

LOCAL DOMINANCE AND TERRITORIAL SETTLEMENT OF NONBREEDING OYSTERCATCHERS

by

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Summary

1. We studied the mechanisms of territory acquisition in an oystercatcher (*Haematopus ostralegus*) breeding population on Schiermonnikoog (1983-1997), competing for low quality (leapfrog) and high quality (resident) territories.

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⁵⁾ An indispensable contribution to this paper was made by Piet Zegers, who very skillfully caught so many nonbreeders. Jan Hulscher never lost his enthusiasm in visiting distant roosts and clubs with few marked birds. Many people participated in the project, of which the following deserve special mention. Alex Brenninkmeijer, Caroline Haverkort, Marcel Kersten, Jan van der Kuil and Ad Stroes did the removal experiments. These, Jan Hulscher and Marcel Klaassen kept the population study running in the early eighties. Kees van Oers gathered many data in the important 1996 season. The pilot study of Nelly van Brederode, carried out with meticulous care, gave us confidence that intrusion rate could be quantified. Intrusion rates in 1993 were determined with Rosalie Blom, Bob van Oort, Merlijn van Weerd, Romke Kats and Marcel Sagel. Leo Zwarts and Klaas van Dijk provided roost counts during 1984-1989. This paper benefited much from stimulating discussions with Rudi Drent, John Goss-Custard, Jaap Kruijt, Joost Tinbergen and Franjo Weissing. We thank the two anonymous referees for their useful comments on the manuscript. The 'Dienst der Domeinen,' 'Staatsbosbeheer' and 'Natuurmonumenten' allowed us to work in their nature reserve 'Oosterkwelder,' one of the last unspoiled parts of the Netherlands. Jan Koenes and his crew took good care of the hides. Jan Nijboer and Ger Veltman made the colour bands. Dick Visser prepared the figures. BE, DH and LB were supported by NWO (grants 811-430-163, 805-30-164 and 805-36-124).

2. Numbers of nonbreeders on the island varied from 960 to 3380 during 1984-1997, compared to *ca* 4620 breeders. We estimated that 50% of the nonbreeding individuals, or 27% of all adult birds (at least three years of age), were capable of breeding but failed to do so.
3. Nonbreeders were apparently active in searching breeding positions by: (a) frequent intrusions into territories and hovering ceremonies above nesting territories, evicting breeders, creating territories or filling vacancies. (b) Forming pair bonds and establishing local dominance positions on the mudflats or clubs to usurp breeders, to fill vacancies or to squeeze between territories. Depending on the location of activity, we distinguished 'aggressive club-birds,' 'hopeful residents' and 'opportunistic nonbreeders' among the nonbreeders.
4. Due to the high survival of breeders, low numbers of primary vacancies became available annually. Additional secondary vacancies became available from breeders deserting their territories for better breeding positions. The relative number of deserting individuals decreased from female leapfrogs, male leapfrogs, female residents to male residents. In the main study area leapfrog territories outnumbered resident territories 2 : 1. Hence, nonbreeders had more opportunities to obtain a leapfrog territory in both absolute and relative terms.
5. Nonbreeders filled only 46% of the resident ($N = 94$), and 32% of the leapfrog vacancies ($N = 179$). This was due to severe competition with single and paired breeders also aiming at these vacant sites. Hence, only 33% of the nonbreeders acquiring a breeding position used a vacancy ($N = 236$). As an alternative, paired nonbreeders squeezed between breeding territories (45%) or more rarely, single/paired nonbreeders usurped single/paired breeders (18%), or single females joined breeding pairs into polygyny (3%).
6. Hopeful residents settled on the shoreline close to their mudflat territory, usually as a resident, sometimes as an adjacent leapfrog. Aggressive club-birds with high dominance positions on the main club in the leapfrog area, settled close to this club as a leapfrog. Opportunistic nonbreeders settled in territories close to where they had intruded in previous year(s), either as a resident or as a leapfrog. A high dominance position at a given locality seems a prerequisite for getting a territory at that locality.
7. By removals of a mate during incubation, experimental breeding vacancies were created. The most interesting results were obtained from permanent removals, which resulted in clutch loss (89%) and territory loss (56% of the 'widowed' birds, $N = 9$). The other 44% of 'widows' got a new, mostly previously nonbreeder, mate. The experiment confirmed that: (a) nonbreeders were capable of breeding; and (b) only cooperative pairs are able to raise a brood and defend a territory.
8. Many nonbreeders settled after severe winters, due to more vacancies arising because of increased mortality. Yet many leapfrog vacancies remained unoccupied, despite nonbreeders being available to fill these vacancies. This at first sight anomalous observation can be explained by the queue model (Ens *et al.*, 1995), since waiting for a vacancy in a resident territory might be more beneficial than immediately accepting a low quality leapfrog territory.
9. We propose that nonbreeders face three trade offs, (a) between sampling a large area and finding many vacancies (*i.e.* opportunistic strategy) *versus* establishing a local dominance position, sampling a small area and finding fewer vacancies, but with a higher chance of successfully competing for that vacancy (*i.e.* hopeful resident or

aggressive club-bird strategy); (b) between competing for a low quality territory with small numbers of competitors *versus* fighting for a high quality territory with many competitors; (c) between finding a breeding position singly, and mating a widowed breeder with breeding experience *versus* pairing with a nonbreeder, thereby finding a breeding position by squeezing between breeding territories.

Introduction

In many species, individuals can only reproduce if they settle into a breeding territory. In natural populations, competition for these breeding sites can easily be observed, *e.g.* when individuals return to these sites in early spring and engage in severe battles for breeding space. Competition often results in closely spaced small territories, particularly in high quality habitat. These high densities might decrease the average productivity or survival of the local population (*e.g.* Englund, 1993), and in many cases individuals get excluded from breeding (see Newton, 1998). Equally important, due to these density-dependent effects on fitness, less suitable habitats might become attractive, because fitness in the high quality habitat might decrease to the level of fitness in the low quality habitat due to this competition (Kluijver & Tinbergen, 1953; Fretwell & Lucas, 1970). In fact, all else being equal, we would expect natural selection to modify habitat selection of organisms, so they will settle in the habitat offering the highest fitness, given the current densities of competitors in each habitat. Accordingly, we would expect organisms to distribute themselves over these habitats so as to level out any fitness differences between the individuals (the 'Ideal Free Distribution,' see Fretwell & Lucas, 1970).

Surprisingly, many species have been found where this general prediction does not seem valid at first glance. For instance, in the oystercatcher (*Haematopus ostralegus*), breeders in the high quality territories produce three times more fledglings than breeders in the low quality territories, although they survive equally well (Ens *et al.*, 1992, 1995). Apparently, density-dependent effects have not taken their toll in the high quality habitat yet. So why do not more birds settle in this high quality habitat? Why has not the density in the high quality area increased, as to level out these fitness differences? We will call this the '*habitat selection paradox*.' Ens *et al.* (1995) discussed four hypotheses offering a solution to this paradox, including: (1) Individuals occupying low quality territories are competitively

inferior to individuals occupying high quality territories (therefore, they are despotically excluded from the best territories); (2) Relatively more individuals compete for vacancies in the high quality territories compared to vacancies in the low quality territories. If many individuals compete for the best habitat, (a) the chances of obtaining a breeding position in the best habitat will decrease; (b) expected age at recruitment will increase; and hence (c) the expected time spent breeding will decrease. They concluded that the second hypothesis is most likely and constructed a model to predict the settlement strategies of nonbreeders (the 'queue' model, which incorporates 'Ideal Free' and 'Ideal Despotic' elements). The model showed that the expected lifetime fitness of a nonbreeder competing for either habitat might be the same. According to the model, new recruits face a trade off between settling at a young age in a territory of poor quality, or improving the chances of settling in a territory of high quality through a delay of settlement, but with the risk of dying before having settled. At the evolutionary equilibrium the density of the nonbreeders (or the length of the queues) is such that the fitness loss from aiming for a high quality territory equals the fitness loss from settling almost 'immediately' in a territory of low quality (Ens *et al.*, 1995).

From a general review of the avian literature, Zack & Stutchbury (1992) concluded that the evidence for the idea that nonbreeders queue is patchy, in part because it is often so difficult to study the behaviour of the nonbreeders. Mock (1985) states that the study of nonbreeding birds 'will be a major logistic challenge because many birds we need to know about are under great social pressure from dominant conspecifics to be inconspicuous.' Luckily for us, nonbreeding oystercatchers gather in clubs at traditional locations in the breeding area, where their behaviour can be studied with unusual ease. Thanks to the openness of the habitat, it is also relatively easy to study how they intrude and recruit into the breeding population. Finally, in our study area it is relatively straightforward to measure territory quality (see Ens *et al.*, 1992). In this paper we shall discuss questions arising from the queue model:

- (1) How many nonbreeders are excluded from breeding? Are these birds in principle capable of breeding? Under the most simple scenario the possibilities for nonbreeders to settle can be equated to vacancies that occur through death of a territory owner. Each vacancy should be quickly occupied by a nonbreeder. Experimental removal of breeders should similarly allow nonbreeders to settle. Additionally, the removal of breeders allowed us to test whether single breeders (experi-

mental widows) can care for the brood and defend the territory simultaneously, without help from a mate.

- (2) How do nonbreeders find breeding positions? How many single and how many paired nonbreeders settle in leapfrog and resident territories?
- (3) Is it possible to distinguish nonbreeders opting solely for resident territories or for leapfrog territories ('queuing')? Ens *et al.* (1995) believe that nonbreeders cannot switch queues, because individuals must develop local site dominance to be able to compete successfully for vacancies at that site. Thus, dominance should change with the location of the bird, there must be specific dominance behaviours and it should be possible to identify nonbreeders as either hopeful resident or hopeful leapfrog.
- (4) Do nonbreeders queue for the resident territories, when vacancies in the leapfrog territories are available? Three severe winters with mass mortality of both breeders and nonbreeders provided us with data to address this question.

In the discussion we reflect on how queues get established, why individuals stick to their positions in the queue, and how queue models provide us with new insight in habitat selection and population demography.

Study population and social system

Study population

Since 1983, oystercatchers inhabiting the Dutch Wadden Sea island of Schiermonnikoog (Fig. 1) have been individually colour marked. On Schiermonnikoog, most oystercatchers breeding in natural habitats, like the salt-marsh, feed almost entirely on the intertidal mudflats throughout the year. No substantial migration occurs during the nonbreeding season, except during periods of extreme cold when some migrate south to estuaries in the southern part of the Netherlands and France (Hulscher, 1989). In winter, all oystercatchers feed up to several kilometers from the shore during low water, while in summer there is a greater tendency to feed close to the shore. Marked nonbreeders settled both inside and outside the main study area. However, outside the main study area usually no detailed observations were available of birds changing territory or mate. Notably, in some areas not all

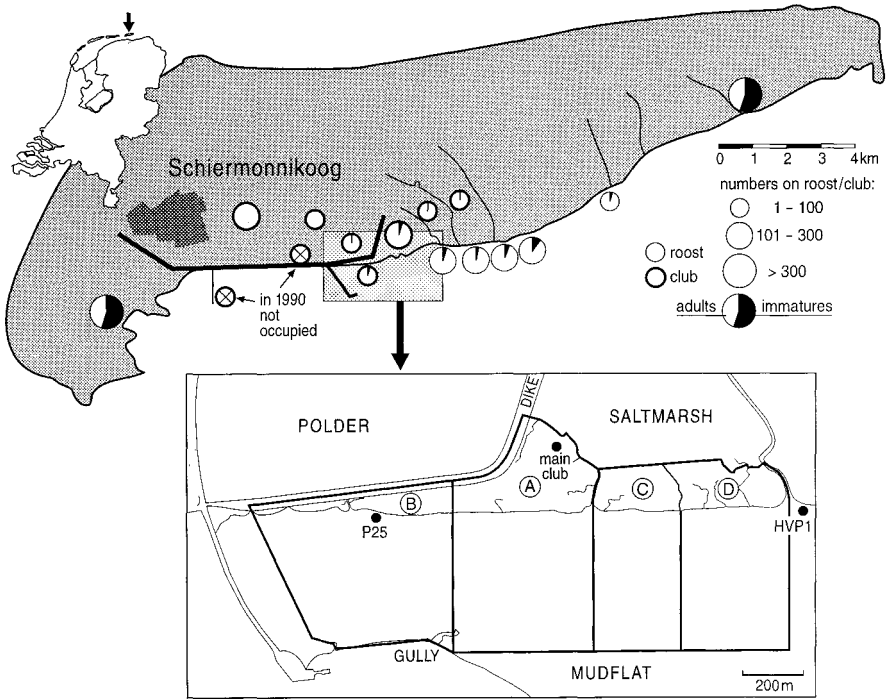


Fig. 1. Map of the island Schiermonnikoog with the main study area, the high tide roosts and the clubs indicated. The main study area was extended twice, in 1986 from area A to AC, in 1992 from area AC to ABCD. Indicated are the subareas A, B, C and D; the local clubs 'main club,' 'P25' and roost 'HVP1' and the adjacent mudflats.

of the breeders were marked, which made it difficult to establish whether a vacancy resulted from a breeder dying or deserting the territory. Therefore, we restricted our analysis of territory changes to the main study area (area A, Fig. 1 panel), which was extended twice (in 1986 to area C, in 1992 to area B and D). In 1983 observations started with banding breeders in the study area, and in 1984 most of the breeders in study area A were marked. In 1985 the first detailed observations of territory changes were conducted.

Definitions and general description of social system

The birds aggregate in two kinds of traditional roosts when the intertidal feeding area is covered: *roosts*, where flocks of up to thousands of oystercatchers rest during high tide in winter, and *clubs* (Fig. 1), where small flocks of at most a few hundred oystercatchers roost at high tide only during

the breeding season (March-August). Some individuals remain at the club during low tide.

Although polygyny sometimes occurs (Heg & van Treuren, 1998), most oystercatchers form monogamous pair bonds, in which male and female share duties in parental care and territory defence. Most breeders return to the same nesting territory and mate with the same partner each spring (Harris *et al.*, 1987; Ens *et al.*, 1993). Given that the birds are absent from the nesting territories in winter, the stability in the location and occupation of the territories is quite remarkable. In the study area, as in many areas, oystercatchers breed as: *resident* pairs, which defend a nesting territory on the edge of the saltmarsh and an adjacent area of mudflat, and *leapfrog* pairs, which defend a nesting territory further inland on the saltmarsh which is therefore separated from the feeding territory further down shore (Fig. 2). Resident pairs fledge about 3.5 times as many chicks per pair as leapfrog pairs (Ens *et al.*, 1992, 1995; Heg, 1999). Although the probability of breeders changing status is very low, some 5% of the leapfrogs manage to acquire a resident territory annually (Ens *et al.*, 1995; Heg, 1999). Moreover, Heg (1999) showed that only leapfrogs breeding close to the resident nesting territories were able to do so. We will refer to these leapfrogs as first row leapfrogs (breeding adjacent to a resident nesting territory) and second row leapfrogs (breeding adjacent to a first row leapfrog nesting territory, but not breeding adjacent to a resident territory) respectively.

We define as *nonbreeder* all individuals that do not defend a nesting territory (although they may defend a feeding territory on the mudflats). Though Harris (1970) referred to breeders in whose nesting territory no clutches were found as nonbreeders, we do not do so, because predation on eggs is high during egg-laying (Ens, 1991), and we suspect that most breeders without a clutch are in fact birds that lost their clutch so quickly that it was not found by us. True nonbreeders can be classified according to their territorial commitments as:

1. *Aggressive club-birds*, which behave very aggressively on the club or the high tide roosts, yet do not succeed in claiming an area there to which they have exclusive access. Aggressive club-birds compete for leapfrog territories adjoining the roost, in cases where the club is located inland (*e.g.* Fig. 2, 1995). If the club or roost is located along the shoreline (*viz.* adjoining resident feeding territories), they compete for resident territories.

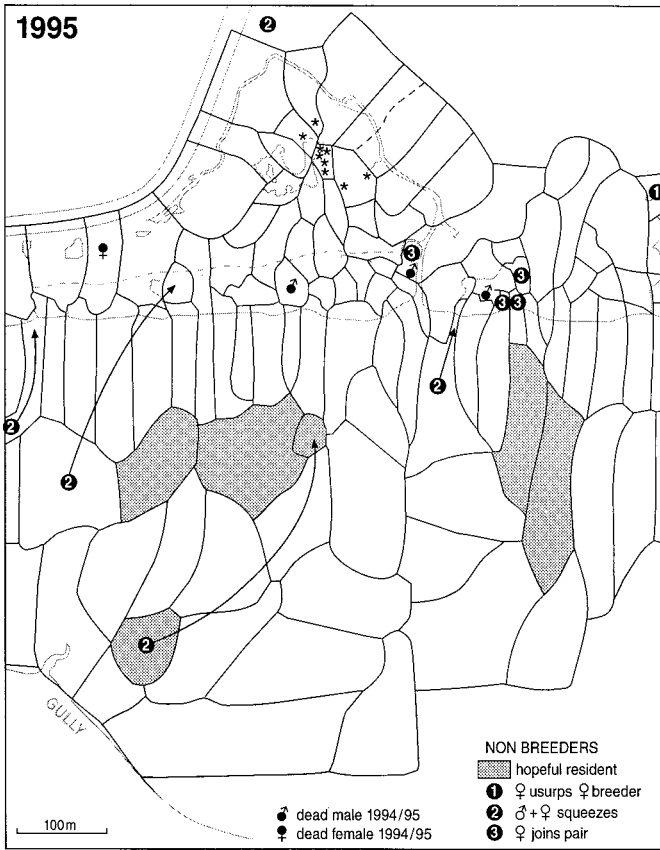


Fig. 2. Territory map of the main study area (area AC, area BD not depicted) in June 1995 (after a mild winter) and June 1996 (after a severe winter). Male and female breeders which had not returned and presumed dead after the previous winter are indicated on the maps. The number of leapfrog territories declined after the severe winter 1995-96. The main club was established in 1988. Stars indicate nine hopeful leapfrog pairs settled from the main club as a leapfrog in the years 1988-1995, six of these territories were still occupied in 1995 (two of them have 'moved away' from the main club). Typical ways in which nonbreeders gained a nesting territory after a mild winter are indicated in the map of 1995: 1. female nonbreeder usurps female breeder; 2. pair of nonbreeders squeeze between territories to gain nesting territory; 3. female nonbreeder joins monogamous pair into polygyny. Filling vacancies were more common after severe winters, as indicated in the map of 1996: 4. female nonbreeder fills vacancy of female breeder; 5. male nonbreeder fills vacancy of male breeder. Nonbreeders have difficulties acquiring resident territories, due to severe competition for these high quality territories. This competition includes breeders taking advantage of changes in the resident population, as indicated in the map of 1996: 6. pair of leapfrogs squeezes between residents to acquire a resident territory; 7. leapfrog widow and neighbouring resident widow join nesting territories; 8. neighbouring resident widows join territories.

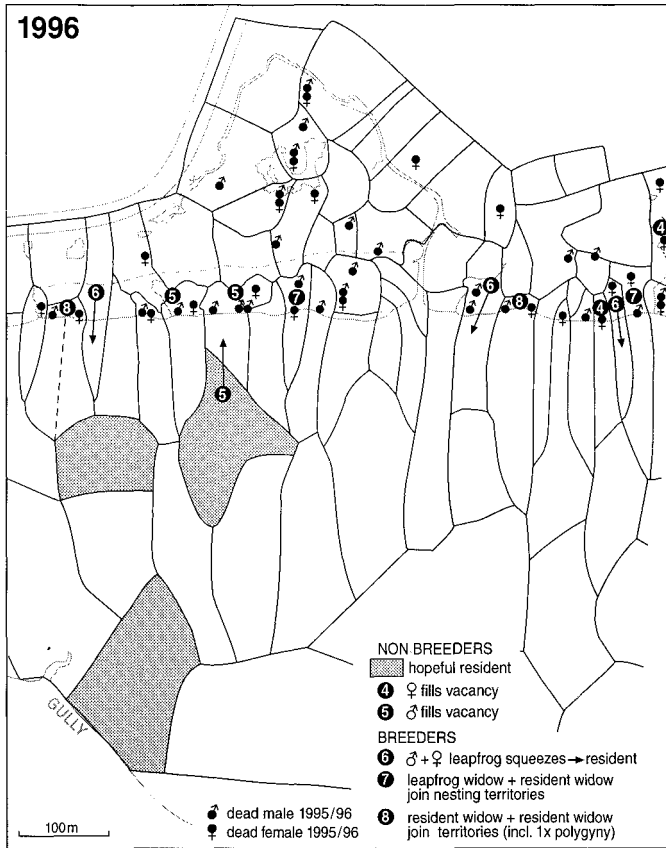


Fig. 2. (Continued).

2. *Territorial nonbreeders*, which defend a feeding territory on the mudflats, often adjoining the feeding territories of the residents. We will show that the latter birds can be identified as 'hopeful residents' (Fig. 2).
3. *Opportunistic nonbreeders*, which are without known aggressive commitments on either the club or the mudflats. However, they are very active with intrusions within a restricted area (5 to 15 territories). Sometimes they intrude as pairs (and they might even copulate with each other during an intrusion).
4. *Uncommitted nonbreeders*, which are without known local commitments on either the club or mudflats. Many juveniles (< 3 years of age) were classified as uncommitted: they arrived at high tide roosts

very late in the tidal cycle (when almost all the mudflats were covered by water) and left it again very soon (as soon as the mudflats were exposed again), flying directly towards the distant mudflats. However, some of these nonbreeders might have defended feeding territories on these distant mudflats or might have intruded in breeding territories outside our study area. Note that we prefer not to refer to uncommitted nonbreeders as 'floaters,' since this term has been used by other authors to denote 'nonbreeders' in general.

Oystercatchers engage in various typical behaviours (see pictures in Goss-Custard, 1996). *Intruders* (usually nonbreeders, sometimes distant breeders) intrude into territories not their own, after a walk, or more commonly, a flight. This category excludes territory owners that persist in chasing an intruder in their own territory into their neighbours' territory, and also victims of chases that enter a new territory being chased by territory owners. However, it includes *gatherings* of between 10 and 40 intruders that may accumulate in a territory, with the majority standing in an alert posture; in a mudflat territory, some intruders may start to forage. Such intruders may behave aggressively toward each other and toward the territory owners. However, most intruders joining a gathering behave very submissively and flee instantly when the territory owners start chasing them. In the *hovering ceremony*, several oystercatchers all perform the 'piping display' (Cramp & Simmons, 1983) together in flight while hovering above a fixed location. Otherwise, piping is done on the ground by territory owners while chasing intruders, in boundary disputes with neighbours and as a 'keep-out signal' against intruders flying overhead or landing at a distance (review in Cramp & Simmons, 1983).

Methods

Observations of breeders

The primary field season lasted from March till August. Each year we tried to catch (usually on the nest) and mark any unmarked adults breeding in the main study area. By 1985, nearly all the *ca* 80 pairs in the *ca* 12 ha main study area had been marked (and also many birds in the surrounding areas). Two hides (since 1992 three hides) placed on the saltmarsh edge and the dyke allowed a complete survey of all nesting territories. Another hide 350 m down shore allowed the survey of many feeding territories defended by both breeders and nonbreeders. On average, the hides were manned once a week for an entire low-water period from March to August. The identity of all pairs and single birds present was determined and their location

marked on a grid of 25 m squares. The location of copulations was noted, along with the identity of the individuals, the initiator and whether cloacal contact occurred. The location of aggressive encounters was noted, along with the encounter type (see Ens, 1992 for details), the identity of the individuals or pairs involved, and the outcome. These observations allowed us to discover changes in the breeding population and provided the raw material for the territory mapping. Territory boundaries were determined by plotting the positions of the birds and the trajectories of boundary disputes on detailed maps of the main study area. A 50×50 m grid of sticks on the mudflat (450×450 m, since 1990: 500×450 m) was used to map the feeding territories. Thus, any changes in the breeding and feeding territories could be identified, *i.e.* change of mate, change of mating system (unpaired, monogamy, polygyny), change of territorial status (leapfrog, resident or nonbreeder: including location of mudflat territories), and the month in which the change occurred. Also, the cause of the change could be determined by monitoring which focal individual, focal pair or competitors (*i.e.* neighbouring breeding pairs or individuals, nonbreeding pairs or individuals: hopeful residents, aggressive club-birds or other nonbreeders) initiated aggressive interactions and/or deserted the territory leading to these various changes.

Observations of nonbreeders

Between 1987 and 1992 birds were caught with a canon net on the clubs and high tide roosts and most of them were colour marked (Heg, 1999). We caught predominantly adult nonbreeders of unknown age, many of which might have had a previous breeding history. Our pool of individually recognizable nonbreeders was further increased by colour-marked fledglings from the study area (1985 onwards), which survived their first winter and mixed with the other nonbreeders. All the high tide roosts around the main study area, and most of the other roosts on the rest of the island were visited at least once every second week. The total number of birds present, the number of marked birds and the number of immature birds was determined. Immature birds retain their neck collar throughout the summer, which makes them easily recognizable (Cramp & Simmons, 1983). Marked birds that roosted on the club, but were not known to defend a nesting territory, were classified as nonbreeders. Hence, these observations and the observations in the nesting areas allowed us to identify changes in the status of the nonbreeders, *e.g.* the time and place of successful establishment of a resident or a leapfrog territory during the course of the breeding season.

Nonbreeders defending a feeding territory on the mudflats were classified as territorial nonbreeders (mainly hopeful residents), and were observed weekly. Nonbreeders with a dominance score on the club exceeding 50% (see later) that had engaged in daily encounters on the club were classified as aggressive club-birds. The remaining nonbreeders were classified as opportunists or uncommitted nonbreeders.

When the main club formed in the main study area from 1988 onwards (Fig. 1), a small hide was placed nearby to allow detailed behavioural observations. From 1989 to 1996, aggressive encounters on this club were used to calculate a dominance score for each individual. An individual was considered 'winner' when it successfully chased other individuals (usually other nonbreeders) or when it piped and was not chased itself (a 'draw', usually in encounters with the local breeders). An individual was considered 'loser' when it was chased or evaded aggressive individuals. The dominance score was calculated as the number of 'wins' ('win + draw') divided by the total number of encounters ('win + draw + lost'). Additional information was gathered in 1990. In 1990, the main club was watched at

least once a week for 8 to 9 hours from low tide until all the birds had left after high tide. Every hour all birds present, and the marked birds in samples where both legs were visible, were counted. If possible, all marked birds were identified and the arrival time of marked birds seen landing was noted.

Vacancies

When a bird known to be alive the previous year did not show up the next year anywhere (on its territory, on any of the clubs or roosts, or on the feeding grounds), it was presumed dead. No less than 24% of the missing birds in the period 1983-1996 were actually recovered and reported dead (see Fig. 2 in Camphuysen, *et al.*, 1996). So far, no individual presumed dead after it had bred in the main study area in one year, was ever observed in later years, underlining the reliability of this method.

In the following we will indicate vacancies that resulted from the death of a territory owner as *primary vacancies* (Table 1, Fig. 2). These vacancies were mostly quickly filled in February/March, when most breeders regularly started to visit their feeding territories. When a breeder deserted its territory, *e.g.* to occupy a primary vacancy, thus creating a vacancy in its former territory, we refer to the latter as a *secondary vacancy* (Table 1, Fig. 2). When a bird obtained a new partner, while the old mate was still alive, the pair had divorced. We assumed that the focal bird had *deserted* its old mate, if the focal bird was seen to move, or if the old mate was for a substantial period of time alone in its territory. Usually, the deserting bird occupied a neighbouring breeding territory, leaving the old mate alone in the former territory. We assumed that the old mate had been evicted by a *usurper*, if there was no time lag between the appearance of the new mate and the disappearance of the old mate from the territory, or more rarely, if the actual takeover fight was observed (see also Ens *et al.*, 1993). Both breeders and nonbreeders could evict territory owners. Another method to obtain or improve one's breeding position was to '*squeeze*' between territories. For instance, leapfrogs adjacent to resident territories (so called 'first row' leapfrogs) were frequently observed to secure a small piece of the resident's feeding territories to feed on with their chicks, by initiating aggressive encounters on the mutual territory boundary of the two adjacent resident pairs occupying this mudflat area. Thus, they could get a small, 'V'-shaped resident territory without actually completely evicting a resident pair (*e.g.* Fig. 2). Since they retained their former nesting territory, changes from leapfrog to resident by squeezing did not result in secondary vacancies. Similarly, paired nonbreeders could squeeze between the nesting territories of the breeders and obtain a breeding position (*e.g.* Fig. 2).

Observations of intrusions

In 1990, four rectangular areas, measuring 100 by 150 meters each were divided into 10 by 10 meter squares using small sticks. Two of the areas were close to the saltmarsh edge, while the other two were on the adjacent mudflat, including (major parts of) 29 territories. Within these four areas, observations on intruders were made daily between 5 a.m. and 11 p.m. during several hours in the 1990 breeding season, at both high and low water (April-June). In 1991 (March-July), 1992 (April-July) and 1993 (March) the two rectangular areas close to the saltmarsh were again observed. Additionally, in 1993 another rectangular area close to the edge, the three areas on the adjacent mudflats, and one area close to the club was observed. For each intruder, the exact landing (intruders hardly ever arrived by walking) and

leaving sites were mapped. The presence or absence of territory owners was recorded, along with their reactions, all aggressive encounters between owners and intruders, the duration of the intruders' stay and any other birds (mostly neighbours) involved. Though males and females are similar in appearance, experienced observers can identify the sex from slight but consistent differences. Females are slightly larger, with a slightly longer bill and a slightly paler plumage and bill colour (Cramp & Simmons, 1983): sexing marked intruders revealed that few errors were made. For each observation period, intrusion rate was calculated as the number of intruders per hour per hectare.

Gatherings and hovering ceremonies

Observations on gatherings were collected subsidiary to other observations. Whenever gatherings occurred, the location, the total number of birds participating and the number of marked birds among them were counted. If possible, all marked participants were identified.

Detailed observations on hovering ceremonies were only collected in 1990. Due to the conspicuousness of this behaviour and the openness of the habitat we would have missed few hovering ceremonies. Radio contact between an observer scanning the club and an observer scanning from one of the large hides allowed us to identify many participants. Of all hovering ceremonies observed, the number of participants, duration, origin and location above which they took place were noted. Identifying individuals in flight was difficult, but usually birds would leave the ceremony singly or in small flocks, some landing nearby, thus making it possible to identify retrospectively some of the birds involved. In 32 hovering ceremonies the identification of all participants was possible.

Removal experiments

In total twenty male breeders and five female breeders were caught and temporarily or permanently removed from the territory. These included temporary removals: (1) breeders caught on the nest and released again the same or the next day from a distant part of the Netherlands (> 10 km away) to measure flight costs ($N = 11$); (2) breeders caught on the nest or in the territory and released after one or two days in captivity ($N = 5$); and permanent removals: (3) breeders caught on the nest and transported to the university ($N = 9$). These birds were used for several behavioural and physiological experiments and were not released. Thus in total, sixteen breeders were temporary removed (days since start incubation: 17.7 ± 2.5 , range 8 to 28, $N = 15$; one pair did not produce a clutch during the experiment), and nine breeders permanently removed (days since start incubation: 18.9 ± 2.1 , range -4 to 28, $N = 9$, one male was caught four days before incubation started).

Statistical analysis

Statistical analyses were performed using SPSS PC+ V2.0 and 4.0 (Norusis, 1990). Hierarchical log-linear models were used to analyse cross-classifications with more than two variables (Norusis, 1990). Logistic regressions were used to analyse probabilities (Norusis, 1990). In each case, full models containing all main effects and their interactions were constructed. Subsequently, nonsignificant terms were removed (on the basis of the likelihood ratio chi square, LR χ^2 or G) until the final model contained only significant terms. All statistical tests are two-tailed. We use the abbreviation 'NS' to indicate *non significant* differences.

TABLE 1. Annual number of resident and leapfrog nesting territories in the main study area (separately given for area A + C and area B + D), and the number of hopeful resident territories

Area:	Number of territories						Number of primary vacancies						Number of secondary vacancies						Number on roosts (whole island) ^f		
	Residents		Leapfrogs		Hopeful residents		Resident		Leapfrog		Resident		Leapfrog		Resident		Leapfrog		Total number	Estimated number of nonbreeders	
	AC	BD	AC	BD	AC	BD	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀			
1984	14 ^a	-	41 ^a	-	?	-	0	0	0	0	0	0	0	0	0	0	0	0	3440	2649	
1985	14 ^a	-	42 ^a	-	2 ^a	-	0	0	0	1	0	0	0	0	0	0	0	0	2625	2021	
1986	28 ^b	-	59 ^c	-	7	-	2	0	1	0	0	0	0	0	0	0	0	0	2770	2133	
1987	28	-	50	-	4	-	5 ^g	7 ^g	9	12	0	1	2	5	1340	1032	2091	2715	2087	1908	
1988	28	-	55	-	4	-	0	0	1 ^g	2 ^g	0	0	0	0	0	0	0	0	2710	3381	1975
1989	23	-	54	-	7 ^d	-	0	0	3	0	0	0	2	1	4391	2087	1908	2565	1193	1862	
1990	25	-	54	-	7 ^d	-	0	0	3	1	0	1	1	2	2478	1975	1549	2418	1862	1862	
1991	27	-	57	-	7 ^d	-	0	1	1	2	0	0	0	0	2478	1975	1549	2418	1862	1862	
1992	25	35	56	38	7	5	4 ^g	1 ^g	1	1	0	0	0	0	2565	1975	1549	2418	1862	1862	
1993	26	39	50	38	5 ^e	7	3	4	2	3	0	0	0	0	1549	1193	1549	2418	1862	1862	
1994	26	39	53	41	6 ^e	7 ^d	1	1	2 ^g	2 ^g	0	0	2	3	2418	1862	1549	2418	1862	1862	

TABLE 1. (*Continued*)

Area:	Number of territories				Number of primary vacancies				Number of secondary vacancies				Number on roosts (whole island) ^f			
	Residents		Hopeful residents		Resident	Leapfrog	Resident	Leapfrog	Resident	Leapfrog	Resident	Leapfrog	Total number	Estimated number of nonbreeders		
	AC	BD	AC	BD	♂	♀	♂	♀	♂	♀	♂	♀				
1995	26	39	48	43	6	6	2 ^g	3 ^g	7 ^g	1 ^g	0	1	2	3	2519	1940
1996	22	36	29	25	3	5	25 ⁱ	14 ⁱ	29 ^h	18 ^h	0	1	6	13	1850	1425
1997	22	35	23	19	3	2	6	8	6	2	0	3	3	10	1243	957
Total number of vacancies					48	39	65	45	0	7	18	51				
Percentage secondary vacancies of all vacancies									0	15	22	53				

The number of primary and secondary vacancies arising in each year was established in relation to the number of territories and the area studied in the previous year (see Methods for definitions of vacancies). The number of nonbreeders is given as the sum for the whole island of Schiermonnikoog. Years printed in bold refer to breeding seasons following a severe winter. The main study area was extended in 1986 from A to AC and in 1992 from AC to ABCD. Observations started in 1983 with marking breeders (area A: 8 pair of residents, all marked and 13 pair of leapfrogs, 8 marked; only a limited number of breeders in area A were located and marked).

^a Only area A.
^b Main study area extended to C, number of territories in A: 16, number of territories in C: 12.
^c Main study area extended to C, number of territories in A: 42, number of territories in C: 17.
^d Including one polygynous trio.
^e Including two polygynous trios.
^f Counts in mid-May, estimated number of nonbreeders = 77% of the total number (see text).
^g Including one vacancy for a pair (both male and female died).
^h Including five vacancies for a pair (both male and female died).
ⁱ Including three vacancies for a pair (both male and female died).

Results

The number of nonbreeders and breeders

Estimating the number of nonbreeders

Clubs were occupied when breeders took up their nesting territories in early spring. In the period from the 5 March to the 9 June 1990, between 48 and 278 ($\bar{x} = 172$, $SD = 58$, $N = 32$) oystercatchers roosted on the main club during high tide, but the numbers showed no consistent seasonal pattern within this period.

On average, 54% of the roosting adults on the main club during this period were unmarked. These unmarked individuals were almost certainly nonbreeders for the following reasons. All of the areas surrounding the main club were visited to identify any marked breeders, and only a few marked birds roosting on the main club were from distant breeding areas. Indeed, the proportion of tides that a breeder roosted on the main club rapidly declined with the distance between its territory and the main club (see later). Further, in the course of the season breeders progressively occupied their nesting territories more often, and by mid-May most of the breeders visited the club only occasionally (mainly after disturbance in the breeding areas). Thus, unmarked birds will be regarded as nonbreeders in the rest of this paper. On this assumption, we calculated that 77% of the birds on the main club were nonbreeders (marked plus unmarked), while 23% of the birds belonged to the local breeding population.

When we applied this figure of 23% to other clubs and all high tide roosts, we calculated from the high water counts in mid-May 1990, that Schiermonnikoog harboured 3381 nonbreeding oystercatchers, including 1744 fully adult individuals (at least three years of age). As the breeding population was estimated at 4620 individuals (Theo Bakker & Jan B. Hulscher, pers. comm.), it appeared that 27% of the individuals capable of breeding did not breed. So a substantial fraction of the adult oystercatcher population seems excluded from breeding.

Year-to-year variation in the number of nonbreeders

The numbers of nonbreeders varied from *ca* 960 (1997) to *ca* 3380 (1990, years 1984-1997, Table 1, subtracting 23% breeders). There were four years with exceptionally low numbers of nonbreeders: three years following severe winter mortality of oystercatchers (1987, 1996 and 1997, see Camphuysen

et al., 1996; Heg, 1999), and one year (1993) following three years with low fledging production (see Ens *et al.*, 1995; Heg, 1999). Thus, the potential number of nonbreeders competing for breeding territories varied considerably from year to year. The counts from 1996 and 1997 (after two consecutive severe winters), point at a marked reduction in the pool of nonbreeders. Nevertheless, adult nonbreeders were still present on the island in 1997. These included nonbreeders with a previous breeding history, so in each year of the study period nonbreeders with breeding experience were available to fill vacancies.

Year-to-year variation in the number of breeders

The number of resident territories in the central part of the study area was almost constant between 1984 and 1997 (Table 1). In contrast, the number of leapfrog territories declined sharply after severe winter mortality (1987, 1996 and 1997), despite the fact that nonbreeders were available to fill the primary (and secondary) vacancies following the mass mortality.

Social structure of nonbreeders

Feeding grounds: evidence for hopeful residents

Occasional searches for marked birds on the mudflats indicated that both leapfrogs and nonbreeders could defend feeding territories up to two kilometres from the saltmarsh. It appears that an unknown proportion of nonbreeders roosting on the club defended a feeding territory on the mudflats with a mate, before acquiring a nesting territory. Territorial nonbreeders were invariably mated, though pair bonds were less stable. We were able to identify all nonbreeder pairs with mudflat territories within 500 m from the shoreline. These pairs defended 5 to 13 feeding territories adjacent to the resident feeding territories (Table 1, *e.g.* Fig. 2). The nonbreeder pairs were actively squeezing between the resident mudflat territories towards the shoreline (Fig. 2). They initiated numerous boundary disputes with the resident breeding pairs. For this reason, nonbreeders that defend a feeding territory adjoining a resident territory were named *hopeful residents*. On average, there was one hopeful resident territory occupied for every 5.8 ± 0.6 resident territories ($N = 13$ years, range 3.3-11.4), and usually they shared boundaries with only two to four resident pairs, focusing their attention on squeezing between two of them (*e.g.* Fig. 2). Consequently, only about 35%

of the resident pairs were severely affected by the aggressive behaviour of these hopeful residents. New hopeful resident territories were established, starting with frequent intrusions by nonbreeders on the boundary of resident and leapfrog feeding territories on the mudflat (*e.g.* Fig. 2, 1995). Severe competition among the nonbreeding females for establishment in a hopeful resident territories is suggested by the occurrence of polygyny among the hopeful residents (three cases lasting 2, 2 and 3 years respectively, 10% of the territory with marked males $N = 69$, or 11% of the males were at least once mated polygynously). In contrast, no polygynous aggressive club-birds on the main club were observed, and polygyny was extremely rare amongst the breeders (*ca* 2%, Heg & van Treuren, 1998).

The main club: evidence for hopeful leapfrogs

Most roosting oystercatchers were inactive on the club at high tide, but sexual and aggressive activities were commonly observed at the beginning and end of the high tide period. Probably some pair formation occurred on the club, though the feeding grounds may be much more important in this respect (Heg *et al.*, 1993). Indeed, nonbreeders that were very aggressive on the club (the aggressive club-birds) were also most often engaged in sexual behaviour on the club (Heg *et al.*, 1993). Thus, pair formation on the club may have mainly occurred among a selected number of aggressive club-birds as part of the attempt to establish a territory on or near the club (*e.g.* Fig. 2, 1995).

Detailed information on dominance hierarchies were gathered only from the main club (Fig. 1). Individuals, including both breeders and nonbreeders, that were dominant on the main club in 1990 tended to arrive long before high tide, while individuals with a low dominance on the main club tended to arrive very late (Fig. 3, $r = -0.55$, $N = 84$, $p < 0.0001$). In all years, breeders whose territory adjoined the main club were primarily occupied with chasing away nonbreeders wandering into their territory. This explains why adjoining breeders always had very high dominance scores (Fig. 4). Breeders of distant territories frequently attended the clubs in the early breeding season (March, April) and engaged in aggression there. These breeders were less often engaged in aggression and were less dominant compared to breeders adjoining the main club (Fig. 4). However, close to egg laying these breeders did not attend clubs and roosts anymore, except when disturbed from their nesting territory.

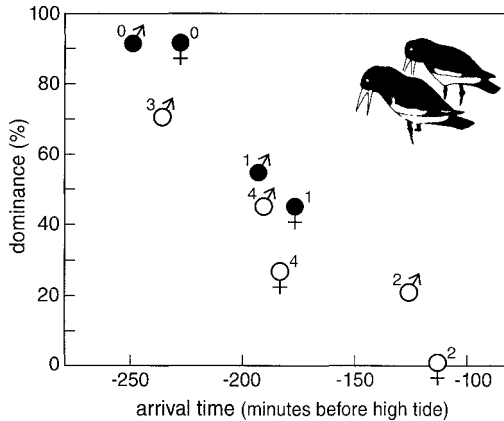


Fig. 3. Average dominance on the main club (% encounters won) plotted against mean time of arrival on the club (minutes before high tide) for males and females belonging to the following social categories: (0) leapfrog breeders whose territory adjoins the main club, (1) leapfrog breeders from more distant territory, (2) hopeful residents, (3) aggressive club-bird (in this case hopeful leapfrogs, because the main club is situated within leapfrog area), (4) other nonbreeders (nonbreeder without known territorial commitments).

A minority of nonbreeders was aggressive on the clubs and roosts. Also, some of these nonbreeders were paired. If they were aggressive on a roost (*i.e.* close to the shoreline in resident area), they tried to reach the shoreline and build nestcups there. Thus, they were very active in securing a (small) nesting area between the breeders adjoining the club or roosts. However, both the nestbuilding and aggressive behaviour were interrupted by chases from adjacent breeders, and attacks by several pairs were quite common. So nonbreeders usually failed in securing a nesting area. Judged from these behaviours, aggressive club-birds on the main club can be considered *hopeful leapfrogs* (*e.g.* Fig. 2, 1995). As stated before, detailed information on hopeful leapfrogs was only available from the main club. Only 5 out of 18 (1990) and 6 out of 22 (1991) male nonbreeders (*ca* 28%), and 2 out of 19 (1990) and 3 out of 18 (1991) female nonbreeders (*ca* 14%) observed in at least five aggressive encounters had a dominance score exceeding 50% in that year. If all the roosting nonbreeders that simply avoided aggressive encounters were counted as well, the proportion of dominant nonbreeders would be even lower. The most dominant nonbreeders tended to arrive early and were also most often observed in aggressive encounters (male nonbreeders in 1991: $r_s = 0.43$, $N = 22$, $p < 0.05$; female nonbreeders in 1991: $r_s = 0.61$, $N = 17$, $p < 0.01$). Dominance in 1990 did not

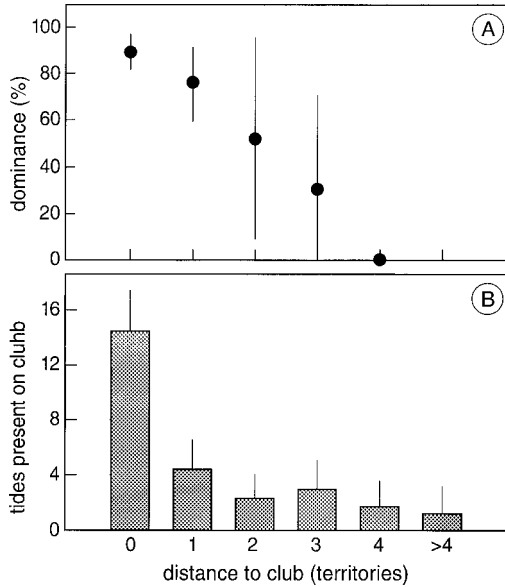


Fig. 4. (a) Mean dominance of 36 breeders (males and females, resident and leapfrogs combined) on the main club in relation to the distance (measured in territories) of their nesting territory to the main club in 1990. (b) Mean frequency (bars represent SD) with which 96 breeders (males and females, residents and leapfrogs combined) were observed roosting on the main club in relation to the distance (measured in territories) of their own nesting territory to the main club, based on 23 tides in 1990.

significantly correlate with dominance in 1991. This was true when birds were excluded whose dominance could not be ascertained in 1990 or 1991 (male nonbreeders: $r_s = 0.05$, $N = 8$, NS; female nonbreeders: $r_s = -0.02$, $N = 9$, NS), or when it was assumed that birds not observed in aggressive encounters in a year had a dominance of 0% in that year (male nonbreeders: $r_s = 0.11$, $N = 20$, NS; female nonbreeders: $r_s = -0.08$, $N = 13$, NS). This is due to the many nonbreeders quickly achieving high dominance positions in a particular year. For instance, two males, both fledged in 1988, returned to the study site in 1990 (one of them roosted on another site), but were not observed in aggressive interactions on the main club in 1989-1990. Nevertheless, they were the two top-dominant male nonbreeders in 1991 (only losing disputes with neighbouring leapfrog breeders). Of the four top-dominant males on the club in 1991, three secured a nesting area in the club (leapfrog territory) in subsequent years (1992-1995). However, high dominance on the club did not appear a necessary prerequisite for

females' successful settlement in a (subsequent) year. Of 9 marked female nonbreeders that settled in a breeding territory only 1 had a dominance score exceeding 30% on the club in the preceding year. Remarkable is the case of one female (code GB210B6, fledged in 1988) which was not observed on the club in 1990, and had a low overall dominance in 1991, yet settled in June of that year in a territory directly adjacent to the club.

Previously, we suggested that hopeful residents were in the best position to obtain a resident territory. Yet, hopeful residents were always subordinate on the main club (Fig. 3), again suggesting that the club should not be thought of as a flock of nonbreeders where an absolute hierarchy determines priority in the filling of vacancies. Rather, hopeful residents and aggressive club-birds seem strongly committed to obtaining a nesting territory in a particular location and it is only there that they enjoy a high dominance.

Territorial commitment and intrusion behaviour

We expect that strong commitment to defend dominance at a given locality (*e.g.* hopeful resident, aggressive club-bird) will restrict the possibilities for sampling alternative options elsewhere. Indeed, nonbreeders without known territorial commitments had by far the highest tendency to intrude (Table 2). We corrected for the frequency with which individuals roosted on the club in this table, because of a positive correlation between roosting frequency and intrusion frequency for nonbreeders ($r = 0.48$, $N = 114$, $p < 0.0001$). The correction did not significantly influence the results though.

Hovering ceremonies

Actual fights between individuals were rare in our study population. Most of them were seen in May, when breeders laid eggs and pairs of nonbreeders often established a nesting territory (Ens, 1992).

Ritualized aggressive encounters were much more common, both among breeders and nonbreeders. Both males and females, breeders and nonbreeders, engaged in piping ceremonies on the ground and piping ceremonies in the air (hovering ceremonies). Since the nonbreeders are immediately chased from both the feeding and breeding territories if they perform aggressive displays on the ground, hovering ceremonies might be an alternative to establish local dominance relationships among nonbreeders without much interference from the breeders.

TABLE 2. *Intrusion index, expressed as the number of times an individual was observed as an intruder, per ten observations of the same individual on the main club, averaged for different social categories*

	Females			Males		
	\bar{x}	SE	<i>N</i>	\bar{x}	SE	<i>N</i>
<i>Breeder</i>						
territory near club	0.10	0.10	7	0.15	0.15	7
distant territory	0.37	0.26	39	0.36	0.25	43
<i>Nonbreeder</i>						
hopeful residents	0.63	0.63	2	0	0	4
aggressive club-birds	–	–	–	0.93	0.38	4
other nonbreeders	1.80	0.44	43	1.50	0.50	35

The breeder group was subdivided in breeders with territories within two territories from the main club or more distant, nonbreeders were categorized on the three principal settlement strategies.

A two-way ANOVA showed that the intrusion index varied significantly with social status ($F_{4,175} = 4.02, p = 0.004$), but not with sex ($F_{1,175} = 0.19, p = 0.66$).

It is estimated that 57% of the birds in a hovering ceremony were nonbreeders ($N = 481$, assuming that all unmarked participants are nonbreeders as well). In only 32 hovering ceremonies could all participants be identified before they flew away. In eight cases, no breeders participated, whereas in five no nonbreeders participated. In these five cases where only breeders participated, the nesting territories of the participants were separated by 1 territory (3 cases), 2 territories (1 case) and 4 territories (1 case). These findings support the idea that hovering ceremonies were primarily contests over local dominance among nonbreeders, between nonbreeders and breeders defending their territory, and among breeders over space that was not part of either of their territories. That they were contests is supported by the observation that individuals sometimes pecked at each other in flight and that on 16 occasions a hovering ceremony ended in a chase flight: the persistent persecution in flight at high speed for a considerable period of time.

Many hovering ceremonies originated on the club. If hovering ceremonies served to determine an absolute dominance ranking among nonbreeders that roosted on the club, there should have been no spatial bias in the tendency of those nonbreeders to join a hovering ceremony. Spatial biases were obvious for four non-breeders observed more than once in a hovering ceremony in 1990 (see Fig. 11, p. 61 in Ens, 1992). The observation of spatial biases in

the tendency of nonbreeders to join hovering ceremonies supports the view that nonbreeders joined hovering ceremonies to display and/or defend their local dominance.

Hovering ceremonies were most frequent above resident territories and the leapfrog territories directly adjacent to the resident territories (Fig. 5). Only leapfrogs breeding in the first two rows of nesting territories adjacent to the resident nesting territories were seen to gain a resident territory in subsequent years (annual probability *ca* 5%, Heg, 1999). As in the hovering ceremonies, intruders landed more often in the best territories during 1990-1993 (Fig. 5). These observations suggest that competition was most intense for the resident territories. Further, nonbreeders appear to compete more for the leapfrog territories close to the shoreline than for the leapfrog territories further inland. Although we measured intrusion frequency far inland only in 1993, we have no reason to believe that the intrusion frequency in distant leapfrog territories increases again compared to the low intrusion frequency of leapfrogs breeding around the main club. During our visits to these areas to locate breeders we only occasionally saw intruders.

Thus, nonbreeders seemed fully equipped to locate vacancies within the breeding population. More importantly, the localized activity of many nonbreeders suggested that most of them were competing for a limited number of territories. In the next part of this paper we will analyse how (and how many) nonbreeders acquire breeding positions and whether locally active nonbreeders actually acquire local breeding positions.

Vacancies in the breeding territories

Filling breeding vacancies is the most obvious method for a nonbreeder to acquire a breeding position. However, as the annual survival rate averaged 92% for both sexes (Heg & van Treuren, 1998), the annual number of vacancies arising was low (Table 1, residents: 5.7 ± 2.6 , leapfrogs: 7.7 ± 3.2 , $N = 14$ years). Moreover, nonbreeders could expect more vacancies to arise in the leapfrog territories than in the resident territories, both in relative and absolute terms, although the survival rates of residents and leapfrogs were comparable (Ens *et al.*, 1995; Heg, 1999). Why was this the case? First, although the probability of a primary vacancy (male or female) arising was comparable between residents and leapfrogs, leapfrogs were significantly more likely to desert their territory to occupy a resident vacancy

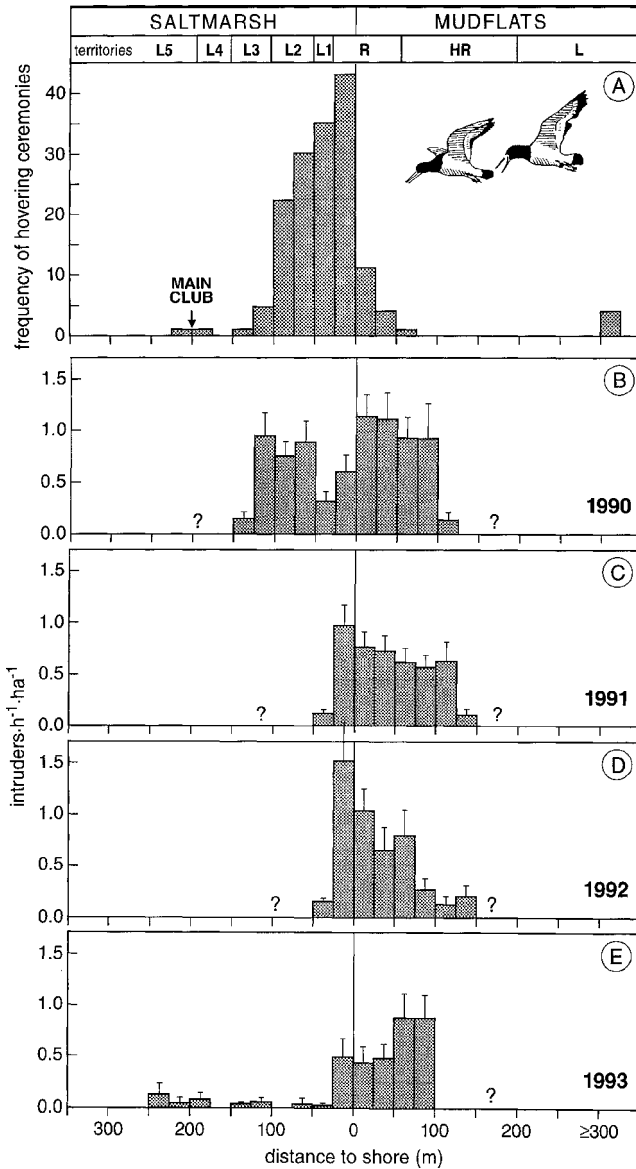


Fig. 5. (a) Occurrence of hovering ceremonies relative to the edge of the saltmarsh in 1990 and intrusion rate relative to the edge of the saltmarsh in (b) 1990, (c) 1991, (d) 1992 and (e) 1993. Territory boundaries are schematically indicated (L1-L5: first to fifth row leapfrog nesting territories, L: feeding territories of first and second row leapfrogs, R: resident nesting and adjoining feeding territories, HR: hopeful resident territories).

TABLE 3. Annual probability \pm SE of a primary or secondary vacancy arising, depending on sex and territory quality of the breeder involved

	Vacancy	
	primary	secondary
<i>Resident</i>		
male	0.08 \pm 0.03	0.00 \pm 0.00
female	0.06 \pm 0.02	0.01 \pm 0.005
Z	-0.42 NS	-2.02*
<i>Leapfrog</i>		
male	0.06 \pm 0.02	0.02 \pm 0.005
female	0.05 \pm 0.02	0.05 \pm 0.02
Z	-1.33 NS	-2.50*
Comparing territory qualities		
males Z	-0.39 NS	-2.34*
females Z	-1.07 NS	-2.70**

Probabilities are calculated in reference to the number of breeders in the previous breeding season, 1984-1997, $N = 14$. Wilcoxon's matched pairs tests (Z-values) comparing the probabilities in relation to sex and comparing the probabilities in relation to territory quality, are indicated in the table.

* $p < 0.05$

** $p < 0.01$

(in particular female leapfrogs, Table 3). In contrast, male residents were never seen to desert their territory, and female residents only occasionally (Table 3). Second, the number of leapfrog territories exceeded the number of resident territories five to one (measured from Wadden Sea coastline to North Sea coastline, see Heg, 1999), so nonbreeders could expect more vacancies to occur in the leapfrog population in absolute terms (in the main study population leapfrogs outnumbered residents two to one). Further, a noteworthy consequence from the high annual survival rate of breeders was the low probability of both mates in a pair dying in the same winter. Between 1984 and 1997 we observed only fourteen such cases (Table 1, nine cases occurred following a severe winter). Thus in most cases paired nonbreeders were unable to find a vacancy for a pair, but instead had to compete with a widowed male or a widowed female for access to a territory. In this section we analyse (1) whether nonbreeders can take advantage of primary and secondary vacancies arising, (2) which nonbreeders fill the resident vacancies and (3) which nonbreeders fill the leapfrog vacancies. Then we

proceed by analysing other methods by which nonbreeders could settle into a breeding territory, namely: evicting a breeder or a breeder pair (usurpation), squeezing between nesting territories or females joining a monogamous breeding pair to form a polygynous bond (males were never seen to join pairs into a polyandrous trio, although we saw one case of polygynandry, Heg & van Treuren, 1998).

Resident vacancies

Nonbreeders filled only about half of the resident vacancies (Table 4), the rest being filled by breeders. Breeders took advantage of the vacancies in various ways. First, widowed residents mated with each other, instead of a nonbreeder, merging the two territories into one big territory (Table 5). Second, resident pairs enlarged their territories, often at the expense of the widowed resident. Third, leapfrogs deserted their territory (and sometimes their mate) and filled the resident vacancies (Table 5). Fourth, leapfrog pairs moved their territory into the resident vacancy, evicting the widowed resident in due course (Table 5). In particular leapfrog females were prone to leave their territory to occupy a primary resident vacancy. Thus, in many cases nonbreeders were unable to take advantage of these high quality vacancies arising.

Leapfrog vacancies

Leapfrog vacancies were less likely to be filled by nonbreeders compared to resident vacancies. Only a third of the leapfrog vacancies were filled by nonbreeders (Table 6). Comparing the different types of single vacancies (resident or leapfrog, male or female, primary or secondary), resident vacancies were significantly more often filled by nonbreeders than leapfrog vacancies (see Appendix for statistics). Additionally, female nonbreeders were significantly less likely to fill resident vacancies and more likely to fill leapfrog vacancies than male nonbreeders. Whereas female nonbreeders were more likely to fill primary leapfrog vacancies compared to secondary leapfrog vacancies, for resident vacancies the opposite was true (see Appendix). We detected no significant differences in nonbreeder success rate for paired vacancies, although nonbreeders tended to have more success in taking advantage of paired resident vacancies ($p = 0.12$, see Appendix). Despite many secondary leapfrog vacancies arising because of leapfrogs moving into the

TABLE 4. *Changes in the breeding population when a resident (= high quality) vacancy arose*

Filled by:	Resident vacancy for:								
	Male			Female			Pair		
	prim	sec	total	prim	sec	total	prim	sec	total
resident	4 ^{d,f}	0	4	8 ^d	0	8	0	0	0
resident pair	8 ^a	0	8 ^a	1 ^a	0	1 ^a	2 ^a	0	2 ^a
leapfrog	5	0	5	11 ^e	1	12	0	0	0
leapfrog pair	3 ^{b,g}	0	3 ^b	1 ^b	2 ^b	3 ^b	1	0	1
nonbreeder	20	0	20	10	4	14	0	0	0
nonbreeder pair	2 ^c	0	2 ^c	2 ^c	0	2 ^c	3	0	3
total	42	0	42	33	7	40	6	0	6
% filled by breeder	48	–	48%	64	43	60%	50	–	50%
% filled by nonbreeder	52	–	52%	36	57	40%	50	–	50%

All vacancies were filled: prim = primary vacancy, sec = secondary vacancy.

^a Neighbouring resident pair(s) extending their territory at the expense of the territory owner(s).

^b Neighbouring leapfrog pair(s) extending their territory at the expense of the territory owner(s).

^c Nonbreeder pair filling vacancy at the expense of the resident widow.

^d Including two cases of two neighbouring resident widows joining their territories.

^e Including two cases of a resident widow and a leapfrog widow joining territories into one resident territory.

^f Including one case of a polygynandrous territory where one male died and the second male mated with the first female, this female ousted the second female from the territory.

^g Including one case of polygyny: the widowed resident female was joined by a neighbouring leapfrog male, but this male also retained his old leapfrog female.

resident area, the remaining leapfrog area was seldom occupied by nonbreeders. In fact, 3.7% of all single leapfrog vacancies ($N = 163$), mostly female vacancies, remained unfilled by either nonbreeders or breeders, whereas all resident vacancies were eventually filled (these were significant differences, see Appendix). Nevertheless, neighbouring leapfrogs often took advantage of both primary and secondary vacancies arising: they enlarged their nesting territories (Table 7). Some single leapfrogs combined their territories with neighbouring single leapfrogs and paired males enlarged their territory to

TABLE 5. *Characteristics of breeders filling resident primary and secondary vacancies*

Filled by:	Resident vacancy for:					
	Male		Female		Pair	
	prim	sec	prim	sec	prim	sec
<i>Resident</i>						
widows joining territories	2	0	2	0	0	0
deserter	2 ^a	0	3	0	0	0
deserter of polygynous territory	0	0	2	0	0	0
victim of usurpation ^d	0	0	1	0	0	0
neighbouring pairs enlarging territory	8 ^b	0	1 ^b	0	2	0
<i>Leapfrog</i>						
leapfrog widow joins territory with resident widow	1	0	2	0	0	0
deserter	4	0	9	1	0	0
victim of usurpation ^d	0	0	0	0	0	0
neighbouring pairs enlarging territory	3 ^c	0	1 ^b	2 ^b	1	0
Total	20	0	21	3	3	0
% filled by resident	60	–	43	0	67	–
% filled by leapfrog	40	–	57	100	33	–

^a Including case of dissolving polygynandry: first male has died, first female usurps second female and mates with second male.

^b Neighbouring pair(s) extending their territory at the expense of the remaining territory owner.

^c Neighbouring pair(s) extending their territory at the expense of the remaining territory owner, except in one case the widowed resident female was not evicted by the pair but remained polygynously mated to the male.

^d Breeder evicted from old territory.

include a single, second female resulting in polygyny (Table 7). Leapfrog pairs squeezing between the residents to obtain a portion adjacent feeding area on the mudflat were never immediately penalized by nonbreeders obtaining (part of) their nesting territory. Usually they lost some nesting space to neighbouring leapfrogs, though. We compared the types of breeders taking advantage of either resident or leapfrog vacancies (see Appendix). The types of breeders taking advantage of the vacancies, varied significantly with the status of the vacancy (*e.g.* residents did not compete for leapfrog vacancies), the type of vacancy (*e.g.* secondary vacancies were relatively often used by

TABLE 6. *Changes in the breeding population when a leapfrog (= low quality) vacancy arose*

Filled by:	Leapfrog vacancy for:								
	Male			Female			Pair		
	prim	sec	total	prim	sec	total	prim	sec	total
resident	1 ^b	1 ^b	2	3 ^h	3 ^m	6	0	0	0
resident pair	1 ^k	0	1	1 ^l	0	1	0	0	0
leapfrog	17 ^c	1	18	12 ^c	8	20	0	0	0
leapfrog pair	20 ^{a,e}	12 ^{a,e}	32	3 ^a	19 ^a	22	5 ^j	2 ^j	7
nonbreeder	17	1 ^f	18	17	15	32	0	0	0
nonbreeder pair	3 ^g	0	3	0	2 ^g	2	1	0	1
not filled	0	1 ⁱ	1	3 ⁱ	2 ⁱ	5	0	0	0
total	59	16	75	39	49	88	6	2	8
% filled by breeder	66	94	71%	56	65	56%	83	100	87%
% filled by nonbreeders	34	6	28%	44	35	39%	17	0	13%

Note that some vacancies remained unfilled, in contrast to the resident vacancies: prim = primary vacancy, sec = secondary vacancy.

^a Neighbouring leapfrog pair(s) enlarging their nesting territory at the expense of the territory owner.

^b Leapfrog widow and an adjacent resident widow joined territories to form one resident territory.

^c In seven cases neighbouring leapfrog widows joined territories to form one leapfrog territory.

^e In one case a female leapfrog joined her territory with a neighbouring leapfrog male into one polygynous territory.

^f In one case a male from the polder (adjacent to the main study area), entered a neighbouring leapfrog territory within the main study area. The secondary vacancy in the polder was probably filled by an unmarked nonbreeder.

^g Nonbreeding pair filling vacancy at the expense of the single territory owner.

^h In all three cases a widowed resident female deserted her territory to fill the leapfrog vacancy, because she was a victim of usurpation.

ⁱ Widow remained unmated within the territory.

^j Neighbouring leapfrog pair(s) enlarged their nesting territory into the vacant area.

^k A case of polygyny: neighbouring resident male enlarged his territory to encompass the widowed female leapfrogs territory, but remained mated to his resident female as well.

^l Neighbouring resident pair enlarged their nesting territory at the expense of the territory owner.

^m In two cases a widowed resident female deserted her territory to fill the leapfrog vacancy, because she was a victim of usurpation; in one case the leapfrog widow and an adjacent resident widow joined territories to form one resident territory.

TABLE 7. *Characteristics of breeders filling leapfrog primary and secondary vacancies*

Filled by:	Leapfrog vacancy for:					
	Male		Female		Pair	
	prim	sec	prim	sec	prim	sec
<i>Resident</i>						
leapfrog joins territory with resident widow	1	1	0	2	0	0
widow joins resident pair into polygyny	1	0	0	0	0	0
deserter	0	0	0	0	0	0
victim of usurpation ^h	0	0	3	1 ^a	0	0
neighbouring pairs enlarging territory	0	0	1 ^b	0	0	0
<i>Leapfrog</i>						
widows joining territories	8 ^c	0	7	0	0	0
deserter	9	1 ^d	5 ^e	6 ^f	0	0
victim of usurpation ^h	0	0	0	1	0	0
neighbouring pairs enlarging territory	20 ^b	12 ^b	3 ^b	20 ^{b,g}	5	2
Total	39	14	19	30	5	2
% filled by resident	5	7	21	10	0	0
% filled by leapfrog	95	93	79	90	100	100

^a Victim of usurpation by pair.

^b Neighbouring pair(s) extended their territory at the expense of the remaining territory owner.

^c In one case a lone leapfrog male joined territories with a widowed neighbouring female.

^d In one case the deserted female was joined by a widowed neighbouring male.

^e In two cases the vacancies were filled by leapfrogs deserted by their mates in the early season.

^f In one case the vacancy was filled by a widowed female, who decided to desert her territory at the moment the secondary vacancy arised; and in three cases the deserted males joined territories with widowed neighbouring females.

^g In one case the secondary vacancy resulted from a female widow trying to usurp a neighbouring female, but in the end polygyny was the result.

^h Breeder evicted from old territory.

leapfrog pairs) and sex of breeder died (*e.g.* particularly female victims and deserters took advantage of female vacancies).

Usurpations and squeezing

Thus, due to competition with breeders, nonbreeders were not able to acquire the majority of the breeding positions resulting from breeders dying or moving. In particular the leapfrogs took advantage of these opportunities

in various ways. Instead, most nonbreeding oystercatchers recruited through usurpation and squeezing (Table 8). Single birds evicted breeders of identical sex and mated with the remaining partner. Usually single nonbreeders evicted single breeders (78% of all 36 usurpations), but sometimes nonbreeder pairs evicted single or paired breeders (22%). Another important avenue for mated nonbreeders to obtain a breeding position was via active competition for space on the shore with several breeding pairs, by squeezing between other territories. These nonbreeding pairs established a nesting territory at the expense of parts of the territory of a breeding pair, or parts of the territories of several breeding pairs. (Note that this occurs without chasing the territory owner(s) away, otherwise we would count it as an usurpation). Not surprisingly, those nonbreeders that took advantage of natural vacancies did so early in the breeding season, while acquisition of territories through usurpation and squeezing was also common later in the breeding season, when established breeders had eggs or chicks to take care for (Fig. 6).

Polygyny

An alternative method of acquiring a breeding territory was to join a breeding pair. This was only observed in females, and resulted from 'failed' usurpation attempts (Heg & van Treuren, 1998). We observed three different outcomes of usurpation attempts. First, a nonbreeder successfully usurps a breeder, and mates monogamously with the mate (as described in the previous section, see also Ens *et al.*, 1993). Second, a nonbreeder repeatedly intrudes, fights with the breeder of identical sex, but fails and retreats. Third, a nonbreeder repeatedly intrudes, fights with the breeder of identical sex, is unable to evict the breeder from the territory, but does not retreat (a 'stalemate,' see Heg & van Treuren, 1998). The third possibility was seen only in females. The polygynous females usually divided the nesting territory between themselves and were assisted by the male in territory defence and brood rearing on either side of their territory boundary (so called 'aggressive polygyny'). However, Heg & van Treuren (1998) describe how in half of the cases, polygynous females start to cooperate and join efforts in territory defence, egg laying and brood care, instead of remaining aggressive (so called 'cooperative polygyny'). In the main study area only six female nonbreeders settled by joining a monogamous breeding pair, thus forming a polygynous trio (other polygynous territories resulted from breeding females, usually widows, joining neighbouring pairs). They were more likely to join a resident pair,

TABLE 8. *The frequency of the different strategies followed by male and female nonbreeders to obtain resident and leapfrog territories*

Strategy of nonbreeder	Territory obtained by nonbreeder	
	<i>Resident</i>	<i>Leapfrog</i>
<i>Single males</i>		
fills vacancy	18	16
usurps male breeder	5	4
<i>Single females</i>		
fills vacancy	14	27
usurps female breeder	7	12
joins pair of breeders	5	1
<i>Pair</i>		
pair fills vacancy for pair	2	0
pair usurps single male breeder	6	0
pair usurps single female breeder	0	0
pair usurps pair of breeders	2	0
male squeezes with mate	8 ^a	46 ^b
female squeezes with mate	8 ^a	44 ^c
Total Males	41	66
fills vacancy	49%	24%
usurps	32%	6%
squeezes	19%	70%
Total Females	44	84
fills vacancy	37%	32%
usurps	34%	14%
squeezes	18%	52%
joins pair	11%	2%

Squeezing was only performed by pairs and only females were observed to join pairs to establish polygynous pair bonds.

Hierarchical loglinear analysis with backward elimination of the terms: nonbreeder sex ('sex': male or female), nonbreeder strategy ('strategy': fills vacancy, usurps, squeezes or joins pair), acquired territory ('status': resident or leapfrog) and their interactions ($N = 235$), revealed two significant interactions: strategy \times status ($LR\chi^2 = 45.6$, $df = 3$, $p < 0.0001$) and strategy \times sex ($LR\chi^2 = 9.4$, $df = 3$, $p = 0.025$).

^a In all cases with nonbreeder mate; except one case with leapfrog widow.

^b In 43 cases with nonbreeder female; in three cases with breeding female: one case with male resident widow victim of usurpation by pair, one case with male leapfrog victim of usurpation by single and one case with male leapfrog deserting his territory to obtain other territory.

^c In 43 cases with nonbreeder male; one case with leapfrog male deserted by his mate.

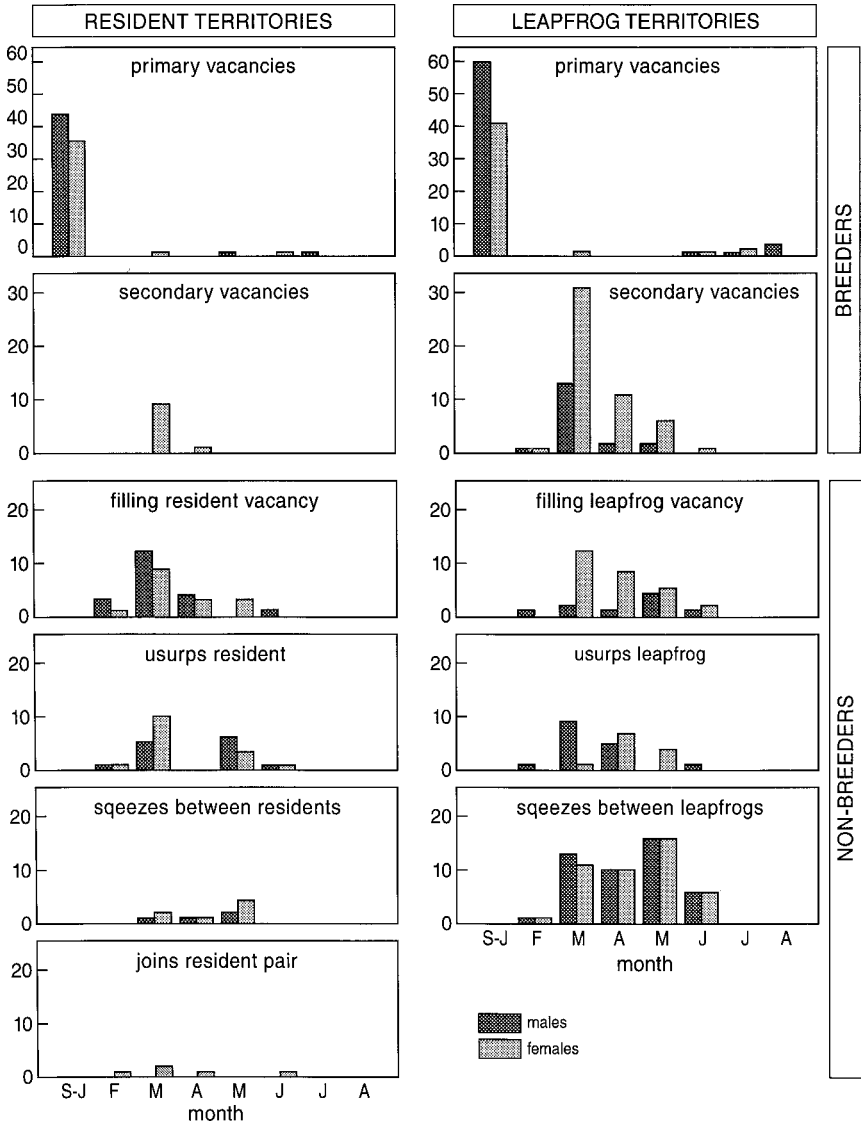


Fig. 6. Seasonal distribution of primary and secondary vacancy of residents and leapfrogs, males and females. Seasonal distribution of male or female nonbreeders acquiring a resident or a leapfrog territory, separate for the different settlement strategies (filling vacancy, usurpation, squeezing, joining pair). S-J: five months during the winter season combined (September to January).

than a leapfrog pair (Table 8). Nonbreeding females joined pairs throughout the season (Fig. 6).

In summary, nonbreeders used four different avenues to acquire a breeding territory, of which filling vacancies was the most common (Table 8). These ways varied significantly both with the nonbreeder's sex and with the quality of the breeding territory acquired.

Local dominance and settlement

So far, we have treated all nonbreeders as equals. However, in practice the settlement of the nonbreeders greatly depended on whether and where they had acquired a local dominance position. In the following section, we show that nonbreeders dominant at site X, settle as breeders at site X, instead of a more distant site Y.

Hopeful residents and aggressive club-birds

Hopeful residents always settled close to their mudflat territory along the shoreline, usually as a resident, but sometimes as a 'first row' or 'second row' leapfrog (Table 9). In contrast, aggressive club-birds on the main club ('hopeful leapfrogs'), settled as leapfrogs close to the main club (Table 9), at least ten territories away from the nearest other club or roost. Most of them settled adjacent to the main club, as a 'fourth row' ($N = 7$) or 'fifth row' ($N = 2$) leapfrog, but some of them settled closer to the shoreline.

Other nonbreeders

Many nonbreeders were difficult to classify as either 'hopeful resident' or 'hopeful leapfrog.' However, most of the adult nonbreeders were engaged in hovering ceremonies and frequent intrusions within a limited area. Subsequently, these nonbreeders settled (usually in a vacancy) close to where they had previously intruded (Fig. 7). We named these birds 'opportunistic nonbreeders.' For instance, one male (code GB101B2, born in a resident territory in 1986) predominantly intruded in area C during 1990-1994 (Fig. 7), and often engaged in disputes with other intruders as well. In 1992 he attempted but failed to usurp a male resident near the boundary of area A and C. Eventually he filled a vacancy for a male resident in 1995, about four territories west from the territory where he was born. Another case history is provided by a male (code WR011G3), who was predominantly active in area A, including

TABLE 9. *Number of hopeful residents and aggressive club-birds that settled in our main study population*

Settled as:	<i>Resident</i>	<i>Leapfrog</i>		
		zero	first	second
<i>Hopeful resident</i>				
Male	14	4	1	0
Female	13	3	1	0
<i>Aggressive club-bird</i>				
Male	0	0	3	5
Female	0	0	0	6

Leapfrog rows are counted as the number of territories from the nesting territory to the nearest resident nesting territory: the first row is adjacent to a resident nesting territory, the second row adjacent to a first row leapfrog nesting territory *etc.*

Hierarchical loglinear analysis with backward elimination of the terms: nonbreeder sex ('sex': male or female), nonbreeder strategy ('strategy': hopeful resident or aggressive club-bird), acquired territory ('status': resident or leapfrog) and their interactions ($N = 50$), revealed one significant interaction: strategy \times status ($LR\chi^2 = 28.5$, $df = 1$, $p < 0.0001$).

vigorous piping ceremonies and chasing of other nonbreeders (Fig. 7). He finally filled a resident vacancy two territories from his natal territory. A more complicated case is represented by a female (code RB200W1, Fig. 7). Active in area C, she established a mudflat territory on the border of area A and C in 1991 with a male (territory 'A'). In 1992 she moved the mudflat territory with the same male towards the resident mudflat territories, became hopeful resident, but was unable to reach the shore (territory 'B'). Instead, she joined a nearby resident pair twice (polygyny), in 1993 and 1995 (arrow), until she filled a resident vacancy in a nearby territory in 1996 (hatched territory). Similarly, 'opportunistic nonbreeders' were able to acquire leapfrog territories. For instance, a male (code RB220W5) almost exclusively active in resident and leapfrog areas close to the shore in area C (intrusions, piping and chasing other nonbreeders and challenging breeders), established a leapfrog nesting territory in area C in 1996 (Fig. 7). He managed to squeeze between adjacent residents at the end of the breeding season 1996. Another example is provided by a female (code GB110B6), who was not often seen between 1988-1993, until in the beginning of the season 1994 when she failed to usurp a late arriving female resident in area A. In the end of the season of 1994 she was seen on the mudflats of area B, and subsequently in 1995 squeezed between the leapfrogs acquiring both a nesting territory and a nearby feeding

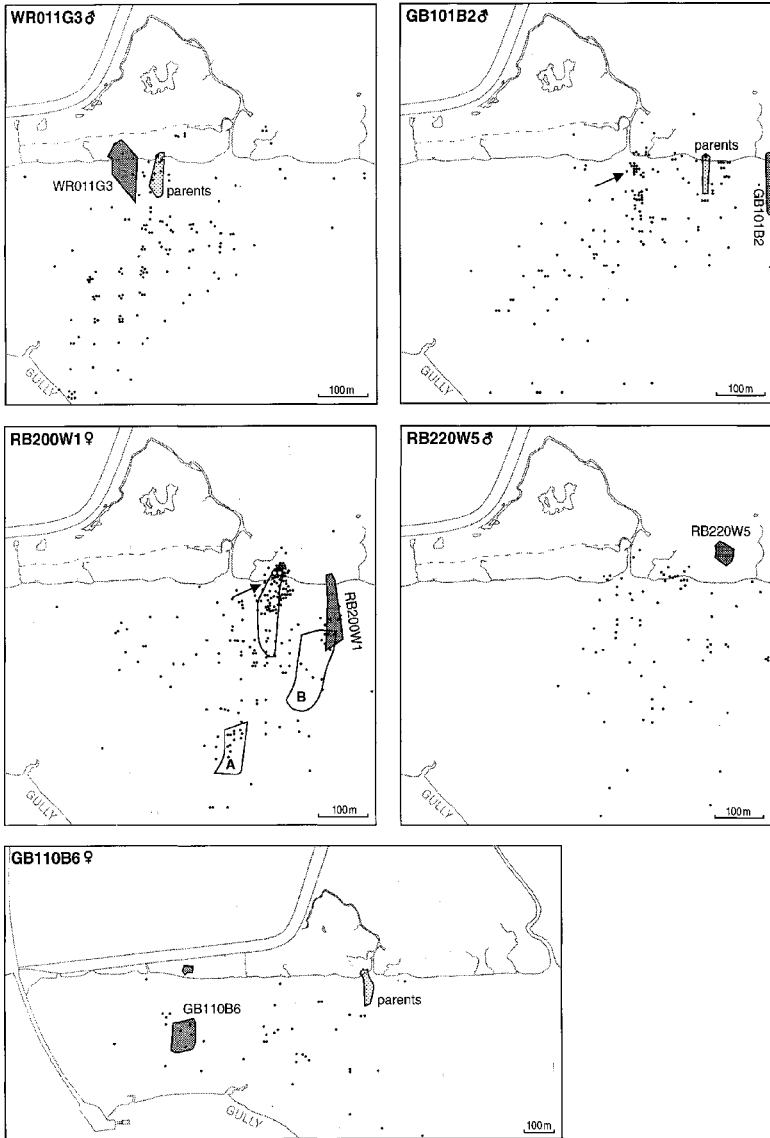


Fig. 7. Five examples of floaters which eventually settled as resident (WR011G3, GB101B2 and RB200W1) or as leapfrog (RB220W5 and GB110B6). Indicated on the maps are: their activity (intrusions, joining gatherings, piping etc.) in previous years; territory and year of birth (not known for RB200W1 and RB220W5); territory and year of settlement. Note the separate feeding and nesting territory for GB110B6. See text for further explanation.

territory (Fig. 7), remarkably close to the location where she was seen feeding in 1994. Thus, we have clear evidence that most nonbreeders are active in a limited area, and recruit within this limited area. However, it proved very difficult to construct detailed activity ranges and dominance hierarchies of all nonbreeders in our study population. Therefore, the frequency and success of the various strategies remain to be assessed.

Experimental vacancies

The previous results indicate that breeders prevent many nonbreeders from settling. Further evidence that breeders restricted the recruitment of nonbreeders was obtained from removal experiments carried out in the breeding season (May-July) when egg-laying had started and territory owners could be caught on the nest or in the nesting territory (Table 10). Only one territory owner was (temporarily) removed at a time. The removal experiments indicated that nonbreeders were available and capable of filling experimental vacancies. In 32% of all the cases a new bird filled the vacancy (Table 10), including seven nonbreeders (28%) and one neighbouring breeder (4%). New mates were acquired within 1.6 ± 0.6 days ($N = 7$, range 0-5 days, in one case the exact date of new mating was unknown), or if the neighbouring breeder is excluded from the analysis, within 1.7 ± 0.7 days ($N = 6$). There might be a bias in this estimate, since the temporary removals might not have lasted long enough for new birds to get established. However, it is questionable whether widowed birds would be able to keep the territory for a long time and wait for a new mate to arrive. The permanent removals indicated that experimentally widowed birds needed to acquire a new mate very quickly, otherwise they lost the clutch and the territory altogether. Permanently widowed birds lost the clutch within 2.6 ± 0.5 days ($N = 8$, range 1-5 days), except in one case when the male was removed just before the clutch hatched two days later: in this case the widowed female (code WR201R5) was capable of successfully completing the incubation on her own for the remaining two days (clutches hatch after *ca* 28 days of incubation). Only about half of the widows were able to acquire a new mate and keep the territory, while the other half did not acquire a new mate and lost the territory (Table 10). Territories were lost to neighbouring breeders extending their range at the expense of the widow. These permanent widows were ousted from their territory within 7.4 ± 2.4 days since removal of their mate ($N = 5$,

TABLE 10. *Fate of males and females when the mate was caught on the nest and either permanently or temporarily removed. Mates temporarily removed were released within two days from capture*

	Temporarily		Permanent		Logistic Regressions		
	male	female	male	female	sex	removal	territory quality
Numbers of widows/widowers							
Residents	3	7	1	4			
Leapfrogs	1	5	0	4			
Fate of widows/widowers							
<i>Deserted nest?</i>							
Residents	0	1 ^a	1	3			
Leapfrogs	1	1 ^a	0	4			
<i>Lost territory?</i>							
Residents	0	0	1	3			
Leapfrogs	0	0	0	1			
<i>Acquired new mate?</i>							
Residents	1	2	0	1			
Leapfrogs	0	1	0	3			
Total % deserted nest (sample size)	25 (12)^b		89 (9)^c		$\chi^2 = 0.05$ $p = 0.82$	$\chi^2 = 9.3$ $p < 0.01$	$\chi^2 = 0.3$ $p = 0.61$
Total % lost territory (sample size)	0 (16)		56 (9)		$\chi^2 = 1.3$ $p = 0.26$	$\chi^2 = 12.7$ $p < 0.001$	$\chi^2 = 0.001$ $p = 1.00$
Total % new mate (sample size)	25 (16)		44 (9)		$\chi^2 = 1.1$ $p = 0.3$	$\chi^2 = 0.3$ $p = 0.6$	$\chi^2 = 0.2$ $p = 0.6$

Logistic Regressions with backward elimination of terms and interactions, where the main effects 'widow/widower' (male or female, $df = 1$), 'territory quality' (resident or leapfrog, $df = 1$) and 'removal' (temporary or permanently, $df = 1$) entered as categorical variables, were used to test for significant effects.

^a Two cases excluded, because the eggs were removed at capture of the mate.

^b $N = 12$, because four cases were excluded from analysis, since the eggs were removed at capture of the mate.

^c Only one female did not desert the brood, the eggs hatched two days later.

actual values 4, 5, 5, 6, 17). This estimate however, is strongly influenced by the only widow caring for young (WR201R5). She was ousted from her territory after 17 days.

Temporarily removed birds were released within two days from capture (frequency distribution: several hours later on the same day: $N = 9$, one day later: $N = 3$, two days later: $N = 4$). All sixteen birds regained their

territory. To regain their territory, three males and one female had to fight severely with the new mate of their partner for one or two days.

Discussion

What limits recruitment?

Our observations and removal experiments leave little doubt that the presence of the territory owners restricted recruitment of the nonbreeders into the breeding population (*cf.* Watson, 1967; Harris, 1970; Vines, 1979; Newton, 1992, 1998). Nevertheless, nonbreeders often failed to profit from vacancies because established breeders tried to improve in breeding status (*i.e.* moving from leapfrog to a resident territory); or had a very strong 'urge' to enlarge their territories whenever the opportunity arose early enough (this 'urge' should relate to the cost and benefits of territory enlargement, depending on the number of competitors, *e.g.* Gill & Wolf, 1975; Parker & Knowlton, 1980; Davies & Houston, 1984). Similar findings have been obtained in other experimental and observational studies, where breeders tried to improve the quality of their breeding territory (*e.g.* Watson & Jenkins, 1968; Krebs, 1971; Korpimäki, 1988; Newton, 1991; Montalvo & Potti, 1992; Holmes *et al.*, 1996). This 'urge to expand' is also evident from our observations that neighbouring territory owners chased intruders from temporarily vacated territories and that territory owners engaged in hovering ceremonies when their territories were not contiguous. Hence, though some nonbreeding oystercatchers recruited by taking up primary or secondary vacancies, most nonbreeders recruited into the breeding population by conquering space or ousting rival partners, as has been observed in other bird species (*e.g.* Arcese, 1989; Stutchbury, 1991).

Why do nonbreeders often fail to exploit natural vacancies?

The suggestion that established territory owners continually strive for better breeding positions is only half of the explanation for the fact that nonbreeders often fail to exploit natural vacancies. Several (non-exclusive) hypotheses might explain why nonbreeders often fail to fill vacancies or decide not to fill vacancies: (1) '*the inferior phenotype hypothesis*'; (2) '*the sampling cost hypothesis*'; and (3) '*the queue hypothesis*.' We will address these hypotheses in turn.

First, '*the inferior phenotype hypothesis*' states that most nonbreeders do not have the quality to find or defend a (high quality) vacancy against neighbours. Hence, many vacancies are not filled by nonbreeders, because there are not enough high quality nonbreeders available to fill these vacancies. Suggestive in this respect is that in several other species where nonbreeders fill only a minority of vacancies, these nonbreeders tend to arrive late at the breeding sites as well (Coulson & Thomas, 1983; Porter, 1988, 1990). Maybe only high quality individuals are able to arrive early, occupy a territory and breed (*e.g.* Lanyon & Thompson, 1986; Bensch & Hasselquist, 1991; Cristol, 1995; Aebischer *et al.*, 1996), leaving only poor quality territories or no territory at all for latecomers. For instance, yearling male sage grouse *Centrocercus urophasianus* settle at the periphery of the lek late in the season (Wiley, 1973). Moreover, in two species where the arrival date has been experimentally altered, the first arriving birds achieved dominance over the late arriving birds (Grahn *et al.*, 1993; Cristol, 1995). However, in case of the oystercatcher the inferior phenotype hypothesis is not a likely explanation, for the following reasons. Although nonbreeders were not successful at filling all vacancies, *at the same time* they used other methods to establish themselves, *i.e.* by squeezing between breeding territories or usurping breeders. For instance, hopeful residents occupied their mudflat territories for many years, and arrived in these territories about the same time in the breeding season as residents did (February-March). Besides, it would be difficult to maintain that all nonbreeders are competitively inferior to breeders, since some of them manage to usurp breeders later in the season.

Second, '*the sampling cost hypothesis*' states that nonbreeders incur considerable costs locating vacancies, for instance because of high predation risk when sampling territories for vacancies (see Johnson & Gaines, 1990; Sutherland, 1996 and references therein). If sampling costs are high, nonbreeders should fail to locate some of the vacancies arising. However, observations suggest nonbreeding oystercatchers locate all vacancies without difficulty: (a) Ens (1992) estimated that every nonbreeder in the main study population, visited each territory in the main study population about six times, on average. Also after severe winters (1987, 1996, 1997) nonbreeders were seen to intrude in both resident and leapfrog areas (D. Heg, pers. obs.). (b) Only the peregrine falcon *Falco peregrinus* might impose a serious predation risk during territory sampling, but is nowadays absent from the island during April-August. We have lost only two of our birds (a couple) on the

periphery of our study population during the breeding season to a predator (a feral cat). Hence, nonbreeders might spend time locating vacancies, incurring only the costs of flight time and intrusion, if they restrict this activity to high tide. Thus, we expect that all vacancies, including those within low quality territories, are discovered by nonbreeders during the breeding season.

Third, '*the queue hypothesis*' states that some vacancies remain unfilled, because they are of low quality. Instead, nonbreeders might benefit more from delaying breeding and wait for a vacancy in a high quality territory to arise (Ens, 1992; Newton, 1992; Ens *et al.*, 1995). Many of our results are in agreement with this hypothesis. For instance, more high quality (resident) vacancies were filled than low quality (leapfrog) vacancies. After high breeder mortality, the number of occupied low quality territories declined, despite a surplus of nonbreeders was available to fill these vacancies. If the fitness consequences of accepting a certain vacancy or delaying breeding is known, removal experiments can be used to test the validity of queue-models to explain these findings. Newton (1992) reviews the evidence of territoriality limiting the number of breeders, based on studies creating experimental vacancies. He finds evidence in 45 of 56 species studies (80%). However, the quantitative results were very variable. The queue model provides an explanation for this variability, if we assume that some removal experiments have been performed in poor quality habitat or in a mix of good and poor quality habitat. The prediction is that nonbreeders might not accept low quality vacancies, because it pays them to wait ('queue') for a vacancy in a high quality habitat. Hence, it might appear there are no nonbreeders available to fill the vacancies, whereas in fact it does not pay them to fill the low quality vacancies. Thus, one would misleadingly conclude that territoriality does not limit the number of breeders. Indeed, several removal experiments indicate that in other bird species queuing processes might explain some of the results. For instance, in Cassin's auklet (Manuwal, 1974), blue grouse (Lewis & Zwickel, 1980) and sparrowhawks (Newton & Marquiss, 1991) replacement occurred on good territories, but seldom on poor territories, or replacement occurred on good territories when poor sites remained vacant (Newton, 1992).

The structure of the queue: local site dominance

Queuing processes in breeding systems like the oystercatcher and delayed dispersal in cooperative breeding systems have many features in common

(e.g. Koenig & Mumme, 1987; Stacey & Ligon, 1987; Pruett-Jones & Lewis, 1990; Komdeur, 1992; Emlen & Wrege, 1994; Emlen, 1997). In both situations, waiting for a vacancy in a high quality territory to arise might be beneficial, instead of accepting a low quality territory and breeding immediately. The only difference between both situations is that in the cooperative system, nonbreeders (the helpers) might gain some fitness benefits while waiting for a vacancy in the (nearby) territory to arise: if they help rearing a brood when (1) they are related to the chicks they help raising and/or (2) they are able to inseminate some of the eggs in the nest, or dump eggs, in the nest they help. Delayed dispersal and helping might occur with (e.g. Komdeur, 1992) and without habitat saturation (e.g. Emlen & Wrege, 1994), as long as helping in a high quality territory is more beneficial than accepting a low quality territory, *i.e.* even when low quality territories are widely available. For nonbreeders of cooperatively breeding species the queue can be easily characterized by the number of same sex helpers in the territory and their dominance hierarchy (e.g. Pruett-Jones & Lewis, 1990).

For oystercatchers we propose that the structure of the queue is represented by local dominance positions. Between breeders in a territorial system social dominance, by definition, depends on the geographical location of the encounter, *i.e.* dominance is site-dependent. The following observations suggest that the social system of the nonbreeders has this same property. We have provided evidence that the club is not a flock, where an absolute dominance ranking determines priority in the filling of vacancies over a wide area. Instead, the club can be viewed as a lens that allows determination of local dominance relationships that are otherwise 'unobservable.' Thus, nonbreeders dominant on the main club, which is located within the leapfrog area, were able to acquire leapfrog breeding territories on or near that club. That is why we named those nonbreeders *hopeful leapfrogs*. Similarly, nonbreeders that are strongly committed to obtain a nesting territory elsewhere have a very low dominance on the club. For instance, *hopeful residents* are paired and have mudflat territories close to the resident mudflat territories. They appear to squeeze between the resident territories to acquire a piece of shoreline to nest. Although they are completely dominant in their mudflat territories, chasing away breeders and nonbreeders, they hardly engage in aggressive disputes on the clubs and are always subdominant there. Finally, *opportunistic nonbreeders* show spatial biases in their participation in hovering ceremonies and intrusions, engaging in elaborate chases with other nonbreeders.

Some of these nonbreeders appeared very active in chasing other nonbreeders away, for instance when intruding into the nesting area. Subsequently, they acquired breeding positions within their activity range. This strategy bears resemblance to the 'disperser strategy' in juvenile magpies *Pica pica*, which encounter relatively more vacancies but have a lower annual survival compared to more sedentary juveniles (Eden, 1987; see also Smith, 1984; Smith & Arcese, 1989). Local dominance positions among nonbreeders and subsequent local recruitment has been demonstrated in several other species as well (Krebs, 1971; Knapton & Krebs, 1976; Smith, 1978, 1984, 1987, 1994; Drent, 1983; Birkhead & Clarkson, 1985; Stutchbury, 1991; Pravosudov, 1993; Poston 1997). The local dominance hierarchy ('queue') we envisage is somewhere in between the orderly queue among male stripe-backed wrens *Campylorhynchus nuchalis* or superb fairy-wrens *Malurus cyaneus* waiting to inherit the natal territory (Wiley, 1981; Pruett-Jones & Lewis, 1990), and the fights among female stripe-backed wrens for vacancies, where it is still the case that proximity to the natal territory and senior age favour success (Zack & Rabenold, 1989). This queue might be schematically outlined as in Fig. 8. Locally topdominant nonbreeders will acquire the local breeding vacancies, and the remaining nonbreeders will move one position in the hierarchy. The nonbreeder vacancy thus arising is filled by a new juvenile. Figure 8 depicts queuing for territories of the same quality, but this can easily be extended to queuing for territories with different qualities. Queues for high quality breeding positions will be long and queues for low quality breeding positions will be short.

Why do nonbreeders not jump the queue?

At this stage several questions emerge. Why should newcomers respect the hierarchy of the queue (*cf.* Wiley & Rabenold, 1984; Grafen, 1987), and line up at the end of the queue? Why should nonbreeders delay breeding and wait for a vacancy to arise, instead of fighting and acquiring a breeding position immediately? Given that usurpations are sometimes observed and that nonbreeders often recruit via active competition for breeding positions or space, the concept of a 'queue' may appear incomplete to account for this behaviour. Hence, we have to ask ourselves how stable queuing processes can evolve. Structural integrity of the queue can only be achieved if all birds in or joining the queue can expect highest pay-offs when sticking to their

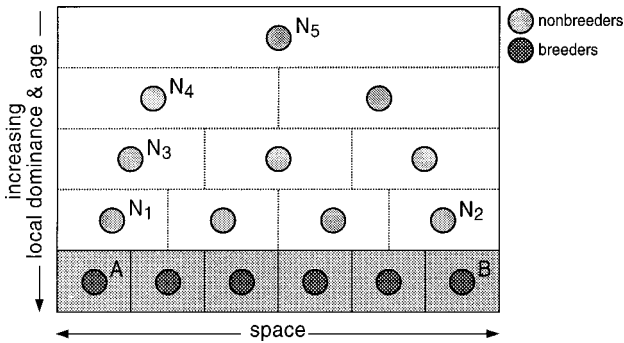


Fig. 8. A schematic representation of local dominance of nonbreeders and breeders. Nonbreeders with the highest local dominance will fill vacancies at that site (*e.g.* if breeder A dies, nonbreeder N1 fills the vacancy; if breeder B dies, nonbreeder N2 fills the vacancy). Subsequently, lower ranking nonbreeders (N3-5) will move to higher positions (*e.g.* N3 → N1).

local dominance position, instead of ‘jumping’ the queue and, for instance, fight immediately for a better position. In other words, all contests between two individuals within the queue must be somehow asymmetric (Parker, 1974). Asymmetry in a contest can be due to a difference in fighting ability, a difference in the value of the resource to each of the contesting individuals, or a difference in ‘private information’ about the value of the resource (Parker, 1974; Eshel & Sansone, 1995). We propose four general mechanisms which could stabilize the queue: (1) assuming improvement in quality with time spent in the queue, when quality correlates with fighting ability (*i.e.* age); (2) assuming the value of the resource is the highest for the individual longest in the queue; (3) assuming improvement in ‘private information’ of the local resources the birds are queuing for; (4) assuming individuals jumping the queue are more challenged by other birds in the queue, than birds which don’t jump the queue. We will address these four possibilities separately.

First, if individuals somehow improve in quality while waiting in the queue, which enables them to win fights and maintain a dominant position against individuals behind in the queue, this might stabilize the queue. It is conceivable that individuals improve in quality with age, due to experience they gather, both in summer and in winter. For instance, in oystercatchers older individuals achieve higher intake rates in the wintering area (*e.g.* Goss-Custard, 1996), and increase in dominance with age on wintering sites (Caldow & Goss-Custard, 1996). This might influence their time of arrival at the breeding sites, summer condition and fighting ability during the breeding

season. Older birds dominating younger birds is a widespread phenomenon (*e.g.* Arcese & Smith, 1985; Komers, 1989; Sandell & Smith, 1991; Koivula *et al.*, 1993).

Second, if individuals longest in the queue somehow rate the value of the territories they are competing for higher than individuals shorter in the queue, this would stabilize the queue. Individuals longer in the queue will be more willing to fight for the resource if challenged, and individuals shorter in the queue will subdue (*e.g.* in a war of attrition, Parker & Rubinstein, 1981). We can think of two mechanisms: (a) increased mortality with age; (b) increased parental ability with age. We have evidence that mortality increases with age (Heg, 1999). Thus, if a vacancy arises, nonbreeders longest in the queue might fight to exhaustion to get the breeding position, because due to their higher mortality rate it might be the only reproductive position they will ever get before they die. If older nonbreeders are more efficient in converting the same amount of resources to offspring, *e.g.* because they are more efficient feeders (Orians, 1969), then they would value the same amount of resources higher than younger nonbreeders (*cf.* Newton & Marquiss, 1991). We have some evidence suggesting this might be true (see above).

Third, nonbreeders should attach a low value to space which they have poorly sampled for two reasons. The risk of misjudging territory quality or the risk of misjudging the quality of local competitors might be high. In both cases, changing to other spatio-social positions or reluctance in fighting for better local positions might be more beneficial (Hammerstein, 1981). Nonbreeders at the tail of the queue should be more reluctant to fight and more willing to change from queue, than nonbreeders higher up in the queue.

Fourth, nonbreeders jumping the queue might be challenged more than individuals that stay put. This phenomenon is known as 'the neighbour-stranger effect' or 'the dear enemy effect' (Fisher, 1954). When contests over local dominance are treated as a war of attrition (Parker & Rubenstein, 1981), role mistakes are more likely when the opponents do not know each other and this might increase fighting with strangers (*e.g.* Krebs, 1971, 1982; Ydenberg *et al.*, 1988; Fox & Baird, 1992; Godard, 1993; Eason & Hannon, 1994). The rationale is that neighbours should challenge newcomers, to find out whether these newcomers can defend (*i.e.* derive net benefits from) the same resources as the individual who disappeared. If they would not challenge the newcomer, they might mistakenly leave too many resources (*e.g.* a too high position in the queue) to the newcomer, despite the newcomer being

of inferior quality compared to the neighbour who disappeared. Familiar neighbours have been extensively challenged in previous contests, and social positions have been divided according to their differences. Therefore, familiar neighbours are no longer challenged intensively. These four factors combined, might make 'jumping' the queue a very unprofitable strategy.

In conclusion, we view these conflicts over queuing positions as a variant of frequency-dependent asymmetric contests (Selten, 1980, 1983; Hammerstein, 1981; Hammerstein & Parker, 1982; Enquist, 1985; Eshel & Sansone, 1995; Mesterton-Gibbons & Dugatkin, 1995). The contests are frequency-dependent, because the number of contestants in the queue will depend on the local habitat quality (*e.g.* resident or leapfrog area), and will depend on the density of breeders and the total number of nonbreeders competing. Nonbreeders, which have been longest active in the local surroundings ('queuing') have the best private information, might be competitively superior and will thus be dominant over nonbreeders shorter in the queue. Nilsson (1990) performed an interesting experiment in this respect: he released captive fledged marsh tits (*Parus palustris*) at different moments during the breeding season. The juveniles released early established more local dominance positions and recruited more often into the breeding population than later released juveniles.

We expect young birds first to sample over a large area and gradually concentrate their activity, sometimes in response to the disappearance of an individual from the local queue. We did find that noncommitted nonbreeders showed more intrusion behaviour than committed nonbreeders. Because of this decrease in intrusion behaviour committed nonbreeders should progressively revise the value of more distant space downwards as their acquired knowledge on the local social relationships of these distant places becomes obsolete.

Why are nonbreeders reluctant to fight breeders?

Our results show that nonbreeders are reluctant in evicting breeders. Nevertheless, usurpations were more likely to occur in high quality territories (residents) than in low quality territories (leapfrogs), both in males and females. This might be expected, since theory would predict an increase in the probability of fights if the value of the resource increases, all else being equal (*e.g.* Parker, 1974). However, given the large number of breeders available

annually to confront, and the large number of nonbreeders to challenge them, fights are relatively rare. Why is this the case? Similar arguments as we have advanced on the stability of the queue can be advanced answering this question, and most of them have already been mentioned by Ens *et al.* (1995). However, there are some additional arguments which we would like to address shortly. The presence of rival competitors in the local queue should lead a nonbreeder to discount the net benefits from escalated fighting, as each competitor might need to be confronted or must be outlived. If the local queue has at least two competing nonbreeders lining up, escalated fighting with the local bird higher in rank (in this case the local breeder) might be unprofitable: (a) when the nonbreeder escalating has to incur considerable direct costs fighting with the first opponent (*e.g.* the breeder); and (b) when a lower ranking nonbreeder in the queue might take advantage and start fighting with the exhausted winner of the previous contest and gain the position (in this case the territory) in the end. Indeed, we have once observed a hopeful resident male (male A) usurping the local resident male, but subsequently he lost severe fights with the new hopeful resident male taking his original place. In the end, male A lost his newly acquired nest, mate and breeding territory.

Cooperation

Another striking result of our study was the high percentage of nonbreeders acquiring a breeding territory cooperatively, as a pair (48%). For instance, *only* paired hopeful residents were able to defend a mudflat territory and *only* paired aggressive club-birds on the main club were eventually successful in obtaining a leapfrog nesting territory. Thus, successful squeezing between the breeding territories seems to rely entirely on the cooperation between mates. In accordance, the removal experiments indicated that single breeders ('experimental widows') had great difficulties in keeping their nesting territory (56% lost their territory). Only breeders acquiring a new mate quickly were able to defend the territory, or they lost the territory altogether and became nonbreeders. However, most of these removal experiments were performed close to the shoreline in attractive territories: within the high quality resident territories and the first two rows of leapfrog territories. This is where we expect all vacancies should get filled: all natural resident vacancies were eventually filled or neighbours took advantage ($N = 94$). In contrast, some

leapfrog vacancies remained unfilled, the unmated leapfrogs defended their territory alone during the whole breeding season (6 cases or 3.3%, $N = 179$). Unmated leapfrogs were predominantly found in low quality leapfrog territories, *i.e.* leapfrogs without a creek in their territory to feed in with their chicks ($N = 5$, Ens *et al.*, 1992) and/or with low prospects of acquiring a resident territory on the long run ('third' and 'fourth row' leapfrogs, $N = 4$: Heg, 1999).

The study of cooperation between nonbreeders and its effect on local dominance and territory acquisition needs more attention in the future. In oystercatchers it is likely that pairing has a direct effect on dominance because males and females assist each other in defence (pecking, chasing and fighting against opponents of the opposite sex regularly occurs, see Ens, 1992). In other studies, however, it is as yet unclear whether pairing status has a direct or an indirect effect on dominance. For instance, Björklund (1989), Yokel (1989) and Sandell & Smith (1991) found that paired males dominated unpaired males, but in both studies pairing status might have signalled male fighting ability (only high quality males being able to attract females). Experimentally altering the pairing status of males and females might solve the point.

Population demography and density-dependence

How do our ideas of nonbreeders locally competing for access to breeding territories relate to habitat selection, population demography and density-dependence? We believe that queuing processes provide us with important insights in all three of them. Our study population appeared stable during years with mild winters, but particularly in recent years large declines occurred in the number of birds occupying poor territories and especially in the number of birds without a nesting territory. This overall decline may be linked to increased mortality in winters due to extremely cold weather conditions in combination with recent food shortages in the Wadden Sea (Camphuysen *et al.*, 1996). However, as we have shown, the numbers of leapfrog territories declined after severe winters, despite the fact that a surplus of nonbreeders survived the cold and might have filled these territories. We term this phenomenon the '*paradox of the unsaturated low quality habitat*,' and we will show how queuing processes solve this paradox. First, we will start by discussing the original ideas about the

relationship between population size and habitat saturation. If territories have a fixed minimal size in a given habitat as assumed by Brown (1969) and Klomp (1972, 1980), each habitat can be divided in a fixed maximum number of territories. When the habitat is 'saturated' (*i.e.* the population has reached the critical population level 3 distinguished by Brown, 1969), the local breeding population is stable and additional birds are forced to become nonbreeders (Fig. 9, 'Brown's model'). Under the hypothesis of Brown (1969), the number of occupied poor territories cannot decline in the presence of nonbreeders capable of filling the gaps. Yet, this is what we observed. How is this possible? Under a simplistic queue scenario, *i.e.* retaining some Brownian thinking, we expect the following with increasing population size. First, the high quality habitat is saturated. Then birds start to queue for the high quality habitat. At some stage the profitability of queuing equals the success expected from immediately settling in a poor habitat. From then onwards, the birds will settle in the poor habitat. Once the poor habitat is also fully occupied, the lengths of the queues for both poor and good territories will increase (Fig. 9, 'Queue 1 model'). Although the queue model of Ens *et al.* (1995) assumes that the number of nesting territories is fixed, such a restriction does not seem a necessary condition under the queue hypothesis. It is more likely that the optimal territory size will vary with the total population density (leading to the 'Queue 2 model' or variants thereof, Fig. 9). Summarizing, we believe that incorporating density-dependent effects among nonbreeders competing for access to breeding sites, provides an additional important mechanism which might level out apparent reproductive differences between habitats (others include cost of dispersal, costs of migration, predation rates *etc.*: Boulinier & Lemel, 1996; Petit & Petit, 1996; Nicholson *et al.*, 1997). Moreover, queuing processes might provide an explanation for the generally high proportion of nonbreeders reported at breeding sites (40-70% of the total population is quite usual, Newton, 1998), while they could have settled instead. We have theoretical reasons for believing that queuing is not restricted to longlived species. This conviction is supported by a discovery of a queuing process in a non-helper passerine (the boat-tailed grackle *Quiscalus major*, Poston, 1997), which is considerably shorter-lived than our oystercatcher. Hence, we believe there is no *a priori* reason why queuing processes should not play a role in habitat selection and population dynamics in many organisms.

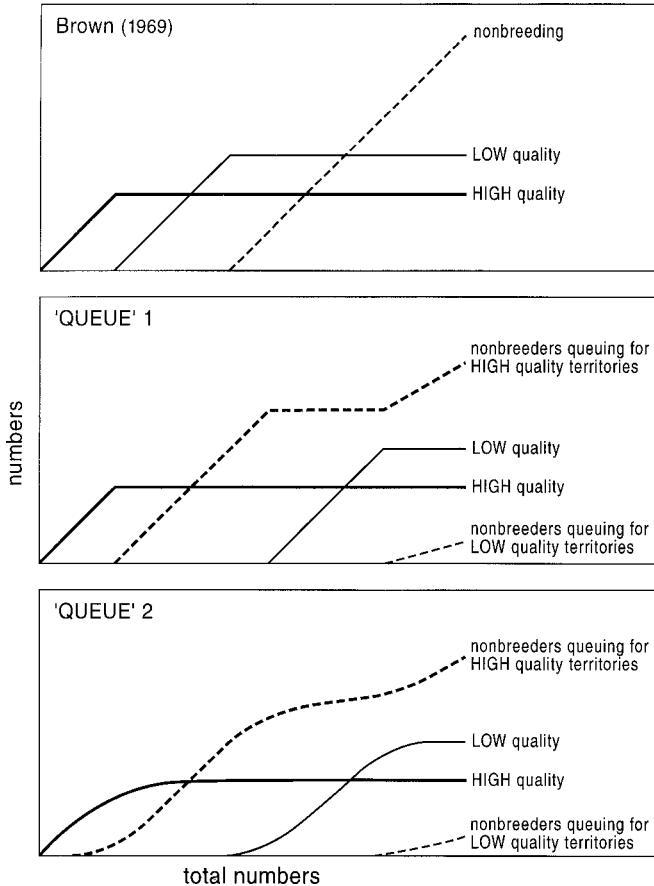


Fig. 9. (a) The sequence of habitat or territory occupancy according to Brown (1969). Individuals can choose between high and low quality habitat. Initially all arriving individuals settle in the good habitat, until the benefits obtained in this habitat equals the benefits obtained by settling in the poor habitat. The next arriving individuals settle in the poor habitat, this is continued until this habitat is saturated. Settlers to arrive after both habitats are 'saturated' (*i.e.* settled individuals derive net benefits from evicting newcomers, instead of saving time and energy to invest in reproduction and accept the newcomers), are forced to become nonbreeders. (b) Queue 1: an alternative outcome of the Brown-model, when queuing processes are incorporated. In this case, it pays some late arriving individuals to wait for a vacancy to arise in the good habitat, instead of settling immediately in the poor habitat. Nonbreeders will accept the poor habitat, once the benefits of settling in this habitat outweigh the expected benefits of waiting for a vacancy in the good habitat to arise. (c) Queue 2: idem as (b) but now following a more realistic density-dependent scenario.

Fundamental trade-offs

Fundamental trade-offs derive from inescapable constraints. In respect to habitat selection we can think of two important constraints: (1) only one behaviour can be performed at a time, (2) only one site can be visited at a time. Understanding animal behaviour requires that we succeed in predicting how individuals should behave, given the costs and benefits of the particular behaviour, given it might be performed at certain places and at certain moments in life. Our observations suggest the following trade-offs for prospecting oystercatchers that we think can be derived from these constraints:

(1) Sampling territories *versus* establishing and defending a local dominance position: the problem of time allocation. If birds stop sampling the environment and choose to compete for a local breeding position, they might fail to find a more suitable locality in terms of net pay-offs (*e.g.* higher territory quality or shorter queue). This trade-off resembles a foraging problem investigated by Krebs *et al.* (1978), where great tits had to decide when to stop sampling feeding stations offering rewards at different rates and start exploiting the feeding station estimated to be the most profitable. The period of sampling should be reduced when the difference in reward probability was small, while sampling should be continued for longer when the time horizon (*i.e.* the duration of the experiment) was longer. This is exactly the problem we think nonbreeding oystercatchers face when sampling breeding territories of different quality.

(2) Establishing site dominance at a certain location *versus* establishing site dominance somewhere else: the problem of site choice. When dominance depends on prior residence (and/or frequency of presence), it is physically impossible to achieve high status in a large area. We think this trade-off underlies the 'global' trade-off in the queue model between queuing for a high quality or a low quality territory.

(3) Attempting to establish a nesting territory before forming a pair bond, *versus* attempting to form a pair bond before establishing a nesting territory: the problem of mate choice. It is conceivable that the presence of a nonbreeder mate is a handicap when prospecting for natural vacancies, since most vacancies are for singles. A widowed breeder will probably prefer an unmated nonbreeder to a mated nonbreeder, because a mated nonbreeder introduces a competitor to the widowed breeder as well. Likewise, if a

vacancy arises, the prospecting paired nonbreeder might prefer mating with the experienced widowed breeder. But since the nonbreeder is paired, a severe battle between the widowed breeder and her nonbreeder mate is likely to occur, and he or she might end up with the less preferred mate or lose one breeding season due to fights between the two potential mates. On the other hand, nonbreeders pairing before establishing a nesting territory open an alternative route to a breeding position. We have only seen *paired* nonbreeders successfully squeezing between breeding territories (*e.g.* hopeful residents, aggressive club-birds). Hence, nonbreeders deciding to act singly or to act paired might trade-off these various settlement strategies with their respective pay-offs (likelihood of successful establishment, quality of the mate or territory).

Experiences and decisions during the years spent as a nonbreeder appear of vital importance in determining the age of first breeding and the quality of the breeding territory acquired. Since there are clear reasons to believe that these decisions will depend on the decisions made by other competitors, individual decisions will both depend on, *and* affect, habitat selection and population dynamics. Determining the shape of this interaction, and identifying the events and the phenotypic attributes that make individuals chose different ontogenetic trajectories (*sensu* Wiley, 1981) will remain an exciting challenge to future students.

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Appendix

Statistical analysis of which and how many individuals filled vacancies, in relation to which breeder(s) died ('sex': male, female or pair), status of vacancy ('status': resident or leapfrog), type of vacancy ('type': primary or secondary) and status of individual who filled the vacancy ('statusf': leapfrog, pair of leapfrogs, resident, pair of residents, nonbreeder, pair of nonbreeders, not filled). Significant interactions between factor 'a' and 'b' are indicated by 'a * b'.

Are the different types of vacancies filled by different types of individuals?

Hierarchical Loglinear analysis with backward elimination of terms ($N = 259$), effects of sex, status, type, statusf and interactions.

Effect	df	LR χ^2	<i>p</i>
statusf \times status	29	49.5	0.01
status \times type	1	32.0	< 0.0001
sex \times type	1	29.6	< 0.0001

Are certain single vacancies more often filled (yes or no) than other single vacancies?

Logistic Regression with backward elimination of terms ($N = 245$), effects of sex, status, type and interactions.

Effect	df	LR χ^2	<i>p</i>
type	1	5.4	0.02
type \times sex	1	7.9	0.005
sex \times status	1	6.6	0.01

Are certain single vacancies more often filled by nonbreeders (yes or no, paired and single nonbreeders lumped) than other single vacancies?

Logistic Regression with backward elimination of terms ($N = 245$), effects of sex, status, type and interactions.

Effect	df	LR χ^2	p
status	1	7.2	0.007
sex \times status	1	7.1	0.007
type \times status	1	5.1	0.02

Are certain paired vacancies more often filled by nonbreeders (yes or no, paired and single nonbreeders lumped) than other paired vacancies?

Logistic Regression with backward elimination of terms ($N = 14$), effects of sex, status, type and interactions.

Effect	df	LR χ^2	p
status	1	2.4	0.12

Are there differences in which type of breeders use the various vacancies?

Type of breeder ('breeder'): resident widow, resident deserter, resident victim, resident neighbour(s), leapfrog widow, leapfrog deserter, leapfrog victim or leapfrog neighbour(s). Monogamous and polygynous situations were lumped. Hierarchical Loglinear analysis with backward elimination of terms ($N = 156$), effects of sex, status, type, breeder and interactions. (Note: the significant interaction terms type \times status and type \times sex indicate that the availability of vacancies varied).

Effect	df	LR χ^2	p
breeder \times sex	14	41.4	0.0002
breeder \times status	7	40.9	< 0.0001
breeder \times type	7	40.9	< 0.0001
type \times status	1	9.2	0.002
type \times sex	2	22.8	< 0.0001