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CONSPECIFIC REPRODUCTIVE SUCCESS AND BREEDING HABITAT SELECTION: IMPLICATIONS FOR THE STUDY OF COLONIALITY

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Abstract. Habitat selection is a crucial process in the life cycle of animals because it can affect most components of fitness. It has been proposed that some animals cue on the reproductive success of conspecifics to select breeding habitats. We tested this hypothesis with demographic and behavioral data from a 17-yr study of the Black-legged Kittiwake (*Rissa tridactyla*), a cliff-nesting seabird. As the hypothesis assumes, the Black-legged Kittiwake nesting environment was patchy, and the relative quality of the different patches (i.e., breeding cliffs) varied in time. The average reproductive success of the breeders of a given cliff was predictable from one year to the next, but this predictability faded after several years. The dynamic nature of cliff quality in the long term is partly explained by the autocorrelation of the prevalence of an ectoparasite that influences reproductive success. As predicted by the performance-based conspecific attraction hypothesis, the reproductive success of current breeders on a given cliff was predictive of the reproductive success of new recruits on the cliff in the following year. Breeders tended to recruit to the previous year's most productive cliffs and to emigrate from the least productive ones. Consequently, the dynamics of breeder numbers on the cliffs were explained by local reproductive success on a year-to-year basis. Because, on average, young Black-legged Kittiwakes first breed when 4 yr old, such a relationship probably results from individual choices based on the assessment of previous-year local quality. When breeders changed breeding cliffs between years, they selected cliffs of per capita higher reproductive success. Furthermore, after accounting for the potential effects of age and sex as well as between-year variations, the effect of individual breeding performance on breeding dispersal was strongly influenced by the average reproductive success of other breeders on the same cliff. Individual breeding performance did not appear to influence the probability of dispersing for birds breeding on cliffs with high local reproductive success, whereas individual breeding performance did have a strong effect on dispersal for birds that bred on cliffs with lower local reproductive success. This suggests that the reproductive success of locally breeding conspecifics may be sufficient to override an individual's own breeding experience when deciding whether to emigrate. These results, which are supported by behavioral observations of the role of prospecting in recruitment, suggest that both first breeders and adults rely on the reproductive success of conspecifics as ''public information'' to assess their own chances of breeding successfully in a given patch and to make settling decisions. A corollary prediction is that individuals should attempt to breed near successful conspecifics (a form of social attraction) in order to benefit from the same favorable local environmental conditions. Such a performance-based conspecific attraction mechanism can thus lead to an aggregative distribution of nests and may have played a role in the evolution of coloniality.

Key words: breeding habitat selection; conspecific reproductive success; dispersal; ectoparasitism; environmental predictability; evolution of coloniality; metapopulation; performance-based conspecific attraction; public information; Rissa tridactyla.

Introduction

The environment of most animal species is heterogeneous at different spatial and temporal scales for various characteristics that can directly affect components of fitness. The processes of habitat selection are thus likely to be under strong selective pressures (Cody 1985, Martin 1993). Basic theoretical models indicate that, at equilibrium, individuals should distribute themselves among patches in an Ideal Free or Ideal Despotic distribution, depending on local density and frequency-dependent effects on fitness and on the type of competition (Fretwell and Lucas 1970). This implies that individuals use some knowledge of environmental quality to choose among habitat patches on the basis of their current relative quality (Wiens 1976).

Animals can use a variety of physical cues to assess environmental suitability (Buckley and Buckley 1980, Cody 1985, Danchin and Wagner 1997). More parsi-

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moniously, they can use some integrative cue such as the presence and activities of conspecifics (Kiester 1979, Shields et al. 1988, Stamps 1991, Boulinier and Danchin 1997, review in Danchin and Wagner 1997). The role of the presence of conspecifics in attracting individuals to particular patches of habitat (i.e., Social Attraction) has been suggested by several authors (Fisher and Fisher 1969, Shields et al. 1988, Brown et al. 1990, Stamps 1991, Reed and Dobson 1993, Forbes and Kaiser 1994), and demonstrated experimentally in various groups of vertebrates (e.g., Burger 1988, reviewed in Smith and Peacock 1990, Danchin and Wagner 1997) and invertebrates (Meadows and Campbell 1972, Grosberg and Quinn 1986). However, the mere presence of conspecifics may not always be a good indicator of local quality, because feeding groups or breeding colonies can show dramatic differences in foraging or reproductive success resulting from spatial variations in the quality of the habitat patches that are occupied (Brown et al. 1990, Danchin and Monnat 1992). Conversely, the fact that most current breeders on some patches were successful in a given year demonstrates that these particular patches provided favorable conditions at least in the current breeding season. Current reproductive success of conspecifics may thus be a reliable cue for predicting the reproductive success that can be expected on a given patch in the next breeding season (Chabrzyk and Coulson 1976, Burger 1982, Shields et al. 1988, Boulinier and Danchin 1997, Switzer 1997). Such a mechanism of patch choice, in which individuals use the local success of conspecifics as ‘‘public information,’’ has been proposed and tested in the context of optimal foraging (Clark and Mangel 1984, Valone 1989, 1991, Valone and Giraldeau 1993, Templeton and Giraldeau 1995), but less so for breeding habitat selection. Despite good evidence that individuals use their own breeding performance in deciding whether to be faithful to their breeding site (e.g., Newton and Marquiss 1982, Beletsky and Orians 1987, 1991, Marzluff 1988, see Switzer 1993 and 1997 for a review), tests of the value of conspecific reproductive success as a cue for breeding site selection are scarce (Burger 1982, Bollinger and Gavin 1989, Danchin et al. 1991, Orians and Wittenberger 1991, Boulinier 1996, Boulinier et al. 1996).

An iteroparous animal selects its breeding site at first recruitment as a breeder (natal dispersal) and for each subsequent breeding attempt (breeding dispersal). In both cases, the local reproductive success of conspecifics may represent a valuable supplementary cue that an individual can use to gauge its own chances of breeding successfully in a given area. Theoretical investigations of the hypothesis that individuals use the reproductive success of conspecifics for breeding patch selection (hereafter referred to as the ‘‘performance-based conspecific attraction hypothesis’’) have led to testable assumptions and predictions (Boulinier and Danchin 1997). In particular, comparing the fitness of random settling strategies and strategies based on patch reproductive success, it was shown that a key assumption for such a habitat selection mechanism to be selected is that the environment is patchy and predictable at the scale considered. Key predictions concern expected patterns of local demography and individual behavior. In this paper, we use the Black-legged Kittiwake (*Rissa tridactyla*), a cliff-nesting seabird, to test some of these assumptions and predictions. That species is well suited for testing this hypothesis because it feeds on nondefendable food far from its actual nesting patches (i.e., breeding cliffs), which permits the investigation of factors affecting breeding patch choice independently from foraging constraints.

We examined two key assumptions: (1) that the environment is composed of patches of different quality; and (2) that local breeding patch quality in one year is a predictor of its quality in the next year (i.e., the quality of the patches is autocorrelated, or predictable, in time [Stephens 1987, Switzer 1993]). As local patch quality may have been difficult to infer independently from the quality of local breeders, we tested whether the reproductive success of current breeders was positively correlated with the success of new local recruits in the next year. If this was the case, then it would confirm the predictability of breeding patch quality.

We also explore different key predictions of this hypothesis: (1) that high average reproductive success of the breeders on a given cliff patch (hereafter called local reproductive success) should lead to net local recruitment of breeders in the following year (even though Black-legged Kittiwakes first breed when 3 yr old), while low local reproductive success should lead to net emigration of local breeders; (2) that individuals changing cliffs between year $t - 1$ and year t should move to better cliffs (i.e., those with higher local reproductive success) in year t. Because such choices are based on information gathered in year $t - 1$, breeders changing cliffs should have selected cliffs that were of high quality in year $t - 1$, i.e., at the time of prospecting; finally, (3) that breeding patch fidelity should be influenced not only by individual breeding performance, but also by the current success of the other pairs breeding on its home cliff, which together constitute complementary sources of information on current cliff quality. Failed breeders are expected to be more likely to disperse from patches with low local reproductive success than failed breeders from patches with high local reproductive success. Testing prediction 1 involved using yearly nest counts only (demographic data); testing predictions 2 and 3 involved data of the monitoring of individually marked birds (behavioral data).

We discuss the implications of such a mechanism of breeding habitat selection for the evolution of grouping behavior in animals (Pulliam and Carraco 1984, Shields et al. 1988, Stamps 1988). Indeed, Boulinier and Danchin (1997) and Danchin and Wagner (1997) proposed that a performance-based conspecific attraction mechanism may explain the origin and maintenance of colonial breeding (i.e., breeding among densely distributed territories that contain no resource other than breeding sites; Perrins and Birkhead 1983).

METHODS

Black-legged Kittiwake study colonies are situated in the Cap Sizun (Brittany, France) where 6682 adults and chicks had been individually color banded between 1979 and 1992 (Danchin and Monnat 1992). Yearly population size has varied between 800 and 1300 pairs in six clearly separate colonies, which among them include 45 breeding cliffs. Each colony was checked for banded birds at least 80 times every year and the breeding performance of every pair was monitored. Pairs were considered as having bred successfully if (1) their marked chicks had been seen alive after leaving the nest, or (2) their chicks left the nest for the first time when >35 d old (for pairs with unmarked chicks). These two criteria gave us equivalent results. Chicks were checked for the presence of feeding ticks (*Ixodes uriae*) at banding and tick numbers were recorded (Danchin 1992, Boulinier et al. 1997). Individual breeding performance was rated according to the final stage of the breeding attempt: (1) nest constructed, no egg laid, (2) no egg hatched, (3) no chick fledged, (4) fledged one chick, and (5) more than one chick.

Intensive demographic and behavioral monitoring resulted in 12 901 bird-years of observations. The sex of individuals was determined by recording behavior during mating. We were able to assess with considerable precision the factors influencing the decision of individuals to emigrate in a given year, because (1) the rate of resighting of breeders, estimated by capture-recapture models (Pollock et al. 1990, Lebreton et al. 1992, Nichols 1992), was almost 1 (Danchin and Monnat 1992, Cam et al., *in press*; only 27 birds were missed in one year among 4124 individuals with complete information in two successive years); (2) 81.4% of the adult nonbreeders were seen regularly during the years they did not breed, and (3) we checked for marked breeders at all colonies within 150 km of our colonies, a distance beyond which even young birds are unlikely to emigrate (Coulson and Nève de Mévergnies 1992). The reproductive life-span of any individual was divided into three ''age'' categories: (1) year of first reproduction, (2) years between first reproduction and the last year of life, and (3) last year of life.

Geographical scale

For practical survey purposes, at the beginning of the study, the colonies were subdivided into several distinct breeding cliffs (or subcolonies) on the basis of topographic features of the coastline. This permitted us to investigate breeding habitat selection at a scale intermediate between the nest site and the colony. Because different cliffs within a given colony showed important variations in local reproductive success associated with local effects of ectoparasitism and predation (see Danchin and Monnat 1992 and results of assumption 1), all the analyses in this paper used those cliffs as the spatial units of breeding habitat. For instance, birds changing nests within a given cliff were considered as ''faithful,'' whereas birds moving from one cliff to another were considered as having ''dispersed.'' However, we obtained similar results from analyses using either the actual nest site or the colony as the spatial unit. The average number of chicks fledged per nest by other pairs nesting on the same cliff (local reproductive success) was used to test whether neighbors' reproductive success affected individual dispersal decisions. Cliffs were included in the data set if they had hosted at least ten nests in a given year. The number of nests per cliff built in a given year thus varied from 11 to 121.

Cliff annual demographic trend

We describe the annual demographic trend of the different cliffs with two different variables. The annual multiplication rate in the local numbers of breeders on a cliff between year $t - 1$ and year t was computed as the ratio of the numbers of pairs on that cliff in the two successive years $N(t)/N(t - 1)$. That parameter reflects the demographic balance of the positive effect of local recruitment against the negative effect of adult mortality and emigration. Thus, for each cliff in a given year, we compared the annual multiplication rate with the corresponding year-specific annual adult survival rate to estimate whether net emigration or net recruitment had occurred. Annual rates of increase higher than the upper limit of the 95% confidence interval of the year-specific adult annual survival rate reveal net recruitment of new breeders, while values lower than the lower limit of that interval imply net emigration of former local breeders (i.e., numbers of breeders decreased more than predicted by mortality alone). This defines a variable taking three levels: net emigration, net recruitment, and cases where the estimated annual multiplication rate of the local population of breeders was within the 95% confidence interval of the annual survival rate (mortality alone could explain changes in local numbers of breeders).

Statistical methods

We used analyses of variance and analyses of covariance for continuous dependent variables (GLM procedure in SAS [SAS 1990]) and logistic regressions for binary dependent variables (CATMOD procedure in SAS [SAS 1990]). We checked fit of logistic regression models with likelihood-ratio goodness-of-fit tests. Except when specified, we started with the full model containing the main effects plus all the possible interactions. Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance (α set at 0.05), starting with the highest-order interactions down to the main effects.

Accounting for nonindependence in the data.—Data used to test predictions 2 and 3 had two potential sources of nonindependence. First, the different records concerning the same individual (mean of 2.82 observations per individual; SD = 2.1; range = 1–11) could not be considered as independent statistical events. Second, birds breeding on the same cliff in the same year (i.e., cliff-year) were not independent because they each experienced the same local conditions (mean of 7.3 marked individuals per cliff-year; SD = 8.7; range 1–45). One method that has been used in such cases to avoid biases due to such nonindependence is to select a single record per source of nonindependence and to perform the analysis on the resulting data set. If this random selection is done only once, such approach can lead to wrong conclusions, as for instance the P value associated with an effect may have a 50% chance of being below the significance level, depending on the data set (Massot et al. 1993, Potvin and Roff 1993; see Fig. 4). It is thus necessary to study the distribution of the P values associated with the different potential effects by performing multiple random resamplings of one record per independent unit (Massot et al. 1993, Potvin and Roff 1993).

We used such a resampling technique to analyze factors affecting breeding patch fidelity of individuals. We performed the analyses in two steps. First, the analyses were performed on the whole data set. This permitted the selection of final models incorporating the significant effects. In a second step, we used data sets containing statistically independent records by randomly selecting one record per individual, and a single record per cliff-year. This was repeated 1000 times to obtain the distribution of the P value of the independent variables (or their interactions). The distribution of the P values associated with each effect allowed us to determine their significance. If the higher value of the 95% confidence interval of the P values associated to a given effect (hereafter called 95% CI) was lower than 0.05, then the effect was significant. Conversely, if the lower value of the confidence interval was higher than 0.05, the effect was not significant.

When the 95% confidence interval of the distribution of the P values included 0.05, following Crowley (1992), Efron and Tibshirani (1993), and Massot et al. (1993), we performed randomization tests to determine the probability P' of obtaining the observed proportion of significant values by chance. Randomization tests use random permutations of the values of each independent variable of the statistical model: for each permutation, we performed 200 resamplings of one value per individual and cliff-year as described above to obtain the proportion of significant tests resulting from that permutation. We did 500 permutations, and the final value P' for each effect was given by the proportion of the permutations that led to an equal or larger proportion of significant values than that observed in the resamplings without permutation. If $P' < 0.05$, we reject the null.

TABLE 1. Variations of the probability of successfully rearing at least one chick in different years according to the cliff (logistic regression).

Year	No. of nests	df	χ^2	P of cliff effect
1981	98	1	19.72	0.0001
1982	786	16	135.78	0.0001
1983	755	15	79.94	0.0001
1984	655	15	53.57	0.0001
1985	540	14	66.16	0.0001
1986	808	20	43.50	0.0018
1987	753	20	64.52	0.0001
1988	489	14	48.28	0.0001
1989†	310	9	10.50	0.3112
1990	678	15	58.57	0.0001
1991	679	14	35.98	0.0011
1992	772	17	60.69	0.0001

† This was an unusual year during our 17-yr study: a very low proportion of adults bred (~35% vs. ~10% in other years; Cam et al., *in press*), laying was very late, and there was a very low reproductive success in all cliffs.

RESULTS

Assumption 1: patchiness of the environment

We analyzed the probability of a pair breeding successfully according to year and cliff (Table 1). Because the interaction between those factors was significant (Year × Cliff: $\chi^2_{139} = 477.19$, $P < 0.0001$), we analyzed the effect of the cliff separately for each year. In 11 out of 12 yr, the cliff effect was highly significant. Thus, the probability of breeding successfully varied among cliffs within years, and the relative quality of different cliffs varied in time. This suggests that cliffs were breeding patches of varying quality.

Assumption 2: predictability of the environment

The average reproductive success of the pairs of a given cliff was autocorrelated from one year to the next ($n = 205$, $r^2 = 0.22$, $P < 0.0001$, slope $\pm$ 1 SD = 0.87 $\pm$ 0.03), indicating that cliff quality was predictable between years. The interactions between the previous year's local reproductive success with the year effect ($F_{10,181} = 1.22$, $P = 0.28$) and with the cliff effect ($F_{30,140} = 1.00$, $P = 0.47$) indicated that these relationships did not differ among years and cliffs.

Two local environmental factors are likely to explain the main part of the predictability of local average reproductive success independently of the quality of the local breeders: ectoparasitism by cliff ticks and predation. In particular, each cliff's density of tick (*Ixodes uriae*, an ectoparasite linked to the breeding substratum; Eveleigh and Threlfall 1974) was negatively correlated with the local number of chicks fledged per pair (ANOVA, $F_{1,139} = 50.51$, $P < 0.0001$, $r^2 = 0.26$), suggesting a negative effect of that ectoparasite on local reproductive success. Furthermore, tick density on a

TABLE 2. Predictability of breeding cliff quality as assessed through temporal autocorrelation of local reproductive success (RS).

A) Correlation of local reproductive success in year *t* and local reproductive success of the same cliff at different time lags before year *t*

Year	R^2	Sample size	df	*P*
$t - 1$	0.2227	205	1	0.0001
$t - 2$	0.0934	169	1	0.0001
$t - 3$	0.0452	148	1	0.0095
$t - 4$	0.0166	126	1	0.1510

B) Existence of additive or multiplicative effects of the local reproductive success of the four last years on current reproductive success (analysis of covariance, $n = 103$)

Independent variables	df	*F*	*P*
Year	7	2.88	0.0090
Local RS($t - 1$)	1	21.89	0.0001
Local RS($t - 2$)	1	3.26	0.0741
Local RS($t - 3$)	1	0.00	0.9604
Local RS($t - 4$)	1	2.33	0.1301
Selected model	8	4.98	0.0001

Note: The starting model included the local reproductive success in the four previous years plus all the possible interactions, as well as the year effect plus its interaction with the previous-year local reproductive success.

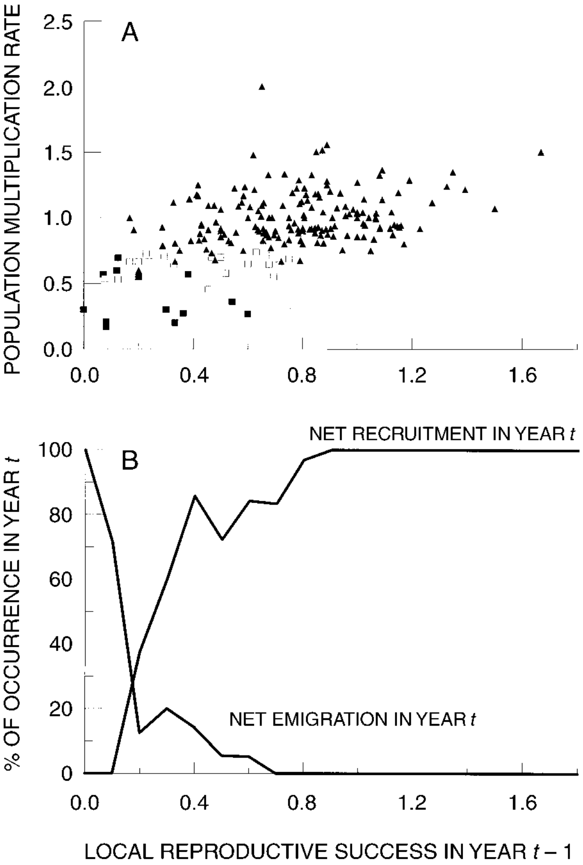

FIG. 1. Local population trend of a group of Black-legged Kittiwakes breeding on a cliff between year $t - 1$ and year *t* as a function of local reproductive success of year $t - 1$ (average number of chicks fledged per pair; $n = 173$ cliff-years; see Table 3 for statistics). (A) Local multiplication rate in number of breeders $N(t)/N(t - 1)$. Some of these values imply net emigration of former breeders (■); others imply net recruitment of new breeders (▲); and others correspond to cases in-between (□) (see *Methods*). (B) Proportion of net emigration and net recruitment for breeders.

cliff was autocorrelated between years ($n = 66$, $P < 0.0001$, $r^2 = 0.54$, slope ± 1 SD = 0.99 ± 0.06). This parameter, which influenced environmental quality, was thus predictable from one year to the next. Finally, the probability of breeding successfully for young local recruits was correlated with the local reproductive success in the previous year (logistic regression, $n = 673$ young recruits, $P = 0.0003$), showing that the reproductive success of current breeders was predictive of the success of new recruits. Thus, factors other than the quality of the local breeders explain the temporal autocorrelation of the local reproductive success.

The temporal autocorrelation of local reproductive success fades with time (Table 2A), showing that the environment was only weakly predictable after a few years. The prediction of the local reproductive success in a given year as a function of local reproductive success in the previous year was not improved by adding information about the local reproductive success 2, 3, and 4 yr before, either as additive or multiplicative effects (Table 2B). This shows that this system is dynamic in space and time, but that cliff quality can nevertheless be predicted from one year to the next, but not over several years.

Prediction 1: local demographic trend and cliff reproductive success

There was a strong relationship between local reproductive success and local demographic trend in the following year (Fig. 1, Table 3). High local reproductive success always led to high annual multiplication rate in the number of local breeders (Fig. 1A) resulting from net recruitment of new breeders (Fig. 1B) in the following year. Conversely, low local reproductive success led to low annual local population multiplication rate and net emigration of breeders (Fig. 1). Breeders were thus deserting cliffs with low local reproductive success. Furthermore, the relation between annual local population multiplication rate and the previous year's local reproductive success was positive in every year, significantly so in 8 out of 10 yr (interaction between local reproductive success and year effects $P = 0.20$), and was positive and significant in each of the six colonies (interaction between year and colony effects, $P = 0.80$).

In this population as in others (Coulson and Thomas 1985), the youngest age at which Black-legged Kittiwakes first breed is 3 yr, and the modal age of first breeding is 4 yr (percentage recruiting at age 4: 45.4%; $n = 445$; mean age at recruitment: 3.98 yr). Therefore,

TABLE 3. Factors explaining the local annual population trend of Black-legged Kittiwakes.

A) Annual local multiplication rate in the number of breeders $N(t)/N(t-1)$ as a function of year, previous-year local reproductive success (RS, average number of chicks fledged per pair), and colony (analysis of covariance)†.

Independent variables	df	F	P
Local RS in year $t-1$	1	170.92	0.0001
Year	10	15.66	0.0001
Colony	5	7.27	0.0001
Model	18	20.54	0.0001

B) Probability of occurrence of net emigration or net recruitment in relation to the previous-year local reproductive success of the cliffs (logistic regression, $n = 173$ cliff-years).

Independent variable	df	F	P
Local reproductive success in year $t-1$	1	17.22	0.0001
Selected model likelihood ratio	139	38.09	1.000

Notes: Net recruitment was detected when local population increased more than predicted by year-specific annual adult survival rate. Cases of net emigration were those in which local population decreased more than predicted by this parameter.

† The starting model of the analysis included the three independent variables plus all the possible interactions (n = 173 cliff-years).

recruits in a given year could not have hatched in the preceding year, and there should be a 4-yr delay in the effect of local reproductive success on local population trend under the assumption of natal philopatry to the breeding cliff. However, after accounting for the effect of local reproductive success in year $t-1$ on the multiplication rate in the numbers of local breeders from year $t-1$ to t, there was no additive or interactive effect of the local reproductive success in the years before (final model as in Table 3A; starting model included as independent variables year, colony, and local reproductives successes in year $t-1$, $t-2$, $t-3$, and $t-4$ and the interactions; all independent effects removed in the selection process had $P > 0.30$): the demographic trend was best explained by the previous year's local reproductive success only. Adding information on years before did not improve the model. This shows that active recruitment involving nonlocally born individuals occurred immediately following high local reproductive success.

Prediction 2: breeding patch selection of experienced breeders

Birds that changed breeding cliffs between year $t-1$ and year t settled in higher proportions on cliffs of better reproductive success in the year t than if they had settled at random [(i.e., equally likely among cliffs; $\chi^2_2 = 13.5$, $P < 0.01$; three levels of local reproductive success: high (>75% of successful pairs), average (between 75 and 50%) and low (<50% of successful pairs)]. This biased spread of the former breeders that changed cliffs can be explained by an active choice made while prospecting at the end of year $t-1$. Indeed, the reproductive success of the cliffs to which individuals dispersed in year t was significantly better in year $t-1$, at the time of prospecting, than if selected at random in year $t-1$ (comparison of the different proportions of cliffs with three levels of local reproductive success, $\chi^2_2 = 34.13$, $P < 0.001$).

Prediction 3: individual breeding patch fidelity and local reproductive success

First step: analysis of the whole data set.—To analyze the effect of the average reproductive success of local breeders on fidelity to the breeding cliff, we had to account for the effect of other factors known to influence breeding patch fidelity in other species. Such factors are the sex and age, as well as individual's last-year breeding performance (e.g., Shieck and Hannon 1989). We also included a year effect to account for between-year variations (Table 4). Because the model explaining adult fidelity to the cliff in year t showed an interaction between individual breeding performance and local reproductive success in year $t-1$ (Table 4A; Figs. 2 and 3), individuals having experienced a success or a failure in their year $t-1$ breeding attempt were analyzed separately.

For failed breeders in year $t-1$, the average reproductive success of other pairs breeding on the same cliff in year $t-1$ had a strong effect on adult fidelity to the breeding cliff in the following year (Figs. 2 and 3; Table 4B). For birds having bred successfully the previous year, only sex had an effect, with females being trivially less faithful to site than males (96.1 and 98.1% faithful, respectively; Table 4C). Successful breeders were highly faithful to their breeding cliff regardless of the reproductive success of the other pairs on their breeding cliff (Table 4C; Figs. 2 and 3). However, in productive cliffs (Figs. 2 and 3) birds appeared faithful to their breeding cliff regardless of their individual breeding performance ($\chi^2_1 = 0.35$, $P = 0.55$, breeding failure at the nest stage against the other stages; Fig. 2). Conversely, in less productive cliffs (Figs. 2 and 3), individual breeding performance played a prominent part ($\chi^2_4 = 107.42$, $P < 0.0001$), and females were more likely to emigrate ($\chi^2_1 = 22.51$, $P < 0.0001$). When both individual breeding performance and the average reproductive success of other pairs on the same cliff were very low, breeding dispersal was the most common behavior observed (Fig. 3).

Second step: numerical resamplings to control for nonindependence.—We checked the validity of the previous analyses with a resampling technique to select one record per individual and cliff-year to obtain independent data (see *Methods*). Resamplings confirmed that in productive cliffs (Figs. 2 and 3), birds were faithful to their breeding cliff regardless of their previous-year individual breeding performance (95% of the P values associated to that effect were between

TABLE 4. Fidelity to the breeding cliff in year t according to individual breeding performance and local reproductive success in year $t - 1$, and sex, age, and year (multiple logistic regression, on the whole data set). In the three cases, the starting models contained the main effects plus all the pairwise interactions.

A) Analysis on all categories of breeders ($n = 1395$)

Independent variable	df	χ^2	P†
Sex	1	8.54	**0.0035**
Age	2	6.90	**0.0317**
Year	7	8.17	0.3177
Individual breeding performance in year $t - 1$‡	1	17.08	**0.0001**
Local reproductive success in year $t - 1$§	1	5.80	**0.0160**
Individual breeding performance × Local reproductive success	1	6.57	**0.0104**
Model likelihood ratio	478	382.44	0.99

B) Analysis on breeders that failed in year $t - 1$ ($n = 491$)

Independent variable	df	χ^2	P
Sex	1	4.91	**0.0267**
Age	2	2.97	0.2268
Year	7	14.68	**0.0229**
Individual breeding performance in year $t - 1$‖	2	11.67	**0.0029**
Local reproductive success in year $t - 1$§	1	35.59	**0.0001**
Model likelihood ratio	217	208.52	0.6482

C) Analysis on breeders that bred successfully in year $t - 1$ ($n = 1197$)

Independent variable	df	χ^2	P
Sex	1	3.93	**0.0474**
Age	2	3.98	0.1364
Year	7	5.27	0.6265
Individual breeding performance in year $t - 1$¶	1	0.87	0.3508
Local reproductive success in year $t - 1$§	1	0.64	0.4233
Model likelihood ratio	1	0.31	0.5792

† Significant P values are in boldface.

‡ Fledged at least one chick vs. complete breeding failure.

§ Local reproductive success in year $t - 1$ is the average number of chicks fledged per nest by other pairs nesting on the same cliff. Similar results were obtained by using the three categories of cliff quality (as in Fig. 2) or the percentage of breeding failure per cliff (arcsine transformed) as a descriptor of local reproductive success.

‖ Failed at the nest, egg, or chick stage.

¶ Fledged one vs. two or more chicks.

0.049 and 0.97 among the analyses carried out on 1000 resamplings of the data set), whereas in less productive cliffs individual breeding performance played a prominent part (95% of the P values were below 0.004).

For successful breeders, when using successive resamplings, the lower limits of the 95% confidence intervals of the significance levels obtained in 1000 iterations were above 0.05 when testing the final model obtained on the whole data set (Table 4C): specifically, the lower limit of the 95% CI was 0.078 for the effect of the previous-year individual breeding performance and 0.102 for the effect of sex. This confirms the results obtained on the whole data set (Table 4C), that successful breeders were highly faithful to their breeding cliff regardless of their age, sex, level of breeding success, and the average breeding success of the other pairs on the same cliff.

For failed breeders, when testing the model selected on the whole data set (see Table 4B) on randomly selected independent records, the 95% CI of the significance levels obtained in 1000 iterations included 0.05 for all the effects (Fig. 4). Randomization tests (see *Methods*) showed that the probability P' of obtaining similar proportions of significant values by chance was 0.002 for the effect of local reproductive success, 0.004 for individual breeding performance, and 0.102 and 0.132 for sex and year effects, respectively. This confirms that, for failed breeders, fidelity to the breeding cliff was strongly influenced by the average reproductive success of the other pairs breeding on the same cliff as well as by the stage of the breeding cycle at which the breeding failure occurred. Those results confirm that, for a given individual breeding performance, as well as age, sex, and year, breeders did not behave in the same way according to the average reproductive success of their neighbors.

DISCUSSION

The hypothesis that animals cue on the reproductive success of conspecifics to select breeding patches (i.e., performance-based conspecific attraction) was strongly supported by our results. They provide the first empirical evidence that individual animals use local average reproductive success of conspecifics as a source of public information (Valone 1989) to select their breeding environment (Chabrzyk and Coulson 1976, Burger 1982, Shields et al. 1988, Bollinger and Gavin 1989, Beletsky and Orians 1991, Switzer 1997). A similar hypothesis has been proposed on the basis of theoretical and experimental considerations for feeding site selection, with foraging success of conspecifics being the cue to assess the quality of a feeding area (Clark and Mangel 1984, Valone 1989, 1991, Templeton and Giraldeau 1995, Valone and Giraldeau 1993).

The major assumptions of the hypothesis that animals use the reproductive success of conspecifics for breeding habitat selection (Boulinier and Danchin 1997) were fulfilled: the environment was patchy (Table 1) and current patch quality was predictive of next-year patch quality (Table 2). The predictability of breeding patch quality was supported by (1) a positive temporal autocorrelation of local reproductive success, (2) the autocorrelation from one year to the next of an ecological parameter acting on reproductive success (the prevalence of an ectoparasite, the tick *Ixodes uriae*, which appears correlated to local quality), and (3) the correlation between reproductive success of current breeders with that of new local recruits in the following year. However, this temporal autocorrelation fades in a few years (Table 2A), and local population dynamics were explained by local reproductive success only on

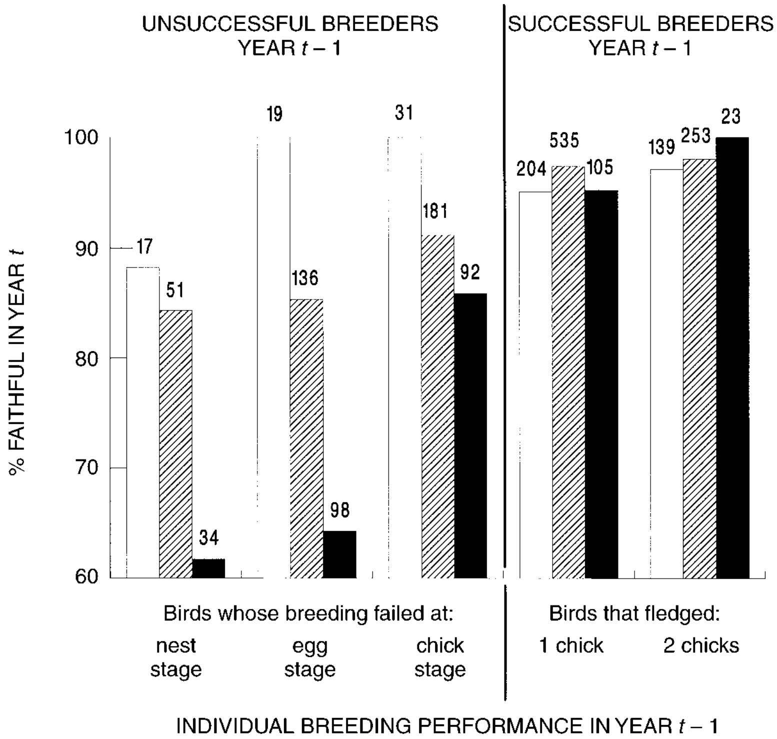

FIG. 2. Fidelity of adult Black-legged Kittiwakes to the breeding cliff in relation to individual breeding performance and average reproductive success of the pairs on the same cliff in the previous year (open bars, breeding cliffs in which <25% of the pairs failed in their breeding attempt; hatched bars, between 25 and 50% failed; black bars, >50% failed). Sample sizes are above bars (whole data set).

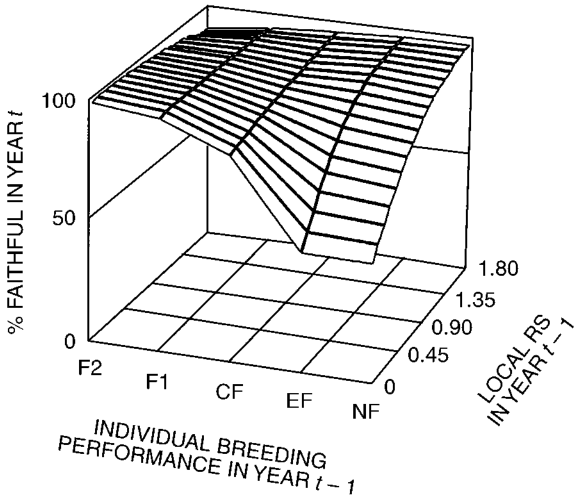

FIG. 3. Fidelity to the breeding cliff in year *t* according to individual breeding performance and the average number of chicks fledged per nesting pair on the cliff (local reproductive success [RS]) in year $t - 1$ (multiple logistic regression). Individual breeding performance: F2, fledged two or more chicks; F1, fledged one chick; CF, chick failure—none of the chicks fledged; EF, egg failure—none of the eggs hatched; NF, nest failure—nest built, no egg laid.

a year-to-year basis (Table 4B). Because Black-legged Kittiwakes typically first breed when 4 yr old, it would not be valuable for first-time breeders to have assessed the quality of their natal cliffs when they were chicks: the information about that quality would have faded by the time they first breed 4 yr later. The observed relationship between local demographic trend and the previous year's local reproductive success (Fig. 1) thus suggests an active selection by potential recruits of last year's most productive cliffs. In the same way, the high frequency of net emigration after a year of poor local reproductive success (Fig. 1B) showed that former breeders deliberately deserted currently low-quality cliffs. Our monitoring of individually marked birds demonstrated that deserting birds were failed breeders of the previous year, and in agreement with prediction 3, their decision to desert was strongly influenced by the breeding success of their close neighbors in the previous year.

Alternative hypotheses

Could our findings result from different dispersal strategies rather than by a performance-based conspecific attraction? Alternative mechanisms could be philopatry or breeding-patch selection based on the presence of conspecifics. Philopatry to the birth cliff would generate a 3 or 4 yr delay in the relationship between

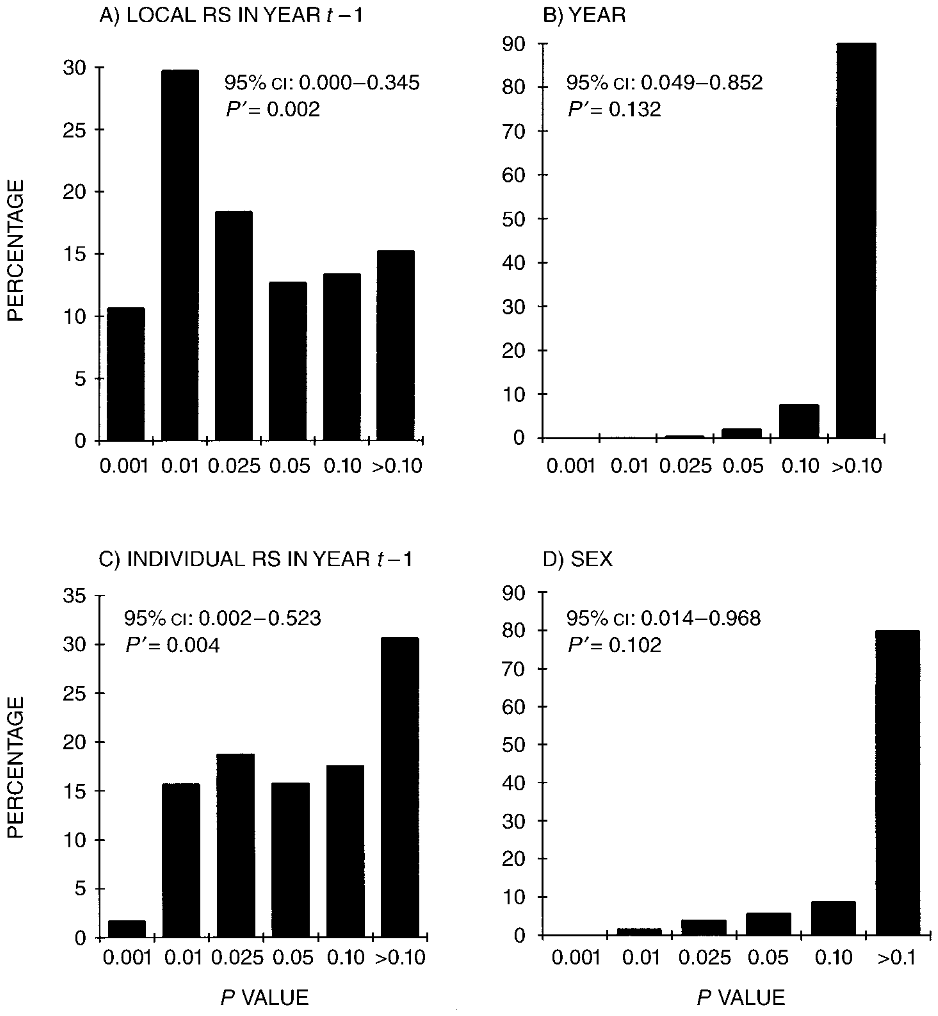

FIG. 4. Distribution of the *P* values obtained in 1000 analyses following the random resamplings of one record per individual and per cliff-year (95% CI: 95% Confidence Intervals of the distributions). Effect of (A) local RS of conspecifics in year $t - 1$, (B) year, (C) individual breeding performance in year $t - 1$, and (D) sex on fidelity to the breeding cliff between year $t - 1$ and t in breeders that failed in their breeding attempt in year $t - 1$. P' values are the actual significance levels obtained after randomization tests.

local dynamics and local reproductive success. No such relationship was found, and only 14.5% of 807 individuals recruited in the study colonies first bred on their natal cliff (Boulinier et al. 1997). Similarly, individuals apparently may have relied on the mere presence of conspecifics to select a breeding cliff. However, this could not be a major effect because local reproductive success was only slightly explained by the size of the breeding group in the previous year ($P = 0.0437$, ANCOVA with previous year local reproductive success as a second covariate $P = 0.0001$, and year as a class effect, $P = 0.0001$). Finally, individuals could use different cues acting on local reproductive success, but the use of the reproductive success of conspecifics is likely to be a more parsimonious strategy because it integrates the effect on fitness of all these factors into a single parameter.

Our results on breeding-patch fidelity could also result from at least two different mechanisms: birds may actually have assessed local reproductive success (or some correlates), or in highly predictable environments, individuals may simply rely on their own previous long-term breeding experience (Boulinier and Lemel 1997). However, we have seen that the temporal autocorrelation of cliff quality breaks down in a few years, and the relative quality of cliffs also varied in time. Consequently, a bird's long-term memory could not generate the detected relationship between local reproductive success and breeding-patch fidelity. In an environment presenting such patterns of variation, and if dispersal is not too costly, individuals should present a dispersal strategy based on a year-to-year appraisal of their environment. Prospecting several years prior to recruitment, or memorizing breeding experience over a long period, should not necessarily improve breeding-patch selection. This is supported by our observation that net recruitment and breeding dispersal (Fig. 1B) were strongly related to local reproductive success in the previous year.

The performance-based conspecific attraction hypothesis also assumes that there is no important phenotypic differences between the prospector and the local breeders. Reproductive success is indeed influenced by local environmental factors (Boulinier and Lemel 1997) but also individual components such as age, genetics, body condition, and pair bonding (Coulson and Thomas 1985, Wooller et al. 1990, Hamer and Furness 1991, Pärt et al. 1992, Weimerskirch 1992). In the present study, however, environmental factors seem more important than individual components because the reproductive success of current breeders is a good predictor of the success of local recruits in the next year.

Breeding dispersal

Prediction 3 is that breeding dispersal should be affected by various factors, including local reproductive success. This might appear to contradict previous studies on Black-legged Kittiwakes, given that Coulson and his collaborators almost never observed significant emigration of breeders in their long-term study (Coulson and Nève de Mévergnies 1992), and suggested that once established, breeding Black-legged Kittiwakes never emigrate (Aebisher and Coulson 1990). Their study also showed that prior individual experience influenced the relationships between nest site and mate fidelity (Fairweather and Coulson 1995). In fact, the only significant breeding failure event in Coulson and his collaborators' studies was followed by the only significant emigration event (Coulson and Nève de Mévergnies 1992). In other words, except in that particular case, their colony probably corresponded to the highly productive cliffs of the present study (open bars in Fig. 2 or rear part of Fig. 3) from which none of our birds emigrated either. Moreover, our study presents results on fidelity to subcolony rather than to colony. That scale appeared particularly meaningful in our case because of the patchiness resulting from local environmental factors (ectoparasitism and predation). Besides, we documented 62 cases of infidelity to the colony, and we conducted similar analyses that showed that dispersal between colonies was also influenced by the same variables, including local reproductive success.

For various practical reasons, ecologists often study growing or stable populations, rather than rapidly declining ones (Pulliam 1988). This may have precluded the finding of some important processes that are expressed only in unfavorable situations. For instance, Bollinger and Gavin (1989) found results similar to ours on the influence of neighbors' reproductive success when comparing populations with very different average reproductive success, whereas Beletsky and Orians (1991) did not find this within a productive population. Finally, breeding dispersal should not be neglected since even a low rate of breeding infidelity can have important effects on individual fitness, as well as on metapopulation dynamics and gene flow (Barton 1992, Danchin and Monnat 1992, Lebreton and Gonzáles Dávila 1993, Spendlow et al. 1995, Prévot-Julliard et al., *in press*). In cases where local resighting probabilities are below one, the use of multistate capture–recapture models should allow the effect of local habitat characteristics in a given year on dispersal probabilities to be studied (Nichols and Kendall 1995, Spendlow et al. 1995).

Behavioral evidence of habitat assessment before recruitment

Our results strongly suggest that potential recruits actually assess some parameter highly correlated with the current reproductive success of conspecifics. This may be the reproductive success itself and/or the local social context (resulting from the activities of the individuals of the breeding group), which has been shown to influence individual behavior (Southern 1974, Danchin 1988). In the Black-legged Kittiwake, several behavioral observations explain the results of predictions 1, 2, and 3. The two categories of individuals most likely to be seeking a nesting site (i.e., immatures and failed breeders), prospect colonies towards the end of the breeding season (Hodges 1974, Porter 1990, Danchin et al. 1991, Cadiou et al. 1994, Boulinier et al. 1996). During the course of this study, 92.9% of the 807 birds that were banded as chicks and recruited into our study colonies were seen in the year preceding their first recruitment. Most failed breeders on productive cliffs remained on their nest for the rest of the season, while on less productive cliffs failed breeders tended to desert their nest immediately after failure and squat on (i.e., occupy) successful nests on other cliffs that often belong to other colonies (Cadiou 1993, Cadiou et al. 1994). This can explain how, in certain circumstances, some measure of current local environmental quality (here estimated by the local reproductive success) can override individual breeding experience, as shown by our results on breeding-patch fidelity.

Furthermore, the timing of prospecting in this species corresponds to the period when the value of information on relative cliff quality is the highest (Boulinier et al. 1996). More generally, the widespread avian habit of prospecting (Danchin et al. 1991, Baker 1993, Reed and Dobson 1993, Reed et al. 1998) occurs when young individuals and failed breeders can actually assess the relative quality of the patches they visit. In burrow-nesting species, where nest contents cannot be assessed from a distance, prospectors visit burrows during chick rearing (reviewed in Reed et al., 1998), which is probably the best strategy to assess current reproductive success. In the common Goldeneye (*Bucephala clangula*), for instance, adults whose nesting attempt failed, and nonnesting yearlings are commonly captured in nest boxes while prospecting (Zicus and Hennes 1991). Active nests received up to 25 visits per day, and adults appeared to prospect more in nest boxes that had contained successful nests during the current season than in those where nests were abandoned or unused. As a consequence, previously successful nest sites are used preferentially in the following season (Dow and Fredga 1985, Zicus and Hennes 1991). In some cliff-nesting species, nest ownership depends on the individual's capacity to land on the nest during fights, and nest appropriation is based on repeated landings on the actual nest site (Danchin and Nelson 1991). Prospectors in these species try to land and squat on nests with chicks as soon as they are left unattended (Monnat et al. 1990, reviewed in Danchin and Nelson 1991, Danchin et al. 1991, Cadiou 1993). In the Black-legged Kittiwake, squatters recruit preferentially to one of the squatted nests (Monnat et al. 1990, Cadiou 1993, Cadiou et al. 1994), thus showing a link between prospecting and recruitment.

Performance-based conspecific attraction and dynamics of subdivided populations

According to the performance-based conspecific attraction hypothesis, when local conditions deteriorate, individuals ''vote with their feet'' by moving to more productive locations and prospectors can choose to breed in the currently best places. Indeed, in our study, birds that dispersed finally settled on cliffs of currently higher than average quality. Some individuals, however, may be unable to fulfil their choices because of density-dependent intraspecific competition for sites and mates. This may lead individuals to skip breeding opportunities (while queuing for breeding vacancies) or to pioneer new colonies (Forbes and Kaiser 1994). At the scale of a metapopulation (Hanski 1991), such individual behavior would lead to preferential recruitment to the most productive areas at a given time. The effect of this form of conspecific attraction on the probability of persistence of metapopulations would need specific investigations (Smith and Peacock 1990, Ray et al. 1991, Reed and Dobson 1993, Boulinier and Lemel 1997).

Our results underscore the complexity of settling decisions in interaction with the spatial and temporal scales of habitat variation (Orians and Wittenberger 1991, Desrochers and Magrath 1993, Switzer 1993, 1997, Prévot-Julliard et al., *in press*). The performance-based conspecific attraction hypothesis relates breeding-patch selection to the evolution of dispersal. Recent models have underlined the importance for the evolution of dispersal of the ability to alter dispersal propensity according to environmental cues (McPeek and Holt 1992, Lemel et al., 1997). Using the current reproductive success of conspecifics may provide such cues, allowing animals to track spatiotemporal variations of the environment (Stephens 1987).

Performance-based conspecific attraction and coloniality

Dispersal and recruitment based on the assessment of the spatiotemporal variation in local reproductive success could aggregate nesting territories (Boulinier and Danchin 1997), as other conspecific-based habitat selection strategies (Shields et al. 1988, Brown et al. 1990, Stamps 1991, Wagner 1993, 1997). This may have led to coloniality in species feeding on nondefendable resources (Shields et al. 1988, Brown et al. 1990, Boulinier and Danchin 1997). The performance-based conspecific attraction hypothesis may thus cast new light on the evolution of coloniality, a breeding pattern observed in many taxa, in spite of its costs for the individual (reviewed in Brown and Brown 1996, Danchin and Wagner 1997). The main difficulty of the classical cost-and-benefit approach to that question is that the balance of these different effects is difficult to estimate because the various costs and benefits cannot be expressed in a single currency (Pulliam and Caraco 1984, Wittenberger and Hunt 1985, Shields et al. 1988). However, one important reason for nesting close to conspecifics may be that they provide information on the current quality of the breeding patch (Shields et al. 1988, Stamps 1991, Brown et al. 1990, Forbes and Kaiser 1994, Boulinier and Danchin 1997). In fact, as a component of fitness, reproductive success integrates the effects of most factors acting on fitness, including the costs and benefits of coloniality, so that it can be considered as the ''common currency'' biologists have been seeking. Thus, its use eliminates the problem of weighing the costs and benefits of coloniality (Danchin and Wagner 1997). It also avoids the risk of overemphasizing any one factor in studies of habitat selection (e.g., food resources, as emphasized by Stamps [1994]).

More generally, the use of any conspecific cue as a way to select all the commodities necessary to breed can generate aggregations of breeders, thus paving the way to coloniality (Danchin and Wagner 1997). This may provide an initial seeding of nest clumping, which allows some or several of the other colony-based selective advantages proposed in the literature (e.g., social defence against predators, social foraging; Wittenberger and Hunt 1985, Brown and Brown 1996) to take effect and promote colony growth. However, the efficiency of breeding-patch selection based on conspecific reproductive success is self-amplified because, once nests are aggregated, individuals can more easily assess the local reproductive success on a large sample of nesting conspecifics within each patch. This is likely to diminish the costs of prospecting and increases the reliability of the estimation of current local environmental quality. Thus, breeding-patch selection based on conspecific cues may contribute to both the formation and the maintenance of colonies.

Counterintuitively, however, reputed costs of coloniality (e.g., predation and parasitism) may have indirectly promoted coloniality. Indeed, the negative effects on individual fitness of such costs may have produced environmental patchiness in the ancestral species, which was likely to have been solitary (Rolland et al., *in press*). This could have increased the necessity of habitat selection strategies based on current fitness components of conspecifics. This may, in turn, have favored the evolution towards colonial breeding to which the formerly negative effects secondarily became costs. Similarly, any factor acting on environmental quality (either positively or negatively) may have indirectly caused the evolution of coloniality. The performance-based conspecific attraction mechanism of colony formation thus integrates the effect of all the previously proposed mechanisms in a single framework, that of breeding habitat selection based on conspecifics (i.e., the commodity selection hypothesis of Danchin and Wagner [1997]). By studying individual decisions, this framework emphasizes the proximate mechanisms of aggregation rather than the resulting patterns. Ultimate causes of coloniality and proximate cues of habitat selection are connected, the reproductive success of conspecifics being the proximate cue that ultimately allows individuals to optimize their own reproductive success.

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