SHORT COMMUNICATION

Viability and expression of sexual ornaments in the barn swallow *Hirundo rustica*: a meta-analysis

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Abstract

Sexual selection results in the evolution of exaggerated secondary sexual characters that can entail a viability cost. However, in species where sexual ornaments honestly reflect individual quality, the viability cost of secondary sexual characters may be overwhelmed by variation in individual quality, leading to expect that individuals with the largest secondary sexual characters show higher, rather than lower viability. Here, we used meta-analyses to test whether such expected positive relationship between sexual ornamentation and viability exists in the barn swallow *Hirundo rustica*, which is one of the most studied model species of sexual selection under field conditions. We found a mean positive effect size of viability in relation to the expression of secondary sexual characters of 0.181 (CI: 0.084–0.278), indicating that in this species the more ornamented individuals are more viable, and therefore of high quality. Analyses of moderator variables showed similar effects in males and females, the *H. r. rustica* subspecies rather than others and tail length rather than other secondary sexual characters. Future research emphasis on other subspecies than the European one and secondary sexual characters than tail length may help identify the sources of heterogeneity in effect sizes.

Introduction

Sexual selection is the process arising from competition among individuals of one sex, usually males, for access to individuals of the sex that limits reproduction, usually females (Andersson, 1994). Already Darwin (1871) noticed that males seem to benefit from displaying exaggerated secondary sexual characters in a sexual selection context despite the fact that such characters can be costly to produce and/or maintain. The evolution of extravagant sexual ornaments is therefore expected to exact a viability cost, as suggested by comparative analyses showing higher mortality in species in which the intensity of sexual selection is larger (Promislow, 1992; Promislow *et al.*, 1992; Liker & Szekély, 2005). However, many intraspecific studies reported exactly the opposite pattern, with individuals bearing larger ornaments also

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showing higher survival (Alatalo *et al.*, 1991; Hill, 1991; Møller, 1991; Kotiaho *et al.*, 1999; Török *et al.*, 2003; Hasegawa *et al.*, 2014). Should there be a positive or a negative correlation between expression of secondary sexual characters and survival?

In species where sexual ornaments are subject to pure Fisherian processes (Lande, 1981), that is when traits are preferred for entirely arbitrary reasons, more attractive individuals should pay a larger cost in terms of survival because they are more exposed to predators, subjected to parasite infections and have to devote a considerable amount of their limited energetic resources to produce sexual displays (reviewed in Kotiaho, 2001). Under such circumstances, a negative relationship between longevity or survival and the expression of sexually selected characters should thus be predicted (e.g. Godin & McDonough, 2003). On the other hand, in species in which sexually selected traits honestly signal individual quality and/or condition, individuals of the competing sex can modulate their investment in ornaments in relation to their ability to sustain the costs associated with the expression of those traits. In

this case, as predicted by the handicap principle (Zahavi, 1975; Grafen, 1990; Johnstone, 1995), individuals in prime condition are able to sustain the large costs of developing extravagant secondary sexual characters. When the expression of secondary sexual characters is condition-dependent, a positive covariation between viability and increased ornamentation should thus be expected (e.g. Møller, 1991; Jennions *et al.*, 2001; but see Kokko, 2001). In addition, we should also expect that individuals in better condition are better able to sustain the costs of experimental exaggeration, as shown in tail manipulation experiments on barn swallows (*Hirundo rustica*; Møller & de Lope, 1994) and other species (Murai *et al.*, 2009). In summary, the relationship between viability and the expression of sexually selected traits is expected to depend on the mode of evolution of the ornaments.

More complex are the cases of species displaying multiple sexually selected traits, which can be selected through different modes of sexual selection (Møller & Pomiankowski, 1993; Pomiankowski & Iwasa, 1993; Candolin, 2003). The relationship between survival and ornamentation can therefore vary depending on the ornament under scrutiny. In addition, in polymorphic species showing geographical variation in sexual selection, we might also expect a difference in the relationship between survival and expression of sexually selected traits among geographical populations/subspecies. However, to the best of our knowledge, these predictions have never been tested in any species.

In the present study, we quantified effect size of the expression of secondary sexual characters on viability in the barn swallow. This species has become a model system for studies of sexual selection, and a large number of studies about the fitness consequences of the expression of different plumage ornaments have been published (Møller, 1994; Turner, 2006; Scordato & Safran, 2014; Romano *et al.*, 2017). Such a large number of studies, carried out in some geographical subspecies, allows for robust estimation of predictions from sexual selection and for generation of novel hypotheses (Romano *et al.*, 2017). Here, we extracted effect sizes from the literature in order to quantify the magnitude and the direction of the relationship between the expression of different plumage ornaments and survival. In addition, as sexual selection has been suggested to vary according to subspecies and sexually selected character (Scordato & Safran, 2014; Romano *et al.*, 2017), we also attempted to assess whether effect sizes vary among subspecies or plumage ornaments.

Materials and methods

Literature survey and database preparation

We considered the published studies where survival was tested in relation to the expression of six sexually dimorphic characters which have been suggested to be under sexual selection in at least one of the barn swallow subspecies (see Romano *et al.*, 2017 for details): tail length, tail asymmetry, size of white spots on the tail, ventral plumage colour, throat plumage colour, and throat colour patch size. We first collected all papers (including associated supplementary results) focusing on the relationship between survival and these plumage traits that were published in scientific journals before 21 April 2017. In-depth details about literature screening and selection of the studies are provided in Romano *et al.* (2017). For the purpose of the present study, we searched on Scopus, Web of Science and Google Scholar the combination of the key words 'barn swallow' or '*H. rustica*' with any one of the following: 'tail', 'colo*r', 'plumage' or 'feather*', 'ventral', 'belly', and 'throat', as well as with and 'survival' or 'viability' (Fig. S1). We included information about both annual survival (e.g. probability to survive from one breeding season to the next) and survival during the breeding season (e.g. survival from predators and severe weather; Fig. S1). We emphasize that in our model species, both breeding dispersal and emigration from one breeding site to another are extremely rare (Møller, 1994; Turner, 2006). Considering that all the studies included in the analyses have been performed during the breeding season, the effects of dispersal and emigration on individual survival are therefore virtually absent.

Statistical relationships where plumage ornaments were hypothesized to determine survival were included, irrespective of how the test was designed. The results of analyses where survival was predicted by any of the aforementioned plumage ornaments (e.g. survival probability according to tail length) as well as analyses testing for differences in ornament expression between groups of individuals with different survival prospect (e.g. tests comparing tail length of survivors vs. nonsurvivors) were therefore included. As in Romano *et al.* (2017), tests of the potential costs of ornaments (e.g. annual survival after manipulation of tail length) were not considered (Fig. S1).

For each statistical relationship, we recorded information on (i) sex (male, female or both sexes) of individuals to which the data referred; (ii) plumage ornament; (iii) barn swallow subspecies on which the study was performed; (iv) sample size; and (v) year(s) when the study was performed. All statistical effects were converted into Fisher's Z (Z_r) using standard formulae (Rosenberg *et al.*, 2000; Nakagawa & Cuthill, 2007; Koricheva *et al.*, 2013; see Romano *et al.*, 2017 for details). The direction (sign) of each value of Z_r was assigned based on the sign of the relationship between the expression of plumage ornaments and survival. In practice, a positive sign was assigned in case of positive relationship between ornaments and survival (but a 'negative' one was assigned for tail asymmetry; see Romano *et al.*, 2017 for details).

When different studies reported information on the relationship between a plumage ornament (e.g. tail length) and the same proxy of survival (e.g. survival from 1 year to the next) in the same group of individuals (e.g. same study area during the same years), only the effect size based on the largest sample size was included in the analyses (Fig. S1).

In total, 46 effect sizes from 20 different studies performed on three barn swallow subspecies (the European *H. r. rustica*, the North American *H. r. erythrogaster*, the Asian *H. r. gutturalis*) were retrieved. However, since one of the aims of the present study was to test for possible differences between survival and expression of plumage ornaments in different barn swallow subspecies, only plumage ornaments for which information was available for at least two subspecies were considered for the analyses (Fig. S1). This procedure resulted in the removal of three effect sizes referring to ventral colour and throat patch size, because information on survival according to these plumage ornaments was available for only one subspecies. At the end of this step, the number of effect sizes suitable for meta-analyses was 43 from 19 different studies (Table S1), concerning tail length, tail asymmetry, white spots on tail and throat colour. However, we note that the vast majority of the database was based on tail length and on the *H. r. rustica* subspecies.

Meta-analyses

Some of the studies included in the database reported multiple effect sizes (e.g. effect of tail length on survival of males and females in the same population). Therefore, we accounted for nonindependence of effect sizes by adopting the random effects hierarchical linear mixed (HLM) modelling approach proposed by van den Noortgate *et al.* (2013, 2015; see Musitelli *et al.*, 2016 and Romano *et al.*, 2017 for details). Variation in effect size weighted by (sample size − 3) was analysed in models including two random effects: 'study ID', which accounts for nonindependence of multiple effect sizes obtained from the same study, and 'effect size ID' nested within 'study ID', while assuming equal variances among studies (van den Noortgate *et al.*, 2013, 2015). In addition, in all models, residual variance was constrained to be equal to one (van den Noortgate *et al.*, 2013, 2015).

We firstly investigated whether mean effect size of survival according to plumage ornaments differed significantly from zero by running an HLM model including only the intercept as a predictor (van den Noortgate *et al.*, 2013). In this model, effect sizes of different barn swallow subspecies were considered together. Secondly, we ran separate HLM models including the different fixed effects (i.e. sex, subspecies and plumage ornament) as moderators to test for differences in effect size

according to sex, subspecies (*H. r. rustica*, *H. r. erythrogaster*, *H. r. gutturalis*) and plumage ornament (tail length, tail asymmetry, white spots on tail, throat colour). An additional analysis including all the moderators simultaneously was also performed to test for the effect of any variable while accounting for the effects of the others. The few effect sizes referring to data of both sexes pooled were omitted from the analyses in which 'sex' was used as a predictor.

The expression of plumage ornaments is larger in males than in females, and the intensity of sexual selection differs between the sexes (Andersson, 1994; see also Romano *et al.*, 2017). All the analyses were also run on data on males only, whereas we did not perform analyses on data on females only due to the small sample size.

Analyses were carried out with the SAS 9.3 PROC MIXED (SAS Institute Inc., Cary, NC, USA) by using a restricted maximum-likelihood (REML) estimation procedure, while degrees of freedom were set with the Satterthwaite approximation. Mean effect sizes and their 95% confidence interval (CI) for different levels of each moderator variable and their difference from zero were computed using the models including the moderator as a fixed effect. Because large heterogeneity of variances was observed between different levels of the moderators (e.g. among different plumage ornaments), we allowed for heterogeneity of variances at both levels of random effects by using the GROUP option in the RANDOM statement. Using these settings, estimated marginal means from the HLM models provided by the LSMEANS statement are identical to the mean estimates obtained from separate meta-analyses for each level of a moderator including only the intercept effect (see Musitelli *et al.*, 2016 for details).

Publication bias analyses

Publication bias was checked using different indirect tests. First, we calculated the Rosenthal fail-safe number (i.e. the number of studies with effect size equal to zero that are required to make the mean effect size not significantly different from zero; Rosenberg *et al.*, 2000). Second, we estimated the Egger regression to test for asymmetry in the distribution of data (Egger *et al.*, 1997). Third, we performed a trim-and-fill test, assuming that in the absence of publication bias, a plot of effect sizes on sample sizes should be symmetric around the 'true' effect size (Duval & Tweedie, 2000a, b). Therefore, we estimated the number of apparently 'missing' data on the side of relatively small effect sizes for the distribution of effect size on sample size (i.e. left side of the funnel plot; Duval & Tweedie, 2000a, b). Finally, we measured the heterogeneity in effect sizes, using the parameter I^2 (Higgins *et al.*, 2003), which represents the proportion of observed variation in the data that is not attributable to random error, and spans

between 0% and 100%, with larger values indicating increasing heterogeneity (Higgins *et al.*, 2003). Publication bias and heterogeneity analyses were run using the *metafor* library (Viechtbauer, 2010) in R 3.2.1 (R Core Team, 2014).

Results

The overall mean effect size of the association between the expression of plumage ornaments and survival was $Z_r = 0.181$ (CI = 0.084–0.278; $N = 43$ effect sizes; Table 1). Despite that the biological effect was not large (Cohen, 1988) and accounted for approximately 2–3% of total variance, this value was significantly larger than zero.

The effect sizes of plumage ornaments on survival of males were medium and significantly larger than zero, while that was not the case for females (Table 1). However, mean effect size did not differ significantly between males and females ($F_{1,14.2} = 2.54$, $P = 0.13$). In addition, mean effect sizes were very similar among the three subspecies included in the analyses (Table 1; $F_{1,2} = 0.00$, $P = 0.99$). Nevertheless, only the mean value for *H. r. rustica* was significantly larger than zero, probably due to the small sample size available for the remaining subspecies. A similar result was obtained for the effect of plumage ornament. Indeed, despite the mean Z_r of all but one (i.e. white spots) plumage ornament was between 0.16 and 0.21, only the value for tail length differed significantly from zero (Table 1). No significant difference in mean effect size among plumage ornaments was thus observed (Table 1; $F_{1,3} = 1.07$, $P = 0.59$).

Qualitatively similar effect sizes were obtained when the analyses were limited to data on males only (Table S2). In addition, no significant effect of any moderator variable was detected when all the moderators were simultaneously included in the models (sex: $F_{1,34} = 3.62$; $P = 0.07$; subspecies: $F_{2,10} = 0.01$; $P = 0.99$; plumage ornament: $F_{3,32.1} = 1.00$; $P = 0.41$).

Rosenthal's fail-safe number associated with the mean effect size was large (2849 studies). In addition, the trim-and-fill test did not reveal the presence of any 'missing' study (mean ± SE: 0 ± 3.315) on the left side of the distribution of mean effect size on sample size. Moreover, Egger regression testing the symmetry of the funnel plot of all the effect sizes indicated that no significant asymmetry occurred in the distribution of data included in the analyses ($Z = -0.48$, $P = 0.63$). To conclude, these results indicate no publication bias in our data. However, there was large heterogeneity in effect sizes across the entire data set ($I^2 = 88.45\%$; Cochran test for heterogeneity: $Q = 606.20$, d.f. = 42, $P < 0.0001$).

Discussion

We estimated the direction and the magnitude of the relationship between survival and the expression of secondary sexual characters in the barn swallow. The small overall estimate of 0.181 was statistically larger than zero and was also significant for males alone, the *H. r. rustica* subspecies alone and for tail length and marginally so for asymmetry in tail length. Finally, we found considerably heterogeneity among estimates implying that one or more undetected factors accounted for variation in effect sizes. These findings were robust, as shown by indirect tests of publication bias.

Overall, our findings indicate that individual barn swallows displaying more exaggerated plumage ornaments are more viable therefore suggesting that the more ornamented individuals are of high quality. Males, and to a smaller extent females, showing exaggerated plumage ornaments therefore accrue fitness advantages both in terms of reproduction (Romano *et al.*, 2017) and in terms of survival (present study). In addition, a comparison of the mean effect in relation to the expression of the same sexually selected traits computed for different phases of the breeding season (see

Table 1 Meta-analyses of the relationship between survival and the expression of secondary sexual characters in the barn swallow. The number of effect sizes (N), mean effect size (Z_r) weighted by their variance (equal to sample size – 3), standard error (SE), *t*-value, degrees of freedom (d.f.), 95% confidence interval, and *P*-values are reported. The analyses were performed by considering all studies ('all') and separately for males or females, for different subspecies and plumage ornaments.

Effect	N	Z_r	SE	t	d.f.	95% CI	P
All	43	0.181	0.045	4.00	14.4	0.084 to 0.278	0.001
Males	26	0.229	0.066	3.46	11.5	0.084 to 0.374	0.005
Females	15	0.085	0.062	1.38	4.76	−0.076 to 0.246	0.23
H. r. rustica	34	0.190	0.056	3.38	11.2	0.066 to 0.314	0.006
H. r. erythrogaster	6	0.184	0.126	1.46	1	−1.415 to 1.782	0.38
H. r. gutturalis	3	0.118	1.002	0.12	1	−1.906 to 2.142	0.91
Tail length	26	0.207	0.058	3.56	12.1	0.081 to 0.334	0.004
Tail asymmetry	12	0.162	0.078	2.09	14.4	−0.004 to 0.328	0.05
White spots on tail	3	−0.031	0.122	−0.26	1	−1.586 to 1.523	0.82
Throat colour	2	0.202	0.108	1.87	1	−1.168 to 1.572	0.31

fig. 5 in Romano *et al.*, 2017) with that of the present study revealed a high degree of overlap of confidence intervals. This overlap implies that the benefits of sexual selection in terms of early breeding, mating success, sperm competition, fecundity, parental care and offspring quality do not statistically differ from the benefits from large viability in this species. Since in the barn swallow ornament expression is heritable (Møller, 1994; Saino *et al.*, 2013; Hubbard *et al.*, 2015; Vortman *et al.*, 2015), mating with a highly ornamented individual can therefore confer indirect fitness benefits to both males and females by producing a progeny which should be more attractive with a larger reproductive success in any single breeding season and also more viable with the possibility to breed for a larger number of breeding seasons. Therefore, our results suggest that the sexually selected traits considered here currently act as honest signals of individual quality and of 'good genes' and that the fitness benefits obtained by mating with highly ornamented individuals should favour the maintenance of these traits. However, it is important to note that the current association between trait expression and individual quality does not necessarily imply that plumage ornaments initially evolved as honest signals of quality. Indeed, a trait initially evolved through a Fisherian process could become a condition-dependent trait with time (Rowe & Houle, 1996; Kokko, 2001; Prum, 2010). Our findings should thus be considered with this caveat in mind.

Our results also show very similar mean effect sizes among different subspecies and plumage ornaments, thus suggesting a highly consistent association between survival and sexual selection in geographically different subspecies and sexually selected traits. However, we note that the present study was mainly based on tail length and *H. r. rustica*, whereas there were few estimates of effect size for other secondary sexual characters and subspecies. The very small sample size available for the other subspecies and plumage ornaments might therefore have obscured existent, maybe weak differences. More importantly, the present database prevented us from testing for the interaction effect between subspecies and plumage ornament. This is unfortunate because previous studies suggested that the intensity of sexual selection on different plumage ornaments varies among subspecies (Scordato & Safran, 2014; Romano *et al.*, 2017). Future targeted studies of barn swallows may therefore considerably help alleviate this large variation in sampling effort, and explain some of the heterogeneity of the relationship between effect size and moderator variables.

The findings reported here can be also compared with a number of estimates from the literature that help us relativize the magnitude of the statistical effects. The mean effect size reported in the present study compares well with the estimate of 0.084 (95% CI 0.068–0.099) from the meta-analysis by Jennions *et al.* (2001) focused

on viability in relation to secondary sexual characters in vertebrates. The 95% CIs of the two studies overlap, although the mean estimate from the present study was almost twice that from Jennions *et al.* (2001). However, the estimate from Jennions *et al.* (2001) for birds was only 0.066 (95% CI 0.049–0.084), therefore, indicating that the association between survival and sexual ornamentation in the barn swallow seems to be particularly large compared to bird species in general. The estimate from the present study can also be compared with viability in the next generation, which is an estimate of the effect of good genes (Møller & Alatalo, 1999). That study reported a very similar effect size of 0.122 (95% CI 0.085–0.159) that largely overlaps with the estimate from the present one, suggesting again that sexually selected traits in the barn swallow can be considered honest signals of individual quality (i.e. of 'good genes'). Finally, Møller (1999) estimated a mean effect size of 0.248 (95% CI 0.226–0.267) for viability linked to asymmetry, which is considerably larger than any of the other aforementioned estimates. From all these comparisons, we can conclude that the relationship between survival and the expression of secondary sexual characters is robust and accounts on average for a small effect. Interestingly, the mean effect size weighted by sample size was very similar for the phenotypic relationships (Jennions *et al.*, 2001; present study) and for the genetic relationships across generations (Møller & Alatalo, 1999). This implies that phenotypic associations can be reliable indicators of genetic relationships.

In conclusion, we have shown a small but robust positive effect size for the relationship between survival and the expression of secondary sexual characters in the barn swallow, suggesting that more ornamented individuals benefit from higher viability. However, large heterogeneity in effect size implies that one or more undetected factors account for variation in effect size. Future research emphasis on subspecies other than *H. r. rustica* and secondary sexual characters other than tail length may help identify the sources of such heterogeneity.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1 Flow chart illustrating the different steps of the data file preparation: (a) exclusion of studies on the barn swallow not focused on plumage ornaments; (b) exclusion of studies not focused on survival; (c) exclusion of studies focused on the costs of plumage ornaments (e.g. annual survival after manipulation of tail length), of studies focused on plumage ornaments for which information was not available for at least two subspecies, and of studies including the same information of another study but performed on a smaller sample size.

Table S1 All effect sizes included in the meta-analyses.

Table S2 Meta-analyses of the relationship between survival and the expression of secondary sexual characters in barn swallow males.