

# Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*

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## Summary

1. The hypothesis of site-dependent population regulation predicts that birds utilize available nesting sites in a pre-emptive (ideal despotic) manner, leading to density dependence in heterogeneous habitats as poorer sites are used at higher population densities. At small population sizes adaptive site choice protects populations against fluctuations (the buffer effect).

2. Common guillemots *Uria aalge* (Pontoppidan) breed at high density on sea-cliffs. The population breeding on the Isle of May, Scotland increased by 60% between 1981 and 2000. A good nest-site is a prerequisite for successful breeding and there is much competition for the best sites. Throughout this period, site use correlated with two measures of site quality, and photographs taken in 1936 show that this pattern has been extremely stable.

3. The data indicate declining quality of sites that remain available as the population has increased. Site-dependent regulation was evident in that average breeding success declined over the years, but no declining trend was detected in the best (and most preferred) sites.

4. An individual guillemot generally uses the same nest-site from year to year, but a minority move, usually less than 2 m, between breeding seasons. These movements can be involuntary or voluntary. Involuntarily moving birds that had occupied very good sites before moving often spent several years as non-breeders (floaters) close to their previous site before breeding again, and then occupied poorer sites. Voluntarily moving birds significantly improved their site quality by moving.

5. Birds responded both to the physical site characteristics and to their own experience (breeding failure) when abandoning a site. Their behaviour thus combined aspects of the 'win-stay, lose-switch' strategy with direct assessment of site quality. Our data set is inconclusive with respect to the public information hypothesis, i.e. whether birds use conspecific cues of breeding success when settling in a new site.

*Key-words:* density dependence, fighting, habitat heterogeneity, intraspecific competition, territoriality.

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## Introduction

Fretwell & Lucas (1970) and Fretwell (1972) developed a model of ideal despotic distribution of territorial

animals that leads to density dependence when individuals prevent others from settling in the preferred patches. Later, Rodenhouse, Sherry & Holmes (1997) presented a synthesis of density dependence that arises through pre-emptive use of habitats. When populations grow, some individuals have to use lower quality sites, which reduces *per capita* population growth even if breeding success at individual sites does not change with density (Fretwell 1972; Dhondt, Kempenaers & Adriansen

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1992; Ferrer & Donazar 1996; Holmes, Marra & Sherry 1996; Petit & Petit 1996; Krüger & Lindström 2001). The carrying capacity of the environment thus results from an interaction between the productivity of the habitat and the behaviour of territorial individuals (Kokko & Sutherland 1998). Individually optimal site use reduces the susceptibility of populations to the vicissitudes of small population size. Various mechanisms can reduce population growth at low densities (Courchamp, Clutton-Brock & Grenfell 1999; Stephens & Sutherland 1999), but if habitat quality is a main determinant of productivity, smaller populations tend to increase due to their exclusive use of high-quality habitat. This is termed the 'buffer effect' by Gill *et al.* (2001) and Sutherland & Norris (2002).

Adaptive behaviour can thus be beneficial to population persistence, but if territorial takeovers are possible, individual site changes could also have negative population consequences. Fighting takes time and energy, the victim of usurpation does not necessarily find or accept a new breeding site, and the would-be usurper does not necessarily succeed in securing a site (Danchin & Cam 2002). Furthermore, population performance can be reduced through adaptive behaviour of individuals if they 'float', i.e. spend a season as a non-breeder, instead of breeding on a low quality site (Kokko & Sutherland 1998).

The ideal despotic distribution in its original form assumes that individuals have perfect information about the quality of each site. However, individuals usually have to rely on proximate cues of quality when choosing habitats, and these cues may often be inaccurate (Abrahams 1986; Orians & Wittenberg 1991) or incomplete (Petit & Petit 1996; Bollmann, Reyer & Brodmann 1997; Storch & Frynta 2000), in extreme cases even leading to a reversal of density dependence (i.e. an Allee effect, Delibes, Ferreras & Gaona 2001; Kokko & Sutherland 2001). An alternative to observing habitat characteristics is to use breeding success itself as a cue for choice. Animals may depart after they have themselves experienced a breeding failure (win-stay, lose-switch strategy; Switzer 1993; Schmidt 2001), and they may use the success of conspecifics to determine where to settle (the public information hypothesis, Boulinier *et al.* 1996; reviewed in Valone & Templeton 2002).

Here we study nest-site choice using a long-term data set on the common guillemot *Uria aalge* (Pontopidan), referred to hereafter as guillemot. It is a highly colonial cliff-nesting seabird, breeding at average densities on flat rocky areas of about 20 pairs/m<sup>2</sup> in many parts of the northern North Atlantic and Pacific Oceans (Harris & Birkhead 1985). The guillemot has a single egg clutch and, there being no nest, this is laid on the bare ground, often on small and precarious ledges where any error when birds are changing over on the egg or chick almost invariably results in its loss. Nest-sites are highly traditional, eggs normally being laid

within 5 cm in different years and individuals are highly site-faithful (Harris, Wanless & Barton 1996). Nevertheless, site changes do occur, and birds sometimes remain as floaters for several years before breeding again. Good nest-sites appear to be in short supply: there is serious competition and fighting for the most productive sites, sometimes resulting in physical damage. Where environmental conditions allow, birds attend these sites for much of the year (Birkhead 1977, 1978; Harris & Wanless 1989, 2003).

Temporal variation in site quality can make interpreting dispersal behaviour challenging (Boulinier & Lemel 1996). Here, guillemots are an ideal study system as they are long-lived, extremely site-faithful and observed easily (Harris *et al.* 2000). The 'territory' is simply the site of the nest, with physical properties (e.g. slope) that do not vary from year to year and that are predictably linked to breeding success (Birkhead & Nettleship 1987). Feeding opportunities do not depend on the characteristics of the nest site, and breeding success is easy to quantify: a single chick is or is not raised. These characteristics allow us to combine longitudinal data on individual site use with its population dynamic consequences.

We tested the population regulation model of Rodenhouse *et al.* (1997) by examining breeding success in an increasing population, additionally investigating the details of the behavioural process leading to pre-emptive site use. We examine if guillemots change nest sites adaptively (i.e. changes lead to improved breeding success), if birds are particularly prone to depart when they have failed in their own breeding (the win-stay/lose-switch strategy, Switzer 1993), if takeovers target birds preferentially that have succeeded in breeding (public information hypothesis, Boulinier *et al.* 1996; Boulinier & Danchin 1997; Doligez, Danchin & Clobert 2002; Valone & Templeton 2002) or if site change is directly dictated by a site's physical characteristics.

## Methods

### THE STUDY AREA

The Isle of May, in the entrance to the Firth of Forth, south-east Scotland (56°11' N, 2°33' W), has a long-established colony of common guillemots. In 1981 there were 11 250 pairs, in 2000 there were 18 000 pairs, with the main increase (5.5% per annum) occurring between 1991 and 2000. Between 1982 and 2000 we carried out an intensive study of the breeding of all pairs of guillemots breeding within clearly defined areas of cliff chosen to cover a range of cliff types and bird densities. Photographs of parts of the areas are given in Harris & Wanless (1988). The number of study areas increased during the early years but remained consistent between 1985 and 2000. The carrying capacity of the study area was not reached because the numbers of guillemots breeding in the areas increased further in 2001 and

2002. Breeding sites were numbered on large black-and-white photographs and each site was checked from permanent hides every day during the breeding season. We recorded whether or not a site was occupied, an egg was laid and breeding was successful (the chick survived to the age of at least 14 days when it can be taken to sea by the male parent to complete its development). The physical characteristics of 1119 of the 1252 sites followed were measured in the field, the remainder being inaccessible to us (Harris *et al.* 1997). A total of 725 adults were caught, marked with unique combinations of colour-rings, sexed by observations of copulations and their survival and breeding documented by daily observations made in each season.

#### MEASURES OF SITE QUALITIES

We measured the quality of each site,  $Q$ , as the total number of young reared between 1985 and 2000 (the period over which the study areas remained constant) divided by the number of these years the site was used for breeding.  $Q$  is not a perfect measure of site characteristics: the estimates of rarely used sites were less certain than those used regularly, and breeding success increases with the number of consecutive years that the site is occupied (Harris *et al.* 1997). To overcome these problems, a second measure  $Q_p$  was developed based on the physical characteristics of a site that are known to influence breeding success of both this species and the cogeneric Brünnich's guillemot *U. lomvia* L. (e.g. Birkhead *et al.* 1985; Birkhead & Nettleship 1987). This measure equals the predicted success based on a logistic regression with the following explanatory variables: site type (on a ledge or in a niche), the number of walls surrounding the site, and the slope of the site (Harris *et al.* 1997). Because using  $Q_p$  instead of  $Q$  did not change any of our conclusions, we present results using  $Q$  only.  $Q_p$ -based analyses are available by request from the authors.

#### CLASSIFICATION OF MOVEMENTS BY BIRDS

The data set of 4779 observations (bird-years) includes 718 (15%) cases where a bird breeding at a specific site did not breed there the following year. These were classified (Table 1) according to whether the bird changed site immediately (C) or floated (F) or was never seen again (almost certainly because it had died, D), and whether its site was occupied (most probably indicating involuntary movement or eviction) or not (indicating voluntary movement) after the change. Involuntary movements are denoted IC and IF, and voluntary ones VC and VF. Death never being voluntary, we denote death by D+ or D-, according to whether the site of the bird remained occupied (D+) or not (D-) in the year of its disappearance.

It is possible that some movements reflect mate change (divorce) rather than a desire to change the breeding site. Of all the bird-years where members of a

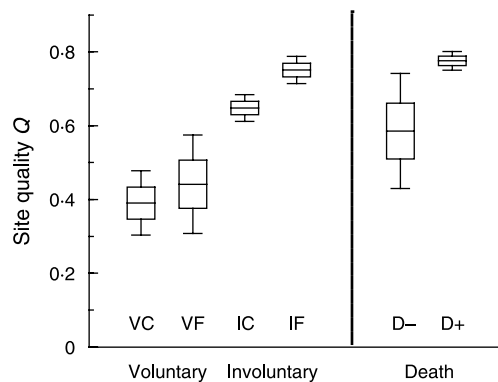
pair were both colour-ringed and could be followed from one year to another, we observed 987 cases where both stayed together, 54 cases where the female moved, 56 cases where the male moved and 39 cases where both moved. Joint movement is much more common than expected by chance ( $2 \times 2$  contingency table for above data:  $\chi^2 = 148.9$ , d.f. = 1,  $P < 0.001$ ), and in 15 of the 39 cases where a pair departed in the same year they ended up breeding together at a different site. These data suggest site change as a more likely motivation to move, rather than mate change. Because this pattern indicates that pairs move non-independently, for all further analyses we have randomly omitted the data for one of the sexes when a pair of colour-ringed birds moved ( $n = 39$  observations omitted).

Guillemots on the Isle of May continue to visit their nest-sites outside the breeding season (Harris & Wanless 1989a) so we were unable to document all fights. However, we recorded all fights involving colour-ringed birds that we saw from a month before egg-laying until the last birds left the colony at the end of the season (Harris & Wanless 2003). All changes of breeding site or status, where a new bird of the same sex occupied the original site in the year that the focal bird had left the site, were classified as 'involuntary'. Changes where the old site was unoccupied the next year were classified as 'voluntary'. The class of involuntary movements undoubtedly contains some voluntary movements, e.g. where a bird left its site that was occupied later by another bird. However, if this was the case, the differences in the fates of apparently involuntarily and voluntarily moving birds should become less pronounced, thus making our tests conservative. In 1982–87, when particular attention was paid to competition for sites involving colour-ringed birds, 23 (32%) of 72 involuntary changes of site involved fighting. The corresponding figures for voluntary changes were one (4%) of 28. Thus the categories very likely reflect true differences in whether a bird changed site voluntarily or involuntarily ( $\chi^2 = 8.90$ , d.f. = 1,  $P = 0.003$ ). Consequently, we distinguish simply between voluntary or involuntary movements, as indicated in Table 1. An involuntarily leaving bird is referred to as the victim, and its replacement as the usurper.

Sexes did not differ in the frequency of the categories of site change ( $2 \times 4$  contingency table for categories VC, VF, IC, IF in Table 1: = 6.26, d.f. = 3,  $P = 0.099$ ), nor in the number of deaths and their relationship to site occupancy ( $2 \times 2$  contingency table for categories D- and D+ in Table 1:  $\chi^2 = 1.81$ , d.f. = 1,  $P = 0.179$ ), or in the mean quality of sites where a bird of each change category bred (two-way ANOVA with sex and category as fixed effects, and  $Q$  as the dependent variable: sex and sex  $\times$  category both non-significant: sex,  $F_{1,659} = 0.20$ ,  $P = 0.888$ ; sex  $\times$  category:  $F_{5,659} = 0.285$ ,  $P = 0.921$ . Excluding the interaction term keeps sex non-significant:  $F_{1,659} = 0.034$ ,  $P = 0.854$ ). In all the following analyses, data for the two sexes are therefore pooled (but, as described above, never for two members of the same pair in the same year).

**Table 1.** Number of departures of marked birds from breeding sites. Changes were rare: the data set includes 2159 bird-years when a male did not change his site, and 1902 bird-years when a female did not change her site. Numbers in brackets indicate the changes that are analysed further (some were omitted randomly when two colour-ringed birds bred together; see text for explanation)

Number of events	Females	Males
Apparently voluntary change in breeding site or status (old site unoccupied)		
Changed site immediately (VC)	28 (25)	36 (30)
Floated for at least 1 year (VF)	25 (24)	13 (10)
Apparently involuntary change in breeding site or status (old site occupied by another bird of the same sex)		
Changed site immediately (IC)	95 (92)	107 (94)
Floated for at least 1 year (IF)	73 (72)	87 (75)
Never seen again – probably dead		
Old site left vacant (D–)	7 (7)	17 (17)
Old site occupied (D+)	93 (93)	120 (120)



**Fig. 1.** Qualities of sites  $Q$  that were occupied by birds in the year prior to a change in breeding site or status. Categories of birds are as in Table 1. Box plots indicate the mean, mean  $\pm$  SE (box), and the 95% confidence interval for the mean (whiskers). See text for significance tests.

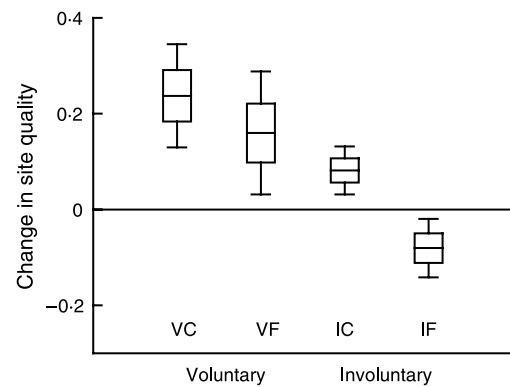
## Results

### OCCUPATION OF SITES LEFT VACANT BY DEATH OF OWNER

Of the 237 sites left vacant by the failure of the owner to return, probably because it had died, 213 were taken immediately by another bird and 24 remained unoccupied that year (Table 1). Those taken over immediately were of significantly higher quality than those that remained unoccupied (Fig. 1, Student's  $t = 4.19$ ,  $n_1 = 213$ ,  $n_2 = 24$ ,  $P < 0.001$ ).

### VOLUNTARY VS. INVOLUNTARY CHANGES IN BREEDING SITE OR STATUS

A total of 102 changes were classified as voluntary, and a total of 362 as involuntary (Table 1). Birds of different categories differed significantly in the quality of their original breeding sites (Fig. 1; ANOVA  $F_{3,421} = 30.86$ ,



**Fig. 2.** Means  $\pm$  SE (box) and the 95% confidence interval for the mean (whiskers) for the change in site quality that a bird experienced when it changed its breeding site, measured as  $Q(\text{new}) - Q(\text{previous})$ . For floating birds (VF and IF), the new site is the site this bird bred next if it ever obtained a new site (the data set did not include birds who floated without ever breeding again). See text for significance tests.

$P < 0.001$ ), and also in how much their site quality changed if they bred again (Fig. 2; ANOVA:  $F_{3,344} = 10.72$ ,  $P < 0.001$ ). Birds that changed site voluntarily (VC) were breeders on low-quality sites before the change and obtained a site of much higher quality after the change (Figs 1 and 2). Birds that left voluntarily to float (VF) also obtained a better site when they bred again after a gap of 1 or more years. The original site of VF birds was of higher quality than that of VC birds (Fig. 1).

Involuntary changes were recorded in birds that had been occupying very high-quality sites (IC, and especially IF in Fig. 1). When these birds bred again, they occupied lower-quality sites if they had been floaters during the intervening periods (IF, Fig. 2). If they changed site immediately (IC, Fig. 2), their new site was better than their old site (Fig. 2). This suggests that the IC category included birds that were evicted, but also birds that changed site voluntarily from a relatively good site to a very good site, and the relatively good vacancy left behind was immediately filled by another bird.

Although Figs 1 and 2 suggest adaptive site choice in guillemots, they could be artefacts because estimates of site quality are difficult to distinguish from the increase in individual breeding success over time (Harris *et al.* 1997). Therefore, we performed a randomization test on a null model (Appendix I), which assumed that all sites were equal in quality, all variation in breeding success arose from previous breeding experience of the bird and from demographic stochasticity, and that patterns of site use (probability of moving after  $n$  years of breeding; life span of birds; number of birds) equalled that of the field data. We assumed that birds keep their high experience score even if they move, making the test conservative as this tends to improve the breeding success scores after site changes. As the test statistic we used  $p_{\text{inc}}$ , the proportion of increases (0  $\rightarrow$  1) of all changes in breeding success following a site change. This proportion had the mean = 0.541 in the 10 000

simulation runs (range 0.448–0.634). The observed value in the field data was 0.766 ( $n_{0 \rightarrow 1} = 317$ ,  $n_{1 \rightarrow 0} = 97$ ), which is outside the range of the randomized null model, indicating  $P < 0.001$ . Birds thus changed sites to improve their breeding success.

For voluntarily leaving birds, we investigated whether they left low-quality sites regardless of their own breeding success, or whether the individual's own experience of breeding failure made it more likely to leave. In the null model, the proportion of site changes that were preceded by breeding failure ( $p_{\text{dep}}$ ; see Appendix I) had the mean = 0.241 and range 0.190–0.300 across all randomizations. In the field data, voluntarily leaving birds (VC and VF) had failed to rear a chick in 77.5% of cases (79 of 102). Thus, voluntary departures were associated strongly with breeding failure (10 000 simulations with range outside the observed value indicates  $P < 0.001$ ).

Failure, however, often occurs disproportionately on poor quality sites. Did birds thus pay attention to site characteristics or to their own experience when leaving a site? Another randomization test took variable site quality into account. In the year prior to moving, the 64 birds of category VC reared a total of 15 fledglings. We calculated the expected distribution of the number of offspring produced prior to the VC birds moving, given the qualities of sites they owned. In a single run of such a randomization test, each site produced a fledgling with a probability equal to its estimated quality  $Q$ . The test statistic was the sum of all fledglings produced, calculated 10 000 times. The null hypothesis was that birds did not fail more often than expected based on the qualities of their sites. Using this null hypothesis, the birds produced 15 or fewer fledglings in 41 of 10 000 randomized cases. VC birds had thus been experiencing more breeding failures than predicted from their site occupancy ( $n = 64$ , two-tailed  $P = 0.0082$ ). The same was true for VF birds ( $n = 38$ ,  $P < 0.001$ ). For victims of usurpation, the patterns were different depending on their category (IC and IF). IC birds had experienced more breeding failures than predicted by the null model ( $n = 202$ ,  $P < 0.001$ ), but the breeding success of IF birds did not differ significantly from expectation ( $n = 160$ ,  $P = 0.29$ ). Overall, the pattern suggests that individuals partly used their own breeding experience to determine whether they should attempt to move and potentially displace owners of higher quality sites. The group IF, that deviates from this pattern, may have consisted of true victims of usurpation (potentially particularly successful birds) and of birds that left voluntarily in search of a better breeding site after being unsuccessful. The opposite predictions for breeding success for these birds would thus cancel out in the data.

The response of birds to a breeding failure was not a simple rule of thumb but conditional on the quality of its site: among failed breeders, subsequent voluntary departure (VC, VF) was more likely if the failed bird bred on a poor quality site (logistic regression between breeding site quality  $Q$  and belonging to the VC or VF

category, as opposed to staying as a breeder:  $\beta = -3.73$ ,  $\chi^2 = 76.26$ , d.f. = 1,  $n = 732$ ,  $P < 0.001$ ). Birds on high-quality sites were thus more site-tenacious after a breeding failure than birds using low-quality sites.

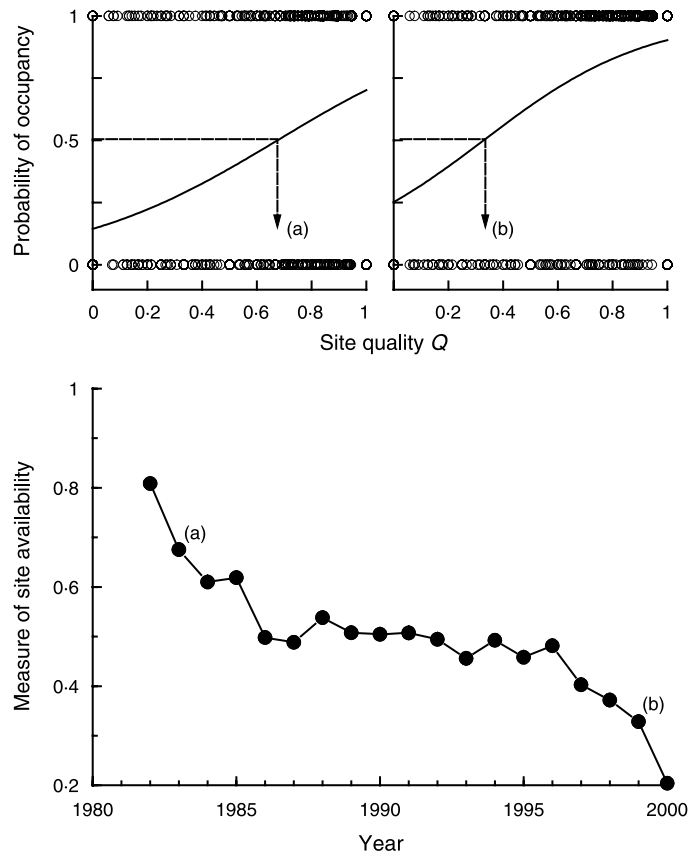
Did usurpers simply target birds that owned sites with good physical characteristics, or did they use others' breeding success as a cue for high-quality sites? If the latter, involuntarily leaving birds should have high breeding success for their sites, but none of the above results indicate this. For some birds of the category IC, this may simply indicate voluntary movement after a breeding failure. More conclusive evidence is provided by involuntarily floating (IF) birds, i.e. birds that are most likely to have been forced to leave. Because IF birds had had average breeding success for their sites, there was no suggestion that birds looking for new sites preferentially targeted neighbouring birds that had been successful in the previous year. In other words, usurpers appeared to vie for the generally high-quality sites occupied by IC and IF birds, whether or not the particular breeding attempt of these birds was successful.

#### CHANGES IN SITE OCCUPANCY AND SITE CHANGE FREQUENCIES OVER TIME

Site quality was significantly positively related to its occupation status in all 19 years (Table 2). We therefore used the quality that predicted 50% site occupancy,  $Q_{50}$ , as an index that reflected the quality of available sites at the current population size (Fig. 3). It is evident that poorer sites remained available as the study progressed (Fig. 3). As poorer sites were used for breeding in years with high population size, average breeding success decreased. This shows as a positive correlation between quality of available sites and average breeding success in all sites (marked and unmarked birds; Fig. 4). However, breeding success in the 316 sites that were occu-

**Table 2.** Logistic regression of site quality as an explanatory variable for site occupancy

Year	$\beta$	$P$
1982	2.29	< 0.001
1983	2.64	< 0.001
1984	2.94	< 0.001
1985	3.29	< 0.001
1986	3.91	< 0.001
1987	3.32	< 0.001
1988	3.77	< 0.001
1989	3.61	< 0.001
1990	3.38	< 0.001
1991	3.73	< 0.001
1992	3.74	< 0.001
1993	3.66	< 0.001
1994	4.12	< 0.001
1995	4.04	< 0.001
1996	4.09	< 0.001
1997	3.78	< 0.001
1998	3.61	< 0.001
1999	3.32	< 0.001
2000	3.02	< 0.001

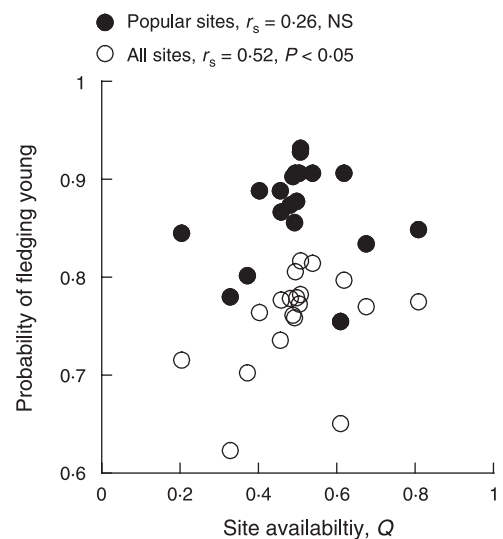


**Fig. 3.** Upper panels: two examples (years 1983 and 1999) of the logistic regression (Table 2) predicting site occupancy based on site quality. The arrow indicates the quality that relates to 50% occupancy probability. This forms the measure  $Q_{50}$  of site availability for each year. Lower panel: site availability measure  $Q_{50}$  for each year, with (a) and (b) denoting  $Q_{50}$  (the location of the 50% arrow) in years 1983 and 1999. The decreasing trend is significant (regression  $Q_{50} = \alpha + \beta \text{ year}$ ;  $\beta = -0.0204$ ,  $F = 63.7$ ,  $P < 0.001$ ).

pied every year between 1982 and 2000 was unaffected by the quality of available sites (Fig. 4). The result supports the interpretation of pre-emptive use of best sites, leading to site-dependent density regulation (Rodenhous *et al.* 1997).

Population regulation was evident in that the poorest available sites at the end of the study did not offer high enough breeding success to sustain a population. The mean survival from fledging to recruitment in 14 years of study was 33%. Available sites offered approximately 20% fledging success at the end of the study period ( $Q_{50} = 0.2$ , Fig. 4), which gives  $1/2 \times 0.2 \times 0.33 = 0.033$  same-sex recruits from one breeding attempt. More than 30 breeding attempts are required for such sites to yield a stable or growing population ( $1/0.033 = 30.3$ ), clearly beyond the average life span of guillemots.

More inexperienced birds could have bred in later years, generating the observed decline in breeding success. Therefore, we checked if the pattern of declining breeding success could have arisen simply through the null model (Appendix I). Breeding success of marked birds followed over years improved with time (regression with mean success of marked birds =  $\alpha \times \text{year} + \beta$ : estimate of  $\alpha = 0.0028$ ), but the null model produced an even stronger positive trend,  $\alpha$  falling below that of the true data set in 308 of 10 000 runs ( $P = 0.031$ ). Thus the data contained more, rather than fewer, experi-



**Fig. 4.** The proportion of occupied sites that fledged an offspring was positively related to the measure of the quality of available sites (open dots). For the 316 popular sites that were occupied in every year between 1982 and 2000, fledging success was not significantly related to the quality of available sites (black dots).

enced birds over time, and the breeding success of birds declined relative to what was expected on the basis of their improving experience. Repeating the randomization by excluding those birds already breeding at the

start of the study, whose true experience status was unknown, produced an even more significant result ( $\alpha$  below observed in 34 of 10 000 runs,  $P = 0.0034$ ).

It is possible that changes in breeding output are due to increasing local density, rather than birds using different site qualities than before. However, this alternative explanation appears unlikely. We had data for the mean number of close (touching) neighbours for individual nest-sites in the years 1985 and 2002. Despite a much higher population density in the latter year, we found no significant difference in the mean number of neighbours (1985:  $1.33 \pm 0.09$ ; 2002:  $1.32 \pm 0.09$ ; Student's  $t = 0.32$ ,  $n_1 = 552$ ,  $n_2 = 472$ ,  $P = 0.75$ ).

Finally, we checked if mortality changed with density. The probability of not returning (likely death) was significantly higher in years when available breeding sites were of low quality ( $Q_{50}$  and probability of not returning: Spearman's  $r_s = -0.50$ ,  $n = 18$ , one-tailed  $P < 0.05$ ).

## Discussion

Territorial behaviour is a common factor limiting bird populations (Newton 1992), and the strategies of site use and dispersal used by individuals can strongly alter the overall size and stability of a population (Holt 1993). Site use can generate density dependence such that populations become buffered against fluctuations (Gill *et al.* 2001), but this occurs only if individuals make adaptive choices of where to breed (McPeck *et al.* 2001). Our results clearly indicate adaptive site choice in guillemots. Breeding sites in use are of higher quality than those which are not, and birds leave low-quality sites to increase their breeding success. Preferences for high-quality sites (sites physically protected by walls, with slopes that prevent eggs rolling into the sea) appear extremely stable. The currently most productive sites were already occupied in 1936 and 1977 when the population was only a tenth and a quarter of its size at the end of our study (Harris *et al.* 1997), although some very productive sites had also been colonized since then.

The adaptive choices of guillemots resulted in density dependence, a result that is in line with the model of site-dependent population regulation (Rodenhouse *et al.* 1997). Average breeding success was correlated with the quality of available sites, i.e. higher in years of smaller population size. While the population carried on growing at the end of the study, the poorest sites used at the end of the study did not contribute enough young to be part of a 'source' population. There was no indication that breeding success declined on individual sites: the best sites remained equally productive regardless of population size.

Evidence for site-dependent population regulation has been previously found for several bird species (e.g. imperial eagle *Aquila adalberti* Brehm: Ferrer & Donazar 1996; goshawk *Accipiter gentilis* L. Krüger & Lindström 2001), as well as for mammals (beaver *Castor fibre* L. Nolet & Rosell 1994; white-footed mouse *Peromyscus leucopus* Rafinesque: Halama & Dueser

1994) and reptiles (side-blotched lizards *Uta stansburiana* Baird: Calsbeek & Sinervo 2002). Our study adds insight to the details of this important density-dependent process, by following individual decisions over the whole lifetime of birds, combining movement data with the consequences of individual behaviour on population growth.

Some evidence was found that adult mortality increased when the population became large. The quality of available sites, an index of population size, correlated with the probability that marked individuals disappeared from the population. It is thus possible that density dependence results from a combination of lower adult survivorship when the population grows large, and site-dependence as modelled by Rodenhouse *et al.* (1997). Site-dependence thus does not necessarily operate in isolation from other processes.

Site-dependent regulation was not solely a result of indirect interactions either. Site-dependent population regulation has been described as density dependence generated in the absence of direct interactions between individuals (McPeck *et al.* 2001). However, pre-emptive use of sites means that one individual, by occupying a site, forces a constraint upon another's site choice and hence reduces its fitness. To us, this qualifies as an interaction (see also Hawkins & Berryman 2000; Hunt & Law 2000; Rodenhouse, Sherry & Holmes 2000). The guillemot system emphasizes the importance of direct interactions: competition for sites often induces takeovers, which obviously shape population regulation as some individuals may have to float instead of breeding.

We also examined proximate mechanisms that birds use to assess site quality. Theory predicts that 'win-stay, lose-switch' (individuals leave sites in which they have been unsuccessful) is a good strategy, especially when habitat quality does not vary much over time, as in our guillemots (Switzer 1993; Schmidt 2001). As an alternative, birds could have innate preferences for certain types of nest sites. In nature, both processes appear to play a role. Greater flamingos *Phoenicopterus ruber* (L.) switched colonies after breeding failures in the Camargue (Nager *et al.* 1996). Switzer (1997a) confirmed experimentally that male dragonflies *Perithemis tenera* (Say) leave sites in which they are prevented from mating. Simultaneously, they were more faithful to a territory if it was of relatively high quality (Switzer 1997b). Haas (1998) presented experimental evidence for responses to breeding failure in American robins *Turdus migratorius* (L.) and brown thrashers *Toxostoma rufum* (L.). In Cassin's auklets *Ptychoramphus aleuticus* (Pallas) nest site fidelity was greater at low densities, but previous experience had no effect on site fidelity (Pyle, Sydeman & Hester 2001). In the black-legged kittiwake *Rissa tridactyla* (L.) birds emigrate from less productive patches, and an individual's own experience has an effect on departure, but only when breeding in poor patches (Danchin, Boulinier & Massot 1998). The behaviour of guillemots matched most closely

that of kittiwakes. Site changes were not solely a response to breeding failure, as birds were more likely to stay after a failure if their breeding site was of high quality. However, voluntary site changes were particularly likely after a breeding failure, after controlling for site quality. Thus, a guillemot's decision to leave a site was influenced both by the site's quality *per se* and by the individual's own experience.

There was no support for the hypothesis that usurpers used the success of conspecifics as a cue when determining which sites to target (Boulinier *et al.* 1996; Valone & Templeton 2002). In several species such as black-legged kittiwake and collared flycatcher *Ficedula albicollis* (Temminck), individuals monitor the breeding success of others and move preferentially to sites that have generated good success in the previous year (Boulinier & Danchin 1997; Doligez *et al.* 2002). Guillemots did not target conspecifics with better than predicted reproductive success. However, our data are somewhat inconclusive in this respect, because we could not document all fights leading to takeovers. Because some 'victims' could have left due to breeding failure, our breeding success estimates for the victims of usurpation may be deflated. However, it is plausible that the physical aspects of site quality, which are easy to assess on a temporally stable cliff-face, offer better cues for guillemots than the success or failure of conspecifics, which unavoidably incorporates demographic stochasticity.

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**Appendix I**

The null model assumes that breeding success is purely determined by the experience of a bird, measured as the number of years,  $x$ , since it first was observed occupying a ledge. The probability that breeding is successful,  $b_x$ , is given for each  $x$  as the mean success of birds in the real data set that had been observed for this number of years. To correspond to the simulation procedure below, birds at the start of the study are assumed to be first-time breeders. The probability that a bird leaves the site after breeding for  $x$  years,  $d_x$ , is calculated similarly from the data set for each  $x$ . Then, the simulation proceeds as follows.

For each real bird of the data set, note the number of years it has been observed (the observation span). In order to obtain unbiased estimates, in this simulation we do not omit paired birds that changed sites, as in other parts of the MS. Start the simulation with  $x = 1$  and record a successful breeding event with probability  $b_x = b_1$ ; otherwise, record a failure. Irrespective of success, make the bird leave the site with probability

$d_x = d_1$ . Then, increase  $x$  by one. Repeat the breeding and leaving up to the observation span of the bird. Repeat the procedure for each bird ( $n = 1118$ ).

For the full simulated data set, record the number of site changes that resulted in no change in breeding success ( $n_{0 \rightarrow 0}$  and  $n_{1 \rightarrow 1}$ ) as well as the number of changes that resulted in a change ( $n_{0 \rightarrow 1}$  and  $n_{1 \rightarrow 0}$ ). As test statistics we used the following:

- To check if, by chance, birds tend to increase rather than decrease their breeding success: the proportion of increases  $p_{\text{inc}} = n_{0 \rightarrow 1} / (n_{0 \rightarrow 1} + n_{1 \rightarrow 0})$ .
- To check if, by chance, birds tend to leave after unsuccessful breeding events: the proportion of departures after unsuccessful breeding,  $p_{\text{dep}} = (n_{0 \rightarrow 0} + n_{0 \rightarrow 1}) / (n_{0 \rightarrow 0} + n_{0 \rightarrow 1} + n_{1 \rightarrow 0} + n_{1 \rightarrow 1})$ .

The distribution of the test statistics was obtained by repeating the above procedure 10 000 times. Additionally, we repeated the procedure assuming that success depends on the number of years that a bird has occupied a given site, rather than on its overall experience. This modification did not change the levels of significance obtained.