

Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American barn swallows

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Sexual adornments often vary markedly across a species' range, which presumably is owing to differences in local environmental conditions and the associated selection pressures, such as natural versus sexual selection or the relative signaling value of different ornamental traits. However, there are only a few reported examples in which the information content of mating signals varies geographically, and even fewer in which a set of secondary sexual traits serves different signaling functions in different populations. Classic studies of sexual selection in the European barn swallow (*Hirundo rustica rustica*) demonstrate that elongate tail-streamers provide several reproductive advantages to males and females and are used as reliable signals of mate quality. Here, we show that tail-streamers do not appear to confer these same benefits in a population of barn swallows from North America (*Hirundo rustica erythrogaster*). Instead, ventral plumage coloration, which is more exaggerated in North American swallows compared with their European counterparts, predicts patterns of assortative mating and annual reproductive success in *H. r. erythrogaster*. These observations support the idea that ornamental traits can serve different functions among animal populations and suggest that geographic variation in different sexual signals may facilitate population divergence, which may ultimately lead to speciation. *Key words*: geographic variation, *Hirundo rustica*, population divergence, sexual selection, sexual signals. [*Behav Ecol* 15:455–461 (2004)]

Sexually selected traits are generally thought to be the result of strong directional selection and provide consistent advantages in competition for mates (Andersson, 1994), but their expression can vary considerably across a species' range (Panhuis et al., 2001). The colorful skin of male Trinidadian guppies (*Poecilia reticulata*) is a well-known example (Endler, 1992). Variability in natural selection pressures, such as predation risk or lighting conditions, is often responsible for such geographic differences in sexual displays, and the extent of sexual selection (e.g., intensity of female mate-choice) is known to track environmental changes in ornamentation in several species (Endler and Houde, 1995; Marchetti, 1993).

How competing selection pressures interact to shape trait expression has been mostly studied only for single ornaments in isolation. However, many animals exhibit multiple ornamental traits that may serve the same, different, or no signaling function (Møller and Pomiankowski, 1993). Theoretical models have emphasized the importance of considering how sexual selection pressures for different ornamental traits may also shape geographic variation in trait expression and function (Schluter and Price, 1993). In fact, variable ecological conditions may favor the use of wholly different sexual signaling systems in allopatric populations of the same species.

For nearly 15 years, tail-streamers in barn swallows (*Hirundo rustica rustica*) from Europe have served as a classic illustration of sexual selection in animals (Møller, 1988, 1994). Females prefer to mate with the longest-tailed males both as social and extrapair partners (Møller, 1988; Saino et al., 1997), and by breeding earlier and completing more seasonal breeding attempts, long-tailed males produce the most offspring within a year (Møller, 1988, 1994). European barn swallows also

display patches of rust-colored feathers in the face and throat regions, but this trait is more exaggerated in barn swallows from North America (*Hirundo rustica erythrogaster*), which develop pigmented plumage that extends down the breast and belly of the animals to the vent (Cramp, 1988; Møller, 1994).

In the present study, we investigated the reproductive benefits of possessing variable tail and color ornaments in a breeding population of North American barn swallows. We measured tail length and symmetry of all birds following previously established methods (Møller and Höglund, 1991; Shykoff and Møller, 1999), objectively quantified plumage coloration with a reflectance spectrophotometer (Hill, 1998), and observed nesting behavior throughout the season to determine the relationship between plumage coloration, tail-streamer characteristics, patterns of mate selection, and reproductive performance (date of breeding onset and annual reproductive success).

METHODS

Field methods

We studied a population of barn swallows at 12 breeding sites in Tompkins County, New York, from May–August 2001. By using mist nets, we captured male ($n = 47$) and female ($n = 73$) swallows during the first 2 weeks of the breeding season. The reason our sample of females is greater is because capture of females was considerably easier and more females that were captured during the early part of the season remained at sites throughout the breeding season.

We uniquely marked individuals with enamel-based paints following methods used by Shields and Crook (1987) and numbered aluminum rings for later identification. We checked nests daily to determine breeding onset (Julian date on which first egg was laid), number of nesting attempts (one or two), and annual reproductive success (total number of young

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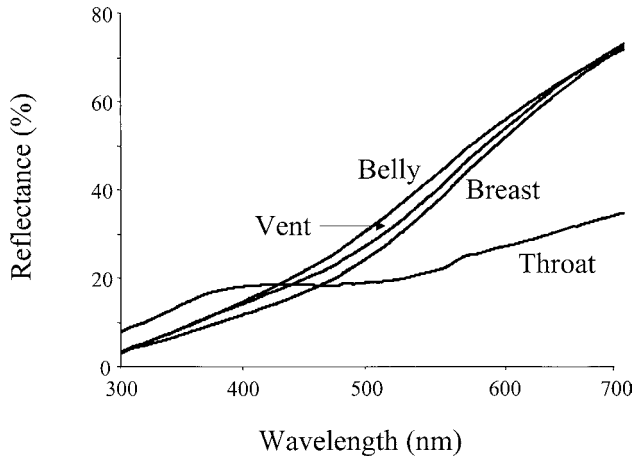


Figure 1

Spectrophotometric data from a representative male indicating no ultraviolet reflectance of ventral feather colors in North American barn swallows.

fledged within the season), and we identified pairs as they constructed nests, incubated eggs, and fed nestlings.

We plucked patches (three to 10 feathers) of ventral plumage from four standardized body regions (hereafter referred to as throat, breast, belly, and vent) and carefully mounted these colored feathers on an index card as to recreate the natural plumage appearance of the bird (Keyser and Hill, 1999). These cards were stored in the dark and saved for later plumage-color scoring (see below).

At capture, we also measured the length and symmetry of tail-streamers of males and females. We measured both the right and left tail-streamer of individual birds to the nearest 0.5 mm with a ruler (Smith et al., 1991). Each tail-streamer was measured three times, and the separate measure of streamers was found to be highly repeatable (streamer repeatability = 0.99, $F_{19,39} = 304.31$, $p < .001$; Lessells and Boag, 1987). For statistical comparisons of tail-streamer length, we used measures from the right side of both males and females (Smith and Montgomerie, 1991) to avoid the problem of using the average of right and left sides in cases in which streamer lengths were asymmetric. We calculated the degree of symmetry between the right and left tail-streamer lengths by using the absolute value of the difference between these measures (Shykoff and Møller, 1999). Our measure of the degree of symmetry between right and left tail-streamers, calculated by subtracting each measure of the right tail-streamer from each measure of the left tail-streamer separately, was highly repeatable ($r = .98$, $F_{24,49} = 100.18$, $p < .001$; Lessells and Boag, 1987). We omitted all birds with broken or missing tail-streamers from our sample ($n = 9$ females and 7 males; Shykoff and Møller, 1999).

Plumage-color scoring

The color of feather samples was scored along three traditional axes of color (hue, saturation, and brightness) with a reflectance spectrophotometer (Colortron; Light Source; Hill, 1998). This unit quantifies visible light only which is sufficient for this species because the ventral plumage of barn swallows does not exhibit a unique ultraviolet reflectance peak (Figure 1). Each plumage patch was scored three times, and we averaged these scores to determine mean hue, saturation, and brightness for the throat, breast, belly, and vent of each swallow. These 12 plumage measures were moderately to highly repeatable for a subsample of individuals ($n = 14$; all $r > .6$

Table 1

Principal components loadings for male and female color variables

	Throat PCI	Breast PCI	Belly PCI	Vent PCI
Male color variables				
Explained variance	0.84	0.83	0.81	0.85
Hue	0.57	0.57	0.55	0.57
Saturation	-0.56	-0.57	-0.58	-0.56
Brightness	0.61	0.59	0.60	0.60
Female color variables				
Explained variance	0.79	0.86	0.82	0.87
Hue	0.55	0.60	0.58	0.58
Saturation	-0.58	-0.58	-0.59	-0.59
Brightness	0.60	0.58	0.56	0.56

and ranged from .60–.94, average $r = .82 \pm .12$, median $r = .88$, all $F > 3.0$, all $p < .01$). Color scores were significantly intercorrelated within (all $p < .001$) but not among ventral regions, so we devised a color-scoring scheme to summarize data separately for each of the four plumage areas. We used principal components analysis (PCA) to collapse hue, saturation, and brightness scores within each plumage region. The first principal components (PCI) for throat, breast, belly, and vent explained more than 80% of the variation in the color scores of each plumage region in both sexes. Thus, we used these four measures of color in our statistical analyses. Birds with lower PCI scores have browner (lower hue values), more saturated, and darker (lower brightness values) plumage (Table 1).

Statistical analyses

In many cases, our data (raw or transformed) did not conform to the assumptions of parametric analyses. Therefore, we used Mann-Whitney U tests to examine sex differences in plumage coloration, tail-streamer length, and tail-streamer symmetry. We examined differences between males and females in the variability of these sexual traits by using Levene's tests (Neter et al., 1996). Spearman rank-correlations were used to examine correlations among ornamental traits and to explore the associations of ornaments in breeding pairs. We used general linear models (SAS PROC GENMOD, v.8.2) to explore the relationships between measures of fitness and ornamental traits. We analyzed the distribution of each dependent variable in order to choose the most appropriate linear model; reproductive success was normally distributed and, therefore, appropriately modeled by using a general linear model, whereas clutch initiation date was best modeled by using Poisson regression. We used locally weighted scatter plot smoothers (LOWESS curves) to explore the relationship between two variables without fitting a specific model (such as a straight line or predefined distribution). These LOWESS curves enabled us to determine whether linear or higher-order terms (quadratic, or cubic, functions) would be suitable for modeling the relationships between two variables (Neter et al., 1996).

We applied Bonferroni-corrected significance tests ($\alpha = 0.05$ divided by the number of multiple tests for each variable) in cases in which we used the same data for multiple comparisons. Tests are two-tailed and $\alpha = 0.05$ in all cases. Sample sizes vary owing to the exclusion of individuals having either frayed or missing tail-streamers or an inadequate sample of ventral feathers for color scoring.

RESULTS

Sexual dimorphism in tail-streamer characteristics

Male tail-streamers were longer and more variable in length ($n = 42$, mean \pm SD = 89.75 ± 7.14 mm) than those of females in our study population ($n = 67$, 76.83 ± 3.87 mm; two-sample t test, $t = -10.80$, $p < .0001$; Levene's test, $F = 16.1$, $p < .0001$). There were no sex differences in the degree of tail-streamer symmetry in our population (male: 1.94 ± 4.96 mm, $n = 38$; female: 1.8 ± 2.00 mm, $n = 63$; Mann-Whitney test $W = 3464$, $p > .07$), nor did symmetry vary more among males than females (Levene's test, $F = 0.14$, $p > .70$).

Sexual dichromatism in ventral plumage

Males differed significantly from females in our four composite (PC1) measures of plumage color (Figure 2), with males having lower scores and thus exhibiting browner, more saturated, and darker plumage. Color scores were not more variable in males than in females, however (all Levene's test, $F < 2.5$, all $p > .1$), nor did the different plumage regions differ in color variability in either males or females (all Levene's test, $F < 1.5$, all $p > .5$).

Intercorrelations among ornamental traits

Males and females with more colorful plumage in one ventral region generally displayed colorful plumage in all regions (Table 2). However, plumage-color expression was not significantly correlated with tail-streamer length or symmetry in either sex (Table 2).

Pairing by ornament expression

The coloration of paired individuals was correlated in the throat region (Figure 3a), and breast region (Spearman rank correlations, $r_s = .47$, $p < .04$, $n = 20$; $p > .15$ for other color measures). However, we found no correlations between paired individuals in tail symmetry ($r_s = -.38$, $p > .16$, $n = 15$) or length of tail-streamers (Figure 3b).

Plumage ornaments as predictors of breeding performance

Timing of breeding

Neither male tail-streamer length nor symmetry was correlated with breeding onset, but male throat and vent coloration predicted the date of clutch initiation of his mate (Table 3 and Figure 4). Similarly, neither female tail length nor symmetry predicted the onset of breeding, but female belly and breast coloration were significantly related to lay date, with more colorful females nesting earlier (Table 3 and Figure 4).

Female Male

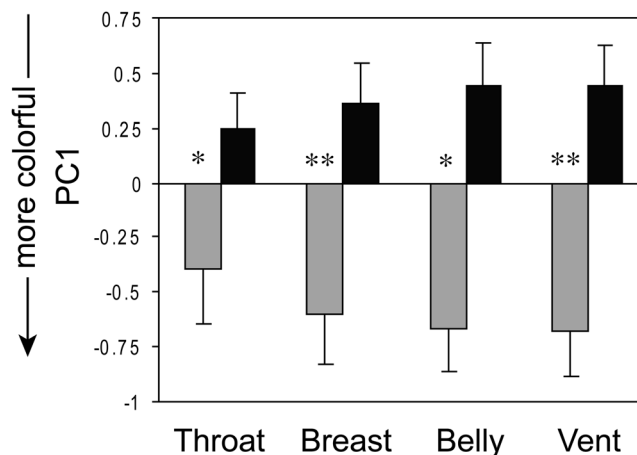


Figure 2 Sexual dichromatism in the ventral plumage of North American barn swallows (mean \pm SE). Male plumage was significantly more colorful than that of females (differences between male and female PC1 scores are all significant; Mann-Whitney U tests, $*p < .05$; $**p < .01$). Birds with lower PC1 scores have browner (lower hue values), more saturated, and darker plumage.

Annual reproductive success

Male belly and vent coloration significantly predicted the number of young produced in a season (Table 4 and Figure 5). In males, tail symmetry was not correlated with reproductive success (Table 4). In one of four cases, a cubic function of tail-streamer length did predict variation in reproductive success; birds with intermediate tail lengths had a greater number of fledged young (Table 4). Neither female tail length nor symmetry predicted reproductive success (Table 4 and Figure 5). However, females with more colorful belly feathers fledged more offspring in a season than did drab females (Table 4 and Figure 5). Females with more than one successful breeding attempt were also more colorful (breast: $U = 916$, $p < .05$, $n = 51$ and belly: $U = 303$, $p < .01$, $n = 46$) compared with females who raised only one brood (data not shown; $p > .05$ for other color and tail measures).

DISCUSSION

Sexually selected traits are usually characterized by the following patterns: (1) they are sexually dimorphic, (2) they predict patterns of mate selection, and (3) they correlate with

Table 2 Correlations among ornamental traits in male (italics) and female North American barn swallows

	Throat	Breast	Belly	Vent	TSL	AA
Throat						
Breast	0.32* (67)				0.21 (37)	-0.31 (37)
Belly	0.26 (67)	0.52* (42)			0.16 (35)	-0.03 (37)
Vent	0.30* (72)	0.47* (66)	0.48* (44)		0.06 (37)	-0.11 (35)
TSL	-0.10 (64)	0.38* (71)	0.32 (43)	0.50* (45)		-0.31 (38)
AA	0.22 (64)	0.01 (64)	0.43* (42)	0.24 (45)	0.02 (38)	0.36 (38)
			-0.25 (59)	-0.23 (63)	-0.06 (64)	
			0.04 (59)	0.19 (63)		

Data are presented in each cell as Spearman's rank coefficients, r_s . TSL indicates tail-streamer length (mm); AA, degree of absolute symmetry between right and left tail-streamers.

* $p < .01$, (sample size). Significance tests are Bonferroni-corrected at $\alpha = 0.05/5 = 0.125$.

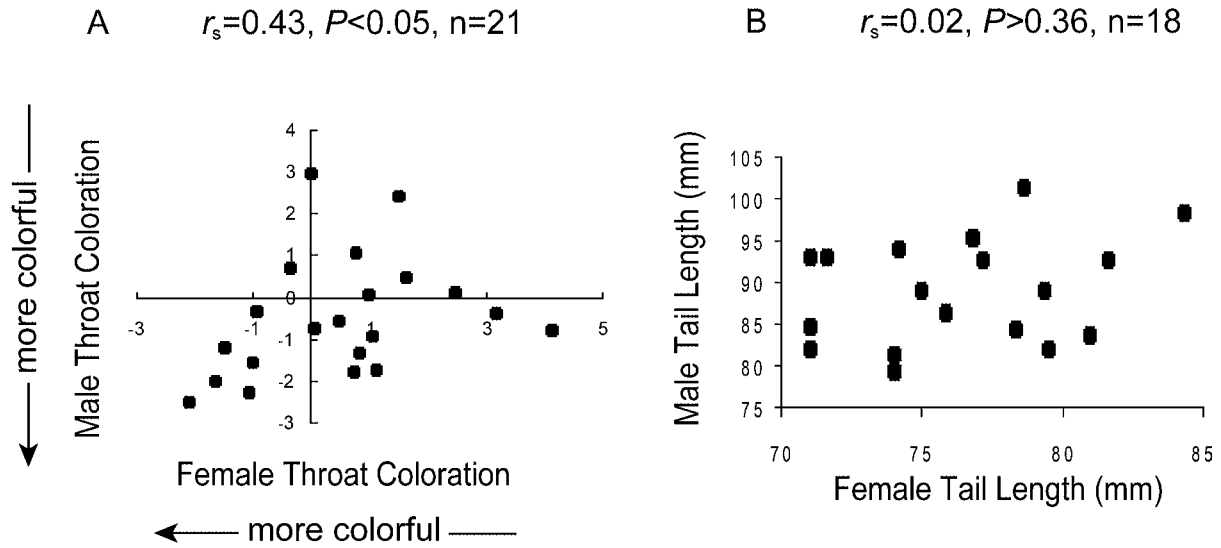


Figure 3 Evidence of pairing based on feather coloration (a), but not tail-streamer length (b), in North American barn swallows.

measures of seasonal reproductive success (Andersson, 1994). Here, we considered the relative signaling function of two traits that are both sexually dimorphic in a North American population of barn swallows. Contrary to previous studies of the signaling function of tail-streamers in European barn swallows (Møller, 1994), barn swallows in our study population that displayed longer and more symmetrical tails failed to gain any reproductive advantages. Instead, plumage coloration predicted patterns of pairing and seasonal reproductive success.

Tail-streamers

An interesting finding is that in one of four cases (Table 4), a cubic function of tail-streamer length significantly predicts variation in reproductive success, suggesting that natural selection may favor males whose streamers are intermediate in length and close to an aerodynamic optimum (Buchanan and Evans, 2000; Evans, 1998). However, in previous years (1999, 2000) of another study of the same population of barn swallows, there was no relationship between tail-streamer length and reproductive success (Safran RJ, unpublished data). Two other studies of North American barn swallows suggests that tail-streamers do not function in the same way as they do in European populations (Briceno 2002; Smith and Montgomerie, 1991; Smith et al., 1991). In Ontario, Canada (300 km north of our study site), Smith and Montgomerie

(1991) conducted similar tail-streamer manipulations as did Møller (1988), although they did not include control groups in their experimental design. Although females appeared to begin breeding earlier when mated to males with experimentally elongated tail-streamers, these males did not have a higher frequency of multiple clutches or experience greater reproductive success as a result. Moreover, although we have not yet measured the incidence of extrapair young in our sample of birds, Smith et al. (1991) found no extrapair mating advantages for longer-tailed males in North America. Thus, from these results and our 1-year study, it is clear that tail-streamers do not provide the full spectrum of sexually selected benefits to male swallows in North America as they characteristically do in Europe.

Ventral feather coloration

North American swallows exhibit a much larger patch of rust-colored ventral feathers than do their European counterparts. In our study population, feather coloration is variable and sexually dimorphic; male swallows exhibited more brightly colored plumage than did females. Most importantly, males with more colorful patches of throat feathers formed pairs with females who initiated nesting earliest in the breeding season. These results demonstrate that the function of ventral feather coloration in male barn swallows in North America is similar to

Table 3 Results of Poisson regression models to predict variation in clutch initiation date

	Males				Females			
	Throat (n = 29)	Breast (n = 27)	Belly (n = 28)	Vent (n = 29)	Throat (n = 52)	Breast (n = 52)	Belly (n = 47)	Vent (n = 51)
Color	4.51 (0.03)	2.06 (0.15)	0.27 (0.60)	4.40 (0.04) ^a	0.06 (0.80) ^a	4.48 (0.03)	8.84 (0.003)	1.07 (0.30)
TSL	0.50 (0.47) ^a	0.00 (0.96) ^a	0.02 (0.87) ^a	0.03 (0.86) ^a	1.41 (0.23)	1.31 (0.25)	0.06 (0.80)	0.71 (0.40)
AA	0.10 (0.74)	0.79 (0.37)	0.82 (0.37)	0.15 (0.70)	0.62 (0.68)	0.39 (0.53)	0.58 (0.44)	0.32 (0.57)

Separate models were run for each color trait and for each sex. Each column represents the results of a single Poisson regression model: chi-square tests of each coefficient, *p* values are in parentheses. Bold *p* values indicate significance after the Bonferroni adjustments for multiple comparisons using tail-streamer and symmetry variables (*n* = 4, initial α = 0.05). Sample sizes are given for each region (males, females); sample sizes vary owing to the ability to adequately score the collected feathers.

^a Variable modeled as a cubic function.

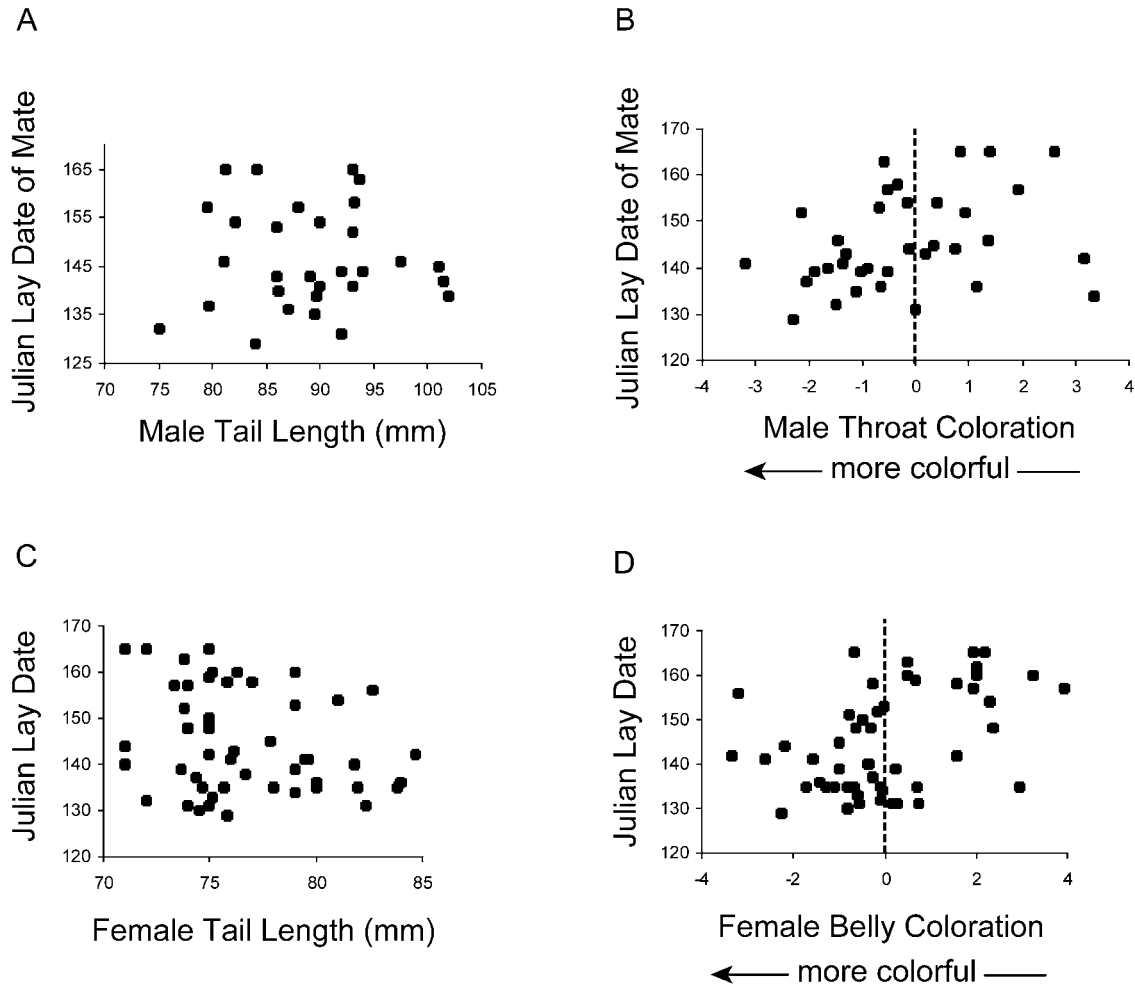


Figure 4
 In male and female barn swallows, tail-streamer length does not correlate significantly with clutch initiation date (a, c), but feather coloration is correlated with the onset of breeding in both sexes (b, d).

patterns for color described in other species. Several researchers have demonstrated a relationship between male feather coloration and seasonal reproductive success in a number of avian species, including house finches (*Carpodacus mexicanus*; Hill et al., 1994, 1999; McGraw et al., 2001), northern cardinals (*Cardinalis cardinalis*; Wolfenbarger, 1999), and arctic skuas (*Stercorarius parasiticus*; O’Donald, 1980).

The links between breeding performance and color expression were not limited to male barn swallows in this study,

however. The belly and breast coloration of females predicted the onset of breeding, the capacity to produce more than one brood in a year, and overall reproductive success during the year. Studies demonstrating functional female ornaments are rare among birds, and many argue that display traits in females are the result of correlated selection on male ornamentation (Amundsen, 2000). In fact, we are aware of no other studies that demonstrate a direct fecundity advantage to female birds that are the most colorful. Ironically, one of the only other

Table 4
 Results of general linear models to predict variation in seasonal reproductive success

	Males				Females			
	Throat (n = 29)	Breast (n = 27)	Belly (n = 28)	Vent (n = 29)	Throat (n = 52)	Breast (n = 52)	Belly (n = 47)	Vent (n = 51)
Color	0.45 (0.50) ^a	0.03 (0.84) ^a	4.65 (0.03) ^a	3.78 (0.05)	1.10 (0.29)	0.10 (0.74)	7.93 (0.005)	0.19 (0.65)
TSL	4.13 (0.04) ^b	3.80 (0.05) ^b	5.47 (0.02) ^b	6.15 (0.01) ^b	0.00 (0.98) ^b	0.00 (0.98) ^b	0.62 (0.43) ^b	0.01 (0.92) ^b
AA	0.14 (0.71)	0.29 (0.59)	0.86 (0.35)	1.93 (0.16)	1.97 (0.16)	1.29 (0.25)	1.40 (0.23)	1.05 (0.30)

See note to Table 3.

^a Variable modeled as an exponential function.

^b Variable modeled as a cubic function.

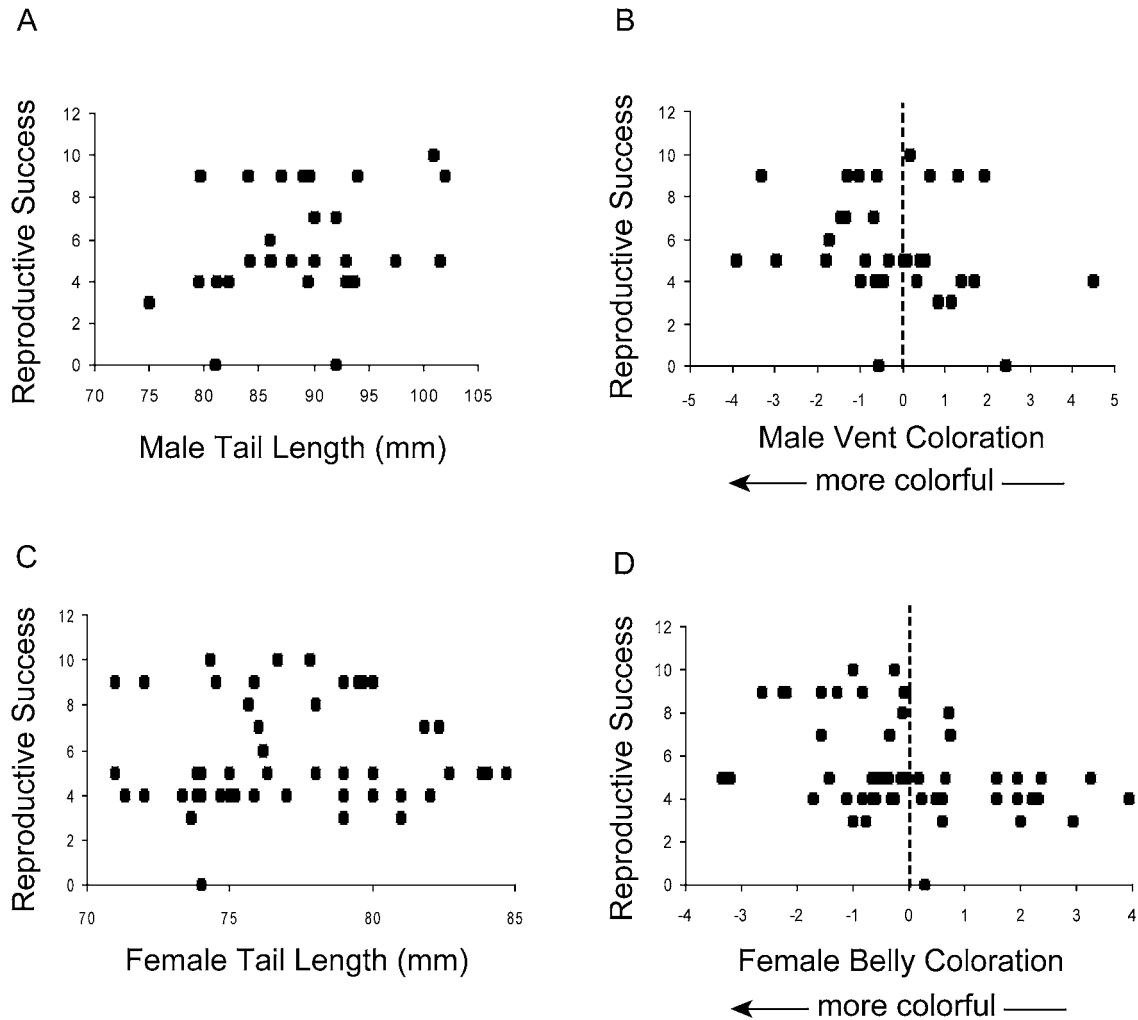


Figure 5

Tail-streamer length does not linearly predict seasonal reproductive success in male (a) and female (c) barn swallows, but feather coloration is correlated with the number of fledged young produced during the breeding season for both males (b) and females (d).

female ornaments that signals offspring production in birds is tail length in female European barn swallows (Møller, 1993; but see Cuervo et al., 1996). It remains to be determined in both sexes whether color ornaments are maintained by intersexual mate choice or intrasexual mate competition.

Why do different color regions correlate with different features of reproductive performance? In females, breast and belly coloration were correlated with Julian lay date, whereas throat and vent coloration in males correlated with the onset of his mate's egg-laying. Interestingly, patterns of mate selection seem to indicate that at least two of these traits, breast and throat coloration, are positively correlated in pairs. Although we have no a priori expectation that color regions would vary in their relative functions, it is possible that it is easiest to assess the coloration of feathers in these regions in contrast to the dark collar band that nearly completely separates the throat and breast. Another possibility is that the extent of coloration in these regions is differentially costly to produce. To better understand costs, it is necessary to understand the mechanistic basis of how this trait is produced.

Geographic differences in signals

Our study suggests that the sexual selection of tail-streamers and ventral feather coloration may vary geographically. Why

might these traits serve different functions in Europe and North America? Male barn swallows incubate their eggs approximately 12% of the time in North America (Ball, 1983; Smith and Montgomerie, 1992) but not at all in Europe (Møller, 1994), and this has been proposed as a reason for shorter streamers, on average, among Nearctic *H. rustica*, either by direct damage to streamers while on the nest or higher foraging demands (Smith and Montgomerie, 1991). Evans (1998) and colleagues (Buchanan and Evans, 2000; Rowe et al., 2001) have determined that only a small proportion of the total length of the tail-streamers of European barn swallows (approximately 10–15 mm) is sexually selected, whereas the majority of the length of streamers confers naturally selected benefits in terms of flight performance. Interestingly, on average, the streamer lengths of European barn swallows are about 10–15 mm longer than the average streamer lengths of North American barn swallows (Cramp, 1988), suggesting a reduction in sexual selection in this population. However, the maintenance of sexual dimorphism is not explained by this hypothesis. Another possibility is that, in North America, ventral coloration may provide more information about individual quality than about tail-streamers. If this is true, individuals may favor the use of feather coloration, rather than tail-streamer length, and the former trait may take precedence as a signal used to assess either mate

choice or dominance (Schluter and Price, 1993). Although both the results from experimental and observational data suggest no role of tail-streamer length in female mate choice in North American populations of *H. rustica* (Briceno, 2002; Smith and Montgomerie, 1991; Smith et al., 1991), similar manipulations of feather coloration should be performed to determine its role in mate choice or intrasexual competition.

These results are not the first to demonstrate differences in the function of sexual signals among populations of the same species. Pied flycatchers (*Ficedula hypoleuca*), for example, exhibit large white forehead patches that are sexually selected in Spain, but are small and not correlated with mating success in Norwegian populations (Dale et al., 1999). Interestingly, in Norway, female pied flycatchers appear to use feather color for mate selection instead of the size of white forehead patches (Sætre et al., 1995; Slagsvold and Lifjeld, 1988). Although feather coloration is variable in Spanish populations of this species, it does not appear to be as reliable an indicator of male quality (Potti and Montalvo, 1991). These patterns have recently been explained by selection for species recognition. Males of a closely related species, the collared flycatcher (*Ficedula albicollis*), also possess a white forehead patch. In areas where pied and collared flycatchers are sympatric, female pied flycatchers appear to choose males on the basis of feather coloration, not characteristics of the forehead patch (Sætre et al., 1997). This explanation for the pattern of trait divergence in pied flycatchers does not seem to apply to geographically isolated populations of *H. rustica* in North America and Europe because neither population is sympatric with heterospecifics that are similar in appearance. Instead, our results are consistent with hypotheses that advocate sexual selection as a mechanism that drives character divergence and ultimately speciation (Panhuis et al., 2001).

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