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Multi-modal signalling in estrildid finches: song, dance and colour are associated with different ecological and life history traits

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ABSTRACT

Sexual traits (e.g., visual ornaments, acoustic signals, courtship behaviour) are often displayed together as multi-modal signals. Some hypotheses predict joint evolution of different sexual signals (e.g., to increase the efficiency of communication), or that different signals trade-off with each other (e.g., due to limited resources). Alternatively, multiple signals may evolve independently for different functions, or to communicate different information (multiple message hypothesis). We evaluated these hypotheses with a comparative study in the family Estrildidae, one of the largest songbird radiations, and one that includes many model species for research in sexual selection and communication. We found little evidence for either joint evolution or trade-offs between song and colour ornamentation. Some negative correlations between dance repertoire and song traits may suggest a functional compromise, but generally courtship dance also evolved independently from other signals. Instead of correlated evolution, we found that song, dance and colour are each related to different socio-ecological traits. Song complexity evolved together with ecological generalism, song performance with investment in reproduction, dance with commonness and habitat type, whereas colour ornamentation was shown previously to correlate mostly with gregariousness. We conclude that multi-modal signals evolve in response to various socio-ecological traits, suggesting the accumulation of distinct signalling functions.

Keywords: Multi-modal signals, Sexual selection, Song, Courtship dance, Colour ornamentation, Estrildidae.

INTRODUCTION

Sexual selection has generated a great diversity of secondary sexual traits and ornaments in animals (Andersson, 1994). Courtship can make use of multiple sexual signals, often involving different signalling modalities (e.g., visual and acoustic), but we still know little about the evolutionary interactions among signalling modalities. For example, in birds, which are among the most ornamented and most studied animals in this respect, some past studies focusing on birdsong and colour ornamentation found evidence for trade-offs between these signal modalities (e.g., Badyaev et al., 2002; Shutler, 2011), whereas others found evidence for positively correlated evolution (e.g., Catchpole & McGregor, 1985; Shutler & Weatherhead, 1990; De Repentigny et al., 2000; Gonzalez-Voyer et al., 2013), or a lack of consistent associations (e.g., Ornelas et al., 2009; Mason et al., 2014; Matysioková et al. 2017). The reason for these apparently inconsistent results is not yet clear (reviewed in Shutler, 2011; Gonzalez-Voyer et al., 2013; Mason et al., 2014).

In addition to song and colour, birds have other sexual signals such as odours (e.g., Whittaker et al., 2011; Whittaker et al., 2013), extended phenotypes (e.g. nests or bowers; Gilliard, 1956; Mainwaring et al., 2014), and courtship dances (including movements of the body, wings, tail, bill, and erection of feathers; Dakin & Montgomerie, 2009; Ota et al., 2015; Soma & Mori, 2015; Ullrich et al., 2016). Courtship dance is particularly interesting because it typically interacts with other signals, being performed together with vocalizations or emphasizing conspicuously coloured body parts (Cooper & Goller, 2004; Byers et al., 2010; Dalziell et al., 2013). This might give rise to functional compromises and/or correlated evolution of different signal modalities.

Even without functional interactions, sexual selection is hypothesized to yield positively correlated evolution among different sexual signals, especially if they have identical functions and collectively improve signal reliability (redundant or unreliable message hypotheses; Moller & Pomiankowski, 1993; Johnstone, 1996; Bro-Jorgensen, 2010), and in the absence of limitations for investing in multiple signals (Shutler, 2011). Conversely, if resources are limited (Shutler, 2011) or if it is costly for receivers to evaluate multiple signals (Pomiankowski & Iwasa, 1993; Schluter & Price, 1993; Iwasa & Pomiankowski, 1994), then sexual selection should lead to the evolution of one type of sexual signal to the exclusion of others, resulting in negatively correlated evolution of different sexual signals across species.

Alternatively, different modalities of sexual signals or different traits within a signalling modality may communicate different kinds of information (multiple message hypothesis; Moller & Pomiankowski, 1993; Johnstone, 1996; Candolin, 2003; Bro-Jorgensen, 2010) or may function in different social contexts (e.g., when different song traits attract mates or convey aggressiveness; Catchpole, 1983; Nemeth, 1996; Leitão & Riebel, 2003; Cardoso et al., 2007; Funghi et al., 2015), and in these cases they may evolve in response to different selective factors. Correlated evolution among multiple sexual signals would then depend on the extent to which relevant selective pressures are correlated across species. Many differences in ecology and life history among species (e.g., parental care, gregariousness, habitat) can influence the evolution of sexual signals, either by changing the strength of sexual selection, the detectability of different signalling modes, or the relative costs of different secondary sexual traits (Endler, 1992; Bradbury & Vehrencamp, 1998). Therefore, the apparently inconsistent results from comparative studies of multimodal signalling might be resolved by asking if different sexual signals evolve under the same or different socio-ecological circumstances. This would help determine whether correlated or independent evolution of different signalling modalities is attributable to evolutionary interactions among multiple sexual signals, or to the co-occurrence of relevant selective factors across species.

Here we use estrildid finches, a large songbird family that includes many model species for research in sexual selection and animal communication (e.g., Pryke et al., 2010; Soma, 2011; Crowhurst et al., 2012; Van Rooij & Griffith, 2012; Cardoso et al., 2014; Ota et al., 2015; Soma & Mori, 2015; Ullrich et al., 2016; Young et al., 2016), to test whether different modalities of sexual signals evolve independently or in a correlated manner, and whether different modalities are associated with particular ecological or life history traits. Finch species in the family Estrildidae vary considerably in their songs, which are thought to function primarily as inter-sexual signals in this group (Hall, 1962), and exhibit a broad diversity of colour ornamentation (Clement et al., 1993). Many species also perform stereotypical courtship dances (Goodwin, 1982; Baptista et al., 1999; Payne, 2010; Soma & Garamszegi, 2015). Estrildid species also differ in ecological and life history traits that can affect sexual selection, including the degree of gregariousness, which is correlated with ornamental coloration (Gomes et al., 2016). In a previous study focused on female ornamentation, we also found that the complexity of courtship dances was unrelated to the extent of colour ornamentation or the occurrence of female song across estrildids, perhaps because these traits evolve primarily as male sexual signals (Soma & Garamszegi, 2015).

We use detailed measurements of male sexual signals and ornamentation (song complexity, song performance, size of dance repertoires, the extent, saturation and contrast of ornamental colours) to study how multimodal signalling evolves. If the different traits strongly influence each other, we expect to find correlated evolution among different types of sexual signals, and ask if such correlations are positive or negative, the latter reflecting potential trade-offs among sexual signals (Shutler, 2011). If the components of multimodal signalling are functionally equivalent, as suggested by the redundant or unreliable message hypotheses (Moller & Pomiankowski, 1993), we also expect them to be correlated with similar ecological or life history traits. Alternatively, if the different sexual signals have different functions or information content, as suggested by the multiple message hypothesis (Moller & Pomiankowski, 1993), we expect them to be correlated with different ecological or life history predictors, in which case the different types of sexual signals may evolve independently of each other.

MATERIAL AND METHODS

We quantified song traits, colour ornamentation and courtship dance repertoires of male estrildid finches, and gathered information on the ecology and life history of each species. We chose to only measure males because many estrildid finch species lack female song (Hall, 1962), and also because in many species males are more ornamented and experience stronger sexual selection than females.

Song

We obtained 535 audio recordings representing 86 species of estrildid finch species from the National Sound Archive at the British Library and the web-based library Xeno-Canto (http://www.xeno-canto.org). Based on sound quality, we selected up to ten songs per recording for analyses, and also consulted published descriptions of song (Payne, 2010) in order to distinguish the song of the focal species from other kinds of vocalizations or species captured in the recordings; all ambiguous cases were excluded. We define syllables as the units that repeat to form a trill or, in the non-trilled parts of song, as individual sound elements or tight groups of elements linked by intervals noticeably shorter than the typical between-syllable intervals. Individual songs were identified as groups of syllables separated from other songs by at least three times the typical inter-syllable intervals in the recording.

Songs that appear interrupted at the end of the recordings were not measured. We measured a total of 659 songs from 164 different recordings representing 51 estrildid species (7.3 ± 3.37 SD song/species). Spectrograms were generated with AvisoftProLab (AvisoftBioacustic, Berlin) on 16-bit files with sampling frequency of 44Hz, using 512 FFT length, Hamming window and 50% overlap, which corresponds to a resolution of 86 Hz by 5.8ms. We measured song duration from spectrograms, and used Avisoft automatic parameter tools to measure the peak frequency, maximum and minimum frequencies of each song. Peak frequency was measured as the frequency of highest amplitude across the song; maximum and minimum frequencies were measured as the frequency at which sound amplitude drops below 14 dB relative to the peak frequency. We checked the accuracy of these frequency measurements by visual inspection of spectrograms, and excluded measurements of minimum frequency that were caused by background noise. In addition to these song measurements, we used higher-resolution spectrograms (settings as above except for window overlap of 75%, resulting in 2.9 ms. time resolution) to count or measure the total number of syllables per song, the number of different syllables, and, for species with trills, the duration of trills and the number of syllable repetitions per trill. Trill measurements were made on trills that repeated at least three times the same syllable, or a syllable that changes gradually. From these raw measurements, we analysed 3 traits related to complexity (song duration, frequency bandwidth, and syllable diversity) and 4 traits related to performance (syllable rate, trill rate, sound frequency corrected for body size, and deviation from expected sound frequency).

Song duration was measured in seconds for each song, averaged across songs from the same recording, and then across recordings of the same species (the same averaging procedure was used for all the other traits below). Frequency bandwidth was computed as the difference between log-transformed maximum and minimum frequencies (i.e. the ratio of maximum to minimum frequency) of each song. Log-transformation was used because perception and modulation of sound frequency both function on a ratio scale (Cardoso, 2013). These two traits are used here to quantify song complexity under the assumption that longer songs and songs with wider frequency bandwidth can accommodate more varied sounds. In addition, these measures may also reflect song performance if singing longer songs and/or wider frequency bandwidth is physiologically demanding. Finally, syllable diversity was computed as the proportion of different syllables relative to the total number of syllables in the song; this quantifies syllable diversity while controlling for song duration.

We quantified acoustic traits likely related to song performance, in the sense that they should increase challenges to the motor system, the respiratory system, or other physiological processes involved in singing. We calculated syllable rate as the number of syllables divided by song duration, and trill rate as the number of syllable repetitions divided by trill duration. We also compared the ability of different species to sing at high sound frequencies, under the assumption that this may be physiologically demanding, requiring greater muscular contraction at the syrinx and/or build-up of greater air pressures (Goller & Riede, 2013). Controlling for body size is important because of the strong allometry between sound frequency and body size among birds (Wallschläger, 1980; Ryan & Brenowitz, 1985), a consequence of the basic physics of larger species having larger vocal tracts (Bradbury & Vehrencamp, 1998; Fletcher, 2004). Thus, we $\log_{10}$-transformed the peak frequency of each song (see explanation above, and Cardoso, 2013), and regressed species mean values on body size to obtain residual peak frequency for each species. For this we used body size data from Gomes et al. (2016), which comprises the first principal component of a Principal Component Analysis on morphometric measures (tarsus length, bill length and depth, tail and wing lengths, all $\log_{10}$-transformed) from skins of estrildid species. These residual peak frequencies, in $\log_{10}$Hz, are henceforth referred to as sound frequency corrected for body size. In addition, because it may be demanding to produce sound frequencies more distant from those predicted for a given species' body size, either very high or very low sound frequencies, we also analysed the absolute values of these residual frequencies, henceforth referred to as deviation from expected sound frequency. As noted above, song data was available for 51 different estrildid species.

Dance

We used male dance repertoire data identical to Soma and Garamszegi (2015). Based on published descriptions of courtship dance for each species (Goodwin, 1982), we counted the number of different dance movements that males perform. The categories of dance movements are: bobbing; horizontal body movements; wing movements; tail movements; erection of feathers on body; hopping or stepping; holding nest material in the bill; bill wiping; and opening the bill or showing the tongue. Dance repertoires including a greater number of different movements are considered to be more elaborate displays (see Soma & Garamszegi, 2015). Data on male courtship dance repertoire was available for 85 species.

Colour

We used the colour ornamentation data from Gomes et al. (2016), based primarily on reflectance spectrophotometry and digital photography of specimens at the Natural History

Museum of London. The five metrics below allow comparisons of the extent of ornamentation, and chromatic and achromatic aspects of colour, among species with diverse colour hues. Maximum and mean saturation of ornamental colours, which quantify the chromatic conspicuousness of plumage colours, were calculated using models of avian vision (Endler & Mielke, 2005; Stoddard & Prum, 2008), as the maximum or mean value of colour saturation (distance to the achromatic centre of perceptual colour space) in each of seven body parts (crown, throat, mask, back, belly, tail and wing). Maximum achromatic difference quantifies the non-chromatic contrast among plumage colours, and was computed as the maximum absolute value of all pair-wise differences in log-reflectance among the seven body parts noted above. Extent of ornamental coloration is an index of the proportion of plumage area with ornamental coloration (i.e., yellow-to-red, green, blue, or homogeneous black), and was computed from dorsal, ventral and lateral photographs of each specimen. Finally, we noted whether bills had ornamental red colour. For detailed methods on these metrics, see Gomes et al. (2016). Data on male colour ornamentation was available for 132 species.

Ecological and life history traits

We gathered information from the literature (Clement et al., 1993; Payne, 2010) on several ecological and life history traits of estrildid fiches. We used 14 of the 15 ecological and life history traits in Gomes et al. (2016), chosen for having been shown or suggested to affect sexual signals in other taxa, and for which information was available for most estrildid species. These traits are: vegetation density of the habitat, maximum altitude and altitudinal range, commonness, migration, gregariousness, feeding height and range, length of the breeding season, clutch size, lengths of the incubation and nestling periods, nest height, and vulnerability to brood-parasitism. See Gomes et al. (2016) for methods used to quantify these traits, and for the rationale for their potential relationships with sexual signals (see Table 1 in Gomes et al., 2016). Unlike Gomes et al. (2016), we did not use the trait “diet” (extent of granivory), because this trait has a predicted relationship only with colour ornamentation, and not song or dance.

Phylogeny and comparative analyses

For comparative analyses, we used a molecular phylogeny for the estrildid finches comprising all extant species recognized by Payne (2010) and for which we had information on song, dance or colour ornamentation. This phylogeny was based on two mitochondrial DNA regions comprising ~2,170 base pairs. The analyses reported here are based on the maximum clade credibility tree from BEAST (Drummond et al., 2012). For detailed information on the molecular phylogeny, see Gomes et al. (2016).

We tested for correlated evolution between phenotypic traits associated with different modalities of sexual signals — song, courtship dance repertoire, and colour ornamentation — using two approaches. The first approach used bivariate phylogenetic generalized least squares (PGLS) regressions to test for correlation among traits while controlling for phylogenetic relationships among species (Pagel, 1999). The choice of which traits to use as predictor or dependent variable in these models was arbitrary (we choose to use colour traits always as predictors, and dance repertoire always as dependent). Sample sizes differ for the different regression models because data on sexual signals and on ecological and life history traits were available for different subsets of species (see Supplementary dataset). We analysed each song and colour trait separately because phenotypic traits within the same signal modality (song or colour) did not generally show strong positive covariation: all bivariate PGLS regressions coefficients (β) among song traits were either negative or were lower than 0.38, except for syllable and trill rates, which are alternative ways of assessing the same aspect of performance (Table S1). Likewise, β were lower than 0.23 among all colour traits, except for mean and maximum saturation, which is expected because they summarize the same saturation measurements (Table S2).

The second approach used PGLS multiple regression models to include the various song traits, or the various colour traits, together as independent variables in the same statistical model, rather than testing their effects in separate analyses. This has the advantage of accounting for complementary effects that different song or colour traits may have on the evolution of each trait in the other signalling modalities. It has the limitation that sample size for some multiple regression models is quite low compared to bivariate models because there are missing values for some species (e.g., no data on trill rate for species without trills). For PGLS multiple regression models using song traits as independent variables, we excluded sound frequency corrected for body size and syllable rate to avoid multicollinearity problems (sound frequency corrected for body size is strongly negatively related with frequency bandwidth and with deviations to expected sound frequency, and syllable rate is strongly negatively related with syllable diversity and positively with trill rate; all other $|\beta| < 0.39$, Table S1). Similarly, in PGLS multiple regression models using colour traits as independent variables, we excluded maximum saturation to avoid multicollinearity with mean saturation ($\beta = 0.80$; all other $|\beta| < 0.24$).

We testes whether statistically significant results obtained in the above analyses were robust to uncertainty in the phylogenetic tree we used (i.e., the maximum clade credibility tree) by replicating statistically significant analyses using multiple trees sampled from the posterior distribution of trees generated by BEAST. We randomly selected 1000 trees from the posterior distribution and then replicated each of these significant analyses across the 1000 trees. Following Garamszegi & Mundry (2014) and Rubolini et al. (2015), we averaged results weighted by the fit of each tree to the analysis (evaluated by its Akaike Information Criterion, AIC).

We tested whether species differences in song traits or dance repertoires are predicted by the above set of 14 ecological and life history traits. Ecological and life history correlates of estrildid colour ornamentation are reported elsewhere (Gomes et al., 2016). Since the ecological and life history traits differ in samples sizes (i.e., number of species with information available), we completed this test in two steps: (1) we ran PGLS simple regressions with each ecological or life-history trait as the single predictor of the song or dance trait (Table S3); (2) we selected ecological and life history traits showing suggestive associations with song or dance ($P < 0.1$) for inclusion in a PGLS multiple regression for each signalling trait. This procedure avoids excessive reduction in sample size for the multiple regression, while allowing the inclusion of all relevant predictors. We also report these PGLS multiple regression models as averaged across 1000 different phylogenetic trees, to account for phylogenetic uncertainty, as described above. All PGLS regressions were calculated in the R (R Core Team, 2015) package Caper (Orme, 2013), and in all cases we estimated the parameter λ of the regression model in order to assess and adjust the degree of phylogenetic correction (Freckleton et al., 2002).

RESULTS

Few of the song and colour traits studied appear to evolve in a correlated manner. PGLS bivariate regressions found three nominally significant relationships were: 1) a positive association between sound frequency corrected for body size and the extent of ornamental coloration ($\beta_{st} = 0.35$, N = 50 species, P = 0.02); 2) a positive association between deviation from expected sound frequency and maximum achromatic difference ($\beta_{st} = 0.35$, N = 50, P = 0.01); and 3) a negative association between syllable diversity and maximum achromatic difference ($\beta_{st} = -0.43$, N = 50, P = 0.004; all other $|\beta_{st}| < 0.26$, P > 0.07; Table 1). However, these associations between song and colour are not robust to correction for the multiple comparisons included in Table 1. Similarly, PGLS multiple regressions found little support for coevolution of song and colour. The above two associations between maximum achromatic difference and song traits were retrieved in some of the PGLS multiple regression models, especially those using various colour traits simultaneously as independent variables (Table S4 and S5). No additional associations between song and colour traits were discovered, except for the model regressing mean colour saturation on the various song traits being marginally significant ($F_{5,32} = 2.57$, $P = 0.05$), albeit with no significant effects for individual song traits (Table S4). All these results remained statistically significant when averaged across analyses using 1000 trees sampled from the posterior distribution, to account for phylogenetic uncertainty (Table S6).

The dance repertoire of males was negatively related to syllable diversity in songs (PGLS bivariate regression: $\beta_{st} = -0.32$, N = 36, P = 0.03; result remained significant when analysed across multiple phylogenetic trees; Table S6), and there was also a negative trend between dance repertoire and trill rate ($\beta_{st} = -0.27$, N = 27, P = 0.14; in all other PGLS bivariate regressions, $|\beta_{st}| < 0.20$, $P > 0.12$; Table 2). Similarly, PGLS multiple regression suggested the above negative associations between male dance repertoire and syllable diversity or trill rate (partial $\beta_{st} = -0.40$, P = 0.07, and partial $\beta_{st} = -0.33$, P = 0.08, respectively) and also a positive association with frequency bandwidth (partial $\beta_{st} = 0.54$, P = 0.06; Table S4). Although these partial regression coefficients are higher than in the previous bivariate analyses (between 0.33 and 0.54), their statistical significance is only suggestive (all $P \leq 0.08$) perhaps because the sample size for this multiple regression model (25 species) is lower than in bivariate analyses. PGLS multiple regressions also did not find evidence for associations between colour traits and males dance repertoire (Table S5).

Bivariate PGLS regressions found between one and four ecological and life history candidate traits for inclusion in PGLS multiple regression models (Table S3). Multiple regression models then revealed that most song traits and dance repertoires are related to different ecological or life history traits (Table 3; Figs. S1, S2, S3). Results of PGLS multiple regression models were identical when using 1000 trees sampled to account for phylogenetic uncertainty (Table S7).

The strongest association we found was between a song complexity trait, frequency bandwidth, and the range of feeding heights, an aspect of ecological generalism ($\beta_{st} = 0.64$, N = 44, P = 0.004; Table 3), although the number of species that feed across a range of heights is very small (Fig. S1 A). Another song complexity trait, song duration, was also marginally related to a measure of ecological generalism (range of altitudes of the habitat: $\beta_{st} = 0.40$, N =

36, P = 0.06; Table 3; Fig. S1 B). Both results, suggest that ecologically generalist species evolved more complex songs.

None of the song complexity traits were positively related to measures of investment in reproduction (Table 3); on the contrary, syllable diversity was negatively related to clutch size (β_{st} = -0.37, N = 49, P = 0.02; Fig. S1 C). Nonetheless, nestling period, a measure of the investment in reproduction, was the life-history trait most often related to song. It was positively related to most song performance traits (trill rate, β_{st} = 0.49, N = 40, P = 0.02; syllable rate, β_{st} = 0.31, N = 43, P = 0.02; and deviation in sound frequency relative to body size, β_{st} = 0.37, N = 43, P = 0.01), and was marginally related to lower sound frequency (β_{st} = -0.27, N = 43, P = 0.05; Table 3; Fig. S2 A-D). Some of these results, however, are influenced by a single species with longer nestling period than the remaining estrildids (Fig. S2 A-C). Nonetheless, these results suggest that species investing more in their offspring growth evolved higher performance songs (faster trill and syllable rates, and larger deviations relative to the sound frequency predicted by their body size).

Faster trill rates were associated with less migratory species (β_{st} = -0.35, P = 0.04, Fig. S2 E), and larger dance repertoires were associated with higher-altitude habitats (β_{st} = 0.34, N = 45, P = 0.04) and commonness (β_{st} = 0.32, P = 0.04; Table 3, Fig. S3).

DISCUSSION

Past comparative studies on the joint evolution of birdsong and colour ornamentation have reported inconsistent results, although most did not find significant associations between these two signalling modalities (reviewed in Mason et al., 2014). Our results for estrildid finches are comparable; despite considering many traits related to song complexity, song performance, the extent, saturation and contrast of colour ornamentation, most evolutionary correlations among signalling modalities were weak and non-significant, even before correcting for multiple comparisons. Of the three nominally significant correlations between song and colour (i.e., prior to correcting for multiple comparisons), one is similar to a result previously reported for North American wood warblers (extent of colour ornamentation related to higher-frequency songs; Shutler & Weatherhead, 1990), and another (syllable diversity negatively related to achromatic contrast) matches results for Cardueline finches (Badyaev et al., 2002). Collectively, however, our results show largely independent evolution of song and colour ornamentation.

For courtship dance too, strong correlations with other signalling modalities were few. No significant associations were found with the saturation, contrast or extent of ornamental colours, supporting previous work finding that dance repertoires are not related to the extent of estrildid colour ornamentation (Soma & Garamszegi, 2015). The only nominally significant association (i.e., before accounting for multiple comparisons) was species with larger dance repertoires having less syllable diversity in their songs. Since many estrildids sing during courtship (Goodwin, 1982; e.g., Ota et al., 2015; Soma & Mori, 2015; Ullrich et al., 2016), these simpler and more repetitive songs could be interpreted as a functional adaptation to synchronize dance with singing. The same could be said of the second strongest, although non-significant, bivariate association with dance repertoires: slower trill rates. As for the associations between song and colour, however, most correlations involving dance repertoires were weak and non-significant. Therefore, we conclude that interactions among signalling modalities, whether positive or representing trade-offs (Shutler, 2011), are not among the most important factors shaping the evolution of estrildid sexual signalling.

Instead of correlated evolution among sexual signals, we found that each signalling modality was associated with different ecological and life history traits, suggesting that each is subject to a different set of selective factors and constraints. Song complexity evolved together with ecological generalism, measures of song intensity or performance correlated mostly with investment in reproduction, dance correlated with habitat type and commonness, whereas colour ornamentation is related mostly to gregariousness, as reported previously (Gomes et al., 2016).

The association of song complexity (larger frequency bandwidths and longer songs) with ecological generalism agrees with comparative studies finding that generalist species on average experience stronger sexual selection or have more elaborate sexual signals (Badyaev & Ghalambor, 1998; Tobias & Seddon, 2009; Östman & Stuart-Fox, 2011; Cardoso et al., 2012; see Table 1 of Gomes et al., 2016). Migration also is thought to increase sexual selection because of increasing breeding synchrony and likelihood of extra-pair fertilizations (Spottiswoode & Møller, 2004; Table 1 of Gomes et al., 2016). Estrildid species with faster trill rates (a song performance trait) were less migratory, providing no support for a link between migration and sexual selection, at least for this trait. Investment in reproduction is another life-history trait that may select for sexual signals that indicate good parental qualities, for example (the good parent hypothesis; e.g., Germain et al., 2010; Gladbach et al., 2010). Higher song complexity was not associated with greater investment in reproduction, whereas syllable diversity decreased with clutch size across species. This suggests that song complexity in estrildids has not evolved to signal parental care, but on the contrary, may evolve in species with less demanding parental duties, such that males can more easily invest in sexual signals to pursuit extra-pair matings (the trade-off and differential allocation hypotheses; Badyaev & Hill, 2002; Mitchell et al., 2007; Table 1 of Gomes et al., 2016). Several song performance traits (syllable rate, trill rate, and deviations in sound frequency relative to body size), however, were positively correlated to the length of the nestling period, suggesting that song performance may evolve to signal male parental ability in species that require longer parental care.

In contrast to song, ecological generalism and investment in reproduction were not the most important correlates of non-acoustic sexual signals. Although some colour traits are positively related to investment in reproduction, colour ornamentation is most strongly associated with gregariousness, with gregarious species having more saturated and contrasting ornamental colours (Gomes et al., 2016). In this study, we find that male courtship dance repertoires, which should be sexually selected (Johnson, 2000), are larger in more common species and those that live at higher altitudes. These correlates of dance repertoires are not simple to interpret because potential relationships between sexual selection and commonness or altitude are debated; costly sexual signals were proposed to reduce commonness and promote extinction (e.g., McLain et al., 1995; Bro-Jørgensen, 2014), but in some circumstances sexual selection may facilitate adaptation to changing environments (reviewed in Candolin & Heuschele, 2008) or increase with population density (reviewed in Kokko & Rankin, 2006). In other avian species song complexity increases with latitude (reviewed in Singh & Price, 2015), which may have similar ecological consequences as increasig latitude. In contrast, cardueline finches at higher altitudes were found to be less ornamented (Badyaev, 1997). Overall, it is clear that different modalities of sexual signals in estrildid finches are not correlated with the same ecological and life history predictors.

Several explanations might account for the lack of consistent evidence for an evolutionary correlation between elaboration of song and colour ornamentation across avian taxa. These include methodological limitations in quantifying these complex phenotypes, differences in the importance of joint evolution versus trade-offs across avian lineages (Shutler, 2011), or evolution of these sexual signals for different functions or under different socio-ecological constraints (see Gonzalez-Voyer et al., 2013 and Mason et al., 2014 for review and discussions of this). Our work on estrildid finches reinforces the conclusion of Mason et al. (2014) that a general correlation among song and colour is unlikely for songbirds and tentatively expands this conclusion to courtship dance, despite suggestive evidence for a functional compromise between dance and song. Having analysed several aspects of song complexity, song performance, chromatic and achromatic aspects of colour, our results also argue against explanations based on methodological limitations. Instead, finding that each mode of sexual signalling (including song complexity and performance separately) tends to be associated with distinct socio-ecological traits suggests that these sexual signals communicate different information (multiple message hypothesis; Moller & Pomiankowski, 1993; Johnstone, 1996), and/or respond to different selection pressures or constraints. We therefore suggest that the co-occurrence of different sexual signals across avian species is shaped by the alignment of the relevant socio-ecological factors that influence the evolution of each signalling modality, and that this may help explain the inconsistent results of comparative studies on different avian clades.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Scatterplots of species values illustrating relationships between song complexity and ecological or life history traits.

Fig. S2. Scatterplots of species values illustrating relationships between song performance and ecological or life history traits.

Fig. S3. Scatterplots of species values illustrating relationships between dance repertoire and ecological or life history traits.

Table S1. Bivariate phylogenetic regressions between pairs of song traits.

Table S2. Bivariate phylogenetic regressions between pairs of colour traits.

Table S3. Exploratory bivariate phylogenetic regressions of song and dance traits on each of 14 socio-ecological traits.

Table S4. Phylogenetic multiple regression models regressing each colour or dance trait on various song traits.

Table S5. Phylogenetic multiple regression models regressing each song or dance trait on various colour traits.

Table S6. Bivariate phylogenetic regressions between pairs of song traits, accounting for phylogenetic uncertainty.

Table S7. Phylogenetic multiple regression models relating each song or dance trait to socio-ecological predictors, accounting for phylogenetic uncertainty.

Dataset. Dataset with values per species.

REFERENCES

Andersson, M.B. 1994. Sexual selection. Princeton University Press, Princeton NJ.

Badyaev, A.V. 1997. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. Behav. Ecol. **8:** 675-690.

Badyaev, A.V. & Ghalambor, C.K. 1998. Does a trade-off exist between sexual ornamentation and ecological plasticity? Sexual dichromatism and occupied elevational range in finches. Oikos **82:** 319-324.

Badyaev, A.V. & Hill, G.E. 2002. Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. Behav. Ecol. **13:** 591-597.

Badyaev, A.V., Hill, G.E. & Weckworth, B.V. 2002. Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. Evolution **56:** 412-419.

Baptista, L.F., Lawson, R., Visser, E. & Bell, D.A. 1999. Relationships of some mannikins and waxbills in the estrildidae. Journal für Ornithologie **140:** 179-192.

Bradbury, J.W. & Vehrencamp, S.L. 1998. Principles of animal communication. Massachusetts: Sinauer Associates., Sunderland.

Bro-Jorgensen, J. 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. Trends Ecol. Evol. **25:** 292-300.

Bro-Jørgensen, J. 2014. Will their armaments be their downfall? Large horn size increases extinction risk in bovids. Anim. Conserv. **17:** 80-87.

Byers, J., Hebets, E. & Podos, J. 2010. Female mate choice based upon male motor performance. Anim. Behav. **79:** 771-778.

Candolin, U. 2003. The use of multiple cues in mate choice. Biol. Rev. **78:** 575-595.

Candolin, U. & Heuschele, J. 2008. Is sexual selection beneficial during adaptation to environmental change? Trends Ecol. Evol. **23:** 446-452.

Cardoso, G.C. 2013. Using frequency ratios to study vocal communication. Anim. Behav. **85:** 1529-1532.

Cardoso, G.C., Hu, Y. & Mota, P.G. 2012. Birdsong, sexual selection, and the flawed taxonomy of canaries, goldfinches and allies. Anim. Behav. **84:** 111-119.

Cardoso, G.C., Leitão, A.V., Funghi, C., Batalha, H.R., Lopes, R.J. & Mota, P.G. 2014. Similar preferences for ornamentation in opposite- and same-sex choice experiments. J. Evol. Biol. **27:** 2798-2806.

Cardoso, G.C., Mota, P.G. & Depraz, V. 2007. Female and male serins (Serinus serinus) respond differently to derived song traits. Behav. Ecol. Sociobiol. **61:** 1425-1436.

Catchpole, C.K. 1983. Variation in the song of the great reed warbler Acrocephalus arundinaceus in relation to mate attraction and territorial defence. Anim. Behav. **31:** 1217-1225.

Catchpole, C.K. & McGregor, P.K. 1985. Sexual selection, song complexity and plumage dimorphism in European buntings of the genus Emberiza. Anim. Behav. **33:** 1378-1380.

Clement, P., Harris, A. & Davis, J. 1993. Finches & sparrows: An identification guide. Princeton University Press. Princeton, NJ.

Cooper, B.G. & Goller, F. 2004. Multimodal Signals: Enhancement and Constraint of Song Motor Patterns by Visual Display. Science **303:** 544-546.

Crowhurst, C.J., Zanollo, V., Griggio, M., Robertson, J. & Kleindorfer, S. 2012. White Flank Spots Signal Feeding Dominance in Female Diamond Firetails, Stagonopleura guttata. Ethology **118:** 63-75.

Dakin, R. & Montgomerie, R. 2009. Peacocks orient their courtship displays towards the sun. Behav. Ecol. Sociobiol. **63:** 825-834.

Dalziell, A.H., Peters, R.A., Cockburn, A., Dorland, A.D., Maisey, A.C. & Magrath, R.D. 2013. Dance choreography is coordinated with song repertoire in a complex avian display. Curr. Biol. **23:** 1132-1135.

De Repentigny, Y., Ouellet, H. & McNeil, R. 2000. Song versus plumage in some North American Oscines: Testing Darwin's hypothesis. Écoscience **7:** 137-148.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. **29:** 1969-1973.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. Am. Nat. **139 (suppl.):** S125-S153.

Endler, J.A. & Mielke, P.W. 2005. Comparing entire colour patterns as birds see them. Biol. J. Linn. Soc. **86:** 405-431.

Fletcher, N.H. 2004. A simple frequency-scaling rule for animal communication. J. Acoust. Soc. Am. **115:** 2334.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Nat. **160:** 712-726.

Funghi, C., Cardoso, G.C. & Mota, P.G. 2015. Increased syllable rate during aggressive singing in a bird with complex and fast song. J. Avian Biol. **46:** 283-288.

Garamszegi, L.Z. & Mundry, R. 2014. Multimodel-inference in comparative analyses. In Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice, ed L.Z. Garamszegi (New York, NY: Springer), 305–331.

Germain, R.R., Reudink, M.W., Marra, P.P. & Ratcliffe, L.M. 2010. Carotenoid-based male plumage predicts parental investment in the American Redstart. Wilson J. Ornithol. **122:** 318-325.

Gilliard, E.T. 1956. Bower Ornamentation versus Plumage Characters in Bower-Birds. Auk **73:** 450-451.

Gladbach, A., Gladbach, D.J., Kempenaers, B. & Quillfeldt, P. 2010. Female-specific colouration, carotenoids and reproductive investment in a dichromatic species, the upland goose Chloephaga picta leucoptera. Behav. Ecol. Sociobiol. **64:** 1779-1789.

Goller, F. & Riede, T. 2013. Integrative physiology of fundamental frequency control in birds. J. Physiol. Paris **107:** 230-242.

Gomes, A.C.R., Sorenson, M.D. & Cardoso, G.C. 2016. Speciation is associated with changing ornamentation rather than stronger sexual selection. Evolution **70:** 2823-2838.

Gonzalez-Voyer, A., den Tex, R.J., Castelló, A. & Leonard, J.A. 2013. Evolution of acoustic and visual signals in Asian barbets. J. Evol. Biol. **26:** 647-659.

Goodwin, D. 1982. *Estrildid fin*ches of the world. NY: Cornell Univeristy Press, Ithaca.

Hall, M. 1962. Evolutionary aspects of estrildid song. Symp. Zool. Soc. Lond.

Iwasa, Y. & Pomiankowski, A. 1994. The evolution of mate preferences for multiple sexual ornaments. Evolution **48:** 853-867.

Johnson, K.P. 2000. The evolution of courtship display repertoire size in the dabbling ducks (Anatini). J. Evol. Biol. **13:** 634-644.

Johnstone, R.A. 1996. Multiple Displays in Animal Communication:`Backup Signals' and `Multiple Messages'. Philos. T. Roy. Soc. B **351:** 329-338.

Kokko, H. & Rankin, D.J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. Philos. T. Roy. Soc. B **361:** 319-334.

Leitão, A. & Riebel, K. 2003. Are good ornaments bad armaments? Male chaffinch perception of songs with varying flourish length. Anim. Behav. **66:** 161-167.

Mainwaring, M.C., Hartley, I.R., Lambrechts, M.M. & Deeming, D.C. 2014. The design and function of birds' nests. Ecol. Evol. **4:** 3909-3928.

Mason, N.A., Shultz, A.J. & Burns, K.J. 2014. Elaborate visual and acoustic signals evolve independently in a large, phenotypically diverse radiation of songbirds. Proc. Biol. Sci. **281**.

Matysioková, B., Friedman, N., Turčoková, L. & Remeš, V. 2017. The evolution of feather coloration and song in Old World orioles (genus Oriolus). J. Avian Biol. Doi: 10.1111/jav.01175.

McLain, D.K., Moulton, M.P. & Redfearn, T.P. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. Oikos **74:** 27-34.

Mitchell, D.P., Dunn, P.O., Whittingham, L.A. & Freeman-Gallant, C.R. 2007. Attractive males provide less parental care in two populations of the common yellowthroat. Anim. Behav. **73:** 165-170.

Moller, A.P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? Behav. Ecol. Sociobiol. **32:** 167-176.

Nemeth, E. 1996. Different singing styles in mated and unmated Reed Buntings Emberiza schoeniclus. Ibis **138:** 172-176.

Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. Available online at: http://cran.r-project.org/web/packages/caper/vignettes/ caper.pdf.

Ornelas, J.F., Gonzalez, C. & Espinosa de los Monteros, A. 2009. Uncorrelated evolution between vocal and plumage coloration traits in the trogons: a comparative study. J. Evol. Biol. **22:** 471-484.

Östman, Ö. & Stuart-Fox, D. 2011. Sexual selection is positively associated with ecological generalism among agamid lizards. J. Evol. Biol. **24:** 733-740.

Ota, N., Gahr, M. & Soma, M. 2015. Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird. Sci. Rep. **5:** 16614.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature **401:** 877-884.

Payne, R. 2010. Family Estrildidae (Waxbills). In: Handbook of the Birds of the World - Weavers to New World Warblers, Vol. 15 (J. del Hoyo, A. Elliott & D. A. Christie, eds). Lynx Edicions.

Pomiankowski, A. & Iwasa, Y. 1993. Evolution of Multiple Sexual Preferences by Fisher's Runaway Process of Sexual Selection. Proc. Royal Soc. B **253:** 173-181.

Pryke, S.R., Rollins, L.A. & Griffith, S.C. 2010. Females use multiple mating and genetically loaded sperm competition to target compatible genes. Science **329:** 964-967.

R Core Team 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rubolini, D., Liker, A., Garamszegi, L.Z., Møller, A.P. & Saino, N. 2015. Using the BirdTree. org website to obtain robust phylogenies for avian comparative studies: A primer. Curr. Zool. **61:** 959-965.

Ryan, M.J. & Brenowitz, E.A. 1985. The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. Am. Nat. **126:** 87-100.

Schluter, D. & Price, T. 1993. Honesty, perception and population divergence in sexually selected traits. Proc. Royal Soc. B **253:** 117-122.

Shutler, D. 2011. Sexual selection: when to expect trade-offs. Biol. Lett. **7:** 101-104.

Shutler, D. & Weatherhead, P.J. 1990. Targets of sexual selection: song and plumage of wood warblers. Evolution **44:** 1967-1977.

Singh, P. & Price, T.D. 2015. Causes of the latitudinal gradient in birdsong complexity assessed from geographical variation within two Himalayan warbler species. Ibis **157:** 511-527.

Soma, M. & Garamszegi, L.s.Z. 2015. Evolution of courtship display in Estrildid finches: dance in relation to female song and plumage ornamentation. Front. Ecol. Evol. **3**: 1-11.

Soma, M. & Mori, C. 2015. The songbird as a percussionist: syntactic rules for non-vocal sound and song production in Java sparrows. PLoS One **10:** e0124876.

Soma, M.F. 2011. Social Factors in Song Learning: A Review of Estrildid Finch Research. Ornithol. Sci. **10:** 89-100.

Spottiswoode, C. & Møller, A.P. 2004. Extrapair paternity, migration, and breeding synchrony in birds. Behav. Ecol. **15:** 41-57.

Stoddard, M.C. & Prum, R.O. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. Am. Nat. **171:** 755-776.

Tobias, J. & Seddon, N. 2009. Sexual selection and ecological generalism are correlated in antbirds. J. Evol. Biol. **22:** 623-636.

Ullrich, R., Norton, P. & Scharff, C. 2016. Waltzing Taeniopygia: integration of courtship song and dance in the domesticated Australian zebra finch. Anim. Behav. **112:** 285-300.

Van Rooij, E.P. & Griffith, S.C. 2012. No evidence of assortative mating on the basis of putative ornamental traits in Long-tailed Finches Poephila acuticauda. Ibis **154:** 444-451.

Wallschläger, D. 1980. Correlation of song frequency and body weight in passerine birds. Experientia **36:** 412-412.

Whittaker, D.J., Gerlach, N.M., Soini, H.A., Novotny, M.V. & Ketterson, E.D. 2013. Bird odour predicts reproductive success. Anim. Behav. **86:** 697-703.

Whittaker, D.J., Richmond, K.M., Miller, A.K., Kiley, R., Bergeon Burns, C., Atwell, J.W. & Ketterson, E.D. 2011. Intraspecific preen oil odor preferences in dark-eyed juncos (Junco hyemalis). Behav. Ecol. **22:** 1256-1263.

Young, C.M., Cain, K.E., Svedin, N., Backwell, P.R.Y. & Pryke, S.R. 2016. The role of pigment based plumage traits in resolving conflicts. J. Avian Biol. **47:** 167-175.

Tables

Table 1. Bivariate phylogenetic regressions of seven song traits on five colour traits. Statistically significant results indicated by an asterisk; λ is the estimated phylogenetic signal of each regression model; N is the number of species.

	Song complexity			Song performance			
	Song duration β (P; λ)	**Frequency bandwidth**	**Syllable diversity**	**Sound frequency corrected for body size**	**Deviation from expected sound frequency**	**Syllable rate**	**Trill rate**
Maximum saturation	0.10 (0.45; 0.00)	0.15 (0.27; 0.00)	0.08 (0.56; 0.37)	0.17 (0.21; 0.00)	-0.12 (0.39; 0.00)	-0.09 (0.53; 0.00)	0.19 (0.20; 0.00)
Mean saturation	-0.03 (0.80; 0.00)	0.17 (0.21; 0.00)	0.21 (0.14; 0.34)	0.05 (0.69; 0.00)	-0.06 (0.66; 0.00)	-0.08 (0.58; 0.00)	0.18 (0.24; 0.00)
Achromatic difference	0.07 (0.65; 0.00)	0.14 (0.39; 0.00)	* -0.43 (0.004; 0.29)	-0.26 (0.07; 0.00)	* 0.35 (0.01; 0.00)	0.17 (0.23; 0.00)	0.09 (0.59; 0.00)
Extent of ornamental colours	0.14 (0.37; 0.00)	-0.08 (0.63; 0.00)	0.16 (0.32; 0.32)	* 0.35 (0.02; 0.00)	-0.15 (0.35; 0.00)	-0.19 (0.23; 0.00)	-0.03 (0.84; 0.00)
Bill ornamental colour	-0.01 (0.96; 0.00)	0.23 (0.12; 0.00)	0.01 (0.96; 0.41)	0.01 (0.94; 0.00)	-0.06 (0.69; 0.00)	-0.22 (0.12; 0.00)	-0.06 (0.72; 0.00)
N	50	46	50	50	50	50	40

Table 2. Bivariate phylogenetic regressions between male dance repertoire and each of seven song traits and five colour traits. Statistics as in Table 1.

	Males dance repertoire	
	β (P; λ)	**N**
Song duration	-0.07 (0.62; 0.09)	36
Frequency bandwidth	0.15 (0.47; 0.14)	32
Syllable diversity	* -0.32 (0.03; 0.00)	36
Sound frequency corrected for body size	-0.07 (0.69; 0.06)	36
Deviation from expected sound frequency	0.001 (0.99; 0.09)	36
Syllable rate	0.08 (0.60; 0.03)	36
Trill rate	-0.27 (0.14; 0.00)	27
Maximum saturation	0.08 (0.48; 0.30)	
Mean saturation	0.06 (0.64; 0.31)	
Achromatic difference	0.19 (0.12; 0.16)	82
Extent of ornamental colours	-0.13 (0.34; 0.28)	
Bill ornamental colour	0.07 (0.59; 0.29)	

Table 3. Phylogenetic multiple regression models relating each song or dance trait to their respective candidate set of socio-ecological predictors. Statistics as in Table 1.

	Song complexity			Song performance				
	Song duration	**Frequency bandwidth**	**Syllable diversity**	**Sound frequency corrected for**	**Deviation from expected sound**	**Syllable rate**	**Trill rate**	**Males Dance repertoire**

	β (P)			body size	frequency			
Vegetation density								
Altitude of habitats	0.07 (0.80)							* 0.34 (0.04)
Range of altitudes of habitats	0.40 (0.06)							
Commonness	-0.25 (0.27)							* 0.32 (0.04)
Migration							* -0.35 (0.04)	0.25 (0.09)
Gregariousness							0.22 (0.28)	
Range of feeding heights		* 0.64 (0.004)						
Clutch size			* -0.37 (0.02)					
Incubation period						0.17 (0.23)		
Nestling period				-0.27 (0.05)	* 0.37 (0.01)	* 0.31 (0.02)	* 0.49 (0.02)	
Nest height								-0.001 (1.00)
Brood-parasitized	-0.14 (0.39)							
λ (N)	0.00 (36)	0.00 (44)	0.00 (49)	0.00 (43)	0.26 (43)	0.00 (43)	0.00 (40)	0.49 (45)