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Evolution of patterned plumage as a sexual signal in estrildid finches

Running title: Plumage patterns as a sexual signal

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Abstract

Colour patterns, such as bars or dots, that cover the body surface of animals are generally thought to play roles in signalling and camouflage. In birds, however, the macroscopic aspects of plumage colouration are less well understood as past studies typically described plumage colourations by using spectrophotometric analyses. To provide insight into the evolution of plumage patterns as sexual signals, we characterised interspecific and intersexual variations in the plumage patterns of estrildid finches and tested their associations with other courtship signals and life-history traits using a comparative phylogenetic approach. Our results support the idea that plumage patterns in estrildids are favoured by sexual selection because large-sized conspicuous plumage patterns are possessed by species with an elaborate courtship dance. These plumage patterns may also play roles in social signalling because patterns are more conspicuous in species with intraspecific brood parasitism. We predict that pattern traits can be favoured by mate choice or intra-sexual competition when they can serve as honest indicator of individual condition. As our results are consistent between the sexes, we suggest that the same selective force is acting on the evolution of plumage patterns in males and females in parallel. Finally, we also found a trade-off between large size and vivid colour patterns, suggesting that too conspicuous patterns are costly, presumably because of the risk of catching the eyes of potential predators. Therefore, plumage patterns are also shaped by natural selection.

Keywords: plumage colour pattern, sexual signal, estrildid finch, phylogenetic comparison

Many animals are not uniformly coloured. They can have colour patches, spots, or stripes, which have likely evolved through predator–prey interactions, or for intraspecific communication (Caro 2005; Stevens and Merilaita 2009). Even though the definition of colour pattern varied among studies or species, a number of previous studies reported on the functions of what they call 'patterns'. In particular, body colour patterns are shown to function for camouflage in diverse species, like moths (Bond and Kamil 2002), squirrels (Ancillotto and Mori 2016), and carnivores (Ortolani 1999; Allen et al. 2011), while bold patterns (e.g. red spots on black) that make animals conspicuous serve as aposemantic signals in spiders (Brandley et al. 2016) and poison frogs (Darst et al. 2006). Social living has also promoted the evolution of body colour patterns that can code individual information in cetaceans (Caro et al. 2011; Krzyszczyk and Mann 2012), or face colour patterns in some mammals (squirrels: Ancillotto and Mori 2016 ; primates: Santana et al. 2012). Lastly, and most importantly for this study, colour patterns can affect mating, which has been well documented in fish (e.g. Endler 1983; Puebla et al. 2007).

Although colour patterns have long been discussed in the context of conspicuousness vs. camouflage (Endler 1978; Gluckman and Cardoso 2010), few empirical studies on birds exist on this topic. Considering that birds play essential roles in predator-prey interactions, and can possess colourful plumage that functions for signalling, it would be of great importance to look into plumage colour patterns in birds from such viewpoint. In contrast with conspicuous plumage colours (e.g. carotenoid, UV) that have been extensively studied using pin-point data relying on the spectrometry techniques (Andersson 1994; Hill and McGraw 2006), the signalling functions of plumage colour patterns are only beginning to be understood in an evolutionary context (cf. Gluckman and Mundy 2013; Gluckman 2014; Marshall and Gluckman 2015). We suggest that the extensive interspecific variations in the macroscopic aspects of plumage colouration deserve an evolutionary explanation for a complete understanding of how feather colours function as visual stimuli (cf. Endler 2012; Dale et al. 2015). Patterns focused in this study are defined as repetitive and regular appearances of colour patches of a certain shape (i.e. dot, bar, and mottle) covering some background color (see also methods and Fig. 1). Considering that many birds have these patterns limited to small areas of the body surface, and that males and females can differ in the presence or conspicuousness of the patterns (Gluckman and Cardoso 2010) (see examples in Fig.

1a–g), we hypothesize that in addition to colours, plumage patterns have important signalling roles in birds.

So far, several studies have indicated that plumage patterns are used as visual signals among conspecifics. In the zebra finch *Taeniopygia guttata*, a popular model species of sexual selection with sexually dimorphic plumage patterns, males but not females have black and white stripes on the chest. The melanin colouration of these stripes is shaped by body condition during the juvenile stage (Birkhead et al. 1999), and females prefer males with symmetric chest stripes (Swaddle and Cuthill 1994). Similarly, in common waxbills *Estrilda astrild*, the regularity of barred plumage on the back is more salient in males than females, and is positively related to body condition and to the expression of coloured ornamental traits (Marques et al. 2016). Moreover, patterns can play roles in broader social contexts not strictly limited to male signalling: in the diamond firetail *Stagonopleura guttata*, the characteristics of flank spots predict social dominance in females (Crowhurst et al. 2012), while in the red-legged partridge, both males and females show off flank stripes during agonistic displays (Bortolotti et al. 2006).

Despite the list of within-species evidence for the use of feather pattern traits in signaling, one fundamental question remains: why some species have patterns while others do not, which begs for evolutionary explanation and between-species comparisons. One straightforward approach to this is to provide insight into the interspecific variations in plumage patterns and to identify their relationships with other morphological or behavioural sexual signals. Multiple traits (e.g. plumage patterns and courtship displays) can evolve in the same direction (e.g. general conspicuousness) under the same selective force, such as strong sexual selection, where redundant or multiple ornamentation is favoured (Møller and Pomiankowski 1993; Johnson 2000; Candolin 2003). Conversely, it is also possible that both morphological ornamentation and behavioural displays become less favoured when organisms are exposed to higher predation risks. Such correlated evolution would also be expected when the traits are under the control of the same pleiotropic mechanisms, e.g. hormones, genes or neurotransmitters. Moreover, when birds have both morphological ornamentation and behavioural displays, the latter signals may work as an "amplifier" of ornamentation (Zahavi 1978; Hasson 1991). As a textbook example, peacocks *Pavo cristatus*, which are known for having long trains with eyespots, perform courtship displays facing towards

the sun to highlight the iridescent colour patterns of the erected feathers (Dakin and Montgomerie 2009). Similarly, visual displays of some birds are performed in a way that enhances the signal efficacy of ornamentation (Candolin 2003; Fusani et al. 2007; Olea et al. 2010; Bortolotti et al. 2011).

In addition, the idea of correlated evolution may hold true for the association among different facets of patterns, i.e. colouration and size. Depending on the strength of the selective force, a plumage pattern may become conspicuous or less conspicuous in terms of both colour and size. In contrast, if it is too costly to have large-sized vivid colour patterns at the same time because of intense predation risks, there might be a trade-off between the two aspects of the patterns. Considering that some birds show sexual dichromatism in melanin- and carotenoid-based colouration (Hill and McGraw 2006), such a relationship between size and colour could also differ between the sexes.

Lastly, comparing the evolution of plumage patterns between sexes would provide insight into their potential roles as sexual signals. Although sexual traits in birds, such as songs and ornamental colours, tend to be male-biased (Dale et al. 2015), it has been reported that plumage patterns are female-biased, suggesting that they function as cryptic sexual signals, which are particularly widespread in females (Gluckman and Cardoso 2010).

Estrildid finches (family: Estrildidae) are ideal candidates to investigate the possible role of plumage patterns in sexual selection. First, within-species evidence in some estrildids suggest that patterns can have signalling functions (zebra finch: Swaddle and Cuthill 1994; Birkhead et al. 1999; diamond firetail: Crowhurst et al. 2012; Zanollo et al. 2013, 2014; common waxbill: Marques et al. 2016). Second, a relatively larger number of species has plumage patterns in this taxonomic group (57.5%), with some showing sexual dimorphism in the presence or conspicuousness of patterns (e.g. Marques et al. 2016, Fig. 1), suggesting the possibility that plumage patterns may be linked to sexual selection. Third, estrildid finches are characterised by elaborate courtship signals, including acoustic and behavioural displays (Goodwin 1982; Baptista et al. 1999; Soma and Garamszegi 2015). Most importantly, when potential mating partners come close, often perching side by side, they show a ritualised courtship dance (Goodwin 1982; Soma and Garamszegi 2015), which is performed by males of some species (Zanollo et al. 2013; Ullrich et al. 2016) or by both

sexes in other species (Ota et al. 2015, 2017; Soma and Iwama 2017). Such behavioural features of estrildid finches often involve display positions in which the plumage colour patterns are exposed and might explain why they frequently have flank patterns (e.g. Crowhurst et al. 2012, see also Fig. 1a–g). Plumage colouration has been studied from evolutionary perspectives in estrildids, but plumage patterns have not been investigated in a comparative phylogenetic context. In our previous comparative phylogenetic studies of estrildid finches (Soma and Garamszegi 2015; Gomes et al. 2017), we did not find a link between the evolution of dance displays and ornamental colouration, measured based on the coverage and reflectance spectrophotometry. In another comparative phylogenetic study, ornamental colouration in males was higher in species with a gregarious nature, suggesting that social selection affects the evolution of plumage colouration (Gomes et al. 2016).

In this study of estrildid finches, we characterised plumage patterns and tested the following set of predictions by applying a phylogenetic comparative approach to provide insight into the evolution of plumage patterns as sexual signals. (1) As visual signals, the conspicuousness of plumage patterns (e.g. size) may have evolved in association with other visual traits, such as pattern colour and courtship displays. (2) The sexes may undergo different selection regimes, which can be detected by comparing the evolution of plumage patterns between the sexes. (3) Interspecific variations in life history can be potentially linked to the interspecific variations in plumage patterns because it has already been shown to be related to plumage colouration (Gomes et al. 2016).

MATERIALS AND METHODS

Collecting the plumage pattern data

We collected data on plumage patterns by taking pictures of skin specimens at the Natural History Museum at Tring, U.K and Yamashina Institute for Ornithology at Chiba, Japan. We sampled five individuals of each sex for each estrildid finch species, when possible, and took pictures from four angles (ventral, dorsal and left and right sides) with a scale using a digital camera (α5000; Sony, Tokyo Japan). We also took UV photos (digital camera: D70s, Nikon, Tokyo Japan; lens: UV-105 mm F4.5, Tochigi Nikon, Tochigi Japan; filter: U360, Hoya Optronics, Tokyo Japan; light: Handy UV Lamp 365nm; AsOne, Osaka Japan), considering that estrildids are likely to have

UV vision (Ödeen and Håstad 2003), to verify that there was no pattern in the non-visible part of the spectrum that was apparent only under UV light. We collected data on both sexes from 126 species, and male data from one species, of the 134 estrildid species. Based on the fact that some estrildid species show intermediate patterns between bars and dots (e.g. overlapped dots forming lines), we applied the definition of pattern trait in a broad sense (i.e. a repetition of the same shape regardless of whether patterns form bars, dots, or mottles) instead of setting small categories depending on unit shape.

We calculated the following four geometric features of patterns from the digital images, using ImageJ 1.48v (Schneider et al. 2012). We measured pattern coverage on the dorsal, ventral and side (average of left and right sides) views, calculated as the percentage of patterned area per total body surface in each picture. As an index of pattern conspicuousness, we measured the size of the unit shape that constituted the pattern, by taking the width of a bar or the diameter of a mottle or a dot (in mm). After checking that each of the four variables showed fairly high repeatability within the same sex of each species ($r > 0.86$, $P < 0.0001$; Garamszegi 2014), we used sex-specific average values for each species in subsequent analyses. As some species had multiple types of patterns (e.g. zebra finch males having flank dots, chest stripes, and tail bars), we counted the total number of patterns for each sex of each species. The above four measures were treated as 0, respectively, when no plumage pattern was evident. To avoid potential interobserver bias, all measurements were performed by the same observer (MS). Using the species for which we measured specimens in the two museums, we checked for potential biases originating from the fact that different museums may store specimens differently or may have collections of different ages. However, we found no differences between the museums (linear mixed model including species as a random effect and sex and museum as fixed effects: effect of museum on side coverage, $t = 1.01$, $P = 0.32$; effect of museum on ventral coverage, $t = 1.11$, $P = 0.27$; effect of museum on dorsal coverage, $t = 0.69$, $P = 0.49$; effect of museum on pattern unit size, $t = 0.53$, $P = 0.60$).

In addition, we recorded whether the patterns that each species/sex had were composed of melanin-based or carotenoid-based colouration or a mixture of both. Melanin and carotenoid are the two main pigment types in birds that are responsible for red, and orange, or black, gray, and brown, respectively (Hill and McGraw 2006). Both pigmentations, including pigment-based patterns, are

argued to play roles in signaling individual conditions (Griffith et al. 2006; Pérez-Rodríguez et al. 2017). Based on the visual inspection of the feather colors, they were scored as melanin (0); melanin and carotenoid (1); or carotenoid (2). Melanin patterns are colored with combinations of black, grey, brown and white, while the carotenoid patterns are colored with red and white (see Fig. 1a,d for the comparison of melanin and carotenoid patterns expressed in females and males respectively). As we observed that some birds have white spots on the basis of a black-to-red gradation background, they were categorized as 'melanin and carotenoid' patterns.

Other sexual signals and life-history traits

As potential signals that can co-evolve with plumage patterns, we characterised the degree of expression of courtship displays of each sex. Specifically, we quantified the dance repertoires of males and females, under the prediction that the complexity of a visual display (i.e. courtship dance) evolved jointly with plumage conspicuousness to emphasise showiness. Courtship dance is stereotyped within species and is expressed as a combination of several simple actions (e.g. Restall 1996; Zanollo et al. 2013; Ota et al. 2015; Ullrich et al. 2016; Soma and Iwama 2017). We counted the number of dance categories that constituted the courtship displays of each species, separately for males and females (see also Soma and Garamszegi 2015).

In addition, we also considered life-history variables that likely affect the cost of reproduction, such as median clutch size, and body size taken as body length. As some estrildid finches in Africa are targets of interspecific brood parasitism by birds in the genus Vidua (Sorenson et al. 2004), the presence or absence of interspecific brood parasitism was scored as 0 or 1 (parasitism absent–present, respectively). Furthermore, some estrildid finches show intraspecific brood parasitism (Yom-Tov 2001), which was scored as 0 or 1 (parasitism absent–present, respectively). Although most species do not defend territories, the degree of gregariousness varies among species and was scored as follows: colonial breeders or species with social systems in which multiple pairs keep contact with each other even during the breeding season were given a score of 3; highly social and gregarious species, in which aggregations mainly occur outside the breeding season were given a score of 2; species that breed usually in pairs or in small parties were given a score of 1; and strictly territorial species were given a score of 0. All of these data were compiled

from an earlier study (Soma and Garamszegi 2015), and the number of focal species was limited (n = 85) because of the availability of information.

Phylogeny

For the comparative phylogenetic analyses described below, we could not obtain an overwhelmingly supported consensus phylogenetic tree with branch lengths, but were able to derive multiple equally likely candidate trees from Jetz et al. (2012). We derived 1,000 trees from the dataset for the focal species in each analysis and used their consensus tree without branch length to reconstruct the ancestral state or used each of them in phylogenetic regressions followed by multi-model inference (see below).

Statistical analyses

Principal component analysis (PCA)

The four geometric variables that describe plumage patterns (dorsal, ventral and side coverage and unit size) are mutually dependent and may be related with the number of pattern types of each species/sex. We conducted a principal component analysis (PCA) to define independent axes that have distinct biological meaning from the raw variables, in which we used square root values for coverage, pattern unit size, and the number of patterns of each sex. We performed a single conventional PCA for a mixed sex dataset, instead of repeating phylogenetic PCA for each sex, in order to obtainin PC scores comparable between sexes. Specifically, using data from 127 males species and 126 females species, we aimed to achieve dimension reduction by extracting principal component axes (PCs) that account for most of the variance (i.e. >70%), have eigenvalues larger than 1 and have biologically interpretable component loadings. Below we show PCA results for PC1 and PC2, but based on the above criteria we used PC1 only in the subsequent analyses (see Results). We confirmed that these PC scored obtained from a conventional PCA were highly correlated with those obtained from phylogenetic PCA ($r > 0.997$, $P < 0.0001$). We used R 3.3.1 software (R Core Team 2016) for the analyses described here and below, except otherwise stated.

Ancestral state reconstruction

To characterise the evolutionary history of plumage patterns, and to compare it between sexes, we reconstructed the ancestral state using the PC scores in Mesquite (Maddison and Maddison 2011). A consensus phylogenetic tree was obtained based on 1,000 trees from the dataset (Jetz et al. 2012). We had to use parsimony methods instead maximum likelihood because the latter is not available for our data, i.e. multi-furcating tree.

The phylogenetic relationship between colour and patterns

We investigated the association between geometric features and colours of the patterns with the aim of revealing a positive or negative correlation between the two different aspects under our predictions. We used species that have a plumage pattern, and tested the effects of pattern colour (i.e. melanin, carotenoid or mixture of both) and sex on PC1. Non-independence of the data due to the phylogenetic relatedness of species was controlled by Bayesian phylogenetic mixed models (Hadfield and Nakagawa 2010) in R package 'MCMCglmm' (Hadfield 2010) because it allows multiple data entries (i.e. male and female PC scores) per species. In the model, we used a Gaussian error distribution, and the priors [G = list(G1= list(V = 1, nu = 0.02), G2 = list(V = 1, nu = 0.02))]. We repeatedly fit the same model using each of the 1,000 phylogenetic trees obtained from the dataset (Jetz et al. 2012), all of which successfully converged, and obtained the mean coefficients for the predictor variables and their 95% confidence interval by model averaging the 1,000 outcomes. We weighted parameter estimates based on the DIC of the respective model corresponding to a particular tree.

For this particular analysis, we relied on MCMCglmm because we needed to analyse the data with multiple entries (i.e. male and female variables) per species that requires approaches based on phylogenetic mixed modeling. In the rest of the analyses as below, we applied the phylogenetic generalised least-squares (PGLS) regression technique available in the package phylolm (Ho et al. 2016) that could be run separately for males and females.

The phylogenetic relationship between courtship dance and plumage patterns

To examine the potential relationships between plumage patterns and courtship dance, we tested if the PC1 co-varied with the dance repertoire at the interspecific level, separately in the two sexes. We fitted PGLS regressions to control for phylogenetic dependence by using the 1,000

phylogenetic trees as explained earlier, in which we entered PC1 as predictor variables and dance repertoire as a response variable. As dance repertoires are discrete values (count data), we used regression with Poisson error distribution. For each tree, we fitted models with identical predictor/response structure, and then derived mean and confidence estimates across trees for the estimated parameters (slopes and intercepts). Summary statistics were obtained via model averaging Garamszegi and Mundry 2014). For the PGLS modeling we used the R package 'phylolm' that allows Poisson distribution (Ho et al. 2016)

The phylogenetic relationship between plumage patterns and life-history variables

We tested for the relationship between plumage pattern and life-history variables that likely affect the cost of reproduction. Specifically, we used PGLS framework available in R package 'phylolm' again, and constructed models in which clutch size, body size, presence of interspecific and intraspecific brood parasitism and sociality were entered as predictor variables and PC1 were used as a response variables (different models for males and females), using Gaussian distribution. As in the above analyses, we used the same set of 1,000 phylogenetic trees and applied model averaging to obtain mean and confidence estimates for the estimated parameters (intercept and slopes for each predictor). Parameter estimates from each model were weighted according to their relative fit to the data (Garamszegi and Mundry 2014).

RESULTS

Principal component analysis

PC1 accounted for 72.8% of the total variation in the variables that were taken to describe plumage pattern and had positive loadings (>0.36) for all five variables (Table 1, Fig. 1h). Therefore, higher PC1 scores can indicate larger and conspicuous patterns. In contrast, PC2 accounted for only 15.2% of the total variation and had a higher positive loading (>0.8) only for dorsal coverage but negative loadings (<−0.30) for ventral coverage and pattern unit size (Table 1, Fig. 1h). Given the low eigenvalue of PC2 (Table 1), we mainly focused on PC1 (conspicuousness) hereafter.

Comparison of pattern evolution between sexes

The reconstruction of ancestral states revealed that the plumage colour patterns evolved in a similar fashion in males and females (Fig. 2, see also Supplementary Material Fig. S1). Additionally, we also directly compared PC1 between the sexes using the paired t-test and found that PC1 did not differ significantly between the sexes (paired t-test: $t = 1.04$, $P = 0.302$, $N = 124$ species).

The phylogenetic relationship between color and patterns

We examined whether geometric features and the colours of patterns were inter-related by focusing on species that had plumage patterns and for which information on the phylogenetic relationships was available (male: $N = 63$ species; female: $N = 65$ species). We found an interspecific relationship between colour and conspicuousness of patterns: PC1 scores were lower in species in which patterns were carotenoid-dependent than in species that had melanin-dependent trait expression in both sexes (Fig. 3, Table 2).

The phylogenetic relationship between courtship dance and plumage patterns

Using the species data for which dance and pattern data were available, we examined the potential relationship between PC1 and complexity of the dance repertoire, and found that PC1 co-varied positively with dance repertoire in each sex (Table 3, Fig. 4). These associations indicate that species with conspicuous plumage patterns have more complex dances.

The phylogenetic relationship between plumage patterns and life-history variables

In both males and females, we found a significant association between plumage pattern and intraspecific brood parasitism, as PC1 was positively correlated with this trait (Fig. 5, Table 4). The remaining life-history traits were not related significantly to the PC 1 (Table 4)

DISCUSSION

The present phylogenetic comparative study focusing on geometric features of plumage patterns in estrildid finches revealed that they might have evolved for signaling function, for at least two reasons. First, the PCA showed that interspecific variations in patterns could be described along the spectrum of conspicuousness.. The PC1 reflected larger and bold patterns that are possibly composed of multiple shapes (e.g. Fig. 1b). Second, through the phylogenetic comparative analyses of PC1, we found evidence that plumage patterns may be co-evolutionarily related to another sexual signal (i.e. dance repertoire), and to intraspecific competition (i.e. presence of intraspecific brood parasitism). As these trends were consistent between sexes (Tables 2–4), and males and females showed very similar levels of conspicuousness (Figs. 1–2) we can infer that basically the same selective force is acting on the evolution of plumage patterns in males and females. Alternatively, selection may favor the trait in one sex only, but its effect is also manifested in the other due to strong genetic correlation between sexes.

Lack of sex-biased evolution of plumage patterns

Evolution of female ornamentation is a challenging question, and discussed in relation to the presence of intersexual genetic correlation, and/or sexual and social selection (West-Eberhard 1979; Tobias et al. 2012), which is generally applicable to behavioral and morphological traits of estrildid finches (Soma and Garamszegi 2015). Specifically, estrildids are characterised by multiple sexual traits that can be shared between sexes. Females of some species sing courtship songs like males (Goodwin 1982; Geberzahn and Gahr 2011, 2013), whereas females of other species perform courtship dance displays identical to those of males (Ota et al. 2015; Soma and Garamszegi 2015; Soma and Iwama 2017) or have plumage ornamentation comparable to that of males (Zanollo et al. 2014; Marques et al. 2016). However, these sexual signals (song, dance and plumage colouration) are generally male-biased with regard to presence/absence or degree of elaboration in estrildids (Soma and Garamszegi 2015; see also Dale et al. 2015), which is contrasted with the plumage colour pattern (cf. Gluckman and Cardoso 2010). Only a few species (*Spermophaga spp*.) show female-biased sexual dimorphism with regard to the presence of patterns, and there was no sex

difference in PC1. Moreover, the sexes showed similar evolution of PC1 (Fig. 2). This is quite different from what was found in peafowls and their related taxa, where eyespot patterns likely have evolved primarily in males for female choice (Sun et al. 2014). Presumably, plumage patterns in female estrildids would function either for sexual signaling to get mates (sexual selection), or for status signaling to repel rivals even outside the reproductive context (social selection)(e.g. Kabasakal et al. 2017). Although there is limited empirical evidence available showing that selection operates on female estrildid finches, a study on one species supports this idea. Diamond firetail *S. guttata*, females have more flank spots than males on average (Zanollo et al. 2014), and the number of spots reflects physical condition (Zanollo et al. 2012) and predicts social dominance in females (Crowhurst et al. 2012). Therefore, similar selection forces may mediate the interspecific variation in plumage patterns in both males and females.

Hiding vs. signaling

Diversity of colour patterns in animals can be explained in the light of hiding vs. signaling strategy (Endler 1978; Stevens and Merilaita 2009; Gluckman and Cardoso 2010). Some animals balance the two by having cryptic patterns over the body and conspicuous patterns on small areas that are important for communication, like face or tail (Caro 2005; Ancillotto and Mori 2016), while others have dual-purpose colour patterns (e.g. squids: Mäthger and Hanlon 2006; Mäthger et al. 2012). In line with these previous insights into non-bird species, our findings indicate that plumage patterns in estrildid finches are also the product of a compromise between hiding and signalling, as suggested by Endler (1978). Estrildid finches need to escape potential predators, but they also need to be showy enough to attract or deter conspecifics. As a consequence, they cannot have patterns that are large and red at the same time (Fig. 3), or otherwise their appearance would stand out too much; thus, making it difficult to avoid predation. The gregarious nature and colonial breeding of estrildid finches are likely a response to high predation risks, at least in some species (Zann 1996). Although we did not find a direct link between gregariousness and plumage patterns in this study, some estrildid species build nests in a thorny tree or near a wasp nest (Goodwin 1982; Barnard and Markus 1990; Beier et al. 2006), while others add carnivore scat to their nest to prevent predation (Schuetz 2004). These strategies may indirectly suggest how much predation pressure can

affect the life of estrildid finches. Phylogenetic comparative studies particularly focusing on this aspect of breeding biology could be designed in the future into this promising direction.

Some finches are also known for their showy plumage patterns that play roles in sexual/social contexts (Swaddle and Cuthill 1994; Crowhurst et al. 2012; Zanollo et al. 2013, 2014; Marques et al. 2016). Consistent with such earlier findings, in this comparative study, we gained results that support the hypothesis that plumage patterns evolve alongside their signaling roles in sexual selection. Specifically, we found that the complexity of courtship dance has evolved in the same direction as the conspicuousness of plumage patterns (Table 3, Fig. 4). This supports the idea that the two visual traits evolved under the same selective force, and our findings thus meet the prediction of the 'amplifier' hypothesis (Zahavi 1978; Hasson 1991). However, more detailed investigations are needed to clarify how gestural displays functionally enhance signal efficacy of plumage patterns (or vice versa) in estrildid finches. In general, we expect that motions (i.e. direction, speed) might play an important role in how patterns are perceived by receivers (cf. Dakin and Montgomerie 2009). In the context of predator-prey interactions, it was already reported that particular patterns make animals less detectable especially while they are moving (e.g. Halperin et al. 2017). Such potential roles remain to be explored in the context of sexual signaling.

The function of plumage patterns could also include social signaling in addition to the sexual context. Having signaling traits that facilitate individual recognition is favored especially in species living in colonies and having agonistic competitions (Tibbetts and Dale 2007). Here, we uncovered that the presence of intraspecific brood parasitism was associated with conspicuous plumage patterns (Table 4). This is also consistent with our previous study (Soma and Garamszegi 2015), in which we detected associations between dance complexity and intraspecific brood parasitism in both sexes. Apparently, the two visual signals, dance and plumage patterns, evolved in the same direction in response to intraspecific parasitism (Table 4). Intraspecific parasitism can cause intense within-species competition, where for instance, host and parasite females can have higher chance to directly interact or fight (e.g. Semel and Sherman 2001; Åhlund 2005). In that case condition-dependent honest indicators of quality (e.g. Marques et al. 2016) would be effective for avoiding escalated costly aggression. This is comparable to the findings from the passerine-wide phylogenetic comparative study showing that females of cooperative breeding species are more

likely to have ornamental colouration due to female competition (Dale et al. 2015).

To conclude, we have shown that plumage patterns constitute an important visual trait that can be the subject to both natural and sexual selection forces. Such a finding could not have been discovered solely with spectrometric techniques that are more commonly applied for examining the evolution of plumage traits of birds. Our results strongly suggest that the macroscopic aspects of plumage traits may open a new research agenda for understanding the evolution of complex plumage traits in birds, as done in other taxonomic groups (Ortolani 1999; Seehausen et al. 1999; Caro 2005; Caro et al. 2011; Allen et al. 2011; Santana et al. 2012; Allen et al. 2013; Kelley et al. 2013; Ancillotto and Mori 2016). We suggest that colour and geometric features should be integrated to reach a comprehensive understanding of the physical appearance of complex plumage traits in animals (Endler 2012).

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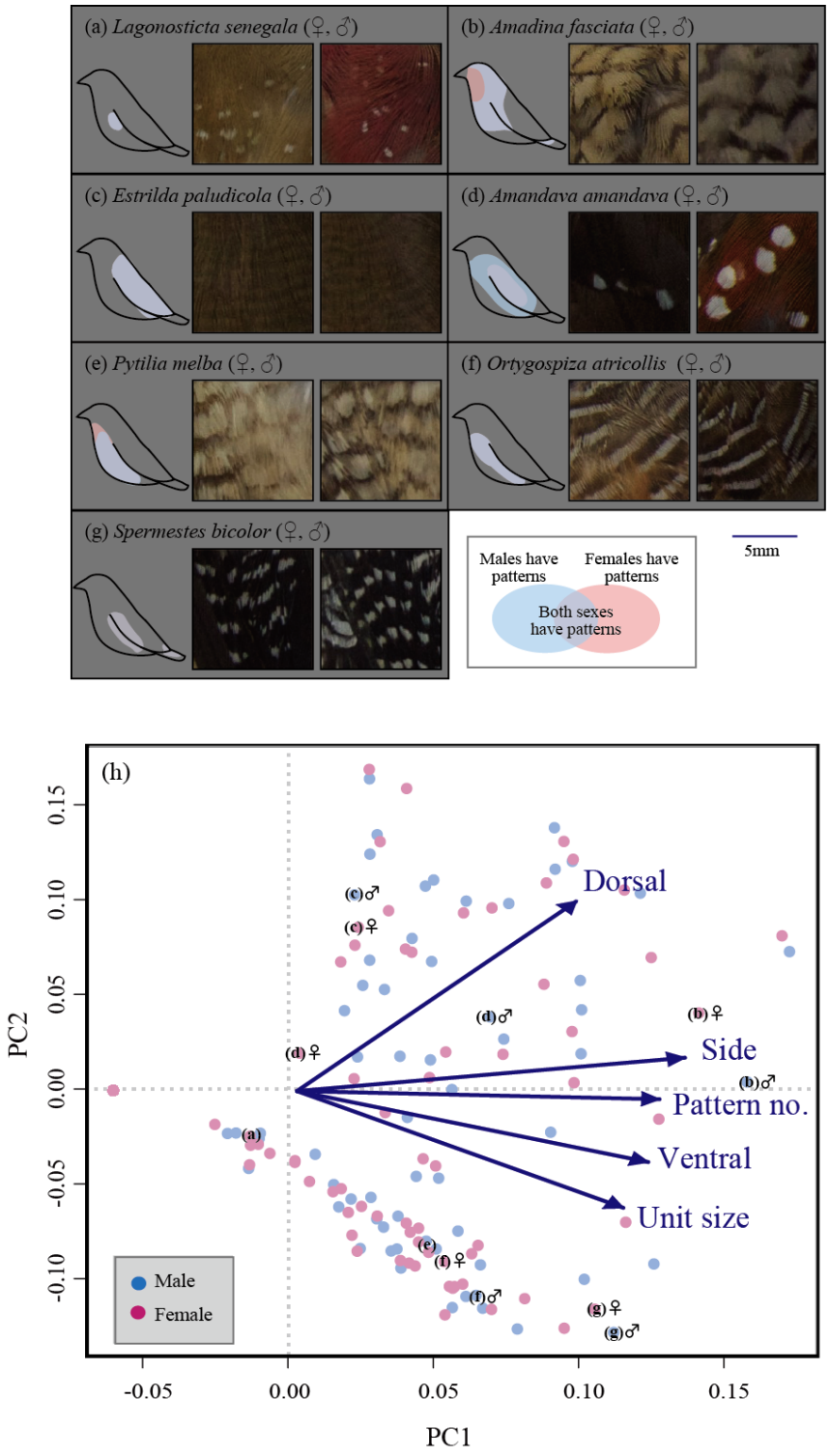

Figure 1. Examples of interspecific and intersex variations in plumage colour patterns (a–g), and the loading plot for the principal components analysis on the geometric features of plumage patterns (h). The patterned area on the body surface is schematically shown in the illustrations (a–g). Data points of the examples (a–g) are shown on the scatter plot, where the data points of males and females overlap for some species (a, e). Note that we performed a single PCA for a mixed sex dataset (see methods), but that we plotted male and female in different colors only for illustrative purpose.

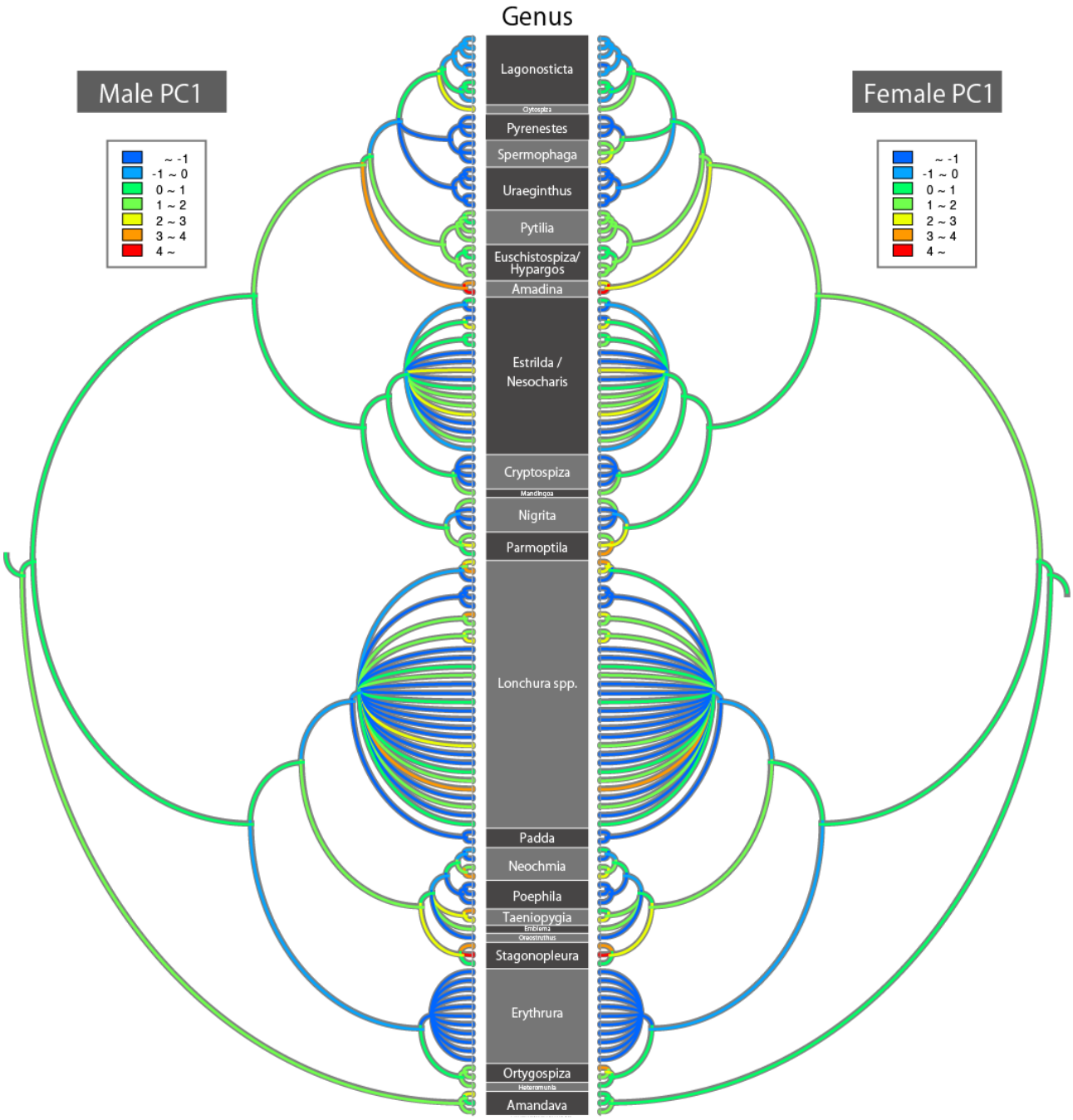

Figure 2. Reconstruction of ancestral states of plumage colour patterns (PC1) in males and females (see Supplementary Material Fig. S1 for PC2)

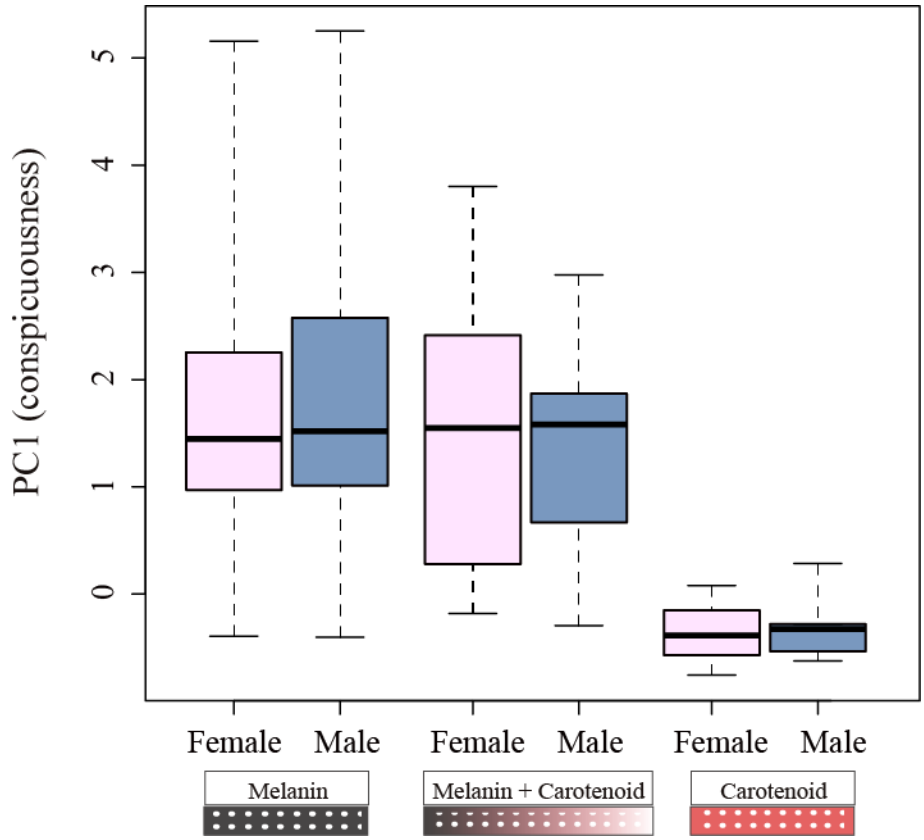

Figure 3. Comparison of principal component 1 (PC1) (pattern conspicuousness) of males and females in species with melanin- or carotenoid-based plumage patterns (see Table 2 for statistical outcomes). Square bars at the bottom show a schematic view of the plumage colour categories ('Melanin and carotenoid' patterns typically have black-to-red gradation background with white spots, while the other two patterns have monotone backgrounds).

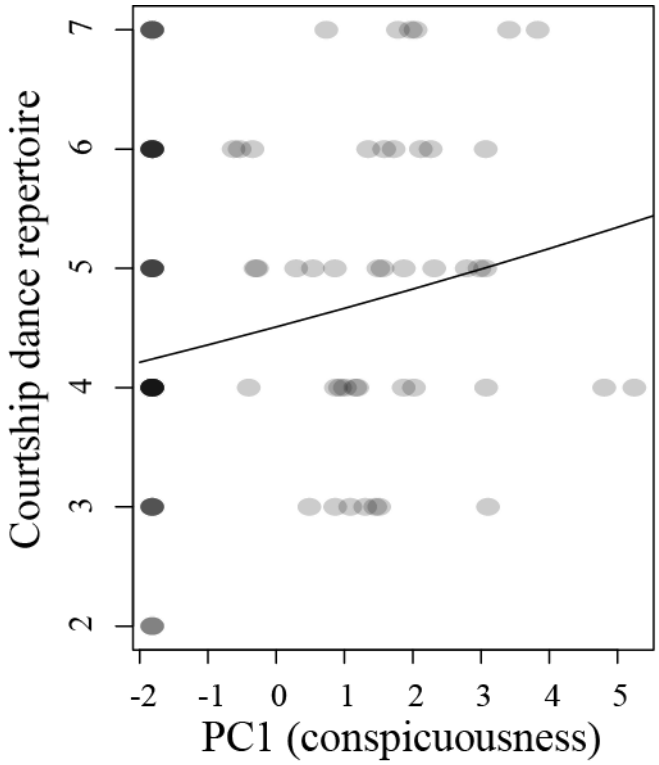

Figure 4. Relationship between the complexity of courtship (dance repertoire) and PC1) in males. Species data are shown with semi-transparent plots and the regression lines are drawn based on estimated parameters from the phylogenetic analyses summarized in Table 3.

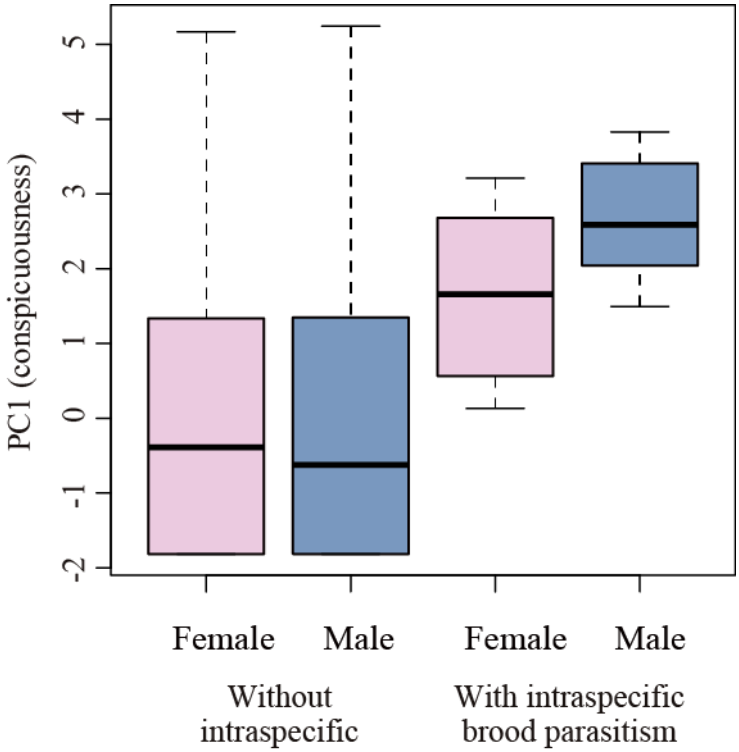

Figure 5. Comparison of male and female PC1 between species with and without intraspecific brood parasitism.

Table 1. The results of the principal components analysis on mixed sex data of patterned variables.

	PC1	PC2
Side coverage (square root)	0.505	0.141
Ventral coverage (square root)	0.457	-0.300
Dorsal coverage (square root)	0.364	0.803
Pattern unit size	0.425	-0.494
Number of pattern types	0.472	-0.035
Eigenvalue	3.638	0.761
Proportion of variance	0.728	0.152
Cumulative proportion	0.728	0.880

Table 2. Effects of colour of plumage pattern (0: melanin; 1: melanin and carotenoid; 2: carotenoid) and sex on PC1. Bold typeface is used when 95% confidence interval (CI) does not contain zero; thus, it can be interpreted as a significant effect.

	Coefficient	95% CI	
Intercept	1.776	[1.208	2.297]
Color	**-0.841**	**[-1.365**	**-0.282]**
Sex	0.029	[-0.158	0.217]

Table 3. Effects of PC1 on the dance repertoire of each sex. Bold typeface is used when 95% confidence interval (CI) does not contain zero; thus, it can be interpreted as a significant effect.

	(a) Male dance repertoire				(b) Female dance repertoire			
	Coefficient	SE	95% CI		Coefficient	SE	95% CI	
Intercept	1.532	0.108	[1.317	1.747]	0.672	0.381	[-0.090	1.434]
PC1	**0.029**	**0.009**	**[0.011**	**0.047]**	**0.090**	**0.039**	**[0.012**	**0.167]**

Table 4. Effects of life-history traits on PC1 (plumage pattern conspicuousness) in males (a) and females (b), as estimated from the appropriate phylogenetic generalised least-squares models. Bold typeface is used when 95% confidence interval (CI) does not contain zero; thus, it can be interpreted as significant association.

	(a) Male PC1				(b) Female PC1			
	Coefficient	SE	95% CI		Coefficient	SE	95% CI	
Intercept	1.736	2.268	[-2.801	6.273]	0.952	2.126	[-3.301	5.205]
Clutch size	-0.106	0.271	[-0.648	0.437]	-0.203	0.236	[-0.676	0.270]
Body size	-0.107	0.146	[-0.399	0.184]	0.010	0.141	[-0.272	0.293]
Interspecific brood parasitism	0.999	0.508	[-0.017	2.015]	0.831	0.506	[-0.182	1.843]
Intraspecific brood parasitism	**3.286**	**0.673**	**[1.940**	**4.633]**	**2.539**	**0.716**	**[1.107**	**3.872]**
Sociality	-0.125	0.241	[-0.607	0.358]	-0.212	0.233	[-0.678	0.253]