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Geographic variation in sexual selection and implications for speciation in the Barn Swallow

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Abstract

Barn Swallows (*Hirundo rustica*), a group of passerine birds comprised of six closely related subspecies, are well known throughout their nearly worldwide distribution, in part because of their close association with human settlements. A tractable species for both individual-based and population-level studies, Barn Swallows are a prominent model system in evolutionary, ecological, and behavioral research. Here we review work on sexual selection and population divergence in this species complex, focusing on comparative studies among populations and subspecies. We summarize variation in the targets of mate choice and in the information conveyed by sexually selected traits, and conclude that the benefits advertised by different traits may vary geographically. Finally, we consider the role of sexual selection as a driver of population divergence in this widespread and phenotypically variable species complex.

Keywords: Barn Swallow, Geographic variation, Natural selection, Sexual selection, Speciation, Tail streamers, Ventral color

Introduction

A spring and summer inhabitant of the Holarctic, the Barn Swallow (*Hirundo rustica*) is the most widespread species of the swallow family, Hirundinidae. The extensive breeding range of the Barn Swallow is believed to be due in part to their close association with human populations. Based on patterns of human colonization in Eurasia and recent phylogenetic studies in swallows, it appears that this association with humans has persisted for millennia (Zink et al. 2006). Indeed, swallows will nest nearly everywhere there are barns or bridges, especially if these are situated near water and fields. In addition to human structures providing nest sites, swallows benefit from agriculture: the insects surrounding livestock are an excellent food source for these aerial insectivores. The Barn Swallow is thus well known and easily recognizable throughout rural areas worldwide, and has been the subject of extensive behavioral, ecological, and evolutionary research since the early part of the 20th century (reviewed in Møller 1994a; Turner 2006).

Barn Swallows are divided into six subspecies (del Hoyo and Elliott 2014, Figure 1). The nominate form, *H. r. rustica*, breeds throughout Europe, North Africa, and western Russia and migrates to the Mediterranean and sub-Saharan Africa in the winter. Further east in Russia, *H. r. tytleri* occurs in the Baikal region and south into Mongolia, and is believed to overwinter in India and Southeast Asia. The phenotypically variable *H. r. gutturalis* overwinters in Southeast Asia and breeds in the Russian Far East, China, Japan, and Korea (although it has sometimes been divided into as many as four different subspecies throughout this range, del Hoyo and Elliott 2014). Two subspecies with comparatively restricted ranges also occur in the Middle East and North Africa: *H. r. savignii* is a year-round resident in the Nile Valley in Egypt, and *H. r. transitiva* is a short-distance migrant breeding in Israel, Jordan, Lebanon, and Syria. A single subspecies, *H. r. erythrogaster*, occurs throughout North America and overwinters in Central and South America. A breeding population has also recently established itself in Argentina (Martínez 1983).

There is extensive phenotypic variation among these six subspecies, particularly in body size, the length of the "tail streamers" (the outermost tail feathers), and ventral color, which ranges from nearly pure white in some populations to a dark rusty orange in others (Figure 2, reviewed in del Hoyo and Elliott 2014). These latter two traits have been the subject of sexual selection research in several populations. Males of the European *H. r. rustica* are on

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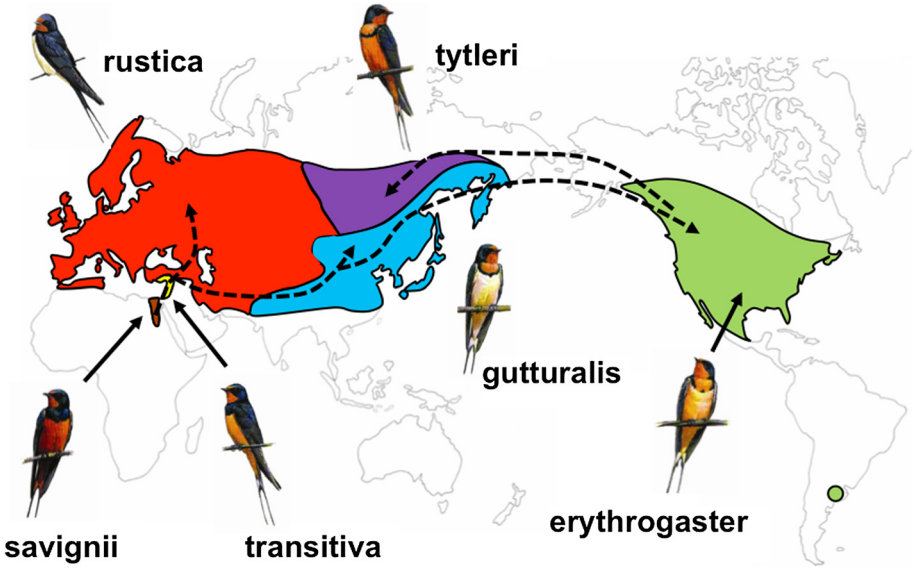

Figure 1 Range map of the six barn swallow (*Hirundo rustica*) subspecies. Dashed arrows show hypothesized directions of colonization from an African common ancestor. Note the back-colonization of the Baikal region by North American swallows, which eventually gave rise to *H. r. tytleri*. Figure adapted from Dor et al. (2010).

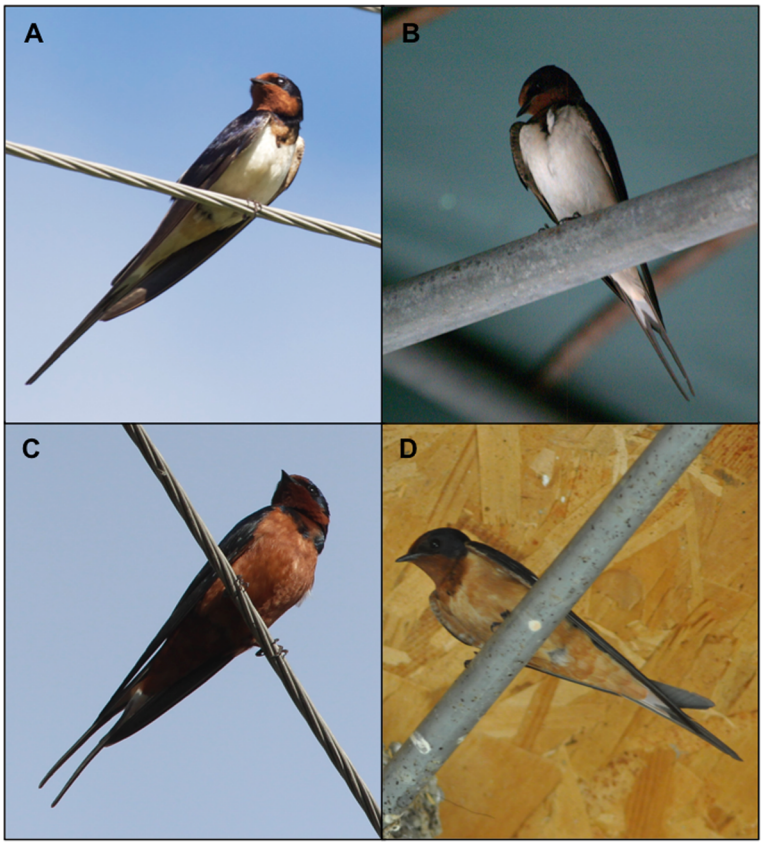

Figure 2 Four of the six barn swallow subspecies. A) nominate European *H. r. rustica*, with pale ventral coloration and long tail streamers **B)** East Asian *H. r. gutturalis*, with pale ventral coloration and short streamers; **C)** Baikal region *H. r. tytleri* with very dark ventral coloration and intermediate streamers; and **D)** North American *H. r. erythrogaster* with dark ventral color and short streamers. Note that *tytleri* is much more similar in coloration to *erythrogaster* than to the geographically proximate Eurasian subspecies, supporting phylogenetic data that suggest it has re-colonized Asia from a North American ancestor. Photos courtesy of M. Wilkins.

average largest in body size, palest in ventral color and have the longest tail streamers of all of the subspecies (Møller 1994a, Safran et al. in review). The North American populations are on average much darker in ventral color, with tail streamers tending to be intermediate in length to other subspecies (Safran et al. in review). Populations of the two sedentary subspecies (*H. r. savignii* in Egypt and *H. r. transitiva* in the Middle East) have relatively large body size, dark plumage coloration, and long streamers (although *H. r. savignii* is darker and shorter-streamered than *H. r. transitiva*, (Vortman et al. 2013)). *H. r. tytleri*, in the Baikal region, is of intermediate body size and exhibits intermediate streamer lengths with dark ventral color, while East Asian *H. r. gutturalis* has very small body size, pale orange-brown ventral color, and the shortest tail streamers of all subspecies. Despite these broad phenotypic differences, there is latitudinal variation within subspecies and some overlap in some trait values between subspecies (Møller 1994a). Within subspecies, there is sexual dimorphism in both streamer length and ventral color, although variation in female phenotype among subspecies mirrors male variation to some extent (Møller 1994a, del Hoyo and Elliott 2014).

Phylogenetic reconstructions of the species complex indicate an African common ancestor, of which the Middle Eastern *H. r. savignii* and *H. r. transitiva* are likely the closest relatives (Figure 3, Zink et al. 2006; Dor et al. 2010). Barn swallows then expanded their range throughout Eurasia, with *H. r. rustica* and *H. r. gutturalis* likely diverging a via vicariance events (Zink et al. 2006). Birds from the Asian populations also crossed the Bering Strait to populate North America an estimated 100000 years ago, giving rise to the *H. r. erythrogaster* subspecies. Most interestingly, these North American swallows apparently re-crossed the Bering Strait and recolonized the Baikal region, as mtDNA indicates that *H. r. tytleri* is nested within the *erythrogaster* clade, and these two subspecies are much more phenotypically similar than *H. r. tytleri* is to the more geographically proximate *rustica* or *gutturalis* (Figure 2). This range expansion and concomitant phenotypic differentiation among the six subspecies has occurred on a rapid evolutionary timescale (estimates are approximately 100000 years ago for the Asian-North America split and 27000 years ago for the North America-Baikal dispersal event, Zink et al. 2006). Indeed, divergence is not complete, as hybridization and gene flow occur at most subspecies borders (Turner 2006; Dor et al. 2012). The patterns of phenotypic differentiation among subspecies, coupled with recent divergence and ongoing gene flow, have made the Barn Swallow system one of particular interest in the fields of sexual selection and speciation, which are the focus of this review.

The first studies of sexual selection in Barn Swallows were conducted in European populations of *H. r. rustica*, and focused primarily on the role of tail streamer length in mate choice. However, when research began on North American *H. r. erythrogaster* in the 1990s, it became apparent that streamer length played a different role in reproductive success in this subspecies than it did in Europe, although sample sizes for these studies were small (Smith and Montgomerie 1991; Smith et al. 1991). Geographic variation in the targets of mate choice has subsequently drawn attention to the role that sexual selection may play in population divergence and speciation in the Barn Swallow complex. Here, we first review what is known about the evolution and social function of streamer length and ventral coloration in different subspecies of Barn Swallow; these two traits have been the subject of the most extensive research. We also consider the role of song in sexual selection, which is less well studied than color and streamer length but nonetheless seems to play a role in both male competition and mate choice. We summarize data related to sexual selection on these traits in the different subspecies, and then consider the role of geographic variation in sexual selection pressures in population divergence and speciation. We do not discuss traits that have been studied in only a single subspecies of Barn Swallows (e.g., nest size, asymmetry, senescence),

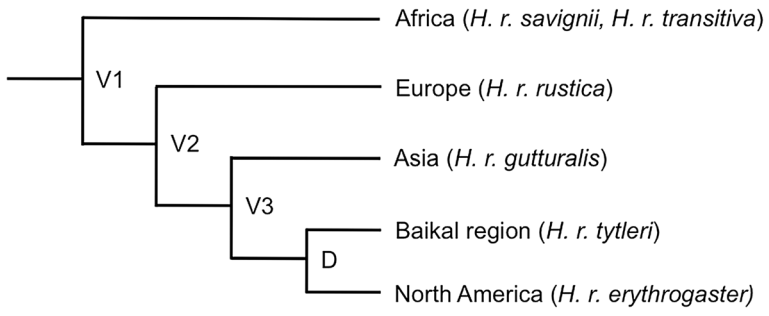

Figure 3 Major clades within the barn swallow complex. The splits between African and Europe (V1), Europe and Asia (V2), and Asia and North America (V3) likely arose via vicariance events, whereas the split between North America and the Baikal region (D) is likely due to dispersal of North American birds into Eastern Russia. Figure modified from Zink et al. (2006).

as there is no comparative data available. We conclude by highlighting future directions for ecological and evolutionary research on this species complex.

Review

Sexually selected traits in the Barn Swallow

Sexual selection was originally conceived by Darwin (1871) to explain the widespread presence in nature of elaborate and conspicuous traits that do not contribute to an organism's survival, and indeed often seem detrimental to its fitness. Darwin postulated that these traits evolve because they are attractive to members of the opposite sex and/or aid in competition for mates; hence, costly and elaborate traits could persist because they enhanced an individual's mating success, if not its survival. A sexually selected trait is therefore defined as any trait that assists an individual in the acquisition of mates or fertilizations (Andersson 1994). These traits can evolve via female choice (i.e., females mate with males that display the most elaborate traits), or by male-male competition (i.e., males with the most elaborate traits are best able to monopolize access to fertile females). Both cases result in directional selection on traits because males with the most elaborate sexually selected traits are often those that enjoy the greatest reproductive fitness.

A central question in sexual selection research is why females prefer males that display showy and presumably costly traits. The most common explanation is that elaborate male traits advertise benefits a female may obtain by mating with that male. These benefits fall into two categories: direct benefits which affect female fitness, such as a male's ability to provide resources, good paternal care or high quality territories to his mate (Price et al. 1993; Kirkpatrick 1996); and indirect, or genetic benefits, which advertise a male's ability to produce attractive, healthy, or high-quality offspring (Iwasa et al. 1991; Kirkpatrick 1996). Both types of benefits models rely on sexual signals being "honest indicators" of male quality (Zahavi 1975); that is, only the highest quality males have the surplus resources available to bear the costs associated with developing and maintaining elaborate traits (Grafen 1990). More elaborate signals therefore advertise higher quality males who can provide better benefits, and females should choose to mate with males that exhibit the most elaborate version of the preferred trait (Grafen 1990). A major focus of sexual selection studies is thus identifying the costs and benefits (both direct and indirect) associated with putative sexually selected traits.

Determining whether or not a trait is sexually selected requires extensive empirical work. Although it is often tempting to assume that any elaborate or sexually dimorphic trait (e.g., bright colors, ornamental feathers, or weapons) is sexually selected, these traits can also evolve for other purposes, such as mimicry, aposematic signaling, and species recognition (e.g., Jiggins et al. 2004; Maan and Cummings 2008; Price 2008). To show that a trait is subject to sexual selection, a causal relationship between trait variation and reproductive success must be demonstrated. The best way to do this is using field experiments that manipulate a trait to be more or less exaggerated than average and then measuring the effects of this manipulation on some aspect of fitness, such as timing of breeding, pairing success, or number of offspring. Barn Swallows are a favored model system in sexual selection studies, as their most obvious sexually selected traits, tail streamers and color, are both relatively easy to manipulate (e.g., tail streamers: Møller 1988, 1989; color: Safran et al. 2005). Substantial work has thus been devoted to identifying the costs and benefits advertised by these traits.

Tail streamers in European H. r. rustica

The best studied of the Barn Swallow's sexually selected traits are the tail streamers. Since this trait is strongly sexually dimorphic in European populations, scientists studying *H. r. rustica* quickly suspected that these traits were under sexual selection in males. To determine whether there is a relationship between tail streamer length and male mating success, Møller (1988) artificially elongated and shortened streamer length and examined whether this affected a male's ability to attract a mate. Males with artificially elongated tail streamers mated earlier than their short-streamered neighbors - the first demonstration of a causal relationship between male tail length and female mate choice in Barn Swallows. Indeed, since that initial study and the dozens that have followed (reviewed in Møller et al. 1998a; Turner 2006), tail streamers in European *H. r. rustica* have become a textbook example of sexual selection. Further experimental and correlational studies confirmed that females prefer males with the longest tail streamers: 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 (reviewed in Møller 1994a; Møller et al. 1998a). Naturally long-streamered males likely breed earlier because they are in better condition and arrive on the breeding grounds earlier than shorter-streamered males (Møller 1994a; Møller et al. 2003; Ninni et al. 2004), which gives them an advantage for obtaining high quality nest sites and mates, as well as producing more broods.

Barn Swallows are socially monogamous and exhibit biparental care (Møller 1994a). However, they also pursue extra-pair matings. This means that in any given nest, some offspring are likely not genetically related to the male caring for them, and counting the number of chicks in a nest is thus not necessarily an accurate reflection of the male nest owner's reproductive output. Molecular parentage analyses provide a definitive measure of a male's

reproductive success, and allow a more accurate assessment of the strength of sexual selection associated with different traits. In European populations of Barn Swallows, the proportion of extra-pair young (EPY) in a nest averages 17.8–34% (Saino et al. 1997b; Møller et al. 1998b). Møller's (1988) tail manipulation study was replicated in Europe and confirmed that males with the longest streamers obtained a significantly greater share of genetic paternity in their nests and in the nests of others, relative to their short-streamered neighbors (Møller and Tegelström 1997; Saino et al. 1997b).

Tail streamers are a particularly interesting sexually selected trait because they have a clear function unrelated to mating. As aerial insectivores, Barn Swallows must fly efficiently, a task that is substantially aided (or hindered) by the shape of their tails. Thus, rather than evolving under directional sexual selection alone (as would be predicted if the longest-streamered males always had the highest fitness), this trait is predicted to be shaped by a balance between sexual and natural (viability) selection. This appears to be borne out by empirical data: individuals with longer streamers suffer from impaired aerodynamic performance that may result in lower foraging efficiency (Møller et al. 1998a; Bro-Jørgensen et al. 2007), and population-level survival is lower when male streamer length is longer on average (Møller and de Lope 1994). There is some evidence that high condition males with naturally longer tails have higher survival (Møller 1991a; Møller 1994a), although more recent mark-recapture analyses of annual population means shows that males with naturally longer tails have lower survival (Møller and Szép 2002). Swallows with too short a set of streamers also suffer from reduced flight skills (Buchanan and Evans 2000; Rowe et al. 2001). The balance between tail feathers that are too long or too short implies that there is a naturally-selected optima for tail length, and that sexual selection may drive tail length away from this optima (Møller et al. 1995; Evans and Thomas 1997; Buchanan and Evans 2000; Bro-Jørgensen et al. 2007).

The apparent costs associated with elongated tail streamers led researchers to hypothesize that tail length is an honest signal of male quality: only high condition males can bear the costs of elongated tails. If this is true, females should gain benefits from mating with longer-tailed males, which leads to directional sexual selection on streamer length that will ultimately be opposed by viability selection when the survival costs of long tails outweigh the benefits from increased mating success. There is some evidence for the type of "quality" that long-tailed males might be signaling: European males with longer tails had fewer ectoparasites (Saino and Møller 1994) and more robust immune responses (Saino et al. 1997a, 2002), suggesting that tail length advertises information about immune system quality. Experimental data manipulating tail length also found that long-tailed males were better able to cope with the immune costs of their elaborate traits (Saino and Møller 1996). Some aspects of the immune response appear to be heritable, as a positive correlation was found between ectoparasite loads on fathers and sons (Møller 1990; Møller et al. 2004), meaning that females paired to long-tailed males may gain indirect benefits in the form of healthy sons. Females may gain direct benefits from mating with healthy, long-tailed males as well, via less exposure to contagious ectoparasites.

Long tails seem to advertise additional qualities besides immune function: males with longer tails had higher levels of circulating testosterone, which may be related to competitive ability (Saino and Møller 1994), and the sons of long-tailed males had greater longevity than those of short-tailed males (Møller 1994b), which could be due to good genes, better parental care in nests with long-tailed fathers, or other heritable components of longevity. These latter effects are difficult to partition, particularly because long-tailed males obtained high-quality females as mates (Møller 1991b), high quality females also had long tails (Møller 1991b; Cuervo et al. 1996b), and females mated to attractive, long-tailed males invested more in reproductive effort (de Lope and Møller 1993). Thus, some of the benefits experienced by the offspring of long-tailed males are likely due to their high-quality mothers, although offspring may also suffer due to reduced investment from their long-tailed fathers (de Lope and Møller 1993). Taken together, long tail streamers seem to be indicators primarily of indirect benefits: females mated to long-streamered males do not obtain better paternal care (indeed, elevated testosterone and longer tails resulted in poorer parental care, de Lope and Møller 1993; Saino and Møller 1995a), but they produce healthy, long-lived offspring and long-streamered sons.

However, another hypothesis suggests that tail streamer length is not an honest signal of a male's ability to withstand a "too long" streamer, but rather is optimized to individual-specific flight performance and thus subject to natural selection (Cuervo et al. 1996a; Evans and Thomas 1997; Buchanan and Evans 2000). To differentiate these alternatives, Bro-Jørgensen et al. (2007) utilized an individual-based approach to study flight performance as a function of streamer length. They analyzed aerodynamic performance after manipulating tail streamers to multiple different lengths, and found no evidence to support the view that the sexually selected component of this trait reflects individual variation in flight performance. Instead, the optimal streamer length for efficient flight varied among males, but beyond a certain point, any additional length to the streamer, presumably caused by sexual selection, did not vary among individuals. The conclusion is that the naturally, rather than 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. Bro-Jørgensen et al. (2007) speculate that tail streamer lengths may simply serve to signal the age and sex of the individual (adult male vs. female or juvenile), and indeed, older males typically have longer tails, although the benefits associated with streamer length are still found when controlling for the effect of age (Møller et al. 1998a). The relative roles of natural and sexual selection in shaping elongated tail streamers thus remain debated (e.g., Evans 1998, 1999; Hedenström and Møller 1999; Evans 2004; Evans et al. 2012; Aparicio and Møller 2012), particularly because an explicit link between flight performance and fitness has not been demonstrated. Further experimental studies that adopt a within-individual experimental approach with additional treatments related to mate-selection may provide a definitive test for understanding the relative contributions of sexual and natural selection to variation in streamer length.

Geographical variation in sexual selection on tail streamers

All of the above studies were conducted in European populations of *H. r. rustica*. However, there are five other Barn Swallow subspecies, and there is mounting evidence that the function of tail streamers is not the same in all groups. This may to some extent be predicted by variation in streamer length among subspecies: for example, despite some latitudinal variation, tail streamers are on average shorter in North American than European populations, and the extent of sexual dimorphism in streamer length is much reduced (Safran and McGraw 2004). This leads to the *a priori* suggestion that this trait may be subject to weaker sexual selection in North America compared to Europe.

Available correlational and experimental data generally bear out this prediction. For example, in contrast to European *H. r. rustica,* streamer variation in males and females did not significantly predict patterns of assortative pairing in North American *H. r. erythrogaster* (Safran and McGraw 2004). Male streamer length was not a significant predictor of measures of seasonal reproductive success in some correlational data sets (Safran and McGraw 2004; Neuman et al. 2007), but in a Canadian population males with naturally long streamers bred earlier (Smith and Montgomerie 1991) and had increased extra-pair mating success compared to shorter-streamered males (Kleven et al. 2006). In the same Canadian population, a positive correlation was found between streamer length and fertilization success, but much of this relationship was explained by the age-dependence of streamer length: older males had both greater fertilization success and longer streamers, making it difficult to separate these effects on reproductive success (Lifjeld et al. 2011).

Additional components of reproductive success vary with respect to streamer length between European and North American populations. In Europe, there is a significant positive association between streamer length and the proportion of offspring sired in first breeding attempts (Saino et al. 1997b), whereas no such significant association was found between these two variables using the same test statistic in North American population (Neuman et al. 2007). Likewise, males with longer tails sired more offspring in their own nests in Europe (Saino et al. 1997b) but the relationship was not significant in North America (Neuman et al. 2007). A negative correlation was found 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 (Møller and Tegelström 1997), indicating that longer-tailed males are less likely to be cuckolded, but no such correspondence between a male's streamer length and his probability of being cuckolded was found in New York with the same test statistic (Neuman et al. 2007). Finally, a study that replicated the experimental design of Møller's (1988) tail manipulation study in Europe did not find a significant effect of artificial streamer elongation on male reproductive success in a North American population of swallows (Safran et al. in review).

Despite latitudinal variation in streamer lengths within Europe, the function of streamers, in terms benefits related to social and genetic reproductive success, vary little among European populations of *H. r. rustica* (Møller 1995). By contrast, male *H. r. erythrogaster* with elongated streamers in New York did not obtain the same reproductive benefits as males with elongated streamers in Italy (see above). Considered in concert, the results of studies in North America and Europe demonstrate that the pattern of sexual selection on tail streamers varies among subspecies.

Two other Barn Swallow subspecies have been the subjects of additional sexual selection studies: *H. r. transitiva* in Israel, and *H. r. gutturalis* in Japan. Again, there appears to be variation in sexual selection on tail streamers among these subspecies. Male *H. r. transitiva* have tail streamers that are nearly as long as those in *H. r. rustica*, and, accordingly, males with longer streamers breed earlier and have fewer extra pair young in their nests in both correlational (Vortman et al. 2011) and experimental (Vortman et al. 2013) studies. By contrast, male *H. r. gutturalis*, which have much shorter streamers than *H. r. rustica* and *H. r. transitiva*, do not gain any significant reproductive benefits based on tail length in correlational datasets (Kojima et al. 2009; Hasegawa et al. 2010).

Ventral coloration in North America

Although North American swallows have shorter tail streamers than their European counterparts, they have

much darker ventral coloration. Accordingly, ventral coloration, not streamer length, was found to correlate with patterns of pairing and seasonal reproductive success in two populations of North American Barn Swallows (Safran and McGraw 2004; Neuman et al. 2007; Eikenaar et al. 2011a), but not in another (Lifjeld et al. 2011), suggesting that darker coloration may be a target of mate choice in some *H. r. erythrogaster* populations. Experimental manipulations of male coloration further demonstrated that females use ventral color to assess male quality. In North American populations, males with experimentally darkened ventral color gained greater paternity relative to the amount obtained in their first breeding attempts, prior to the color manipulation (Safran et al. 2005), but experimentally elongated tail streamers did not predict increased paternity allocation; in fact, males with *reduced* streamer lengths actually obtained greater paternity (Safran et al. in review).

It is unclear why females favor the use of color for mate selection in some populations and streamer length in others. Feather color in Barn Swallows is not as obvious a "costly signal" as elongated streamers, as darker ventral color probably doesn't hinder foraging ability, and darker birds are unlikely to be more conspicuous to predators (as is the case for some costly, bright-colored signals). There is evidence in other systems that bright red and orange carotenoid-based colors are costly and/or honest signals, because carotenoid pigments must be obtained from the diet and physiologically modified before deposition in tissues (reviewed in Hill and McGraw 2006). However, the orange-brown throat and ventral color in Barn Swallows is caused by eu- and phaeomelanin pigments rather than carotenoids, which can be synthesized endogenously (McGraw et al. 2005) and are not generally believed to be costly to produce (Hubbard et al. 2010). However, recent studies have revealed that there may indeed be costs to deposition of melanin pigments. In addition to stimulating melanogenesis in external tissue, the melanocortin pathway serves non-signaling functions such as regulation of stress and immune responses via binding of peptide derivatives to different melanocortin receptors (Ducrest et al. 2008). Allocation of melanocortins to different receptors may result in a tradeoff between pigment deposition and hormonal function (e.g. Roulin et al. 2008). Melanin-based signals can also be sensitive to oxidative stress (Galván and Alonso-Alvarez 2008, 2009), and thus have the potential to function as an honest signal of antioxidant levels.

Several recent studies have illuminated some of the physiological mechanisms underlying color variation, and shed light on the type of information that darker males may be signaling to prospective mates and competitors. Dark melanin pigmentation appears to be linked to hormonal state: in North American populations, artificially darkened females adjusted their physiological state to have lower levels of testosterone and reactive oxidative metabolites than prior to manipulation (Vitousek et al. 2013). Likewise, naturally darker males were found to have higher levels of circulating testosterone, and experimentally darkening an individual's color increased his testosterone levels (Safran et al. 2008). These experimental findings demonstrate feedbacks between external phenotype and physiological state: experimentally darkened birds likely had different types of social interactions than when they had lighter feathers, resulting in an adjustment of hormonal state to match their new phenotype.

It may be beneficial for naturally dark-colored males to advertise their high levels of testosterone. If these dark, high-testosterone males are more aggressive, they could be more competitive in obtaining high quality nesting territories early in the breeding season (Safran et al. 2008), making them more attractive to females. Indeed, females paired to darker males increased feeding rates of their chicks, although dark males themselves did not give more paternal care than lighter males (Maguire and Safran 2010). This finding suggests that females invest more in their offspring when paired to attractive mates. If darker males can obtain and defend better nest sites, this represents a direct benefit to their mates; however, there is also a potential cost in that high-testosterone males tend to be poorer parents in both Barn Swallows and other bird species (e.g., Ketterson et al. 1992; Saino and Møller 1995a, but see Eikenaar et al. 2011b). In both Europe and North America, therefore, there is evidence that the main target of female choice (tail length and ventral color, respectively) is linked to high levels of circulating testosterone and may advertise a male's competitive ability. Dark coloration in North America is also heritable to some extent (Hubbard et al. in review), suggesting that females paired to dark colored males may obtain indirect benefits in the form of attractive offspring.

Plumage coloration in other populations

Darker ventral color is also associated with greater breeding success in Middle Eastern swallows (*H. r. transitiva*), a subspecies that exhibits elongated tail streamers and dark ventral color. Experimental work in this subspecies has shown that both ventral color and tail streamer length predict different aspects of breeding success, with darker males raising more young over the course of a season, and males with longer tail streamers breeding earlier and having fewer extra-pair chicks in their nests (Vortman et al. 2011, 2013).

Ventral color needn't be the only target of sexual selection on plumage- indeed, in a subspecies with pale ventral coloration, it appears that the size of the dark orange-brown throat patch is the trait most preferred by females. In a Japanese population of *H. r. gutturalis,* females preferred males with larger throat patches, and, accordingly,

the throat patch is on average twice as large in *H. r. gutturalis* as in the closely related *H. r. rustica* (Hasegawa et al. 2010; Hasegawa and Arai 2013a). Males with larger, darker throat patches obtained high-quality females who initiated clutches earlier than females paired to lighter males (Hasegawa et al. 2010, Hasegawa and Arai 2013b). Darker-throated males also had greater survival probability (Hasegawa et al. 2013), and obtained higher quality territories and reduced their paternal care (Hasegawa et al. 2014), relative to small- and pale-throated males. Male tail streamer length was linked to survival rate but unrelated to measures of reproductive success (Kojima et al. 2009; Hasegawa et al. 2010), consistent with the relatively short length of male streamers in this population.

Studies of melanin-based coloration in European populations of Barn Swallows have thus far focused primarily on the potential for melanic signals to advertise information about viability, immunocompetence, and stress. These populations have paler ventral coloration in comparison to males in other subspecies (e.g., *H. r. gutturalis*, *H. r. transitiva*, and *H. r. erythrogaster*), and studies show that paler males have higher survival between years (Saino et al. 2013b). Moreover, naturally paler birds have a stronger primary immune response, but not cell-mediated immune response (Saino et al. 2013a), suggesting a possible immune cost to darker ventral plumage in this population. If darker coloration is associated with poorer immune response, this may be an important source of "honesty" in melanin-based signals. Interestingly, although birds with darker ventral color have a weaker immune response, individuals with darker throat color have higher survival in a Danish population (Galván and Møller 2013), similar to Japanese *H. r. gutturalis* (Hasegawa et al. 2013). Melanic throat color is heritable in Italian populations (Saino et al. 2013c), suggesting that different color patches could advertise different information.

There may also be a relationship between the stress hormone corticosterone and coloration, but this only emerged in experimentally stress-reduced males in Europe (i.e., among males with artificially reduced brood sizes, paler males had less corticosterone and may thus have been less stressed, Saino et al. 2013a). Moreover, a North American study of melanin color in males (both nestlings and adults) found no correlation between color and different measures of corticosterone (Jenkins et al. 2013). The relationship between stress and melanin-based color thus remains unclear. Some of the complication in interpreting the costs of melanin production and deposition comes from the different physiological pathways associated with producing eu- vs. phaeomelanin (Saino et al. 2013a, b), which remain poorly understood in most natural populations. Additionally, feathers are a static signal that likely reflect the hormonal state of the individual when the feathers were grown; thus, measuring hormones months after the trait has developed may not provide useful information about the costs or benefits being signaled. Further research on the relative signaling roles of the two different melanin pigments, as well as on temporal variation in hormone responses, will help elucidate the role of melanin-based ornaments in sexual selection.

Additional plumage characters that have been the focus of some research are the white spots on the underside of the tail feathers. These are sexually dimorphic, and area of white spots is significantly correlated with streamer length. In European populations, males with experimentally reduced white spot sizes fledged fewer offspring, likely because they were less likely to have second broods (Kose and Møller 1999). The white portions of the feather are more prone to breakage (Kose and Møller 1999) and are also the preferred feeding sites of feather lice, although males with larger white spots have fewer lice (Kose et al. 1999). This suggests white spots could signal ectoparasite infestations (Kose et al. 1999). In Japanese *H. r. gutturalis*, males with larger white tail spots bred earlier in the season, suggesting this trait may be sexually selected in these populations as well (Hasegawa et al. 2010).

Song in mate choice and male competition

Though not nearly as well studied as streamer length and ventral color, some work has been done on the social function of Barn Swallow song, primarily in European populations of *H. r. rustica*. Unlike color and morphology, song is learned and culturally inherited. It is also a dynamic signal, capable of changing with season, social context, and physiological state. It thus stands to reason that song may advertise different information than comparatively static signals like color or streamer length. However, interpreting song variation can be difficult, particularly in Barn Swallows, in which males sing enormously complex and variable songs and have relatively large repertoires of unique syllables (Figure 4, Galeotti et al. 1997). This creates problems for researchers both in determining which song variables to measure and in correcting for large numbers of comparisons. Studies of song variation typically examine a variety of parameters related to song structure (e.g., number of syllables, length of syllables, number of syllable types, total repertoire size) and acoustic characteristics (e.g., peak, maximum, and minimum frequencies of different song components). Additionally, song rate (the number of songs produced per unit of time) is often measured independently of song structure. One feature of Barn Swallow song that has received particular attention is the "rattle", a harsh trill appended to the end of most songs that varies in length among males (Figure 4).

Studies of European Barn Swallow song suggest that different song features serve different functions and advertise different information. For example, males with more neighbors produced longer rattles, and shorter, less complex

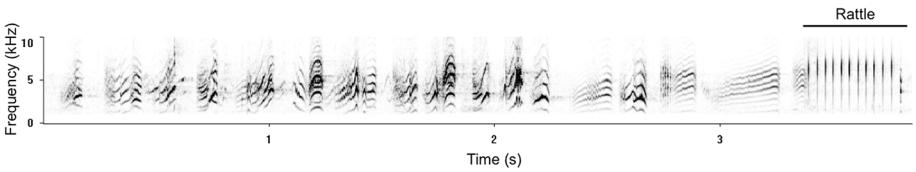

Figure 4 Example song spectrogram from *H. r. rustica*. Note 'rattle' component at terminal end of song and the large variety of complex syllables. Song spectrogram courtesy of M. Wilkins.

songs; additionally, males with longer rattles had higher levels of circulating testosterone, and these song features may therefore be involved in competitive interactions (Galeotti et al. 1997). Further, experiments showed that males with artificially elongated tails produced longer rattles (Saino et al. 2003), and immune challenged males reduced the lengths of their rattles (Dreiss et al. 2008), indicating that this trait is somewhat plastic and can respond to social and physiological cues. Longer rattles and longer tails are both linked to higher levels of circulating testosterone (Saino and Møller 1994; Galeotti et al. 1997, respectively), suggesting that a hormone-mediated social feedback loop similar to the one demonstrated with color in North American birds (Safran et al. 2008; Vitousek et al. 2013) may exist for song as well.

There is also some evidence that females consider song in mating decisions. Males with both long tails and higher song rates had fewer extra pair young in their nests (Møller et al. 1998b); however, the effect of tail was much more important in this relationship, indicating that short-tailed males cannot compensate for their unattractiveness by singing at higher rates. Additionally, males that sang overall longer songs paired more successfully and had lower ectoparasite loads (Garamszegi et al. 2005). Together, these data suggest that in European populations, some song components are used in territory defense and intrasexual competition, while other components may advertise condition and have a role in mate choice. Since clear links between tail streamer length and male-male competition have not been demonstrated in *H. r. rustica* (e.g. Saino and Møller 1995b), males may use different signaling modalities to communicate with potential mates vs. competitors.

Thus far there has been little research on song in non-European Barn Swallow populations. However, recent work in North America found that some song features are important for male-male competition and while other components are used in female choice (Wilkins 2014), possibly implicating a greater role for song in mate choice in this short-streamered subspecies. Future comparative work on the information conveyed by song and melanin-based traits should further illuminate the costs and benefits associated with different types of signals across subspecies.

From geographic variation in sexual selection to speciation

It is clear that many traits, at least some of which are sexually selected, vary among the different Barn Swallow subspecies. But what causes geographic variation in phenotype? And what are the consequences of this variation for population divergence and speciation? Answering these questions entails examining the roles of selective and non-selective processes in shaping phenotypic variation and patterns of reproductive isolation. New species form when individuals from different populations no longer recognize one another as potential mates, or opportunities for mating become limited by differences in habitat use or reproductive schedules (Mayr 1942). In these cases, individuals are reproductively isolated and thus do not exchange genes; this is the first step towards speciation. Work in the field of speciation frequently focuses on identifying the processes that create barriers to gene flow among divergent populations. In this section we discuss the potential roles of natural selection, sexual selection, and drift in forming these barriers and driving phenotypic and population divergence in the Barn Swallow complex.

Speciation by natural selection, or "ecological speciation", occurs when populations living in different environments undergo adaptive evolutionary change via divergent natural selection. This process can form barriers to gene flow when divergent selection results in individuals being physically isolated from each other (i.e., in different ecological niches) or on different reproductive schedules (reviewed in Nosil 2012). Ecological speciation can often be inferred if ecologically divergent pairs of populations exhibit greater reproductive isolation than ecologically similar pairs of populations of similar age (e.g. Funk et al. 2006). Moreover, in cases of ecological speciation, the traits involved in divergent ecological adaptation should also contribute to reproductive isolation, and levels of gene flow in nature should decrease as ecological differences between populations increase (Nosil 2012).

Reproductive isolation can also emerge via divergent sexual selection (Panhuis et al. 2001; Ritchie 2007). In this scenario, divergence in traits related to reproductive success contributes to barriers to gene flow among populations. If reproductive isolation is caused by divergent sexual selection, pairs of populations might be expected

to be ecologically similar but possess divergent mating traits (Panhuis et al. 2001).

Controversy has surrounded the role of sexual selection in speciation, particularly with respect to its relationship with divergent natural selection. At the center of this discussion is whether sexual selection alone can drive speciation, or whether ecological divergence is a prerequisite for the completion of reproductive isolation (Panhuis et al. 2001; Bussière et al. 2007; Safran et al. 2013). Although there are some cases in which sexual or natural selection is the dominant process driving divergence (reviewed in (Kraaijeveld et al. 2011)), the most common scenario is that sexual and natural selection act together to drive variation in the traits used in reproductive isolation (Safran et al. 2013; Scordato et al. 2014). The pertinent question then becomes not which process is most important in causing speciation, but how the two processes interact, how the phenotypic traits used in mate selection and reproductive isolation are shaped by this interaction, and if interactions are consistent or predictable across systems (Arnegard et al. 2010; Wagner et al. 2012; Safran et al. 2013).

Finally, some models of speciation do not include selection as a driver of divergence and reproductive isolation, but rather invoke a key role for chance events. These cases include speciation by genetic drift and founder-events/population bottlenecks. Although such models have a long history in speciation research, for example in the context of small populations colonizing islands, clear empirical support is relatively limited (reviewed in Coyne and Orr 2004). However, when examining the causes of divergence and reproductive isolation among populations, adaptive divergence via selection cannot be assumed, and ruling out a role for random processes is critical.

Divergent ecological and sexual selection in Barn Swallows

Because the Barn Swallow complex has been the subject of extensive sexual selection research for decades and has several phenotypically variable subspecies that are tractable subjects for field studies, it is an ideal system in which to investigate the relative roles of ecological selection, sexual selection, and random processes in population divergence.

Several ecological variables could contribute to population and phenotypic divergence in Barn Swallows. There is variation in migratory distance among subspecies: some subspecies embark on migrations of many thousands of miles (i.e. European and North American populations), where as others are short-distance migrants or entirely sedentary (Middle Eastern populations; Møller 1994a; Turner 2006). Variation in migratory distance can exert natural selection on morphological factors like body size (Alerstam et al. 2003) and the shape of the wings (Mönkkönen 1995; Lockwood et al. 1998). Moreover, different wintering grounds and migratory routes can result in variation in the length and timing of the breeding season: birds that migrate longer distances typically have shorter and more synchronous breeding seasons than short-distance migrants (Garamszegi et al. 2008), which can translate into variation in selection on life history traits such as clutch size and incubation time, as well as mating strategies and parental care. Divergence in any of these traits could contribute to reproductive barriers, particularly if hybrids are unfit; for example, there is some evidence that the hybrid offspring of populations with different migratory pathways follow intermediate and maladaptive migration routes (Irwin 2009).

Geographic variation in sexual selection pressures may also drive phenotypic divergence and generate reproductive barriers in Barn Swallows. As we have discussed in this review, decades of work on the different sexually selected traits in this species show that the relative roles of streamer length, coloration, and possibly song in mate choice and male-male competition vary among subspecies. Even among European populations there is variation the strength of selection on tail length, although it remains consistently positive among populations (Møller et al. 2006). Likewise, the information conveyed by these traits varies geographically, with some evidence suggesting that long tail streamers in Europe advertise indirect benefits (Møller 1994a; Møller et al. 1998a); but see (Bro-Jørgensen et al. 2007) for alternative explanations), whereas coloration has been suggested to advertise direct and indirect benefits in Japan(Kojima et al. 2009; Hasegawa et al. 2012), and could relate to both direct and indirect benefits in North America (Safran and McGraw 2004; Safran et al. 2005). If the relative importance of different types of benefits varies among populations, this may result in mate choice, and consequent directional selection, on different traits, leading to phenotypic divergence and reproductive isolation based on sexually selected signals.

There is some evidence that sexually selected traits act as reproductive barriers in Barn Swallows: in an Israeli population of *H. r. transitiva,* males with color and tail length manipulated to look like the geographically proximate *H. r. savignii* were not attractive to females, suggesting there may be some selection against heterotypic matings in this populations (Vortman et al. 2013). These reproductive barriers are not complete, however: there is evidence for hybridization between *H. r. rustica* and *H. r. tytleri* in central Siberia, between *H. r. tytleri* and *H. r. gutturalis* in eastern Siberia (Turner 2006), and between *H. r. rustica* and *H. r. transitiva* in Israel (Dor et al. 2012), despite morphological differences between all these subspecies. Hybridization, if substantial, has the potential to reverse incipient differences among Barn Swallow subspecies. For example, it has been suggested that formerly geographically isolated subspecies in Asia may have been

brought into contact by recent human settlement (Turner 2006). If reproductive barriers are porous, there may be an eventual loss of differentiation between subspecies, resulting in a uniform hybrid swarm.

To understand the action of ecological and sexual selection and their relative roles in generating (or breaking down) reproductive barriers, we ultimately need to study the substrates on which selection acts; that is, sexually and naturally selected traits and, in the case of sexual selection, their associated preferences. Future work explicitly measuring natural and sexual selection on different aspects of the phenotype will continue to shed light on how these processes operate in the Barn Swallow system. New techniques for obtaining genome-wide estimates of selection are greatly advancing our ability to study the loci involved in reproductive isolation and identify signatures of divergence via adaptation versus random processes.

Conclusions and future directions

Here we have reviewed sexual selection research in Barn Swallows dating back nearly 30 years. Although this vast body of work has made Barn Swallows a model system in evolutionary biology, recent comparative studies show that much remains to be discovered in this species complex. Future comparative research addressing the relative roles of tail streamers, plumage coloration, and song in mating decisions across the different subspecies, as well as determining the information conveyed by these different signals, would help illuminate why the targets of female preferences appear to vary geographically. This work would be enhanced by ecological studies that focus on how different mating traits are shaped by natural selection as well as sexual selection, and by carefully designed experiments that can test the relative contributions of different selective processes to variation within and among subspecies. Finally, advances in genomic methods for detecting ongoing gene flow and the genetic basis of reproductive isolation present the possibility of studying reproductive barriers and causes of diversification among the different subspecies. Integrations of experimental, geographic, ecological, and genomic approaches are likely to yield new insight into sexual selection and speciation in the Barn Swallow complex over the coming decades.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

ESCS and RJS devised and wrote the manuscript. All authors read and approved the final version of this manuscript.

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