

Settlement patterns of female barn swallows *Hirundo rustica* across different group sizes: access to colorful males or favored nests?

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Abstract In most avian species, individuals are faced with two critical decisions at the start of a breeding season: choosing a breeding site and a mate. An analysis of these decisions in light of population-level patterns, such as group size variation in social breeders, can illuminate the causes and patterns of habitat selection behavior. Group sizes are variable in barn swallows; however, no clear and consistent benefits of group breeding have been found in this species, and it is puzzling as to why individuals breed socially. Previous analyses demonstrated that individuals aggregate to gain access to nests that were constructed during previous seasons; however extra-pair matings are also prevalent in this species, raising questions about the mate-selection strategies of females across different group sizes. In this paper, I address the question of how females make their first site-selection decisions in terms of two features known to be causally related to seasonal reproductive success: (1) colorful males or (2) old nests. Using experimental and observational data, I tested, but found no support for, the hypotheses that propose female settlement decisions are a function of (1) the prevalence of colorful males or (2) the increased opportunity for extra-pair matings at group sites. Instead, it is apparent that female

settlement patterns are strongly tied to the availability of old nests at a site. Extra-pair fertilizations are equally common across all group sizes in this population, suggesting that females do not face a trade-off between old nests and the possibility of extra-pair mating decisions when making settlement decisions.

Keywords Barn swallow · Extra-pair paternity · Feather color · Group size · Habitat selection · *Hirundo rustica* · Mate selection · Nest reuse · Nest selection

Introduction

While traditional models of group breeding have focused on the types of costs and benefits that are incurred (e.g., Alexander 1974), on average, to individuals living in groups, more recent approaches have focused on the actual decision rules that individuals employ when joining groups at the start of the breeding season (e.g., Danchin and Wagner 1997; Safran 2004; Doerr et al. 2006). A focus on individual- instead of group-level patterns is fruitful because it recognizes that population-level patterns—such as the nearly universal existence of variation in breeding group sizes within populations of socially breeding species—reflect the underlying decision rules employed by individuals. In other words, variation in group-level characteristics may thus be seen as arising from variation in the input to or output from algorithms that individuals use in selecting the groups to which they belong. Most importantly, from an evolutionary perspective, natural selection shapes population-level patterns (such as group size) through its effects on individual decision rules rather than by directly affecting properties of groups per se (Safran 2004). As such, it is these decision rules that should be

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the focus of studies interested in explaining the maintenance of patterns in group breeding, such as variation in group size.

An important contribution to the study of individual-based decision rules and their consequences for population-level patterns, like the formation of breeding groups, has been the development and testing of the conspecific attraction (CA) hypothesis (Shields et al. 1988; Reed and Oring 1992; Cadiou et al. 1994; Boulinier and Danchin 1997; Danchin et al. 1998). The CA hypothesis proposes that individuals use habitat-based cues and conspecific signals for making settlement decisions at one site over another. In particular, Danchin and Wagner (1997) highlighted the CA hypothesis as an explanation for colony formation in birds and emphasized its focus on individual decisions. Recent models for studying the maintenance of group size variation have included an analysis of nest-site- (Danchin and Wagner 1997; Safran 2004) and mate-selection decisions (Morton et al. 1990; Wagner 1993; Wagner et al. 1996; Hoi and Hoi-Leitner 1997; Danchin and Wagner 1997). These two parameters (breeding sites and mates) comprise critical resources for survival (e.g., shelter) and reproduction (e.g., aspects of mates that affect seasonal reproductive success), and as such, natural selection has likely shaped settlement patterns that incorporate these factors (Safran 2004).

A focus on individual-based decision rules is applicable to a number of different social breeding systems, including those in which individuals do (e.g., cooperative defense against predators and social foraging) and do not derive benefits from breeding in close association with neighbors. In fact, these hypotheses are better suited to the latter case because traditional cost and benefit models for group breeding would yield equivocal results when no group-average benefits are found for these populations. Indeed, there is evidence that group living may occur in species that do not obtain benefits from breeding close to neighbors as a consequence of individuals seeking critical mate or habitat resources that are patchily distributed (Alexander 1974; Danchin and Wagner 1997; Brown and Brown 2001), including barn swallows *Hirundo rustica* (Snapp 1976; Shields and Crook 1987; Shields et al. 1988; Safran 2004; but see Møller 1987). In these cases, it is most efficient to examine the maintenance of group breeding as an emergent property of individual-level decisions about where to breed and with whom to mate.

Throughout their extensive Holarctic breeding range, barn swallows breed in solitary pairs or with groups of conspecifics; they are not obligately social breeders (Brown and Brown 1999). Typically, colony sizes range from 2 to 200 breeding pairs (Cramp 1988). In North American populations, the majority of individuals typically breed either solitarily or in groups ranging from 9 to 35 pairs

(Shields et al. 1988; Brown and Brown 1999; Safran 2004). 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; Safran 2004). Further, research on barn swallow sociality has shown either no relationship between average reproductive success and group size (e.g., Snapp 1976; Safran 2004) or a negative relationship between average reproductive success and group size (e.g., Shields and Crook 1987), leaving open the question of why individuals breed socially.

Group size variation in barn swallows, and other social breeders, offers a natural experimental setting in which to test the role of nest-site and mate-selection rules for the process of site selection in the context of both solitary and social breeding. In terms of nest-site selection, it has been previously demonstrated that the reuse of nests that were constructed in previous breeding seasons (hereafter 'old nests') strongly predicts settlement patterns and the eventual group size at breeding sites (Safran 2004). Once constructed, old nests can persist in the environment for decades, and the majority of breeding pairs at site will attempt to refurbish or reuse these structures instead of constructing new ones (Barclay 1988; Hill 1982; Shields et al. 1988; Briceno 2002; Safran 2006). Experimental studies have demonstrated a strong relationship between old nest reuse and seasonal measures of reproductive success such that individuals settling in old nests have advantages over individuals spending up to 2 weeks constructing a new nest at the start of a breeding season, regardless of their previous breeding experience (Safran 2006). Whereas the reuse of previously constructed nests explains much of the variation in breeding group size in barn swallows such that the number of old nests at a site at the start of the season is a strong predictor of the number of breeding pairs that eventually settle there (Safran 2004), the relative significance of this variable compared to attributes of social and genetic mates is not known.

Indeed, mate-selection decisions are also likely to play an important role in the settlement decisions of females. Previous research on this population of barn swallows identified a causal relationship between male ventral coloration and female mate-selection decisions, such that the most colorful males and their mates have greater seasonal reproductive performance (both social and genetic reproductive success) compared to duller-colored males and their mates (Safran and McGraw 2004; Safran et al. 2005). Extra-pair fertilizations (EPFs) are prevalent in this species (Smith et al. 1991; Safran et al. 2005; Kleven et al. 2006; Neuman et al. 2007) and may also influence the site-selection decisions of individuals (e.g., Morton et al. 1990; Wagner 1993; Hoi and Hoi-Leitner 1997), thus warranting a test of whether a benefit of group breeding to females is greater access to extra-pair males.

As is typical in many migratory birds that are territorial during the breeding season, male barn swallows arrive earlier to breeding sites to defend a potential nest location (Wolinksi 1981; Brown and Brown 1999). As such, later-arriving females are likely able to simultaneously assess both site and male quality when making settlement decisions. Thus, in this study, I used observational and experimental data to determine whether females choosing breeding sites for the first time prioritize access to colorful males or sites with available old nests, or an interaction of these two variables, when they are making site-selection decisions (Table 1) and how these decisions may vary among different group sizes. Because site fidelity is strong, but natal philopatry is very weak in barn swallows (Shields 1984; Safran 2004), I examined the settlement patterns of first-year breeding females that have no prior experience as a breeder in our study area.

Materials and methods

From 1999–2002, 15 field assistants and I studied a population of barn swallows comprising 29 breeding sites (a subset of our larger study area) ranging in size from 1 ($n=7$ solitary sites) to 35 pairs in Tompkins County, NY (42°30'N, 76°28'W). Sample sizes are indicated for each experiment and analysis below. Sample sizes for each analysis vary owing to, for example, the inclusion or exclusion of various sites depending on the experiments conducted there and whether or not I was able to capture all individuals in two successive years for robust estimates of recapture status.

Using mist nets, we captured swallows during the first 2 weeks of the breeding season. The individuals were uniquely marked with numbered aluminum rings and

enamel-based paints, and a variety of standard morphological measurements were recorded (e.g., tail streamer length). We checked nests daily to determine breeding onset, number of nesting attempts (1 or 2), and annual reproductive success (total young fledged). We also identified pairs as they nested.

Plumage-color scoring We sampled patches (three to ten feathers) of ventral plumage from four standardized body regions along a ventral transect of each individual (throat, breast, belly, and vent regions) and carefully mounted these colored feathers on an index card as to recreate the natural plumage appearance of the bird. These cards were stored in the dark until plumage-color scoring. The color of feather samples was scored along three traditional axes of color (hue, saturation, and brightness) using a reflectance spectrophotometer (Colortron™; Light Source, San Rafael, CA; Hill 1998); this spectrophotometer does not quantify light in the ultraviolet range, which is sufficient for this species because the ventral plumage of barn swallows does not exhibit a unique ultraviolet reflectance peak (Safran and McGraw 2004). Each plumage patch was scored three times, and we averaged these scores to determine the mean hue, saturation, and brightness for the throat, breast, belly, and vent of each swallow. These 12 plumage measures were moderately to highly repeatable ($r=0.64–0.94$) for a subsample of individuals (Safran and McGraw 2004). Color scores were significantly intercorrelated within (all $p<0.001$, all r between 0.67 and 0.82), but not among, ventral regions, so a color-scoring scheme to summarize data was devised separately for each of the four plumage areas. Principal components analysis was used to collapse hue, saturation, and brightness scores within each plumage region. The first principal component (PC1) for throat, breast, belly, and vent explained 81–85%

Table 1 Hypotheses with predictions

Question	Hypothesis/prediction	Test
Is the distribution of males across different group sizes non-random?	Relationship between male quality and group size	Analyzed the throat color of males as a function of group size and nest-site treatment (nest removal experiment)
Does male distribution influence the settlement and reproductive decisions of females across different group sizes?	Females settle at sites with the greatest number of colorful males; predicts a positive relationship between male color and the number of females that settle at a site	Analyzed the number of new females at sites as a function of male at sites using observational and experimental (nest removal) data
	Females settle at sites in order to gain access to extra-pair males; predicts positive relationship between group size EPF rate	Analyzed relationship between extra-pair fertilizations and group size using observational and experimental data
What is the relative significance of the number of old nests and the color of males on the settlement decisions of females across different group sizes?		Analyzed the number of new females at sites as function of both the proportion of dark males and the number of old nests at a site

of the variation in the color scores of each plumage region in both sexes. Birds with lower PC1 scores have redder (lower hue values), more saturated, and darker (lower brightness values) plumage.

Although color in all four ventral patches is intercorrelated, throat coloration in the males is most strongly correlated to indicators of seasonal reproductive success (Safran and McGraw 2004). As such, I report patterns of female settlement as a function of male throat coloration, although data collected from other regions provide similar results.

Male distributions Because the number of new females at a site, the response variable in many analyses in this study, is a group-level measure, I also needed a group-level measure for male color. Instead of using average color at a site, which may be confounded by the sample size and variability of the males at a site, I calculated for each site the proportion of the males that were in the top 50% of color distribution of all the males in the population and used this as a group-level indicator of the color of the males present at a site.

Nest removal experiment To tease apart the potential confound between male and nest quality, I used nest removal experiments to compare distributions of the males at sites with and without available old nests at the start of the breeding season. Nests were removed at eight sites where measurements of male quality were also recorded later in the season. The group sizes at these removal sites in the previous year were highly correlated with the number of old nests there (83% of the variation in group size is explained by the number of old nests at a site; Safran 2004) and ranged from 4 to 19 breeding pairs (mean \pm SD=11.14 \pm 5.87). All old mud nests that remained intact from previous breeding seasons were removed, and their scars were scraped away and covered during the late winter, well before the birds returned in mid-April (Safran 2004).

Within-pair paternity and group size To evaluate predictions related to the prevalence of extra-pair matings and group size, I assessed the within-pair paternity in the first broods of 53 females across 22 sites that varied in size, ranging from 1 to 35 pairs. I used three polymorphic microsatellite loci for genetic parentage analyses: HrU6, HrU7 (Primmer et al. 1995), and HrU10 (Primmer et al. 1996), two of which are hypervariable (Saino et al. 1997; Brohede et al. 2002). The mean heterozygosities of these three loci were 0.92, 0.47, and 0.95, respectively, and the total probability of paternal exclusion using all three loci is 0.997. Details about our laboratory methods and analyses can be found in Safran et al. (2005) and Neuman et al. (2007).

EPF experiment I experimentally simulated the nest failure of 17 pairs across different group sizes to test the prediction that the males in groups will lose more paternity in their replacement clutches compared to the males at solitary sites. I analyzed within-pair paternity before and after a nest failure for 17 pairs at sites ranging in size from 1 to 23 pairs. At ten sites I (1) allowed a female to settle with a mate to lay a complete clutch of eggs, (2) experimentally removed this first clutch of eggs, and thereby induced her to (3) lay a replacement clutch. I collected a DNA sample from each embryo in the first clutch and from each nestling in the replacement brood to compare differences in paternity between two breeding attempts as a function of group size. I calculated differences in paternity between the two breeding bouts as the paternity in the replacement clutches minus paternity in the first clutches. Thus, the males that lost paternity from their social mates had a difference value lower than zero, and the males that gained paternity had a difference value greater than zero.

The males included in this experiment were from two different types of control groups as part of a larger experiment. Before pooling males from the two different control groups for this investigation, I made the following comparisons to ensure that aspects of these males would not confound the results of this analysis. First, the average clutch initiation dates of males in both control groups did not differ (Student *t* test, $t=0.54$; $P=0.60$; $df=14$). I found no differences in the within-pair paternity of first (unequal variance *t* test, $t=0.55$; $P=0.59$; $df=13.18$) and replacement clutches (unequal variance *t* test, $t=-1.150$; $P=0.28$; $df=8.13$).

Statistical analyses SAS (version 9.1) was used for all statistical analyses. Locally weighted scatter plot smoothers (LOWESS curves) were used to explore the relationship between two variables without fitting an a priori functional form. These LOWESS curves enable one to determine whether linear models would be suitable for modeling the relationships between two variables (Neter et al. 1996). Nonparametric analyses were applied when aspects of the data did not conform to the restrictions of parametric analyses, e.g., severe nonlinear relationships that could not easily be modelled with higher order terms in linear models (Hollander and Wolfe 1999). These cases are noted in Results.

I employed mixed linear models (Littell et al. 1996; Neter et al. 1996) in cases where the data included repeated observations from one sample unit (e.g., the color of multiple males within one breeding site). In these cases, the variable 'site' was included as a random effect in the model.

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).

Results

Male distributions

After controlling for repeated samples of the males within breeding sites, I detected a negative relationship between how colorful the males were and group size, suggesting that the males at solitary sites are actually darker in color compared to the males in group sites (mixed linear model with 'site' as a random effect: $F_{1,26}=5.44$, $P=0.02$; no effect of site per se; Fig. 1; note that Fig. 1 shows a positive relationship because a lower color score is indicative of a more colorful individual; see [Materials and methods](#) for explanation). The effect of the nest removal treatment (intact or removed) was also significant in this model where the color of the males differed at control sites (old nests were intact at the start of the breeding season), and nest removal sites (mixed linear model, $F_{1,1}=4.57$; $P=0.03$); the average least square mean differences for the color of the males at removal sites (PC1 score for throat color \pm SE = -0.27 ± 0.19) is lower (males are darker in color) compared to the color of the males at control sites where old nests from previous breeding seasons remained intact (-0.24 ± 0.17 ; t test, $t=2.40$, $P=0.02$, $df=229$).

The average group size for males in the top 50% of the throat color distribution was significantly lower (mean \pm SD = 14.87 ± 11.06) compared to males in the lower half of the throat color distribution (mean \pm SD = 19.35 ± 10.89 ; two-sample t test with unequal variances; $t=3.08$, $P=0.002$, $df=$

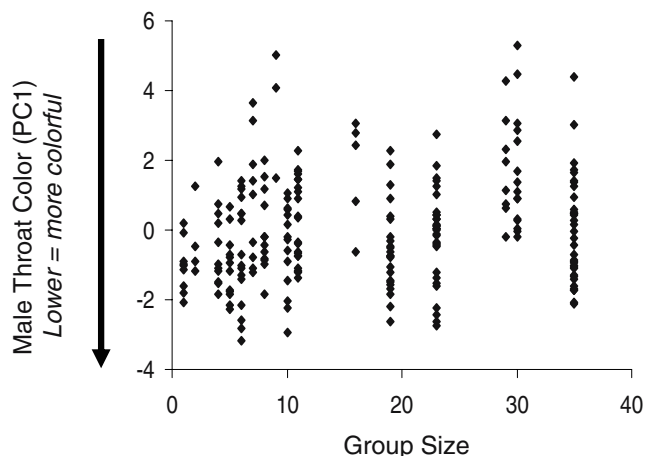


Fig. 1 Darker males were found at smaller sites ($n=229$ males across 27 sites ranging in group size from 1 to 35 breeding pairs)

226.87), corroborating the pattern that darker males are found in smaller sites.

Female settlement patterns and male coloration

No statistically significant relationship was detected between the number of new females and the proportion of dark males at a site, regardless of the presence or absence of old nests (multiple regression $F_{1,14}=0.63$, $P=0.54$: effect of proportion of males: $t=1.11$, $P=0.28$, Fig. 2, effect of nest removal treatment: $t=-0.12$, $P=0.91$). Interestingly, group size had an effect on the color of the males to which new females were paired; new females at solitary sites were paired to darker males compared to the color of mates that new females paired with at group sites (linear regression, $F_{1,22}=4.94$; $P=0.04$).

Female settlement patterns and the prevalence of EPFs

I found no statistically significant relationship between group size (which is strongly correlated to the number of new females at a site; Safran 2004) and within-pair paternity (mixed model: $F_{1,51}=0.05$, $P=0.82$, random effect site is not significant; Fig. 3). I also analyzed EPFs as a function of different group size categories that have previously been employed in analyses of barn swallow social behavior (Snapp 1976) and found no relationship between paternity and group size using this test (one-way ANOVA, $F_{1,52}=0.18$; $P=0.91$). Finally, I found no statistically significant difference in the within-pair paternity for first clutches when I grouped pairs into categories based on whether they bred solitarily (mean within-pair paternity \pm SD = 0.8 ± 0.28 , $n=7$) or in groups (mean \pm SD = 0.75 ± 0.30 , $n=46$; two sample t test: $t=-0.36$, $P=0.72$, $df=51$).

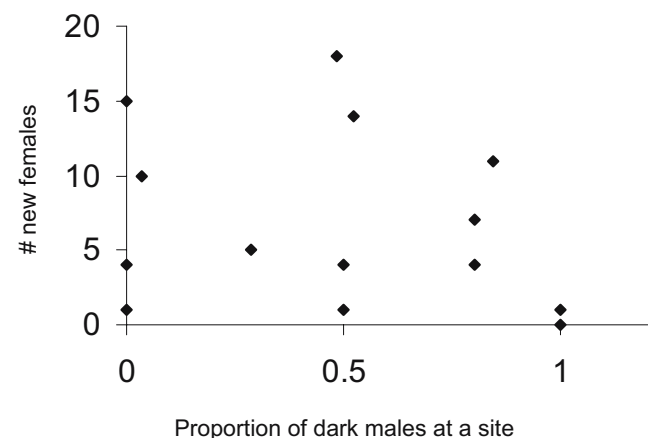
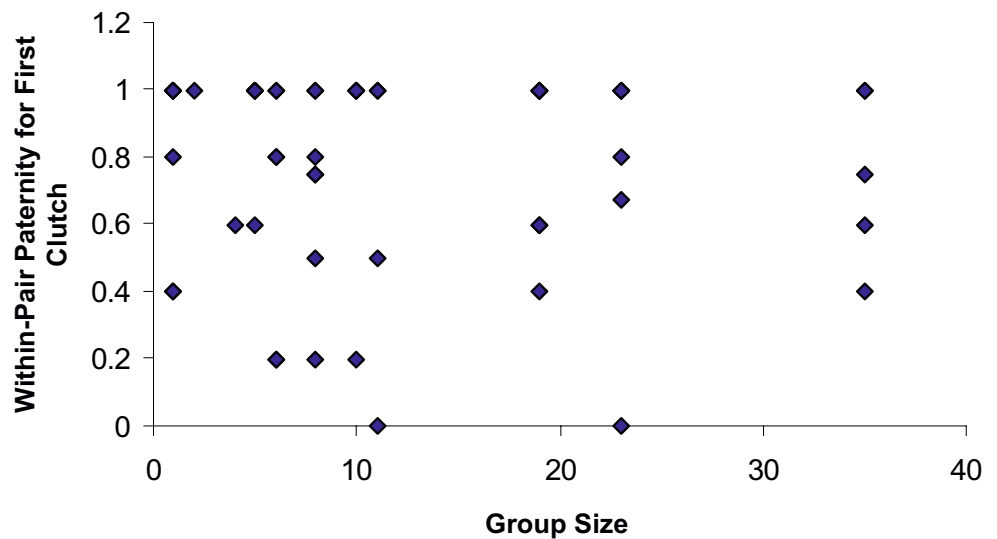


Fig. 2 The settlement patterns of first-time breeding females as a function of the proportion of dark males at 14 sites in Tompkins County, NY

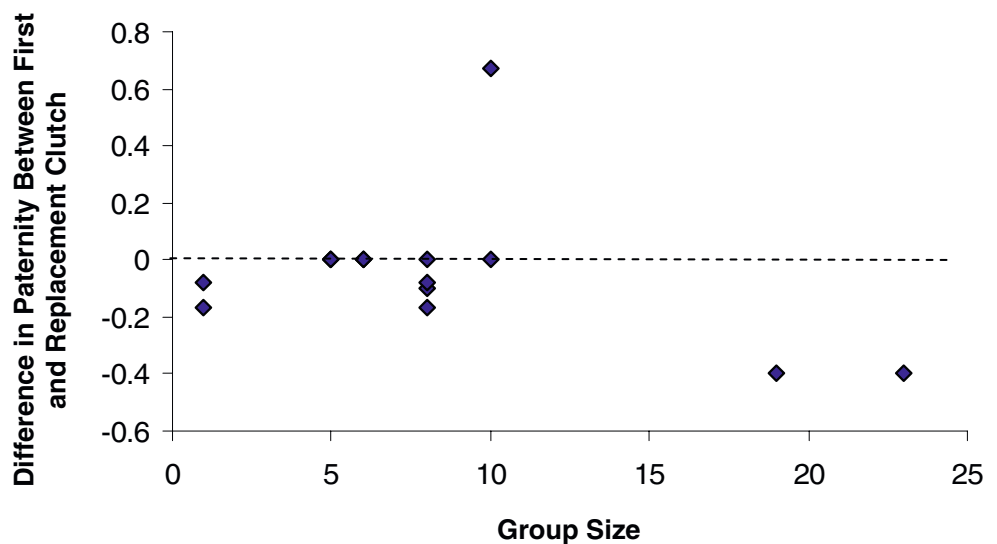
Fig. 3 Relationship between within-pair paternity for first breeding attempts and group size (number of breeding pairs at a site); $n=53$ pairs, 22 sites



EPF experiment

Only 2 of 17 (12%) experimental pairs did not initiate replacement clutches after their first clutch was experimentally removed. All of the remaining 15 females initiated clutches with the same social mate, but one of these pairs laid a replacement clutch that was abandoned before the embryos were developed enough to obtain DNA. Thus, the final sample size for this experiment is 14 pairs. Of the 14 pairs, eight moved to different nests (all within the same breeding site) for their second breeding attempts; moving to a different nest within the same territory did not affect the paternity outcomes of males in this experiment (unequal variance two-sample t test, $t=-1.82$, $P=0.11$, $df=7.48$). I found no differences in the within-pair paternity of first and replacement clutches as a function of group size (Spearman rank nonlinear correspondence; $r_s=-0.20$, $P=0.47$, $n=14$; Fig. 4).

Fig. 4 Changes in paternity in between first and replacement broods after the first clutch of eggs was experimentally removed to simulate a nest failure; $n=14$ pairs, 10 sites. *Dashed line* is equivalent to no changes in within-pair paternity between first and replacement broods. Values below this line indicate that males received less paternity in the replacement broods



Female settlement patterns: old nests vs male color

When examined together simultaneously using multiple regression, I found that the number of old nests, not the proportion of dark males at a site, strongly predicted the number of new females that settled at a breeding site (multiple regression: $F_{2, 7}=46.81$, $P<0.001$, adjusted $R^2=0.93$; number of old nests: $t=8.97$, $P<0.001$, proportion of males in the top 50% of the distribution of throat color: $t=-0.26$, $P=0.81$; Fig. 5).

Discussion

Recent approaches for understanding the maintenance of patterns in group breeding have focused on identifying individual-based settlement decisions, rather than group-based costs and benefits (Danchin and Wagner 1997; Safran

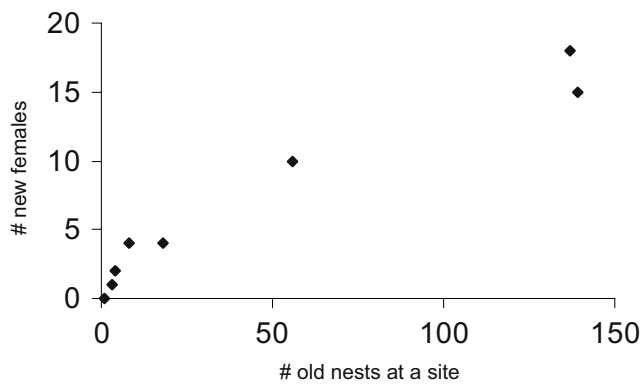


Fig. 5 The number of old nests at a site predicts 95% of the variation in the number of new females that settle there as breeders; $n=8$ sites.

2004; Doerr et al. 2006). The former approach uses known signals and cues related to decision rules that are likely formed by natural selection because they have significant reproductive consequences. The use of these conspecific signals can be instrumental in identifying the underlying causes of group breeding, in addition to the proximate cues that individuals use when making site-selection decisions. This approach can be particularly illuminating in cases where there are no obvious benefits associated with breeding close to conspecifics—as is the case in barn swallows (Shields and Crook 1987; Safran 2004)—because group-average analyses are likely to yield confusing results (Safran 2004).

In this study, I analyzed the settlement patterns of new females as a function of two signals previously identified as being causally related to seasonal reproductive success in a large population of barn swallows (Safran 2004; Safran and McGraw 2004; Safran et al. 2005; Safran 2006): (1) a measure of male quality (ventral color); and (2) a measure of site quality (the presence of an old nest). Following the CA hypothesis outlined in Danchin and Wagner (1997), this study was designed to test the relative significance of mate and habitat characteristics across different breeding group sizes. Taking advantage of the fact that barn swallows breed both solitarily and in large groups, I examined the relative significance of these signals for explaining group size variation, a pattern of group breeding that is nearly ubiquitous, but often puzzling, among socially-breeding organisms.

The results of this paper suggest a biased distribution in the males with respect to ventral color: the darker males tended to settle at solitary and smaller sites, while the lighter males were more often found in large groups (Fig. 1). How does the distribution of the males, based on a known signal of quality, affect the settlement patterns of the females? A priori, I predicted that a possible explanation for why females settle in groups is that there are more

colorful males as potential social or genetic mates at large breeding sites; however, such an explanation would predict the opposite of what was found. Indeed, fewer new females were found at sites with the greatest proportion of dark males (Fig. 2), as these dark males were found most often at solitary and small sites. The females at solitary and small sites were paired with the darker males, on average, compared to the females at group sites, corroborating evidence that the number of new females at a site is not strongly associated with this measure of male quality. While additional aspects of male quality are known to predict seasonal reproductive performance in other populations of barn swallows (e.g., age and tail streamer length; Saino et al. 1997 and 2003) and could influence the settlement patterns of first-time breeding females, previous analyses in this population did not detect any patterns with additional phenotypic measures of males (RJS unpublished data). Thus, it does not appear that male color, per se, or other indicators of male quality that I have analyzed, strongly influenced the settlement patterns of female barn swallows in this study.

While evidences for relationships between EPF rates and breeding density are not consistent among species (e.g., Westneat and Sherman 1997; Griffith et al. 2002), at least one investigator found an increase in extra-pair copulations with group size in barn swallows (Møller 1994). Therefore, in barn swallows, it is plausible that females choose to settle in groups where they may have increased opportunities for extra-pair matings, as has been observed in other systems (e.g., Wagner 1993; Hoi and Hoi-Leitner 1997). However, the results of this study suggest that the females are just as likely to seek extra-pair mates in solitary and small sites as they are at group sites (Fig. 3), countering some of the predictions of the Hidden Lek Hypothesis (Morton et al. 1990; Wagner 1993; Danchin and Wagner 1997; Tarof et al. 2005) and other theoretical considerations that propose a relationship between EPFs and breeding density (Møller and Birkhead 1993).

More compelling than a lack of a pattern between group size and within-pair paternity are the experimental results of our study. Failures of first nesting attempts are common in barn swallows. Regardless of group size, approximately 20% of all first clutches are lost to predators or abandoned during bad weather (Safran unpublished data). Divorce rates between breeding seasons are higher after a failed breeding attempt in other species (Coulson 1966; Streif and Rasa 2001) suggesting that females base their decisions on the success of previous breeding bouts. As such, if females breed in groups to gain additional access to extra-pair males, one might predict that after a nest failure, females in groups will also be more likely to have mixed paternity in replacement clutches compared to females at solitary sites. However, I found that males at solitary sites and in groups

were equally as likely to lose paternity between the successive reproductive bouts (Fig. 4).

A potential weakness of these data is the measure of within-pair paternity (via paternity exclusions) across different group sizes, rather than both within and extra-pair paternity (via paternity assignments). However, that solitary pairs have EPF rates similar to group-breeding pairs (Fig. 3) provides persuasive evidence that access to extra-pair males per se is neither a limitation for solitary breeding females, nor a benefit of group-breeding females only. Although barn swallows maintain discrete territories around their nests (Wolinski 1981), within-pair copulations have been observed primarily away from the nest site (Safran, personal observation) and it is common for individuals to forage far away from nest sites. Thus, it is likely that the pursuit of extra-pair matings is not tied to one's choice of a breeding site, as potential extra-pair mates are likely encountered far from one's breeding site. Still, in another study of extra-pair mating in barn swallows, Kleven et al. (2006) determined that extra-pair males are typically members of the same colony as their extra-pair mates.

When analyzed simultaneously, the effect of the number of old nests, not the proportions of the dark males, is a significant predictor of female settlement patterns in this population of barn swallows (Fig. 5). This analysis corroborates previous experimental tests on the role of old nest reuse and settlement decisions where the experimental removal of a critical breeding resource, old nests, significantly affected the settlement patterns of first-year breeding birds (Safran 2004), suggesting that resources, not conspecifics, affect the settlement decisions of breeding barn swallows. This study confirms that male color does not as strongly influence site-selection decisions as the presence of a critical resource, old nests. Old nests are an important commodity for breeding pairs (Shields et al. 1988; Safran 2004; Safran 2006), and individuals appear to seek these out when making site-selection decisions, the number of pairs that eventually settle at a site closely correlates with the availability of suitable old nests, and experimental tests indicate that group size changes as a function of the availability of old nests (Safran 2004).

Collectively, these results and previous studies on barn swallow social behavior (e.g., Snapp 1976; Shields and Crook 1987; Shields et al. 1988; Safran 2004) are consistent with the idea that barn swallows do not breed in groups to derive direct benefits from conspecifics (here, in the form of greater access to high quality social mates and extra-pair partners) but rather that groups form as a consequence of resource-based decisions (Safran 2004). Once paired with a social mate, the females from all group sizes are able to adjust their mate-selection decisions by seeking extra-pair mates (Safran et al. 2005; Neuman et al. 2007). An alternative possibility is that females have

different site-selection strategies such that some attempt to settle at solitary sites with the darkest males and others attempt to secure a high quality breeding territory at larger sites where these are more available. However, this hypothesis would predict a pattern that was not detected in this study: a lack of, or lower rates of extra-pair matings at solitary sites.

To my knowledge, this is the first study to simultaneously examine the relative significance of habitat and mate selection decisions within the context of variation in breeding group size. One study, conducted in pied flycatchers, revealed a similar hierarchy in the nest-site- and mate-selection decisions of females. In this species, as is also the case in barn swallows, males arrive earlier than females and defend breeding sites. By experimentally manipulating the quality of the site after a male began to defend it, Slagsvold (1986) determined that females principally chose males based on the quality of his territory, rather than his own quality. That is, in pied flycatchers, females did not settle with males whose territory contained an unsuitable nest, regardless of his quality (Slagsvold 1986). Interestingly, in barn swallows there exists a relationship between female age and the age of the nest she settles in, suggesting a higher probability that older females secure a high quality breeding territory more often than young females (Safran 2006). Because there is a premium on early breeding in barn swallows (Safran 2004; Safran and McGraw 2004), as is the case for most migratory songbird populations (Drent and Daan 1980; Rowe et al. 1994; Price 1998; Winkler and Allen 1995; 1996; Ardia 2005), it seems likely that females try to secure a mate who is defending a territory with an old nest in it as soon as possible. EPFs are prevalent in this species, suggesting the possibility that females first choose a nest site and make mate-selection adjustments afterwards.

A focus on individual-based decision rules for understanding patterns of group breeding is particularly valuable for individuals who do not derive benefits from breeding in close association with neighbors, such as barn swallows. The identification of individual-level decision rules related to evolutionarily relevant variables associated with reproduction and survival are likely to yield more explanatory power for patterns of social living compared to traditional cost and benefit models for group breeding. In the case of barn swallows, the group-average approach previously yielded equivocal results because no group-average benefits of social breeding are found for populations of barn swallows (e.g., Snapp 1976; Shields and Crook 1987; Shields et al. 1988; Safran 2004). Instead, group breeding in this species appears to be a consequence of the distribution of a critical nest-based resource.

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