



RESEARCH ARTICLE

Predictors and consequences of nest-switching behavior in Barn Swallows (*Hirundo rustica erythrogaster*)

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ABSTRACT

Nest-switching is an important breeding strategy for multiple-brooded bird species. When deciding whether or not to switch nests for subsequent breeding attempts, pairs must weigh the costs and benefits of various factors related to the number of fledglings of the first breeding attempt, the likelihood of nest predation, and qualities of the nest environment, such as nest ectoparasites and the age of the nest. In this study, we analyzed the predictors and consequences of nest-switching behavior at 6 breeding sites of North American Barn Swallows (*Hirundo rustica erythrogaster*), where 60% of pairs that raised 2 broods within a season switched nests for a second breeding attempt. Pairs often reused existing (old) nests constructed during previous years, and pairs that settled in old nests for their first breeding attempt were the most likely to switch nests for a second breeding attempt. Contrary to previous studies, nest predation and nest ectoparasitism had no influence on whether or not pairs switched nests. Moreover, second breeding attempts overall had significantly more mites than first breeding attempts, but there was more variation in the change of mite intensities for those pairs that switched nests for a second breeding attempt compared to pairs that did not switch. Furthermore, pairs that switched from one old nest to another nest between breeding attempts decreased the time between first and second breeding attempts when compared to pairs that reused their first nest for a second breeding attempt. Because nest-switching led to greater fledging success for second breeding attempts compared to birds that reused their nests, our results suggest that switching between nests is an adaptive reproductive strategy for Barn Swallows.

Keywords: Barn Swallow, ectoparasites, nest age, nest mites, nest predation, nest reuse, nest-switching, reproductive success

Predictores y consecuencias del comportamiento de cambio de nido en *Hirundo rustica erythrogaster*

RESUMEN

El cambio de nido es una estrategia reproductiva importante para las especies con nidadas múltiples. Al momento de decidir si cambiar o no de nido en los subsiguientes intentos reproductivos, las parejas deben pesar los costos y beneficios de varios factores relacionados al número de volantones del primer intento reproductivo, la probabilidad de depredación del nido y las cualidades del ambiente del nido, como los ectoparásitos del nido y la edad del nido. En este estudio, analizamos los predictores y las consecuencias del comportamiento de cambio de nido en seis sitios de anidación de *Hirundo rustica erythrogaster*, donde el 60% de las parejas que criaron dos nidadas dentro de una estación cambiaron el nido para el segundo intento reproductivo. Las parejas usualmente reusaron los nidos existentes (viejos) construidos durante los años previos, y las parejas que se establecieron en los nidos viejos para su primer intento reproductivo fueron las más propensas a cambiar de nido para su segundo intento reproductivo. Contrariamente a los estudios previos, la depredación del nido y el ectoparasitismo del nido no tuvieron influencia en el cambio o no de nido que realizaron las parejas. Más aún, los segundos intentos reproductivos en general tuvieron significativamente más ácaros que los primeros intentos, pero hubo más variación en el cambio de intensidad de los ácaros en aquellas parejas que cambiaron de nido para un segundo intento reproductivo que en las parejas que no cambiaron. Más aún, las parejas que cambiaron de un nido viejo a otro nido entre intentos reproductivos disminuyeron el tiempo entre el primer y el segundo intento reproductivo, en comparación con las parejas que reutilizaron su primer nido para un segundo intento reproductivo. Debido a que el cambio de nido derivó en un mayor éxito de emplumamiento en los segundos intentos reproductivos en comparación con las aves que reusaron sus nidos, nuestros resultados sugieren que el cambio de nido es una estrategia reproductiva adaptativa para de *H. rustica*.

Palabras clave: ácaros del nido, cambio de nido, depredación del nido, ectoparásitos, edad del nido, éxito reproductivo, *Hirundo rustica*, re-uso del nido

INTRODUCTION

Avian reproductive strategies are presumed to balance various costs and benefits to achieve the greatest lifetime reproductive success (Martin 1995b). While some species of birds construct one nest per season in which to raise one brood, other species have several broods within the same breeding season (Geupel and DeSante 1990). For bird species that have multiple breeding attempts, there are opportunities between within-season breeding attempts to remain in the first nest, switch to a new location in which a nest already exists, or switch to a new location and construct a new nest (Hansell 2000, Lima 2009). Nest-switching, like many behaviors that balance ecological and evolutionary costs and benefits, is thus predicted to affect reproductive success (Barclay 1988, Lima 2009). Factors implicated in nest-switching include the reproductive success of the first breeding attempt, nest predation, and qualities of the first nest site, including nest ectoparasite abundances and nest age (e.g., old nests may harbor more ectoparasites and harmful detritus) (Greig-Smith 1982, Collias and Collias 1984, Barclay 1988, Hart 1990, Brown and Brown 1992, Safran 2006, Lima 2009).

Offspring mortality in one nest location can predict whether or not pairs switch nest sites within a breeding season. For example, Eastern Bluebirds (*Sialia sialis*) dispersed to new nests within the same breeding season more readily after an unsuccessful reproductive attempt than after a successful one (Gowaty and Plissner 1997). Common causes of nestling mortality are predators and nest ectoparasites. Predators can destroy entire broods and nest ectoparasites, which live in the nest and feed on nestling blood, weaken nestlings enough to cause indirect mortality by decreasing nestling immune defenses and overall nestling quality (Rothschild and Clay 1952, Brown and Brown 1986, 1996; Møller 1990, Lima 2009, Proctor and Owens 2000).

Some species react to nestling mortality due to nest predation or nest ectoparasitism by nest-switching. For example, Spotted Antbirds (*Hylophylax naevioides*) switched nests after predation to prevent future discovery by predators (Styrsky 2005), and Brewer's Sparrows (*Spizella breweri*) responded to depredated nests by moving to new nest sites with higher and denser shrubs for subsequent breeding attempts (Chalfoun and Martin 2010). Additionally, Møller (1990) found that ectoparasitic mites were associated with smaller body mass at fledging for European Barn Swallows (*Hirundo rustica rustica*) and a greater chance of adults moving to a new nest for a second breeding attempt. Therefore, nest-switching may be an attempt to avoid either or both nest predation and nest ectoparasites in subsequent breeding attempts (Hart 1990, Møller et al. 1990, Styrsky 2005, Lima 2009).

Whether or not the nest was built during a previous season (old nest) or constructed at the start of the breeding season (new) may also be an important predictor of nest-switching behavior. For example, European Starlings (*Sturnus vulgaris*) that nested in old nests with an increased abundance of ectoparasitic mites responded by increasing feeding rates of nestlings to counteract effects by the mites on the growth of the nestlings (Mazgajski 2007, but see Rendell and Verbeek 1996). There are also benefits associated with reusing old nests, as pairs save time by reusing old nests rather than building new ones (Barclay 1988, Safran 2004). New nests, or nests built upon arrival to a breeding site, may be initially free of nest ectoparasites, but the added time investment of nest construction can delay reproduction (Møller 1990, Brown and Brown 1996, 1999; Safran 2006). Building a new nest may be a pair's only option for breeding if no other preexisting or suitable nest is available to them at a breeding site (Barclay 1988).

To date, research on the predictors and consequences of nest-switching within a breeding season has often tended to focus on single factors (e.g., only nest predation or reproductive success), yet we still do not have a clear understanding of how complex environmental aspects and reproductive outcomes influence nest-switching behavior. Therefore, we aimed to collectively analyze various predictors and consequences of nest-switching to fully examine this behavior. In this study, we asked 2 questions: (1) Which factors predict nest-switching behavior? We examined how the number of nestlings fledged, nest predation, nest ectoparasites, and nest age affected whether or not pairs switched nests between their first and second breeding attempts; and (2) What are the consequences of nest-switching between breeding attempts? We examined how nest-switching affected the relative number of ectoparasites during a pair's second breeding attempt as compared to their first, the time between the first and second breeding attempt, and the number of nestlings fledged in the second breeding attempt. We predicted that factors such as lower fledging success of the first nest, incidence of nest predation, higher intensities of nest ectoparasites, and old first nests would increase the likelihood of pairs switching between nests for a second breeding attempt. We also predicted that nest-switching would decrease the number of mites in the second nest when compared to the first, decrease the time between breeding attempts, and lead to an increase in fledging success of the second nest.

METHODS AND MATERIALS

Study System

We analyzed field-collected data from a long-term study of North American Barn Swallows (*Hirundo rustica eryth-*

rogaster) in Colorado, USA. Barn Swallows are insectivorous and migratory passerines that nest in barns, culverts, and bridges (Brown and Brown 1999, Safran 2007). Breeding colonies are defined as discrete populations breeding in one specific location, such as a bridge or barn, and can range in size from 1 to 200 pairs (Cramp 1988, Safran 2004). Within each breeding season, 45–82% of pairs will reuse previously constructed nests, rather than repair broken nests or build new nests entirely, which can delay breeding by up to 2 weeks (Brown and Brown 1999, Safran 2006). Pairs typically have 2 broods per season, although they can have up to 3, and often pairs switch nests between these breeding attempts (Shields 1984, Brown and Brown 1999).

After their first breeding season as adults, individuals exhibit strong site fidelity, returning each year to the same breeding site (Shields 1984). On average, males arrive on the breeding grounds earlier than females to claim and defend territories within a colony. Females arrive later and choose a mate based on his territory and phenotype (Møller 1994, Safran 2007). Within-season divorce was rare in our population (2 confirmed cases in 7 yr, out of 427 pairs with second breeding attempts). Unlike in other populations of *H. r. erythrogaster*, where divorce was higher (Shields 1984, Crook and Shields 1985), we did not observe infanticide, a factor implicated in divorce; therefore, we consider pairs as a single unit when analyzing nest-switching behavior.

The nest predators and nest ectoparasites of Barn Swallow eggs and nestlings can strongly influence reproductive success (Brown and Brown 1999). Predators are locally variable and include domestic cats (*Felis catus*), House Sparrows (*Passer domesticus*), European Starlings, gopher snakes (*Pituophis catenifer*), raptors (e.g., *Buteo jamaicensis*, *Falco sparverius*), and corvids (e.g., *Pica hudsonia*) (Møller 1987, Brown and Brown 1999). Nest ectoparasites were common within our study sites, albeit unequally distributed as is typical for parasites (Woolhouse et al. 1997). We chose to examine nest infestation by northern fowl mites (*Ornithonyssus sylviarum*) due to their ubiquity (40.5% of the population infested) and documented costs to nestlings (Brown and Brown 1999). Other nest ectoparasites of Colorado Barn Swallows were excluded from this study due to their low prevalence in our study population, including blowfly larvae (Calliphoridae, 1% of the population infested) and bat bugs (*Cimex lectularius*, 3% of the population infested) (Brown and Brown 1999).

Field Methods

We observed Barn Swallows in Boulder County, Colorado, USA, from early May through late August, from 2008 to 2014, at 6 breeding sites (see Appendix Figure 5). Adults were captured in mist-nests and banded with USFWS

bands and unique combinations of color bands and colored tail spots for matching individual breeding pairs to their respective nests. We defined nest-switching as a pair's movement from their first nest to a different nest located at the same site for a second breeding attempt within the same breeding season. A breeding attempt (at least one egg laid) in the previous nest had to have occurred for movement to qualify as nest-switching. Nests were checked twice weekly to note clutch initiation and completion and to count the numbers of eggs and nestlings per breeding attempt. Hatch date was determined by checking the nest daily beginning 2 weeks after a female laid her penultimate egg (e.g., Safran 2004, 2006; Hund et al. 2015a). We measured and banded nestlings 12 days after hatching, which is near fledging (17–20 days). Handling nestlings past day the twelfth day increased the risk of premature fledging. Thus, on the twelfth day after hatching, the number of nestlings in the nest minus the number unhatched in the nest or presumed dead was our estimate of reproductive success.

Quantifying Nest Predation

We inferred nest predation when all nestlings or eggs disappeared from the nest on the same day. If nestlings or eggs were found unhatched, dead underneath the nest, or dead in the nest before fledging age, we considered these nests abandoned by the adults or failed due to other causes (e.g., falling) and did not include them in our nest predation analyses. The barns in our study gave the nestlings and eggs added protection from poor weather (e.g., wind, rain, or snow) and other causes of nest failure that may affect more exposed nests (see Ricklefs 1969). Moreover, because we checked nests often, we could track the progression of the nesting cycle closely. Thus, we were fairly certain that predation was the most plausible form of nest failure in cases when active nests were suddenly found empty. We collected eggs from nests at 2 of the 6 breeding sites within our study area during the 2009 season to synchronize female laying dates for a different experiment, which mimicked predation events (Safran et al. 2016). Because pairs did not differ in their nest-switching responses to nest predation or egg collection, we pooled these data for analyses (chi-square test: $\chi^2 = 0.3$, $df = 1$, $P = 0.59$).

Quantifying Nest Ectoparasites

To quantify the abundance of ectoparasitic mites in each nest, nestlings were removed from the nest and placed in a container. We then placed a cupped hand in the nest for 30 s and counted any mites that were found on the hand. Other studies (e.g., Møller 1990, Saino et al. 2002, Hund et al. 2015a) have used the hand method to measure ectoparasite loads as a valid estimate for mite abundance through comparisons with estimates obtained from

sampling of swallow nests using Berlese funnels (e.g., Møller 1990, Hund et al. 2015b). We used the sum of mites counted on each nestling, the container used to hold the nestlings, and the number of mites on the hand after it was inside the nest for 30 s as an estimate of the mite abundance for the entire nest. Northern fowl mites are typically the only mites visible to the naked eye within the nests and are usually red or dark brown in color; mistaking the identification and presence of nest mites was highly unlikely, especially when compared to the other nest ectoparasites (e.g., blowfly larvae and bat bugs).

All 6 of the study sites were also included in nest ectoparasite manipulations that took place during the summers of 2013 and 2014. In 2013, mites were added or removed from second broods during a cross-fostering experiment. Nest mites were added when nestlings were 3 days old. We removed these 2013 experimental nests from analyses looking at the change in mites between broods, as mite manipulations occurred during second broods. In 2014, before males arrived in the spring (early April) damaged or partial nests at these sites were removed and complete nests were emptied of their old contents (e.g., feathers and feces) and then disinfested with a heat gun (see Hund et al. 2015b). Three of the sites were left as disinfested control sites without mites. At the other 3 sites, half of the nests were randomly assigned to a mite treatment and had 100 live, field-collected mites added to mimic typical overwintering population levels. Nest mites were added to nests before Barn Swallows arrived at the sites from spring migration, allowing individuals to naturally assess nest mite abundances. Consequently, for all data except those from the experimental sites in 2013, we treated experimentally manipulated and naturally occurring mite intensities in the nests equally among years and sites.

Nest Age

The ages of nests were classified as either “new” or “old” based on the presence of the nest in the previous breeding season, as detailed by Safran (2004). If a nest existed before the start of the breeding season, it was classified as “old.” Nests built by pairs after they arrived at the breeding site were classified as “new.” New nests that remained intact for the following year were then reclassified as “old.” Five destroyed or partially destroyed nests were rebuilt during the study. Rebuilding a partial nest requires similar effort as building an entirely new nest. Therefore, we classified rebuilt nests as “new.”

Statistical Analysis

We analyzed all data in R v3.2.2 (R Core Team 2015). We first analyzed the proportion of pairs that switched nests vs. those that stayed for a second breeding attempt by the number of vacant nests available to a pair for their second

breeding attempt with a generalized linear model (GLM) using a binomial error distribution. To correct for overdispersion detected in our model, we then used a quasibinomial response error (Zuur et al. 2009). We estimated the number of vacant nests available to a pair for their second breeding attempt by subtracting the number of active first nests from the total number of nests at a site per year.

To analyze the row-by-column independence of count data, we used a chi-square test of independence. We also used a Wilcoxon Rank Sum test to analyze the differences between nonparametric data, such as the differences between ectoparasitic mite populations in old vs. new nests and between first and second breeding attempts. We listed medians and interquartile ranges (IQR) for reference. Mite data were transformed by taking the natural log of total mite counts plus one.

For all mixed effect models, we used the lme4 package, linear mixed-effects models using Eigen and S4 (Bates et al. 2015). We tested the significance of a fixed effect by dropping it from the model and comparing the updated model and the original model using a likelihood ratio test (LRT). We also included the additive random effects of year, site, and the identity of the first nest. The random effects are additive because some years lacked certain sites, and active nests were not always present at the same site from year to year. We included the identity of the first nest to avoid pseudoreplication and overdispersion (Harrison 2014), as some pairs reused the same nests between years. Random effects are included in each model due to their biological importance in the system and to control for site and year effects.

To understand which factors best predicted nest-switching, we used a generalized linear mixed model (GLMM) with a binomial response error (“stay” or “switch”). Various fixed effects such as the number of fledglings of the first breeding attempt, whether or not nest predation occurred, and the abundance of ectoparasitic nest mites were analyzed as separate models, each with nest age included. This was due to various correlations among fixed effects, such as nest predation and ectoparasitic nest mites which did not co-occur in our study because mites, counted on day 12, could not be counted on already depredated nestlings. Additionally, nest predation directly influenced fledging success. Furthermore, models with nest ectoparasites as a fixed effect used reduced data sets compared to the other models because only nests at certain sites and years have nest ectoparasite data.

To understand how nest-switching influenced the time between the first and second clutch initiation dates, we used a linear mixed model (LMM). We calculated the time between clutch initiation dates by transforming the dates into an ordinal date (the number of days since 1 January) and taking the difference between them. The fixed effects

TABLE 1. The number of pairs that originally nested in either new or old nests and their subsequent decision to have either one or two breeding attempts. Percentages were calculated by the box count out of the total number of all pairs (chi-square test: $\chi_2^2 = 13.4$, $P < 0.001$).

Age of first nest	Decision for a second breeding attempt		Total
	Only one breeding attempt (%)	Second breeding attempt (%)	
New nest	48 (8)	41 (6)	89 (14)
Old nest	183 (29)	368 (57)	551 (86)
Total	231 (37)	409 (63)	640

included in this model were the clutch initiation date of the first breeding attempt (as a covariate), the decision to switch nests or not, the age of the first nest, as well as the 3 possible pairwise interactions.

We also used a GLMM with a binomial response error to see which factors influenced the number of fledglings in the second breeding attempt. We used a binomial response because the response variable was a proportion of those nestlings that fledged vs. the number of nestlings that did not fledge. The fixed effects for this model included the clutch initiation date of the first breeding attempt, the decision to switch nests or not, the age of the first nest, and the 3 possible pairwise interactions.

RESULTS

Summary Statistics

Overall, 409 out of 640 pairs initiated a second breeding attempt (64%; Table 1). Nest-switching was a common

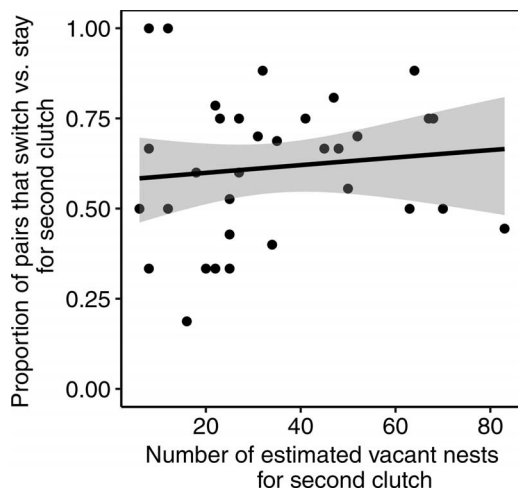


FIGURE 1. The proportion of pairs that switch nests vs. those that stay in their first nest for a second breeding attempt remains constant as the number of estimated vacant nests available to a pair for the second breeding attempt increases. Each point represents one site for one year; 95 % confidence bands are shown as grey shading around the black trendline.

TABLE 2. The number of pairs that originally nested in either new or old nests and their subsequent decision for a second breeding attempt: stay in the same nest, switch to a new nest, or switch to an old nest. Percentages, shown in parentheses, were calculated by the count for a particular combination (e.g., stay / new nest) out of the total number of all pairs in the study ($n = 406$).

Age of first nest	Decision for a second breeding attempt			Total
	Stay (%)	Switch to new (%)	Switch to old (%)	
New nest	23 (6)	12 (3)	6 (2)	41 (11)
Old nest	139 (34)	34 (8)	192 (47)	365 (89)
Total	162 (40)	46 (11)	198 (49)	406

behavior when averaged across all sites and years of this study, with 60% of pairs ($n = 244$ of 406) switching nests between their first and second breeding attempts (see Appendix Figure 6). We found that even as the number of estimated vacant nests available to a pair for a second breeding attempt increased, the proportion of pairs nest-switching remained constant (GLM: estimate = 0.01, SE = 0.007, $t_{53,98,31} = 1.6$, $n = 33$, $P = 0.11$; Figure 1), suggesting that the degree of nest-switching is not simply a function of the available opportunities for moving to new locations.

Pairs were more likely to settle in old nests (86%, $n = 552$) than new nests (14%, $n = 89$) for their first breeding attempts. Also, pairs were more likely overall to switch to an old nest (81% of those that switched) rather than to a new nest (19%), and were especially more likely to switch to an old nest if they had first occupied an old nest (chi-square test: $\chi_2^2 = 26.9$, $P < 0.001$, Table 2).

Natural rates of nest predation were 27% for first breeding attempts and 10% for second breeding attempts across years and sites. During first breeding attempts, old nests (median = 0, IQR = 1.61, $n = 183$) had nearly 50% fewer nest mites on average than new nests (median = 0.69, IQR = 3.29, $n = 19$; Wilcoxon test: $W = 2159.5$, $P = 0.05$). For second breeding attempts, we found no differences in mite abundances between new and old nests (new: median = 1.10, IQR = 3.82, $n = 14$; old: median = 1.10, IQR = 2.90, $n = 82$; Wilcoxon test: $W = 591.5$, $P = 0.85$).

Which Factors Predict Nest-switching?

Pairs were more likely to switch to a different nest between breeding attempts if their first nest was old than if it was new (GLMM: estimate = 2.14, SE = 1.44, LRT: $\chi_1^2 = 4.5$, $P = 0.03$). Nest-switching was not predicted by the number of fledglings of the first nest (LRT: $\chi_1^2 = 0.2$, $P = 0.66$), whether or not the first nest was depredated (LRT: $\chi_1^2 = 0.5$, $P = 0.49$), or as a function of ectoparasitic nest mites abundances (LRT: $\chi_1^2 = 1.5$, $P = 0.22$). These results suggest that settling in an old nest influences nest-switching behavior more than factors including fledging

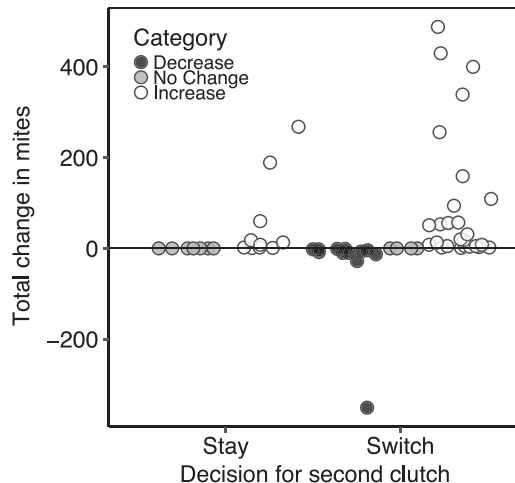


FIGURE 2. Pairs that remain in their first nest for a second breeding attempt (“Stay”) only increased or maintained their mite abundances. Switching nests for a second breeding attempt (“Switch”) led to a potential decrease in mites for some second breeding attempts. The total changes in mites are shown as raw totals, untransformed. Data are overlaid, or “jittered,” to better show all values.

success, nest predation, and ectoparasitic nest mite abundances.

What are the Consequences of Nest-switching as Measured in the Second Breeding Attempt?

Across all nests, there were 33% more mites in second breeding attempts (median = 1.10, IQR = 3.18, $n = 96$) compared to first breeding attempts (median = 0, IQR = 1.61, $n = 202$; Wilcoxon: $W = 7565.5$, $P < 0.001$). On average, this was true for those pairs that remained in their first nest for a second breeding attempt (first breeding attempt: median = 0, IQR = 0.69, $n = 52$; second breeding attempt: median = 0.35, IQR = 2.62, $n = 36$; Wilcoxon: $W = 689$, $P = 0.02$) and also for those that switched nests between breeding attempts (first breeding attempt: median = 0, IQR = 1.61, $n = 99$; second breeding attempt: median = 1.39, IQR = 3.77, $n = 59$; Wilcoxon: $W = 2105$, $P = 0.002$).

Nest-switching, however, did give some pairs the opportunity to decrease nest mites in their second nest when compared to their first. For pairs that remained in the same nest between breeding attempts, nest mite abundance always stayed the same or increased (stayed: 41% no change, 53% increased, 0% decreased); however, for pairs that switched nests, nest mite abundance decreased some of the time (switched: 9% no change, 63% increased, 28% decreased). This suggests that switching nests may offer some birds the opportunity to reduce nest mites for their second breeding attempt, particularly if they faced high infestations during their first (Figure 2).

When looking at the time between breeding attempts, we found that there was a significant interaction between the clutch initiation date of the first nest (the covariate) and the decision to switch nests (LRT: $\chi_1^2 = 13.5$, $P < 0.001$). Nest age and the decision to switch nests or not was also a significant interaction (LRT: $\chi_1^2 = 9.3$, $P = 0.002$), though the effect on the time between clutches was driven only by pairs that first nested in old nests (LRT: $\chi_1^2 = 10.9$, $P < 0.001$; Figure 3A). Moreover, pairs that stayed in old nests for a second breeding attempt had no change in the time between breeding attempts (LRT: $\chi_1^2 = 0.1$, $P = 0.77$; Figure 3B), and pairs that switched from old first nests decreased the amount of time between breeding attempts (LMM: estimate = -0.39 , SE = 0.08, LRT: $\chi_1^2 = 20.9$, $P < 0.001$; Figure 3C).

We found that the number of fledglings of the second breeding attempt was best explained by both the age of the first nest and the decision to switch nests for a second breeding attempt, where birds that settled in an old nest and then switched nests had the highest number of nestlings fledged (GLMM: estimate = 1.18, SE = 0.40, LRT: $\chi_1^2 = 8.3$, $P = 0.004$; Figure 4). These results suggest that the best strategy for a second breeding attempt, in terms of maximizing fledging success, is using old nests first and then switching to a different nest, compared to nesting in new nests first or deciding to stay in the first nest, even if it is an old nest, for a second breeding attempt.

DISCUSSION

We examined the predictors and consequences of nest-switching behavior in 6 populations of North American Barn Swallows in Boulder, Colorado, over 7 breeding seasons. Barn Swallows switched nests 60% of the time when initiating a second breeding attempt, regardless of the number of nests present at each site. Pairs that settled in old nests for their first breeding attempt were more likely to switch nests compared to pairs that constructed new nests for their first broods. We found that on average second breeding attempts had more mites than first breeding attempts for pairs that both stayed and switched for a second breeding attempt, and that only 12 out of 43 pairs (28%) switched to nests with fewer mites than their first nests. Pairs that switched from an old nest to either an old or new nest also decreased the amount of time between their breeding attempts and on average increased the number of fledglings in the second nest compared to pairs that did not switch or switched from a new nest. Thus, switching nests is most likely a way for some pairs to decrease ectoparasitic nest mites for subsequent breeding attempts and is an adaptive behavior that increases the number of fledglings and allows pairs to have a shorter time interval between breeding attempts.

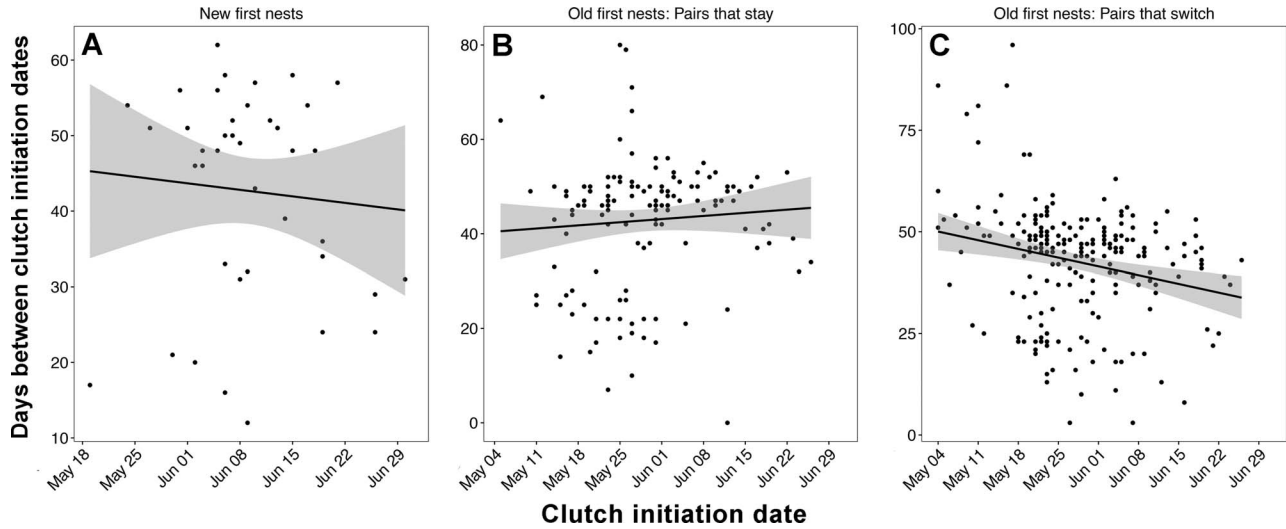


FIGURE 3. The relationships between the days between clutch initiation dates and the first clutch’s initiation date, all as ordinal dates. **(A)** For pairs that constructed new nests at the start of the breeding season there is no significant interaction between the first clutch initiation date and the time between clutch initiation dates and whether or not pairs decided to move for a second breeding attempt; for all new first nests, the time between clutch initiations remains constant. **(B)** There is no significant trend when looking at pairs that stayed in their first old nest for a second breeding attempt; the time between clutch initiation dates is independent of when the pair laid their first breeding attempt. **(C)** For those pairs that switched out of old nests, the time between clutch initiation dates decreased as the first clutch initiation date increased (See Table 2 for sample sizes).

Which Factors Predict Nest-switching?

We found that the proportion of pairs that switched to a different nest vs. those that re-nested remained constant with the varying number of old nests available for a second breeding attempt, suggesting that the rate of nest-switching is independent of nest availability.

Furthermore, fewer pairs switched nests when they constructed a new nest for their first breeding attempt compared to pairs that used old nests for their first breeding attempt. This may be indicative of the benefits of building new nests, such as securing a territory when suitable old nests are limited (Barclay 1988). We did not

assess the effects of intraspecific competition on nest-site selection as part of this study. However, as pairs that build new nests are typically younger in age and start breeding later when compared to older individuals (Safran 2004, 2006), these individuals may have less time in the breeding season or reduced access to suitable nests to switch to for a second breeding attempt, and thus must remain in their first nest despite the potential costs of doing so (e.g., Brown 1969).

Pairs that switched between old nests may do so to save time and energy (Hansell 2000; Safran 2004, 2006), while also avoiding the costs of re-nesting in old nests, such as harmful bacteria from detritus, nest ectoparasites, or deteriorating nest conditions (Rothschild and Clay 1952, Collias and Collias 1984, Shields 1984, Møller 1990, Mazgajski 2007). We found, however, that new nests had significantly more ectoparasitic mites than old nests during first breeding attempts, a finding corroborated in a northeastern USA population of Barn Swallows (R. J. Safran personal observation). While new nests have more mites than old nests, our results still suggest that mite abundances do not affect nest-switching. Our results differ from the findings of other studies of Cliff Swallows (*Petrochelidon pyrrhonota*) and Barn Swallows, which demonstrated that pairs tend to switch nests or nest sites as a function of high ectoparasite densities (Barclay 1988, Møller 1990, Møller et al. 1990, Brown and Brown 1992, 1996; Safran 2006). These differences could result from our use of hierarchical statistical models, which account for

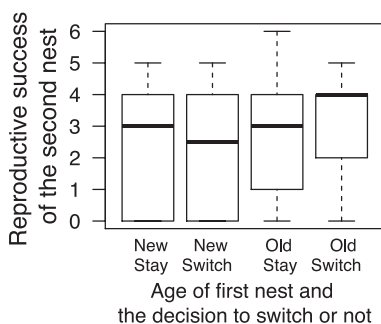


FIGURE 4. The number of fledglings of the second breeding attempt varied by pairs’ decisions to either stay or switch for a second breeding attempt, which depends on the age of the first nest (see Table 2 for sample sizes). The number of fledglings of those that first nested in old nests and then switched best explains overall second nest fledging success.

variation among sites, years, and individuals. It is also possible that our results differ as a function of variation in parasite intensities in other populations (e.g., Barclay 1988, Møller 1990, Brown and Brown 1992, 1996).

Other factors, such as poor reproductive success and nest predation, have also been implicated in other studies of within-season nest-switching (Greenwood and Harvey 1982, Lima 2009), although in this study neither were significant indicators of nest-switching. Perhaps the high rate of nest-switching for a second breeding attempt (60%, $n = 244$ of 406 pairs) evolved as a way to offset the potential costs of nest predation or nest ectoparasitism (e.g., Eggers et al. 2006, Lima 2009, Hua et al. 2013), or nests infested with ectoparasites (e.g., Barclay 1988, Hart 1990, Safran 2006). Although we did not find any clear predictors of nest-switching behavior, this may suggest that other components of old nests (e.g., microclimate), or other aspects of Barn Swallow behavior (e.g., territoriality), might play a larger role in nest-switching.

What are the Consequences of Nest-switching as Measured in the Second Breeding Attempt?

We found that second breeding attempts had much higher ectoparasitic nest mite abundances than first breeding attempts. Yet, nest-switching allowed some pairs to decrease mite intensities in their second nest when compared to their first, which went against the population trend of increasing mites later in the breeding season. The number of pairs that decreased mite intensities when they switched nests (28%, $n = 12$ out of 43) was much greater than for pairs that stayed in their original nest (0% decreased mites). Typically, mites multiply rapidly when feeding on nestlings over the course of the breeding season, so increases in mite populations were expected, especially within nests that were infested during the first breeding attempt (Brown and Brown 1986, Barclay 1988, Møller 1990, Proctor and Owens 2000, Stanback and Dervan 2001, Safran 2004). An overall trend of increasing ectoparasite intensities in the second nest may signify the importance of nest-site competition if pairs can differentiate between subsequent nests with higher or lower nest mite abundances. If pairs cannot quantify nest mite abundances, they may be gambling each time they switch nests.

Pairs that switched nests also were able to shorten the amount of time between clutch initiation dates, but only if they switched from an old nest. A pair's ability to increase the number of breeding attempts they have during a breeding season can result in higher total seasonal reproductive success (Safran 2006), a feat made easier by decreasing the time between reproductive attempts (Møller 1990, Safran 2006). Moreover, using old nests allows a pair to initiate their first clutch earlier in the breeding season than those building new nests (Jackson et

al. 1989, Safran 2004, 2006). Nest-switching may decrease the time between breeding attempts because it allows the female to lay the second clutch in a different nest while her older nestlings are still roosting in the first nest (Jackson et al. 1989, Howlett and Stutchbury 1997). Pairs staying in their first nest for a second breeding attempt must wait for those nestlings to permanently leave (fledge) the nest and its immediate vicinity before the female can lay her eggs. Thus, in terms of minimizing time between the first and second breeding events, pairs that switch nests might have an advantage over those that stay in the same nest.

Another consequence of nest-switching was that pairs that switched from old nests had more fledglings in the second nest when compared to pairs that switched from new nests, or did not switch at all. This suggests that nest-switching is an adaptive behavior that increases fitness for a majority of Barn Swallow pairs. One explanation for this pattern is that pairs that nest in old nests and then switch are the most experienced breeders. More experienced breeders are likely to have more fledglings in both their first and subsequent breeding attempts compared to naïve pairs (Lawton and Lawton 1980, Greenwood and Harvey 1982, Hatchwell et al. 1999, Safran 2006). The experience that comes with returning to a site each year may aid a pair in choosing the best ultimate strategy for seasonal fledging success, such as switching between old nests for successive breeding events while having a second breeding attempt sooner in the breeding season (Greenwood and Harvey 1982, Curio 1983, Marzluff 1988, Fowler 1995, Martin 1995a, but see Weimerskirch 1992, Redmond et al. 2007, Jiménez-Franco et al. 2014).

Conclusion

Birds that have multiple broods within a single breeding season must balance the costs and benefits of switching between nests for subsequent reproductive attempts (Bowler and Benton 2005). While nest predation and nest ectoparasites have been cited as the major causes for pairs to leave their first nest and move to another (Greig-Smith 1982, Collias and Collias 1984, Barclay 1988, Marzluff 1988, Hart 1990, Brown and Brown 1992, Safran 2006, Lima 2009), we found that the only predictor of nest-switching behavior were old first nests. There were benefits of nest-switching; switching allowed some pairs to decrease the number of mites in their second nest, it decreased the time between breeding attempts, and increased the number of fledglings for the second breeding attempt. Thus, nest-switching is important for understanding how individuals maximize reproductive success.

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Ethics statement: Behavioral observations and handling of adults and nestlings were done in accordance with guidelines set by the University of Colorado Institutional Animal Care and Use Committee (IACUC). All procedures in this study were approved by IACUC (protocol number 1303.02). Birds in experimental treatment groups did not appear to suffer from nest manipulations or from measurements and blood collection.

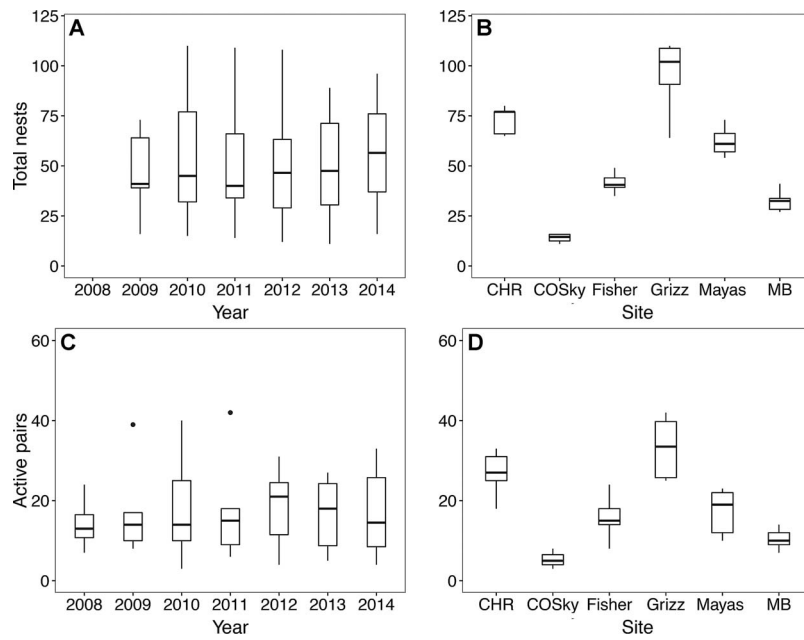
Author contributions: K.J. Donahue conceived the idea, design, and experiment (supervised research, formulated question or hypothesis). A.K. Hund, I.I. Levin, and K.J. Donahue performed the experiments (collected data and conducted the research). K.J. Donahue, R.J. Safran, I.I. Levin, and A.K. Hund wrote the paper. K.J. Donahue, A.K. Hund, and R.J. Safran developed or designed methods. K.J. Donahue analyzed the data.

LITERATURE CITED

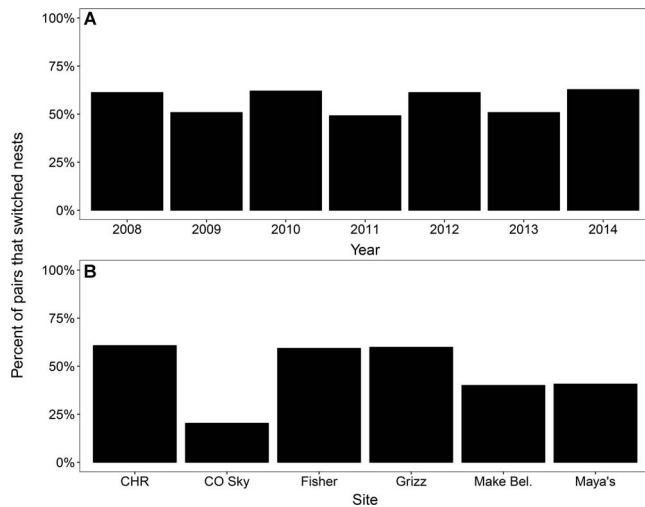
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APPENDIX



APPENDIX FIGURE 5. (A and B) The variation in the total number of old nests that were available to Barn Swallow pairs between years and sites. (C and D) The variation in the number of active pairs (i.e. the number of nests actually used out of the total number of nests) between years and sites. Data for 2008 for total nests were unavailable.



APPENDIX FIGURE 6. Percentage of pairs that switch nests for a second breeding attempt by year (above) and site (below).