

# Population differences in density and resource allocation of ornamental tail feathers in the barn swallow

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Many organisms show well-defined latitudinal clines in morphology, which appear to be caused by spatially varying natural selection, resulting in different optimal phenotypes in each location. Such spatial variability raises an interesting question, with different prospects for the action of sexual selection on characters that have a dual purpose, such as locomotion and sexual attraction. The outermost tail feathers of barn swallows (*Hirundo rustica*) represent one such character, and their evolution has been a classic model subject to intense debate. In the present study, we examined individuals from four European populations to analyze geographical variation in the length and mass of tail feathers in relation to body size and wing size. Tail feather length differed between sexes and populations, and such variation was a result of the effects of natural selection, acting through differences in body size and wing size, as well as the effects of sexual selection that favours longer tails. The extra enlargement of the tail promoted by sexual selection (i.e. beyond the natural selection optimum) could be achieved by increasing investment in ornaments, and by modifying feather structure to produce longer feathers of lower density. These two separate processes accounting for the production of longer and more costly tail feathers and less dense feathers, respectively, are consistent with the hypothesis that both Zahavian and Fisherian mechanisms may be involved in the evolution of the long tails of male barn swallows. We hypothesize that the strength of sexual selection increases with latitude because of the need for rapid mating as a result of the short duration of the breeding season at high latitudes. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **105**, 925–936.

**ADDITIONAL KEYWORDS:** aerodynamics – Fisherian process – flight – handicap – migration – sexual selection.

## INTRODUCTION

Geographical variation in morphology is common in many organisms including animals (Imasheva, Bubli & Lazebny, 1994) and plants (Hodgins & Barrett,

2008). Such variation is presumably attributable to natural selection because environmental conditions and intensity of selection vary in space. Among the most prominent patterns of geographical variation are an increment in body size (Bergmann's rule) and a reduction of extremities with latitude (Allen's rule) that appear to represent physiological adaptations to prevent heat loss in cold climates. However,

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other factors may affect such latitudinal clines in geographical variation. For example, migration distances appear to increase with latitude, and this selects for different wing lengths and shapes (Winkler & Leisler, 1992; Lockwood, Swaddle & Rayner, 1998; Pérez-Tris & Tellería, 2001). In addition, life-history traits such as clutch or litter size also vary with latitude (Lack, 1948; Moore, 1949; Lord, 1960; Fleming & Gross, 1990; Iverson *et al.*, 1993). There are exceptions to these rules of geographical variation, which are interpreted as consequences of local adaptation (Laugen *et al.*, 2003). In any case, it is obvious that natural selection varies quantitatively and/or qualitatively in space, and this posits an interesting scenario with different prospects for the action of other selective pressures such as sexual selection. Indeed, mating systems vary geographically in several species (Shine & Fitzgerald, 1995; Perrin & Mesnick, 2003; Gosselin, Sainte-Marie & Bernatchez, 2005), as does the size of secondary sexual characters (Møller, 1995; Candolin, Salesto & Evers, 2007; Olsen *et al.*, 2010), as well as the degree of sexual dimorphism (Ralls & Harvey, 1985; Møller, 1995; Shine & Fitzgerald, 1995; Pearson, Shine & Williams, 2002).

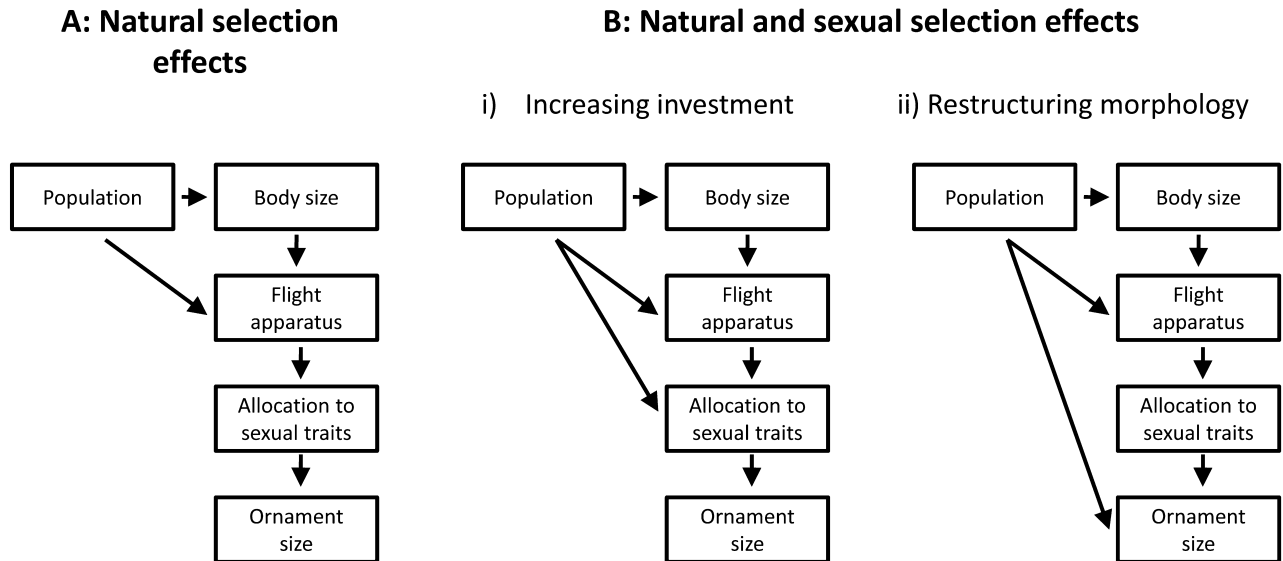
Inter-population differences in ornament size could evolve by natural selection if there is spatial changes in optimal phenotype or variation in general morphology, which in turn may affect secondary sexual traits. In addition, sexual selection could also produce differences in tail length among populations, and this could occur through two processes: by differences in resource allocation to ornaments and/or by differences in the cost of production, which allows for the development of longer ornaments with the use of fewer resources. The first process may occur when populations differ with respect to the costs and benefits of investment in secondary sexual traits (Møller *et al.*, 2006). For example, an increment in size of a secondary sexual character is more costly at low than at high latitude in Europe as a result of the effects of ornament size on capture of prey at different ambient temperatures (Møller, de Lope & López Caballero, 1995). Such variation occurs even within populations when certain individuals tend to spend more resources on ornaments than expected from their phenotypic quality (Candolin, 1999; Muñoz, Aparicio & Bonal, 2008).

The cost of producing ornaments could be altered by restructured morphology (Backwell *et al.*, 2000; Aparicio, Bonal & Cordero, 2003). In birds, interspecific comparisons of feather length and structure have shown that males have evolved the trait chosen by females at the expense of modifying the structure and diverting resources from other components that do not appear to be taken into account by females (Aparicio *et al.*, 2003). We have found variability in feather structure among individuals, even within a

barn swallow (*Hirundo rustica* L.) population, and this variability is repeatable among moults (Muñoz, Aparicio & Bonal, 2011). This implies that some males consistently produce long and heavy feathers, whereas others produce feathers of similar length, although with a much reduced density, implying that males display their size for show rather than as reliable indicators of quality.

The study of spatial variation in phenotype provides a good opportunity for quantifying the selective pressures that drive the evolution of morphological characters, particularly for traits affected by both natural and sexual selection. Classic examples of characters that evolve by sexual selection are long tails of male birds (Andersson, 1982; Møller, 1988). The so-called U-shaped tails, in which the outermost feathers are the longest ones, such as the tail of the barn swallow, are a good model system for analyzing the role of natural and sexual selection on the evolution of characters because their enlargement may have been favoured by sexual selection (Møller, 1988) combined with natural selection to reduce flight costs (Norberg, 1994; Evans & Thomas, 1997; Evans, 1998). Indeed, the relative role of natural and sexual selection for the evolution of long tails has been the subject of intense debate (Møller, 1994; Norberg, 1994; Evans & Thomas, 1997; Evans, 1998; Møller *et al.*, 1998; Barbosa & Møller, 1999; Hedenström & Møller, 1999; Matyjasiak *et al.*, 1999, 2004; Buchanan & Evans, 2000; Cuervo, 2000; Rowe, Buchanan & Evans, 2001; Bro-Jørgensen, Johnstone & Evans, 2007). By contrast to males, females do not obtain any mating advantages from elongated tails but, instead, pay a cost in terms of increased natural selection (Cuervo, de Lope & Møller, 1996, 2003), thus preventing females from evolving tails as long as those in males.

The present study aimed to examine the potential selective forces that drive the evolution of the sexually size dimorphic outermost tail feathers of the barn swallow by comparing individuals from four populations located at different latitudes in Europe, with different climatic conditions and migration distances between breeding grounds and African winter quarters. In theory, inter-population variation in tail feather length could be exclusively determined by causes related to natural selection, such as latitudinal clines in temperature or migration distances that affect body size and size of the flight apparatus (i.e. wings and wing muscles), which, in turn, may affect tail length (Fig. 1A). Alternatively, inter-population variation in ornamental tail feathers could be caused by sexual selection. In this case, if the strength of sexual selection differs among populations, we would expect stronger selection for long-tailed individuals in some populations compared to others, and this selective pressure could lead to two processes: a stron-



**Figure 1.** Hypothetical selective pressures explaining the evolution of ornaments. A, the only effect is a result of natural selection, so the size of the ornament will co-evolve in accordance with the size of the body and/or flight apparatus. After controlling for these effects, there would be no differences among populations in ornament size. B(i), there are differences among populations in the amount of resources invested in ornaments, which are not completely explained by differences in size of the flight apparatus. B(ii) there are differences among populations in ornament size, which are not completely explained by differences in the amount of resources invested in ornaments. Note that scenarios (i) and (ii) may occur simultaneously.

ger selection for higher quality individuals, increasing the amount of resources allocated to sexual characters (Fig. 1B, i), or, alternatively, a modification in the structure of the signal so that the ornament increases in size at the expense of other components not valued by choosy females (Fig. 1B, ii). Therefore, we hypothesized that inter-population differences in tail length could be caused by differences in: (1) body size as reflected by body mass; (2) size of the flight apparatus as reflected by wing length; (3) allocation to ornaments as reflected by feather mass or (4) morphological structure as reflected by feather density (Fig. 1). In a first analysis, we examined whether there is variation among populations in these four factors, and then we tested whether each component could account for variance in tail length among populations. To the best of our knowledge, there has been no previous attempts to assess whether populations differ in these components of morphology for traits that have a double function: sexual attraction and flight performance.

## MATERIAL AND METHODS

Barn swallows are small (approximately 20 g), socially monogamous, semi-colonial passerine birds feeding on insects caught on the wing. Morphology is clearly adjusted to aerial insectivory, as demonstrated by the streamlined body, the long and slender wings,

and the forked tail. Males have much longer tails than females, which have longer tails than juveniles (Møller, 1994).

We collected outermost tail feathers from four barn swallow populations, located at different latitudes in Denmark (57° N), Ukraine (51° N), Italy (45° N), and Spain (39° N). The number of birds sampled was 138, 100, 30, and 218 respectively. In each population, feathers were collected within a radius of 25 km. The Spanish population migrates to West Africa for winter, travelling approximately 3000 km, whereas the Danish and the Ukrainian populations migrate more than 10 000 km to South Africa, and the Italian population is intermediate in terms of migration distance (Ambrosini, Møller & Saino, 2009). Males arrive in Denmark and Ukraine during April and May, whereas females, on average, arrive 1 week later (Møller, 1992). Italian males arrive in April. In Spain, arrival takes place between February and March.

We used mist nets placed in open doors and windows for trapping adult birds during the breeding season. This method is highly efficient during the breeding season. Each adult barn swallow was weighed upon capture to the nearest 0.1 g with a Pesola spring balance. We examined wing and tail feathers and took at least one outermost tail feather from each bird, excluding broken or growing feathers. Wing length was measured on each bird with a ruler to the nearest 0.5 mm. All birds were individually marked with a

numbered aluminium band. Sex was determined by the presence or absence of a brood patch and by the shape of the cloacal protuberance, which is considerably larger in males than in females (Svensson, 1984). Details on field procedures are provided in Møller (1992, 1993, 1995) and Muñoz *et al.* (2008).

The feathers were taken to the laboratory, where they were cleaned and inspected for breakage or damage. Most of the collected feathers were in perfect condition and only a few feathers were excluded as a result of incomplete growth or breakage. Feathers were measured with a calliper (to the nearest 0.5 mm) and weighed with a digital high-precision balance (to the nearest 0.1 mg). Both the length and mass of feathers were measured for 17 females and 14 males twice in nonconsecutive order by different individuals, and measurements showed high repeatability (for all measures on females:  $F_{1,16} \geq 1529$ ,  $r \geq 0.99$ ,  $P < 0.0001$ ; for all measures on males:  $F_{1,13} \geq 2200$ ,  $r \geq 0.99$ ,  $P < 0.0001$ ).

#### STATISTICAL ANALYSIS

We considered body mass to represent a measure of overall body size, wing length to represent a measure of the size of the flight apparatus and the mass of a tail feather to represent a measure of resource allocation to tail feathers. Body mass has a disadvantage compared to other measures, such as tarsus length, that can vary with time of day or breeding state, especially in females. However, tarsus length and other measures of body size have been dismissed as a result of the risk of lack of consistency among the measures taken by different researchers in different populations. In a first general linear model (GLM), we examined whether there were population and sex differences in body mass, wing length, and mass and length of tail feathers. Subsequently, we performed successive GLM analyses to test for a role of each variable, according a hypothesized causal chain (Fig. 1). Sex and population were included as factors in each analysis, as well as the appropriate indepen-

dent variable in each case (as hypothesized in Fig. 1) and the interaction between population and sex. As a result of allometry of continuous morphological variables, these were log-transformed. All analyses were performed with SPSS, version 19 (SPSS, Inc.).

Because there is no significant genetic population structure among populations of barn swallows in Europe (Santure *et al.*, 2010), we can treat populations as statistically independent observations. Any two populations are as different genetically as the two most distant populations in Europe.

## RESULTS

### DIFFERENCES IN MORPHOLOGY BETWEEN SEXES AND POPULATIONS

All morphological parameters that we examined (body mass, wing length, tail feather length, and tail feather mass) differed significantly between sexes and populations. Population explained most of the variance in body mass and wing length, whereas sex was the main factor explaining variance in tail feather characteristics (Table 1). The interaction population  $\times$  sex was only significant for tail feather length, indicating that sexual dimorphism in this trait differed between populations, whereas differences in sexual dimorphism for the other characters among populations did not reach significance (Fig. 2).

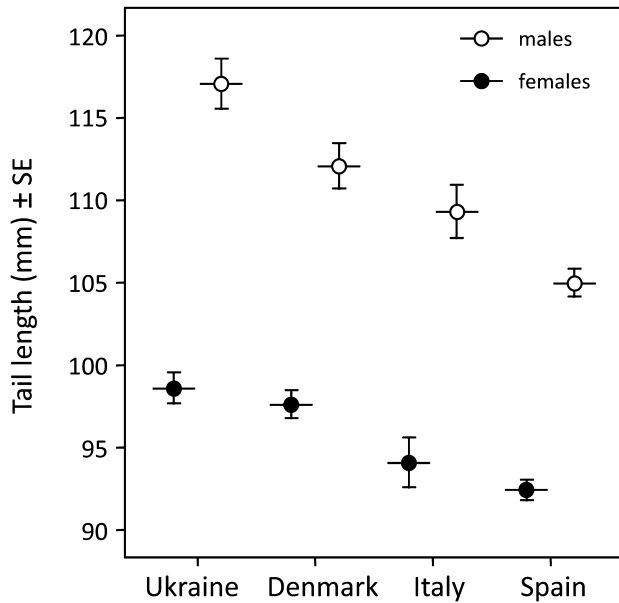
### BODY SIZE

We attempted to explain factors that determine differences among populations in tail length. We examined the effect of body size on tail feather length by performing a GLM similar to that outlined above for tail feather length, at the same time as including body mass as a covariate. The effect of body mass was significant, although the new model only increased by 0.4% in terms of variance explained with respect to the previous model (49.1% versus 48.7%), and a high percentage of the variance in tail length was still explained by population (Table 2).

**Table 1.** General linear model analyses relating several morphological traits to sex, population, and the interaction between sex and population of barn swallows

Trait	<i>N</i>	Sex			Population			Sex $\times$ Population		
		<i>F</i>	<i>P</i>	$\eta^2$	<i>F</i>	<i>P</i>	$\eta^2$	<i>F</i>	<i>P</i>	$\eta^2$
Body mass	480	29.54	< <b>0.0001</b>	0.06	25.58	< <b>0.0001</b>	0.14	1.29	0.28	0.01
Wing length	478	15.89	< <b>0.0001</b>	0.03	72.82	< <b>0.0001</b>	0.32	1.26	0.29	0.01
Tail feather length	481	287.63	< <b>0.0001</b>	0.38	38.21	< <b>0.0001</b>	0.20	3.50	<b>0.02</b>	0.02
Tail feather mass	481	120.81	< <b>0.0001</b>	0.20	29.65	< <b>0.0001</b>	0.16	2.17	0.09	0.01

$\eta^2$  reflects the amount of variance explained by the partial effect of a given variable. Significant *P*-values in bold.



**Figure 2.** Outermost tail feather length (mm; mean  $\pm$  SE) of barn swallows in relation to sex and population.

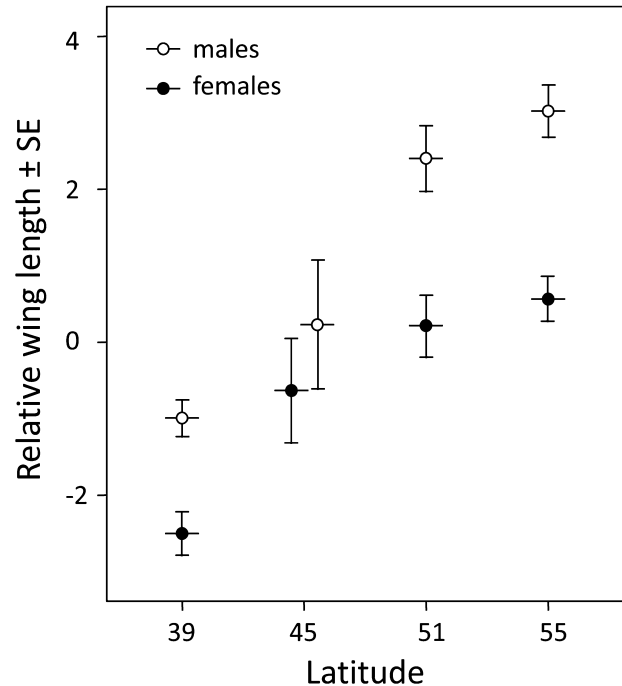
**Table 2.** General linear model analysis relating tail feather length to body mass, population, sex, and the interaction population and sex of barn swallows

	<i>F</i>	d.f.	<i>P</i>	$\eta^2$
Body mass (log)	7.73	1,471	<b>0.006</b>	0.016
Population	28.20	3,471	<b>&lt; 0.0001</b>	0.152
Sex	297.30	1,471	<b>&lt; 0.0001</b>	0.387
Population $\times$ Sex	3.91	3,471	<b>0.028</b>	0.024

$\eta^2$  reflects the amount of variance explained by the partial effect of a given variable. Adjusted  $R^2 = 0.55$ . Significant *P*-values in bold.

#### SIZE OF FLIGHT APPARATUS

Individuals from different populations may differ in the size of their flight apparatus for various reasons. For example, individuals in populations with longer migration distances produce longer wings than individuals with short migration distances (Winkler & Leisler, 1992; Lockwood *et al.*, 1998; Pérez-Tris & Tellería, 2001). A GLM analysis including wing length as dependent variable, sex and population as factors, and body mass as a covariate, showed differences in size of the flight apparatus (measured as wing length) among populations, which are greater than that expected merely from differences in body size (Table 3, Model A). A second GLM analysis controlling for body mass and sex, and including latitude rather than population, showed that relative wing length indeed did increase with latitude (Fig. 3, Table 3, Model B).



**Figure 3.** Mean  $\pm$  SE relative wing length after controlling for body mass, according to Model B in Table 3, in the two sexes of barn swallows breeding at different latitudes.

**Table 3.** General linear model analyses relating wing length to body mass, population, sex, and the interaction population and sex of barn swallows (Model A); Model B includes latitude rather than population

	<i>F</i>	d.f.	<i>P</i>	$\eta^2$
Model A: Adjusted $R^2 = 0.36$				
Body mass (log)	13.36	1,468	<b>0.0003</b>	0.028
Population	56.01	3,468	<b>&lt; 0.0001</b>	0.264
Sex	22.38	1,468	<b>&lt; 0.0001</b>	0.046
Population $\times$ Sex	1.14	3,468	0.33	0.007
Model B: Adjusted $R^2 = 0.36$				
Body mass (log)	16.91	1,473	<b>&lt; 0.0001</b>	0.035
Sex	45.20	1,473	<b>&lt; 0.0001</b>	0.087
Latitude	164.75	1,473	<b>&lt; 0.0001</b>	0.258

$\eta^2$  reflects the amount of variance explained by the partial effect of a given variable. Significant *P*-values in bold.

#### ALLOCATION OF RESOURCES TO ORNAMENTS

The lengthening of tail feathers could simply follow the elongation of the wings for aerodynamic reasons or optimal resource allocation (regardless of sexual selection). If so, we would expect a positive correlation between the amounts of resources allocated to different parts of the flight apparatus (wing and tail). Moreover,



**Table 4.** General linear model analysis relating tail feather mass to wing length, population, sex, and the interaction population and sex of barn swallows

	<i>F</i>	d.f.	<i>P</i>	$\eta^2$
Wing length (log)	120.99	1,469	< <b>0.0001</b>	0.205
Population	5.78	3,469	<b>0.001</b>	0.036
Sex	104.32	1,469	< <b>0.0001</b>	0.182
Population $\times$ Sex	1.27	3,469	0.28	0.008

$\eta^2$  reflects the amount of variance explained by the partial effect of a given variable. Adjusted  $R^2 = 0.50$ . Significant *P*-values in bold.

if the allocation rules were the same for all populations, we should expect the variance in wing length to explain the variance in tail mass, thereby eliminating any population effects. A GLM analysis including tail feather mass as dependent variable, sex and population as factors, and wing length as covariate, showed that wing length and sex accounted for most of the variance in tail feather mass. However, the effect of population was still significant (Table 4), indicating the existence of population differences in allocation rules. At equal wing length, tail feather mass decreased from Ukraine to western populations in Spain (Fig. 4).

#### MORPHOLOGICAL STRUCTURE

Another factor that may explain variation in tail length among populations is the structure of tail feathers. Morphological structure of feathers could be modified so that longer feathers would not cause additional production costs, whereas maintenance costs could be similar to that of other individuals with equal tail length. The length/cost ratio is the so-called signalling rule in general signalling theory (Grafen, 1990a; Aparicio *et al.*, 2003; Muñoz *et al.*, 2011). If all populations use the same rule of signalling, we should expect no population effect on the length of tail feathers after controlling for feather mass, individual body size, and wing length. However, we found that population continued to have a significant effect on feather length after controlling for the previously listed independent variables (Table 5). Differences among populations arose because, at equal feather mass, some populations produced longer feathers than the others (Fig. 5).

#### DISCUSSION

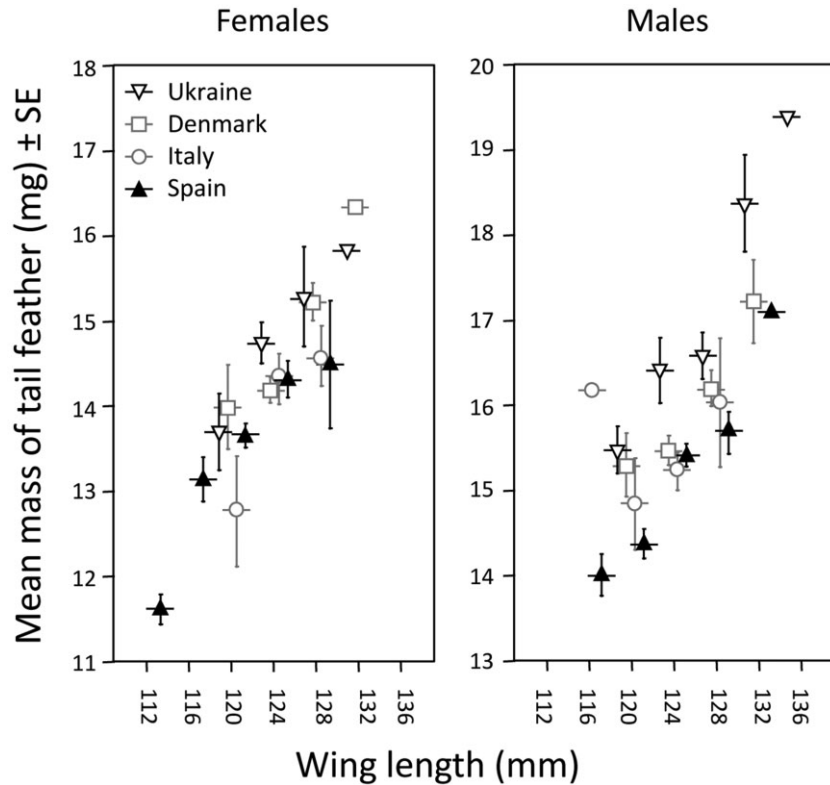
We examined factors accounting for differences in the outermost tail feathers of four European barn swallow populations. Tail length is a morphological

**Table 5.** General linear model analysis relating tail feather length to body mass, wing length, feather mass, population, sex, and the interaction population and sex of barn swallows

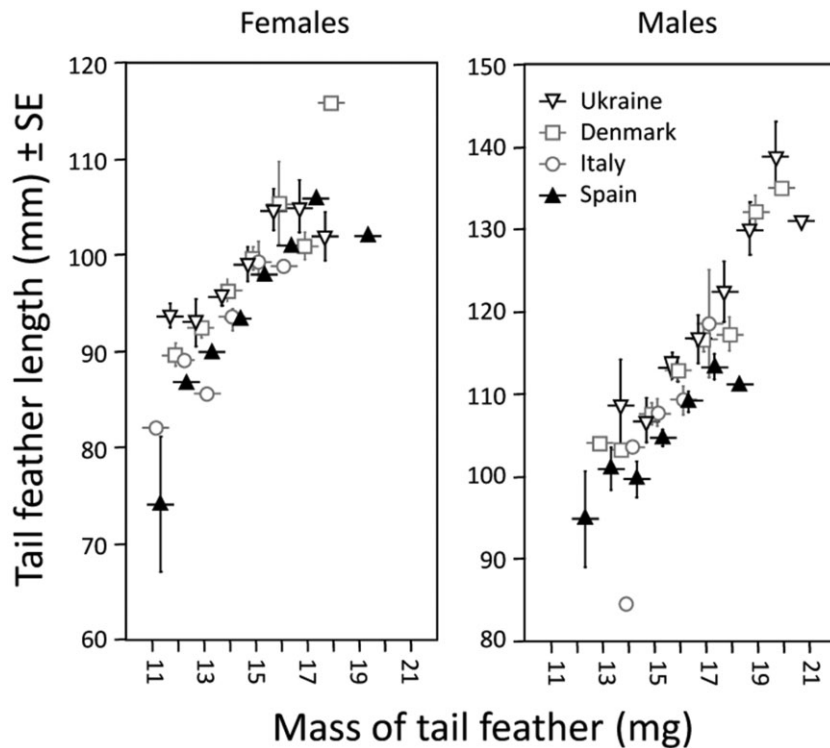
	<i>F</i>	d.f.	<i>P</i>	$\eta^2$
Body mass (log)	0.74	1,466	0.39	0.002
Wing length (log)	7.02	1,466	<b>0.008</b>	0.015
Feather mass (log)	216.29	1,466	< <b>0.0001</b>	0.317
Sex	119.87	1,466	< <b>0.0001</b>	0.205
Population	3.63	3,466	<b>0.013</b>	0.023
Population $\times$ Sex	0.79	3,466	0.50	0.005

$\eta^2$  reflects the amount of variance explained by the partial effect of a given variable. Adjusted  $R^2 = 0.72$ . Significant *P*-values in bold.

character that serves to aid flight manoeuvrability, improve stability, and enhance lift generation at low flight speeds (Thomas, 1993; Norberg, 1994; Maybury & Rayner, 2001; Maybury, Rayner & Couldrick, 2001; Hedenström, 2002). Moreover, it is a secondary sexual trait that reflects male attractiveness because females choose long-tailed males for mating and extra-pair copulations (Møller, 1988, 1994). Thus, there has been intense debate on whether variation in ornament size simply reflects variation in the size of the underlying naturally selected optimum trait value (Norberg, 1994; Evans & Thomas, 1997; Evans, 1998) or include variation in the degree of sexually selected exaggeration (Møller, 1994; Møller *et al.*, 1998; Barbosa & Møller, 1999; Hedenström & Møller, 1999). As in previous studies, we found that tail feather length differed between sexes and populations (Møller, 1994). Our results showed that population differences were associated with differences in body size, the size of the flight apparatus, resource allocation between wing and tail feathers, and tail feather structure. The elongation of the tail associated with an increment in body size and the size of the flight apparatus appears to be related to natural selection because a larger size of the body or the flight apparatus would require a larger tail for maintenance of flight performance. However, tail elongation through allocation of more resources to its production than expected from the length of wings, as well as the modification of tail feather structure appears to be a consequence of sexual rather than natural selection. This is because longer tails made of more slender feathers can break more easily than more robust feathers (Møller, 1989; Barbosa & Møller, 1999). Indeed, this weakening of structure does not improve the bearer's flying ability but enhances male attractiveness to females if the resources saved by production of more slender feathers are re-allocated to



**Figure 4.** Tail feather mass (mg; mean  $\pm$  SE) in relation to sex, population and wing length (mm) of barn swallows. Individuals were grouped by wing length.



**Figure 5.** Tail feather length (mm; mean  $\pm$  SE) in relation to sex, population and tail feather mass (mg) of barn swallows. Individuals were grouped by tail feather mass.

produce longer tails. In agreement with this finding, inter-specific comparisons also showed that the enfeeblement of ornamental feathers was positively related to the increment of sexual dimorphism in a phylogenetic comparison of 36 bird species (Aparicio *et al.*, 2003). Therefore, these results are consistent with the idea that tails are the product of both natural and sexual selection, and that sexual selection is responsible for part of the difference in tail length among populations (Møller *et al.*, 1998).

The two phenomena of tail elongation shown in this study, by producing either large feathers with low density of keratin or higher resource allocation, suggest different modes of sexual selection. On the one hand, increased resource allocation to ornamental traits is what we should expect if the evolution of characters occurs through a process of good genes, through which the ornaments are becoming more costly to produce and maintain (Zahavi, 1975, 1977; Grafen, 1990b; Iwasa, Pomiankowski & Nee, 1991). By contrast, a reduction in density of feathers allows a reduction in production costs and (at equal investment) increases the length of the feather (Fig. 5). That is, they increase the level of signalling but not the quality of feathers. We should recognize that, at the beginning of these processes of cost reduction, pioneer individuals reducing feather density would signal above the level expected for their condition only, and then their ornament would reflect signalling capability rather than the quality of the individual as expected for a Fisherian process (Fisher, 1958; Lande, 1981; Kirkpatrick, 1982; Pomiankowski, Iwasa & Nee, 1991). Given that such long feathers are also preferred by females and this extra enlargement does not convey reliable information on male quality, we consider that the process of tail enlargement through cost reduction is a Fisherian rather than a Zahavian process. However, a reduction in the cost of producing ornaments does not imply the end of the handicap signalling process because the handicap can also operate with low cost signals whenever these are condition-dependent (Getty, 1998) and, once the new signalling rule has spread in the population, the system can function again as a Zahavian process.

A Fisherian process was also argued by Bro-Jørgensen *et al.* (2007) after examining the prey size and manoeuvrability of male barn swallows exposed to different tail shortening treatments because the extent of tail feathers beyond the optimum size (attributed to sexual selection) did not vary among males and was independent of original tail length. However, they excluded the existence of a mixed process of sexual selection probably because their experimental methodology did not allow alternative results (Aparicio & Møller, 2012).

The co-existence of these two modes of evolution of secondary sexual traits in a single species supports the hypothesis of a mixed process that includes stages of honest signalling followed by stages in which a new and better advertising rule of signalling may extend in the population as a Fisherian process of sexual selection (Aparicio *et al.*, 2003). The joint evolution (apparently so different) is possible because mating with ornamented males has benefits for females, in the form of both viability of offspring and attractiveness of sons (Kokko *et al.*, 2002).

Variability in the amount of resources allocated to secondary sexual characters has also been observed within single populations (Candolin, 1999), including a Spanish barn swallow population (Muñoz *et al.*, 2008), in which each male allocates a different proportion of resources to ornamental feathers in relation to wing length, and these differences in resource allocation within a single individual are repeatable across moults among years. Similarly, there were individual differences among males (and to a lesser extent also among females) in the structure of their tail feathers within this population (Muñoz *et al.*, 2011). Hence, some individuals appear to grow longer feathers than others with the same amount of resources thus producing large but fragile structures. The existence of variability in investment of resources in feathers or larger size of feathers within a single population suggests that there may still be potential for selection and evolution of these traits if their variability has a genetic basis, as shown by parent-offspring resemblance and animal models (Møller, 1994; Teplitsky *et al.*, 2011).

The two mechanisms of elongation of the tail associated with sexual selection were significantly affected by sex, although not by the interaction between sex and population (Tables 4, 5), probably because the variability in resource allocation and signalling rules in females is lower than in males (Muñoz *et al.*, 2008, 2011). These results support the idea that selection on a character in one sex causes not only a direct response for the character in the selected sex, but also a correlated response for the homologous character in the other sex (Lande, 1980; Møller, 1993; Cuervo *et al.*, 1996, 2003).

It is also interesting to note that the effects of both natural and sexual selection on tail length appear to be parallel, because the two mechanisms of elongation of the tail associated with sexual selection are more pronounced in populations where natural selection has selected for large body mass and long wings. This parallelism could occur (1) because a larger body size allows greater opportunity for exaggeration of sexual traits or (2) because both natural and sexual selection are subject to similar constraints imposed by latitudinal clines (Møller *et al.*, 1995). The



amount of variation in resource allocation (Table 4) and feather density (Table 5) explained by the population factor is small in relation to variation in wing length (Table 3) or body mass (Table 1), suggesting that geographical differences in morphology caused by natural selection could be much stronger than those promoted by sexual selection.

Correlations between size and sexual dimorphism are common in the animal kingdom. For example, Rensch's rule suggests that sexual size dimorphism decreases with size when females are the larger sex, although it increases with size when males are the larger sex (Rensch, 1950; Fairbairn, 1997). This pattern can be explained by the interaction between the form and strength of sexual selection acting on each sex in relation to body size. In species with elaborate male aerial displays, the two components of sexual selection that appear to determine this pattern are the intensity of sexual selection acting on males and the agility of the males' display (Székely, Freckleton & Reynolds, 2004; Raihani *et al.*, 2006; Dale *et al.*, 2007). This hypothesis could also explain variation in size dimorphism among barn swallow populations if aerial displays during courtship decrease with latitude in favour of more static displays.

As for the question whether natural and sexual selection are subject to similar latitudinal clines, there are two obvious mechanisms that can explain the latitudinal cline that favours longer tails at higher latitudes by natural selection: the positive relationship of body size and migration distance with latitude selects for greater investment in the flight apparatus in northern compared to southern populations. The question that arises is why sexual selection should be stronger at higher latitudes. We hypothesize that decreases in the duration of the mating season at higher latitude may impose a latitudinal cline in strength of sexual selection (Møller *et al.*, 2006). This could occur in migratory species because the time elapsed from arrival to breeding decreases with latitude, and there is strong pressure to breed at the beginning of the season given that breeding date largely determines the fitness of parents and their offspring in a wide variety of organisms (Perrins, 1970; Brinkhof, Cave & Perdeck, 1997; Svensson, 1997). In Spain, barn swallows arrive up to two months before egg-laying (Gordo, Sanz & Lobo, 2007; Balbontín *et al.*, 2009), whereas, in Denmark, the earliest pairs barely spend approximately 2 weeks before breeding just to prepare the nest and produce eggs (Møller, 1992, 1994). In the north, it is essential to arrive at the breeding area as soon as environmental conditions allow the acquisition of a mate in the shortest possible time. A long tail is not a great problem for travelling long distances at high speed because tails can be furled to minimize drag (Heden-

ström, 2002), whereas it confers a clear advantage for mating (Møller, 1988; Møller & Tegelström, 1997; Saino *et al.*, 1997). Because females have less time to choose, males should highlight the differences in their signal with respect to other males even more than when the time for mating is longer. Therefore, the strength of sexual selection should increase with latitude even when the potential number of females obtained by a male remains constant. Alternatively, although the Spanish population only migrates 3000 km to West Africa, the Danish and the Ukrainian populations migrate more than 10 000 km to South Africa, and the Italian population is intermediate in terms of migration distance. Long-distance migration can be considered a test of endurance, especially if accompanied by a handicap such as the long outermost tail feathers of a male barn swallow. The Spring arrival date of barn swallows at the breeding grounds is strongly negatively correlated with tail length (long-tailed individuals arrive the earliest), although only in males, and more so in Danish than in Italian or Spanish barn swallows (Møller, de Lope & Saino, 2004). Such an earlier arrival is related to body condition, parasitism, and immunocompetence, implying that early arriving individuals indeed are in better condition.

In conclusion, we have shown that variation in length of ornamental tail feathers among barn swallow populations is a result of the effects of both natural and sexual selection because a larger body and flight apparatus are positively associated with longer tail feathers in northern populations that have longer migration distances. In addition, sexual selection acts by increasing investment in ornaments and modifying feather structure to produce longer feathers of lower density for a given length of feather. These two mechanisms of sexual selection are consistent with an evolutionary mixed process, in which females may obtain different indirect benefits from their mate choice.

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