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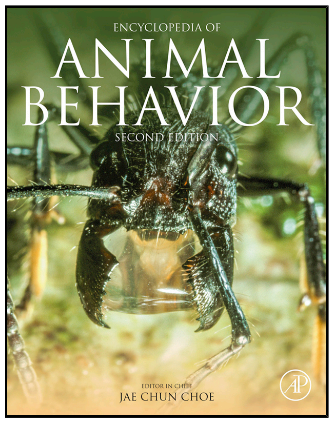

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The Sexual and Social Behavior of the Barn Swallow☆

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Glossary

Extra-pair paternity (molecular analyses of) Using DNA tests, researchers have discovered that many males care for young that are not actually their own, but sired by other males in the population instead. Extra-pair paternity in barn swallows is calculated as the paternity a social male has in his own nest plus those that he has sired in neighboring nests; parentage analyses are important for calculating the role and strength of sexual selection in shaping traits that are used in the process of mate-selection.

Holarctic the northern continents of the world.

Melanin a pigment that underlies the rusty-coloration of ventral feathers of the barn swallow and many other birds. Melanins are produced endogenously rather than acquired through diet like carotenoid pigments that add red and orange colors to the feathers of many other birds like house finches.

Sexual Selection Darwin's famous theory that explains the evolution of traits that confer mating advantages to their bearers. In particular, these traits were puzzling to Darwin because they defy explanation by selection for survival alone.

Social network A graphical and quantitative representation of all individuals in an interacting population that depicts the connections (social interactions) between those interacting individuals.

Tail Streamer the elongated outer tail feathers (rectrices) of the swallow tail, giving the tail its forked appearance.

Abstract

Barn swallows, Hirundo rustica, are well known throughout their nearly worldwide distribution, in no small part because of their close association with human settlements. A tractable species for both individual-based and population-level studies, barn swallows are prominent research subjects at the interface of behavioral, ecological and evolutionary biology. In this short article, we review a fraction of what we have learned from studies of barn swallows with a special focus on discoveries related to sexual selection and variation in social behavior.

Keywords

Aerodynamic function; Geographic variation; Mate selection; Nest construction; Sexual selection; Social network; Sociality; Tail streamers; Ventral color

An inhabitant of most of the Holarctic (with the exception of Greenland I), the barn swallow is the most widespread species of the swallow family, *Hirundinidae*. The extensive breeding range of the barn swallow is believed to be due to their close association with human populations. Based on human colonization patterns across Eurasia and recent studies of the colonization of swallows, it appears that this close association with humans has persisted for millennia (Turner, 2006). Indeed, nearly everywhere you find a barn, building, or bridge, especially if these are situated near water and fields, you find the swallow's mud cup nest tucked in under the eaves or constructed along beams and planks. As such, the barn swallow, or simply swallow as it is called throughout much of range, is well-known. Swallows are also well-loved as evidenced by hundreds of examples of their portraiture in fine and folk art. Some of the earliest discoveries of barn swallow art date back to the Bronze Age where recent discoveries of cave paintings from the ancient society, Thera, feature swallows in flight fighting over feathers used as nest lining – a behavior that persists today (Foster, 1995).

Formal studies of barn swallow behavior began with publications in the early part of the last century and number well into the high hundreds. These studies represent a tremendous amount of breadth ranging from classic ethological studies of parental behavior to sophisticated molecular studies of physiology and reproductive biology. Much of the detail of this research is covered in one of two academic books published on barn swallows. The first, written by Anders Møller in 1994, focuses on sexual selection,

☆*Change History*: September 2018. Rebecca J Safran added a co-author, Dr. Iris Levin, added in-line citations to references throughout, updated information throughout on sexual selection, geographic variation, and sociality and added a reference section which incorporated many of the items in the previous 'suggested reading' section.
This is an update of R. Safran, Barn Swallows: Sexual and Social Behavior, In Encyclopedia of Animal Behavior, edited by Michael D. Breed and Janice Moore, Academic Press, Oxford, 2010, Pages 139-144.

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with an emphasis on his incredible long-term data set on swallows. The second, published in 2006, entitled *The Barn Swallow* by Angela Turner, is a comprehensive review, ranging from conservation status to taxonomy. In this short review, it is difficult to even scratch the surface of the incredible wealth of knowledge accumulated on this 17–20-g bird, and we will first focus on a trait that these birds are arguably the most famous for: their tail streamers. Indeed, much research on the barn swallow revolves around this trait, as their streamers impacts mate-selection, nest construction, flight aerodynamics, parental care, and physiology. Moreover, the tale of tail streamers has as many interesting twists and turns as this trait causes its bearer in flight; the tail of the swallow appears to be constantly evolving and changing in different ways depending on where you study it. Even within populations, there is great debate as to what information this trait is conveying to conspecifics. In the latter half of this review, we summarize what is known about the fascinating variation in social behavior of swallows and how new technology allows us to understand variation in social behavior with unprecedented detail.

For Fancy, or Flight, or Both: The Controversy About Tails

One of the best-known studies on barn swallows and on the role of sexual selection in trait evolution was written by Anders Møller in 1988. This article, published in Nature and cited nearly 600 times, employed techniques of tail manipulation pioneered by Andersson (1982) to examine the relationship between the streamer length of male barn swallows and their mating success. The elegant experimental design involved looking at the pairing date of males randomly assigned to four treatment groups: males whose streamers were artificially elongated 20 mm, males whose streamers were artificially shortened by the same amount, a control group whose streamers were cut and re-glued and yet another control group of males whose streamers were not manipulated at all (Møller, 1988).

That males with elongated streamers attracted mates earlier than their short-streamered neighbors was the first demonstration of a causal relationship between male tail length and female mate choice. Indeed, since that article and the dozens that have followed it (e.g., summarized in Scordato and Safran, 2014; Romano *et al.*, 2017), tail streamers in the European population of the barn swallow, *Hirundo rustica rustica*, have become a textbook example of sexual selection. Experimental and correlational studies show that females prefer males with the longest tail streamers, and, among paired individuals, female tail length is positively correlated with male streamer length, providing evidence for assortative mating based on this trait (Møller, 1994; Turner, 2006). Long-tailed males produce the most offspring (in their first clutches and total number of young per season) each year because they pair and breed earlier and successfully fledge more broods than shorter-tailed males (Møller, 1994; Turner, 2006).

Of course, merely counting the number of chicks in the nest that a male is provisioning is not enough to truly understand his evolutionary fitness. Barn swallows, like so many other social animals, have complicated sex lives. They form a cooperative social pair bond that can last throughout an entire breeding season or longer, but they also pursue extra-pair mating strategies on the side. Therefore, molecular parentage analyses provide the only definitive way to measure the reproductive activities of a male; using these methods allows more accurate assessment of the amount of sexual selection associated with streamer lengths.

To confirm the correlation between a male's streamer length and his social mating success, researchers in Europe also showed that males with the longest streamers enjoy a significantly greater share of paternity in their nests and the nests of others, relative to their short-streamered neighbors. In this experiment, Saino *et al.* (1997) replicated Møller's (1988) classic tail manipulation experiment to look for paternity differences among males in the four treatment groups and, as predicted, found that males whose streamers were elongated sired more offspring in his nest and others compared to males in the shortened and control groups. Studies of extra-pair mating strategies in other populations of barn swallows (throughout Europe and North America) found that the percentage of broods with extra-pair young ranges from 33% to 50% (Scordato and Safran, 2014). As shown in the Geographic Variation section of this article, the relationship between extra-pair mating success and ornamental traits becomes very important when comparing the role of sexual selection for shaping male appearance both within and among populations of swallows.

Tail streamers are also critical for barn swallow flight performance, as they need to function efficiently for these acrobatic aerial insectivores. For evidence that tails are important outside of mating, one needs to look no further than female and juvenile barn swallows – they too exhibit extensively forked tails that are used in flight control. Research has also shown that males with the longest tail streamers pay costs associated with bearing this trait; a year after publishing his first experimental paper on tail streamer manipulations, Møller demonstrated lower survival for males carrying elongated streamers, suggesting that these traits are cumbersome in flight (reviewed in Møller, 1994).

If longer streamers impose a burden, this trait could convey honest information about a male's ability to bear the costs of his long tail and to also maintain a high-quality nest location. Interestingly, rather than appearing to be solely under directional sexual selection (as would be predicted if long-streamered males were always chosen as the favorite mates), this trait appears to be an interesting balance of both sexual selection and natural, or survival-based, selection. Previous studies suggest that individuals with longer streamers suffer from impaired aerodynamic performance that may result in lower foraging efficiency. Swallows with too short of a set of streamers also suffer from reduced flight skills. The balance between too long and too short implies that natural selection already shaped the morphology of this species to accommodate elongation and sexual dimorphism of tail streamers. It appears that tail streamer lengths represent a tug-of-war consequence between sexual and natural selection; how much of each form of selection has contributed to the evolution of this trait has generated great controversy, stirred by the elegant aerodynamic performance studies of Matthew Evans and colleagues (e.g., Evans, 1998, reviewed in Safran and Hauber, 2007).

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Brø-Jorgensen *et al.* (2007) utilized an experimental approach to identify the extent to which variation in the length between a male's streamers either reflects differential ability to withstand the costs of 'too long' streamers, as predicted by sexual selection, or represents the individual-specific match between body size and tail streamer length to optimize flight and foraging performance, as predicted by survival-based natural selection. Through the analysis of aerodynamic performance in a flight maze after a series of manipulations of the same individuals' tail lengths, these researchers, working in a Scottish population of swallows, worked out the relative importance of natural and sexual selection contributing to the variation in the length of the tail streamer (Brø-Jorgensen *et al.*, 2007, reviewed in Safran and Hauber, 2007).

The conclusions of the flight performance study by Brø-Jorgensen *et al.* (2007) are surprising as they found no evidence to support the prevailing view that the sexually-selected component of this trait reflects individual variation in some aspects of male quality which would serve as advertisements to choosy females or competitive males. Instead, the authors suggest that the optimal streamer length for flight varies significantly among males, but that the additional component of the streamer – assumed to be caused by sexual selection – does not. The conclusion, which counters the patterns predicted for variable sex-dimorphic traits under sexual selection, is that the naturally – and not the sexually-selected component of the streamer – conveys information about a male's flight and foraging performance, leaving open the question of why streamers are elongated past this optimal value. To interpret their findings, Evans and colleagues (Evans, 1998; Brø-Jorgensen *et al.*, 2007; Safran and Hauber, 2007) speculate that tail streamer lengths may simply serve to signal the age and sex of the individual (adult male vs. female or juvenile). Further experimental studies that adopt this highly powerful within-individual experimental approach with additional treatments related to mate-selection may provide a definitive test for understanding the likely contributions of both sexual and natural selection on this trait.

Geographic Variation in Phenotypes

The pursuit of whether natural selection, sexual selection, or likely both, cause streamer elongation is far from over. Intriguing phenotypic differences in tail streamer length and plumage color exist among the six most well-known subspecies of barn swallows (it is speculated that there are several more sub-species throughout the enormous breeding range of swallows). Combinations of tail and color are not correlated, that is, dark plumage color does not come with longer streamers; variation in one trait does not at all predict variation in the other. Looking at the average phenotypes of males from throughout the Holarctic region, one sees nearly all possible pair-wise combinations of color and streamer length. Males of European *Hirundo rustica rustica* swallows have nearly the palest ventral color and the most exaggerated tail streamer lengths of all of the barn swallows, while swallows from the North American populations are substantially darker in plumage, with streamers that are amongst the shortest of all sub-species. Intriguingly, populations from the two Middle Eastern sub-species (*Hirundo rustica savignii* along the Nile and *Hirundo rustica transitiva* throughout Israel, Lebanon, Jordan, and Syria) have combinations of dark plumage coloration with streamer lengths that are nearly as long as the European sub-species. Populations in northern Asia (*Hirundo rustica tytleri*) possess intermediate values of streamer lengths and feather color relative to their conspecifics while *Hirundo rustica gutturalis*, which occurs throughout much of Asia, has among the least exaggerated features of all, with the palest ventral color and shortest tail streamers. Though differentially sexually dimorphic with respect to both streamer lengths and color, differences in female morphology are highly concordant with differences in males throughout the entire range of this species complex. Ongoing research is focused on determining the underlying causes of these fascinating phenotypic differences (Scordato and Safran, 2014; Safran *et al.*, 2016a,b; Wilkins *et al.*, 2016; Romano *et al.*, 2017).

Differential Sexual Selection?

What causes differences in the phenotypic variation among the sub-species of barn swallows? Several ecological variables are likely to play a key role. First, most populations are migratory but the Middle Eastern populations are not (Turner, 2006). Even within migratory populations, migratory behavior itself may be influential in the evolution of phenotype differences (e.g., Safran *et al.*, 2016a). Second, there are interesting differences in the extent to which males participate in parental care, which could influence trait evolution if competition for mates varies among populations (Turner, 2006). Third, parasites associated with barn swallows vary across their range; these may be playing important roles in trait evolution in closely related populations in different ways (Hund, 2017).

Sexual selection may interact with all of these ecological factors and may also be playing a role in trait variation since many of the phenotypic differences among populations are seen in sexually-dimorphic traits (Scordato and Safran, 2014). The hypothesis that sexual selection operates differently on streamer length and color among various populations is currently under study in four subspecies: *Hirundo rustica rustica*, *Hirundo rustica gutturalis*, *Hirundo rustica erythrogaster*, and *Hirundo rustica transitiva*, for which phenotype manipulation experiments and a meta-analysis of within-population studies already reveal interesting differences in the role of mate-selection decisions related to these traits (e.g., Safran *et al.*, 2016b; Romano *et al.*, 2017).

Sexually-selected traits are often sexually dimorphic, predict patterns in mate- selection, and show a relationship with various measures of reproductive success. While streamer lengths are sexually dimorphic in North America (though to a lesser extent than the dimorphism of streamers in western Europe), studies on the sexual selection of tail streamers of North American

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populations of barn swallows have yielded mixed results, with an overall impression that sexual selection is at the very least a lot weaker on this trait in North America (Safran *et al.*, 2016b; Romano *et al.*, 2017). For example, streamer variation in males and females does not predict patterns of assortative pairing in *Hirundo rustica erythrogaster*, as is the case in European populations (Safran and McGraw, 2004). Male streamer length is not a predictor of many measures of seasonal reproductive success in most correlational data sets, with the exception of a paternity study conducted by Kleven *et al.* (2006).

To date, two studies have experimentally manipulated the streamer length of North American barn swallows. Unfortunately, the first experiment, designed to replicate Møller's 1988 study, is difficult to interpret due to small sample sizes. Though Smith and Montgomerie (1991) found that males whose streamers were experimentally elongated attracted social mates earlier in the breeding season than those whose streamers were shortened, these long-tailed males received less paternity from their social mates, compared to males with shortened tails. Another recent experimental manipulation of tail streamers in a different North American population of barn swallows suggests that shorter-tailed males have paternity advantages over longer-tailed males (Safran *et al.*, 2016b).

The Color of Feathers

If tail streamers do not drive mate choice, what does? Safran and McGraw (2004) found that ventral coloration, not streamer length, is correlated with patterns of pairing and seasonal reproductive success in a population of North American barn swallows. Experimental manipulations of male coloration demonstrated that individuals use this trait to assess male quality (Safran *et al.*, 2005, 2016b). Studies on plumage color variation also indicate variation in the signaling function of this trait among closely related populations (summarized in Romano *et al.*, 2017). Specifically, data about the relationships between reproductive success, tail streamer length and aspects of plumage variation, including the size of white tail spots, the size and color of the throat patch and breast color were compiled from studies of four subspecies (*Hirundo rustica rustica*, *Hirundo rustica gutturalis*, *Hirundo rustica erythrogaster*, and *Hirundo rustica transitiva*) by Romano and colleagues for a meta-analysis on sexual selection in barn swallows (2017). Within each of these subspecies there is some evidence of sexual selection on various plumage color traits: white tail spots are associated with reproductive performance in *Hirundo rustica rustica*, *Hirundo rustica gutturalis*, ventral color variation is associated with reproductive performance in *Hirundo rustica erythrogaster*, and *Hirundo rustica transitiva*, and throat color variation is associated with reproductive performance in *Hirundo rustica gutturalis*, *Hirundo rustica erythrogaster* (see Fig. 6 in Romano *et al.*, 2017).

Feather color in barn swallows is derived from melanin-based pigments; these are produced by the birds and, as such, do not reflect an individual's diet directly, as is the case with the beautiful pink feathers of the flamingo or the bright red beak of the zebra finch. Though we know little about why females might favor the use of color for mate-selection in one population and streamer length in another, Safran *et al.* (2008) demonstrated a causal relationship between coloration and testosterone, a sex steroid often linked with aggressive and sexual behavior. Darker males with higher levels of circulating testosterone in the early part of the breeding season may be more competitive for high quality nesting territories. Further studies on the underlying production and associated expression costs of plumage color traits would be particularly illuminating, both in contrast to signaling costs of tail streamer length variation as well as among closely related populations with variable rates of sexual selection on these plumage color traits.

Tail Streamers, Ventral Color, or Both?

In a direct comparison in which male tail streamers and plumage color were simultaneously experimentally manipulated, Safran and colleagues found evidence that manipulations of these traits result in different reproductive consequences in two subspecies of barn swallow: (*H.r. erythrogaster* in North America and *H.r. transitiva* in the East Mediterranean). In Colorado, males with either (1) darkened ventral coloration or (2) shortened streamers gained paternity between two successive reproductive bouts. In contrast, males in Israel with a combination treatment of darkened ventral coloration and elongated streamers gained paternity between two successive reproductive bouts.

Further, a recent meta-analysis of sexual selection on barn swallows by Romano *et al.* (2017) summarizes additional work on barn swallow populations from Japan, initiated by Masaru Hasegawa and colleagues and within Israel by Yoni Vortman, Arnon Lotem, and colleagues. Here, direct comparisons of sexual selection on various plumage traits, including tail streamer length, tail asymmetry, the size of white tail spots, the size and color of the throat patch and breast color demonstrate divergent sexual selection on male tail length and throat color in comparisons of *Hirundo rustica rustica*, *and Hirundo rustica erythrogaster*, and male tail length, size of white tail spots, and throat color between *Hirundo rustica rustica* and *Hirundo rustica gutturalis* (see Table 3, Romano *et al.*, 2017). Additional experimental studies that manipulate trait variation in consistent ways and thus provide direct comparisons among populations are warranted (see Safran *et al.*, 2016b).

Explanations for Geographic Variation in Tail Streamers

Despite pronounced latitudinal variation in streamer lengths in European populations (males in Denmark have longer streamers compared to males in Italy), the function of streamers, in terms benefits of social and genetic reproductive success, do not vary

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tremendously between these two populations. Although the breeding latitude of males in North America most closely corresponds to males in the Italian study areas, there were no similarities in the benefits from elongated streamers in a population in New York to males in the intensively studied population in northern Italy (e.g., Saino *et al.*, 1997). In the Italian population, benefits associated with this sexual signal are apparent, while they are not in New York. Considered in concert, the results of studies in North America demonstrate that the pattern of sexual selection on tail streamers varies geographically. Smith and Montgomerie (1991) suggest that this geographic variation may relate to differences in male behavior during the incubation period, as male barn swallows in North American spend approximately 12% of daylight hours on the nest during the incubation stage of the breeding cycle while males in the European population do not participate in incubation. It is possible that the longer-tailed males in North America may be at a higher risk of tail streamer breakage during incubation at nests as streamers often brush against a wall or roof. The resulting broken streamers may be shorter than the aerodynamic optimum, thereby decreasing the fitness of the bird.

This explanation is not entirely compelling because the average length of male streamers in North America is equivalent to those of females in Europe. The females' streamers would be even more subject to abrasion during entry into the nest as the female is the sole incubating parent in that population. Potentially, males in North America have less time to forage due to their incubation duties, and therefore they must be more efficient flyers. The additional time constraint of incubation may be sufficient enough to select against those individuals whose tails are beyond the aerodynamic optimum. Consistent with this explanation, previous studies have found that only a small distal region of the tail streamer (approximately 10–15 mm) in the European population appears to be under sexual selection, while the majority of the tail streamer length has evolved to a naturally selected aerodynamic optimum that is very similar to the shorter mean streamer length in the North American population (Neuman *et al.*, 2007).

Because male ventral coloration predicts patterns of social and genetic reproductive success in addition to influencing his mate's rate of parental care (females feed more to shared offspring when paired to darker males), feather coloration may be a more reliable signal of male quality than tail streamer length in North American populations. As mentioned earlier, the jury is still out as to why this trait might be more informative than streamer lengths. A newer piece of evidence suggests that parasites may be playing an important role in providing relevant about plumage color in North American male barn swallows (Hund, 2017).

Sociable Swallows

The physical appearance of barn swallows is not the only highly variable feature of this fascinating species. In fact, early studies of this species by Snapp (1976) in Ithaca, New York and later by Møller (1987) in Denmark and Shields (1987) in a separate population in northern New York focused on variation in the sociality of barn swallows. Throughout their extensive breeding range, barn swallows breed in solitary pairs or with groups of conspecifics; they are not obligately social breeders. Typically, colony sizes range from 2 to 200 breeding pairs, with the majority of individuals breeding either solitarily or in groups ranging from 9 to 35 pairs (Brown and Brown, 1999; Turner, 2006).

Early studies demonstrated few benefits and many costs for group breeding for barn swallows. Snapp's (1976) pioneering studies on social behavior found none of the benefits to group-breeding barn swallows that are typically found in other highly social organisms. Barn swallows in her study area near Ithaca, New York received no benefits from social foraging or collective predator defense. Snapp (1976) concluded that barn swallows breed in groups as a function of limited nest sites. Similarly, Møller (1987), working in Denmark, found no net social foraging benefits to group breeding, yet he did detect slightly faster reaction times in larger colonies to the experimental presentation of a potential nest predator.

Møller (1987) concluded that group breeding in barn swallows may be beneficial to older males and unpaired males. These males gain extra-pair mating opportunities in social groups, but this does not explain why females or younger males tolerate the costs of sociality. Møller defined the costs in terms of competition for food, infanticide, nest parasitism, and parasite transmission. Another long-term study of barn swallow sociality in New York by Shields and Crook (1987) generated an overall assessment of group breeding that was similar to Snapp's – that ideal nest sites are limiting. As a consequence, these researchers developed the traditional aggregation hypothesis which predicts that group breeding is related to nest-site selection behavior.

Overall, research on group living in barn swallows has shown either no relationship between average reproductive success and group size or a negative relationship between average reproductive success and group size, leaving open the question of why individuals breed socially (Safran, 2004).

A distinctive attribute of many species in swallow family (Hirundinidae) is the persistent use of mud nests across breeding seasons. The re-use of old nests is a predominant nest-site selection strategy of barn swallows across their extensive breeding range. Anywhere from 45% to 82% of pairs re-use old nests for their first breeding attempts (Brown and Brown, 1999; Safran, 2004). Once constructed, nests can persist in the environment for decades, and the majority of breeding pairs at a site attempt to refurbish or re-use these structures instead of constructing new ones. Pairs settling in old nests for first breeding attempts lay eggs earlier and have greater numbers of fledged young compared to pairs that construct new nests at the start of the breeding season, regardless of their previous breeding experience. A primary benefit from re-using old nests is that these pairs breed earlier than those who construct new nests at the start of the season (Safran, 2004). Evidence also suggests that individuals avoid the costs associated with ectoparasites by selectively avoiding old nests with remnant mite populations (Turner, 2006). Because nests and nest scars are only rarely completely removed from sites between breeding seasons, it is logical to assume that these nests offer important information to individuals making decisions about where to breed.

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A fascinating consequence of nest re-use is that the number of old nests at a breeding site strongly predicts the number of breeding pairs that settle there (Safran, 2004). Because site fidelity is the rule in barn swallows with prior breeding experience (natal philopatry – the return to the birth site in a following season – is incredibly low), group breeding persists even in the absence of old nests, suggesting strong benefits of site familiarity. In order to truly demonstrate that group size is a function of individuals searching for old nests, a critical experiment tested for a relationship between the number of immigrants that settle at sites and the number of old nests at the site at the start of the season. In the same breeding population as Snapp's (1976) studies but nearly three decades later, Safran (2004) compared the return and immigration rates of adults at sites where all old nests had been experimentally removed and sites where old nests remained untouched between breeding seasons. That the proportion of immigrants was significantly lower during removal years and the number of immigrants was positively related to the number of old nests collectively provided compelling evidence that group size is strongly influenced by the number of new breeders at a site. In turn, the number of immigrants was experimentally shown to be related to the number of old nests at a site at the start of the breeding season (Safran, 2004). This strong relationship between the number of old nests and the number of immigrants settling at a site suggests that immigrants not only use old nests as a cue for settlement decisions, but that they settle with a probability that is proportional to the number of old nests at a breeding location. Experiments designed to analyze further the benefits of site fidelity *per se* in the absence and presence of old nests would provide further resolution on the relationship between group size and the number of old nests present at a site.

Social group size is an important aspect of social living that likely influences another key component of social behavior: social interactions. Quantifying social interactions in the wild can be a real challenge for behavioral ecologists, particularly in an aerially acrobatic species like the barn swallow. Although barn swallows breed colonially, the males are still territorial around their nest, so there are frequent male-male and male-female interactions among individuals during the breeding season. The difficult part is finding a reliable, accurate measure of social interactions that is as unbiased as possible. Simply observing color banded birds (or bird with white tail spots colored for easier identification in flight) captures only a small fraction of interactions, and even with many simultaneous observers, the data are likely biased towards interactions in a particular place or between particular pairs of individuals.

Recently, Iris Levin and Rebecca Safran started to measure social interactions between barn swallows using miniaturized digital transceiver tags that measure close-proximity interactions between tagged birds. These tags each emit a unique identification pulse every 20 s and they can be programmed to recognize the identification codes of nearby tags given a user-set detection distance (Levin *et al.*, 2015). Levin and Safran typically restrict an interaction to a conservative $\leq$10 cm, although in lower density colonies this can be relaxed to investigate how interactions change with different proximities (Levin *et al.*, 2016). The tags record hundreds of interactions during the short period of time the birds carry them. Once a tag has amassed a certain number of tag-tag logs, the data will download to one of several receiver stations set within the breeding colony (Levin *et al.*, 2015). Any remaining logs can be retrieved when the bird is recaptured for tag removal. If the bird is not recaptured (which happens in $<$10% of cases in this study), the tag's harness degrades and falls off. Although close proximity does not guarantee an interaction between individuals, Levin has video-validated the tags and demonstrated that the set detection distance for a tag-tag log to be considered an interaction is quite conservative and thus the tags sub-sample the total social interactions. The pros of this system are: unprecedented, pair-wise social interaction data with precise information about time and duration of the interactions. The cons include a battery-limited, short sampling period, and the fact that the data for the entire social network are only as good as the number of functional tags (battery life varies) and the proportion of the colony tagged.

Proximity tags have given researchers a window into the social lives of barn swallows. In a small pilot study, Levin and Safran found that males who had darker ventral plumage, long tail streamers, and stronger responses to stress (these traits were correlated in this particular sample) had the most interactions with females (Levin *et al.*, 2016). Males who had higher numbers of the closest-proximity interactions with other males tended to have strong responses to stress (higher stress-induced corticosterone levels) and lower diversity of microbes in their gut, measured by DNA sequencing of microbes from a fecal sample (Levin *et al.*, 2016). Contrary to the pattern found between males, females who interacted more at the closest proximities with males had higher gut microbial diversity. Females tend to be far less interactive with other females than males are with other males, leading to lower overall levels of interactivity (Levin *et al.*, 2016). Therefore, more interactive females may increase their acquisition of gut microbes via social interactions. On the other hand, highly interactive males may pay a cost of interaction due to increased stress, which may be the cause of their lower gut microbial diversity. Stress has been implicated in shaping gut microbial communities in a number of other vertebrate systems.

Iris Levin and Rebecca Safran followed-up on this preliminary research with a social network experiment aimed at testing whether male ventral plumage color played a causal role in male-female interactivity and whether changes in interactivity induced predictable changes in physiology (e.g., testosterone and stress-induced corticosterone levels). They did this by tagging a large population of barn swallows with proximity tags to collect baseline (pre-manipulation) social network data. After several days of data collection, the tags were programmed to turn off for several days at which point a random half of the males in the population had their ventral plumage darkened using a non-toxic art marker. Afterwards, the tags turned back on again to measure how social interactions changed as a result of the plumage manipulation. The results of this experiment did show that male ventral plumage color is important in social behavior; the greater the positive change in plumage color (pale to dark), the greater the increase in interactions between the manipulated male and his social mate post-manipulation compared to pre-manipulation. This work is still ongoing as

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Levin and Safran continue to piece together the morphological and physiological traits that mediate social interactions and investigate how aspects of physiology respond to changes in social interactivity.

The Past, Present and Future

Having been featured so prominently in the biological literature, it is difficult to leave out the dozens of other reasons why barn swallows are wonderful subjects for studies related to animal behavior. Besides being tractable, easy to handle, robust to manipulation both during and after handling, and fairly numerous, they are highly variable in so many morphological and behavioral dimensions. We have mentioned a few here and the suggested readings are offered to provide more details. Turner's (2006) book will be extremely helpful to those who want more information.

Sadly, it is common these days to finish an article like this with the bad news. Like so many other species on our planet, barn swallow populations appear to be declining. Formal demographic studies throughout Europe and anecdotal stories from elsewhere are providing sobering evidence that this once hugely abundant species is dwindling throughout its range (Nebel *et al.*, 2010). Though still common enough to observe swallows in flight most everywhere you look, changes in agricultural practices and the move towards metal and concrete over the use of wood for barn construction, in addition the usual detrimental effects related to human population growth, appear to be taking their toll. One can purchase artificial nests or provide wooden ledges within buildings that might otherwise prove inhospitable to attract these beautiful birds. Reduced pesticide use will also help boost the populations of aerial insects these birds rely on.

See also: **Hormones and Behavior:** Female Sexual Behavior: Hormonal Basis in Non-Mammalian Vertebrates. **Reproductive Behavior:** Sexual Selection and Speciation.

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Further Reading

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