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A choice between two adjacent islands: is switching nest sites related to weather or nest density in the Common Eider (*Somateria mollissima*)?

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Birds change nest sites between years in response to breeding success in previous years, activities of other breeders, or weather conditions. Sixteen years of banding data and nest counts of the Common Eider in Rif, western Iceland, were used to evaluate probability of switching nest islands. The two man-made islands studied had different substrates (grass vs. rock) and in some years, different nest-initiation dates. Nest numbers were not related to weather. The apparent survival was not related to annual variation, weather or nest density. Conversely, the probability of switching islands (movement probability) was plausibly affected by three covariates: (1) winters with higher precipitation decreased the probability of switching from the grassy to the rocky island; (2) as winters became milder from 1993 to 2008, the probability of switching islands decreased; and (3) as the nest numbers increased from 155 to 606 during 1993–2008, the probability of switching islands decreased. Winter weather may have affected nest switching primarily via precipitation, which partly determined water levels in the colony. An inverse relationship between nest density and the probability of switching islands is consistent with conspecific facilitation in colonially-nesting bird species.

1. Introduction

Habitat suitability is determined by many biological parameters, such as the number of predators and conspecifics, and physical parameters such as microclimate and its association with weather (Sutherland 1996, Montes-Medina *et al.* 2009). Individuals may estimate habitat suitability by actions or success, and even mere presence or absence, of conspecifics. For example, the breeding success of neighbors may yield information that helps to decide whether to return to a previous breeding site or to search for a new one (Danchin *et al.* 1998, Brown *et al.* 2000, Valone 2007). Conversely, colonially-nesting species may experience negative effects of crowding or even compete for nest bowls, particularly in denser colonies, and this can negatively affect nest success (McCracken *et al.* 1997, Stokes & Dee Boersma 2000). Estimation of negative and positive factors can improve survival chances of breeders and their young when choosing the optimal nest site, which in turn should maximize relative fitness via a combination of survival of nest and parent (Brown et al. 2008, Öst & Steele 2010).

Many species show natal philopatry, including the Common Eider (*Somateria mollissima*) for which up to 98% of females return to their natal colony (Swennen 1990). While philopatry to the colony may be high, fidelity to patches within a colony or the actual nest bowl is more variable (Reed 1975). When selecting nest sites Common Eiders are also influenced by age and body condition, nest concealment and shelter against wind, and aspects of microclimate (Robertson 1995, Bolduc *et al.* 2005, Öst *et al.* 2008, D'Alba *et al.* 2009, 2010, Öst & Steele 2010). Females are more likely to switch nest sites between years following breeding failure (Milne 1974, Bustnes & Erikstad 1993, Switzer 1993, Robertson 1995, Öst *et al.* 2011). Common Eider may switch nest sites within a colony even if their previous sites are unoccupied (Milne 1974). If new sites become available they will probably be colonized by immigrants from other colonies, first-time recruits, or failed breeders from previous years (Krebs 1971, Switzer 1993).

Climatic variation can influence various aspects of breeding, such as nest-site selection, nest desertion, levels of yolk hormone, and immune function (Robertson 1995, Descamps *et al.* 2010, Love *et al.* 2010, Sénéchal *et al.* 2011). Females in good body condition are the first to nest and will occupy the most optimal nest sites (Bolduc *et al.* 2005, Öst *et al.* 2008). However, in late nesting years, other females may take the preferred nest sites. Arrival dates in the Common Eider were positively correlated with timing of ice melt in southwestern Finland (Lehikoinen *et al.* 2006). In Iceland, females arrived later following warm winters with strong westerly winds (positive NAO values; Jónsson *et al.* 2009). Similarly, mild spring temperatures were related to earlier laying dates in East Bay, Canada (Love *et al.* 2010). Unfavorable winter weather can negatively affect accumulation of endogenous reserves for breeding (Hario & Öst 2002, Hario & Hollmén 2004, Lehikoinen *et al.* 2006, Descamps *et al.* 2010). Furthermore, clutch sizes increase following warm and wet spring seasons (Jónsson *et al.* 2009).

Earlier nesting should lead to improved hatching success, which in turn should decrease breeding dispersal, assuming the "win-stay, lose-switch" strategy in nest-site selection (Switzer 1993, Öst *et al.* 2011). We hypothesized that milder winters are beneficial for nest-site selection because they result in better body condition (cf. Descamps *et al.* 2010) and earlier nest initiation, both of which contribute to better nest success. Conversely, harsh winters reduce individual body condition and delay nest initiation, which may in turn lead to higher turnover of nest sites and higher probability of loss of the preferred nest site to other females.

In nest sites with no overhead vegetation and limited shelter against wind, shifting between adjacent nest sites or orienting towards prevailing winds can reduce thermoregulatory costs (Öst *et al.* 2008). Well-sheltered nest sites can help to preserve endogenous reserves by decreasing heat loss (Jónsson *et al.* 2006, Fast *et al.* 2007, D'Alba *et al.* 2009, Kristjánsson & Jónsson 2011). We studied nest-site switching between two islands at Rif, West Iceland. These islands differ in area and aspects of microclimate (see Material and methods). We considered two alternative predictions for effects of nest numbers on the probability of switching islands. (1) Nest numbers will negatively affect the probability of switching islands if increased nest densities are beneficial to females, through conspecific attraction or public information (Valone 2007, Öst *et al.* 2011). (2) Nest numbers may positively affect the probability of switching if increased nest numbers affect the females in a negative way, possibly because of crowding or interference competition over nest bowls (McCracken *et al.* 1997).

We considered two predictions for effects of weather on the probability of switching islands. (1) Increasing winter mildness will be negatively related to the probability of switching islands because in milder years, earlier nest initiation should increase the likelihood that the preferred nest site is available. Consequently, no switching of nest sites would be required. (2) the probability of switching islands may be positively related to precipitation in the previous seasons, because high precipitation increases water levels, which in turn increases the probability that a favored nest site becomes unavailable, being either submerged or occupied by another female. The first prediction assumes that (a) females compete indirectly for the best nest sites via their arrival date to the colony; (b) the first females to nest are the fattest, fittest females, and thus competitive ability for nest sites is positively correlated with the optimal body condi-

Fig. 1. The Common Eider colony at Rif, western Iceland. View from the north-eastern side of the 2.34 ha pool on 12 May 2009. Note the larger waves, caused by the deeper water surrounding the rocky island on the left, compared to those surrounding the grassy island on the right. Spring-season water levels were high when this picture was taken and the ditch for the grassy island was flooded (far right; see text). Photo by SJL.

tion; and (c) harsh winter conditions are unfavorable for depositing fat reserves and they affect most females. Our assumption that body condition in the Common Eider varies between years within individuals (and can thus respond to variation in winter weather) is supported by findings of Öst *et al.* (2007), who reported that such variation represented 59.1% of the total variation, compared to 40.9% for variation between individuals.

2. Material and methods

2.1. Study area

We carried out this study at Rif, which lies at the western tip of the Snæfellsnes peninsula, western Iceland. A few low-lying, natural pools are scattered over this lowland area, which supports many bird species, most notably a large colony of Arctic Terns (*Sterna paradisaea*). The water level in these pools depends largely on winter precipitation. The studied Common Eider colony is comprised of two islands at one pool(2.34 ha in size, 0.5 km from the Atlantic shoreline; 64°55’14” N; 23°49’23” W). The colony was established by the author SJL and Sævar Friðþjófsson in 1972 (Snæbjörnsson 2001). Nesting of Common Eider at the study pool was hindered by the lack of suitable nest sites until that year, although the pool was previously used by Common Eiders in spring but without nesting attempts (Snæbjörnsson 2001). Common Eider is the only species nesting on the islands, except for 1–5 pairs of Black-headed Gull (*Larus ridibundus*).

Despite the islands being originally man-made, the studied population is wild and free-ranging. The first island (hereafter the rocky island) was 15 m^2 1972–1975 but was increased to 120 m^2 in 1987 by addition of more rocks (Snæbjörnsson 2001). Another artificial island (hereafter grassy island) of 600 m^2 was created in 1990, 40 m from the rocky island, when a grassy peninsula was turned into an island by a 9–10 m wide ditch, dug between the grass island and the mainland (Snæbjörnsson 2001).

Neither island has any scrub or tree cover but both have driftwood logs and car tires as nesting shelters (see Jónsson 2001). Despite their proximity to one another, the two islands differ in many respects. Firstly, the rocky island is lower and smaller than the grassy island (Appendix 1). Secondly, the water depth around the rocky island (measured at 1, 2, 3 & 5 meters from the shore) is generally 0.8–1.0 m, whereas the grassy island is surrounded by water depths ranging from 0.1–0.4 m at 1 m, 0.3–0.6 m at 2–4 m, and 0.5–0.8 m at 5 m from the shore. Thus, a shallow, sloped area surrounds the grassy island, whereas the rocky island is a vertical structure, standing 1.0–1.2 m above the 0.8–1.0 m deep water. This results in larger waves forming and breaking on the rocky than on the grassy island (Fig. 1). Nests in the rocky island (surrounded by deeper water) are more often exposed to water spray, which leads to egg cooling in some years (SJL, unpubl. data), whereas such egg cooling rarely occurs in the grassy island (surrounded by shallower water). Water levels in the pool are particularly high following wet winters.

2.2. Population size, nest counts and nesting chronology

SJL counted all nests annually from 1972, and began banding Common Eider females in 1993. Females were caught with a noose pole, and were subsequently banded as adult breeders on nests. A total of 627 females were banded during 1993–2008. No ducklings or immature (1–2 years old) females were caught. During the study, only fourteen females were recovered dead.

Preference for an island may vary between years in relation to possible island-specific breeding success, occurrence of egg cooling, disturbance, predator presence or absence, or overall arrival date of common eider to the colony. First nest date and nesting chronology were earlier on the rocky than on the grassy island in eight years, i.e., 1993–1996, 2002, 2004–2005 and 2007. The opposite was true in 1998 and 2001, and the dates were similar for the two islands in 1997, 1999–2000, 2006 and 2008 (authors' unpubl. data).

2.3. Weather data

We explored effects of local weather (Stykkishólmur, west Iceland). We used principal component analysis (PCA), to create weather indices from monthly average precipitation (mm), ambient temperature (°C), average wind speed (m/s) and atmospheric pressure (PPM). We ran separate PCAs for each of the three seasons (previous fall October–November, previous winter December–March and previous spring April–May) (see Jónsson *et al.* 2009). We ran two separate PCA to explore the weather during (1) the entire life-span of the colony (1972–2008) for a subsequent analysis of nest numbers; and (2) the duration of the banding effort (1993–2008) for a subsequent analysis of banding data.

For winter weather, the first principal component (winter-PC1) yielded loadings of 0.64 for temperature, 0.54 for atmospheric pressure, and –0.51 for wind speed. Winter-PC1 accounted for 47% of the summed variance of the four input variables. The second principal component (winter-PC2) has a single loading of 0.93 for precipitation. Winter-PC2 accounted for 26% of the summed variance of the four input variables. We used winter-PC1 and winter-PC2 as winter weather indices: positive winter-PC1 values corresponded to milder winters, whereas positive winter-PC2 corresponded to wet winters.

For spring weather, the first principal component (spring-PC1) yielded loadings of 0.49 for temperature and 0.62 for precipitation. Spring-PC1 accounted for 47% of the summed variance of the four input variables. The second principal component (spring-PC2) yielded a loading of 0.68 for atmospheric pressure. Spring-PC2 accounted for 26% of the summed variance of the four input variables. We used spring-PC1 and spring-PC2 as spring weather indices: positive spring-PC1 values corresponded to warm, wet springs, whereas positive spring-PC2 corresponded to springs with high pressures and low wind speeds.

For fall weather, the first principal component (autumn-PC1) had loadings of 0.69 for temperature and 0.72 for precipitation. Fall-PC1 accounted for 32% of the summed variance of the four input variables. We used fall-PC1 as the fall weather index: positive values indicated wet, mild fall seasons. The second principal score for fall proved redundant with the inclusion of other PC scores and thus, was not used for analyses.

2.4. Time-series analysis of population size and density

We used arithmetic moving average models in SAS (PROC ARIMA; Yaffee 2000). We first tested series for non-stationarity (a single mean and constant variation over time) using the Dickey-Fuller test, and subsequently rendered series stationary using differentiation where needed (Yaffee 2000). We then analyzed cross-correlations with indices of local weather (Jónsson *et al.* 2009) 1972–2008 where we included PC scores that explained 25% of the variation for linear combinations of temperature, precipitation, atmospheric pressure and wind speed as explanatory variables.

For a subsequent analysis of switching between islands and female survival (1993–2008), we used nest densities as a linear constraint. The area available for nesting (m^2) was constant at 600 m^2 during the 16 years of banding (i.e., since 1990) and thus, no adjustment was applied to this variable. We then used nest densities, specific for each island, in the analysis of banding data as an index of available nest space within each island (hereafter nesting density).

2.5. Probability of switching islands and female survival

We studied the effects of crowding at the nesting colony using 16 years of mark-recapture data, along with island-specific nesting densities from the same period, to estimate whether local population dynamics (number of nests) or weather indices from the PCA were related to the apparent survival and the probability of switching between adjacent islands (movement probability, Ψ). We used multi-strata models in the MARK software package (White & Burnham 1999) to estimate the apparent survival (S) and the probability of a female switching between the islands (Ψ). Prior to analyzing data, we used U-CARE (Pradel *et al.* 2003) to estimate the goodness-of-fit and to obtain an estimate of the variance-inflation factor, $\hat{c}$. The estimated $\hat{c}$ was 0.93. We followed Cooch and White (2010) and set $\hat{c}$ for these under-dispersed data at $\hat{c} = 1.0$.

In the multi-strata modeling, we constrained the apparent survival (S) and movement probability (Ψ) to be a function of two types of parameters: (1) nesting densities, specific for each island; and (2) local weather in the preceding spring, winter, and fall, as indexed by the PCA but excluded redundant components (a total of five components). We constructed a list of candidate models following Hario *et al.*(2009): (1) constant apparent survival (S) over 16 years (over time), (2) time-dependent (between years) S, (3) constant Ψ over 16 years, (4) time-dependent Ψ over 16 years, (5) linear relationship of nesting densities on S, (6) linear relationship of nesting densities on Ψ, (7) linear relationships of local weather indices on S, and (8) linear relationship of local weather indices on Ψ.

We began model selection by creating all possible models with S and Ψ being either time-dependent or constant in time, and as either differing or being the same between the two islands. We kept the capture probability *p* as both time-dependent and different between islands for each of these candidate models, with the exception that the null model S(.) p(.) Ψ (.) was included. We used the ANODEV test (Grosbois *et al.* 2008, Lebreton *et al.* 2012) in MARK to assess the fit of the covariate models relative to that of the appropriate reference models, constant models (i.e. S(.) p(i*t) Ψ(.), S(i) p(i*t) psi(.), S(.) p(i*t) psi(i)) and time dependent models (i.e. S(.) p(i*t) Ψ(i*t), S(i) p(i*t) Ψ (i*t) and S(i*t) p(i*t) psi(i)). Constant and time-dependent models were identical to covariate models for all parameters other than those involved in the linear constraint.

We used Akaike's information criterion (AIC) to rank the models, and used model averaging unless a single model was clearly supported to fit the data (Burnham & Anderson 2002). Furthermore, we estimated the relative importance of individual explanatory variables by summing Akaike weights from each model that contained a given explanatory variable for each parameter. We then compared the importance of pairs of predictor variables by calculating the ratios between sums of Akaike weights for each predictor variable.

3. Results

3.1. Population size, density and nesting chronology

In the time-series analysis, the statistical assumption of stationarity in the data was met at lags 0–2 by differentiating once. There were no relationships (at false discovery rates of 5%) between PC scores for weather in a given year and nest num-

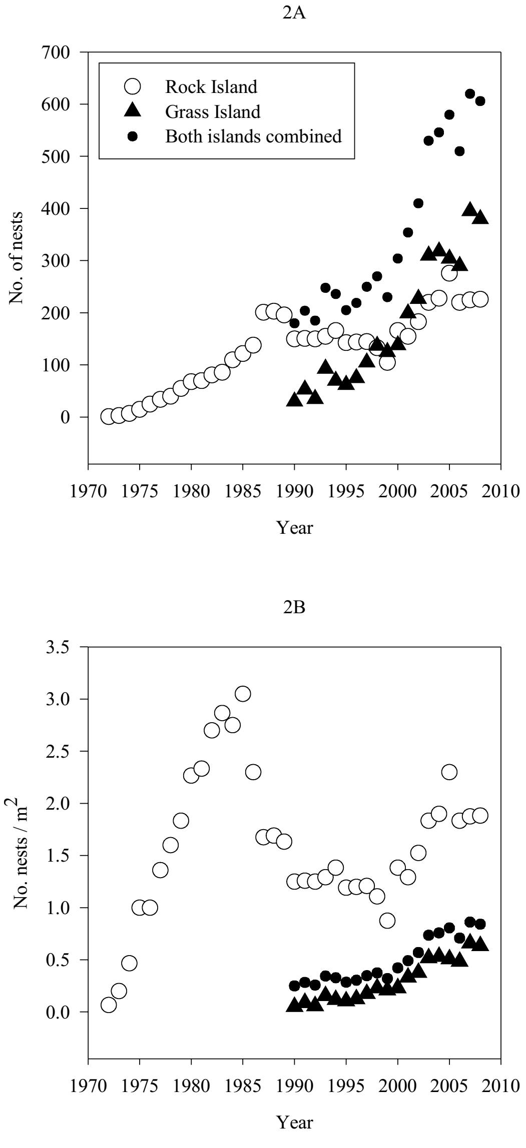

Fig. 2. Nest numbers (A) and nesting densities (nests/m^2: B) of the Common Eider at Rif, western Iceland during 1972–2008.

bers in the same year (lag = 0), next year (lag = 1) or two years later (lag = 2), either for nest numbers or nest density (nests/m^2). Nest numbers increased from one in 1972 to 201 nests in 1987 and further after the addition of the grassy island, from 180 to 606 nests 1990–2008 (Fig. 2A). Nest numbers on the grassy island exceeded that of the rocky island in 1998 and remained higher during 2001–2008. Nest density (nests/m^2) was above 1.5 in 1978–1989 but stayed below 1.0 during 1990–2008 (Fig. 2B). The grassy island added 600 m^2 to the colony, causing overall nest density to decline below 1.0 nests/m^2. The overall nest density increased between 2000–2008 and approached 1.0 nests/m^2 (Fig. 2B). Nest density within the rocky island remained above 1.5 nests/m^2 during 2003–2008.

3.2. Model selection

AIC values indicated that no single model was supported as six models had ΔAIC within 2.0 (Table 1). These top six models had (1) a time-dependent x island effect interaction on p; and (2) constrained time effects on Ψ within each island, with the probability of switching islands (Ψ) constrained by both winter weather indices and the nesting densities (Table 1). The six-top ranked covariate models had ΔAIC values 7.0–8.3 higher than the highest ranked constant model, and had ΔAIC values 83.1–84.4 higher than the null model (Table 1). We applied model averaging to estimate parameters because no single model was preferred by AIC (Table 2).

The ANODEV tests indicated that the null hypotheses, predicting that covariates had no effect on movement probability, could be rejected at the false discovery rate of 5% for the eight highest-ranked models but not for any models ranked lower (#10 and lower) than the highest ranked constant model S(.) p(i*t) Ψ(.) (# 9 in Table 1). Thus, covariates on Ψ only improved models beyond constant models that had S(.) or S(i); these models also were the highest-ranked models by AIC. Conversely, the addition of covariates on S did not improve models beyond constant S(.) models. (Table 1.)

3.3. Model-averaged parameter estimates

Model averaged estimates of Ψ declined between 1993–2008 for both islands and differed between islands in some years (Table 2). According to the six highest-ranked models (Table 1), estimates of Ψ could be plausibly constrained in time by three different parameters. Model averaging indicated a higher Ψ for 1993–2000 than for 2001–2008 (Table 2) and the two of the linear constraints, win-

Table 1. Summary of model selection for estimation of apparent survival (S), capture probability (p) and probability of switching between the rocky and grassy islands (Ψ) for the Common Eider at Rif, western Iceland during 1993–2008. All models that performed better than the survival time dependent model (#47 with ΔAIC) are shown, and the fully time-dependent model (#57) and null model (#63) are also shown. For other than covariate models, ANODEV test is not applicable (na); r^2 = total covariate deviance / corrected total deviance; i = island, all parameters set to differ between rocky and grassy islands; t = time, effect of years 1993–2008; MLH = Model likelihood; NPAR = Number of structural parameters within the model; Dev. = likelihood-ratio statistic for comparing the model to the saturated model.

		AIC model selection					ANODEV		
Rank	Model	ΔAICc	Weights	MLH	NPAR	Dev.	F	p	r^2
1	S(.) p(i*t) Ψ(winter-PC2)	0.0	0.188	1.000	34	1694.2	4.37	0.023	0.245
2	S(.) p(i*t) Ψ(nest density)	0.1	0.179	0.954	34	1694.3	4.33	0.024	0.243
3	S(.) p(i*t) Ψ(winter-PC1)	0.6	0.138	0.736	34	1694.8	4.09	0.028	0.233
4	S(i) p(i*t) Ψ(winter-PC2)	0.7	0.131	0.698	35	1692.8	4.53	0.020	0.251
5	S(i) p(i*t) Ψ(nest density)	0.9	0.121	0.646	35	1692.9	4.45	0.021	0.248
6	S(i) p(i*t) Ψ(winter-PC1)	1.3	0.097	0.516	35	1693.4	4.23	0.025	0.239
7	S(.) p(i*t) Ψ(spring-PC1)	2.3	0.060	0.319	34	1696.5	3.38	0.049	0.200
8	S(i) p(i*t) Ψ(spring-PC1)	2.9	0.045	0.240	35	1694.9	3.52	0.044	0.207
9	Constant model S(.) p(i*t) Ψ(.)	8.3	0.003	0.016	32	1706.8	na	na	na
10	S(winter-PC2) p(i*t) Ψ (.)	8.3	0.003	0.016	34	1702.5	2.03	0.150	0.131
11	S(.) p(i*t) Ψ(i)	8.3	0.003	0.016	33	1704.7	na	na	na
12	S(.) p(i*t) Ψ(spring-PC2)	8.4	0.003	0.015	34	1702.6	1.20	0.317	0.082
13	S(i) p(i*t) Ψ(.)	8.5	0.003	0.014	33	1704.9	na	na	na
14	S(fall-PC1) p(i*t) Ψ(.)	8.7	0.002	0.013	34	1702.9	1.79	0.186	0.117
15	S(nest density) p(i*t) Ψ(.)	9.0	0.002	0.011	34	1703.2	1.67	0.207	0.110
16	S(i) p(i*t) Ψ(spring-PC2)	9.1	0.002	0.011	35	1701.1	1.14	0.334	0.078
17	Constant model S(i) p(i*t) Ψ(i)	9.1	0.002	0.011	34	1703.3	na	na	na
18	S(fall-PC1) p(i*t) Ψ(i)	9.2	0.002	0.010	35	1701.3	1.58	0.224	0.105
19	S(winter-PC1) p(i*t) Ψ(.)	9.3	0.002	0.010	34	1703.5	1.49	0.243	0.100
20	S(winter-PC2) p(i*t) Ψ(i)	9.4	0.002	0.009	35	1701.5	1.46	0.250	0.098
21	S(spring-PC1) p(i*t) Ψ(.)	9.5	0.002	0.009	34	1703.7	1.42	0.260	0.095
22	S(spring-PC2) p(i*t) Ψ(.)	9.9	0.001	0.007	34	1704.1	1.19	0.319	0.081
23	S(.) p(i*t) Ψ(fall-PC1)	10.0	0.001	0.007	34	1704.2	0.72	0.497	0.050
24	S(nest density) p(i*t) Ψ(i)	10.0	0.001	0.007	35	1702.1	1.18	0.322	0.080
25	S(winter-PC1) p(i*t) Ψ(i)	10.2	0.001	0.006	35	1702.3	1.08	0.354	0.074
26	S(spring-PC2) p(i*t) Ψ(i)	10.5	0.001	0.005	35	1702.5	0.96	0.395	0.067
27	S(spring-PC1) p(i*t) Ψ(i)	10.5	0.001	0.005	35	1702.5	0.95	0.400	0.066
28	S(i) p(i*t) Ψ(fall-PC1)	10.8	0.001	0.005	35	1702.8	0.81	0.456	0.057
29	S(fall-PC1) p(i*t) Ψ(t)	12.5	0.000	0.002	49	1673.9	2.30	0.101	0.217
30	S(.) p(i*t) Ψ(t)	12.8	0.000	0.002	46	1680.8	na	na	na
31	S(t) p(i*t) Ψ(nest density)	13.4	0.000	0.001	49	1674.8	3.00	0.050	0.265
32	S(t) p(i*t) Ψ(winter-PC2)	13.7	0.000	0.001	49	1675.1	2.89	0.055	0.258
33	S(t) p(i*t) Ψ(winter-PC1)	13.8	0.000	0.001	49	1675.2	2.86	0.057	0.255
34	S(nest density) p(i*t) Ψ(t)	13.9	0.000	0.001	49	1675.3	1.76	0.180	0.175
35	S(winter-PC2) p(i*t) Ψ(t)	13.9	0.000	0.001	49	1675.3	1.74	0.185	0.173
36	S(winter-PC1) p(i*t) Ψ(t)	14.0	0.000	0.001	49	1675.4	1.72	0.186	0.171
37	S(spring-PC2) p(i*t) Ψ(t)	14.0	0.000	0.001	49	1675.4	1.72	0.190	0.171
38	S(spring-PC1) p(i*t) Ψ(t)	14.1	0.000	0.001	49	1675.5	1.66	0.200	0.166
39	S(t) p(i*t) Ψ(spring-PC1)	16.2	0.000	0.000	49	1677.6	2.19	0.114	0.208
40	S(t) p(i*t) Ψ(.)	20.1	0.000	0.000	46	1681.6	na	na	na
41	S(.) p(i*t) Ψ(i*t)	20.9	0.000	0.000	61	1655.3	na	na	na
42	S(t) p(i*t) Ψ(spring-PC2)	22.1	0.000	0.000	49	1683.5	0.84	0.485	0.092
43	S(t) p(i*t) Ψ(fall-PC1)	23.7	0.000	0.000	49	1685.1	0.54	0.661	0.061
44	S(i) p(i*t) Ψ(i*t)	24.6	0.000	0.000	62	1656.7	na	na	na
45	S(t) p(i*t) Ψ(t)	25.2	0.000	0.000	60	1661.9	na	na	na
46	S(nest density) p(i*t) Ψ(i*t)	27.7	0.000	0.000	64	1655.2	0.04	0.990	0.005
47	S(t) p(i*t) Ψ(i*t)	33.3	0.000	0.000	74	1637.6	na	na	na
57	S(i*t) p(i*t) Ψ(i*t)	55.9	0.000	0.000	88	1626.8	na	na	na
63	S(.) p(.)Ψ(.)	84.4	0.000	0.000	3	1843.1	na	na	na

Table 2. Model-averaged estimates from model selection for parameter estimation: S = apparent survival; p= capture probability; Ψ = probability of switching between the rocky and grassy islands for the Common Eider at Rif, western Iceland during 1993–2008. The top-ranked models indicated that all parameters could differ between islands, but that S was constant (no year effect) whereas p and Ψ were time-dependent. WAE = weighted average estimate; SE = standard error for WAE; USE = unconditional SE for WAE.

		Rocky island			Grassy island		
Parameter	Year	WAE	SE	USE	WAE	SE	USE
Apparent survival (S)	Constant	0.885	0.02	0.02	0.864	0.02	0.02
Capture probability (p)	1994	0.637	0.15	0.16	0.000	0.00	0.00
	1995	0.120	0.06	0.06	0.073	0.04	0.04
	1996	0.205	0.08	0.08	0.192	0.07	0.07
	1997	0.315	0.11	0.11	0.141	0.05	0.05
	1998	0.246	0.09	0.10	0.150	0.06	0.06
	1999	0.364	0.12	0.13	0.042	0.03	0.03
	2000	0.287	0.09	0.09	0.215	0.06	0.06
	2001	0.636	0.14	0.16	0.126	0.04	0.04
	2002	0.395	0.10	0.10	0.323	0.06	0.07
	2003	0.434	0.09	0.09	0.174	0.04	0.04
	2004	0.224	0.07	0.07	0.191	0.05	0.05
	2005	0.552	0.10	0.10	0.158	0.04	0.04
	2006	0.290	0.07	0.07	0.105	0.03	0.03
	2007	0.262	0.07	0.07	0.214	0.05	0.05
	2008	0.291	0.08	0.27	0.307	0.07	0.25
Switching probability	1994	0.421	0.09	0.12	0.318	0.07	0.10
	1995	0.455	0.14	0.20	0.297	0.09	0.18
Ψ	1996	0.403	0.10	0.13	0.321	0.07	0.11
	1997	0.449	0.11	0.14	0.318	0.07	0.09
	1998	0.460	0.12	0.15	0.331	0.07	0.08
	1999	0.483	0.14	0.18	0.343	0.08	0.09
	2000	0.426	0.10	0.12	0.300	0.07	0.09
	2001	0.393	0.09	0.11	0.289	0.06	0.09
	2002	0.387	0.08	0.09	0.239	0.04	0.04
	2003	0.298	0.07	0.08	0.154	0.04	0.06
	2004	0.299	0.07	0.07	0.160	0.04	0.05
	2005	0.306	0.07	0.09	0.222	0.04	0.06
	2006	0.309	0.07	0.08	0.172	0.04	0.05
	2007	0.330	0.06	0.07	0.179	0.04	0.06
	2008	0.383	0.08	0.10	0.277	0.06	0.12

ter-PC1 and nesting densities, showed the same trend with time.

Simultaneously, (1) winter-PC1 had mostly negative values for 1993–2000 and mostly positive ones for 2001–2008; and (2) nesting densities (either for both islands separately or combined) had higher values for 2001–2008 than for 1993–2000 (Fig. 2A). Winter-PC1 indicated winter mildness (a combination of temperature, atmospheric pressure, both inversely correlated with wind speed), with positive scores for milder winters and negative scores for harsher winters).

Winter-PC2 indicated the amount of precipitation during winter. The model with winter-PC2 constraining Ψ indicated lower probabilities of switching islands following the wettest winters (positive scores), i.e., 1995, 2003, 2004 and 2006 but no temporal trend in Ψ (Table 2). Other years with lower Ψ in the grassy island were 2002 and 2007 (Table 2).

Model averaging resulted in two values of S, one for each island (Table 2). The estimates ±SE were 0.885±0.02 and 0.864±0.02 for the rocky and grassy islands, respectively. However, this difference between islands in S was at best marginally significant, as indicated by the overlapping standard errors. Thus, in agreement with the estimate provided by the three top-ranked S(.) models, we parsimoniously report one S for the entire period and for both islands, S = 0.875.

3.4. Sums of model weights

Sums of Akaike weights (Table 1) for apparent survival were 0.577 for constant survival (S.), 0.403 for survival differing between islands (Si), and the combined sum of 0.02 for 12 models where survival was constrained by any of the covariates. Thus, time-dependent models or covariate models were essentially not plausible, and the low ratio between sums for constant apparent survival and an island effect (0.577/0.403 = 1.43) suggests no difference in survival between the two islands.

An island × time effect was the only possibility for *p* (sum of model weight = 1.000). Sums of model weight for probability of switching islands (Ψ) were 0.301, 0.236 and 0.320 for the covariates nest count, winter-PC1 (winter mildness) and winter-PC2 (winter precipitation), respectively. Other models for Ψ, including Ψ(i) and Ψ(.) models, had Akaike weights of 0.06 or lower (22 models, combined sum of 0.143) and thus were not supported. Overall, the top six covariate models were equally plausible, given the data and the set of candidate models: (1) winter precipitation was no more plausible (ratio between sums 0.320/0.236 = 1.36) than winter mildness as an explanatory variable for Ψ. (2) nest densities were no more plausible (ratio between sums 0.301/0.236 = 1.28) than winter mildness as an explanatory variable for Ψ; and (3) the ratios of sums did not favor precipitation and nest count over each other, 0.320/0.301 = 1.06.

4. Discussion

The number of breeding Common Eiders at Rif continuously increased between 1972 and 1990, and at accelerated rates by the addition of the grassy island between 1991 and 2007. The probability of switching islands was high, i.e., females were likely to attempt breeding at both islands. Common Eider females became less likely to switch islands as the study progressed and the colony simultaneously became more densely occupied. The prediction consistent with the conspecific-attraction hypothesis (Valone 2007) was met in that an increase in nesting densities was linked with a decrease in probability of switching islands. Furthermore, probabilities of switching from the grassy to the rocky island (but not the opposite direction), were markedly lowered following the wettest winters.

Unlike estimates for probability of switching islands, the estimate of apparent survival, S = 0.875 was not related to annual variation, weather or nesting densities. This finding is in agreement with that of Hario *et al.* (2009), who reported no significant relationship between population growth rate and survival in Finland. However, annual variation in adult survival rates was reported for Coquet Island, Scotland (Coulson 2010). This estimated S was similar to that reported for sedentary and protected populations from Scotland (0.895), but are slightly lower than those from the Netherlands (0.957), but both are among the highest reported (Coulson 1984, Swennen 2002; see also Hario *et al.* 2009).

Nest success can be a strong driver of breeding dispersal (Catlin *et al.* 2005, Öst *et al.* 2011). We did not monitor nest success, but the observed increase in nest numbers was possibly caused by within-colony recruitment following high nest success. We believe that Rif is a predictable site for Common Eider females, which in turn may allow females to employ a win-stay, lose-switch strategy (Switzer 1993). After all, females may use the same nest area for years once they have found it to be safe (Öst *et al.* 2011). Common Eiders, like other animals, may be more likely to disperse from a colony following a nest failure, but as our results suggest, switching of nesting areas within a colony may also occur (Switzer 1993, Öst *et al.* 2011).

Our modeling approach indicated that Common Eiders became less likely to switch nest sites as winters became milder after 2000. Compared to 2001–2008, winters 2002 and 2008 were not particularly mild and after both, there was a high probability of island switching, similar to that observed in 1993–2000. In our time-series analysis, weather was not related to nest numbers or the apparent survival within any season. For 1993–2008, recent results on 16 other colonies in Iceland showed trends that differed markedly from those reported here for Rif, suggesting increases from 1980 to the early 1990s, but a decline since 1990–1995 (J.E. Jónsson, J.A. Gill, A. Gardarsson, U.K. Pétursdóttir, A. Petersen & T. G. Gunnarsson, in prep.). Thus, the positive warming trend (Winter-PC1) did not induce an increase in nest numbers at Rif, although it probably did not have negative effects either.

Nevertheless, increasing winter mildness is related to nest numbers, first-nest date and clutch size in some other Icelandic colonies (Jónsson *et al.* 2009). Moreover, an advancement of nest initiation was reported in south-western Iceland and attributed to warming climate (D'Alba *et al.* 2010). However, nest-initiation date at Rif did not show any clear trend during the same period (authors' unpubl. data). The warming trend coincides with reduced probabilities of females to switch islands within the Rif colony, although we believe that the trend in nest numbers better explains the decline in the probability of nest-site switching.

The use of nest shelters and successful predator control likely contributed to the increased nest numbers (Chaulk *et al.* 2006, D'Alba *et al.* 2009). The rocky island had served as a nest site for 18 years, i.e., supporting at least one generation of Common Eiders, whereas the grassy island became available in 1990. The rocky island supported higher nest numbers than the grassy island until, but not after, 2001. Moreover, the increase in nest numbers was less rapid in the rocky island during 1993–2008. The carrying capacity of the rocky island may have been reached in the 2000s as, since then, the grassy island seems to have received most recruits.

Switching islands became less probable late in the study, coinciding with peaks in nesting densities. This could indicate a re-enforcing presence of conspecifics, which attract more and more nesters to the island, either as a result of observing the nest success of others ("public information") or that recruits are attracted to patches with the highest nest densities (Danchin *et al.* 1998, Valone 2007). Breeding-season dispersal distances decrease with increasing nest density in the Common Eider (Öst *et al.* 2011). Thus, choosing to nest in the most crowded patches within the colony can be interpreted as being adaptive nest-site selection (Clark & Shutler 1999). Such conspecific attraction may also be reinforced by enhanced dilution of nest-predation risk, which in turn decreases dispersal from these successful patches. Under such conditions, success in competition may become less important than the benefits of colonial nesting.

In colonially-nesting waterfowl, macro habitat selection (here, rocky vs. grassy island) may be a function of habitat availability during nesting, but it also reflects the risk of exposure to adverse weather caused by habitat topography (McCracken *et al.* 1997). Winters with high precipitation (1995, 2003, 2004, and 2006) may have reduced the value of the rocky island as a nest site, by elevating water levels in the pond. Our finding that winter precipitation, which affects water levels, was related to the probability of switching islands can have wide-ranging implications, because Common Eiders prefer to nest close to the shore and are thus sensitive to water levels (Robertson 1995, Bolduc *et al.* 2005). Precipitation or water levels may interfere with nest-site selection by Common Eiders nesting close to ponds, lakes or sea shores. Thus, it is noteworthy that annual precipitation is predicted to increase as much as 20% in the Arctic region, as a result of global climate change (IPCC 2001, ACIA 2005). Sea-levels rise is a future concern, causing habitat loss of breeding waterfowl in coastal areas (Traill *et al.* 2010). Common Eider could be negatively affected by increasing sea levels, perhaps by more restricted nest-site selection or delayed nest initiation.

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Valinta kahden saaren välillä: onko haahkan pesäpaikan vaihto yhteydessä säätilaan vai pesätiheyteen?

Linnut vaihtavat pesäpaikkaansa vuosien välillä riippuen pesimämenestyksestä, muiden pesijöiden toimista ja säätilasta. Pesäsaaren vaihtamisen todennäköisyyttä tarkasteltiin haahkalla (*Somateria mollissima*) Rif'issä, Länsi-Islannissa, perustuen

16 vuoden rengastus- ja pesälaskenta-aineistoon. Tutkimuksessa tarkasteltiin kahta keinotekoista saarta, joista toinen oli kivinen ja toinen ruohostoinen. Pesinnän aloitusajankohta erosi saarten välillä joinakin vuosina.

Saaren vaihtamisen todennäköisyyttä rajoitti kolme taustamuuttujaa: (1) runsaampisateiset talvet laskivat vaihtotodennäköisyyttä ruohostoiselta kiviselle saarelle; (2) talvien lauhtuessa 1993–2008 saarten vaihtamistodennäköisyys laski; ja (3) pesämäärien kohotessa 155:stä 606:en jaksolla 1993–2008 saarten vaihtamistodennäköisyys laski. Talvikauden sää on saattanut vaikuttaa saarten vaihtotodennäköisyyteen ennen kaikkea sateisuuden kautta, sillä tekijä vaikuttaa vedenpinnan tasoon tutkitussa koloniassa. Pesätiheyden ja vaihtotodennäköisyyden käänteinen suhde tukee käsitystä lajikumppanien menestyksen vaikutuksesta yhdyskuntapesijöillä.

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Appendix 1. Characteristics of the study islands at Rif, Snæfellsnes Peninsula, West Iceland

	Rocky Island	Grassy island
First nest found, year	1972	1990
Construction method	Rocks transported with a pickup truck on ice during winter	A peninsula separated from mainland with a 7–10 m wide ditch
Area, m^2	120	600
Cover	Rocky outcrops, driftwood logs	Driftwood logs at center, grass tussocks
Nest substrate	Rock	Grass
Elevation over water level, m	0.5	0.9
Access points for Common Eiders by foot	One on the west side only	Entire shoreline
Adjacent water depth, m	0.8–1.2	0.3–0.6
Shoreline characteristics	Steep edge, 90° vertical to bottom of pond	Gradual incline (30°) from bottom of pond
Distance from mainland to nearest shoreline, m	35	9–10
Vegetation	None	Grasses and tussocks