probability γ, death or injury reduce expected future reproductive success to zero, (3) with probability $1 - \beta - \gamma$, the challenger finds itself back in the status of a nonbreeder. Under these assumptions, the expected outcome of a contest for the challenger is given by

$$F(C) = \beta \cdot F(R) + (1 - \beta - \gamma) \cdot F(NB) . \tag{5}$$

For a nonbreeder, it is profitable to fight if $F(\mathrm{C}) > F(\mathrm{NB})$ or, equivalently, if

$$\beta > \frac{F(NB)}{F(R) - F(NB)} \cdot \gamma . \tag{6}$$

For a leapfrog, fighting is profitable if $F(\mathrm{C}) > F(\mathrm{LF})$ or, equivalently, if

$$\beta > \frac{F(NB)}{F(R) - F(NB)} \cdot \gamma + \frac{F(LF) - F(NB)}{F(R) - F(NB)} . \tag{7}$$

If $F(\mathrm{LF}) = F(\mathrm{NB})$, the conditions (6) and (7) for the spread of fighting behavior are identical for leapfrogs and nonbreeders. If $F(\mathrm{LF}) \neq F(\mathrm{NB})$, the condition for spread will be more easily satisfied for the status that has "less to lose" (i.e., for the status that has the smaller status quo EFRS).

The exclusion of nonbreeders from breeding on a resident territory could be easily explained on the basis of condition (6) if the EFRS of a resident were only slightly larger than the EFRS of a nonbreeder. In such a situation, fighting would be profitable for a nonbreeder only if the probability β of obtaining a resident territory were considerably larger than the probability γ of death or injury. If, for example, $F(\mathrm{R})$ were 10% larger than $F(\mathrm{NB})$, fighting could spread among nonbreeders only if $\beta > 10\gamma$. In other words, fighting would be profitable only if the chance of winning greatly exceeded the risk of losing. In such a situation, it is easily conceivable that residents can despotically exclude other individuals. Waiting for a chance to settle is more profitable than fighting since the risks of fighting outweigh the benefits.

For the Schiermonnikoog population, the situation is different. We estimated $F(\mathrm{R})$ to be roughly twice as large as $F(\mathrm{LF})$, whereas $F(\mathrm{LF})$ and $F(\mathrm{NB})$ are about the same (table 5). Hence, we expect fighting behavior to spread among leapfrogs and nonbreeders if

$$\beta > \gamma \tag{8}$$

(i.e., if the extra probability of getting established successfully as a resident exceeds the extra probability of death or serious injury from fighting). At first sight, it is quite plausible that condition (8) is satisfied. In spite of the fact that oystercatchers have a strong weapon in their pointed bill, physical fights did not result in fatal injury in the more than 100 fights that we observed (Ens 1992). On the other hand, the probability of winning a fight should be about 0.5 if the challenger and resident are in a symmetrical starting position. Why then are escalated fights so rare in oystercatchers?

TABLE 7

MORPHOLOGICAL MEASUREMENTS DEPENDENT ON TERRITORIAL STATUS AND SEX

	RESIDENT			LEAPFROG		
	Mean	SD	*N*	Mean	SD	*N*
Males:						
Wing length (mm)	260	7	69	261	6	136
Bill length (mm)	69	3	71	70	3	144
Body mass (g)	524	33	71	531	35	144
Females:						
Wing length (mm)	263	6	62	263	6	123
Bill length (mm)	79	4	63	78	4	127
Body mass (g)	558	39	63	548	36	125

TABLE 8

RESULTS OF A TWO-WAY ANOVA ON MORPHOLOGICAL MEASUREMENTS WITH TERRITORIAL STATUS AND SEX AS FACTORS

	STATUS		SEX		INTERACTION	
	R^2	P	R^2	P	R^2	P
Wing length	0	.49	4	<.001	0	0.30
Bill length	0	.75	57	<.001	1	0.002
Body mass	0	.78	9	<.001	1	0.02

NOTE.—R^2, Percentage variance explained by each factor.

In the rest of this article, we investigate three hypotheses that try to explain why condition (8) is violated. All three hypotheses posit that β is considerably smaller than 0.5 since residents have a systematic advantage over unsettled individuals. The first hypothesis argues that the chance of a challenger winning is negligible since residents are phenotypically superior. The other hypotheses are based on the idea that winning a single fight is not sufficient to get successfully established as a resident (i.e., β is much smaller than the probability of winning a single fight against a resident).

THE COSTS OF SETTLEMENT

The Inferior Phenotype Hypothesis

To test whether good territories are occupied by good fighters, while poor territories are occupied by poor fighters, we used body size and body condition as indicators of fighting ability. We selected the majority of individuals that had not changed status in the course of the study and averaged the morphological measurements when an individual was caught more than once. There were no large differences between residents and leapfrogs in either males or females, while the variability within a status was high (table 7). Two-way ANOVAs with sex and status as factors showed that for all morphological measurements, sex contributed significantly to the variance, whereas status did not (table 8). Though the interaction between sex and status was significant for bill length and body mass, it explained only 1% of the variance. It is unlikely that measurement errors were so high that the differences between classes were swamped, even for wing length, in which the total amount of variance explained was low, since repeatabilities (see, e.g., Falconer 1981) were high. The lowest repeatability was a value of $r = 0.62$ for the wing length of females. Thus, despite consistent morphological differences between individuals, there were no obvious morphological differences between settled residents and settled leapfrogs. Of course, the absence of gross morphological differences between the two categories of birds does not preclude the possibility of more subtle phenotypic differences determining fighting ability.

The Breeding Skill Hypothesis

Poor territories could serve as "stepping stones" to good territories, if breeding experience augments the chances of getting successfully established on a good territory. Inspection of the transition probabilities indicates that nonbreeders in fact diminish their chances of obtaining a resident territory by settling in a leapfrog territory: in both the original and the reestimated matrix the probability of becoming a resident is two times higher for the average nonbreeder than for the average leapfrog (table 2; fig. 3). Indeed, the combined probability for a leapfrog of dying or becoming a nonbreeder is four times the probability of moving to a resident territory. We can also estimate the importance of recruitment to leapfrog status as an avenue toward becoming a resident taking a long-term perspective. Our calculations (table 6) indicate that only one of every three nonbreeders recruiting into a leapfrog territory moves to a resident territory later in life.

The Queue Hypothesis

Our model of the queue hypothesis assumes that a nonbreeder cannot opt for both types of territory but that it has to concentrate on one type of territory because of the required site-specific experience. Hence, nonbreeders face a decision whether to attempt to obtain a leapfrog territory or a resident territory. Nonbreeders attempting to settle on a leapfrog territory will be called *hopeful leapfrogs,* while nonbreeders attempting to settle on a resident territory will be called *hopeful residents*. The annual probability of territory acquisition for hopeful leapfrogs and hopeful residents will be called λ and ρ, respectively. The annual mortality, μ, will be assumed to be the same for both types of nonbreeders. The resulting model is graphically represented in figure 5. It is obvious that the EFRS of hopeful leapfrogs and hopeful residents satisfies the relations

$$F(HLF) = \lambda \cdot F(LF) + (1 - \lambda - \mu) \cdot F(HLF) \tag{9}$$

and

$$F(HR) = \rho \cdot F(R) + (1 - \rho - \mu) \cdot F(HR), \tag{10}$$

where F(HLF), F(LF), F(HR), and F(R) denote the EFRS of hopeful leapfrogs, leapfrogs, hopeful residents, and residents, respectively. Accordingly, the EFRS for both types of nonbreeders is given by

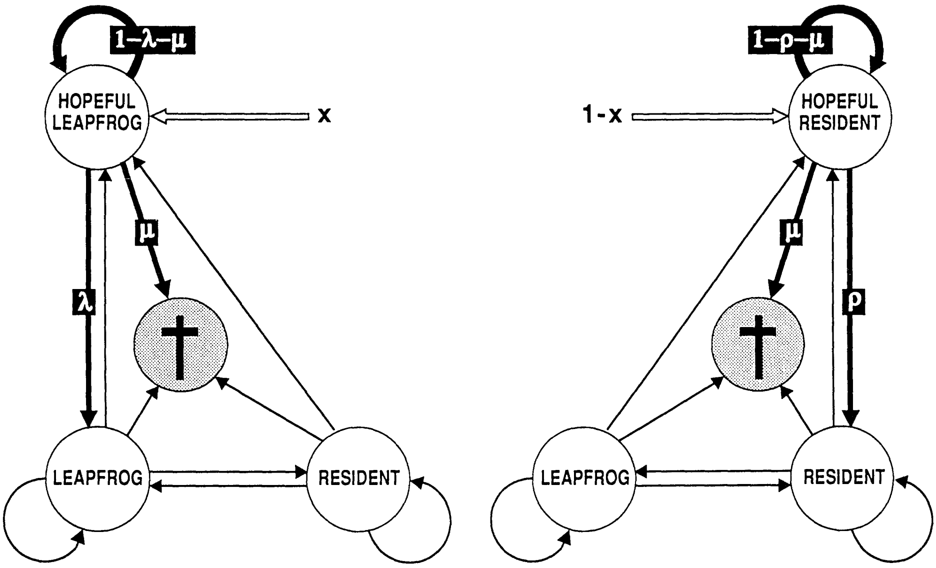

FIG. 5.—Graphical depiction of the queue model, which assumes that nonbreeders are either hopeful leapfrogs or hopeful residents. Hopeful leapfrogs have a probability λ to promote to leapfrog status, whereas hopeful residents have a probability ρ to promote to the status of resident. Both ρ and λ are frequency-dependent (i.e., they both depend on *x*, the relative frequency of hopeful leapfrogs). See text for further explanation.

$$F(HLF) = \frac{\lambda}{\lambda + \mu} \cdot F(LF) \tag{11}$$

and

$$F(HR) = \frac{\rho}{\rho + \mu} \cdot F(R) . \tag{12}$$

The probabilities λ and ρ of territory acquisition will depend on the frequency of competitors in both queues. The more often nonbreeders decide to join the queue for a resident territory, the lower the annual probability of acquiring such a territory. Hence λ and ρ will both be functions of *x*, the relative frequency of hopeful leapfrogs. We can estimate the frequency dependence of λ and ρ if we assume that the annual transition probabilities of nonbreeders to leapfrog and resident status (m_{32} and m_{31}) reflect the rate at which possibilities for settlement open up for hopeful leapfrogs and hopeful residents, respectively:

$$m_{32} = \lambda(x) \cdot x , \tag{13}$$

and

$$m_{31} = \rho(x) \cdot (1 - x) . \tag{14}$$

Accordingly, λ is inversely proportional to the relative frequency of hopeful leapfrogs, *x*, while ρ is inversely proportional to the relative frequency of hopeful

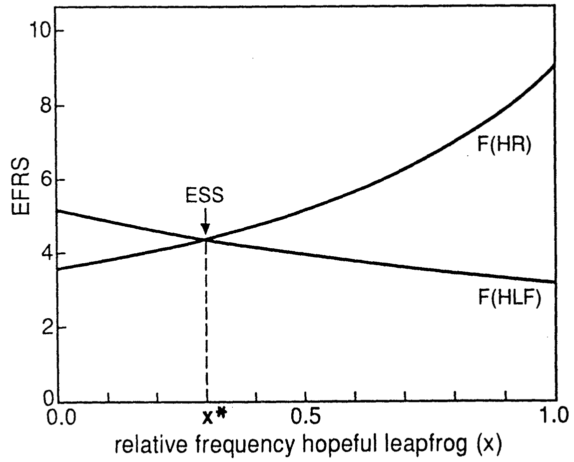

FIG. 6.—The EFRS for hopeful leapfrogs, F(HLF), and hopeful residents, F(HR), plotted against x, the relative frequency of hopeful leapfrogs in the population of nonbreeders.

residents, $1 - x$. Inserting our previous estimates of F(LF) and F(R) (see table 5) and the annual mortality of nonbreeders (m_{34}) in equations (11) and (12), we obtain the EFRS of hopeful leapfrogs and hopeful residents as a function of x (fig. 6). As expected, the EFRS of hopeful leapfrogs is negatively related to the frequency of hopeful leapfrogs, while the EFRS of hopeful residents is positively related to x.

There is exactly one frequency x at which the EFRS of hopeful leapfrogs and hopeful residents are identical. This frequency, x^*, is evolutionarily stable since hopeful leapfrogs have a higher reproductive success when their relative frequency is below x, while hopeful residents have a higher EFRS if the relative frequency of hopeful leapfrogs is above x. The evolutionarily stable value x^* (i.e., the evolutionarily stable strategy, or ESS) is easily obtained by inserting the equilibrium relation $F(\mathrm{HLF}) = F(\mathrm{HR}) = F(\mathrm{NB})$ into equations (9) and (10). In equilibrium, the ratio of hopeful leapfrogs and hopeful residents reflects the ratio of the expected benefits of both types of territory:

$$\frac{x^*}{1 - x^*} = \frac{m_{32} \cdot [F(LF) - F(NB)]}{m_{31} \cdot [F(R) - F(NB)]} . \tag{15}$$

In the case of the oystercatcher, equation (15) yields an ESS value $x^* = 0.30$; that is, the EFRS of hopeful leapfrogs and hopeful residents will be equal if 30% of all nonbreeders queue for a leapfrog territory while 70% queue for a resident territory. Based on this value, figure 7 depicts the cumulative probability of settlement and of premature death for hopeful leapfrogs and hopeful residents, respectively. Almost half of the hopeful leapfrogs settle immediately in the first year ($\lambda[x^*] = 0.46$), and very few will die prematurely in the queue. In contrast, more than half of the hopeful residents will die prematurely in the queue, and less than 10% settle immediately in the first year ($\rho[x^*] = 0.08$). Hence, waiting for a territory of high quality leads to a considerable delay in the age at first breeding.

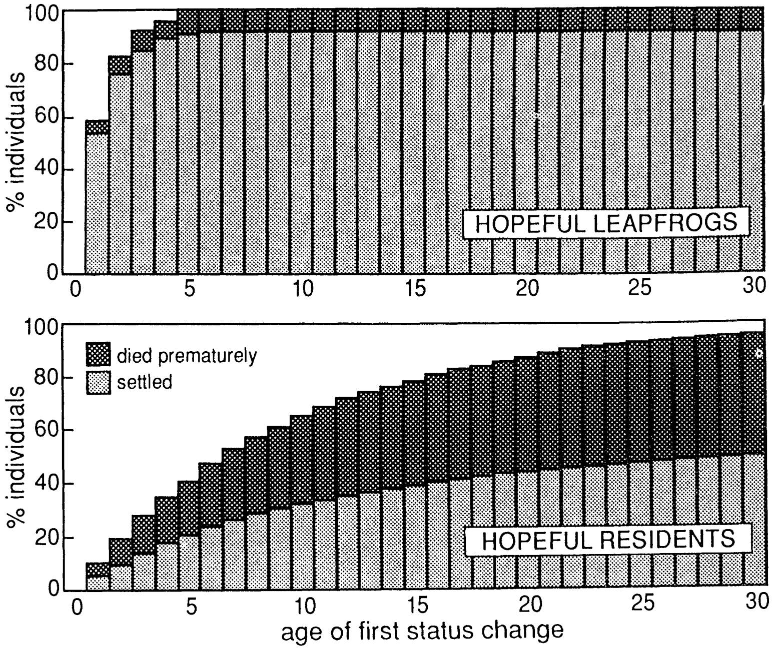

FIG. 7.—Cumulative frequency of settling and of premature death of hopeful residents (*bottom*) and hopeful leapfrogs (*top*) at the evolutionary stable relative frequency of hopeful leapfrogs obtained from eq. (15).

Regrettably, we are not yet able to test these quantitative predictions. Though we can classify some individuals as hopeful residents (see below), we cannot yet classify the majority of nonbreeders, so that we cannot test whether 70% are queuing for a resident territory. Furthermore, our study has not yet lasted long enough to obtain good estimates for the age at first breeding: our current data are necessarily truncated at 7 yr since the first chicks were marked in 1985. However, three lines of evidence provide qualitative support for the queue hypothesis.

First, researchers have shown (Ens et al., in press) that dominance relationships among nonbreeding oystercatchers are site-dependent, a vital condition for queues to evolve. Second, those nonbreeders that defend a feeding territory adjoining the resident territories can be identified as hopeful residents (fig. 1). In all, we watched four hopeful residents gain access to the shore, while they were unsuccessful in 35 bird seasons (i.e., continued to defend their territory). The average waiting time of 10 yr calculated from these data is well above the average age at first breeding of 6 yr determined for Skokholm (Ens 1992), especially if it is realized that to this period of 10 yr we must add 2 yr when the bird was immature, as well as the time that it took to settle in the feeding territory. Thus, there is evidence that nonbreeders that settle in high-quality territories do so at a very late age. Third, evidence also suggests that birds that settle in leapfrog territories are relatively young. Of chicks marked between 1985 and 1989 that returned to the study area, only nine settled so far, but without exception in leapfrog territories. Though a thorough test of the predictions of our model must await more data, the available evidence certainly favors the queue hypothesis.

DISCUSSION

Recruitment in a Life-History Context

The concept of an ideal free distribution, which predicts that individuals should be distributed such that the success on good but crowded habitats is the same as the success on worse but less crowded habitats, has been called "one of the most successful ideas in behavioral ecology" (Kacelnik et al. 1992*b,* p. 314). However, most studies on this concept have been concerned with short-term measures of success such as the rate of food intake in foraging animals. For territorial animals, we know of no well-studied examples that clearly fit the predictions of the ideal free distribution. On the contrary, many bird studies, including ours (Ens et al. 1992), report that the reproductive success in good habitats exceeds the reproductive success in poor habitats despite more intense competition for the former (see, e.g., van Balen 1973; Koenig and Mumme 1987; Newton 1991). Furthermore, as in another study (Ens et al., in press), there is abundant evidence for the presence of nonbreeding individuals that come to breed only when the territory owners are removed (Newton 1992). Apparently, the individuals are "despotically" distributed (sensu Fretwell 1972). The question of how a despotic distribution is generated has, however, received remarkably little attention. This is all the more surprising when it is realized that the mechanisms leading to a despotic distribution are potentially of great significance for the life history and the ecological interactions of the studied organism (see, e.g., Pulliam 1988) and its resources (see, e.g., Oksanen 1990). In fact, they are closely related to the settlement decisions that may have far-reaching consequences for lifetime reproductive success. Our work on oystercatchers suggests that a systematic study of settlement decisions should address at least six questions.

First, are there indeed *consistent differences* between habitats in terms of *long-term reproductive success?* For practical reasons, studies of settlement decisions often focus on the short-term consequences of these decisions in terms of energy uptake, predator avoidance, or fledgling production. It is easily conceivable, though, that the short-term advantages of a settlement decision may be offset by long-term disadvantages. Only if this is not the case, the necessity arises to explain differences in reproductive success. Of course, it will often be difficult to judge the long-term consequences of reproductive decisions. We think that the methods developed in this article not only are applicable to the oystercatcher example but will prove useful for studying long-term reproductive expectations in other species as well. It should be kept in mind, however, that lifetime reproductive success (and, in particular, EFRS) is a reliable measure of fitness only when the population is roughly stationary (see, e.g., Charlesworth 1980; Roff 1992), as seems to be the case for the oystercatcher population on Schiermonnikoog (Ens et al., in press).

Second, are the competitors able to *discriminate* between habitats of different quality? Settling in a habitat of poor quality may easily result if recruits cannot reliably estimate the consequences of habitat choice for future reproductive success. There is abundant evidence that birds can and do select habitats suitable for survival and reproduction (see, e.g., the review in Block and Brennan 1993), but studies that have attempted to quantify the discriminative abilities of the birds are few (see Goss-Custard et al. 1995). However, even if recruits are able to judge habitat quality, a sampling problem remains. Settling in a poor habitat may be adaptive if searching for a better habitat involves large costs in terms of time and energy owing to limited dispersal abilities (Morris 1987) or a shortage of time (Slagsvold et al. 1988). Thus, animals may have the capability to discriminate, but the costs of employing that capability may not be offset by the benefits of improved discrimination. Though we did not measure the costs of sampling in our study of oystercatchers, indirect evidence suggested that the birds were able to, and also did, discriminate between territories differing in quality. More sophisticated measurements must await a more sophisticated theoretical treatment of the problem (cf. Bernstein et al. 1988).

Third, are the differences in habitat quality large enough to *risk a fight* for getting access to a good habitat? Though our fighting model is admittedly simplistic, it obeys the demand that the costs and benefits of fighting should be expressed in terms of their lifetime fitness consequences (Grafen 1987; Enquist and Leimar 1990). If the differences in habitat quality are small, the expected benefits of a good habitat may not outweigh the expected costs of fighting. In such a case, challenging owners of high-quality territories would be maladaptive, and settling in a habitat of lower quality would be the better option in the absence of vacancies in the high-quality habitat. As a consequence, a despotic distribution over habitats should result even in the absence of a clear-cut advantage of established individuals. If, on the other hand, habitats differ significantly in terms of reproductive success, unsettled individuals have a high incentive to risk a fight for a better reproductive opportunity. The absence of fights in such a situation indicates that fighting involves a disproportionately high risk for the challenger. To overcome this large and systematic advantage of established individuals, the unsettled individuals have to pay significant ''costs of settlement.''

Fourth, do owners have a disproportionately high chance of winning because of *phenotypic superiority?* Fighting for a good reproductive position may not be worth the effort if the chances of winning are negligible. Hence, individuals with inferior fighting ability may not gain access to habitats of good quality. This situation does not necessarily mean that inferior phenotypes have to make the best of a bad job. If the fighting ability of an individual is not fixed but dependent on environmental conditions, it may be adaptive to postpone reproduction in order to increase the chances for obtaining a good reproductive position in the future. ''Wait and grow'' may thus be a strategic decision with deferred maturity as a logical consequence (Roff 1992). In contrast to fish and mammals, birds tend not to continue to grow after 1 yr of age, and environmental conditions during growth may strongly affect final body size (see, e.g., Richner 1989; Larsson and Forslund 1991). Only those carrion crows *Corvus corone* that grow to a sufficient size succeed in obtaining a breeding territory (Richner 1989). Though this fact adds some weight to our observation that there were no obvious morphological differences between oystercatchers in poor and good territories, more sophisticated methods to measure fighting ability are clearly needed.

Fifth, do general *breeding skills* improve the effectiveness of individuals in their competition for access to habitats of high quality? It is not enough that birds consistently move from low-quality territories to high-quality territories when possibilities open up, as found by Krebs (1971), Baeyens (1981), de Vos (1983), Petersen and Best (1987), and Newton (1991). What matters is if having bred, albeit in a poor territory, actually helps to overcome the owner advantage of birds in territories of high quality. If so, settlement in a habitat of poor quality may augment the probability of gaining access to high-quality habitats later in life, and it may be adaptive to settle first in a habitat of poor quality. Whether such a decision is indeed advantageous depends, however, not only on the transition probabilities but also on other factors such as habitat-specific mortality rates.

Sixth, can recruits opt for all sites with a reasonable chance of success, or do they have to concentrate on *specific sites?* If site-specific information or integration into a site-specific dominance hierarchy is required to have a reasonable chance of settlement, a specific nonbreeder cannot just settle wherever a vacancy or other opportunity for settlement arises. Instead, previously established social relationships are required to augment the chances of getting successfully established in a given site (see below). This requirement makes it necessary for the prospecting nonbreeder to concentrate its activities on a specific site, which thereby reduces its chances of succeeding elsewhere. It is as if the nonbreeder joined a waiting queue for the site. Furthermore, when the number of competitors increases, the chance of successful recruitment will decrease. Since competition will be more intense for a high-quality habitat, we therefore expect longer "waiting" times for territories in a high-quality habitat. Similar ideas have gradually taken shape during the past decade. Smith (1978) was the first to demonstrate that site-specific experience increased the chances for nonbreeders of successful settlement at that site, while Woolfenden and Fitzpatrick (1978) suggested that in a cooperatively breeding species, the helping nonbreeders did not disperse so as to "inherit" the natal territory. Wiley and Rabenold (1984) were probably the first to suggest that longer queues of nonbreeders would be formed for reproductive positions of high quality, while Stacey and Ligon (1987) and Komdeur (1992) provided compelling evidence for this in two species with helpers at the nest. Reviewing the literature, Zack and Stutchbury (1992) have concluded that the trade-off between waiting a long time for ownership of a territory of high quality or settling immediately in a territory of low quality is not restricted to species with helpers at the nest.

Site-Specific Dominance and Queuing

In our own studies of a population of oystercatchers, we arrived at the conclusion that site-specific dominance relationships indeed play a vital role in the recruitment decision of the individual, and we expect the same to be true in many other species. A possible explanation for site-specific dominance is based on the suggestion that familiarity with the local topography is important during fights. Another possibility is that better knowledge of the local resources is important. In our opinion, however, establishing social relationships (especially dominance relationships) at a locality is a major determinant of recruitment success at that locality. Furthermore, maintaining these social relationships requires regular presence. Thus, there is a trade-off between being regularly present at a few localities and being rarely present at many localities. We think that this trade-off underlies the trade-off suggested by Zack and Stutchbury (1992) that if a nonbreeder increases the number of territories it visits, it thereby reduces its chances of capitalizing on a vacancy that may occur in a visited territory. Our tentative answer to the question why social competition necessitates regular presence has two elements. First, we suggest that the relative value of a unit of space to the contestants may be decisive for the outcome of many territorial contest. Second, the regular presence of an individual in a unit of space may be the best indication of the value of that unit of space to that bird.

Recruitment Decisions and the Timing of Reproduction

So far, we have treated each of the three hypotheses on the underlying mechanism of a despotic distribution independently of the others. However, though the hypotheses are different, they are not mutually exclusive. It could well be that breeding experience, site-specific experience, and good fighting ability all help to improve the chances of successful settlement in a high-quality habitat. In our study of oystercatchers, for instance, evidence favored the queue hypothesis, but the inferior phenotype hypothesis was not definitively rejected. It could be that more subtle phenotypic characters than we investigated determined fighting ability. Thus, ways must be sought to assess the relative contribution of each mechanism. We suggest that one method is to inspect the relationship between lifetime reproductive success (LRS) and the age at first breeding. Under the queue hypothesis we predict a positive correlation between the two variables: birds that settle in poor territories will do so at a young age at the cost of a low LRS, and so forth. Under the inferior phenotype hypothesis we expect a negative correlation: good fighters will settle quickly in a high-quality habitat, while poor fighters will often be displaced before they finally settle in a poor habitat (see Whitham 1978, 1979, 1980). The breeding skill hypothesis does not lead to a specific prediction on this relationship.

The long-term population studies of birds reviewed by Clutton-Brock (1988) and Newton (1989*a*) can be analyzed from this point of view, as there is considerable natural variation in both LRS and the age at first breeding in nearly all studies. From table 17.2 in Newton (1989*b*), it can be calculated that female sparrowhawks *Accipiter nisus* that bred for the first time at 1, 2, or 3 or more years of age, fledged respectively 4.1, 5.8, and 5.2 chicks in their lifetime. Though Newton (1989*b*) states that females that bred at an early age tended to be larger than those that waited and that there was a positive relationship between body size and LRS, these data suggest that queuing was important too. In a study of pied flycatchers *Ficedula hypoleuca* Sternberg (1989) showed that in both sexes reproductive success of the first breeding attempt increased with increasing age at first breeding. However, as in sparrowhawks, LRS was highest for birds with intermediate ages of first breeding. In contrast, in the long-lived short-tailed shearwater *Puffinus tenuirostris,* which rarely breeds before 5 yr old, both annual reproductive success and annual survival were lower for birds that first bred at an early age (Wooller et al. 1989), which suggests there was an advantage in waiting. Comparing these examples, including the oystercatcher, it seems that the best evidence for a positive correlation is found in the longest-lived bird species. Such a relationship would make sense as the likelihood that poor competitors will have died before joining the competition for breeding territories is highest in species that defer breeding longest.

Career Decisions

Although breeding oystercatchers are despotically distributed, the queue model assumes that prospecting nonbreeders are free in their choice of queue, in line with the original proposal of Fretwell (1972) that under the ideal despotic distribution the "apparent suitability" will be equal for all unsettled individuals. That is, unsettled individuals are free to move, as long as they retain the status of unsettled individual. Fretwell (1972) realized that the "apparent suitability" of a habitat "may not be a measure of the success of some members of the habitat, but a measure of the average success of a hypothetical group of individuals which tried to enter a habitat until either successful or dead" (p. 99). Thus, the cost of settlement is paid during the act of settling, which leads to a higher variance in the LRS of birds that attempt to settle in a high-quality habitat, despite average LRS being equal for all potential settlers. In our queue model the difference in variance is due to the difference in waiting time. Fretwell did not explicitly incorporate time in his models. Several of the subsequent extensions and elaborations of density-dependent habitat selection theory have included time through the rate of reward gain in different habitats (see, e.g., Rosenzweig 1981; Sutherland and Parker 1985; Brown 1990). Truly dynamic distribution models, like the simulations of Bernstein et al. (1988), in which predators learn about the average reward rate of the environment on a real-time basis, are few (Kacelnik et al. 1992*a*). Our queue model, in which status is acquired on a real-time (albeit coarse) basis, may be the first dynamic representation of the despotic distribution.

On the other side of the coin, the many ritualized displays that accompany social competition may obscure the fact that this competition ultimately revolves around access to resources vital for reproduction and survival (West-Eberhard 1979). In this context, the recruitment success of an individual typically depends on its previous social position. Social positions have to be built up in the course of time. Because recruitment decisions not only are affected by the preceding social position of the individual but will also affect the future course of its social career, we propose to call them *career decisions*. The concept of a career decision owes much to the concept of an ontogenetic trajectory put forward by Wiley (1981) in a seminal but rarely quoted article. In Wiley's definition the ontogenetic trajectory of an individual describes the ages at which it achieved particular social positions. It is clear that career decisions mark the transitions to new social positions and therefore have long-term fitness consequences. Thus, in order to understand recruitment, one should not focus on successful individuals alone but on expected success at the moment when such a career decision is made (i.e., early in life during the nonbreeding phase). More specifically, the observed distributions of territorial birds cannot be understood from measurements on the territory owners only but must include their years of battle as nonbreeders.

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APPENDIX A

Population Consequences of the Markov Model

In stage-structured population models, the growth rate and the stable stage distribution of a population are usually derived from a life cycle graph or from a corresponding matrix model (see, e.g., Caswell 1989). This approach is not applicable to the oystercatcher since the survival probabilities of young birds (before they return to the breeding grounds) have not yet been estimated reliably. Therefore, we take an alternative approach based on the state transition probabilities m_{ij} and the assumption that the size of the breeding population remains constant (see Ens et al., in press, for empirical evidence). In a stationary population, we may assume that a bird that has died (= status 4) is replaced by a nonbreeder (= status 3):

$$m_{41} = m_{42} = m_{44} = 0, \quad m_{43} = 1 . \tag{A1}$$

Hence, the dynamics of the status frequency distribution (eq. [3]) is governed by a Markov process that is regular since any given state can be reached from any other state. The "fundamental theorem for regular Markov chains" (see, e.g., Kemeny and Snell 1976) guarantees that the process converges at an exponential rate to a unique stable limit distribution p^* that is independent of the starting conditions and characterized by equation (4). Technically, p^* is a left eigenvector of M to the eigenvalue 1. In our example (M given by table 2), the unique solution of equation (4) is $p^* = (0.262, 0.389, 0.292, 0.056)$. The expected limit distribution over the first three states (table 4) is obtained by renormalizing p^* (i.e., dividing p^* by the sum of the first three components). This yields the distribution (0.278, 0.411, 0.310, 0.060).

APPENDIX B

The Estimation of EFRS

From the perspective of a population, it is useful to assume that a dead individual is replaced by a nonbreeder (eq. [A1]). From an individual perspective, however, death is an "absorbing state" that will never be left once it is reached. Accordingly, we posit

$$m_{41} = m_{42} = m_{43} = 0, \quad m_{44} = 1 . \tag{B1}$$

The resulting stochastic process corresponds to an "absorbing Markov chain" that can be analyzed by standard methods (see, e.g., Kemeny and Snell 1976). Let t_{ij} denote the expected number or time steps that the process stays in state j given that it was in state i at time 0 ($1 \leq i, j \leq 3$). For example, t_{31} denotes the number of years that a nonbreeder (= status 3) can expect to spend as a resident (= status 1) in the future. The times t_{ij} can be obtained from the relation

$$t_{ij} = \delta_{ij} + \sum_{k=1}^{3} m_{ik} t_{kj} \tag{B2}$$

(Kemeny and Snell 1976, theorem 3.2.4), where $\delta_{ij} = 0$ if $i \neq j$ and $\delta_{ij} = 1$ if $i = j$. Equation (B2) has a clear-cut interpretation. The time expected to be spent in state j is split into two components: the time spent in state j at time $t = 0$ (given by the first term, δ_{ij}) and the time expected to be spent in j from time $t = 1$ onward. At time $t = 1$, the process will be in state k with probability m_{ik}, and the expected time to be spent in j starting from k is t_{kj}.

The "fundamental matrix" $\mathbf{T} = (t_{ij})$ can easily be calculated from equation (B2). Matrix $\mathbf{T}$ corresponds to the inverse of the matrix $\mathbf{Id}\text{-}\mathbf{M}_0$, where $\mathbf{Id}$ is the identity matrix, and $\mathbf{M}_0$ is the submatrix of $\mathbf{M}$ corresponding to the nonabsorbing states (here, $1 \leq i, j \leq 3$). For the oystercatcher example, the values t_{ij} are presented in table 5.

Some other useful entities are also readily calculated. The variance of t_{ij} is given by the formula (Kemeny and Snell 1976, theorem 3.3.3)

$$\sigma^2(t_{ij}) = t_{ij}(2t_{jj} - t_{ij} - 1)\,. \tag{B3}$$

For a process starting in the transient state i, the expected time before absorption is (Kemeny and Snell 1976, theorem 3.3.5)

$$T_i = \sum_{j=1}^{3} t_{ij}, \quad \sigma^2(T_i) = 2 \cdot \sum_{j=1}^{3} t_{ij} T_j - T_i(1 - T_i)\,. \tag{B4}$$

In the oystercatcher example, T_i corresponds to the life expectancy of a bird in status i (see table 5).

The probability that the process enters state j upon leaving the transient state i can be derived directly from the Markov matrix $\mathbf{M}$ (Kemeny and Snell 1976, theorem 3.5.6):

$$q_{ij} = \frac{m_{ij}}{1 - m_{ii}} \quad (i \neq j)\,. \tag{B5}$$

For example, the probabilities that a nonbreeder (= status 3) will first breed as resident, first breed as leapfrog, or not breed at all (table 6) are directly obtained from equation (B5):

$$q_{31} = 0.196, \quad q_{32} = 0.5, \quad q_{34} = 0.304\,.$$

The probability that the transient state j will eventually be reached once the transient state i is left is given by (Kemeny and Snell 1976, theorem 3.5.7)

$$h_{ij} = \frac{t_{ij} - \delta_{ij}}{t_{jj}}\,. \tag{B6}$$

In the oystercatcher example, the probability that a leapfrog will ever become a resident is $h_{21} = 0.349$. As a consequence, the probability that a nonbreeder will recruit first as a leapfrog and eventually reach the resident status is $q_{32}h_{21} = 0.175$ (table 6).

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