Nest-site selection in the barn swallow, *Hirundo rustica*: What predicts seasonal reproductive success?

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Abstract: Despite hundreds of studies, we know very little about the causes and fitness-related consequences of nest-site selection. For example, it is not typically known whether the rarely reported fitness consequences of site selection are the result of nest, individual, or nest-site variables or combinations of these factors. Reuse of previously constructed nest sites is a prevalent behavior in many animals and offers the opportunity to experimentally tease apart whether seasonal reproductive success is a function of nest, individual, or nest-site characteristics. I used observational and experimental data to test three hypotheses related to these factors in association with barn swallow (*Hirundo rustica* L., 1758) nest reuse. While both nest and individual characteristics explain variation in seasonal reproductive success, nest location per se is not an important factor defining the outcome of nest-site selection. Whereas traits related to habitat and individual characteristics are likely confounded in correlational studies, my experiments demonstrate a causal relationship between seasonal reproductive success and aspects of the nest and individual, the latter explaining more variation in the model than nest characteristics. Knowledge of the relative roles of individual, nest, and nest-site attributes are important for understanding the causes and consequences of habitat selection behavior.

Résumé : On connaît peu de choses sur les causes et les conséquences reliées à la fitness de la sélection des sites de nidification, malgré les centaines d'études faites sur le sujet. Par exemple, on ne sait ordinairement pas si les rares cas rapportés de conséquences de la sélection de site sur la fitness sont le résultat de variables associées aux nids, aux individus, aux sites de nidification ou de combinaisons de ces variables. La ré-utilisation de sites de nidification construits antérieurement est un comportement fréquent chez de nombreux animaux; elle donne l'occasion ici de déterminer si le succès reproductif saisonnier est fonction des caractéristiques des nids, des individus ou des sites de nidification. Des observations et des données expérimentales ont servi à vérifier trois hypothèses reliées à ces facteurs dans la réutilisation des nids chez l'hirondelle rustique (*Hirundo rustica* L., 1758). Alors qu'ensemble les caractéristiques des nids et des individus expliquent la variation du succès reproductif saisonnier, la position du nid en elle-même n'est pas un facteur important dans la détermination de l'issue de la sélection du site de nidification. Bien que les propriétés associées aux caractéristiques de l'habitat et des individus soient vraisemblablement confondues dans les études de corrélation, les expériences faites dans ce travail démontrent l'existence d'une relation de causalité entre le succès reproductif saisonnier et certaines propriétés des nids et des individus; dans le modèle, les traits des individus expliquent une plus grande partie de la variation que les caractéristiques des nids. Une connaissance des rôles relatifs des propriétés des nids, des individus et des sites de nidification est importante, si l'on veut comprendre les causes et les conséquences du comportement de sélection de l'habitat.

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Introduction

Site-selection behavior during the breeding season is known to have important fitness-related consequences in terms of seasonal reproductive success (Badyaev et al. 1996; Martin 1998: Clark and Shutler 1999; Müller et al. 2005; Doerr et al. 2006) and as such is likely to be influenced by natural selection, especially in short-lived organisms that only reproduce a few times during their lives. Despite hundreds of studies related to site-selection prefer-

ences, we know very little about the fitness-related consequences of these behaviors. Even in the few cases where habitat selection behavior has been shown to correspond with measures of seasonal reproductive success, it is not typically known whether these outcomes are the result of characteristics of nests, individuals, nest sites, or a combination of these factors (e.g., Danchin et al. 1998; Lambrechts et al. 2004). As such, teasing apart the effects of these three variables can be difficult in nonexperimental settings because they are likely to be correlated.

In the few cases where researchers have studied the adaptive importance of site-selection rules, measures of seasonal reproductive success were used to indicate adaptive site selectivity (Badyaev et al. 1996; Martin 1998; Clark and Shutler 1999). However, a combination of factors including attributes of the nest location (location within a breeding site where the nest is constructed), the individuals using that nest, and aspects of the nest itself are all likely to play an important role in defining the outcome of nest-site selec-

Table 1. Predictions for various factors influencing the outcome of site-selection behavior in barn swallows (*Hirundo rustica*).

| Hypothesis | Factors that underlie benefits of nest reuse | | |
	Nest	Individual	Nest site
1. Nest reuse is adaptive because of the benefits associated with the nest per se	Reproductive success is greater in old nests	No effect	No effect
2. Aspects related to individuals (not nests or nest locations) explain variation in seasonal reproductive success associated with site selection	No effect	Older individuals have greater reproductive success than younger individuals, regardless of nest age or location	No effect
3. Aspects of the nest site (not nests or individuals) explain variation in seasonal reproductive success associated with site selection	No effect	No effect	Reproductive success is greater in a nonrandom subset of nest locations

tion behavior (Kim and Monaghan 2005; Müller et al. 2005). Knowledge of the relative importance of the (*i*) nest, (*ii*) individual, and (*iii*) nest location allows one to examine the influence of natural selection on the process and patterns of site selection by directly analyzing which factor has the most important fitness-related consequences. Although only rarely considered in studies of habitat selection, an understanding of the variables that contribute to site-selection behavior and its consequences enables one to make important predictions about which phenotypic variables or habitat features are most critical to an individual's seasonal reproductive success (e.g., Doerr et al. 2006).

Complex nest sites are characteristic of many different species of social insects, mammals, and birds such as swallows, weavers, and oropendolas (Hansell 2000). The costs associated with building these structures can be considerable (Conrad and Robertson 1993; Gauthier and Thomas 1993; Hauber 2002), but are often minimized by the reuse of nest sites within and across breeding seasons (Hill 1982; Weeks 1978; Hauber 2002; Hafstad et al. 2005). Examining site-selection strategies in cases where nest reuse is an option provides the opportunity to determine the importance of aspects of the nests and nest locations themselves, in addition to individuals using them, as components of site-selection behavior.

The reuse of old nests is a predominant nest site selection strategy of barn swallows, *Hirundo rustica* L., 1758, across their extensive breeding range (Barclay 1988; Shields et al. 1988; Møller 1990; Brown and Brown 1999; Briceno 2002), where anywhere from 45% to 82% of pairs reuse old nests for their first breeding attempts (Samuel 1971; Hill 1982; Barclay 1988; Shields et al. 1988). Old nests, not conspecific breeding success or group size, are an important site-selection cue for barn swallows (Safran 2004). The number of old nests at a breeding site strongly predicts the number of breeding pairs that settle there, and the presence of old nests is an important settlement cue for first-year breeders (Safran 2004). Collectively, these patterns suggest important benefits associated with nest reuse behavior. However, despite several studies that have provided correlational evidence for the adaptive importance of nest reuse (Hill 1982; Shields et al. 1988; Briceno 2002), we lack experimental evidence of exactly which factors contribute to greater reproductive consequences. For example, many studies have suggested that a primary benefit of nest reuse is earlier clutch initiation dates (Hill 1982; Barclay 1988; Shields et al. 1988; Hauber 2002), but characteristics of the individual

are also an important factor in determining the onset of breeding (Wendeln and Becker 1999; Hasselquist et al. 2001; Blums et al. 2005). Additionally, the benefits associated with nest reuse may be caused by the advantages at favored nest sites per se (the location within the barn or under the bridge where the nests are constructed) if some sites are better protected from predators or harsh weather.

To tease apart the extent to which the nest, individual, and nest site affect seasonal reproductive success, I used observational and experimental data collected on a large population of marked barn swallows at 48 breeding sites in Tompkins County, New York, to examine the following questions: (*i*) Do experiments demonstrate that nest reuse is adaptive? (*ii*) Do characteristics of the individual or nest per se predict seasonal reproductive success? (*iii*) Are the benefits of nest reuse a function of characteristics of the breeding individual, the nest itself, or the nest location per se? Hypotheses and predictions associated with these questions are listed in Table 1.

Methods

From 1998 to 2002, barn swallows were studied at 674 nests within 48 sites (bridges, barns, and other buildings) across Tompkins County, New York, where ~82% of breeding pairs in this area initiate first breeding attempts in old nests. Birds were individually marked with United States Fish and Wildlife Service (USFWS) leg bands and unique color combinations of nontoxic, enamel-based paints (The Testor Corporation, Rockford, Illinois) applied to white spots on the rectrices. The breeding activity of individually marked barn swallows was monitored 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 (only one or two), and the total number of offspring fledged during the year. All nests were checked during every site visit. In the following analyses, second breeding attempts (first attempt did not produce any fledged young) are distinguished from second broods (first attempt did produce at least one fledged young). Because the patterns represented by males and females are similar for all of the questions I address in this study, I present data for females only.

Experimental nest removals

To compare fitness-related differences between old and new nests and examine nest-site preferences in the absence

of old nests, nests were removed at randomly selected sites in 1999 ($n = 12$), 2001 ($n = 5$), and 2002 ($n = 3$). All old mud nests that remained intact from previous breeding seasons were removed, and their scars were scraped away and covered, using spray paint. Piles of old fecal sacs that remained under nests at the end of the season were also removed, as these could be used to detect previous breeding activity at the site. All of these manipulations were conducted during the late winter, well before the birds returned to Ithaca in mid-April.

Individual characteristics

As is common for other organisms (Saether 1990; Martin 1995; Ludwigs and Becker 2005), an individual's experience at a breeding site is a predictor of seasonal reproductive success in barn swallows (females: mixed linear model — effect of age: $F_{[1,232]} = 14.73$; $P < 0.001$; random factors: site and *year* (random factors that were significant in mixed models are italicized); males: mixed linear model — effect of age: $F_{[1,192]} = 4.43$; $P < 0.05$; random factors: site and *year*). Because intensive capturing and marking efforts were initiated at study sites in different years, an individual's recapture status (recaptured or not) was used as a proxy for age. This categorization of the data into two age classes also represents strong biological differences in the reproductive success of first-time and experienced breeders, especially in short-lived animals (e.g., Pärt 2001; Reid et al. 2003). Although dispersal among breeding sites is rare both within and among breeding seasons (Shields 1984; R.J. Safran, unpublished data), individuals appearing anywhere in the study area after they were banded were considered "recaptured".

Nest location characteristics

To determine whether the benefits associated with the reuse of nests are caused by the old nest or the site where the nest is constructed per se (Table 1), nest-site location use was measured at six control sites (where old nests remained intact from previous breeding seasons) and five removal sites (where old nests were experimentally removed before the start of the breeding season). Nest site reuse was quantified as the proportion of nest sites used in one breeding season that were settled in the following breeding season. To test the prediction that certain nest sites are consistently better than others, Pearson correlation analyses were used to determine whether the seasonal reproductive success of a nest site in one year was correlated with its seasonal reproductive success in the following year. To test patterns of nest-site reuse separately from old nest reuse, nest-site choice was analyzed at sites during years where old nests were intact and during years where old nests were experimentally removed.

Statistical models

SAS/STAT® version 9.1 program (SAS Institute Inc. 1990) was used for all statistical analyses.

Locally weighted scatterplot smoothers (LOWESS curves) were used to explore the relationship between two variables without fitting an a priori functional form. These LOWESS curves enables one to determine whether linear or higher order terms would be suitable for modeling the relationships

between two variables (Neter et al. 1996). Nonparametric analyses were applied when appropriate (Hollander and Wolfe 1999).

Condition indices in SAS PROG REG were used to assess the degree of collinearity among independent variables, including clutch initiation date, recapture status, and nest age. These analyses indicated a strong collinear relationship between clutch initiation date and recapture status and also clutch initiation date and nest age, indicating that variance in seasonal reproductive success due to lay dates are accounted for by including the effects recapture status and nest age in each model.

To account for the lack of independence among individuals within each breeding site or nestlings within the same nest, mixed models (PROC MIXED; SAS Institute Inc. 1990) or general linear models (PROC GLM; SAS Institute Inc. 1990) were used in which breeding site and (or) nest were included as random factors or covariates. Among-year differences were accounted for by using year as a random factor or covariate in models that contained data for more than one breeding season. The significance of random factors was assessed using likelihood ratio tests (Neter et al. 1996), but when applicable, factors including nest, site, and year were left in mixed models even if they were not significant to avoid problems associated with pseudoreplication of data (e.g., potential lack of independence of pairs within a site when compared withpairs across sites).

For mixed models, the following algorithms were used: the Kenward Roger method of calculating degrees of freedom, the variance components covariance structure, and the restricted maximum likelihood estimation method. When the statistical significance of more than one covariate was significant at $P < 0.05$, Tukey's pairwise difference tests (individual error rate = 0.05) were used to analyze differences among group means (e.g., by recapture status and age of nest).

In the Results section, random factors that were significant in mixed models are italicized. Sample sizes vary owing to differences in the total number of nests or individuals for which complete histories in each breeding season were collected.
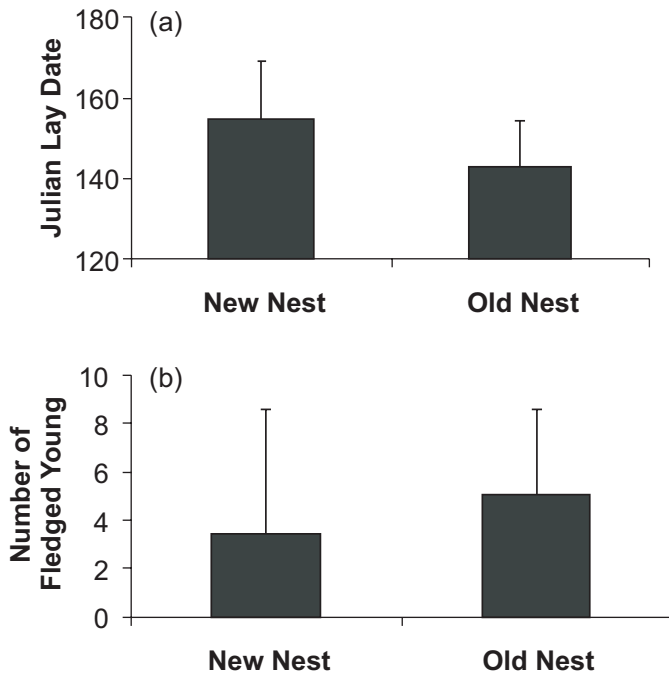
Results

Benefits of nest reuse

Reproductive success in new vs. old nests

Clutch initiation date is a significant predictor of reproductive success within each breeding season among barn swallows (mixed linear model — effect of clutch initiation date: $F_{[1,509]} = 62.81$, $P < 0.0001$; random factors: site and year). This relationship is generated principally by the fact that early breeders have a higher probability of raising two broods (logistic regression: Wald $\chi^2_{[1]} = 54.63$, $P < 0.001$, $n = 469$ pairs, controlling for age of nest and year effects). However, even for pairs that lay a single clutch, there is a seasonal decline in clutch size (mixed linear model — effect of clutch initiation date: $F_{[1,530]} = 23.19$, $P < 0.0001$; random factors: site and year). Thus, selection for early clutch initiation is likely an important influence on the selection of a breeding site.

Birds that use old nests lay their first clutches on average

Fig. 1. The benefits of barn swallow (*Hirundo rustica*) nest reuse: individuals (*a*) breed earlier and (*b*) have greater seasonal reproductive success in old nests compared with individuals that construct new nests at the start of the breeding season. These figures represent least square means + 1 SD that correct for site and year effects.

Table 2. Generalized linear model for the effect of nest age and individual age on seasonal reproductive success of female barn swallows in Tompkins County, New York.

Variable	df	Type III SS	F	P
Nest age	1	50.54	9.37	<0.01
Individual age	1	82.71	15.34	<0.001
Individual age × nest age	1	1.02	0.19	>0.65
Site name	38	542.42	2.65	<0.001

Note: Type III sums of squares (SS) indicate the amount of variation due to a specific effect, controlling for the other factors in the model.

Hypotheses 1 and 2: characeristics of nests and individuals. What explains the consequences of site selection?

If old nest reuse per se strongly influences reproductive success (hypothesis 1), an individual should always have greater fitness-related benefits in old nests regardless of their age class or the location of the nest itself (Table 1). The relationship between reproductive success and age of nest remains significant when lay date is controlled for (mixed linear model — effect of clutch initiation date: $F_{[1,502]} = 44.16$, $P < 0.0001$; effect of nest age: $F_{[1,508]} = 4.19$, $P < 0.05$; random factors: site and year) and when individual age is controlled for in the model (Table 2).

If individual characteristics per se affect the reproductive outcomes of nest-site selection, then individual age, regardless of nest age, should strongly influence reproductive success (Table 1, hypothesis 2).

General linear models demonstrate that both individual characteristics and nest age are significant variables for explaining variation in seasonal reproductive success and that individual age explains more variation in seasonal reproductive success compared with nest age when differences among sites are taken into account (Table 2).
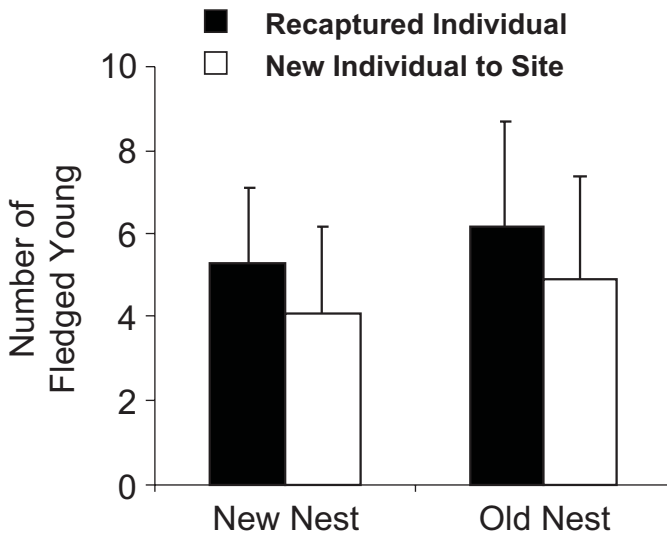
Differences in least square means for the effect of individuals (immigrant vs. recaptured individual: $t_{[206]} = -3.01$, $P < 0.01$) and differences in least square means for the effect of nest age (new vs. old nest: $t_{[226]} = -3.09$, $P < 0.01$) were statistically significant. The effects of nest and individual age were nearly similar (Fig. 2).

Least square means of seasonal reproductive success were significantly different at $P < 0.05$ for recaptured individuals who bred in old vs. new nests and for immigrant individuals who bred in old vs. new nests, demonstrating an important effect of individual age on the number of fledged young produced in a breeding season in either old or new nests.

The effects of year and interaction terms between age of nest and age of individual are not statistically significant in these models. Although the variables nest and individual do not statistically interact in these models, an association between these variables was detected; a significantly greater proportion of immigrant individuals constructed new nests at the start of the season, compared with the proportion of old individuals that bred in new nests ($\chi^2_{[1]} = 14.69$, $P < 0.0001$). The proportions of recaptured and new individuals breeding in old nests did not differ.

At nest removal sites, where all pairs constructed new nests at the start of the season, individual age was a significant predictor of seasonal reproductive success (mixed linear

12 days earlier than birds that construct a new nest for their first breeding attempt (mixed linear model — effect of clutch initiation date: $F_{[1,513]} = 79.47$, $P < 0.0001$; random factors: = site and year; Fig. 1*a*). There is a strong association between age of nest (old vs. new) and the probability of a second brood after a first successful breeding attempt ($\chi^2_{[1]} = 14.28$, $P < 0.0001$), where 38% vs. 17% of pairs that settled in old and new nests, respectively, had second broods. Breeding earlier in old nests translates into a net fitness benefit of, on average, 44% more fledged young in old nests compared with new nests (mixed linear model — effect of clutch initiation date: $F_{[1,533]} = 22.15$, $P < 0.001$; random factors: site and year; Fig. 1*b*).

Nest removal experiments

By experimentally removing old nests at breeding sites before the swallows arrived at Ithaca in the spring, I investigated whether there is a causal relationship between age of nest and clutch initiation date. Overall, clutch initiation dates were significantly later at the nest removal than at control sites (mixed linear model — effect of nest age: $F_{[1,127]} = 9.21$, $P < 0.01$; random factors: year and site); however, there was no difference in clutch initiation dates for those pairs that built a new nest at either the removal or control sites (mixed linear model — effect of experimental treatment at site: $F_{[1,214]} = 1.44$. $P > 0.23$; random factors: site and year), demonstrating a causal basis for the relationship between clutch initiation date and age of nest rather than an effect of the nest removal treatment at experimental sites.

Fig. 2. Nest age and individual age of barn swallows both predict variation in seasonal reproductive success. Data represent least square means + 1 SD that correct for site and year effects. Both within and among age classes, the effect of nest age is significant ($P < 0.05$).

Fig. 3. Neither (*a*) nest reuse at control sites where old nests were intact at the start of the season nor (*b*) nest location reuse at experimental sites where old nests were removed before the breeding season are a function of the reproductive success of barn swallows in that nest during the previous year.

model — effect of individual age: $F_{[1,104]} = 8.70$, $P < 0.01$; random factors: site and year). Differences in least square means indicate that recaptured older individuals had greater seasonal reproductive success than immigrant individuals ($t_{[104]} = -2.95$, $P < 0.01$).

Hypothesis 3: attributes of nest sites and nest reuse

If reproductive success is a function of the nest-site location, then seasonal reproductive success should be variable across nest locations, regardless of aspects of nests or individuals (Table 1, hypothesis 3). Explicit predictions of this hypothesis are that (*i*) favored nest locations should be reused from year to year, regardless of whether an old nest still exists in that part of the breeding site, and (*ii*) reproductive success associated with a nest location should be correlated between years regardless of aspects of individuals or nests.

Prediction 1

The frequency of nest site reuse did not statistically differ between control sites (44%) and experimental sites (32%) where old nests were removed before the breeding season ($\chi^2_{[1]} = 2.03$, $P > 0.10$, $n = 4$ removal and 5 control sites that were studied in 2 consecutive years).

Prediction 2

The seasonal reproductive success at a nest site in 1 year did not predict its reproductive success in the following year (Pearson's $r = 0.15$, $P > 0.45$, $n = 24$ nest sites). Similarly, there was no correspondence between the seasonal reproductive success at 14 nest sites that were used in 2 consecutive years at sites where old nests were experimentally removed at the start of the season in the second year of the comparison (Pearson's $r = 0.40$, $P > 0.15$).

Reproductive success in the previous year did not predict whether a nest site was reused in the following year at either control (logistic regression: Wald $\chi^2_{[1]} = 0.38$, $P > 0.50$; Fig. 3*a*) or removal (logistic regression: Wald $\chi^2_{[1]} = 2.13$,
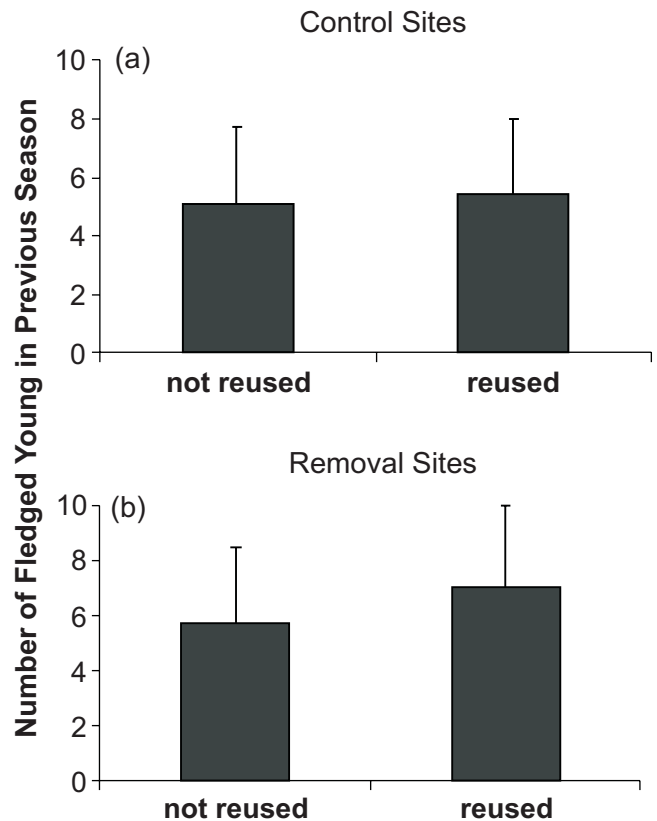
$P > 0.14$; Fig. 3*b*) sites. Both analyses controlled for the effects of site and year differences on the relationship between previous reproductive success at a nest site and its subsequent reuse.

Discussion

Benefits of nest reuse

Although a predominant benefit of nest reuse is the earlier onset of breeding, there are also fitness-related benefits associated with nest reuse that are independent of earlier clutch initiation dates, likely owing to the additive effects of greater reproductive success of site-faithful individuals returning to use old nests. Thus, I found support for a mixture of the predictions associated with hypotheses 1 and 2 (Table 1), demonstrating that both ecological (aspects of nests) and phenotypic (aspects of individuals using nests) variables affect the outcomes of site-selection behavior.

Although individuals within both age classes (immigrants and recaptured individuals) had greater reproductive success in old nests compared with new nests, I found no evidence of a strong, statistically significant interaction between nest age and individual age. Although the interaction of individual age (or phenotypic correlates of age) and nest age were not statistically assessed in other studies, correlations between these two variables have been reported in other populations (e.g., Hill 1982; Shields et al. 1988; Briceno 2002;

but see Barclay 1988), suggesting that older individuals have a greater probability of settling in old nests vs. constructing new ones.

I found no evidence to suggest that the benefits of nest reuse are associated with favored nest sites per se. The rank of a nest site in terms of seasonal reproductive success during the previous year was not a predictor of its rank in the following breeding season. Moreover, at control sites where old nests were left intact, I did not find that previous reproductive success at a nest was a predictor of its reuse (Fig. 3a), suggesting, for example, that a particular nest site is always favored across years. Interestingly, although not statistically significant, at removal sites, pairs tended to reuse nest sites that were the most successful during the previous summer (Fig. 3b). The age structure of the population at removal sites is affected by the experimental removal of old nests; significantly fewer new individuals settled at sites where old nests were removed prior to the breeding season (Safran 2004). Moreover, individuals may reuse the same nest site between years (Shields 1984; R.J. Safran, unpublished data). Thus, site familiarity, nest-site fidelity, and prior experience at the site may be a reason why individuals reused nest sites that were most successful in the previous year.

In barn swallows, nest-site selection is influenced by the presence of old nests (Safran 2004), and this study demonstrates a causal relationship between the reuse of old nests and fitness-related payoffs. On average, all pairs breed earlier and have greater seasonal reproductive success in old nests, regardless of individual age (Fig. 2). However, individual age and its correlates also play an important role in predicting seasonal reproductive success: older individuals breeding in either reused or new nests had greater seasonal reproductive success compared with new individuals in reused and new nests, respectively (Fig. 2). At sites where all nests were experimentally removed before the breeding season, older individuals had greater seasonal reproductive success compared with new individuals at those same sites. Thus, the benefits of nest reuse, in terms of seasonal reproductive success, is affected not only by nest characteristics but also by traits related to the individual settling in a given nest. Although in females, there is a higher proportion of immigrant individuals that settled in new nests compared with the proportion of older individuals in new nests, the same pattern was not apparent in males. Lack of a strong correspondence between nest age and individual age may be due to the fact that nest reuse is highly prevalent (~82%) across sites in my study area, suggesting that many individuals, not just older, more experienced individuals, are able to secure a territory with an old nest.

Although not included in this study, the potential costs of nest reuse, mite infestation, and the probability of falling were weak or nonexistent in Ithaca barn swallows, and they certainly did not outweigh the benefits of earlier lay dates, more frequent second broods, and higher seasonal offspring production associated with nest reuse (Safran 2005). Barn swallows are choosy about which nests they settle in and both avoid settling in old nests with mites and are more likely to switch nests between broods if the first nest is infested with mites. These avoidance tactics likely explain why mites do not appear to affect strongly the reproductive output of pairs in this study area (Safran 2005).

Habitat selection behavior, especially in short-lived organisms, has the potential to strongly influence an individual's lifetime reproductive success. Whereas many studies of habitat selection focus solely on ecological variables (e.g., habitat factors associated with reproductive success) or traits related to individuals (e.g., age-based reproductive success), both are likely to play an important role in the consequences of nest settlement behavior (e.g., Badyaev et al. 1996; Kim and Monaghan 2005; Müller et al. 2005). As such, determining both ecological and phenotypic factors that influence the outcomes of habitat selection are relevant to a number of ecological and evolutionary questions. Namely, what factors greatly influence an individual's probability of success, and how do these shape site-selection behavior? If habitat variables more strongly predict reproductive outcomes, then management plans focused on key ecological resources will be critical (e.g., Webb and Shine 2000; Przybylo et al. 2001; Souter et al. 2004). On the other hand, if aspects of an individual's phenotype is most strongly predictive of seasonal measures of reproductive success (e.g., Murphy 2004), then managers should incorporate demographic features of the population as a priority in conservation efforts, because in these cases, restoration of ecological variables that are not critically related to fitness will not be as effective as managing healthy age-structured populations.

Acknowledgements

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