Short communication

Individual inter-annual nest-site relocation behaviour drives dynamics of a recently established Barnacle Goose *Branta leucopsis* colony in sub-arctic Russia

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Avian breeding colonies are generally in a continuous state of flux, some parts growing whilst others shrink as individuals move within the colony on the search for better nest-sites. We examined the role of experience in breeding patch choice by individually marked Barnacle Geese *Branta leucopsis* in a recently established colony in sub-arctic Russia. Individuals failing to reproduce successfully tended to shift nest location further the following season than did successful pairs, and they did so towards the most dense nest aggregations within the colony, where reproductive success was higher. We suggest that individual decisions on nest-site choice shape the spatial dynamics of this colony.

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Establishment of a bird colony is a complex process, based on breeding site selection by many individuals, some of which have experience of breeding in the site, whereas others arrive unfamiliar with the site, attracted by conspecifics. Individuals are unlikely to possess a perfect knowledge of the quality of all alternative breeding sites when settling (Parker & Sutherland 1986), so habitat assessment may offer the only available criterion on which to make an appropriate decision (review in Boulinier & Danchin 1997). Non-fidelity to the nest-site after breeding failure is a common strategy of breeding patch choice in birds (Switzer 1997). Applying this strategy, failed breeders have to choose from a range of new nest-sites that may be unfamiliar to them. Presence of conspecifics may help these individuals to make the decision and guide faster detection of suitable locations in an unfamiliar environment (Smith & Peacock 1990, Danchin *et al.* 1998). Conspecific attraction promotes clumping of nests in patches of the highest quality (Stamps 1988, Danchin & Wagner 1997). However, in territorial species such as geese the benefits of aggregated nesting may be offset by the costs of competition, which may reduce nesting success (Prop & Quinn 2003). Alternatively, extreme nest-site fidelity may inhibit abandonment of deteriorating breeding areas (Ganter & Cooke 1998). In this paper we present results of breeding patch choice in relation to nesting experience in individual Barnacle Geese *Branta leucopsis* and assess how individual decisions about nest-site choice may affect the dynamics of a colony during the early stages of its formation.

METHODS

Study site

The study colony occupies the peninsula on the northeast coast of Kolokolkova Bay, Malozemelskaya Tundra, Russia (centred at 68°35′N, 52°20′E) and the Chaichi Islands, *c.* 3 km from the mainland. Breeding Barnacle Geese were first observed on the islands in 1994 (Syroechkovsky 1995, van Eerden & Roos 2000). By the early 2000s, Barnacle Geese had started to nest on the mainland saltmarsh (van der Jeugd *et al.* 2003) and the colony progressively occupied the saltmarsh and adjacent elevated dune area. Counts of Barnacle Goose nests were conducted for the period 2002–2009 on the islands, mainland saltmarsh and in the dune area. Information on precise nest location and reproductive success (see

below) was restricted to a focal area (data collected in 2004–2007).

A habitat map of the area (Fig. 1a) was created, based on an ETM+LANDSAT7 image of the area from 29 June 2000, processed in SCANEX IMAGE PROCESSOR v.3.0 software (RDC ScanEx 2009) and using the botanical classification of Lavrinenko and Elsakov (2002), and was subsequently ground-truthed, distinguishing the following habitat types:

Dune area (D), comprising:

DN = Recently formed sandy dunes with sparse vegetation.

B = Complex of shrub and lichen tundra and freshwater bogs on ancient dunes.

Mainland saltmarsh area (M), which included:

LM = Low marsh with sparse vegetation (van der Graaf et al. 2004) and exposed to flooding.

MM = High and middle marsh, supporting the highest green biomass (van der Graaf et al. 2004).

Data collection

We obtained information on reproductive success and geographical coordinates of nests during multiple visits to the focal area. Each of the nests was visited at least twice, and some of them were monitored daily. The focal area included the four habitat types, which allowed us to relate individual reproductive success to habitat type and nest aggregation. Reproductive success was established for 3119 of the 3522 nests found in the area. We scored individual reproductive success as 1 if at least one gosling hatched in the nest (indicated by membranes present or eggshells trampled into down), otherwise 0. Nesting success was defined as the percentage of successful nests. The number of nests in each habitat type each year used in the analysis varied from 119 to 592. No attempts were made to quantify causes of nest failure, which potentially could have been weather conditions (and associated flooding), nest abandonment and predation, mostly by gulls and skuas. Forays by Arctic Fox Alopex lagopus were sporadic, and observed just twice in 2005 and twice in 2007.

For the relationship between reproductive success and nest aggregation, we measured for each nest the average distance to three nearest neighbours (hereafter DNN) using the 'maptools' package in R (Lewin-Koh & Bivand 2010). DNN was considered more effective as a measure of nest aggregation than distance to the nearest neighbour (Clark & Evans 1954), although both parameters were closely correlated (Spearman's $r_s = 0.94$, $P \ll 0.0001$, $n = 3119$). In 2005 most of the nests in habitat LM were flooded and information on nest coordinates was incomplete, which may have led to underestimating nest aggregation in LM.

Observations of colour-ringed individuals were used to relate reproductive success to nest-site choice in the subsequent season, i.e. probability of return to the colony and distance of nest relocation. During 2003–2007
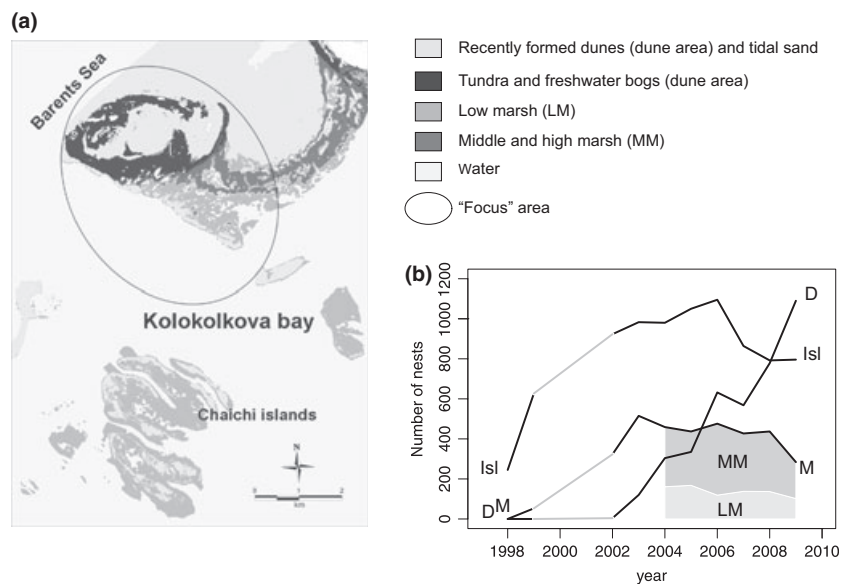
Figure 1. (a) Map of the Kolokolkova Bay study area with main habitat types indicated. (b) Number of nests counted on Chaichi Islands (Isl), on the mainland saltmarsh (M), which includes MM and LM, and in the dune area (D) during 1998–2009. Information for 1998 is from van Eerden and Roos (2000) and for 1999 from Mineev and Mineev (2004). No data are obtained for 2000–2001 (grey line). Distinction of MM and LM within the mainland saltmarsh was made only from 2004 onwards, as indicated by the shading.

we observed 111 nest relocations between two successive years from 15 marked pairs and 61 marked individuals with non-ringed partners. Of these 76 pairs, 10 and 15 pairs were seen nesting 4 and 3 years in a row, respectively. To test whether pairs moved to more densely aggregated parts of the colony in the subsequent breeding season $t + 1$, we calculated ΔDNN ($\text{DNN}_{t+1} - \text{DNN}_t$) (66 and 17 comparisons for successful and failed pairs, respectively). We observed no change of partners in the marked pairs, and we made the likely assumption (Black *et al.* 2007) that no partner changes occurred in the other pairs.

Data analysis

Reproductive success for the period 2004–2007 was entered into generalized linear models using a logit link function, and binomially distributed errors in program R (R Development Core Team 2009). Linear relationships between reproductive success and habitat type, DNN and year (as factor) were explored; a quadratic relationship between success and DNN was also tested. We started with a general model, which included all the variables and their interactions and was simplified by backward elimination of non-significant terms (Zuur *et al.* 2009). Significance of the main effects was tested separately, using the same method but starting with a general model without interaction terms. Planned contrasts were applied to evaluate differences in probability of reproductive success among the four habitat types and among the 4 years.

We analysed observations of colour-ringed individuals by mixed-effects models to cope with pseudoreplication by multiple observations on the same pairs (Zuur *et al.* 2009), incorporating Pair ID as a random variable. The natural log of the distance between nest locations in year$_t$ and year$_{t+1}$ was modelled in response to nest fate in year$_t$, by a generalized additive mixed-effects model

(Wood 2008). We used additive instead of linear models to be able to apply a negative binomial distribution, which we used to cope with the strong overdispersion in the data. ΔDNN was related to the reproductive success in year$_t$ by a linear mixed-effects model (Pinheiro *et al.* 2009).

To compare probabilities of return to the colony in successful and failed nesters (129 pairs) we used GlmmPQL (generalized linear mixed modelling) from the MASS package in R (Venables & Ripley 2002) as resighting cases represented a binary response variable (1 if at least one individual from a pair was seen breeding, otherwise 0). Reproductive success in the first of the 2 years was fitted as a fixed independent variable and Pair ID as a random factor.

RESULTS

Colony dynamics

During 1998–2003, the Barnacle Goose colony at Kolokolkova Bay increased from 245 to more than 2000 nests (Fig. 1b). Numbers of nests changed differently on the islands and across the mainland. Numbers on the Chaichi Islands initially increased, then levelled off and declined slightly after 2006 (Fig. 1b). In the early 2000s we witnessed the colony expanding towards the adjacent mainland. The saltmarsh was colonized first, with numbers peaking in 2003, followed by a decline in numbers in subsequent years. This decline was due to decreasing numbers of breeding pairs in LM. Nest numbers in MM had been stable up until 2009, when mounds of earth-covered ice melted and the MM area became unsuitable for nesting. Initially, numbers in the dune area (DN and B) built up more slowly but they continued to increase until the last year of observation.

In most years, the probability of nesting successfully was lower in LM than in other habitats (Fig. 2; planned
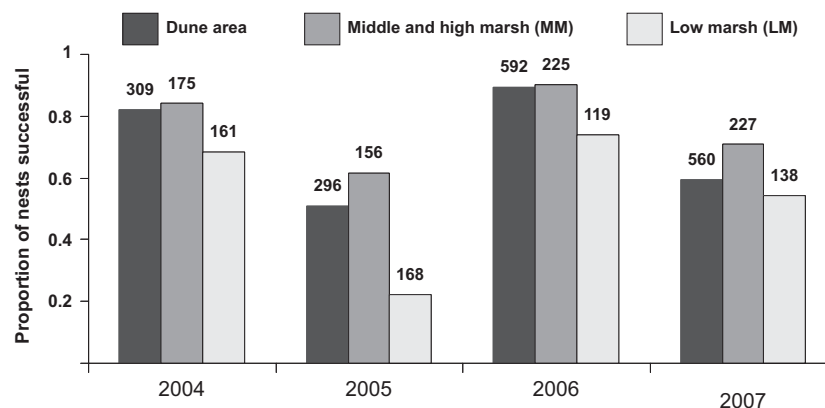
Figure 2. Proportion of nests successful in the dune area, MM and LM. Sample sizes are given above the bars.

contrasts: $P < 0.001$, comparing LM with DN, B and MM; the exception was in 2007 when the difference between LM, DN and B was not significant). Reproductive success in LM was particularly low in 2005 after being flooded by unusually high tides (interaction term between year and habitat: $\chi^2_9 = 24.9$, $P = 0.003$). Controlling for the variation in probability of nesting success due to year ($\chi^2_3 = 364.9$, $P < 0.001$), habitat type ($\chi^2_3 = 87.4$, $P < 0.001$), and the interaction between year and habitat, we found a negative effect of DNN (i.e. a positive effect of nest aggregation) on the probability of reproductive success ($\chi^2_1 = 8.8$, $P = 0.003$).

Nest relocation and previous nesting success

Comparing nest locations of the same individual in two subsequent seasons showed that in year$_{t+1}$ Geese settled at distances between 0 and 4964 m from the location in year$_t$. Birds that lost their clutch moved greater distances than birds that were successful ($P < 0.001$; Fig. 3a) and towards more densely aggregated parts of the colony compared with the first location, as indicated by the ΔDNN being lower than zero ($P < 0.001$; Fig. 3b). In successful pairs, ΔDNN did not differ from zero ($P = 0.82$), i.e. nest aggregation did not change significantly between year$_t$ and year$_{t+1}$. The probability of return to the colony in the next year did not differ between successful and failed pairs ($P = 0.4$); thus, nesting failure was not likely to provoke dispersal from the colony.

DISCUSSION

At Kolokolkova Bay the probability of successful nesting in Barnacle Geese was positively related to nest aggrega-
tion. Accordingly, pairs losing their clutch moved towards parts of the colony of denser nest aggregation in the subsequent season, which was not the case for pairs that were successful. The movements, however, mostly occurred within the colony, and Geese were not more likely to leave the colony after breeding failure than were successful birds. Interestingly, no negative effect of a dense nest aggregation on reproductive success was found, which indicates that Barnacle Geese avoided nesting in extreme aggregations that might impair successful reproduction.

Movements from poor nesting areas towards better nest-sites must have caused a redistribution within the colony. Indeed, nest numbers in the mainland LM declined, in contrast to the stable nest numbers in MM and an increase in the dune area, where reproductive success was higher. The colony initiators originally settled on the islands, which were characterized by LM vegetation, the least favoured mainland habitat. Originally the islands may have been preferred by nesting Barnacle Geese because of their previous experience at other remote breeding sites that associated islands with safety from terrestrial predators (Ganter *et al.* 1999). At the time of colony initiation, in fact, there were almost no terrestrial predators (including humans) on the mainland (van der Jeugd *et al.* 2003, Mineev & Mineev 2004).

Our observations indicate that colony fidelity in Barnacle Geese is strong but that, within the colony, failed breeders can switch from poor patches towards more suitable patches. These individual decisions have maintained the colony in a geographical flux since its establishment, and helped to correct for variation in local nesting conditions, as well as for possible 'mistakes' caused by unfamiliarity with the area – nesting in suboptimal patches while optimal sites remain unoccupied. Thus, an ability to improve nest location over time –
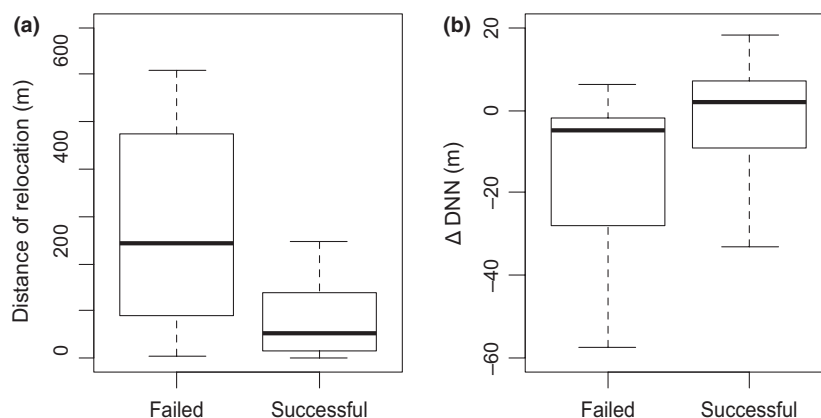
Figure 3. Comparison of (a) distances of relocation and (b) difference in DNN between nests of the same individual in year$_t$ and year$_{t+1}$, related to nesting success in year$_t$. Medians, and upper and lower quartiles are presented.

possibly by taking advantage of colonial nesting (Danchin *et al.* 2004) – may enhance the opportunities to settle in unfamiliar environments.

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