Original Article

The sexual signals of the East-Mediterranean barn swallow: a different swallow tale

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The differential functions of distinct morphological traits as sexual signals among closely related populations are associated with a potential role of sexual selection in population divergence and speciation. The cosmopolitan barn swallow *Hirundo rustica* complex consists of 6 subspecies, which differ substantially in tail streamer length and ventral coloration. Two of these subspecies—the European and North American subspecies—have been extensively studied. Though they are closely related, differentially exaggerated traits in these two subspecies appear to be the result of stronger sexual selection on tail length in Europe and ventral color in North America. The nonmigratory East-Mediterranean subspecies *H. r. transitiva* possesses both elongated long tail streamers and dark (brown-red) ventral coloration. We explored whether the expression of both traits is related to their potential role as sexual signals. In males, dark ventral coloration was the strongest predictor of breeding success, whereas tail streamer length was related to early breeding, and the likelihood of having multiple broods within a season. Older males, which typically have long streamers, were also less likely to have extrapair young in their nests. Tail streamer length and not ventral coloration predicted the breeding success of females. Considered in concert with earlier work on other populations, these findings show how patterns of phenotypic variation in the barn swallow species complex are underlain by differential sexual selection on tail length and ventral color, traits used variably among populations in mate choice and paternity decisions. *Key words:* age, *Hirundo rustica*, multiple signaling, sexual selection, speciation. *[Behav Ecol 22:1344–1352 (2011)]*

INTRODUCTION

Sexual signals may create behavioral barriers to gene flow, thus promoting reproductive isolation and population divergence (e.g., Barraclough et al. 1995; Irwin et al. 2001; Panhuis et al. 2001; Seddon et al. 2008). Several mechanisms may explain why mate preferences and sexual ornaments diverge between closely related populations. One possibility is that such traits are expected to change by drift and other stochastic events, amplified by the Fisherian runaway process (Fisher 1930; Lande 1981; Iwasa and Pomiankowski 1994). Additionally, changes in mate preferences may evolve in response to changing ecological conditions, allowing females to choose the most adapted or most detectable male in the local environment (Schluter and Price 1993; Boughman 2001; Pauers et al. 2004; Seddon 2005; Seehausen et al. 2008). However, these two mechanisms need not be mutually exclusive. Although mechanisms including random or functional changes in trait and preference contribute to our understanding of why a specific trait varies among different populations, an important step in assessing the potential role of sexual trait divergence in speciation is to demonstrate whether there are differences in the functional significance of these geographically variant traits, indicating whether sexual selection serves

as a force in maintaining between population differences. Here, we take advantage of phenotypic variation exhibited by the barn swallow complex, a rapidly formed monophyletic group (Dor et al. 2010) with geographic variation in two traits (ventral color and streamer length) shown to be related to mate selection in at least two subspecies of this group. Because of the known function of tail streamers and ventral color in European and North American populations of barn swallows (*Hirundo rustica*), we, here, determine whether either of these traits behave as sexual signals in a closely related but less studied population of barn swallows in the East Mediterranean (*H. r. transitiva*). The overall objective of our study is to determine the role of sexual selection in maintaining variation in tail streamers and ventral color in both males and females of *H. r. transitiva* population. This information contributes to a growing body of research on geographic variation in sexual signals in barn swallows (Møller 1995; Safran and McGraw 2004; Møller et al. 2006; Santure et al. 2010) and other animal groups (e.g., Seehausen and van Alphen 1998; Gray and Cade 2000; Uy and Borgia 2000; Irwin et al. 2001; Mendelson and Shaw 2005; Seddon and Tobias 2007).

The barn swallow (*Hirundo rustica*) is considered a model species for studies on mate choice and sexual selection (e.g., Møller 1988, 1994a; Smith and Montgomerie 1991; Safran et al. 2005; Kleven et al. 2006; Maguire and Safran 2010). For several decades, the tail streamers of the barn swallow have served as a classic illustration of a sexual signal (Møller 1988; Møller and de Lope 1994; Evans 1998). Within European populations of barn swallows (*H. r. rustica*), several studies have shown that

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females prefer the longest-tailed males both as social and extrapair partners (Møller 1988, 1994b; Saino et al. 1997). Furthermore, Møller and de Lope (1994) demonstrated that long tail streamers are detrimental for survival and thus gave the first empirical evidence to support Zahavi's honest signaling theory (Handicap Principle; Zahavi 1975). Whereas the European subspecies is characterized by long tail streamers and bright ventral coloration, the North American subspecies (*H. r. erythrogaster*) is characterized by darker ventral coloration and relatively shorter tail streamers. Recent correlational and experimental studies in North American populations suggest a potential signaling function of streamer length, but the degree to which this trait is related to reproductive performance appears to be limited. For example, Kleven et al. (2006) provide evidence for extrapair mating benefits for long-streamered males, yet no other indicators of seasonal reproductive performance have been found in association with male streamer length in two other North American populations (Safran and McGraw 2004; Neuman et al. 2007; Maguire and Safran 2010). However, in these North American populations, it has been demonstrated that dark ventral coloration serves as a male sexual signal, and darker males have increased reproductive success (Safran and McGraw 2004; Safran et al. 2005; Neuman et al. 2007; Maguire and Safran 2010).

In comparing geographic variation in traits with potential signaling functions, it is also relevant to examine the potential functional significance of variation in female morphology. Indeed, recent attention is being paid to a signaling function of female morphological variation with a greater emphasis on male mate choice (Amundsen 2000). Theoretically, in the absence of sex-role reversal, female ornaments are expected to evolve either due to a strong genetic correlation between the characters in the two sexes (Lande 1980; Cuervo et al. 1996; Amundsen 2000) or due to direct sexual selection on females (Møller 1993; Johnstone 1996; Amundsen 2000). However, an underlying genetic correlation does not preclude selection on females (Amundsen 2000). In barn swallows, studies conducted on the function of female streamer length indicate that this trait could be under sexual selection (Møller 1993; Cuervo et al. 2003), whereas correlational data from the North American subspecies suggest a potential signaling role of female ventral coloration—but not streamer length (Safran and McGraw 2004).

Here, we considered a poorly known population of barn swallows residing in the East-Mediterranean region. Recent molecular studies demonstrate introgression (recent or historical) among *H. r. rustica* and *H. r. transitiva* (Dor et al. 2010, Dor R, Safran RJ, Vortman Y, Lotem A, McGowan A, Evans MR and Lovette IJ. in review). Despite the genetical similarity of the two subspecies, the East-Mediterranean subspecies is characterized by ventral color that is even darker than that of males in North America (Safran RJ, unpublished data) and tail streamer lengths that are only slightly shorter than males in Europe (Møller 1994b). This combination of exaggerated traits compared with these two well-studied populations raises the question of their roles as sexual signals in *H. r. transitiva*.

We therefore investigated the potential role of sexual selection in shaping variation in ventral coloration and streamer length. We examined the two traits in relation to characteristics typical of sexual signals: the extent of sexual dimorphism and whether either or both of these traits are predictive of both social and genetic measures of seasonal reproductive success.

MATERIALS AND METHODS

Field methods

We studied a population of barn swallows at four breeding sites in the Hula Valley, Israel, from November 2006 to July 2008.

Sites were in remote villages (Kibutz) where swallow nests were typically constructed on the concrete entrances of buildings, usually one to three nests per building; each village was characterized as a site. We captured male ($n = 103$) and female ($n = 97$) swallows using mist nets. One of the four sites had a considerably larger colony comprised of 84 individuals ($n = 46$ males and 38 females); this site was monitored daily through the breeding season in two consecutive years (during 2007 and 2008, we spotted 24 and 27 pairs at this site, respectively). Data on phenotypic variation and trait characteristics are reported here from all sites pooled, whereas the reported measures of reproductive performance are derived only from the larger site where more frequent observations were possible.

In both 2007 and 2008, we individually marked swallows with numbered aluminum rings (Israel bird ringing center). To identify individuals at nests, in 2007, we uniquely marked individuals with enamel-based paints following methods used by Shields and Crook (1987). In 2008, we marked individuals with passive radio-frequency identification (RFID) (Radio-frequency identification) 12 mm, 0.095 g tags mounted on the birds with a Rappole-type harness, made from 0.5 mm elastic cord (Naef-Daenzer 2007). Tag identification was accomplished remotely with a custom-made reader and antenna (Logi Tag Systems ltd, Netanya, Israel). We identified pairs as they constructed nests, incubated eggs, and fed nestlings. With the use of the RFID system, we confirmed individual nest assignment through parental activities at the nest.

All captured adults were measured for wing length, intact tail streamer length (outer rectrices), and the tail feathers adjacent to these streamers. From the brachial vein of each individual, we took a ~20 µl blood sample and preserved each sample in 1 ml of lysis buffer with 2% sodium dodecyl sulfate (White and Densmore 1992). To assess ventral plumage color, we plucked 2–4 feathers from the ventral region (between the breast and the cloaca) of each captured bird and mounted them on an index card for further analysis, following previously established procedures (Safran and McGraw 2004; see color measurements below). All procedures were conducted under the permit of Israel Nature Reserve Authority (permit numbers 28234-2007 and 31345-2008).

We checked nests daily to determine clutch initiation dates (Julian date on which first egg was laid), brood size when nestlings were 10–12 days old to determine breeding performance (mean clutch size = 4.47 eggs ± 0.95 standard deviation), number of nesting attempts (one or two), and annual reproductive success (total number of nestling reaching the age of 10–12 days per season; fledging age is 20–22 days). Using molecular tools (see below), we validated our visual assignment of the genders of breeding individuals and determined each male's genetic breeding success for each brood and for annual reproductive success by excluding extrapair young from brood sizes.

At the age of 10–12 days, nestlings were weighed, banded with aluminum rings, and blood samples were taken in the same manner as from the adults.

Measurements of reproductive success that include both broods within a season, namely "annual reproductive success" and "annual genetic reproductive success," were measured in the first breeding season (2007) only, as in 2008, we initiated manipulative experiments between broods (as part of another, still ongoing study).

Color measurements

To measure ventral coloration, we combined two complementary methods: spectrometry and digital photography. During both years, we plucked feathers of ventral plumage from the ventral region of each captured bird and mounted them on

an index card, stored in the dark, and saved for spectral analysis (Safran and McGraw 2004). During 2008, we also photographed the bird ventral plumage in the field (following guidelines by Stevens et al. 2007) and photographed the feather cards collected in both years for digital color analysis (see below).

We used Ocean Optics USB-4000 spectrometer (range 200–1100 nm, Ocean Optics Inc., Dunedin, FL) to measure the feathers mounted on the cards. However, we found that as a result of a small number of sampled feathers, bright feathers were often penetrated by the diode beam and received spectral data that was strongly biased by the white background of the card. Nevertheless, the spectral analysis allowed us to confirm that there is no ultraviolet reflectance in the ventral feathers (similar to North American populations, Safran and McGraw 2004), which was necessary to validate our digital photography method based on a comparison of color measured accurately with the spectrometer (see below).

We applied digital photography following Stevens et al. (2007), using RAW file formats and Manual White Balance. We used Nikon D-40 digital reflex camera and adjusted white balance manually for each photograph using a white balance card (WhiBal RAW (R) Michael Tapes Design Ltd. Melbourne FL) and a Nikon 18% reflectance gray background. For digital image analysis and color scoring, we developed a MATLAB tool (The Mathworks Inc, Natick MA) that enabled us to exclude pixels with background effect (Vortman Y, Shechtman Y, Roth E, Pines O, Safran RJ, and Lotem A. in review). This was done by applying the Max-lloyd algorithm (Max 1960). Color scoring was done with the sRGB color space, scoring feather's chromatic elements on the R/G (red/green) and G/B (green/blue) ratio, which is consistent with vertebrates' perception of chromatic properties (Hering 1878; Hurvich and Jameson 1957) and with its relative insensitivity to variations in lighting intensity (Kelber et al. 2003).We further simplified our color scoring method after confirming that the variability in green reflectance is negligible in the ventral feathers of our swallows, and therefore, the R/B (red/blue) ratio is sufficiently accurate as a single color score: It was perfectly correlated to a principle component of R/G and G/B ($r_s = 0.9997$, $n = 219$, $P = 0.000$).

For the analysis presented in this paper, we photographed each feather card twice and measured the repeatability of the R/B color score ($r = 0.9969$, $n = 132$). We used 20 feather cards that could be measured accurately by the Ocean Optics spectrometer (i.e., without background bias) and confirmed that their chroma score was highly correlated with the R/B score obtained from the digital photographs of the same feathers ($r_s = 0.86$, $n = 20$, $P < 0.00001$). Here, chroma was calculated as the reflectance sum over the peak reflectance range (between 600 and 700 nm) divided by the total reflectance sum (between 300 and 700 nm). We further validated our R/B color score method by its consistency with human ranking, as human vision can provide a valid proxy for avian perception of sexual dichromatism (Seddon et al. 2010).

Molecular methods and paternity analysis

We extracted DNA from both parent and nestling blood samples using perfect gDNA Blood Kits (Eppendorf, Westbury, NY).

To assess molecular paternity, we used polymerase chain reaction (PCR) to amplify 8 microsatellite loci (Escu6, Hanotte et al. 1994; Ltr6, McDonald and Potts 1994, POCC6, Bensch et al. 1997; Hir11, Hir17, Hir19, and Hir20, Tsyusko et al. 2007; Hru6 Primmer et al. 1995). Individual PCR reactions were combined into multiplex mixes (Multiplex 1(M1); Escu6, Ltr6, POCC6, multiplex 2 (M2); and Hir11, Hir17,

Hir19, and Hir20. Hru6 was amplified as single locus). One locus, Hir17 (Tsyusko et al. 2007), presented a high level of null alleles; therefore it was excluded from the analysis. PCR amplification conditions were as following: initial denaturation at 95 °C for 5 min; 35 cycles of denaturating at 95 °C for 30 s, annealing at 50, 58, or 62 °C for 30 s (specific per multiplex PCR mix M1, M2, and Hru6, respectively), and extension at 72 °C for 30 s; and a final extension at 72 °C for 30 min. Products of PCR were genotyped on an ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA) with LIZ-500 as size standard. Allele sizes were estimated using Genemapper v3.7 (Applied Biosystems) and scored by visual examination.

We assigned paternity using methods implemented in Cervus V3 (Marshall et al. 1998). The combined exclusion probability of seven loci (Hir17 excluded) for the first parent was 0.9983, for the second parent 0.99993, and for the parent pair 0.999999. Offspring were assigned as extrapair young if at least two mismatches between the genotype of the offspring and the social father were found and if the social father was not one of the two most likely fathers. Overall, 43% of 41 first broods hosted one or more extrapair young. Within first broods, the mean proportion of within pair young was 0.84 ± 0.03 standard error.

Sexing

Hirundo rustica transitiva has not been studied previously in relation to its sexual ornaments, and the traditional methods for nonmolecular sexing (tail streamer length differences, Svensson 1975) developed for other barn swallow populations are not completely reliable for assigning gender to breeding adults of this subspecies (see RESULTS). For sexing determination, we therefore used the P2/P8 primer set to amplify the chromo-helicase-DNA–binding genes following Griffiths et al. (1998).

Statistical analysis

During 2007, we caught and measured 47 males and 48 females, and in 2008, we caught and measured 71 males and 67 females. Of these, 15 males and 18 females were caught in both years. In order to avoid pseudoreplication, we included each individual only once, the first year it was entered in our study. Whereas 2007 was a baseline study of the population, in 2008, we initiated a three-year experiment that could potentially influence breeding behavior during the second brood. Accordingly, for 2008, we have descriptive data sets that parallel those of 2007 only for the 2008 first broods; we therefore report annual reproductive success across the entire breeding season, using data from 2007 only. We also excluded from our analyses any pairs whose nests were destroyed due to human activity ($n = 5$).

Statistical analyses were conducted using Statistica V8 (Statsoft Inc, Tulsa, OK), or, when mixed models were applied, using SAS 9.2 (SAS Institute, Cary, NC). We used linear mixed models to test the relationships between ventral coloration, tail streamer length, and reproductive success while incorporating "year" as a random effect to remove the potentially confounding effects of interannual differences; annual differences in reproductive performance were not significant in all our analysis, although this random effect was retained in all models to be most conservative. When both predictive variables in the mixed models contributed similarly to the variance, we used backward elimination to determine which predictive variable is the main contributor to the model's variance. Nonparametric statistics were used for analyzing parameters that did not meet the assumptions of equal variances or that considerably deviated from normality, such as within pair paternity.

RESULTS

Trait characteristics

The ventral coloration and tail streamers of *H. r. transitiva* are sexually dimorphic; males were significantly darker (i.e., more saturated brown-red coloration) than females in their ventral
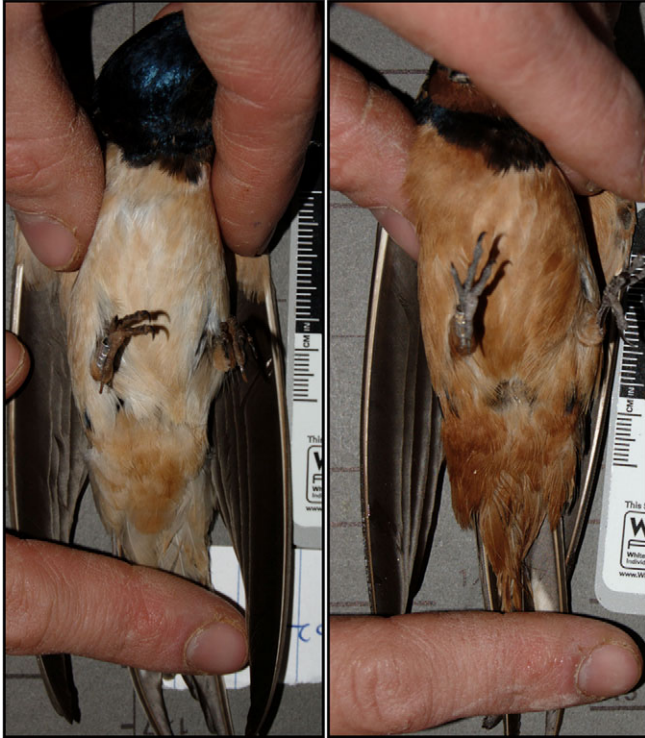

Figure 1
Natural variation in ventral plumage within the *Hirundo rustica transitiva* population. Plumage coloration varies from bright achromatic coloration to dark saturated brown.
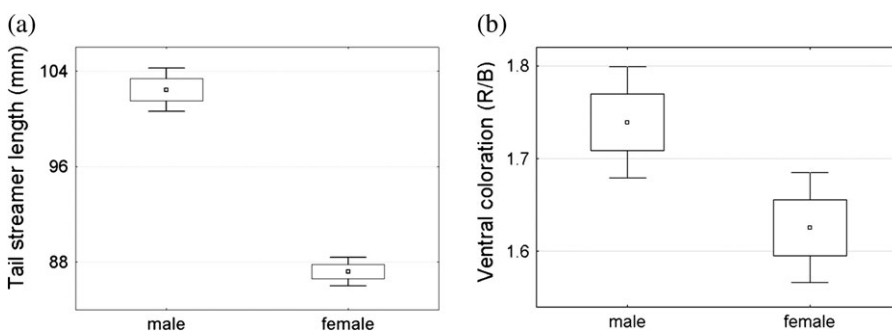
plumage (see Figures 1 and 2) and possessed longer tail streamers (Figure 2). In both males and females, however, ventral coloration and streamer length were not correlated with one another (males: $r_s = 0.1$, $n = 94$, $P > 0.31$, females: $r_s = 0.17$, $n = 87$, $P > 0.11$).

Male traits as predictors of breeding success

The extent of male ventral coloration was positively correlated with the number of young raised successfully in the first brood and over the entire season (i.e., annual breeding success) as well as with the number of genetic young raised in the first brood and over the entire season (Figure 3a–d, respectively, statistical analysis: Table 1 and text below). The length of male tail streamers, on the other hand, was correlated with the annual number of young raised (Figure 4b,d) but not with the number of successful young raised during the first brood (Figure 4a,c statistical analysis: Table 1 and text below). The effects of streamer length and ventral color on the number of young were analyzed using a linear mixed model with year as a random factor when 2007 and 2008 data sets were combined. Ventral coloration significantly predicted social and genetic measures of first brood breeding success (Table 1). Due to the relative small sample size when analyzing annual reproductive success, we validated the correlation of both male tail streamer length and male ventral coloration with annual measures of reproductive success by analyzing them separately. Both male ventral coloration and male tail steamer length significantly correlate with annual reproductive success: (Spearman rank correlation: male ventral coloration and annual reproductive success: $r_s = 0.71$, $n = 12$, $P < 0.008$; male tail streamer length and annual reproductive success: $r_s = 0.67$, $n = 13$, $P < 0.01$) and with genetic annual reproductive success: (Spearman rank correlation: male ventral coloration and annual genetic reproductive success: $r_s = 0.63$, $n = 12$, $P < 0.028$; male tail streamer length and annual genetic reproductive success: $r_s = 0.70$, $n = 13$, $P < 0.006$). Within this subsample of males, tail streamer length did not
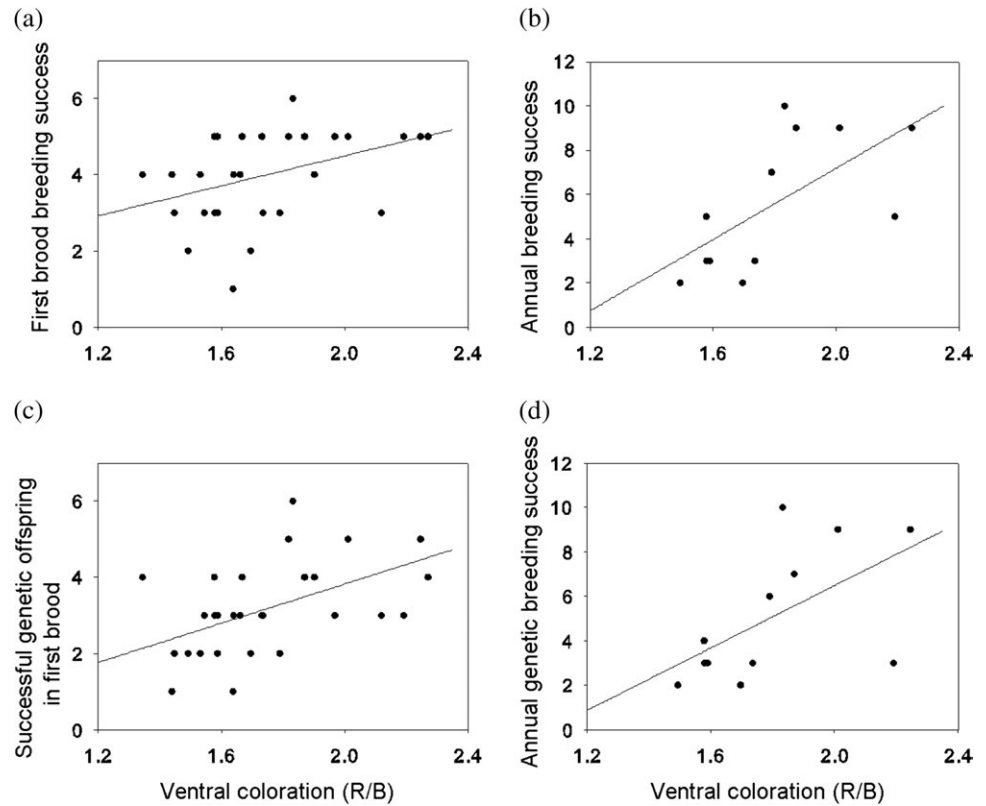

Figure 2
Sexual dimorphism in respect to tail streamer length (a) and ventral coloration (b); small squares in the figure represent the means, large squares mark mean ± standard error [SE], and error bars mark the mean ± 1.96 × SE. Males had longer tail-streamers than females (mean ± standard deviation [SD] = 102.43 ± 9.34 vs. 87.19 ± 5.88 mm, $n = 102$, 95 respectively, Linear mixed model: $F_{1,195} = 184.36$, $P < 0.00001$) and darker ventral coloration (mean ± SD R/B ratio = 1.732 ± 0.288 vs. 1.64 ± 0.273, $n = 95$, 87 respectively, Linear mixed model: $F_{1,181} = 6.92$, $P < 0.009$). Ventral coloration values represent the ratio of red reflectance divided by blue reflectance, as values are higher, the color is more reddish brownish; when values are closer to one, the color is more grayish white (colorless or achromatic).

Figure 3
Male ventral coloration as a predictor of reproductive success: (a) First brood breeding success, (b) Annual breeding success, (c) Successful genetic offspring in first brood, (d) Annual genetic breeding success. The *x* axis values represent the ratio of red reflectance divided by blue reflectance, as values are higher, the color is more reddish brownish; when values are closer to one, the color is more grayish white (colorless or achromatic).

significantly correlate with males' ventral coloration, $r_s = 0.48$, $n = 12$, $P > 0.1$.

In 2007 (the year for which data on annual breeding success were available, see MATERIALS AND METHODS), males with multiple broods had earlier first breeding dates, longer tail streamers, and darker ventral coloration compared with males that had only a single brood (Table 2).

The number of extrapair young in the nest was greater for males with shorter tail streamers (Mixed model: tail streamer length as continuous predictor, number of extrapair young as dependent variable and year incorporated for random effect, $F_{1,15} = 7.51$, $P < 0.016$). However, given the possible relationship between age and streamer length (Balbontin et al. 2011, Vortman Y, unpublished data), this result may reflect the effect of age on paternity. This is consistent with the finding that first-year males (banded as nestlings at the nest in the previous year) had a lower proportion of within-pair paternity compared with older males (males that were banded as adult breeding males the previous year, Mann–Whitney *U* test, $U = 6.5$, $n_1 = 6$, $n_2 = 10$, $P < 0.003$). In fact, almost all the extrapair young identified were within broods of first-year

breeding males (5/6 in first year males vs. 2/10 in older males: $\chi^2 = 4.92$, $P < 0.026$, degrees of freedom = 1).

Female traits as predictors of breeding success

In females, variation in tail streamer length (Figure 5a,b) predicted first brood success and annual reproductive success (Table 3). However, we did not detect a significant relationship between female ventral coloration and female reproductive success (Figure 5c,d, Table 3).

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 measures of seasonal reproductive success (Andersson 1994).

The objective of this study was to examine whether patterns of variation in tail streamers and/or ventral coloration in the East-Mediterranean barn swallow (*H. r. transitiva*) serve as

Table 1

Mixed model results for male's ornaments as predictors of first brood breeding success and first genetic brood breeding success; Variation between years was controlled for random effect in both models

Predictor	First brood breeding success					First genetic brood breeding success				
	Estimate	SE	ddf	*F*	*P*	Estimate	SE	ddf	*F*	*P*
Ventral coloration	2.02	0.78	27	6.65	**0.0157**	2.46	0.75	27	10.68	**0.003**
Tail streamer length	0.016	0.02	27	0.45	0.508	0.03	0.02	27	1.78	0.198

Significant values are marked in bold. SE, standard error; ddf, denominator degrees of freedom.
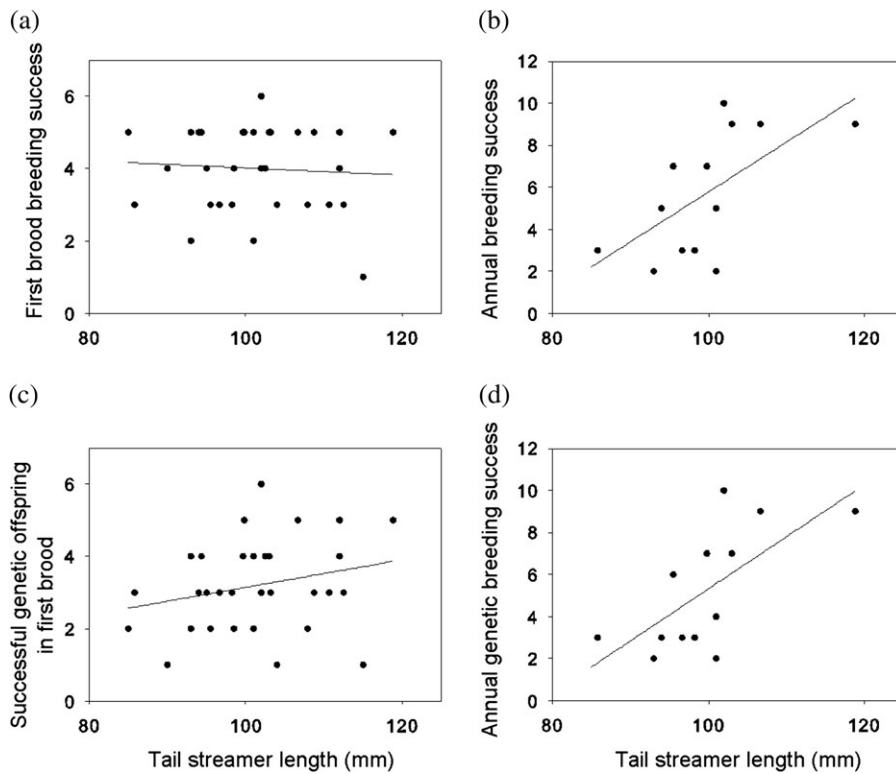
Figure 4
Male tail streamers length as a predictor of reproductive success: (a) First brood breeding success, (b) Annual breeding success, (c) Successful genetic offspring in first brood, and (d) Annual genetic breeding success.

sexual signals. Our data on social and genetic patterns of reproductive performance suggest that both ventral coloration and tail streamer length are sexually dimorphic and related—though in different ways—to seasonal measures of reproductive performance.

Male traits

Males are darker in ventral color compared with females, and darker males have greater reproductive success. Accordingly, our results indicate that variation in male color plays a role in pairing and seasonal reproductive performance—two indications that these traits are sexual signals.

Male East-Mediterranean barn swallows have elongated tail streamers, similar in length to those of males in the European population. In the European population, Møller et al. (2006) have shown that tail streamer length is related to various aspects of health and performance and that elongated tail streamers impose a survival cost (Møller 1988, 1994b; Møller and de Lope 1994). In the North American population, research has shown that streamer length correlates with

paternity and the onset of clutch initiation (Smith and Montgomerie 1991; Kleven et al. 2006). However, other studies from different sites in North America reveal that ventral coloration is the primary sexual signal in that population (Safran and McGraw 2004; Safran et al. 2005, 2008; Neuman et al. 2007). Whereas in North American populations, it appears that the effect of age on reproductive function and tail streamer length has not been carefully accounted for (but see Lifjeld et al. forthcoming); in European populations, it has been shown that older males possess longer streamers (Møller 1991; Garamszegi et al. 2005). This suggests that the relationship between streamer length and reproductive performance may be mediated, to some extent, by the effect of age. Our study reveals that tail streamer length is correlated with annual reproductive success and within-pair paternity. Although the relationship between tail streamer length and annual reproductive success might indicate female preference for tail streamer length, the relation between within-pair paternity and tail streamer length might also be a by-product of the effect of age per se on within-pair paternity (see also Lifjeld et al. forthcoming).

Table 2
Differences in breeding onset, tail streamer length, and ventral coloration for males with single versus double broods

	n	Julian breeding date ± SD (Days from 1 January 07)	Tail streamer length ± SD (mm)	Ventral coloration ± SD (R/B)
Single brood	7	92.7 ± 16.82	95.6 ± 5.3	1.69 ± 0.23
Multiple broods	6	61.8 ± 6.49	104.3 ± 8	1.94 ± 0.18
Mann–Whitney U		1.5	6	4
P value		**0.005**	**0.03**	**0.028**

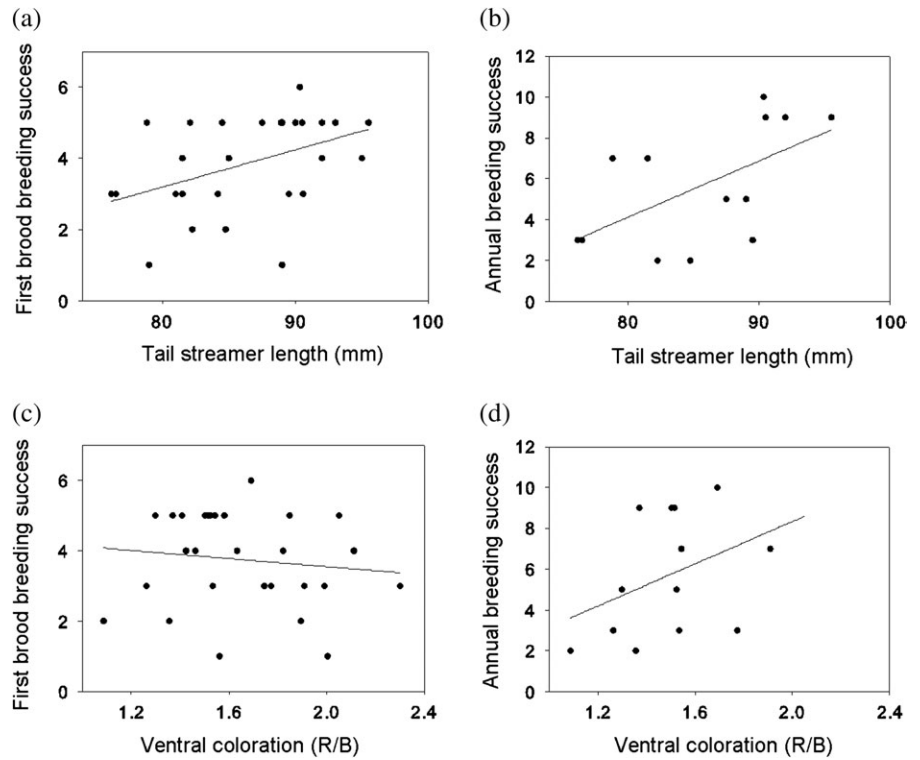Significant values are marked in bold. SD, standard deviation.

Figure 5
Female tail streamers and ventral coloration as predictors of reproductive success: (a) Tail streamer length as a predictor of first brood breeding success, (b) Tail streamer length as a predictor of annual breeding success. (c) Ventral coloration as a predictor of first brood breeding success, and (d) Ventral coloration as a predictor of annual breeding success.

Female traits

Unlike a study on female trait variation from North American barn swallows (Safran and McGraw 2004), we did not find an effect of female ventral coloration on any measures of seasonal reproductive performance. Instead, in *H. r. transitiva*, female tail streamer length correlates with all measures of female reproductive success and also with age. These results parallel those found in the European subspecies (Møller 1993; Cuervo et al. 1996). The expression of tail streamers in females is either due to a correlation of tail streamers with condition and/or due to direct sexual selection by males on this trait. With our present data and without experimental manipulation of female tail length, we cannot infer whether female tail streamer length serves as a sexual signal for male mate choice.

The evolution of sexual signals in the East-Mediterranean barn swallow

Our results suggest that both male tail streamers and dark ventral coloration in the East-Mediterranean barn swallow may function as sexual signals. Furthermore, it seems that this population is

unique among barn swallows in expressing exaggerations in both ornamental traits. Gray and McKinnon (2007) suggest that when adjacent populations differ in morph frequencies, polymorphism within each population can be maintained by gene flow between populations. The gene flow hypothesis is plausible in the case of the East-Mediterranean population because each of the 2 adjacent populations of barn swallows—the long-tailed European (*H. r. rustica*) and the dark-colored Egyptian (*H. r. savignii*)—are characterized by expressing primarily one of these ornaments (Møller 1994b). Molecular evidence for recent divergence and subsequent gene flow between the migratory European population and the sedentary East-Mediterranean populations (Dor R, Safran RJ, Vortman Y, Lotem A, McGowan A, Evans MR and Lovette IJ. in review) suggest that the long tail streamers of the East-Mediterranean males might be attributed to recent coancestry and/or gene flow with the European population. The dark ventral coloration, on the other hand, may reflect recent coancestry or gene flow with the sedentary Egyptian population (*H. r. savignii*). This geographical trait variation may have a recent origin, as the 2 sedentary populations were likely connected ~10 000 years ago, before the recent desertification process of the Sinai

Table 3

Female traits as predictors of first brood breeding success and annual reproductive success; Variation between years was controlled for random effect when analyzing first brood breeding success and had no effect

Predictor	First brood breeding success					Annual reproductive success				
	Estimate	SE	ddf	*F*	*P*	Estimate	SE	ddf	*F*	*P*
Model								12	3.9	0.055
Tail streamer length	0.1	0.04	24	5.71	**0.025**	0.25	0.11	12	5.15	**0.046**
Ventral coloration	−0.66	0.89	24	0.56	0.463	4.3	3.19	12	1.83	0.2

Significant values are marked in bold. SE, standard error; ddf, denominator degrees of freedom.

Peninsula (Goodfriend and Magaritz 1988; BarMatthews et al. 1997; Avner 1998; Miller-Rosen 2003). Future genetic analysis of these populations may allow further testing the gene flow hypothesis, whereas experimental work may reveal whether the presence of both ornaments in the East-Mediterranean population is currently maintained by selection.

FUNDING

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