Adaptive Site Selection Rules and Variation in Group Size of Barn Swallows: Individual Decisions Predict Population Patterns

Rebecca Jo Safran[*]

Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853

ABSTRACT: Variation in group size is ubiquitous among socially breeding organisms. An alternative to the traditional examination of average reproductive success in groups of different sizes is to examine individual decision making by determining the cues used for site selection. Once factors used for decision making are known, one can determine whether group-level patterns, such as group size variation, are emergent properties of individual-level decision rules. The advantage of this alternative approach is that it can explain the distribution of group sizes rather than just the occurrence of optimal group sizes. Using barn swallows, I tested, but did not support, the hypothesis that individuals settle at sites based on the previous success of conspecifics (i.e., performance-based conspecific attraction). Instead, I demonstrate that an adaptive site selection decision rule—to breed where it is possible to reuse previously constructed nests—predicts 83% of the variation in the number of breeding pairs at a site. Furthermore, experimental nest removals demonstrated that settlement decisions are also strongly influenced by site familiarity. I discuss the interaction of the cue-based site selection rule with the occurrence of site fidelity and how, more generally, a consideration of individual-level decision rules can improve our understanding of variation in many social behaviors.

Keywords: conspecific reproductive success, group size, *Hirundo rustica*, nest reuse, site selection.

Group size variation is a ubiquitous characteristic of populations of social animals. Many studies have focused on the consequences of group size variation; however, a long-standing problem for behavioral and evolutionary biologists has been to explain the causes of variable group sizes

* E-mail: rjs37@cornell.edu.

within a population (Brown et al. 1990). The traditional method for studying variation in the number of breeding pairs at a site has been to analyze the relationship between average reproductive success and group size in order to determine the range of group sizes that is optimal (Krebs and Davies 1981; Brown et al. 1990; Brown and Brown 2001). These patterns are then used to determine which sites individuals should favor in their settlement decisions. However, this group average approach has proven unsatisfactory for three reasons. First, many investigators find that no group size is optimal (Pulliam and Caraco 1984; Danchin and Wagner 1997, reviewed in Brown and Brown 2001). Second, even if a particular group size is associated with higher average fitness than others in some species, it is arguable whether group sizes are predictable at the time individuals need to make habitat selection decisions (Brown and Brown 1996) or whether they are stable over the course of the breeding season (Sibley 1983; Pulliam and Caraco 1984) because a wide range of apparently suboptimal group sizes persists in most populations (Shields et al. 1988; Brown et al. 1990; Brown and Brown 1996, 2001). Third, and most important, by comparing only group-level averages rather than examining individual variation, we ignore the fact that, while emergent phenomena certainly can affect selection pressures, natural selection shapes population-level patterns (such as group size) through its effects on individual decision rules rather than by directly affecting properties of a group per se. Put another way, genes within a single individual cannot directly control group size, but they can influence that individual's habitat selection behavior. We thus expect evolution to have equipped individuals with genes for optimal habitat selection rules rather than with genes for an optimal group size per se. This does not prohibit the possibility that patterns of individual site selection decisions may demonstrate an optimal group size in the population.

In studying group size, an alternative approach to analyzing the average reproductive success associated with groups of various sizes is to examine decision making

directly by determining the cues individuals use when selecting breeding sites (Shields et al. 1988; Danchin and Wagner 1997). Once the factors used for decision making are known, one can then begin to determine whether group-level patterns are indeed a consequence of individuals making adaptive decisions.

Indeed, previous models of coloniality have included the use of cue-based decisions (e.g., Shields et al. 1988; Danchin and Wagner 1997), whether the cue of interest is a remnant of previous breeders (e.g., Shields et al. 1988) or a direct assessment of the reproductive success of conspecifics (Danchin and Wagner 1997; Wagner et al. 2000). These models are an excellent alternative to the group average approach because they focus on individual habitat and mate selection decisions. Specifically, one cue-based model predicts that individuals will form aggregations at sites where evidence of previous breeders is apparent (the nest reuse hypothesis; Shields et al. 1988). Alternatively, the performance-based conspecific attraction hypothesis (Boulinier and Danchin 1997; Danchin and Wagner 1997; Danchin et al. 1998) predicts that individuals will aggregate at the sites where, on average, conspecific reproductive success was previously highest.

The ideal free distribution (Fretwell and Lucas 1970) has also been proposed for explaining group size variation (Brown et al. 1990). However, the major predictions of most ideal free models, that individuals receive equal payoffs both within and among different groups, are rarely met in wild animal populations (Whitham 1980; Tregenza 1995). Another approach, advocated recently by Brown and Brown (2000), uses heritability models to examine the maintenance of group size variation in populations of colonial breeders. Indeed, these models do strongly support a heritable element of an individual's choice of group size in cliff swallows (*Petrochelidon pyrrhonota*), but it is impossible to test this hypothesis in species in which juveniles disperse far outside the geographic scope of study. For example, in North American barn swallows (*Hirundo rustica erythrogaster*), only at most 1%–2% of all nestlings return as breeders to their natal or neighboring territories (Brown and Brown 1999; R. J. Safran, unpublished data), whereas up to 21% of young cliff swallows return to the general location of their natal site in subsequent years (Brown and Brown 1996). Interestingly, in barn swallows, individuals will remain site faithful despite a change in group size across years, suggesting that group size per se is not the most important component of their site selection decisions (Shields 1984; Safran 2004).

Here I present results of field observations and experiments designed to test the following hypotheses about the cues used in the process of site selection: first, that individuals copy the habitat selection decisions of successful conspecifics (the performance-based conspecific attraction

hypothesis [PBCA hypothesis]; Boulinier and Danchin 1997; Danchin and Wagner 1997) and, second, that individuals select nest sites based on the presence of old nests (the nest reuse hypothesis; Shields et al. 1988). Next, I test the extent to which these cues (conspecific reproductive success or the presence of old nests) explain patterns of group size variation in a population of breeding barn swallows.

Study System

Throughout their extensive Holarctic breeding range, barn swallows breed in solitary pairs or with groups of conspecifics. Typically, colony sizes range from two to 200 breeding pairs (Cramp 1988). In North American populations, the majority of individuals typically breed either solitarily or in groups ranging from nine to 35 pairs (Shields et al. 1988; Brown and Brown 1999). Previous studies of barn swallows have demonstrated few benefits and many costs for group breeding (Snapp 1976; Møller 1987; Shields and Crook 1987; Shields et al. 1988). These studies have also shown either no relationship between average reproductive success and group size (e.g., Snapp 1976) or a negative relationship between average reproductive success and group size (e.g., Shields and Crook 1987). Similarly, the reproductive success of barn swallows in my study area in Tompkins County, New York, does not vary significantly across the range of group sizes (fig. 1).

Barn swallows migrate long distances from their natal and breeding territories to wintering areas (Cramp 1988; Brown and Brown 1999). Although natal philopatry is extremely uncommon in North American barn swallows (range: 0%–2%; Shields 1984; Brown and Brown 1999; R. J. Safran, unpublished data), adult barn swallows are site faithful (12%–46%; Shields 1984; Brown and Brown 1999; R. J. Safran, unpublished data), and they rarely disperse to different sites within and among breeding seasons (Shields 1984; R. J. Safran, unpublished data). In Tompkins County, New York, the average annual survival rate of adults (mean = 38%, SE = 0.13) coupled with the overall annual rate of breeding site fidelity (mean = 43%, SD = 0.15) suggests that in the vast majority of cases, an individual's first site selection decision determines its lifetime breeding location. Thus, the decision making process for choice of a first breeding site should be under intense selection for these short-lived birds.

The cues that individuals have evolved for site selection decisions should offer reliable information by being tightly correlated with fitness-related benefits (see, e.g., Schlaepfer et al. 2002). A distinctive attribute of many species in the family of swallows (Hirundinidae) is the persistent use of mud nests across breeding seasons (Barclay 1988; Shields
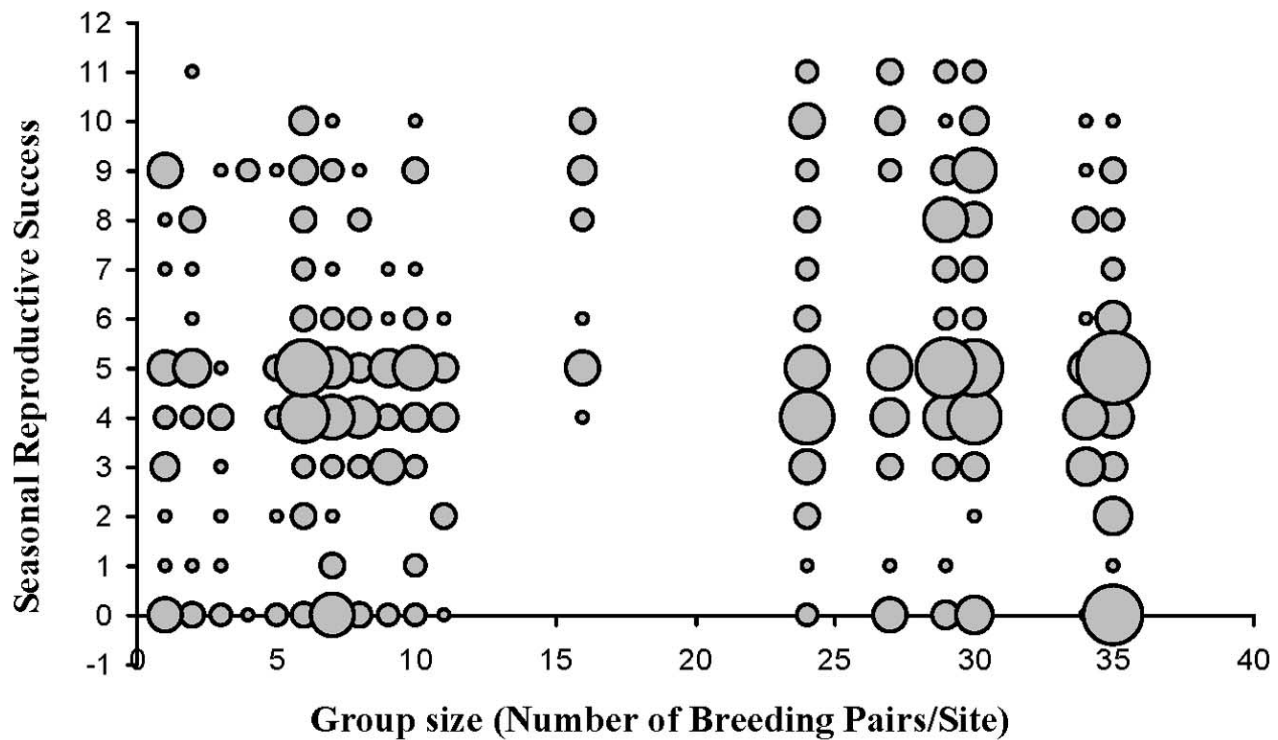
Figure 1: Group size variation does not explain variation in reproductive success (number of fledged young) of barn swallows at 45 sites in Tompkins County, New York, with one to 35 breeding pairs. Mixed linear model: $F = 0.17$, df $= 1, 10.8$, $P > .68$; random effects $=$ site and year; $n = 547$ pairs. Year effects are controlled for in this analysis, and there is no relationship between group size and reproductive success when each year is analyzed separately. Moreover, there is no significant effect of age or quality indicators on this relationship (R. J. Safran, unpublished data).

et al. 1988; Winkler and Sheldon 1993). Barn swallows readily reuse nests that remain intact between breeding seasons because doing so allows pairs to breed earlier than pairs who construct new nests at the start of the season (Hill 1982; Shields et al. 1988; Brown and Brown 1999; Safran 2004). There is also evidence to suggest that individuals avoid the costs associated with ectoparasites by selectively avoiding old nests with remnant mite populations (Møller 1990). Moreover, there is evidence for a net benefit associated with nest reuse because both immigrant and site-familiar pairs have higher reproductive success in old nests compared with pairs within their same age class (immigrant or site familiar) who construct new nests at the start of the season (Safran 2004). Because nests and nest scars are only rarely completely removed from sites between breeding seasons, it is logical to assume that these nests offer important information to individuals making decisions about where to breed.

Methods

General Field Methods

From 1998 to 2002, I and many field assistants studied an individually marked barn swallow population at 52 sites

(barns or bridges) across Tompkins County, New York. At 36 sites, we captured >94% of all breeding individuals ($n = 1,149$) using mist nets. We applied unique paint color combinations to white spots on the rectrices of all adults in order to identify the individuals at each active nest as they incubated eggs and fed nestlings (Shields and Crook 1987). We monitored breeding activity at least every 2 days by noting the seasonal onset of nesting (date on which the first egg was laid), clutch size, the number of complete breeding attempts within a year (one or two), and the total number of offspring fledged during the year. We checked all nests during every site visit. All sampling and experimental methods were approved by the Cornell University Institutional Animal Care and Use Committee (protocol 01-51).

Nest Removals

To determine whether old nests are an important site selection cue, I removed nests at 12 sites in 1999, five sites in 2001, and two sites in 2002. In 2001 and 2002, I removed nests at sites where >94% of breeding adults had been captured and marked during the previous year of the study.

I removed all old mud nests and fecal materials below nests, and I scraped away and covered all nest scars using paint that matched parts of the structure (barn rafters, bridge supports) where no nests were present. I conducted these site manipulations during the late winter, well before the birds arrived in mid-April. The number of breeding pairs during the previous season at the removal sites ranged from one to 29. Nests were collected under permits from the U.S. Fish and Wildlife Service and the New York State Department of Environmental Conservation.

Statistical Analyses

I used SAS (version 8.2) for all statistical analyses presented in this article. I used Spearman rank tests to rank-transform the average reproductive success of individuals at each site in order to test predictions of the PBCA hypothesis. Because the reproductive success at each breeding site was not normally distributed, I compared the average number of fledged young at each site per year (1999–2002) using Kruskal-Wallis tests. To increase the power of the test of the PBCA hypothesis, I included control sites and sites where nests had been removed in the analyses. The overall results are qualitatively the same whether the removal sites are included or not. In the case of two-group analyses where variances are unequal, I used the approximate t computation for unequal variances using SAS PROC TTEST. The degrees of freedom for the approximate t computation are based on Satterthwaite's approximation (SAS Institute 1990). In order to account for the lack of independence among individuals within each breeding site, I used mixed linear models (SAS, PROC MIXED) in which breeding site and year were included as random effects to correct for among-site and among-year differences. I applied transformations or used polynomial regression to model nonlinear relationships. For directional predictions only, I used one-tailed significance tests (Rice and Gaines 1994).

I calculated survival rates using the program MARK (White and Burnham 1999). Because the program MARK cannot calculate recapture probabilities for just two consecutive years of data, I calculated return rates as the proportion of females marked in year n that returned in year $n + 1$ for experiments where I wanted to analyze and compare the return rates of individuals both in the year before and during a site manipulation. I only calculated return rates for sites where the vast majority (>94%) of breeding females were captured for two consecutive years in a row. I analyzed differences in immigrant and returning females (i.e., excluding males) because females are easier to capture and match to a nest, as they do the majority of incubation, and because many males float from one site to another within the same breeding season. Therefore, "site famil-

iarity status" is less reliable in males than it is in females between years of the study.

Results

Performance-Based Conspecific Attraction Hypothesis

One assumption of the PBCA hypothesis is that site quality, or the average reproductive success of individuals within sites, varies within a given year (Danchin and Wagner 1997; Danchin et al. 1998). In my study area I found that the average reproductive success of individuals across sites differed in only two of four years (table 1).

If individuals use the reproductive success of conspecifics to make site selection decisions for the following breeding seasons, then reproductive success at a site should be a reliable indicator of the expected average success of breeding individuals in the subsequent year. Thus, a second assumption of the PBCA hypothesis is that within sites, reproductive success is correlated between at least two successive years (Boulinier and Danchin 1997). However, I did not detect a significant predictive relationship between the success rank of a site in one year and its rank in the subsequent year (table 1).

If individuals rely on variation in conspecific reproductive success across sites to make decisions about site selection, the decision to settle at a site should be a function of the average reproductive success at a site in the previous year. Specifically, a critical prediction of the PBCA hypothesis is that the number of immigrants at a site should be greater at sites with the highest previous reproductive success (Boulinier and Danchin 1997; Danchin and Wagner 1997).

Contrary to this prediction, I found a nonsignificant, negative correspondence in the rank of a site (based on

Table 1: Tests of the assumptions of the performance-based conspecific attraction hypothesis

	Assumption 1					Assumption 2	
Year	Mean reproductive success	SD	n	H	P	Spearman's ρ (no. sites compared)	P
1999	4.54	4.34	34	44.71	.08		
2000	5.34	3.16	14	23.16	.04	.52 (14)	.06
2001	5.04	2.95	30	59.63	<.01	.12 (14)	.66
2002	4.63	2.30	26	26.54	.38	.04 (9)	.91

Note: Assumption 1: Does reproductive success vary across sites within each year? Assumption 2: Is reproductive success correlated within site among years? n = number of breeding sites; total numbers of pairs were 212, 155, 212, and 136, respectively, for 1999–2002. I tested assumption 1 using Kruskal-Wallis tests (H). I tested assumption 2 using Spearman rank tests; results are listed for two consecutive years in a row: 1999 and 2000, 2000 and 2001, and 2001 and 2002.

mean reproductive success) in the previous year and the number of female immigrants at the site in the focal year for all years of the study: 1999–2000: $r_s = -0.39$ ($P >$ .22, $n = 11$ sites); 2000–2001: $r_s = -0.40$ ($P > .50$, $n = 5$ sites); and 2001–2002: $r_s = -0.30$ ($P > .63$, $n = 5$ sites). (Sample sizes differ from year to year owing to annual variation in our ability to catch an acceptable majority of birds at many sites.)

A second critical prediction of the PBCA hypothesis is that colony growth is a function of the success of breeders at the site during the previous year. Thus, the change in the number of pairs at a site between two successive years should be a function of the average reproductive success at the site during the previous year. Specifically, the difference in the number of pairs at a site between two successive years should be positively related to the previous reproductive success at that site. However, in no two consecutive years of this study did I detect such a relationship: 1999–2000 ($r_s = -0.09$, $P > .75$, $n = 14$ sites), 2000–2001 ($r_s = 0.32$, $P > .27$, $n = 14$ sites), and 2001–2002 ($r_s = 0.32$, $P > .34$, $n = 11$ sites). (The sample size in the comparison of pairs between 2001 and 2002 is reduced because of difficulties in accessing several sites in my study area in 2002 due to land ownership changes).

Nest Reuse Hypothesis

The nest reuse hypothesis assumes that the reuse of a nest constructed in a previous breeding season (hereafter, "old nests") is adaptive compared with constructing a new nest. If this assumption is correct, individuals who initiate their first breeding attempts in old nests should have higher seasonal reproductive success than individuals who construct new nests at the start of the breeding season.

To examine differences in reproductive success as a function of nest age, I recorded the number of fledged young at sites where old nests were intact at the start of the breeding season (control sites). Specifically, at control sites I compared the reproductive success of pairs using old nests and pairs who constructed new nests. Individuals who reused old nests had nearly 25% greater reproductive success than individuals who constructed new nests at the start of the breeding season (mixed linear model: $F = 21.95$, df $= 1,479$, $P < .001$, random effects $=$ site and year, $n = 499$ pairs; fig. 2). The lay date of breeding pairs is strongly correlated with seasonal reproductive success, controlling for site and year effects (Safran 2004). Still, the relationship between reproductive success and age of nest remains significant even when lay date, which is correlated with individual age and quality, is controlled for (mixed linear model: $F = 4.47$, df $= 1,457$, $P < .05$, random effects $=$ site and year, $n = 496$ pairs).

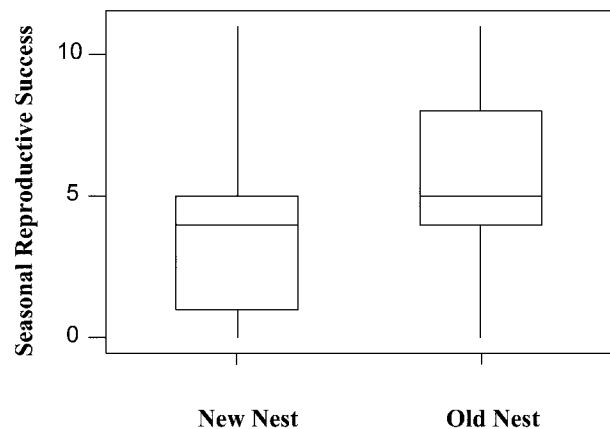If old nests are an important cue for individuals with

Figure 2: Individual barn swallows who reuse old nests have higher reproductive success than those who construct new nests.

no prior experience at the site, a prediction of the nest reuse hypothesis is that the proportion of new individuals (immigrants) settling at sites where all old nests are removed should be lower after the removal compared with control sites, where old nests are intact at the start of the season. Because site fidelity is strong in barn swallows, I analyzed this prediction separately for individuals new to a site versus those with previous experience at a site.

I examined group composition (the proportions of immigrants vs. returning individuals) at seven removal sites and six control sites where the vast majority (at least 94% of females at each site, or a total of 129 pairs across the 13 sites) of breeding females were captured in the previous year. During the subsequent removal year, 98.2% of a total of 127 (or at least 94% at each site) of the breeding females were captured at the same set of 13 sites. The combination of an estimated 38% (SE $= 0.13$) survival rate of adults and an overall breeding site fidelity rate of 43% (SD $= 0.15$) at these sites provide support for the assumption that individual females who arrive unbanded are immigrants and first-time breeders at the site. There is a small probability that I overestimated the number of immigrant females if an individual who was not captured in the previous year returned to the site. However, this problem is eliminated by directly comparing the proportion of immigrant females at control and removal sites where the probability of overestimation should be equivalent. Group sizes did not differ at control and removal sites in the year before the nest removals (equal variances $t = 0.30$, df $= 6$, $P > .78$); thus, there is no inherent bias in the assignment of sites, or group size, for the experimental treatments.

During the year that nests were removed just before the breeding season, a significantly lower proportion of im-

migrant females settled at removal sites compared with the proportion of new females at control sites (unequal variances $t = 3.15$, df $= 10.69$, $P < .01$; fig. 3*A*), and as a consequence, group sizes were smaller at removal sites than at control sites in the year of nest removals. The return rates of individual females with previous breeding experience at the sites did not differ between removal and control sites (control, mean $\pm$ SD $= 0.48 \pm 0.12$, removal $= 0.44 \pm 0.12$; unequal variances $t = 0.61$, df $= 10$, $P > .56$), nor is there a relationship between the probability of returning to a site and group size (polynomial regression: $F = 1.67$, df $= 1, 14$, $P > .20$). Additionally, as predicted if immigrant females use old nests for settlement decisions, there was a significantly higher proportion of immigrant females in the year following the removal year compared with the proportion during the removal year in a different set of four control sites (paired $t = 2.44$, df $= 3$, $P < .05$). Within the same four sites, the proportion of new females was lower during the removal year compared with the proportion before the removal year (paired $t = 2.48$, df $= 3$, $P < .05$; fig. 3*B*).

Group Size Variation Is a Consequence of Individual-Level Decisions

Given the strong support for the hypothesis that immigrants use the presence of old nests as a cue for habitat selection decisions, I next tested predictions of the hypothesis that this individual rule can explain the population-level phenomenon of variation in group size.

Prediction 1. Group size is correlated with the number of old nests at a site at the start of the breeding season. If group size is a consequence of individual decisions to reuse old nests, there should be a significant positive relationship between the number of old nests at a site and group size (number of breeding pairs).

The number of nests at the start of the breeding season at 36 barn swallow sites positively predicted 83% of the variation in the number of breeding pairs that settled at that site (linear regression, $F = 173.61$, df $= 13, 5$, $P < .001$; number of breeding pairs $= 0.116 + 0.756$ number of old nests; fig. 4*A*).

Prediction 2. The number of immigrants at a site is a function of the number of old nests at a site. If old nests are an important cue for the settlement decisions of first-time breeders, group size should be a function of the number of new individuals at a site. Thus, the number of immigrants should increase with the number of old nests at a site at the start of the season. To examine this prediction, I analyzed the relationship between the number of immigrant females as a function of the number of old nests at 11 breeding sites, ranging in size from one to 137 old nests, at the start of the breeding season. The sample
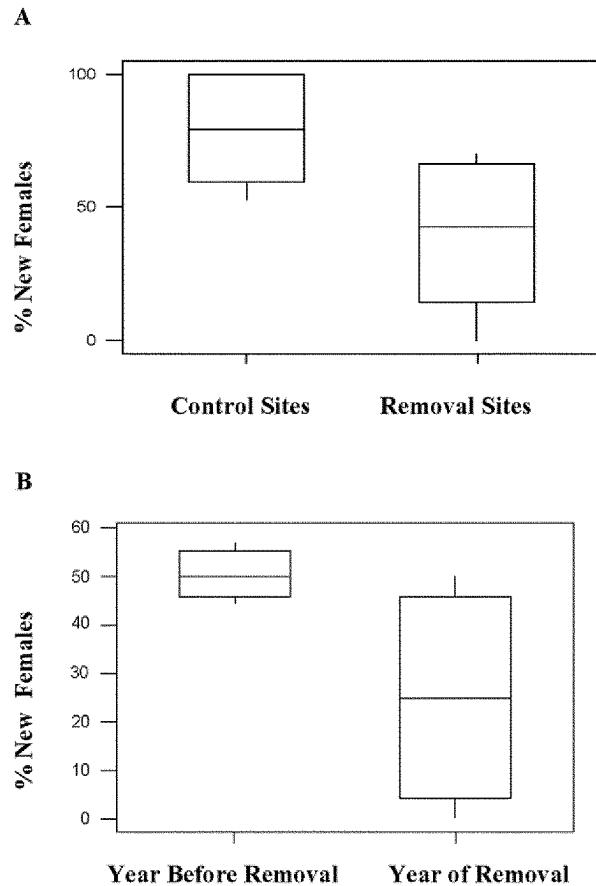

Figure 3: *A*, Group composition as a function of experimental treatment. The proportion of old and new females at control ($n = 6$) and nest removal ($n = 7$) sites. *B*, Difference in the proportion of new (immigrant) females the year before and during nest removal at the same site ($n = 4$).

size for this comparison was limited to sites where >95% of birds were captured in two successive years and where nest removals were not conducted.

The number of nests at the start of the breeding season at 11 barn swallow sites positively predicted 73% of the variation in the number of immigrant females that settled at that site (linear regression, $F = 27.81$, df $= 1, 10$, $P < .001$; number of immigrants $= 0.040 + 0.621$ number of old nests; fig. 4*B*).

Prediction 3. Group size changes with the removal of old nests. If group size is a function of the number of old nests at a site at the start of the season, there should be significantly fewer breeding pairs at sites in the year of the nest removal compared with the year before the nest removal. Similarly, if group size is a function of the presence and number of old nests at the start of the season, then the number of nests constructed during the removal year
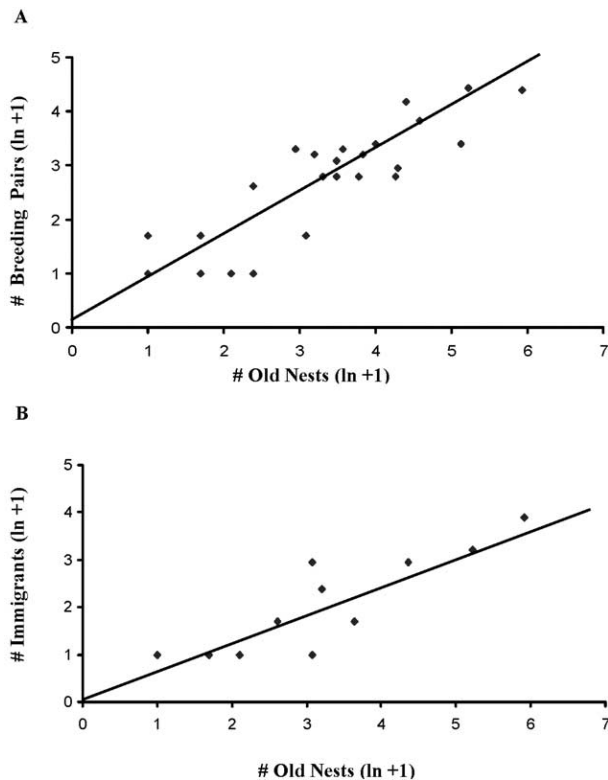
Figure 4: *A*, Number of old nests at a site at the start of the breeding season predicts 83% of the variation in the number of breeding pairs that settle at a site; $n = 36$ different sites ranging in size from one to 31 pairs. *B*, Number of old nests at a site at the start of the breeding season predicts 73% of the number of immigrants that settle at a site; $n = 11$ different sites ranging in size from one to 35 pairs.

should predict the number of breeding pairs that settle at the site in the successive year.

I calculated the differences in group size at the same sites (1) before the nest removal year and during the nest removal year and (2) during the nest removal year and after the nest removal year. Because differences in group size at sites between years may also be a function of larger-scale population demographics, I paired all removal sites with control sites that had approximately the same group size at the start of the experiment. Thus, to control for the possibility of demographic differences between years at sites where nests were removed or left intact, I compared these differences in group size at experimental sites (1 and 2, separately) to (3) differences in group size at the paired (similarly sized nonexperimental) control sites during the same two years.

Relative to differences in group size between years at control sites, there were significant differences in group size between pairs of sites the year before and during nest removals (equal variances $t = -2.52$, df $= 14$, $P < .02$; fig.

5*A*). Relative to differences in group size at control sites, there were no differences in the numbers of breeding pairs during and after the nest removal year (unequal variances $t = 0.47$, df $= 12.91$, $P > .65$; fig. 5*B*).

Discussion

Individual-Level Decisions

Performance-Based Conspecific Attraction Hypothesis. Contrary to studies of other colonial (Danchin et al. 1998; Brown et al. 2000) and noncolonial (Doligez et al. 1999, 2002) birds, I did not find evidence to support the hypothesis that individuals use the average reproductive success of conspecifics as a cue to make site selection decisions in the following year. A primary assumption of the hypothesis, that reproductive success varies among sites within a year, was not strongly supported by data on barn swallows in Ithaca, New York. Another critical assumption of the model, that reproductive success is correlated within a site between years, was not met, suggesting that "public information" in the form of the average reproductive success of individuals at a given site is not reliable between years (table 1). Moreover, I did not find evidence for the predictions of the hypothesis; neither the number of immigrants nor the overall change in the number of breeding pairs was related to the previous success of conspecifics at a breeding site. A primary reason why these results may differ from studies of long-lived black-legged kittiwakes (*Rissa tridactyla*) is that barn swallows, unlike kittiwakes, do not spend several years as nonbreeders before recruiting into the population (Danchin et al. 1998). In a species closely related to barn swallows, cliff swallows (*Petrochelidon pyrrhonota*), Brown et al. (2000) did find evidence to suggest that both first-year breeders and adult cliff swallows settled and moved to sites in a pattern predicted by the PBCA hypothesis. An interesting difference between cliff swallows and barn swallows is that both natal philopatry to the general area and adult breeding site dispersal is much higher in the former species (Shields 1984; Brown and Brown 1996, 1999).

Nest Reuse Hypothesis. In barn swallows, previously constructed nests are both cues and sources of benefits (Hill 1982; Shields et al. 1988; this study). Nest reuse is associated with a 25% increase in seasonal reproductive success compared with individuals who construct new nests for their first breeding attempts (fig. 2). Moreover, as demonstrated by the pattern that fewer immigrants settled at sites where old nests were removed (fig. 3), nests are an important cue for site-unfamiliar individuals. Group composition and size changes as a function of the nest removal treatment because fewer new females settle at sites where
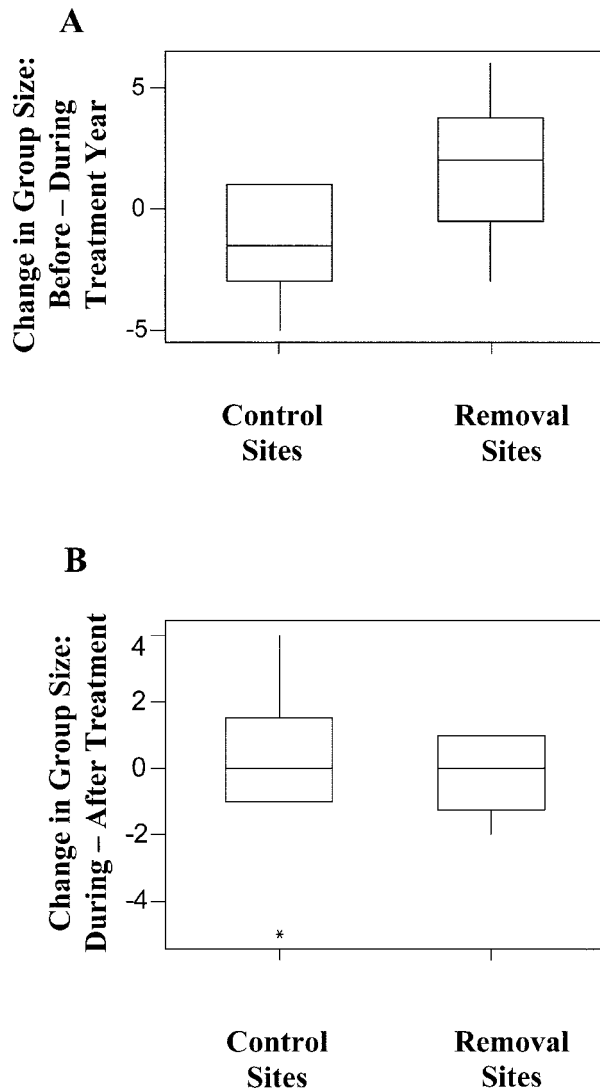
Figure 5: *A,* Changes in group size between the year before nest removal and the year of nest removal are greater than changes in group size during the same two years at control sites with approximately the same number of breeding pairs at the start of the experiment, demonstrating that group size decreases during the removal year (*n* = 8 experimental and control sites). *B,* Changes in group size between the year during and the year after the nest removal are not different from changes in group size during the same two years at control sites with approximately the same number of breeding pairs at the start of the experiment (*n* = 10 experimental and control sites).

old nests have been removed. This pattern is similar when comparing the proportion of new females at different control and removal sites (fig. 3*A*) and within sites that received different treatments in successive years (fig. 3*B*). Taken together, the results of the nest removal experiment demonstrate that new breeders use a site selection strategy

that incorporates the presence of old nests, as suggested by the strong relationship between the number of old nests at a site at the start of a season and the number of immigrants that settle at those sites (fig. 4*B*). Although new females do appear at removal sites, they do so in much lower frequencies than at sites where old nests are intact at the start of the season. I regularly detect an influx of juveniles from outside my study area at the end of the summer who might be prospecting for future breeding locations. However, the results of this study suggest that an important component of their decision making process is the presence of old nests at sites at the start of the breeding season, directly prior to settlement.

Results of this study also demonstrate that, regardless of the removal of old nests, experienced breeders appear to be following the decision rule to be site faithful (fig. 3). In no case did I observe dispersal from a removal site to a nearby site where old nests remained intact at the beginning of the breeding season. However, this does not contradict the hypothesis that old nests are a habitat settlement cue. Because there are strong fitness-related benefits associated with using old nests (fig. 2) and because it may be an evolutionarily novel, if not naturally rare, event for all old nests to be removed at a breeding site between years, a reasonable hypothesis is that site fidelity may, in part, have been selected for as an efficient mechanism for relocation of a site with old nests (see, e.g., Schlaepfer et al. 2002). Put another way, for new breeders, a cue for settlement is the resource, whereas for experienced breeders, site fidelity provides a quick, cheap, and—in the absence of human manipulation—reliable way of locating the same resource.

It could be argued that the traditional approach to explaining group size—looking for differences in average reproductive success across groups of different sizes—could be used to construct a third hypothesis about the decision rules of individuals. Specifically, this hypothesis would be that individuals will settle at sites that have an optimal number of conspecifics. This optimal group size hypothesis predicts that much larger than optimal groups should shrink, whereas smaller than optimal groups should either grow toward an optimum or shrink as individuals move out to settle in better-sized groups. However, note that no predictions can be made without first validating the assumption that one or more group sizes are indeed optimal. Figure 1 falsifies this assumption, making the optimal group size hypothesis inappropriate for consideration in barn swallows.

Group Size Variation

The number of old nests at a site at the start of the season explains a large amount of the variation in group size (fig.

4*A*). However, because site fidelity is the rule in barn swallows that have breeding experience, group breeding will persist even in the absence of old nests, suggesting strong benefits of site familiarity (fig. 3). Thus, in order to truly demonstrate that group size is a function of individuals searching for old nests, it is critical to demonstrate a relationship between the number of immigrants that settle at sites and the number of old nests at the site at the start of the season. The facts that the proportion of immigrants was significantly lower during removal years (fig. 3) and the number of immigrants was positively related to the number of old nests (fig. 4*B*) provide compelling evidence that group size is strongly influenced by the number of new breeders at a site, which is, in turn, a function of the number of old nests at a site at the start of the breeding season. This strong relationship between the number of old nests and the number of immigrants that settle at a site suggests that immigrants not only use old nests as a cue for settlement decisions but that they settle with a probability that is proportional to the number of old nests at a breeding location.

I detected a change in group size from the year before the nest removals to the year during the nest removals. Interestingly, this change was in the opposite direction of changes in group size at pairs of control sites (fig. 5*A*). While group size increased slightly at control sites, the number of breeding pairs decreased at sites where old nests were removed. Thus, the change in group size before and during nest removal years is not a reflection of changes in population size or density. Rather, the reduction in group size is attributable to fewer new settlers at removal sites. Additionally, there were no differences in group size during and after the removal year (fig. 5*B*). This suggests that once new nests are constructed and remain intact for subsequent breeding seasons, they offer important information to individuals who lack prior experience at the site. Thus, these experience-related site selection decisions, demonstrated by shifts in the proportion of new and old individuals at sites where old nests were experimentally removed, have interesting consequences for patterns of group size variation.

Conclusions

Very little progress has been made in explaining the tremendous amount of variation in breeding group size among the many species that breed colonially (reviewed in Brown and Brown 2001). Here, I offer and test a new approach for understanding how and why patterns in group size variation are maintained by examining the site selection decision rules of individuals and determining whether they predict patterns of group size variation. In barn swallows, I demonstrate that an adaptive site selection

rule to reuse old nests has important population-level consequences. The number of old nests at a site, a cue important in site selection decisions of immigrants, explains an extraordinary amount of variation in the number of breeding pairs that settle at the time. Although the use of old nests per se might not function similarly in all species that reuse nests (e.g., cliff swallows; Brown and Rannala 1995), in most systems, we expect that organisms will use cues that predict fitness-related benefits. It has been widely observed that individuals in other taxa prospect for breeding sites before settlement decisions are made (Reed et al. 1999). Thus, in many systems we can ask the question, How does the use of a particular cue relate to larger-scale patterns?

The examination of links between individual-level decisions and population-level patterns is applicable to a number of behavioral and evolutionary questions (Sutherland 1996; Smith et al. 2000; Cam et al. 2002). For example, how do cues in an organism's environment influence individual behavior, and how does this behavior, in turn, affect demographics, population viability, and community structure? Or, as a specific example, how do dispersal strategies of individuals affect characteristics of populations including demographics and genetic structure? Such questions about individual-level behavior and population-level patterns are usually addressed in isolation from one another, but it is the relationship between these two levels that provides powerful predictive information about the effects of individual behavior on the patterns within and dynamics of populations. For example, if long-distance dispersal movements maintain genetic variability within and among populations, it is important to study and be able to predict the behavior of individuals that disperse far from their natal territories. As such, there is an obvious application of this method to a number of conservation- and management-related problems. For example, it is critical to identify the cues animals use for habitat selection and their effects on population dynamics long before management plans are put in place (Bradbury et al. 2001; Sutherland and Norris 2002). Moreover, it is important to recognize cases where animal populations decline as a consequence of using habitat selection cues when they are no longer reliable in a rapidly changing environment (Schlaepfer et al. 2002). The approach of determining the relevant cues and strategies involved in habitat selection thus provides an exciting research protocol for developing rigorous links between behavioral ecology (which has traditionally focused only on within-population dynamics) with population, community, and ecosystem processes.

Acknowledgments

Literature Cited

Barclay, R. M. R. 1988. Variation in the costs, benefits, and frequency of nest reuse by barn swallows. Auk 105: 53–60.

Boulinier, T., and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evolutionary Ecology 11:505–517.

Bradbury, R. B., R. J. H. Payne, J. D. Wilson, and J. R. Krebs. 2001. Predicting population response to resource management. Trends in Ecology & Evolution 16:440–445.

Brown, C. R., and M. B. Brown. 1996. Coloniality in the cliff swallow. University of Chicago Press, Chicago.

———. 1999. Barn swallow (*Hirundo rustica*). The birds of North America, ed. A. Poole and F. Gill. No. 452. Birds of North America, Philadelphia.

———. 2000. Heritable basis for choice of group size in a colonial bird. Proceedings of the National Academy of Sciences of the USA 97:14825–14830.

———. 2001. Avian coloniality: progress and problems. Current Ornithology 16:1–82.

Brown, C. R., and B. Rannala. 1995. Colony choice in birds: models based on temporally invariant site quality. Behavioral Ecology and Sociobiology 36:221–228.

Brown, C. R., B. J. Stutchbury, and P. D. Walsh. 1990. Choice of colony size in birds. Trends in Ecology & Evolution 5:398–403.

Brown, C. R., M. B. Brown, and E. Danchin. 2000. Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. Journal of Animal Ecology 69:133–142.

Cam, E., B. Cadiou, J. E. Hines, and J. Y. Monnat. 2002. Influence or behavioural tactics on recruitment and reproductive trajectory in the kittiwake. Journal of Applied Statistics 29:163–185.

Cramp, S., ed. 1988. The birds of the western Palearctic. Vol. 5. Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology & Evolution 12:324–347.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.

Doligez, B., E. Danchin, J. Clobert, and L. Gustafsson. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. Journal of Animal Ecology 68: 1193–1206.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168–1170.

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Hill, J. R. H. III. 1982. Reproductive success in the barn swallow: effects of nest reuse and age. M.S. thesis. Pennsylvania State University, University Park.

Krebs, J. R., and N. B. Davies. 1981. An introduction to behavioural ecology. Sinauer, Sunderland, Mass.

Møller, A. P. 1987. The advantages and disadvantages of coloniality in the swallow *Hirundo rustica*. Animal Behaviour 35:819–832.

———. 1990. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. Ecology 71: 2345–2357.

Pulliam, R., and T. Caraco. 1984. Living in groups: is there an optimal colony size? Pages 122–147 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Sinauer, Sunderland, Mass.

Reed, M. R., T. Boulinier, E. Danchin, and L. W. Oring. 1999. Informed dispersal: prospecting by birds for breeding sites. Current Ornithology 15:189–259.

Rice, W. R., and S. D. Gaines. 1994. "Heads I win, tails

you lose": testing directional alternative hypotheses in ecological and evolutionary research. Trends in Ecology & Evolution 9:235–237.

Safran, R. J. 2004. From individuals to populations: female decisions and group size variation in barn swallows. Ph.D. diss. Cornell University, Ithaca, N.Y.

SAS Institute. 1990. SAS/STAT user's guide, version 6, 4th ed., vol. 2. SAS Institute, Cary, N.C.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474–480.

Shields, W. M. 1984. Factors affecting nest and site fidelity in Adirondack barn swallows. Auk 101:780–789.

Shields, W. M., and J. R. Crook. 1987. Barn swallow coloniality: a net cost for group breeding in the Adirondacks? Ecology 68:1373–1386.

Shields, W. M., J. R. Crook, M. L. Hebblethwaite, and S. S. Wiles-Ehmann. 1988. Ideal free coloniality in the swallows. Pages 189–228 *in* C. N. Slobodchikoff, ed. The ecology of social behavior. Academic Press, San Diego, Calif.

Sibley, R. M. 1983. Optimal group size is unstable. Animal Behaviour 31:947–948.

Smith, C., J. D. Reynolds, and W. J. Sutherland. 2000. Population consequences of reproductive decisions. Proceedings of the Royal Society of London B 267:1327–1334.

Snapp, B. D. 1976. Colonial breeding in the barn swallow and its adaptive significance. Condor 78:471–480.

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.

Sutherland, W. J., and K. Norris. 2002. Behavioural models of population growth rates: implications for conservation and prediction. Philosophical Transactions of the Royal Society of London B 357:1273–1284.

Tregenza, T. 1995. Building on the ideal-free distribution. Advances in Ecological Research 26:253–307.

Wagner, R. H., E. Danchin, T. Boulinier, and F. Helfenstein. 2000. Colonies as by-products of commodity selection. Behavioural Ecology 11:572–573.

White, G. C., and K. P. Burnham. 1999. Program mark: survival estimation from populations of marked animals. Bird Study 46:120–139.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. American Naturalist 115:449–466.

Winkler, D. W., and F. H. Sheldon. 1993. Evolution of nest construction in swallows (Hirundinidae): a molecular phylogenetic perspective. Proceedings of the National Academy of Sciences of the USA 90:5705–5707.