

# Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice

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## Summary

1. One way that animals may select breeding sites is by assessing the reproductive success of conspecifics in one season and settling the next year in those habitat patches where success collectively had been greatest. This sort of habitat assessment may promote the formation of colonies at high quality sites.
2. We examined whether cliff swallows, *Petrochelidon pyrrhonota*, in south-western Nebraska used conspecific breeding performance to choose colony sites.
3. Reproductive success at colony sites varied spatially within seasons and between seasons, and was autocorrelated at a site from one year to the next, but not over longer time intervals. Cliff swallows thus met the conditions for potential use of information on conspecific breeding performance.
4. Among sites re-used in consecutive years, those with highest collective success in one season showed the greatest rates in colony growth the next season, including the greatest influx of immigrants.
5. The probability of colony-site re-use in successive years increased with collective reproductive success and average breeder body mass (a measure of individual condition) the previous season.
6. Cliff swallows probably use conspecific breeding performance in selecting colonies. This mechanism is one component of habitat selection that also includes attraction to conspecifics and assessment of an individual's own success.

*Key-words:* coloniality, conspecific attraction, fitness, Nebraska, *Petrochelidon pyrrhonota*, social behaviour.

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## Introduction

Breeding habitat for most species is patchy and variable in quality. Individuals presumably select among patches in ways that optimize fitness, but how animals make settlement decisions in general is not well known. In some species, patches may be occupied in direct proportion to local resource availability (Fretwell & Lucas 1970; Brown & Rannala 1995), suggesting that individuals at times directly assess resources in relation to local population size.

Alternatively, animals may use the presence of conspecifics (Kiestler 1979; Shields *et al.* 1988; Stamps 1988; Reed & Dobson 1993; Erwin *et al.* 1998) or their assessment of the local reproductive success of current residents as cues for choosing breeding sites (Boulinier & Danchin 1997; Switzer 1997; Danchin, Boulinier & Massot 1998). Local reproductive success either of an individual or a collective group may be a particularly useful index of habitat quality because it represents the net effect of many different ecological and social factors that may each affect site suitability, but that may be difficult to assess individually (Danchin & Wagner 1997). Information on reproductive success in a patch is valuable only if the habitat quality remains the same during the next breeding period; otherwise, animals cannot accu-

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rately predict site suitability. A prerequisite for habitat choice based on prior reproductive success, therefore, is temporal autocorrelation in local breeding performance (Boulinier & Danchin 1997; Switzer 1997; Danchin *et al.* 1998). Although foraging animals are widely believed to use collective success in a patch as a cue for where and when to feed (Valone 1989, 1991; Valone & Giraldeau 1993; Templeton & Giraldeau 1995, 1996) and many species use their own breeding performance to guide their dispersal decisions (Greenwood & Harvey 1982; Part & Gustafsson 1989), little is known about how local reproductive success is autocorrelated over time or the degree to which species use the success of others in a patch to choose breeding sites (reviewed in Danchin *et al.* 1998).

Recently, Danchin & Wagner (1997) proposed that habitat selection based on local breeding performance may often lead to colony formation. If individuals can assess local reproductive success and one's prospects for success remain autocorrelated between years, over time, individuals will aggregate in successful sites. Other hypotheses for colony formation have suggested that individuals use the presence of conspecifics (that is, group size) as an index of a site's probable success and thus whether to nest there (Shields *et al.* 1988; Brown & Brown 1996). Relatively little data on the mechanisms of colony formation exist, however, and the evolution of coloniality in general is still a mystery (Danchin & Wagner 1997; Rolland, Danchin & de Fraipont 1998) despite extensive study of certain species (Hoogland 1995; Brown & Brown 1996; Danchin *et al.* 1998).

In this paper we evaluate to what degree local reproductive success in colonially nesting cliff swallows *Petrochelidon pyrrhonota* is autocorrelated over time and to what degree individuals may use this information in their choice of colony site. The only previous tests of the performance-based hypothesis of habitat selection in colonial species were those of Danchin *et al.* (1998) for the black-legged kittiwake *Rissa tridactyla* and Erwin *et al.* (1998) for the gull-billed tern *Sterna nilotica*, both of which are relatively long-lived seabirds whose life history and ecology differ substantially from that of passerine birds, such as the cliff swallow. We test the assumptions that breeding habitat patches (that is, colony sites) vary in quality and that quality of a site one year is a reliable predictor of quality there the next year. We then evaluate the predictions that high average reproductive success at a site should lead to re-use of the site and a net gain in number of breeders there the next year, and that fidelity to a breeding site should be influenced not only by individual performance there the previous year, but also by the previous success of other pairs at that site. Finally, we assess the importance of performance-based

habitat choice in the maintenance of coloniality in cliff swallows.

## Methods

### STUDY AREA AND STUDY ANIMAL

Our research was conducted along the North and South Platte Rivers near Ogallala, primarily in Keith and Garden counties, south-western Nebraska. The study area was approximately 150 × 50 km and contained about 160 separate colony sites where cliff swallows breed. The study site has been described in detail by Brown & Brown (1996). The cliff swallow is a 20–28 g neotropical migrant that breeds throughout most of western North America and winters in southern South America. These insectivorous birds build gourd-shaped mud nests, and place them beneath overhanging rock ledges on the sides of steep cliffs or underneath the protected eaves of artificial structures. Cliff swallows often breed in dense colonies. In south-western Nebraska, mean ( $\pm$  SE) colony size is 393.0 ( $\pm$  24.3) nests, ranging from birds that nest solitarily to colonies of 3700 nests (Brown & Brown 1996). Cliff swallows typically have a short breeding season, 10 weeks or less in our study area, and raise only one brood (Brown & Brown 1995). In south-western Nebraska, most birds arrive in May and breeding is largely completed by the end of July.

### FIELD METHODS

Cliff swallow colonies were defined as groups of nesting pairs that interacted behaviourally at least occasionally (Brown & Brown 1996). In most cases, a colony was simply all the nests on a given bridge or highway culvert, which were commonly used as nesting sites in our study area. All birds on a single bridge or culvert usually interacted with each other, as for example, during mobbing of predators or while foraging. In occasional instances, birds nesting on separate, but closely spaced (< 25 m) bridges or culverts tended also to interact, and in these cases we considered both groups to represent a single colony. For birds nesting on the sides of cliffs, we also used the criterion of social interaction to designate groups of nests as colonies (see Brown & Brown 1996). In practice, colonies were almost always highly discrete groups of nests separated from the next nearest colony by  $\geq$  3 km of habitat clearly unsuitable for nesting. Nests within a colony were closely spaced at most sites, often touching each other (see Brown & Brown 1996). In our analyses here, each colony is considered a habitat patch and no attention is given to within-patch dynamics. For example, a bird is considered faithful to a site if it settled anywhere in the colony; only those changing colony sites entirely are considered to have dispersed. Colony size is the maximum number of nests

to have had  $\geq 1$  egg laid; methods of determining colony size at a site are given by Brown & Brown (1996).

Our measure of local reproductive success was the number of nestlings fledged per nest. We determined fledging success by checking contents of nests at intervals of 1–3 days, beginning shortly before egg laying was expected to begin in a nest until either its eggs hatched or the nest failed. Nest contents were observed with a dental mirror and flashlight inserted through a nest's entrance (see Brown & Brown 1996). Once hatching date was determined, we did not check a nest again until the nestlings were 10 days old. At that time nestlings were banded, weighed and examined for ectoparasites. The principal ectoparasites infesting cliff swallows in southwestern Nebraska were the swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) and a bird flea (Siphonaptera: Ceratophyllidae: *Ceratophyllus celsus*). These insects primarily reside inside the cliff swallow nests. All bugs and fleas anywhere on a nestling's body were counted, and the average value for all nestlings in a nest was used in statistical analyses. Nestling survival was the number of young alive at 10 days, which is an accurate relative index of survival to fledging for cliff swallows (Brown & Brown 1996). Nests in 11 colonies had been fumigated to remove ectoparasites for other experiments (see Brown & Brown 1986) and had data relevant to the analyses in this paper. These sites were combined with non-fumigated ones here. Pooling was done for two reasons: (1) parasites or their absence (as caused by fumigation) have no consistent effects on cliff swallow colony-site use (Brown & Brown 1996; see Results); and (2) through its effects on total ectoparasite load and nestling condition (Brown & Brown 1996), fumigation gave us a greater range in mean reproductive success per colony.

Adult breeders were captured at colonies using mist nets strung across culvert entrances or the sides of bridges. We rotated among sites, systematically netting at each throughout the breeding season. At some sites, we colour-marked adults by painting their white forehead patches in unique three-colour combinations, enabling us to identify owners of nests and their associated reproductive success. At other sites, adults were captured inside their nests at night (Brown & Brown 1988, 1996). Breeders were weighed upon each capture. We used our mark-recapture data to estimate age-specific survival probabilities using program SURGE (Brown & Brown 1996, 1998). Data used in this paper were collected from 1982 to 1997.

#### DEMOGRAPHIC CALCULATIONS

We used yearly counts of active nests (colony size;  $N$ ) to estimate the annual rate of increase in the

local number of breeders at a given colony site between year  $t-1$  and year  $t$ . The rate of increase was computed as the ratio of the nest counts at a site in two successive years,  $N_{(t)}/N_{(t-1)}$ . This parameter reflects the demographic balance between the negative effects of adult mortality and emigration, and the positive effects of recruitment of philopatric yearlings and immigration.

To estimate the relative importance of emigration, recruitment of locally born young, and immigration in local site dynamics, we computed the number of individuals involved in each change of colony size at a site using estimates of first-year ( $S_j$ , from fledging to the next breeding season) and adult ( $S_a$ , between breeding seasons) survival probabilities. The number of breeders in year  $t$  [ $2*N_{(t)}$ ] can be expressed as the number of local breeders that survived from last year [ $2*N_{(t-1)}*S_a$ ], plus the first-year birds locally born last year [ $N_{(t-1)}*CRS_{(t-1)}*S_j$ , under the assumptions of complete recruitment at age 1 and strict natal philopatry], where CRS is the colony's mean reproductive success (number of young fledged) per nest, plus the adults recruited in year  $t$  that were not previously born or resident at the site. Thus,

$$2 * N_{(t)} = [2 * N_{(t-1)} * S_a] + [N_{(t-1)} * CRS_{(t-1)} * S_j] + \text{Immigrants} \quad \text{eqn 1}$$

This allows separation of two parameters. Immigrants is defined as  $2*N_{(t)} - [(2*N_{(t-1)}*S_a) + (N_{(t-1)}*CRS_{(t-1)}*S_j)]$  and quantifies the change in colony size between two successive years attributable to birds coming from other colony sites under the assumptions of complete recruitment at age 1 and strict natal philopatry. We assume these assumptions are met, but if they are not, some of the observed gain in colony size attributed to local birds may arise from immigration of non-local birds. Thus, our test for the presence of immigrants is conservative. This term (immigrants) is either positive, reflecting non-locally born birds entering the colony, or negative, reflecting desertion of the colony by former breeders and/or natal dispersal to other sites. New-breeders is defined as  $2*[N_{(t)} - N_{(t-1)}*S_a]$  and quantifies the total number of breeders that did not nest at the site the previous year, including recruits locally born the previous year. The sign reveals whether there was net emigration between years (negative) or a net recruitment of new breeders of all origins (positive).

These parameters allow us to estimate different components of colony-site population dynamics. New-breeders includes the recruitment of locally born individuals, while immigrants accounts only for non-locally born recruits. Under the assumption of natal philopatry alone, we expect new-breeders (but not immigrants) to vary directly with CRS in the previous year. A significant positive relationship

between last year's CRS and immigrants would reveal performance-based conspecific attraction to a site.

In these analyses we used an average adult survival probability ( $S_a$ ) of 0.57, calculated for all birds across all sites and years (Brown & Brown 1996), and an average first-year survival probability ( $S_j$ ) of 0.40.  $S_j$  in this case is greater than in previously reported analyses (Brown & Brown 1996, 1998), reflecting more recent mark-recapture results from 1997 to 1998 with more thorough sampling of colony sites (C. R. Brown & M. B. Brown, unpublished data). Because of the potential error introduced in using a single survival probability across sites and years, we tested the sensitivity of our results to variation in  $S_a$  and  $S_j$  by allowing the survival probabilities to vary from 0.2 to 0.6 (for  $S_j$ ) and 0.3–0.7 (for  $S_a$ , see Results).

#### STATISTICAL METHODS

We used analyses of variance and analyses of covariance for continuous dependent variables (GLM procedure in SAS; SAS Institute 1990). To study the influence of CRS on colony growth in the following year, we ranked CRS and colony growth rate in each year, with rank 1 corresponding to the highest value of each parameter that year. This was a way to account for between-year variation in average reproductive success: a given value for CRS may have been very good in globally poor years, but average or even poor in good years. We then tested whether the colony showing the highest yearly CRS showed the greatest rate of increase in the following season. We used the RANK procedure (SAS Institute 1990) to normalize variables when necessary. The values of CRS were not normally distributed, and thus for the regression of CRS in two

successive years we did two kinds of analyses. We first normalized the distribution of CRS by computing normal scores from ranked values of CRS using the BLOM option of the RANK procedure. In the second analysis, we ranked CRS by year (highest rank = 1) and used those ranks in calculating non-parametric correlations. We used logistic regression (CATMOD procedure; SAS Institute 1990) for binary dependent variables (site use, breeding site fidelity). We checked the fit of logistic regression models with likelihood-ratio goodness-of-fit tests. Except where specified, we started with the full model containing the main effects plus all the possible interactions. Backward model selection was carried out by removing, one by one, the effects that were the farthest from statistical significance ( $\alpha$  set at 0.05), starting with the highest order interactions down to the main effects. When possible, we also tested the normality of the residuals of the selected model. We used the software R (Cliff & Ord 1981; Legendre 1993) to compute Moran's  $I$  over time intervals of increasing length in studying temporal predictability of CRS.

#### Results

##### TEMPORAL AND SPATIAL VARIABILITY IN REPRODUCTIVE SUCCESS

Cliff swallow reproductive success varied significantly with breeding colony site in each of the 11 years for which we had data (Table 1). CRS varied from 0 to 4.0 young per nest within years and average CRS ranged from 1.4 to 2.8 young per nest between years (Table 1). Thus, local reproductive success varied among colonies within years and the relative quality of different colony sites varied over time.

**Table 1.** Effect of colony site on individual reproductive success in cliff swallows by year (one-way ANOVAs testing for differences within years)

| Year | CRS Mean | SE  | <i>N</i> | Range   | <i>F</i> | <i>P</i> |
|------|----------|-----|----------|---------|----------|----------|
| 1982 | 2.6      | 0.3 | 12       | 1.7–4.0 | 3.55     | <0.0001  |
| 1983 | 2.3      | 0.5 | 7        | 0.0–4.0 | 3.41     | 0.003    |
| 1984 | 2.2      | 0.3 | 11       | 1.0–4.0 | 7.12     | <0.0001  |
| 1985 | 2.7      | 0.2 | 9        | 1.3–3.5 | 18.50    | <0.0001  |
| 1986 | 2.0      | 0.3 | 6        | 1.0–2.9 | 22.76    | <0.0001  |
| 1987 | 1.7      | 0.4 | 5        | 0.6–2.6 | 11.27    | <0.0001  |
| 1988 | 1.4      | 0.2 | 11       | 0.0–2.4 | 12.37    | <0.0001  |
| 1989 | 1.5      | 0.5 | 4        | 0.0–2.3 | 39.44    | <0.0001  |
| 1990 | 2.4      | 0.2 | 3        | 2.1–2.8 | 6.73     | 0.001    |
| 1991 | 2.7      | 0.3 | 8        | 0.7–3.6 | 7.20     | <0.0001  |
| 1997 | 2.8      | 0.2 | 5        | 2.5–3.0 | 2.71     | 0.029    |

*N* = number of colonies; total nests was 482, 244, 555, 732, 1232, 1443, 1931, 783, 253, 272, and 570 in each year, respectively.

**Table 2.** Temporal autocorrelation of colony reproductive success (CRS) over time intervals of 1–4 years. Reproductive success at a site in year  $t$  was compared with that of the same site at different time intervals before year  $t$

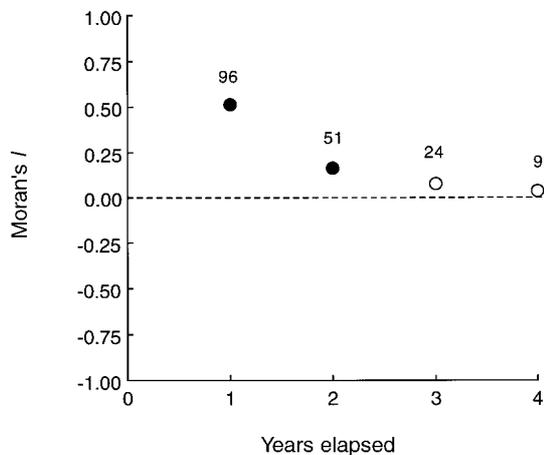
| (a) Normalized values of CRS |     |       |       |        |
|------------------------------|-----|-------|-------|--------|
| Year                         | $n$ | $r^2$ | $F$   | $P$    |
| $t-1$                        | 39  | 0.26  | 13.02 | 0.0009 |
| $t-2$                        | 32  | 0.04  | 1.15  | 0.29   |
| $t-3$                        | 30  | 0.01  | 0.38  | 0.54   |
| $t-4$                        | 22  | 0.10  | 2.21  | 0.15   |

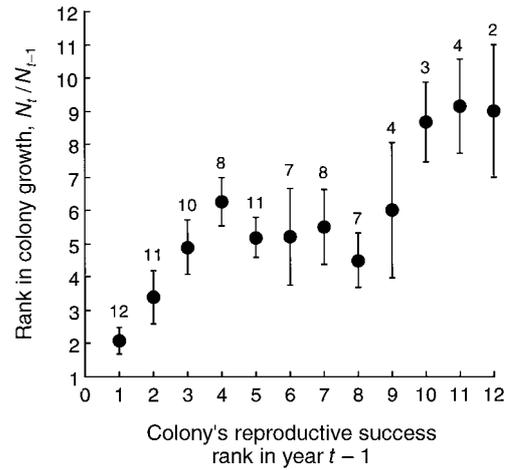
| (b) Ranked values of CRS |     |       |       |          |
|--------------------------|-----|-------|-------|----------|
| Year                     | $n$ | $r^2$ | $F$   | $P$      |
| $t-1$                    | 39  | 0.39  | 23.71 | < 0.0001 |
| $t-2$                    | 25  | 0.18  | 5.18  | 0.033    |
| $t-3$                    | 21  | 0.00  | 0.00  | 0.98     |
| $t-4$                    | 18  | 0.00  | 0.02  | 0.89     |

PREDICTABILITY OF REPRODUCTIVE SUCCESS

Colony reproductive success was significantly autocorrelated over a 1-year time interval, showed a slightly significant autocorrelation over a 2-year time interval and exhibited no significant autocorrelation over longer time intervals. This tended to hold for normalized and ranked values of CRS (Table 2) and for autocorrelation as described by Moran's  $I$  (Fig. 1). Therefore, CRS in one year was a predictor of relative CRS the next year, among sites that were re-used in consecutive years.



**Fig. 1.** Temporal autocorrelation of mean reproductive success at cliff swallow colony sites. Sample sizes (number of colonies) shown by dots. Closed circles are significant autocorrelations; open ones are non-significant ones.



**Fig. 2.** Yearly growth rank of cliff swallow colony sites in year  $t$  (all classes of birds) in relation to yearly rank in colony reproductive success (CRS) in year  $t-1$ . Colony sites with the largest growth in a given year or highest CRS in a given year were assigned rank 1. Ties were assigned the same rank, sometimes resulting in apparent discrepancies in sample sizes between ranks. Mean ( $\pm$  SE) shown; number of years with colony sites of that rank (sample size) are shown above error bars. See Table 3 for significance. Colony sites with the highest CRS in the previous year show the greatest total growth in the current year.

However, birds could not predict CRS at a site based on that from 3 or more years earlier.

COLONY GROWTH IN RELATION TO REPRODUCTIVE SUCCESS

Colony growth, expressed as the ratio of the number of nests in two successive seasons ( $N_t/N_{t-1}$ ), was significantly associated with CRS in year  $t-1$  (Fig. 2, Table 3). Among sites re-used in consecutive years, colonies where birds fledged the most young tended to show the greatest increase in size the following season (Fig. 2). This relationship held only from year  $t-1$  to year  $t$ , however (Table 3). Colony growth was not correlated with CRS over 2 or more

**Table 3.** Relationship between yearly rank in colony growth and colony reproductive success (CRS) over time intervals of 1–4 years. Colony growth at a site in year  $t$  was compared with CRS of the same site at different time intervals before year  $t$

| Year  | $r^2$ | $F$   | slope | d.f. | $P$      |
|-------|-------|-------|-------|------|----------|
| $t-1$ | 0.266 | 30.79 | 0.51  | 1,86 | < 0.0001 |
| $t-2$ | 0.022 | 0.51  | —     | 1,24 | 0.48     |
| $t-3$ | 0.121 | 1.79  | —     | 1,14 | 0.20     |
| $t-4$ | 0.171 | 1.85  | —     | 1,10 | 0.21     |

year time intervals among sites used in consecutive years (Table 3). These results suggest that the parameter new-breeders varied directly with CRS the previous year, and we found a significantly positive relationship ( $P = 0.0002$ ) between new-breeders and CRS when using any value between 0.3 and 0.7 for  $S_a$  in 0.1 increments. Thus, plausible local fluctuations in breeders' survival probabilities could not alter the conclusion that colony growth was related to CRS the previous year. New-breeders varied between -980 and 3280, indicating that yearly turnover at colony sites may be high. Negative values reveal the emigration of former breeders from colony sites with relatively low CRS.

Colony growth as reflected in yearly counts of nests (Fig. 2) or new-breeders at a site includes the birds born at the colony in the previous year. Increased colony sizes at sites where CRS had been high the previous year could simply reflect natal philopatry, with first-year birds recruiting in their birth colony (see Brown & Brown 1992, 1996). To separate natal philopatry from immigration by non-local birds, we analysed the variable immigrants, finding that immigration to a site was positively correlated with the previous year's CRS (Fig. 3). This relationship held for all plausible values for  $S_a$  and  $S_j$  (Table 4). Thus, colonies with the highest CRS relative to other colonies in a given year tended to attract and recruit more birds from other colonies the next year, while colonies with low CRS were unattractive to immigrants the next year. The parameter immigrants varied from -2727 to 1947, indicating that the yearly within-colony turnover may be high. This suggests mass movements of birds into colonies that had high CRS the previous year.

COLONY SITE RE-USE IN RELATION TO REPRODUCTIVE SUCCESS

The above analyses all dealt with the subset of colony sites in the study area that were used in conse-

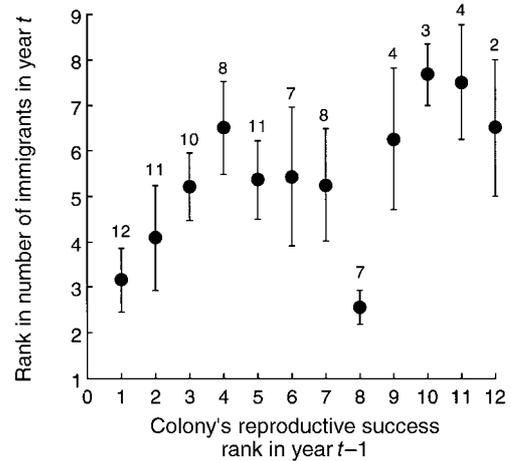


Fig. 3. Yearly rank in number of immigrants to cliff swallow colony sites in year  $t$  in relation to yearly rank in colony reproductive success (CRS) in year  $t-1$ . Colony sites with the most immigrants in a given year or highest CRS in a given year were assigned rank 1. Ties were assigned the same rank, sometimes resulting in apparent discrepancies in sample sizes between ranks. Number of immigrants was estimated using 0.57 and 0.4 for adult and first-year survival probabilities, respectively (see Methods). Mean ( $\pm$  SE) shown; number of years with colony sites of that rank (sample size) are shown above error bars. See Table 4 for significance. Colony sites with the highest CRS in the previous year show the greatest number of immigrants in the current year.

cutive years. However, cliff swallows avoid certain colony sites entirely in some years, with about one-third of the total colony sites not occupied each season (Brown & Brown 1996). We compared CRS and other attributes in year  $t-1$  between sites that were and were not occupied in year  $t$  (Table 5); if at least one nest was active at a site in year  $t$  it was considered occupied. The probability of a colony site being re-used was significantly influenced by CRS and average late-season body mass of breeders the pre-

Table 4. Probability values for regression tests of whether yearly rank in colony reproductive success in year  $t-1$  at a site was significantly related to yearly rank in number of immigrants\* at a site in year  $t$  according to different plausible estimates of annual adult ( $S_a$ ) and first-year ( $S_j$ ) survival probabilities. The probabilities obtained with the most likely estimates of  $S_a$  and  $S_j$  are shown in boldface

| $S_j$ | $S_a$  |        |              |              |              |       |
|-------|--------|--------|--------------|--------------|--------------|-------|
|       | 0.3    | 0.4    | 0.5          | 0.57         | 0.6          | 0.7   |
| 0.2   | <0.001 | <0.001 | <0.001       | 0.005        | 0.005        | 0.006 |
| 0.3   | 0.001  | 0.004  | <b>0.011</b> | <b>0.012</b> | <b>0.008</b> | 0.007 |
| 0.4   | 0.006  | 0.018  | <b>0.023</b> | <b>0.018</b> | <b>0.012</b> | 0.023 |
| 0.5   |        | 0.024  | 0.016        | 0.026        | 0.024        | 0.048 |
| 0.6   |        | 0.022  | 0.035        | 0.055        | 0.053        | 0.076 |

\*Numbers were estimated after accounting for the death of former breeders and philopatric recruitment of locally born birds (see Methods).

**Table 5.** Comparison of colony attributes in year  $t-1$  for cliff swallow colony sites used and not used in year  $t$  (see Table 6 for significance)

| Variable                | Used  |      |          | Unused |      |          |
|-------------------------|-------|------|----------|--------|------|----------|
|                         | Mean  | SE   | <i>n</i> | Mean   | SE   | <i>n</i> |
| Nestling mass (g)       | 22.8  | 0.2  | 43       | 21.7   | 0.4  | 17       |
| Bugs per nestling       | 0.4   | 0.2  | 48       | 0.8    | 0.3  | 22       |
| Fleas per nestling      | 0.6   | 0.1  | 48       | 1.3    | 0.5  | 22       |
| Colony size (no. nests) | 227.1 | 58.7 | 60       | 66.5   | 19.0 | 27       |
| Adult body mass (g)     | 22.6  | 0.1  | 36       | 21.9   | 0.2  | 14       |
| CRS                     | 2.1   | 0.5  | 60       | 1.6    | 0.2  | 27       |

vious year, but not by colony size, fleas per nestling, bugs per nestling or nestling body mass the prior year (Table 6). CRS and body mass of breeders at the end of the nesting season tended to be lower at sites that were not re-used the next season (Table 5).

### Discussion

Our analyses revealed that cliff swallow colony sites vary in their apparent suitability, as measured by the average number of young fledged per nest. This variability occurs among colonies within a season, suggesting that the birds encounter an environment containing patches of breeding habitat of different quality each year. Among sites re-used in two consecutive seasons, site suitability remained similar from one year to the next. A patchy habitat with site autocorrelation in reproductive success between successive years is a prerequisite for habitat choice based on performance of conspecifics (Danchin & Wagner 1997; Danchin *et al.* 1998). Cliff swallows, at least in principle, should be able to gain information on local breeding success at sites one summer and use that to predict the colony sites where relatively high success is likely the next summer. However, because reproductive success shows a strong autocorrelation over only a 1-year time interval, cliff swallows must assess sites each season in

order to potentially predict breeding performance the next year.

That cliff swallows use conspecific breeding performance to select colony sites is suggested by the pattern in colony-site use and growth from one season to the next. Sites where residents had the highest reproductive success relative to others in the study area tended to be re-used and to show the greatest increase in colony size the next year, with a significant part of the growth coming from immigrants. The apparently mass movements of birds into and out of certain colony sites between years is also consistent with assessment based on public information about reproductive success (*sensu* Valone 1989, 1991; Templeton & Giraldeau 1995, 1996). Thus, cliff swallows are the second species for which colony choice based to some degree on assessment of conspecific reproductive success has been found. The other is the black-legged kittiwake (Danchin *et al.* 1998). Conspecific reproductive success is also used by solitarily nesting collared flycatchers *Ficedula albicollis* to choose nesting sites (Doligez *et al.* 1999). However, in colonial gull-billed terns, colony-site re-use one year appears to be unrelated to past success (Erwin *et al.* 1998), possibly because site quality is not autocorrelated between years in this species.

If cliff swallows use the success of others to choose colony sites, one would expect behavioural adaptations for site assessment. In kittiwakes, non-breeders and failed breeders prospect at active colonies, mingling among residents who are tending nests, with prospecting occurring mainly at the end of the breeding season when CRS can be accurately assessed (Cadiou, Monnat & Danchin 1994; Boulinier *et al.* 1996). This sort of behaviour also occurs in cliff swallows. Daily mark-recapture studies at selected colonies have demonstrated extensive daily movement into and out of a site by floaters who do not become established that season (Rannala 1995; C. R. Brown & M. B. Brown, unpublished data), and toward the end of the nesting season there is extensive visitation of active and inactive sites by birds that have finished breeding

**Table 6.** Results of backward multiple logistic regression of factors potentially influencing cliff swallow colony-site use, showing final values for each variable before removal from the regression model

| Variable                | $\chi^2$ | <i>P</i> |
|-------------------------|----------|----------|
| Nestling mass (g)       | 0.06     | 0.81     |
| Bugs per nestling       | 0.14     | 0.70     |
| Fleas per nestling      | 0.64     | 0.42     |
| Colony size (no. nests) | 2.02     | 0.15     |
| Adult body mass (g)     | 4.44     | 0.035    |
| CRS                     | 5.63     | 0.018    |

(Brown & Brown 1996). Colony visitation affords apparent opportunities to assess reproductive performance of residents, and cliff swallows caught as floaters at a colony in one season have been found as breeders at the same site the next year. Whether breeders themselves have opportunities to assess performance at other colonies probably depends on whether they nest successfully. Successful birds do not begin to visit other active sites until the end of the nesting season after they have finished raising their young, and by then many of the residents of the other sites also have finished and departed. Unsuccessful breeders whose nests failed earlier in the season can visit other colonies early enough in the summer to observe reproductive performance of all or most of the colony residents. These failed breeders are more likely to change sites the next year (Brown & Brown 1996).

Colony choice in cliff swallows probably has two components: whether a colony site is used at all in a given season and how many birds settle at active sites (Brown & Brown 1996). In addition to past breeding performance, we found that used and unused sites differed in the body mass of adults at the end of the nesting season, a measure of overall condition that is directly correlated with annual survival (Brown & Brown 1996). Cliff swallows thus may also use their past condition as a cue for site choice, being less likely to return to colony sites where they apparently had poor foraging success or for other reasons were in relatively poor condition the previous season. If fewer of the poor-condition adults from poor sites survive to return the next year, this may further contribute to those sites not being re-used.

Colony choice in cliff swallows may proceed as follows. Sites where breeders had high personal success the previous year are initially reoccupied; these colonies also have larger numbers of past residents available to return by virtue of the adults having been in good condition and more having survived. Non-breeders and failed breeders from the prior year then select among the occupied subset of sites based on their assessment of conspecific performance the previous season, and naive first-year birds settle in the larger colonies because they are attracted to conspecifics (Brown & Rannala 1995; Brown & Brown 1996). This promotes colony growth of previously successful sites. In contrast, an unsuccessful site has fewer past residents return because the birds were themselves unsuccessful and they thus disperse. Such a site is also unlikely to attract immigrants because of its past low success and the reduced number of residents does not attract foreign-born yearlings. Colony growth stops or declines. This scenario incorporates assessment of conspecific breeding performance, attraction to conspecifics, and the obvious importance of individual

reproductive success in breeding dispersal decisions, and it accounts for the dynamic nature of colony-size change at sites in cliff swallows. We believe this is a plausible hypothesis for colony choice that is consistent with the analyses reported here and elsewhere (Brown & Brown 1996), and may describe the maintenance of coloniality in animals more generally.

Previous work has shown that local reproductive success at a site is often strongly correlated with colony size in cliff swallows (Brown & Brown 1996). This is brought about by a variety of group-size effects, both positive and negative, that influence reproductive success and adult survival. The purpose here is not to evaluate all of the potential factors that may influence cliff swallow fitness and site use (see Brown & Brown 1996), but rather to ask only to what degree CRS *per se* provides potential information about habitat quality. Although the birds might base their choice of breeding site on other unidentified proximate cues, our analyses suggest that cliff swallows often use CRS to select the colony sites where expectations are highest. As emphasized by Brown & Brown (1996) and Danchin & Wagner (1997), CRS integrates the costs and benefits of group size into a single fitness measure, and may be the most direct index of reproductive expectations at a site for both researchers and the animals themselves.

Colony size itself may be difficult to predict at a site in advance (Brown & Brown 1996), although the number of birds settling at a site will eventually influence local reproductive success in a variety of ways and over time break down the autocorrelation of reproductive success. If the performance of residents at a site last year is the best single source of information on site quality available, as appears to be the case, we should see relatively successful colony sites grow in size between years and relatively unsuccessful ones decline. The overall pattern of colony-size changes in our population (Brown & Brown 1996) is broadly consistent with this scenario and with the analyses reported here (e.g. Figs 2 and 3). Whenever CRS at a site drops as a result of ectoparasite infestations or any ecological or colony-size effect, fewer birds reoccupy the site. Sites with strong autocorrelation in reproductive success tend to be ones that change relatively little in size between years. Thus, the analyses reported here are consistent with (and extend) the large body of work on the costs and benefits of coloniality in this species (Brown & Brown 1996) and suggest a proximate mechanism for colony-site selection. The fact that two land-dwelling passerines (cliff swallow, collared flycatcher) and a marine gull (black-legged kittiwake) appear to use past performance of conspecifics in making settlement decisions suggests that this may be a common form of habitat selection.

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