



*Avian Conservation and Management*

## Barn Swallow (*Hirundo rustica*) colony relocation in western Massachusetts

### Reubicación de una colonia de Golondrinas Comunes (*Hirundo rustica*) en el oeste de Massachusetts

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**ABSTRACT.** Populations of Barn Swallows (*Hirundo rustica*) have declined throughout northeastern North America. Modern farming techniques, reduced insect prey populations caused by pesticide exposure, and mortality associated with climate changes have been postulated as causes of these declines. Evidence is equivocal that loss of nesting sites has adversely influenced regional population levels. Nonetheless, removal of a nesting site from a wildlife sanctuary created a contentious public debate between local animal protectionists, a statewide conservation organization, and a federal wildlife agency. We implemented and evaluated a two-year project aimed at mitigating the loss of this nesting site. In year one, when the abandoned horse stable that was planned for demolition was occupied by a breeding colony of approximately 40 pairs, we enhanced an existing nearby structure that was occupied by five pairs by placing seed nests that had been harvested from the horse stable, installing artificial nest platforms, and using vocalization playbacks. In year two, we deployed additional seed nests within the alternate nesting site that had been collected during demolition of the stable. Within three years, the alternate site supported a breeding colony that was approximately 93% in size of the colony that had previously been in the stable. There was no evidence that the nesting behavior of birds occupying the alternate site was affected by the forced relocation: the number of second broods, clutch sizes, body masses of both sexes, and within- and among-season survival did not differ significantly between the original and relocated nesting sites.

**RESUMEN.** Las poblaciones de Golondrinas Comunes (*Hirundo rustica*) han disminuido en todo el noreste de Norteamérica. Las técnicas agrícolas modernas, la reducción de las poblaciones de presas de insectos causada por la exposición a pesticidas y la mortalidad asociada con cambios climáticos han sido propuestas como causas de estas disminuciones. La evidencia es equívoca respecto a que la pérdida de sitios de nidificación haya influido negativamente en los niveles poblacionales regionales. Sin embargo, la eliminación de un sitio de nidificación en una reserva natural de vida silvestre generó un polémico debate público entre los proteccionistas de animales locales, una organización estatal de conservación y una agencia federal de vida silvestre. Implementamos y evaluamos un proyecto de dos años con el fin de mitigar la pérdida de este sitio de nidificación. En el primer año, cuando el establo de caballos abandonado que se planeaba demoler fue ocupado por una colonia reproductiva de aproximadamente 40 parejas, mejoramos una estructura cercana existente que estaba ocupada por cinco parejas colocando como señuelos nidos que habían sido recolectados en el establo de caballos, instalando plataformas artificiales para nidos y reproduciendo vocalizaciones de la especie. En el segundo año, colocamos nidos adicionales dentro del sitio de nidificación alternativo que habían sido recolectados durante la demolición del establo. Hacia el tercer año, el sitio alternativo contenía una colonia reproductiva que tenía aproximadamente el 93% del tamaño de la colonia que había estado previamente en el establo. No hubo evidencia de que el comportamiento de nidificación de las aves que ocupaban el sitio alternativo haya sido afectado por la reubicación forzada: el número de segundas nidadas, el tamaño de puesta, las masas corporales de ambos sexos y la supervivencia dentro y entre temporadas no difirieron significativamente entre los sitios de nidificación original y realocizado.

**Key Words:** *aerial insectivores; colony relocation; Hirundo rustica; nesting behavior; survival*

Aerial insectivores are showing steep population declines in North America (North American Bird Conservation Initiative Canada 2012, Rosenberg et al. 2019). Included in this group is the Barn Swallow (*Hirundo rustica*), an iconic bird of many agricultural landscapes throughout the world. In the United States and Canada, U.S. Geological Survey (USGS) Breeding Bird Survey (BBS) data have shown a cumulative population decline of 38 percent since 1970 (Rosenberg et al. 2016, Sauer et al. 2020), with declines most pronounced in the northeastern states and eastern Canada (Nebel et al. 2010).

The causes of Barn Swallow declines are unclear. Spiller and Dettmers (2019) summarized multiple drivers thought to potentially be responsible for aerial insectivore declines in North America, including decreased prey abundance, impacts of

environmental contaminants, habitat loss, phenological effects associated with climate change, and conditions on migratory stopover or wintering grounds. At a worldwide scale, BirdLife International (2016) identified intensification of agricultural practices, pesticide-caused reductions in prey populations, and impacts of climate change on breeding success and overwinter survivorship as possible factors.

Although various studies have shown that Barn Swallow populations increase in response to increased nest site availability (Erskine 1979, Turner and Rose 1990, Ambrosini et al. 2002, Evans et al. 2003), others have concluded that there is no clear evidence that population declines are caused by reduced availability of suitable nesting sites (Holroyd 1975, Robinson et al. 2003, Brown and Brown 2020). Despite this uncertainty of a

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causal relationship between nest site availability and population status, conservation advocates and wildlife managers in northeastern North America have expressed concern that demolition of decaying wooden barns and other structures that provide Barn Swallow nesting habitat may threaten local populations (Mass Audubon 2011, Silver 2012, Connecticut Audubon 2013, Ontario Ministry of Natural Resources and Forestry 2016, Dil and Mohr 2019).

In 2019, a colony of approximately 40 pairs of Barn Swallows nested in an abandoned horse stable located on the Silvio O. Conte National Fish and Wildlife Refuge's Fort River Division in Hadley, Massachusetts. Public safety concerns over the aging structure, administrative directives to eliminate needless buildings on refuge lands, and potential threats to nearby buildings led the U.S. Fish and Wildlife Service (USFWS) to decide to demolish the stable at the end of the 2019 breeding season, despite the structure's obvious value as a nesting site being used by a regionally declining species (USFWS 2019). This decision triggered a contentious public debate among local animal protectionists, a statewide conservation organization (Mass Audubon), and a federal wildlife agency (USFWS; Abel 2019, Hook 2019, Saulmon 2019, WWLP-22News 2019). We conducted a multiyear study aimed at understanding the effects of our mitigation efforts, which consisted of providing alternative nesting options in a nearby, protected structure. We used a combination of metrics, including counts of active nests, body masses, clutch sizes, and estimates of within- and among-season survivorship to compare possible impacts of the forced relocation.

## METHODS

The Silvio O. Conte National Fish and Wildlife Refuge currently totals 153 km<sup>2</sup> located in 22 parcels distributed across four states (Connecticut, Massachusetts, New Hampshire, and Vermont). The overall landscape of the refuge's Fort River Division (42°26' 24"N 72°34'12"W) includes extensive areas of agricultural land that provide foraging habitat to nesting Barn Swallows (Boynton et al. 2020, Brown and Brown 2020, Atwood and Rhodes 2022). Four structures were included on the refuge at the time of purchase in 2009. Three of these—a residence, a shop building, and a former indoor horse exercise arena with an attached room currently used to store boats and other refuge equipment (hereafter referred to as the “Boat House”; 149 m<sup>2</sup> in extent)—were considered key assets to be maintained for refuge operations. The fourth structure was the Bri-Mar Stable (hereafter, “Stable”), a 30-year-old, two-story building, with each floor approximately 1,045 m<sup>2</sup> in extent. The Stable and the Boat House were separated by approximately 70 m. After evaluating various management alternatives and receiving public comments (USFWS 2019), the USFWS demolished and removed the Stable on 7 January 2020.

In March 2019, we moved 12 previously used Barn Swallow nests (hereafter, “seed nests”) from the Stable to the Boat House; in November 2019, a further 24 seed nests were salvaged from the Stable and moved to rafters in the Boat House. Seed nests were attached to 13 X 14 cm wooden shelves. Additionally, 264 artificial nest platforms, patterned after items that had been used to support nests in the deteriorating Stable, were placed in the Boat House rafters in March 2020 to potentially attract prospecting birds when they returned from their wintering grounds. The designs of these nest platforms were unique to this study. Consisting of

**Fig. 1.** Partial view of the Boat House rafters, showing examples of artificial nest foundations. A = electrical conduit; B = electrical box; C = wire mesh; D = wooden shelf; E = hurricane brace; F = corner bracket. G = Seed nests were placed on additional wooden shelves.



readily available, inexpensive hardware materials, the platform types included 15 cm sections of electrical conduit, electrical boxes, wire mesh, 13 X 14 cm wooden shelves, hurricane braces, and corner brackets (Fig. 1). Forty-four examples of each of these six artificial nest platform types (none of which included seed nests) were deployed in the Boat House.

During May–July 2019, we broadcast recordings (<https://xeno-canto.org/56419>), from 0600–1200 h daily, of Barn Swallow twitter–warble songs (Nelson 2009, Brown and Brown 2020) from a speaker positioned at the Boat House's entrance window. The window measured approximately 2 X 1.5 m and was located approximately 6 m from the ground. We did not use playback in 2020–2022 because several active nests had already been established in the Boat House in 2019.

We compared nesting behavior and body condition between pre-displacement (Stable, 2019) and post-displacement (Boat House, 2020–2021) by using five metrics: (1) the number of nests initiated prior to 1 July, (2) the frequency of apparent double-brooding (nests initiated after 1 July) and within-year reuse of specific nest platforms, (3) mean clutch sizes of pre-July 1 and post-July 1 broods, (4) body masses of specific individuals captured in successive years, and (5) survival rates of displaced birds banded in 2019 in the Stable and recaptured in 2020 in the Boat House vs. survival rates of non-displaced birds caught in the Boat House in 2020 and 2021. We also compared frequencies of nests constructed on seed nests with those built on artificial nest platforms. Statistical analyses were provided by JMP 7.0.1 ([https://www.jmp.com/en\\_ca/home.html](https://www.jmp.com/en_ca/home.html)) and included Wilcoxon rank sum or Kruskal-Wallis (clutch sizes), signed-rank (body masses), and chi-square (nest frequencies) tests. Survival rates were compared using the R2jags package in RStudio 0.99.892 (Su and Yajima 2014).

Active nests within the Stable were counted at approximately one-week intervals from mid-May through mid-August 2019. Most nests were located on the Stable's first floor; the building's second floor was searched less often due to safety concerns, but visits were sufficient to document the number of nesting attempts. Nest

contents were examined using a telescopic mirror; once nest checks indicated that clutches had been completed or juveniles had reached approximately 10 days of age, we avoided further inspections of those nests. Similar nest monitoring was conducted in the Boat House during 2020–2022.

Barn Swallows are frequently double-brooded, with laying of second broods typically occurring approximately 50 days after first clutches are initiated (Campbell et al. 1997). Nesting in all years of the study began on approximately 15 May, and second waves of nesting were evident each year during the first week of July. We defined nests begun prior to 1 July as first brood nests; nests where egg laying began on, or after, 1 July were considered to be second brood nests, although it is possible that some of these later nests were actually first broods produced by birds that, for unknown reasons, had been delayed in the onset of their breeding cycle.

We did not trap adults at nests and have no way of knowing whether the same or different individuals used specific nest sites during first and second broods or between years. Other researchers (Anthony and Ely 1976, Shields 1984, Peck and James 1987, Barclay 1988, Iverson 1988) have found that reuse of nests that were occupied earlier in the same year varied widely, from 12–81%. We used the number of first brood nests as an index of the number of breeding pairs present during each year of the study.

Maximum clutch size per nest was recorded during nest monitoring. To avoid undue disturbance, we did not monitor nests after clutch completion (when repeated nest checks encountered the same number of eggs) or assess hatching or fledging success. We excluded from analysis single nests that contained clutches of inviable runt eggs, possibly produced by a single female, that were noted in 2019 and 2020 (for reviews of this rare phenomenon, see Rothstein 1973, Mulvihill 1987 and Czechowski and Zduniak 2008).

We erected mist nets within the Stable to capture birds for banding in 2019 (nine dates, 28 May–13 August) and in the Boat House in 2020 (four dates, 27 May–9 July), 2021 (six dates, 25 May–22 July), and 2022 (four dates, 6 June–13 July). Trapping periods on each date lasted approximately four hours, with approximately one week between occasions. Age and sex were determined using criteria described by Pyle (1997). Only adult (AHY) birds were banded. Individuals were weighed with a digital balance to the nearest 0.1 g, and wing lengths were measured to the nearest 1 mm. Banding was conducted under authorization of Federal (Master Bird-Banding Permit 09996) and State (Massachusetts Scientific Collecting Permit 196.19SCB) permits.

#### *Analysis of recapture rates*

We banded 91 Barn Swallows in the Stable in 2019 and recorded recaptures of these individuals in 2020–2022 as an index of how many of the original breeders relocated to the Boat House after the Stable had been destroyed. Additionally, for each sex, we compared recapture rates of birds banded in the Stable in 2019 and recaptured in the Boat House in 2020 (that is, birds that were displaced by destruction of the 2019 nesting site) with recapture rates of birds caught in the Boat House in 2020 and 2021 (when no disturbance of the nesting colony occurred). The resulting encounter histories were used to estimate survival using Cormack-

Jolly-Seber (CJS) models, which account for detection probabilities that are often less than one (Cormack 1964, Lebreton et al. 1992). We used a hierarchical formulation of the CJS model (Royle 2008, Royle and Dorazio 2008), which allows covariates of both survival probability and detection to be accommodated. The resulting estimates of apparent survival do not distinguish between mortality and permanent emigration. That said, permanent emigration indicates lower persistence, which is a useful correlate of survival (Faaborg et al. 2010). Apparent survival is thus helpful in comparison of demographic rates.

We explicitly defined the period spent on the breeding grounds (25 April–30 August) by consulting eBird records at this heavily banded site to determine arrival and departure dates, thus allowing for estimates of within-season survival over the entire approximately four-month breeding season (including outside of our observation periods) as well as among-season survival during an approximately eight-month period that includes the migratory and wintering seasons (Ritterson et al. 2021). Among-season survival is akin to return rates that account for detection probability. We modeled among-season survival by sex to examine differences before and after demolition of the Stable and subsequent relocation of the colony into the Boat House. Within-season encounter histories were structured by day (versus week or month). In this setup, an individual received a “1” if detected, a “0” if not detected, and no entry (i.e., “NA”) on days with no encounter attempts. Our models thus provided daily survival estimates and allowed for an uneven frequency of, and time between, sampling occasions (Chandler 2010, Ritterson et al. 2021). Monthly survival was calculated by raising daily survival to the 30th power.

We used Bayesian inference with vague prior distributions. All models kept detection probability constant and included an interaction of season (within vs. among) with survival. This base model was used to estimate apparent survival among- and within-season. An interaction of sex with among-season survival was added to examine differences in apparent among-season survival (an indication of return rates) between males and females. Models were run in JAGS 4.2.0 (Plummer 2003) using the R2jags package in RStudio 0.99.892 (Su and Yajima 2014). Convergence was assessed using visual diagnostics (Gelman and Rubin 1992), and variances of derived parameters (e.g., annual survival) were approximated using the delta method (Powell 2007).

## RESULTS

In 2019, approximately 45 pairs of Barn Swallows nested in buildings at the Fort River Division of the Conte National Fish and Wildlife Refuge: 40 in the Stable and five in the Boat House. The number of first brood nests in the Boat House increased to 28 in 2020, 32 in 2021, and 37 in 2022. The size of the Boat House colony in 2022 represented 93% of what was present in the Stable prior to its demolition (Table 1).

Not all individuals present as breeders were captured and banded during each year of the study. Nonetheless, we believe that the majority of birds found in the Boat House during 2020–2022 had been displaced from the Stable, although some may have been recruited from elsewhere. Of 91 individuals initially banded in the Stable in 2019, 28 (31%) were recaptured during limited sampling in the Boat House from 2020–2022.

**Table 1.** Numbers of first and second broods in Barn Swallow (*Hirundo rustica*) nesting sites in the Stable and Boat House.

Year	Location	First brood	Second brood	Ratio
2019	Stable	40	24	0.57
2019	Boat House	5	n/a <sup>a</sup>	n/a
2020	Boat House	28	19	0.68
2021	Boat House	32	22	0.69
2022	Boat House	37	20	0.54

<sup>a</sup> Counts of second brood nests were not conducted in the Boat House in 2019.

Twenty-seven of 36 seed nests (75%) that had been placed in the Boat House were used for nesting in 2020. Only 11 of 264 artificial nest platforms (4%) were used as nest foundations in the Boat House; seed nests were significantly preferred as nesting sites compared with artificial nest platforms ( $\chi^2 = 143.7$ ,  $P < 0.001$ ).

There was no clear evidence of changes in nesting behavior between birds associated with the Stable in 2019 and the Boat House in 2020. The relative frequencies of first and second broods in the two years was not significantly different (Table 1; likelihood ratio  $\chi^2 = 1.5$ ,  $P = 0.22$ ). The relative frequencies with which specific nest platforms were used by first and second broods did not differ significantly before (Stable 2019) and after (Boat House 2020) colony displacement (Table 2; likelihood ratio  $\chi^2 = 2.1$ ,  $P = 0.34$ ). Across the four years of the study (and combining data collected in the Stable and the Boat House), approximately 49% of potential nest platforms were used within a season only by the first brood, 36% were used during first and second broods, and 15% were used only by a second brood.

**Table 2.** Repeated use of specific nest platforms by first and second Barn Swallow (*Hirundo rustica*) broods.

Year	Location	First brood only	First and second broods	Second brood only
2019	Stable	24	18	5
2020	Boat House	17	11	8
2021	Boat House	14	18	3
2022	Boat House	25	12	8

Colony displacement showed no clear evidence of impact on body condition during the following year. Masses of individual birds that were captured in successive years in the Stable (2019) and the Boat House (2020) did not differ (Wilcoxon sign-rank test; females,  $n = 8$ ,  $z = 11.0$ ,  $P = 0.18$ ; males,  $n = 10$ ,  $z = 1.5$ ,  $P = 0.98$ ).

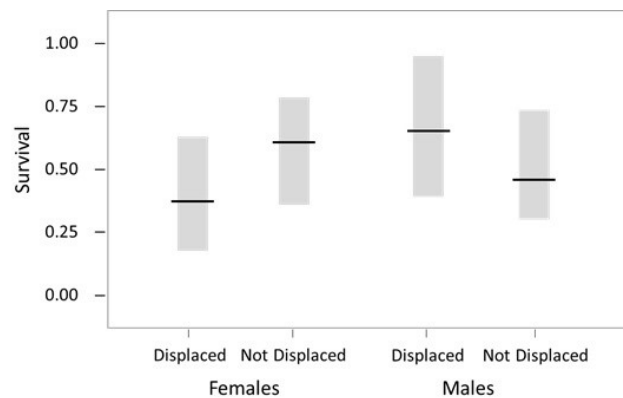
Mean clutch size of first brood nests in the Stable in 2019 was smaller than first brood nests present in 2020 in the Boat House (Wilcoxon rank sum test,  $z = 2.7$ ,  $P = 0.01$ ; Table 3). There was no difference in clutch size of second broods produced during 2019 in the Stable vs. 2020 in the Boat House (Wilcoxon rank sum test,  $z = 0.8$ ,  $P = 0.41$ ). During the three years following displacement of pairs from the Stable into the Boat House (2020–2022), clutch size showed no evidence of significant annual differences in either the first brood (Kruskal-Wallis test,  $\chi^2 = 1.3$ ,  $P = 0.52$ ) or the second brood (Kruskal-Wallis test,  $\chi^2 < 0.1$ ,  $P = 0.99$ ).

**Table 3.** Variation in Barn Swallow (*Hirundo rustica*) clutch size during first and second broods in the Stable (2019) and Boat House nesting sites (2020–2022).

Year	Location	First brood			Second brood		
		n	mean	SD	n	mean	SD
2019	Stable	42	4.50	1.06	26	4.15	0.73
2020	Boat House	30	5.10	0.84	19	4.37	0.83
2021	Boat House	32	5.25	0.67	22	4.32	0.84
2022	Boat House	37	4.97	0.93	20	4.20	1.24

Apparent within-season monthly survival was 0.95 (SD = 0.10), equivalent to a 0.81 (SD = 0.29) probability of surviving the entire approximately four-month period on the breeding grounds. Detection probability was estimated to be 0.29 (SD = 0.04). Apparent survival among seasons was estimated to be 0.46 (SD = 0.10), equivalent to a monthly survival of 0.91 (SD = 0.01). In both sexes, survival rates of birds that were displaced from the Stable in 2019 to the Boat House in 2020, and of birds that nested in the Boat House in 2020 and 2021 without being displaced, were not significantly different (Fig. 2). Annual survival, derived by multiplying within-season survival by among-season survival, was estimated to be 0.37 (SD = 0.18).

**Fig. 2.** Comparison of among-season survival, by sex, between nesting Barn Swallows (*Hirundo rustica*) that were displaced (2019–2020) and not displaced (2020–2021). Means indicated by black lines, 95% confidence intervals indicated by shaded bars.



## DISCUSSION

Several studies have questioned whether replacement of aging barns by modern structures can cause regional population declines (Holroyd 1975, Robinson et al. 2003). However, the regular demolition of buildings that have historically housed Barn Swallow colonies at least draws public attention to the need to mitigate loss of nest sites used by this species, even if such losses have not been conclusively linked to population declines.

Numerous efforts, especially in Canada, have involved the construction of Barn Swallow nesting structures to attempt to compensate for destruction of occupied barns or other structures. Most of this work has focused on building nesting kiosks of



various designs, dimensions, and orientations (Campomizzi et al. 2019, Dil and Mohr 2019; B. Wallace, 2nd Barn Swallow kiosk appears in King [blog entry], *personal observation*). Mitigation efforts have also included deployment of artificial nesting platforms made of wood or clay and efforts to attract birds using decoys and vocalization broadcasts (Silver 2012, Campomizzi et al. 2019).

Despite these efforts, many of the nesting structures created for Barn Swallows have had limited success. Silver (2017) concluded that “alternative nesting structures ... have not been shown to mitigate the loss of nesting habitat provided by larger structures, such as barns.” Campomizzi et al. (2019) found that vocalizations and decoys failed to attract pairs to artificial structures.

We implemented mitigation efforts that slightly modify what have been used elsewhere. Instead of creating new nesting structures intended to attract birds that had been displaced by destruction of an active nesting site, we used a two-year relocation process. In year one, we enhanced an existing structure that was already occupied by a small number of pairs, which was located near an occupied breeding site that was planned for destruction. This enhancement included deployment of seed nests that had been harvested, during the non-breeding season, from the site that was planned for demolition, placement of additional nesting platforms, and vocalization playback. In year two, additional seed nests, collected at the time of demolition, were placed within the alternate nesting site prior to onset of the breeding season.

These efforts successfully established a colony that, after three years, supported approximately 93% of the number of breeding pairs that had originally been present in the nesting structure that was demolished. Although we are unsure of exactly how many of the birds found in the Boat House during 2020–2022 had originally nested in the Stable, limited sampling found that 33% of 89 birds originally banded in the Stable were recaptured in the Boat House within three years of the Stable’s destruction. Some of the birds that nested in the Boat House may have been recruits from fledglings produced in the Stable. However, other workers have found that most one-year-old Barn Swallows do not return to their natal colony: 0.4% (n = 679) in Kansas (Anthony and Ely 1976), 0.6% (n = 524) in Oklahoma (Iverson 1988), 1.0% (n = 1,008) in Pennsylvania (Bell 1962), 2.0% (n = 331) in New York (Shields 1984), and 2.0% (n = 1,718) in Massachusetts (Mason 1953). Once a nesting site has been selected, reported return rates of breeders are higher, ranging from 20% in Oklahoma (Mason 1953) to 42% in New York (Shields 1984).

Seventy-five percent of the 36 seed nests that were deployed in the alternate structure were used, compared with 4% of 264 artificial nest platforms. There was no evidence that nesting behavior or other metrics of performance for birds that nested in the alternate breeding site were impacted as a result of the relocation: clutch sizes, number of second broods, body masses of both sexes, and year-to-year returns of banded birds (as measured by among-season survival estimates) were all comparable between birds using the original and alternate nesting sites. The annual survival rate for Barn Swallows of 0.374 we reported is within the range (0.300–0.641) of other estimates for this species (Møller and Szép 2002, Møller et al. 2005, Robinson et al. 2008, García-Pérez et al. 2014, Romano et al. 2016).

Although actual estimates of fledgling rates were not collected, ad hoc observations suggested that most nesting efforts were successful at both the original and relocated colonies.

We emphasize that harvest of nests to deploy as seed nests in alternate nesting structures should only be used in situations where demolition of an established breeding colony cannot be avoided. Removal of nests from an active colony might negatively affect future colony size because yearling females may cue in on the presence of previous nests when selecting a breeding site (Safran 2004, 2007). Furthermore, Safran (2004, 2006) suggested that nest reuse may confer a slight reproductive advantage when compared with the costs of building a new nest; Donahue et al. (2018) found that 45–82% of pairs will reuse previously constructed nests. Although Barclay (1988) noted that reuse of old nests may lower chick survival due to increased exposure to nest parasites, Donahue et al. (2018) found that mite abundances did not affect nest-switching between broods.

Addressing the causes of Barn Swallow declines will require a multifaceted approach. In addition to the complex array of challenges associated with climate change, conservation of suitable foraging habitats located near established nesting areas, and threats associated with pesticide use along migration routes and on wintering grounds, reduced nest site availability in many agricultural landscapes is one of many issues to be considered. We recommend that, in situations where demolition of structures being used by active breeding colonies cannot be avoided, a multiyear process be pursued in which alternate nesting site(s) are created and determined to be occupied prior to destruction of an established breeding colony. Deployment of seed nests, harvested outside of the breeding season from structures where demolition is planned, and used to enhance alternative nesting structures prior to the following breeding season, may represent an important strategy for successfully mitigating forced colony relocation.

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#### Author Contributions:

*JLA and ACF conceived the idea; ACF and MR oversaw the monitoring program; JLA conducted banding activities and data management; JLA and JDR conducted statistical analyses; JLA authored the paper with contributions from JDR.*

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**Data Availability:**

The data/code that support the findings of this study are openly available at <https://DOI.org/10.17605/OSF.IO/RBUPG>.

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