

# Site attachment of floaters predicts success in territory acquisition

Leo W. Bruinzeel and Martijn van de Pol

Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

In many territorial species, a fraction of all mature individuals are classified as floaters, and little is known about how these animals eventually acquire a breeding territory of their own. We observed intrusion behavior of floaters, subsequently removed breeding birds, and then observed floaters as they were filling these vacancies in an oystercatcher, *Haematopus ostralegus*, population. Birds familiar with the area and its inhabitants filled 80% of the experimentally created vacancies. These could be either neighbors or floaters with a former breeding history nearby, but they were mainly floaters with an intrusion record nearby. Floaters obtaining experimentally vacated territories intruded significantly nearer to this territory before removal compared with floaters not obtaining the vacancy. In general, vacancies that were not occupied by intruding floaters tended to be located in areas where less intruding floaters were seen prior to removal. We show quantitatively that only birds familiar with a site succeed in establishing a territory at that site, suggesting that local information is essential for territory acquisition. We propose that the main aim of intrusion behavior may be the collection of such information. *Key words*: floaters, habitat selection, *Haematopus ostralegus*, intrusion behavior, local dominance, prospecting, queuing, territoriality. [*Behav Ecol* 15:290–296 (2004)]

In many bird species, a proportion of all mature individuals in the population is excluded from reproduction (Hensley and Cope, 1951; Stewart and Aldrich, 1951). These so-called floaters represent a reservoir from which new breeders are recruited and, as such, are important for population regulation (Brown, 1969; Kluyver and Tinbergen, 1953). Although the name “floater” suggests that individuals are randomly roving around (Zack and Stutchbury, 1992), the study of Smith (1978) showed that floaters can live within the territory boundaries of breeders, with a social organization of their own.

In contrast to the wealth of empirical studies on established territorial breeders, little is known about how floaters acquire a territory (Stamps, 1994). Behavior-based theoretical models on territory acquisition (Ens et al., 1995; Stamps and Krishnan, 1999, 2001) assume that time spent in a certain area increases the likelihood that an individual will be successful in that area. This assumption is widely accepted but has rarely been tested (Stamps, 1987, 1995). Only two studies have experimentally tested whether site attachment is associated with territory acquisition. In purple martins, *Progne subis*, floaters settled in experimental vacancies within the intrusion area (created by adding new nest-boxes in the breeding season; Stutchbury, 1991). In *Anolis aeneus* lizards, individuals that were made experimentally familiar with the area (but deprived from entering it) had a higher chance of obtaining that site once released (Stamps, 1987). We tested whether there was a relation between spatial behavior of floaters and the chance of obtaining a breeding position in a wild population of European oystercatchers, *Haematopus ostralegus*. This is the first study that combines a removal experiment with detailed observations on the potential replacement candidates in a territorial species with significant site and mate fidelity.

We first observed intrusions (e.g., short visits to occupied territories) by floaters (mature birds not defending a breeding territory). These observations were followed by the removal of breeding birds, and finally, we observed floaters as they were filling those vacancies.

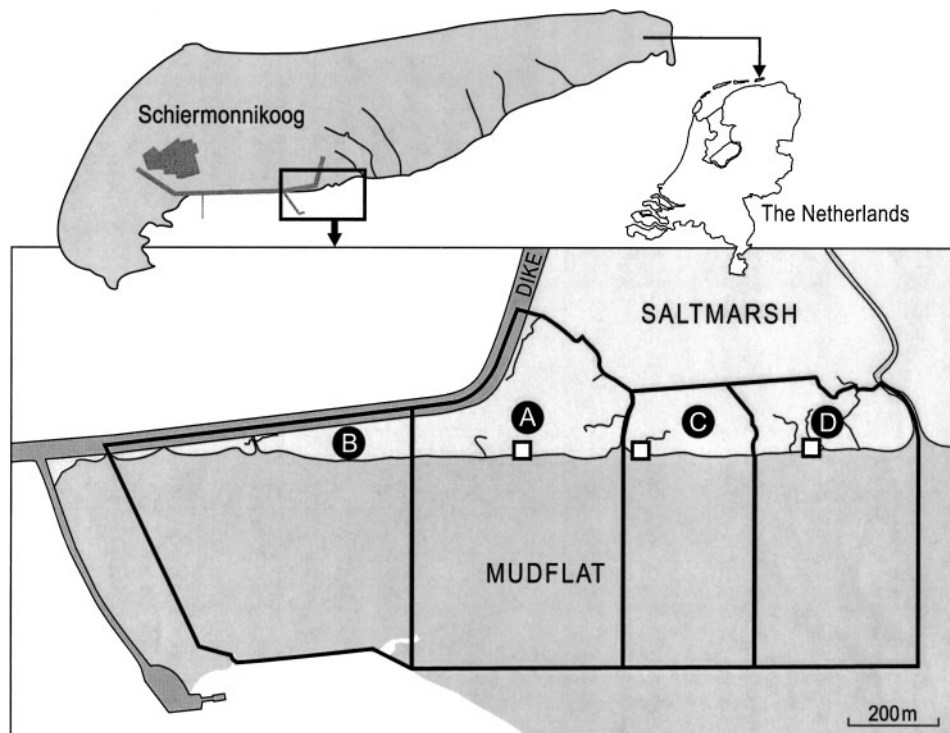
In general, floaters reside secretly on territories that are defended by others (Smith, 1978) or gather in flocks at locations not defended by territory owners (Newton, 1998) and, from here, regularly intrude in occupied territories (Zack and Stutchbury, 1992). There are three hypotheses addressing the function of intrusion behavior: (1) visits are attempts to aggressively evict the territory owner (Arcese, 1987), (2) visits are reproductive strategies (floaters may gain parentage through egg dumping or extrapair copulations) (Møller, 1987), and (3) visits serve to gather information. This information could be about available breeding positions in the population (Stutchbury and Robertson, 1987). Another source of information may be related to territory quality and reproductive success (this behavior is known as prospecting; Schjørring et al., 1999) or related to characteristics of an area and the territory owners (Stamps, 1987).

Previous removal experiments in the oystercatcher revealed the existence of floaters able to reproduce and defend a territory but, prior to removal, prevented from breeding by territorial breeders (Harris, 1970; Heg et al., 2000). In the long-lived oystercatcher, floaters outnumber the vacancies, and those finally obtaining a high-quality territory start breeding at a relatively old age, compared with those settling in low-quality territories (Ens et al., 1995). Hierarchies among floaters in which those with the longest tenure have the highest chance of achieving a breeding position (queuing) cause this difference (Ens et al., 1995).

Oystercatcher floaters can show territorial behavior at communal gatherings (at traditional sites) or when they defend a feeding territory on the mudflats, called “mudflat territorials” (Ens et al., 1995). Floaters that showed either of these behaviors at a certain location usually acquired a breeding territory close to that site (Ens et al., 1995; Heg et al., 2000). However, the majority (78%, see Heg et al., 2000) of new breeders obtained a territory without showing either of these behaviors. It was hypothesized that for these floaters, intrusions to occupied territories may play a key role in their territory acquisition (Heg et al., 2000). Therefore, we tested whether birds that are familiar with an area, and the social environment at the territory level, have the highest chance of obtaining an experimental vacancy at that site. We predicted that site-familiar birds are more successful in occupying the

Address correspondence to L. W. Bruinzeel. E-mail: l.w.bruinzeel@biol.rug.nl.

Received 13 November 2002; revised 16 May 2003; accepted 21 May 2003.



**Figure 1**  
Study area on the Island of Schiermonnikoog (The Netherlands), the location of the main study site (A through D) and the location of the observation hides (squares).

available spot compared with birds that are relatively unfamiliar with that area.

## METHODS

### Study site and social system

We studied a population of oystercatchers on the isle of Schiermonnikoog, The Netherlands ( $53^{\circ}29'N$ ,  $6^{\circ}14'E$ ). All breeding birds in the area (Figure 1, areas A through D) were individually color-marked since 1984 in area A, since 1986 in area C, and since 1992 in area B and D. During this study the area harbored 99 pairs (A, 31 pairs; B, 24 pairs; C, 18 pairs; and D, 26 pairs). Over the years an increasing number of floaters (birds without a breeding territory) in the area and its direct surroundings was 114 in 1998 and 90 in 1999.

We distinguish two types of breeders: residents and leapfrogs. Residents occupy high-quality territories, and leapfrogs inhabit low-quality territories. Resident territories comprise a defended nesting area on the edge of the salt marsh and an adjacent feeding area on the mudflats. Leapfrog territories comprise a defended nesting area located further inland and, usually, a defended feeding area located further offshore. Hence, leapfrogs defend two spatially segregated areas. Oystercatcher chicks are semiprecocial. Resident chicks follow their parents on the mudflats for food, whereas leapfrog chicks have to wait in the nesting territory for aerial food provisioning. For each delivered prey item, the leapfrog parent has to make an energetically costly flight over resident territories. Because of this difference in food provisioning, residents produce three times more young each year compared with that of leapfrogs (Ens et al., 1992). Leapfrog territories can be further subdivided into first row leapfrog territories (adjacent to resident territories) and inland leapfrog territories (surrounded by other leapfrog territories and located further inland). This distinction is made because only birds in first row

leapfrog territories have a chance of promotion to a productive resident territory later in life (Heg, 1999).

### Intrusion behavior

In both years (1998–1999), hides were placed on the edge of the salt marsh in the study area on 3-m scaffolding. In both years the hides were placed in exactly the same place. The wide spacing of the hides enabled us to do observations on intrusion behavior over a large area (Figure 1). Observation periods usually lasted 6 h (from high tide to low tide or vice versa to cover a representative part of the tidal cycle). In total, more than 1000 observation hours were made in 1998 and 1999. Intrusion data were collected from March until the end of June; removals took place in May and June.

Intruders are defined as birds alighting in a territory that is not their own (territory ownership is conclusive because all breeders are marked, and both pair members defend their territory with displays). Visits of neighboring breeders were treated separately from other intrusions, owing to difficulties in separating intrusions from border disputes. The vast majority of intruders consist of floaters. A more general description of intrusion behavior of floaters will be in a forthcoming article. Intruders were discovered by directly observing birds landing in territories or were noticed through breeders making alarm calls. When an individual landed in a territory, we registered the following parameters: individual color code (using a telescope), the arrival and departure time, the exact location, the behavior of the intruder (whether it acted aggressively by starting a piping display or acted sexually by raising the tail), the identity of the territory owners, the time until the owners responded, and the time elapsed between the first response to the intruder and the departure of the intruder. Locations of different actions were recorded using a  $50 \times 50$  m grid in the area (accuracy,  $5 \times 5$  m). One-meter-high sticks were used in the field to mark the grid.

For each intruding individual (defined as individuals

Table 1

Number of vacancies created per sex and territory type, the number of vacancies occupied within the same season (filled vacancies), number of unoccupied vacancies (unfilled vacancies), and the cases in which the removed bird was released before the arrival of a new candidate (release cases)

	Males ( $N = 13$ )			Females ( $N = 15$ )		
	Resident	Leapfrog	Inland leapfrog	Resident	Leapfrog	Inland leapfrog
Vacancies created	5	4	4	6	3	6
Filled vacancies	5	4	2	3	1	5
Unfilled vacancies	0	0	1	2	1	0
Release cases	0	0	1 (13)	1 (10)	1 (11)	1 (9)
Reoccupation latency	$6.6 \pm 1.5$	$3.0 \pm 1.4$	$9.5 \pm 6.5$	$3.7 \pm 1.9$	4.0	$9.6 \pm 2.7$

The average interval (mean  $\pm$  SE) between creation and reoccupation of a vacancy (reoccupation latency) is given in days (sample size equal to the number of filled vacancies). Between parentheses is the number of days the vacancy remained unoccupied.

observed intruding at least four times a year; older than 3 years of age, i.e., sexually mature; and not defending a feeding and/or a breeding territory in that year), we calculated a center of all intrusion attempts. Intrusions took place over a large area, covering different territories. The center was the mean of the  $x$ - and  $y$ -coordinates of all intrusion attempts for this individual.

### Removal experiment

Breeding birds were caught on the nest and held in captivity in 1998 ( $n = 16$ ) and 1999 ( $n = 12$ ). We removed one member of the breeding pair, thus leaving a "widowed" breeder behind. The timing of the removal allowed us to collect data on intrusion behavior before the experiment. Removals were randomly chosen from a subgroup of candidates; however, the subgroup was not chosen randomly. Subgroups were chosen with respect to other removals, territory types, and vicinity of the hides. To ensure that the studied process of reoccupation did not interfere with other experimental vacancies, we removed only three birds at the same time and spaced removals over the study area. Three birds of identical sex were caught on 1 day, originating from the three different territory types (resident, leapfrog, and inland-leapfrog). The next set was comprised of birds of the other sex and was removed, on average, 7 days later. Subgroups were also chosen to be located near (but not within 50 m of) the hides. We removed birds from the main study area where we also observed intrusions ( $n = 15$ ) (Figure 1, areas A, C, and D) and outside the main study area where we lacked those observations ( $n = 13$ ). The latter category was included to study the chance of reoccupation in relation to territory type. On two occasions we removed a bird that was not part of a scheduled set. In 1998 the captive birds were housed at the nearby field station and released in the population later. On four occasions we were forced to release birds because they could not remain in good condition in captivity, all in 1998. Those birds were released before their position was actually filled by a newcomer. In 1999 the birds were permanently removed from the island and released 1 year later in another area. Captive birds in both years were fed with their natural food (the bivalves edible cockle, *Cerastoderma edule*, and edible mussel, *Mytilus edule*) and with artificial trout food.

### Statistics

All data were analyzed by using SPSS/PC (SPSS Inc.). Descriptive statistics in the text are given as mean  $\pm$  SE. For the comparison of characteristics of a small subsample of

individuals with all individuals, we use randomization tests with 5000 replicates (Adams and Anthony, 1996).

## RESULTS

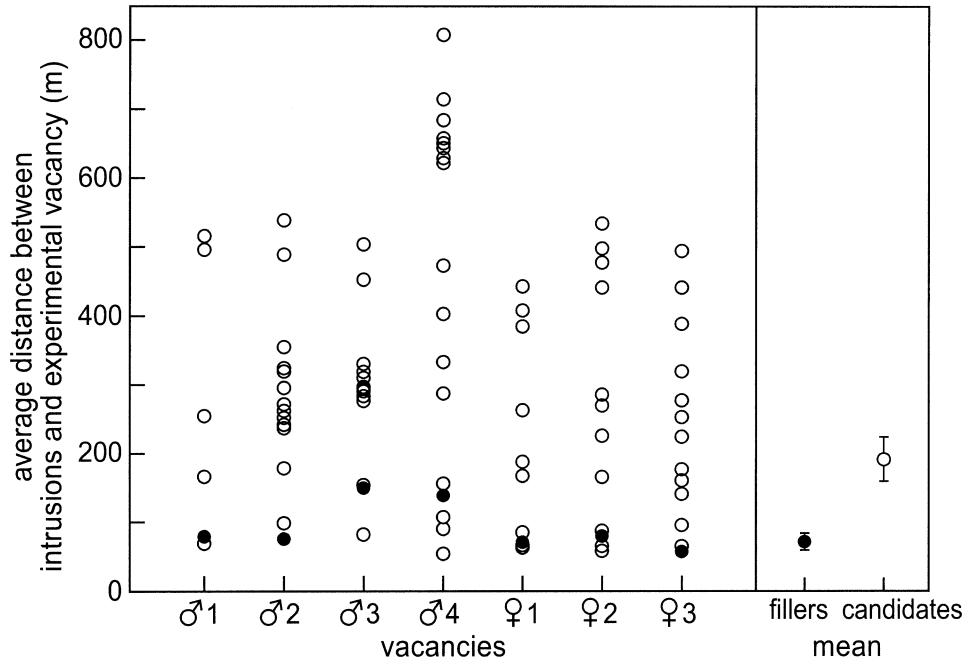
### Reoccupation of experimental vacancies in relation to territory quality

In total, 28 territory owners were removed (13 males and 15 females), distributed over three territory types (Table 1). The chance that a vacancy became reoccupied within the same breeding season was not related to territory type, sex of the removed bird, or date of removal (logistic regression,  $N = 24$ , territory quality:  $W = 0.99$ ,  $df = 2$ ,  $p = .6$ ; sex:  $W = 2.61$ ,  $df = 1$ ,  $p = .11$ ; date:  $W = 0.06$ ,  $df = 1$ ,  $p = .81$ ). In four cases, all in 1998, we released birds before a new owner was present in the territory; these vacancies were not included in this analysis.

The duration between creation and occupation of the vacancy (the filling interval) was analyzed for all vacancies occupied within the season ( $N = 20$ ). The filling interval was not related to sex ( $F = 0.24$ ,  $df = 1$ ,  $p = .63$ ) or territory quality (ANOVA,  $F = 3.0$ ,  $df = 2$ ,  $p = .08$ ). Although there was a trend that the time period until reoccupation differs between territory types, the average values did not tend to change monotonically with territory quality (Table 1). In addition, we tested the differences in filling interval by comparing the filling sequence within a set for all vacancies created on the same day ( $N = 7$ ,  $L = 86$ ,  $p = .70$ , Page ordered alternatives test). We performed a power test to analyze which difference was still detectable with our sample size. The power test was applied to the situation in which all territory types differ in reoccupation rate. We assumed that resident territories with the highest reproductive output become reoccupied first, followed by leapfrogs, and those in turn are followed by inland leapfrogs. For a power of 80% ( $N = 7$  sets,  $\alpha = 0.05$ ), the minimal difference between the categories was 78% (Page ordered alternatives test). This means that if in reality the chance that a resident vacancy is sooner filled than a leapfrog vacancy (which in turn is sooner filled than an inland leapfrog vacancy) within all sets is less than 78%, we cannot detect a difference. However, a difference of more than 78% was detectable with our sample size. Note that the test is two-sided, and a difference of 50% indicates the absence of a difference between the groups.

### Individuals occupying the vacancies

Floater birds that succeeded in occupying an experimental vacancy revisited specific territories more often (before vacancy



**Figure 2**

Distance between the center of all intrusions attempts and the experimental territory (before removal) for intruders who filled an experimental vacancy (fillers, filled circles) compared to a control set of intruders not filling vacancies (candidates, open circles). Candidates were of similar sex, and all were seen intruding at least once within 150 m from the vacancy. The x-axis represents the different experimental vacancies by sex and numbered individually. For each of the seven vacancies, the intrusion distance of the fillers was compared with the candidates. In the right panel, the average distance for fillers and candidates is given.

creation) compared with floaters who filled no experimental vacancies ( $1.8 \pm 0.4$  [ $n = 7$ ] and  $1.3 \pm 0.1$  [ $n = 172$ ] revisitations observed per year, respectively, Mann-Whitney  $U$  test,  $U = 359$ ,  $p < .05$ ). Floaters that acquired an experimental vacancy were seen intruding significantly closer to that vacancy (before the creation of it) compared with a set of control intruders (floaters of the same sex that did not occupy the vacancy but were seen intruding in our study site) (Figure 2; randomization test,  $N = 5000$ ,  $p < .05$ ). Floaters that obtained experimental vacancies intruded within 150 m of the vacancy (Figure 2) and were always among the five intruders whose “center of intrusions” was located nearest to the vacancy (Figure 3, left). Not all birds that occupied a vacancy were intruding floaters. In Figure 3 (right) we plotted the center of intrusions for all candidates in the cases in which an experimental vacancy was not occupied by an intruding floater but by others. In this group there were fewer candidates available with a center of intrusions located within 150 m distance, and the center of intrusion of the nearest intruder tended to be located further from the vacancy (Mann-Whitney  $U$  test  $U = 10.00$ ,  $N = 7,7$ ,  $p = .06$ ).

In three cases a vacancy was not filled by an intruding floater while nearby intruding floaters were present in the area (Figure 3: 5♂, 6♂, 4♀). In all these three cases, a neighbor filled the vacancy (by definition these birds cannot be regarded as potential intruders; see Methods). Experimental vacancies that lacked nearby intruding floaters were occupied by a neighboring breeder (8♂), by a former neighboring breeder (5♀), and by two birds that were not seen intruding or breeding in the area (7♂, 9♂).

In summary, 80% of all vacancy fillers were familiar to the area before the experiment (Table 2). They were familiar because they were socially active nearby (i.e., interacting with other birds by defending a territory within 50 m or performing intrusions within 150 m of the experimental vacancy).

#### Is proximity the only feature that determines territory acquisition?

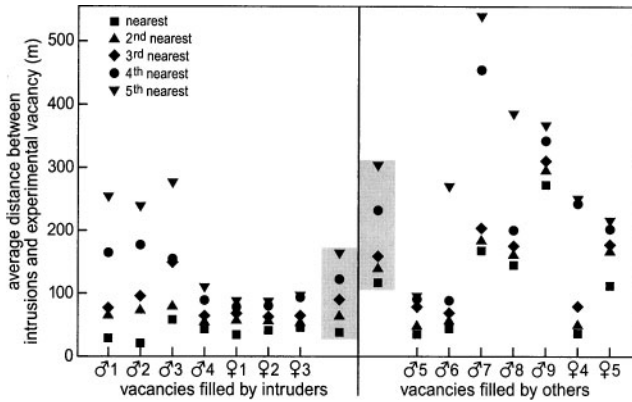
We compared characteristics of intrusion attempts (collected previous to the removal) of floaters that successfully obtained

an experimental vacancy ( $n = 7$ ) with those that did not ( $n = 159$ ). Successful intruders did not show higher incidences of aggressive or sexual behavior during intrusions ( $\chi^2 = 3.055$ ,  $df = 2$ ,  $p = .22$ ). Territory owners responded similarly to both type of intruders; incidence of aggressive or sexual behavior toward intruders did not differ significantly ( $\chi^2 = 1.978$ ,  $df = 2$ ,  $p = .37$ ). The outcome of the interaction between intruder and territory owner did not differ between successful and unsuccessful intruders ( $\chi^2 = 0.611$ ,  $df = 2$ ,  $p = .74$ ). In nearly all cases, the intruder left and “lost.” For both groups of intruders, we found equal incidences of paired intrusion attempts, that is, intrusions in collaboration with a mate ( $\chi^2 = 0.108$ ,  $df = 1$ ,  $p = .2$ ). There was no difference in time interval between landing of the intruder and a response by the owner ( $t = -0.96$ ,  $p = .93$ ), or in the time it took for the owner to get rid of the intruder ( $t = -0.34$ ,  $p = .74$ ). There was no difference in age between the successful and unsuccessful floaters, either for both years combined (Mann-Whitney  $U$  test,  $U = 829$ ,  $n = 161$ ,  $p = .23$ ) or for both years separately (1998:  $U = 268$ ,  $p = .37$ ; 1999:  $U = 137$ ,  $p = .34$ ). A similar proportion of birds with breeding experience was present among the vacancy filling intruders compared with the unsuccessful ones for males ( $\chi^2 = 1.77$ ,  $df = 1$ ,  $p = .18$ ) and females ( $\chi^2 = 0.15$ ,  $df = 1$ ,  $p = .7$ ).

#### DISCUSSION

Intruding floaters with a center of activity located within 150 m of the vacancy and both breeders and exbreeders from the direct vicinity had a much higher chance of obtaining an experimental vacancy compared with that of other birds. Current behavior-based models on competition for space assume that familiarity with an area increases the settlement chance in that area (Ens et al., 1995; Stamps and Krishnan, 2001). Our results confirm this assumption. The probability of effectively confiscating a particular area increases as a function of previous presence in that area.

Several studies have hypothesized about the role of familiarity in settlement patterns (Birkhead and Clarkson, 1985; Smith, 1978). A correlation between local familiarity and settlement as a breeder was found in various bird species:



**Figure 3**  
Distance between the center of all intrusion attempts and the experimental territory (before removal) for experimental territories later filled by an intruder (left) and experimental territories later filled by other birds (right). The x-axis represents the different experimental vacancies by sex and numbered individually. Different symbols mark the intruder who is intruding closest and second closest up to the fifth closest to the place where later a vacancy was created. The shaded boxes in the middle mark the averages for both groups.

red-winged blackbird, *Agelaius phoeniceus* (Yasukawa, 1979); purple martin, *Progne subis* (Stutchbury, 1991); barnacle goose, *Branta leucopsis* (van der Jeugd, 2001); kittiwake, *Rissa tridactyla* (Porter, 1988); spotted sandpiper, *Actitis macularia* (Reed and Oring, 1992); cavity nesting *Bucephala* ducks (Eadie and Gauthier, 1985); and shelduck, *Tadorna tadorna* (Patterson and Makepeace, 1979).

### Function of intrusions

The first and most obvious hypothesis with regard to the function of intrusion behavior is that it serves to aggressively evict the owner (Arcese, 1989). In general, it is often assumed that outcomes of contests over territories are determined by traits of the contestants, such as fighting ability or body size. Thus, territories are acquired through contests (Stamps, 1994). Most studies on this topic rely on observations of social interactions between an individual that occupies a territory (the owner) and an individual that is new for that territory (the intruder). Usually the owner "wins" the encounter and remains in possession of the territory, and the intruder leaves after the interaction. This is often interpreted as a causal relation: the owner retains possession of its territory because it won the fight. However, Stamps (1994) questions the logic of this line of reasoning. First, why should intruders return repeatedly to the same spot after "losing" consecutive interactions with the owner, and second, why do intruders in some species not engage in overt contests with the owners? In our study we classified the intruder as winner in only 1% of all intrusion attempts. These events all occurred when a territory owner aborted an interaction and temporarily left the territory. However, upon return of the owner shortly thereafter, intruders were easily chased away. The owners were classified as winner in all other cases. Stamps (1994) proposed to view intrusion behavior as an attempt to initiate a social relationship with the owner, or to obtain information from the owner and neighbors, rather than an attempt to steal resources or take over the territory (see hypothesis 3). Our observations are in agreement with this prediction.

The second hypothesis explaining intrusion behavior relates to the potential direct fitness benefits through extrapair paternity or egg dumping (Møller, 1987). Empirical evidence

**Table 2**  
**Characteristics of birds filling vacancies in the main study area (N = 15)**

Social category	Distance (m)	♂	♀	Total
<b>Locals:</b>				
Intruder	<150	4	3	7
Neighbor (breeder/mudflat territorial)	<50	3	1	4
Former neighbor breeder	<50	0	1	1
<b>Non-locals</b>				
Unknown commitment	—	2	0	2
Unmarked bird	—	0	1	1

The social category, distance (in meters) between the area where the vacancy later was created and the place where different individuals were socially active (see Results), and the number of individuals (N). Two birds acquired an experimental territory but were not observed intruding, breeding or defending a territory (unknown commitment).

that floaters father offspring is scarce and available for only two species. In tree swallows, *Tachycineta bicolor* (Barber and Robertson, 1999; Kempenaers et al., 2001), and stichbirds, *Notiomystis cincta* (Ewen et al., 1999), male floaters were responsible for part of the extrapair young. However, in oystercatchers, intrusions take place over a much longer period than just the fertile period before egg laying (Heg et al., 2000). Furthermore, despite intensive study, we never observed egg dumping, and this is therefore probably very rare (eggs of a clutch in oystercatchers are all marked with identical female specific patterns and only very occasionally deviant eggs are found; Heg et al., 1993). Moreover, only a marginal fraction of intrusions (2%) was associated with sexual behavior (floaters raising their tail to solicit copulation during their brief intrusion visits). This behavior was directed to both males and females and was not restricted to the fertile period (L.W. Bruinzeel, personal observations). Instead, copulations are thought to signal cooperation, because in polygynous trios, female oystercatchers also copulate with each other (Heg and van Treuren, 1998). We conclude from our study that there is no evidence that intrusion behavior in the oystercatcher is related to gaining parentage through egg dumping or extrapair copulations.

The third hypothesis relates intrusion to the process of information gathering on vacant breeding sites (Stutchbury and Robertson, 1987), reproductive success at different sites (Porter, 1988), the area and the inhabitants (Stamps, 1987), or any combination. We suggest, in part by excluding the alternatives, that in oystercatchers the primary function of intrusions is to become familiar with an area and its occupants. First, vacancies resulting from death or divorce of a mate usually occur early in the season before egg laying (Heg et al., 2000), whereas intrusions occurs throughout the season (Heg et al., 2000). Second, floaters only occupied experimental vacancies after, on average, 6 days. Within this time period, many more potential candidates had noticed the vacancy (L.W. Bruinzeel and M. van de Pol, personal observations) and intruded on it. In some occasions, unsuccessful candidates stayed for a few hours before the successful newcomer arrived, indicating that territory acquisition was not restricted to floaters arriving first at the scene. Third, intrusions were also performed by immatures (less than 3 years of age), and we have never observed a bird younger than 3 years settling in our area (Heg, 1999). These findings suggest that intruders do not only scan for current vacancies. Part of the information collected might concern potential vacancies that may arise in the future.

If intrusions would only serve to scan for territories with a high reproductive output, we would expect most intrusions to occur only at the end of the fledging period, which is not the case. For instance, in colonial waterbirds such as kittiwakes (Porter, 1988); cormorants, *Phalacrocorax carbo* (Schjørring et al., 1999); and barnacle geese (van der Jeugd, 2001) prospective visits are mainly restricted to the nestling phase. However, these species are only present at the breeding grounds during the incubation and nestling phase, whereas oystercatchers are present at the breeding grounds for a much longer period of time. In oystercatchers it seems that those individuals with the most detailed knowledge of the local social circumstances have the best settlement chance. The high annual survival and persistent pair bonds of breeders and the consistency in the location of territory boundaries suggest the possibility of accumulating information over the years.

Ens et al. (1995) and Heg et al. (2000) postulated local dominance instead of familiarity as the key mechanism shaping the hierarchy among floater oystercatchers queuing for a high-quality territory. The difference between local dominance and familiarity is only whether or not familiar individuals defend a resource: "Site dependent dominance might develop from the tendencies of individuals to defend specific resources and it might result simply from the tendency of animals to remain within and become familiar with small areas in the absence of any resource defense" (Piper, 1997). We hardly ever observe interactions among floaters outside the social gatherings, and if so, these are always associated with defense of a feeding territory. In fact, intruders are hardly ever present together in an area, let alone present together sufficiently frequently to establish a dominance hierarchy among themselves.

### The role of the neighbors

Successful floaters did not intrude more frequently in the focal territory where removal later took place compared with neighboring territories, indicating that information about the neighbors and the neighborhood might be important (see also Stutchbury and Robertson, 1987). We got the impression that newcomers frequently engaged in interactions with the neighbors and that successful reoccupation of the territory (defined as joint territory defense and copulations with the new mate) coincided with an interaction frequency with the neighbors lowered to a level that is normal among neighboring established breeders. Floaters that were unsuccessful in acquiring the vacancy despite attempts to do so devoted nearly all of their time to interactions with the neighbors (Bruinzeel LW and van de Pol M, personal observations). Several studies have shown that being familiar with the neighbors may decrease cost of territory defense. In willow ptarmigan, *Lagopus lagopus*, territorial defense against new neighbors required a greater expenditure of time and energy compared with that for familiar breeders (Eason and Hannon, 1994). Similar results were experimentally found for primates; in Wied's black tufted-ear marmosets, *Callithrix kuhli*, living in overlapping group home ranges, males are less aggressive toward familiar intruders (French et al., 1995). Red-winged blackbirds settle near familiar neighbors (Beletsky and Orians, 1991), and those with familiar neighbors have higher breeding success (Beletsky and Orians, 1989), probably owing to fewer or less costly interactions in their neighborhood.

This study wouldn't be possible without the help of students and staff of the University of Groningen. Dik Heg ringed as many fledglings as possible during his project and spent many hours getting L.W.B. accustomed to the oystercatcher society. Nienke Beintema, Folmer

Bokma, Riek van Noordwijk, Peter Vos, and Theodoor Westerhof assisted in observing intruders. Simon Verhulst and Kees Oosterbeek helped catch and transport the birds, and Roelie Wiegman, Sjoerd Veenstra, Tosca Boeré and Adriana Faber took good care for them in captivity. Bruno Ens supplied us with frozen cockles. We are very grateful to Natuurmonumenten and especially its Schiermonnikoog crew (Otto Overdijk, Jan Harthoorn, and Kees Soepboer) for logistic support and allowing us to work and to place hides on the salt marsh (which were always kept in good condition by Jan Koenes and his crew). The experiments were carried out under license of the Animal Experiment Board of the University of Groningen (DEC NR 2099). Rudi Drent, Corine Eising, Henk van der Jeugd, Judy Stamps, Joost Tinbergen, Simon Verhulst, and two anonymous referees gave advice and improved the manuscript. L.W.B. is financed by a grant from NWO (805-36-124).

### REFERENCES

- Adams DC, Anthony CD, 1996. Using randomization techniques to analyse behavioural data. *Anim Behav* 51:733–738.
- Arcese P, 1987. Age, intrusion pressure and defense against floaters by territorial male song sparrows. *Anim Behav* 35:773–784.
- Arcese P, 1989. Territory acquisition and loss in song sparrows. *Anim Behav* 37:45–55.
- Barber CA, Robertson RJ, 1999. Floater males engage in extrapair copulations with resident female tree swallows. *Auk* 116:264–269.
- Beletsky LD, Orians GH, 1989. Familiar neighbors enhance breeding success in birds. *Proc Natl Acad Sci USA* 86:7933–7936.
- Beletsky LD, Orians GH, 1991. Effects of breeding experience and familiarity on site fidelity in female red-winged blackbirds. *Ecology* 72:787–796.
- Birkhead TR, Clarkson K, 1985. Ceremonial gatherings of the magpie *Pica pica*: territory probing and acquisition. *Behaviour* 94:324–332.
- Brown JL, 1969. Territorial behavior and population regulation in birds. *Wilson Bull* 81:293–329.
- Eadie JM, Gauthier G, 1985. Prospecting for nest sites by cavity nesting ducks of the genus *Bucephala*. *Condor* 87:528–534.
- Eason P, Hannon SJ, 1994. New birds on the block: new neighbors increase defensive costs for territorial male willow ptarmigan. *Behav Ecol Sociobiol* 34:419–426.
- Ens BJ, Kersten M, Brenninkmeijer A, Hulscher JB, 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *J Anim Ecol* 61:703–715.
- Ens BJ, Weissing FJ, Drent RH, 1995. The despotic distribution and deferred maturity: two sides of the same coin. *Am Nat* 146:625–650.
- Ewen JG, Armstrong DP, Lambert DM, 1999. Floater males gain reproductive success through extrapair fertilizations in the stich-bird. *Anim Behav* 58:321–328.
- French JA, Schaffner CM, Shepherd RE, Miller ME, 1995. Familiarity with intruders modulates agonism towards outgroup conspecifics in Wied's black-tufted-ear marmoset (*Callitrix kuhli*: Primates, Callitrichidae). *Ethology* 99:24–38.
- Harris MP, 1970. Territory limiting the size of the breeding population of the oystercatcher (*Haematopus ostralegus*): a removal experiment. *J Anim Ecol* 39:707–713.
- Heg D, 1999. Life-history decisions in oystercatchers (PhD dissertation). Groningen: University of Groningen.
- Heg D, Ens BJ, Burke T, Jenkins L, Kruijt JP, 1993. Why does the typically monogamous oystercatcher (*Haematopus ostralegus*) engage in extra-pair copulations? *Behaviour* 126:247–289.
- Heg D, Ens BJ, van der Jeugd HP, Bruinzeel LW, 2000. Local dominance and territorial settlement of nonbreeding oystercatchers. *Behaviour* 137:473–530.
- Heg D, Van Treuren R, 1998. Female-female cooperation in polygynous oystercatchers. *Nature* 391:687–691.
- Hensley MM, Cope JB, 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. *Auk* 68:483–493.
- Kempnaers B, Everding S, Bishop C, Boag P, Robertson RJ, 2001. Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*). *Behav Ecol Sociobiol* 49: 251–259.
- Kluyver HN, Tinbergen L, 1953. Territory and regulation of density in titmice. *Arch Néerlandaises Zool* 10:265–289.

- Møller AP, 1987. Intruders and defenders on avian breeding territories: the effect of sperm competition. *Oikos* 48:47–54.
- Newton I, 1998. Population limitation in birds. London: Academic Press.
- Patterson IJ, Makepeace M, 1979. Mutual interference during nest prospecting in the shelduck, *Tadorna tadorna*. *Anim Behav* 27: 522–535.
- Piper WH, 1997. Social dominance in birds: early findings and new horizons. *Curr Ornithol* 14:125–187.
- Porter JM, 1988. Prerequisites for recruitment of kittiwakes *Rissa tridactyla*. *Ibis* 130:204–215.
- Reed JM, Oring LW, 1992. Reconnaissance for future breeding sites by spotted sandpipers. *Behav Ecol* 3:310–317.
- Schjørring S, Gregersen J, Bregnballe T, 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Anim Behav* 57:647–654.
- Smith SM, 1978. The “underworld” in a territorial sparrow: adaptive strategy for floaters. *Am Nat* 112:571–582.
- Stamps JA, 1987. The effect of familiarity with a neighborhood on territory acquisition. *Behav Ecol Sociobiol* 21:273–277.
- Stamps JA, 1994. Territorial behavior: testing the assumptions. *Adv Study Behav* 23:173–232.
- Stamps JA, 1995. Motor learning and the value of familiar space. *Am Nat* 146:41–58.
- Stamps JA, Krishnan VV 1999. A learning based model of territory establishment. *Q Rev Biol* 74:291–318.
- Stamps JA, Krishnan VV, 2001. How territorial animals compete for divisible space: a learning-based model with unequal competitors. *Am Nat* 157:154–169.
- Stewart RE, Aldrich JW, 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. *Auk* 68:471–482.
- Stutchbury BJ, 1991. Floater behaviour and territory acquisition in male purple martins. *Anim Behav* 42:435–443.
- Stutchbury BJ, Robertson RJ, 1987. Behavioral tactics of subadult female floaters in the tree swallow. *Behav Ecol Sociobiol* 20: 413–419.
- van der Jeugd HP, 2001. Large barnacle goose males can overcome the social costs of natal dispersal. *Behav Ecol* 12:275–282.
- Yasukawa K, 1979. Territory establishment in red-winged blackbirds: importance of aggressive behavior and experience. *Condor* 81: 258–264.
- Zack S, Stutchbury BJ, 1992. Delayed breeding in avian social systems: the role of territory quality and “floater” tactics. *Behaviour* 123: 194–219.