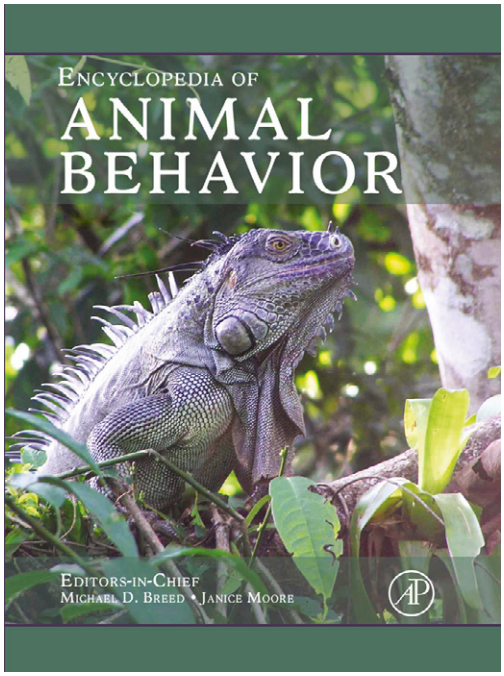

Safran R. (2010) Barn Swallows: Sexual and Social Behavior. In: Breed M.D. and Moore J., (eds.) Encyclopedia of Animal Behavior, volume 1, pp. 139-144 Oxford: Academic Press.

B

Barn Swallows: Sexual and Social Behavior

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An inhabitant of most of the Holarctic (with the exception of Greenland and Iceland), 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. On the basis of 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. 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 the swallow as it is called throughout much of its 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: 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 even today!

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, with an emphasis on the author's incredible long-term data set on swallows. The second, published very recently (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 I 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 (**Figure 1**), as their streamers impact mate-selection, nest construction, flight aerodynamics, parental care (**Figure 2**), and physiology. Moreover, the tale of tail streamers has as many interesting twists and turns as this trait causes its bearer to make in flight; the tail of the swallow appears to be constantly evolving and changing in different ways depending on where one studies it. Even within populations, there is much debate on the kind of information this trait conveys to conspecifics. In the latter half of this review, I summarize what is known about the fascinating variation in the social behavior of swallows.

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

One of the best-known articles on barn swallows was written by Anders Møller in 1988. This article, published in *Nature* and cited over 300 times, employed techniques of tail manipulation pioneered by Malte Andersson 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 dates of males randomly assigned to four treatment groups: males whose streamers were artificially elongated by 20 mm, males whose streamers were artificially shortened by the same length, control males whose streamers were cut and reglued, and yet another control group of males whose streamers were not manipulated at all.

That males with elongated streamers attracted mates earlier than their neighbors with short-streamers 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, tail streamers in the European population of the barn swallow *H. 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

Figure 1 A North American swallow (*H. rustica erythrogaster*) in flight. In North American populations of barn swallows, ventral plumage color is typically darker compared to the European nominate subspecies (*H. rustica rustica*), whereas tail streamers are shorter. Photo credit: © Marie Read.

Figure 2 A North American swallow attending young nestlings. Both males and females participate in feeding of shared offspring, although paternity is typically mixed within each brood. Interestingly, the degree to which males participate in incubation varies among subspecies of swallows, males participating to a greater degree in North America compared to Europe. Photo credit: © Marie Read.

for assortative mating on the basis of this trait. Long-tailed males produce the most offspring (in their first clutch and total number of young per season) each year because they pair and breed earlier and successfully fledge more broods than males with shorter tails.

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. Indeed, molecular parentage analyses provide the only definitive way to measure the reproductive activities of a male; use of these methods allows for 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 fact, Saino and collaborators replicated Møller's 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 their nests and those of 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%. 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.

But tail streamers are also critical to 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. 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.

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 also to 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 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 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 since the 1990s.

Recently, a novel set of experiments conducted by Jakob Brø-Jorgensen, Rufus Johnstone, and Matthew Evans utilized an individual-based 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.

The conclusions of this article 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 sexdimorphic traits under sexual selection, is that the naturally selected – 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 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 subspecies throughout the enormous breeding range of swallows). Combinations of tail and color are not correlated, that is, dark color does not come with longer streamers and statistically, 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 *H. rustica* subspecies 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 more colorful, with streamers that are among the shortest of all subspecies (**Figures 1** and **2**). Intriguingly, populations from the two Middle Eastern subspecies (*savignii* along the Nile and *transitiva* throughout Israel, Lebanon, Jordan, and Syria) have combinations of dark plumage coloration with streamer lengths that are almost the same as those of the European subspecies. Populations in northern Asia (*H. rustica tyleri*) possess intermediate values of streamer lengths and feather color relative to their conspecifics while *H. 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.

Differential Sexual Selection?

What causes differences in the phenotypic variation among the subspecies of barn swallows? Three ecological variables are likely to play a key role. First, most populations are migratory but the Middle Eastern populations are not. Second, there are interesting differences in the extent to which males participate in parental care. Finally, latitudinal differences in streamer length (longer in the north for the most widespread populations in Europe and North America, though not a sweeping generalization for the species complex as a whole) are the rule, though this pattern remains unexplained. Sexual selection is also likely to be playing a role, since many of the phenotypic differences among populations are seen in sexually dimorphic traits. The hypothesis that sexual selection operates differently on streamer length and color among various populations is under current study in three subspecies: *H. rustica rustica*, *H. rustica erythrogaster*, and *H. rustica transitiva*, for which phenotype manipulation experiments will likely reveal interesting differences in the role of mate-selection decisions related to these traits.

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 of the sexual selection of

tail streamers of North American 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. For example, streamer variation in males and females does not predict patterns of assortative pairing in *H. rustica erythrogaster*, as is the case in European populations. 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 Oddmund Kleven and colleagues that I describe later in this article. Collectively, these results may indicate reduced or absent sexual selection on this trait in this continental population.

Some other interesting comparisons between studies of males in North America and Europe are also noteworthy; Nicola Saino and colleagues reported a significant positive association between streamer length and the proportion of offspring sired in first breeding attempts in a northern Italian population of barn swallows, whereas Colby Neuman and others found no association between these two variables in North America using the same test statistic. Likewise, Anders Møller and colleagues report a significant linear relationship between the proportion of offspring sired by the resident male of the nest in relation to his streamer length from a population near Milan, Italy, whereas no such relationship was found in males from Ithaca, New York, using the same type of data analyses. Anders Møller and Håkan Tegelström, in the late 1990s, reported a negative correspondence between the proportion of broods being sired by extra-pair males and the streamer length of the male nest owner in a population in Denmark, indicating that longer-tailed males are less likely to be cuckolded. However, using the same statistical data analyses, Rebecca Safran and colleagues found no such correspondence between a male's streamer length and his probability of being cuckolded.

To date, only one study has experimentally manipulated the streamer length of North American barn swallows. Unfortunately, this experiment, designed to replicate Møller's 1988 study, is difficult to interpret because of the small sample sizes. Though Hendrik Smith and collaborators 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. Interestingly, Oddmund Kleven went back to the same study sites in Ontario, Canada, nearly 15 years after the original experiment was published to conduct a large paternity study. Kleven and colleagues report that males with naturally long streamers received extra-pair benefits from females outside their social pair bond, but not within-pair benefits from their own mates, compared to their shorter-streamered neighbors. It is difficult to reconcile these results with others conducted on this subspecies; and as previously mentioned, large-scale tail manipulation experiments in North American populations of barn swallows currently underway, are sorely needed.

The Color of Feathers

If tail streamers do not drive mate choice, what does? Recently, Rebecca Safran and Kevin McGraw 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. 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 and colleagues recently 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 costs of streamers and ventral color would be particularly illuminating.

Explanations for Geographic Variation in Tail Streamers

There is mounting evidence that the function of elongated streamers varies between European and North American populations, and perhaps others including *H. rustica transitiva* in Israel.

Interestingly, despite latitudinal variation in streamer lengths in European populations so that males in Denmark have longer streamers compared to males in Italy, the function of streamers, in terms of the benefits of social and genetic reproductive success, does not vary 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 compared to males in the intensively studied population near Milan. 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. Hendrik Smith and Robert Montgomerie suggest that this geographic variation may relate

to differences in male behavior during the incubation period, as male barn swallows in North American spend ~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 because of 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 (~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.

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, **Figure 2**), 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.

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 Barbara Snapp in Ithaca, New York, and later by Anders Møller in Denmark and William Shields 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.

Early studies demonstrated few benefits and many costs for group breeding for barn swallows. Barbara Snapp's pioneering studies of 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 concluded that barn swallows breed in groups as a function of limited nest sites. Similarly, Anders Møller, working in Denmark, found no net social foraging benefits to group breeding, yet he did detect slightly shorter reaction times in larger colonies to the experimental presentation of a potential nest predator.

Møller 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 colleagues 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 a negative relationship or no relationship at all between average reproductive success and group size, leaving open the question of why individuals breed socially.

A distinctive attribute of many species in swallow family (Hirundinidae) is the persistent use of mud nests across breeding seasons. The reuse 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 reuse old nests for their first breeding attempts. Once constructed, nests can persist in the environment for decades, and the majority of breeding pairs at a site attempt to refurbish or reuse 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 reusing old nests is that these pairs breed earlier than those that construct new nests at the start of the season. Evidence also suggests that individuals avoid the costs associated with ectoparasites by selectively avoiding old nests with remnant mite populations. 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.

A fascinating consequence of nest reuse is that the number of old nests at a breeding site strongly predicts the number of breeding pairs that settle there. 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 Barbara Snapp's studies but nearly three decades later, Rebecca Safran 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. This strong relationship between the number of old nests and the number of immigrants settling at a site suggests that not only do immigrants use old nests as a cue for settlement decisions, but they also 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.

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 common, they are highly variable in so many morphological and behavioral dimensions. I have mentioned a few here and Further Reading is offered to provide more details. Angela Turner's recent book will be extremely helpful to those who want more information.

Sadly, it is common these days to conclude 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. Though it is still common enough to observe swallows in flight almost everywhere you look, changes in agricultural practices and the move toward metal and concrete over the use of wood for barn construction, and 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 these beautiful birds. Reduced pesticide use will also help boost the populations of aerial insects upon which these birds rely.

Two comprehensive reviews of barn swallows have been published and are recommended here. The first is a treatment of sexual selection in European barn swallows published in 1994 by Anders Møller; as such, I provide suggestions related to sexual selection that were published after this book or that deal with sexual selection in North American populations. Many of the references given in the Further Reading are studies that were published after Angela Turner's wonderful synthesis of recent literature on barn swallows in 2006.

See also: Mate Choice in Males and Females; Social Selection, Sexual Selection, and Sexual Conflict; Visual Signals.

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