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ORIGINAL ARTICLE

Ventral colour, not tail streamer length, is associated with seasonal reproductive performance in a Chinese population of Barn Swallows (*Hirundo rustica gutturalis*)

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Abstract

Phenotypic differentiation is common among populations that have large geographic distributions. One proposed mechanism driving phenotype divergence is sexual selection, which predicts that trait differences among closely related populations are underlain by variation in reproductive performance. Here, we examined a population of Asian Barn Swallows (*Hirundo rustica gutturalis*) in northeastern China. We ask whether traits shown to be under divergent sexual selection in other Barn Swallow populations are under sexual selection in this north Asian population by determining whether two features of phenotype variation, tail streamer length and ventral plumage colouration (including both throat and belly regions), are sexually dimorphic, associated with patterns of assortative mating and predictive of reproductive success. In this population, the length of tail streamers did not correlate with ventral plumage colouration in either males or females. The length of tail streamers was sexually dimorphic, but we did not find assortative mating by tail streamer length. By contrast, we found no sexual dichromatism but we did find assortative mating by throat colouration. Our correlational results indicated that the breeding performance of male Barn Swallows was associated with differences in their ventral plumage colouration, suggesting that ventral plumage colouration is likely a target of sexual selection in this population. Our finding that tail streamer length is unlikely to be under sexual selection is consistent with studies of other *H. rustica gutturalis* populations. The result that ventral plumage colour is likely to be under sexual selection is partially consistent with previous studies on Japanese *H. rustica gutturalis*, in which male throat but not belly plumage colour is the sexually selected trait.

Keywords Assortative mating · *Hirundo rustica* · Plumage colour · Reproductive success · Sexual selection

Zusammenfassung

Die Bauchfärbung, nicht die Länge der äu ßeren Schwanzfedern ist assoziiert mit der saisonalen Reproduktionsleistung einer chinesischen Population von Rauschwalben (*Hirundo rustica gutturalis*).

Phänotypische Differenzierung ist verbreitet zwischen Populationen mit einer weiten geografischen Verbreitung. Ein möglicher Mechanismus, der die phänotypische Divergenz antreibt, ist die sexuelle Selektion, die bestimmt, dass der Merkmalsausprägung zwischen nah verwandten Populationen die Variation der Reproduktionsleistung zugrunde liegt. In der vorliegenden Studie untersuchten wir eine Population asiatischer Rauchschwalben (*Hirundo rustica gutturalis*) in Nordostchina. Wir gingen der Frage nach, inwiefern Eigenschaften, die sich unter sexueller Selektion in anderen Rauchschwalbenpopulationen divergent zeigten, in dieser untersuchten nordasiatischen Population sexuell selektiert wurden. Wir bestimmten, ob zwei Eigenschaften der phänotypischen Variation, die Länge der äußeren Schwanzfedern und die Farbe des Bauchgefieders (inklusive Kehle und Bauchregionen) geschlechtsdimorph sind, im Zusammenhang mit Mustern der assortativen Verpaarung

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und prognostiziertem Bruterfolg. In der untersuchten Population korrelierte die Länge der äußeren Schwanzfedern weder bei Männchen noch bei Weibchen mit der Färbung des Bauchgefieders. Die Länge der äußeren Schwanzfedern war bei den Geschlechtern unterschiedlich, jedoch fanden wir keine assortative Verpaarung über die Schwanzlänge. Dagegen fanden wir keinen Geschlechtsdichromatismus, allerdings eine assortative Verpaarung über die Kehlfärbung. Unsere korrelierenden Ergebnisse zeigen, dass die Brutleistung männlicher Rauchschwalben assoziiert war mit Unterschieden in der Färbung ihres Bauchgefieders. Dies deutet darauf hin, dass die Farbe der Bauchfedern möglicherweise ein Ziel der sexuellen Selektion in dieser Population ist. Die Länge der äußeren Schwanzfedern unterliegt wahrscheinlich nicht der sexuellen Selektion. Dies ist konsistent mit Studien an anderen *H. rustica gutturalis* Populationen. Die wahrscheinlich der sexuellen Selektion unterliegende Bauchgefiederfärbung ist in Teilen übereinstimmend mit früheren Untersuchungen an japanischen Rauchschwalben, in denen die Kehlfärbung der Männchen, jedoch nicht die Bauchfärbung die sexuell selektierte Eigenschaft ist.

Introduction

Sexual selection and natural selection are important forces driving evolutionary changes within and between populations (Coyne and Orr 2004; Panhuis et al. 2001). Recent debates about the role of sexual selection in speciation have moved away from addressing whether sexual selection could be involved in the buildup of population divergence (e.g. Panhuis et al. 2001; Ritchie 2007) to considering the details of how populations evolve in different directions under sexual selection (e.g. Maan and Seehausen 2011; Safran et al. 2013). Indeed, differentiation of secondary sexual ornaments among closely related populations is common (Bro-Jørgensen 2010; Candolin 2003). However, it is necessary to conduct within-population analyses to test whether these phenotypic differences are underlain by sexual selection (e.g. Safran et al. 2005, 2016; Safran and McGraw 2004; Vortman et al. 2011a, b, 2013) or if they are attributable to other processes, such as natural selection or genetic drift.

The Barn Swallow *Hirundo rustica* is a small passerine that has become a model system in evolutionary and behavioural studies of sexual selection. Barn Swallows have a Holarctic distribution and consist of six subspecies that vary in a suite of morphological traits (Scordato and Safran 2014; Turner 2006). In particular, Barn Swallow populations differ in body size, colour of ventral plumage (ranging from white to dark red-brown) and the length of the outer rectrices (tail streamers) (Scordato and Safran 2014). For instance, the nominate European subspecies *Hirundo rustica rustica* is relatively large in size with long tail streamers and pale ventral plumage, while the North American subspecies *Hirundo rustica erythrogaster* is smaller, with short tail streamers and dark ventral colouration. In Europe, the tail streamer is the primary sexually selected trait (reviewed by Møller 1994): male Barn Swallows with long tail streamers arrive at breeding sites earlier, acquire their mates more quickly, and are more likely to raise more nestlings and have second clutches within a single season than males with short tail streamers (Møller 1990). Additionally, male swallows with either naturally long or experimentally elongated tail streamers were cuckolded less frequently and produced more biological offspring over the breeding season than males with naturally short or experimentally shortened tails (Saino et al. 1997). Additionally, recent research using lifetime reproductive success to estimate selection on life span and male ornaments also found selection on tail length and tail white spots, but not on ventral plumage colouration in European Barn Swallows (Costanzo et al. 2017). In North American *H. rustica erythrogaster*, by contrast, there is assortative mating [defined as "the correlation between male and female phenotypes or genotypes across mated pairs" (Jiang et al. 2013)] by ventral plumage colouration but not tail streamer length, and the number of fledglings per season is associated with male ventral colour, suggesting that dark plumage colouration is the primary sexually selected trait in this subspecies (Neuman et al. 2007; Safran and McGraw 2004; Safran et al. 2016, but for a contrasting view see Kleven et al. 2006). Male *H. rustica erythrogaster* individuals with naturally dark ventral plumage colour were cuckolded less frequently than males with pale plumage (Eikenaar et al. 2011), and this result was replicated experimentally by artificially enhancing ventral plumage colouration (Safran et al. 2005, 2016). Finally, in Middle Eastern Barn Swallows (*Hirundo rustica transitiva)*, which possess both long tail streamers and dark ventral colouration, both traits appear to be under sexually selection: darker males with longer tail streamers have greater reproductive success than paler males with shorter streamers (Vortman et al. 2011a, b, 2013).

Although European and North American Barn Swallows have been the subject of the most intense study, there are two additional subspecies that breed in eastern Asia. *Hirundo rustica gutturalis* breeds throughout eastern China, Japan and eastern Russia and generally have smaller body size and paler ventral colour compared to other subspecies of Barn Swallows (Scordato and Safran 2014). Previous observational research on Japanese populations of *H. rustica gutturalis* showed that throat colour and the size of white spots on the tail feathers may be sexually selected in this subspecies (Hasegawa et al. 2010b), and males with large throat patches acquired older and heavier females with higher viability as their mates (Hasegawa and Arai 2013), while male tail length was not significantly related to either within- or

extrapair paternity (Kojima et al. 2009). A second subspecies, *Hirundo rustica tytleri*, breeds in central Siberia, has a body size intermediate between *H. rustica rustica* and *H. rustica gutturalis*, very dark brown ventral plumage colouration, and tail streamers that are intermediate to *H. rustica rustica* and *H. rustica gutturalis* (Scordato and Safran 2014). *H. rustica tytleri* has not been the subject of any studies of sexual selection. A recent meta-analysis of sexual selection in Barn Swallows utilized these previous studies to show that different plumage ornaments are targets of equally intense sexual selection among different Barn Swallow populations (Romano et al. 2017).

Barn Swallows have an unusual biogeographic history: phylogenetic analysis based on mitochondrial DNA and nuclear loci shows that about 100,000 years ago, Barn Swallows from Asia (*H. rustica gutturalis*) crossed the Bering Strait and established the North American populations, giving rise to the *H. rustica erythrogaster* subspecies. Approximately 27,000 years ago, North American Barn Swallows re-crossed the Bering Strait and colonized the Baikal region, giving rise to the *H. rustica tytleri* subspecies (Dor et al. 2010; Zink et al. 2006). Currently the distributions of *H. rustica tytleri* and *H. rustica gutturalis* meet in northern Asia. The *tytleri* and *gutturalis* subspecies are most clearly differentiated by their red-brown vs. white ventral colouration, respectively. However, in northeastern China there are Barn Swallow populations with intermediate ventral colour and short tail steamers (Fig. 1). These populations have at times been designated a separate subspecies, *Hirundo rustica mandschurica* (Zheng 1987), but more recently they have been considered to be an intergrading form between the northern Asian subspecies *H. rustica tytleri* and the southern Asian subspecies *H. rustica gutturalis* (Turner 2006). In this study, we refer to this northern Chinese population as *H. rustica gutturalis,* consistent with the current designation. The targets of sexual selection have never been studied in Chinese *H. rustica gutturalis,* and the purpose of this study is to determine whether and how sexual selection differs in this population compared to other populations of *H. rustica gutturalis* as well as other subspecies of Barn Swallow. We test for patterns of sexual selection on tail streamer length and ventral plumage colour (including both throat and belly regions) by analysing the degree to which these traits are sexually dimorphic, whether there is evidence of assortative mating by these traits, and whether these traits are significantly associated with various measures of seasonal reproductive success.

Methods

Fieldwork methods

We studied a population of Barn Swallows in Shuangyashan City, Heilongjiang Province, China (46°35′N, 131°14′E) from May to September 2013 and June to September 2015. In this population, Barn Swallows usually start breeding in May, during which time each pair establishes and defends

Fig. 1 Morphological variation among three Chinese Barn Swallow populations. *Left panel Hirundo rustica gutturalis* in southern China. *Middle panel Hirundo rustica tytleri–Hirundo rustica gutturalis* intergrading population in northeastern China. *Right panel Hirundo rustica rustica* in western China. Note that the middle swallow has more red-brown ventral plumage colouration. The brightness of this figure has been adjusted to present the colour clearly

a separate territory. We identified active nests and visited them every 2 days to record the laying date and the number of eggs in the nest. Nests where we knew the exact laying date were visited daily after 12 days into the incubation period to determine the hatching date. We checked nests with unknown laying dates daily to identify and record the hatching date. As it usually takes more than 1 day for all nestlings to hatch out, we defined the hatching date (day 0) as the date that the first chick(s) hatched for each brood. We considered the number of nestlings present on day 15 to be the total number of fledglings associated with a particular nest (Vortman et al. 2011a, b). The same monitoring procedures were followed for both first and second broods. In total, there were 84 first broods (2013, $n=38$; 2015, $n=46$) and 20 (2013, $n=5$; 2015, $n=15$) second broods.

Adult swallows were captured using mist nets at night during the first 5 days after their first-brood nestlings hatched, as experience suggested that there was a high risk of them abandoning their nests if they were caught earlier. In total 165 adult swallows (2013, male, $n=36$; female, $n=39$; 2015, male, $n=44$; female, $n=46$) were captured; no individuals included in this study were caught in both 2013 and 2015. At the time of capture, usually between 21:00 and 24:00 hours, swallows were marked with a unique combination of coloured plastic rings on each of their legs. Sex was determined by checking the presence (females) or absence (males) of a brood patch. For each bird, the length of both wings was measured to the nearest 1 mm using a wing rule and the length of both streamers were measured to the nearest 0.01 mm with digital calipers (Jazooli, UK) following Evans (1998), and body mass was measured to the nearest 0.01 g with a digital balance (CX-168; ChangXie, China). All measurements were taken by the same person (Yu Liu) to avoid differences between observers. Feather samples were taken from throat and belly regions for quantification of colour, and we divided feather tract regions following Svensson et al. (2011). For each region, four to ten feathers were plucked and taped to white paper cards following Safran and McGraw (2004). These samples were stored in the dark for future measurement using a spectrophotometer.

Plumage colour measurement

We measured feather samples with a reflectance spectrometer (USB4000, light source; PX-2; Ocean Optics, US) following Safran et al. (2010). Each feather patch was measured three times with 20 scans per measurement, and the three measures were then averaged for further analysis. We calculated colour variables according to three dimensions of colour vision: hue, brightness and chroma (HSB colour space). Calculation of colour variation is based on spectra with wavelengths between 300 and 700 nm, which is the range of spectral sensitivity in birds (Cuthill et al. 2000). Hue is represented by the wavelength that shows the maximum slope for a red-brown plumage spectrum; red chroma is the proportion of total reflectance occurring in the red region (600–700 nm) as a measure of spectral saturation; and brightness is the mean reflectance over the spectra. Ventral plumage in Barn Swallows does not reflect in the ultraviolet range (Safran and McGraw 2004) so little colour information is lost by using the HSB colour space.

Statistical analyses

Principal component analysis on colour traits

Principal component analysis (PCA) was used to reduce the dimensionality of plumage colour traits using the function prcomp from the R package stats, and variables were scaled to have unit variance before analysis. PCA was conducted on throat and belly regions separately. The first PC explained more than 60% of the variation in colour for each region, and therefore PC1 of throat and belly colour were used for further analysis (Table 1). To facilitate comparisons between patches, we multiplied throat colour PC1 loadings by − 1 before the analyses. Swallows with higher PC1 values have darker (lower brightness values), redder (lower hue values, higher chroma values) throat and belly plumage than swallows with lower PC1 values (Table 1).

Correlations between morphological traits and among potential sexually selected traits

Pearson correlations were used to test whether morphological traits, wing length and body mass were correlated within individuals in males and females, separately. Similarly, we tested whether potential sexually selected traits—the length of tail streamers and ventral plumage colour—were correlated within individuals.

Table 1 Principal component (*PC*) loadings for colour traits

	Throat PC1	Belly PC1
Brightness	*− 0.58*	*− 0.66*
Hue	*− 0.52*	− 0.31
Chroma	*0.62*	*0.69*
SD	1.39	1.35
Cumulative proportion of variance	63.97%	60.82%

Correlation values (opposite numbers for throat PC1) and cumulative proportion of variance for colour traits are shown. Traits strongly correlated with PC values (loading > 0.5) are in *italic*

Degree of sexual dimorphism in morphological and potential sexually selected traits

Levene's tests were performed to test the equality of variances in potential sexually selected traits (the length of tail streamers and ventral plumage colour) for the two sexes. Due to different sample sizes of males and females, Welch's two-sample *t*-tests were performed to test the sexual dimorphism of morphological and potential sexually selected traits. Throughout the results, positive *t*-values correspond to larger values in females.

Assortative mating by morphological or potential sexually selected traits

Partial Pearson correlations were used to explore assortative mating based on morphological and potential sexually selected traits in Barn Swallow breeding pairs. We included year as the third controlled variable in the function pcor.test from the R package ppcor. All statistical tests were two-tailed and were performed in R (R Core Team 2016).

Correlation between reproductive success and morphological/potential sexually selected traits

Reproductive success was assessed for each pair of Barn Swallows by recording the chick hatching date, the number of eggs, and the number of fledglings produced during the entire breeding season. Hatching date is considered to be an important index of reproduction timing of birds (Tomás 2015). Generalized linear mixed models (GLMM) were used to analyse the relationship between reproductive success and different traits, using the functions lmer or glmer from the R package lme4 (Bates et al. 2015). A maximal GLMM model (Table S1) was constructed for each measure of reproductive success, with morphological traits (wing length and body mass of both members of the pair) and potential sexually selected traits (streamer length, throat and belly colour PC1 of both sexes) included as fixed effects, and the year (2013 and 2015) as a random effect. We assumed a normal distribution when modelling hatching date and a Poisson distribution when modelling the number of eggs and the number of fledglings. To deal with data overdispersion, nest identifier was also included as a random effect in GLMMs when modelling the number of eggs and the number of fledglings. Models were simplified from the maximal model through stepwise dropping of factors non-significantly correlated with the dependent variable until all factors were significant with $\alpha = 0.05$. ANOVAs were performed on the minimal models to calculate the proportion of variance explained by each factor. Maximal GLMM models are shown in the appendices (Table S1). All analyses were conducted with (R Core Team 2016).

Results

Correlations between morphological traits and among potential sexually selected traits

The wing length and body mass were not significantly correlated in either males or females (Pearson correlation—male, $r = 0.11$, $n = 80$, $p = 0.33$; female, $r = 0.03$, $n = 84$, $p = 0.80$). The length of tail streamers was not significantly correlated with colour traits in either males or females (throat PC1 and belly PC1 values; Pearson correlation—male, $r = -0.12$ to -0.08, $n = 80$, all $p > 0.30$; female, $r = -0.02$–0.07, $n = 83$–84, all $p > 0.54$). Throat and belly PC1 values were significantly correlated in both males and females (Pearson correlation—male, $r = 0.43$, $n = 81$, $p < 0.01$; female, $r = 0.58$, $n = 83$, $p < 0.01$).

Sexual dimorphism in morphological and potential sexually selected traits

In this population, male and female Barn Swallows were sexually dimorphic in wing length and body mass (Welch two-sample *t*-test—wing length, $t_{162.69} = -4.34$, $p < 0.01$; body mass, $t_{131.19} = 3.20$, $p < 0.01$), with males exhibiting longer wings (male, mean ± SD = 112.11 ± 2.64 mm, $n = 80$; female, mean ± SD = 110.31 ± 2.68 mm, $n = 85$) and lighter body mass (male, mean ± SD = 15.31 ± 0.89 g, $n = 80$; female, mean ± SD = 15.96 ± 1.63 g, $n = 85$) than females. Male tail streamer length was significantly longer than that of females (male, mean ± SD = 100.99 ± 7.72 mm, $n = 80$; female, mean ± SD = 84.25 ± 5.22 mm, $n = 85$; Welch two-sample *t*-test, $t_{137.74} = -16.23$, $p < 0.01$) and was more variable (Levene's test, $F_1 = 16.31$, $p < 0.01$). Neither throat nor belly colour PC1 values were significantly different between the two sexes (Welch two-sample *t*-test—throat PC1, $t_{163.9} = -1.30$, $p = 0.19$; belly PC1, $t_{162.86} = -1.37$, $p = 0.17$). There were also no significant differences in variance of colour traits (throat and belly PC1 values) between males and females (Levene's test, $F_1 = 0.065$–0.072, $p = 0.79$–0.80).

Assortative mating by morphological and potential sexually selected traits

We found some evidence for assortative mating by phenotype in our Barn Swallow population. Male body mass was positively correlated with female mass within the same pair (partial Pearson correlation, $r = 0.37$, $n = 77$, $p < 0.01$), but wing length was not significantly correlated between males and females in the same pair (partial Pearson correlation, $r = -0.12$, $n = 77$, $p = 0.28$). There was also no evidence for assortative mating by streamer length between males and

females in each breeding pair (partial Pearson correlation, $r=0.09$, $n=77$, $p=0.46$; Fig. 2). Throat colour PC1 was correlated within pairs (partial Pearson correlation, $r=0.22$, $n=78$, $p=0.05$; Fig. 2) while belly colour PC1 was marginally non-significantly correlated within pairs (partial Pearson correlation, $r=0.19$, $n=77$, $p=0.09$). Together, these results show assortative mating by body mass and throat colour in Barn Swallows breeding in northeastern China.

Reproductive success and potential sexually selected traits

Hatching date of first clutches

Hatching date was significantly associated with male and female body mass, female streamer length and male throat colour PC1 (Fig. 3, Table 2). Phenotypic variables with the greatest influence on hatching date were: male throat PC1 (explaining 9.71% of the total variance), female body mass (8.45%), male body mass (7.49%) and female streamer length (6.90%). The negative associations between hatching date and male body mass and throat PC1 suggest that heavier male Barn Swallows with darker, redder throat plumage started breeding earlier than lighter, paler males (Fig. 3; Table 2). Heavier females with longer tail streamers also bred earlier than lighter, shorter-tailed females (association between hatching date and female body mass and streamer length; Fig. 3; Table 2).

Number of eggs and number of fledglings over the breeding season

Variation in the total number of eggs laid by female Barn Swallows over the course of the entire breeding season (i.e. first plus second clutches) was explained by female body mass and male belly colour PC1 (Table 2). Similar to hatching date, the variance explained by the minimal GLMM model suggested that the number of eggs was mainly influenced by male belly colour PC1 (explaining 13.00% of total variance) and female body mass (12.39%) (Table 2). Female swallows with heavier body mass and/or longer tail streamers laid more eggs in a breeding season, and so did females mated to males with darker, redder belly plumage (Fig. 3).

In addition to examining the total number of eggs produced by females across the entire breeding season, we also considered the total number of fledglings, which can be a more direct measure of reproductive success. In the study population, breeding failures involved unhatched eggs and nestling deaths in the nest (15%, 69 out of 460 eggs/nestlings), which leads to a difference between the total number of eggs and the total number of fledglings in a nest. In the minimal GLMM model testing the correlation between the total number of fledglings and adult phenotype, 23.25% of the variance in the number of fledglings was explained by female tail streamer length (Table 2), indicating that females with longer tail streamers tended to produce more fledglings than females with shorter streamers. There were no other significant associations between adult traits and number of fledglings (Table 2).

Discussion

In this study, we aimed to identify traits under sexual selection in a northeastern Chinese Barn Swallow population that has been the subject of taxonomic debate based on variation in body size and ventral plumage colouration (Turner 2006). We found that the colour of ventral plumage, including both throat and belly regions, predicted patterns of pairing and reproductive performance of male swallows. Females with longer tail streamers also had higher annual reproductive success, including earlier hatching dates and greater

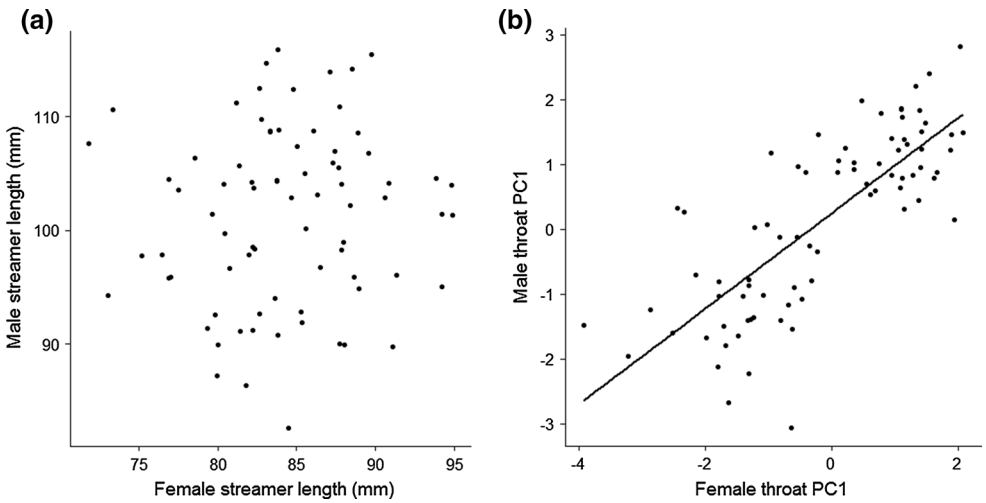

Fig. 2 Assortative mating by streamer length (**a**) and throat (**b**) plumage colour in northeastern Chinese Barn Swallows. Note that there is no significant relationship between male and female streamer length, but evidence for assortative mating by throat colour. Simple regression lines are shown in **b**

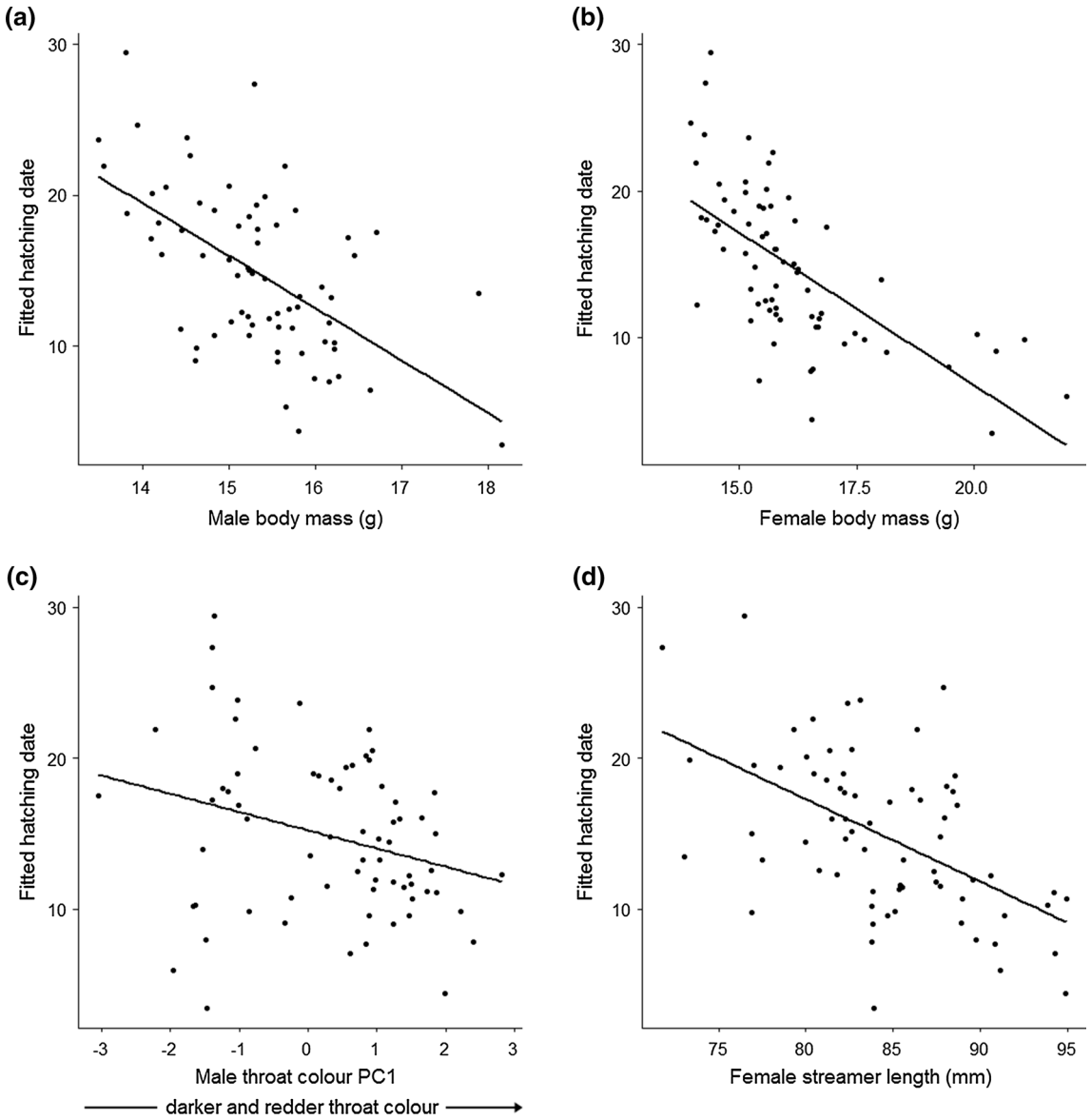

Fig. 3 Relationship between hatching date and male (**a**, **c**) and female (**b**, **d**) morphology. Hatching date was negatively correlated with **a** male body mass, **b** female body mass, **c** male throat colour principal component (PC) 1 and **d** female streamer length in the minimal generalized linear mixed model (GLMM). Fitted values of the hatching date from the minimal GLMM and simple regression lines are shown

numbers of fledglings. By contrast, the length of male tail streamers (the primary sexually selected trait in European populations) did not significantly correlate with any measure of reproductive success. Based on these results, we find that ventral plumage colour, not the length of tail streamers, is likely to be the primary sexually selected trait in this Barn Swallow population.

Assortative mating can be an important mechanism driving speciation by sexual selection (Servedio 2016). In European Barn Swallows, it has been shown that the tail length of female Barn Swallows is positively correlated with the tail length of their mates, after considering age effects; this result supports the suggestion that both male and female tail lengths honestly reflect individual quality (Møller 1993). In contrast, assortative mating based on throat and belly colouration, not tail length, was found in North American Barn Swallows (Safran and McGraw 2004). In Japanese *H. rustica gutturalis*, the height of the throat patch did not significantly correlate between paired swallows (Hasegawa and Arai 2013), while patterns of assortative mating by other sexual ornaments (white spots in the tail, throat colour) have never been reported. In this study, we found assortative pairing by throat colouration rather than tail length. The mechanism that produces this assortative mating is at present unclear.

Table 2 Morphological and potential sexually selected traits predicting reproductive success in this Barn Swallow population

	Hatching date				Number of eggs				Number of fledglings			
	Coefficient	*t*	*p*	% Var.	Coefficient	*Z*	*p*	% Var.	Coefficient	*Z*	*p*	% Var.
Morphological traits												
Male												
Body mass	*−2.96*	*−2.67*	*<0.01*	*7.49%*	−0.06	−0.73	0.47	–	−0.06	−0.60	0.54	–
Wing length	0.52	1.52	0.13	–	−0.02	−0.86	0.39	–	−0.04	−1.17	0.24	–
Female												
Body mass	*−1.68*	*−2.83*	*0.01*	*8.45%*	*0.07*	*2.47*	*0.01*	*12.39%*	0.04	1.04	0.30	–
Wing length	0.57	1.60	0.12	–	−0.003	−0.11	0.91	–	0.002	0.06	0.96	–
Streamer length												
Male	−0.14	−1.11	0.27	–	0.003	0.37	0.71	–	0.008	0.80	0.42	–
Female	*−0.45*	*−2.56*	*0.01*	*6.90%*	0.02	1.77	0.08	–	*0.04*	*3.11*	*<0.01*	*23.25%*
Colour traits												
Male												
Throat PC1	*−2.18*	*−3.04*	*<0.01*	*9.71%*	0.06	0.75	0.45	–	0.05	1.17	0.24	–
Belly PC1	0.61	0.81	0.42	–	*0.10*	*2.16*	*0.03*	*13.00%*	0.06	1.15	0.25	–
Female												
Throat PC1	0.06	0.06	0.95	–	0.06	1.31	0.19	–	0.04	0.53	0.60	–
Belly PC1	1.04	1.26	0.21	–	−0.07	−1.24	0.22	–	−0.08	−1.32	0.19	–
R-squared			0.35				0.15				0.17	

The year (2013 and 2015) and the identifiers of nests were included as random effects when modelling number of eggs and number of fledglings, and the year was included as a random effect when modelling hatching date. Final models including all significant variables ($p < 0.05$) are shown in *italic*. Values of non-significant terms are from the model immediately prior to the elimination of that factor. Variance explained by each fixed significant factor is shown (*% Var.*). Sample size (number of swallow pairs): hatching date, $n = 69$; number of eggs, $n = 54$; number of fledglings, $n = 55$

For northeastern Chinese Barn Swallows, females with longer tails and heavier body mass bred earlier and produced larger clutches over the breeding season (Figs. 3, 4). Although male ornaments are usually considered to be the primary targets of sexual selection, female ornaments can also be functional (Clutton-Brock 2009; Tobias et al. 2012). For instance, the length of tail streamers indicates female quality in European Barn Swallows (Møller 1993), and females with longer tails and more colourful throat patches have a reproductive advantage via earlier clutch initiation in Japanese Barn Swallows (Hasegawa et al. 2017). Our results further support the view that the relationship between reproductive success and ornaments differs between the sexes, with tail length providing more salient information about individual quality in females, and ventral colouration likely advertising information

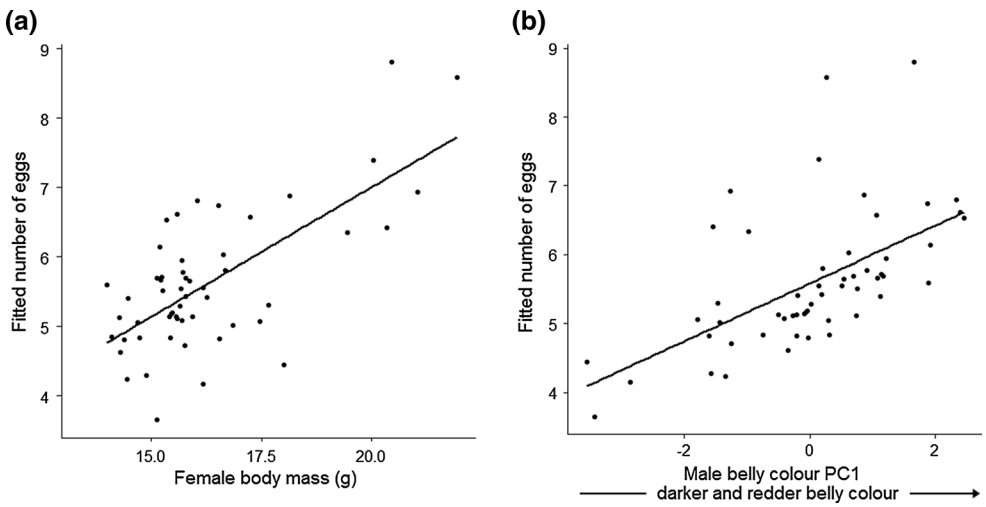

Fig. 4 Relationship between number of eggs and adult morphology. Number of eggs was positively associated with **a** female body mass and **b** male belly colour PC1 in the minimal GLMM model. Fitted values of the number of eggs from the minimal GLMM model and simple regression lines are shown. For abbreviations, see Fig. 3

about quality in males in this study population. We also found a discrepancy between the results for the number of eggs versus the number of fledglings: the ventral colouration of male Barn Swallows predicted the number of eggs, but failed to predict the number of nestlings. This discrepancy could be due to both sexual and natural selection operating throughout the reproduction process, resulting in female Barn Swallows investing more in reproduction for darker males by laying more eggs, but perhaps greater mortality occurring for individuals in large broods.

Although clutch initiation and number of offspring are two major and representative components of sexual selection in the Barn Swallow (Møller 1992 1993), extra-pair paternity is also an important factor which may influence the reproductive fitness of male Barn Swallows (Møller 1994). Although we did not test the effect of extra-pair mating on male fitness in this study, the ratio of extra-pair offspring to all offspring is relatively low in this population [11.6%, 28 extra-pair offspring out of 241 nestlings (Liu 2017)] compared to *H. rustica rustica* or *H. rustica erythrogaster* [*H. rustica rustica*, 18–29%; *H. rustica erythrogaster*, 23–31% (Turner 2006)], so extra-pair mating is not likely to be a major component of sexual selection (but also see Hasegawa et al. 2010a; Kojima et al. 2009). Even so, in swallow populations in which sexual selection via extra-pair mating has been examined, the targets of sexual selection are consistent for both social and extra-pair mating success (e.g. Safran and McGraw 2004; Safran et al. 2005; Vortman et al. 2011a, b, 2013). Another possible confounding factor in our study is that the age of the swallows was not known, and the size of sexually selected traits can change with age, e.g. tail length in European Barn Swallows (Møller 1991) and throat colouration in Japanese Barn Swallows (Hasegawa et al. 2010b). However, it has also been shown that the intensity of sexual selection in Barn Swallows does not differ significantly between age classes (Romano et al. 2017). To test the effect of age on sexual selection in our Barn Swallow population, further research is needed with age-identified individual swallows as samples.

Secondary contact between divergent populations can lead to either fission or fusion of divergent taxa, and sexual selection can be an important force driving this process (Coyne and Orr 2004; Panhuis et al. 2001; Rundle and Nosil 2005). In our population of Barn Swallows, males with overall darker, redder plumage colour bred earlier and had higher annual reproductive success compared to males with pale plumage. We hypothesize that the intermediate ventral colour of northeastern *H. rustica gutturalis* may be the result of introgression of dark colouration from northern *H. rustica tytleri* populations into southern pale-coloured populations, potentially driven by sexual selection. If this is the case, we would predict that darker males in the zone of intergradation would have higher fitness, which could lead to the introgression of alleles for dark plumage colour into the genetic background of the pale-plumage populations.

This study confirms that darker males in northeastern China do indeed have better reproductive performance than paler males. However, some questions remain unresolved. For example, the targets of female preferences and male competition in the parental subspecies, *H. rustica tytleri* and southern Chinese *H. rustica gutturalis,* are unknown. The north Asian subspecies *H. rustica tytleri* derives from recolonization of Asia by the North American subspecies, *H. rustica erythrogaster*. These two subspecies are similar in morphology, and therefore may have similar behaviour patterns, including behaviour related to sexual selection (Dor et al. 2010; Scordato and Safran 2014; Turner 2006; Zink et al. 2006). Observational analyses in Japan on *H. rustica gutturalis* have suggested that the red throat patch and the white spots in the tail are under sexual selection, as males with less saturated throat plumage and larger white spots in the tail bred earlier than other males (Hasegawa et al. 2010b) and males possessing either "less saturated throat colour and shorter tails" or "more saturated throat colour and longer tails" tended to form pairs with females more than other males (Hasegawa and Arai 2017), while pale ventral plumage is unlikely to be a sexual signal (Hasegawa et al. 2017). Our finding that tail length is unlikely to be sexually selected is consistent with previous studies of both North American and Japanese Barn Swallows. The result that belly colouration is associated with reproductive performance is more similar to observations in North American swallows than Japanese populations; however, we do find assortative mating by throat colour, suggesting that this trait may be important in the northeastern Chinese population as well as in Japan. We did not measure the size of white tail spots in this study; this would be an interesting avenue of future research. Our findings also indicate that the targets of sexual selection differ among closely related but phenotypically differentiated populations, which implies that sexual selection may be an important force driving divergence in this system (Romano et al. 2017; Scordato and Safran 2014). In the future, more studies on the behaviour and genetics of the two parental Barn Swallow populations, *H. rustica tytleri* and *H. rustica gutturalis,* are required to fully determine if sexual selection drives asymmetric introgression of plumage colour, and whether this trait contributes to erosion of reproductive isolation between these two subspecies.

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