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Ana Cristina Ribeiro Gomes

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Dissertação de Mestrado apresentada à
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2014

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, _____/_____/_____

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Abstract

Sexual selection is a component of natural selection largely responsible for the evolution of ornaments. Sexually-selected ornamentation tends to evolve rapidly and mediates species recognition and reproductive isolation, and it has been proposed that stronger sexual selection leads to an increase in speciation. But, collectively, comparative work has failed to demonstrate a relationship between the strength of sexual selection and speciation. Since evolutionary changes in ornaments often involve repeated gains and losses, I suggest that rates of phenotypic evolution may not increase with the strength of sexual selection, because alternation of gains and losses becomes rarer in species where ornamentation is already widespread. Therefore, stronger sexual selection may not increase speciation rates, even if changes in sexually-selected ornamentation do promote speciation. Furthermore, sexual selection can also mediate ecological speciation because sexually-selected ornamentation might be influenced by several socio-ecological conditions, in ecologically differentiated populations.

In my thesis I address two main issues: (1) I test the relation between changes in sexual ornamentation and speciation, and in addition test if stronger sexual selection, as evaluated by the degree of ornamentation across species, promotes speciation increase; and (2) I test which ecological and social traits influence differences in sexual ornamentation among species, in order to better understand how ornaments evolve. To test these ideas robustly, I used Estrildidae finches, one of the largest and fastest radiations of songbirds, to study colour ornamentation. I studied several aspects of colour ornamentation: maximum and mean plumage colour saturation, maximum achromatic contrast, extent of ornamental coloration, and bill colour; additionally, for some analyses, I also looked specifically at yellow-to-red and ultraviolet(UV)/blue saturation.

I found that increased colour ornamentation was not related to the quantity of speciation through the Estrildidae phylogeny, or to the time since the most recent speciation. Most ornamental traits fitted a model of speciational evolution better than a model of gradual evolution, for both sexes, meaning that changes in ornamentation are associated with, and perhaps promote, speciation. Together, these results indicate that diverging ornamentation, rather than the strength of sexual selection per se, is implicated in speciation. I conclude that past work relating the strength of sexual

selection to speciation may have greatly underestimated the importance of sexually-selected ornamentation in speciation.

Among a large set of social and ecological traits, the degree of gregariousness was the trait more strongly associated with differences in ornamental coloration, with more gregarious species having more saturated plumage colour, including more short- (blue/UV) and long-wavelength (yellow-to-red) plumage colour saturation, in both sexes, and additionally having higher achromatic difference in males, and more ornamented bill (more carotenoid-content) in females. These results suggest that individuals in flock-living species interact more with each other which can increase the opportunity for sexual selection and for the evolution of ornamentation. Some other ecological and social variables appeared associated with individual ornamental coloration traits, but those effects were not as strong or consistent. The stronger relation between gregariousness and sexual ornamentation could maybe result from the great variation in social systems, among estrildid finches.

Keywords: Estrildidae, colour ornamentation, sexual selection, speciation, ecological speciation.

Resumo

A seleção sexual é uma componente da seleção natural responsável pela evolução dos ornamentos. Os ornamentos selecionados sexualmente tendem a evoluir rapidamente e influenciar o reconhecimento das espécies e isolamento reprodutivo, pelo que tem sido proposto que quanto mais forte a seleção sexual, maior o aumento na especiação. Mas, coletivamente, trabalhos comparativos falharam na demonstração de uma relação entre a força da seleção sexual e a especiação. Uma vez que as mudanças evolucionárias nos ornamentos muitas vezes envolvem sucessivos ganhos e perdas, eu sugiro que as taxas de evolução fenotípica podem não aumentar com a força da seleção sexual, porque a alternância entre ganhos e perdas torna-se mais rara em espécies onde a ornamentação está amplamente distribuída. Por isso, um grau de seleção sexual mais forte pode não levar ao aumento da taxa de especiação, mesmo que as mudanças na ornamentação sexualmente selecionada promovam a especiação. Para além disso, a seleção sexual pode também ter um efeito sobre a especiação ecológica, porque a ornamentação sexualmente selecionada pode ser influenciada por várias condições socio-ecológicas, em populações ecologicamente diferenciadas.

Na minha tese eu estudo dois assuntos principais: (1) estudo a relação entre as mudanças nos ornamentos sexuais e especiação, e ainda averiguo se um grau de seleção sexual mais forte, avaliada pelo grau de ornamentação entre espécies, promove o aumento da especiação; e (2) estudo quais as características ecológicas e sociais que influenciam as diferenças na ornamentação sexual entre espécies, de forma a uma melhor compreensão sobre a evolução dos ornamentos. Para testar estas ideias robustamente, eu estudo a cor da ornamentação de espécies da família Estrildidae, que constituem uma das maiores e mais rápidas radiações de aves canoras. Para o estudo obtive várias características da cor ornamental: saturação máxima e média da cor, contraste acromático máximo, extensão da cor ornamental, e a cor do bico; adicionalmente, para realizar algumas análises, eu também estudei especificamente a saturação amarelo-a-vermelho e ultravioleta (UV)/azul.

O aumento da cor ornamental não está relacionado com a quantidade de especiação através da filogenia de Estrildidae, ou com o tempo desde a especiação mais recente. A maioria das características ornamentais é melhor suportada pelo modelo de evolução especiacional, que pelo modelo de evolução gradual, em ambos os sexos, o que significa que as mudanças na ornamentação estão associadas com, e

talvez promovam, a especiação. Em conjunto, estes resultados indicam que é a divergência da ornamentação, em vez da força da seleção sexual per se, que está envolvida na especiação. Estudos anteriores que relacionam a força da seleção sexual com a especiação, provavelmente subestimaram a importância da ornamentação, sexualmente selecionada, na especiação.

De entre um grande conjunto de características sociais e ecológicas, o grau de gregariedade foi a característica associada mais fortemente a diferenças na coloração ornamental, com as espécies mais gregárias a possuírem uma cor de plumagem mais saturada, incluindo uma coloração com mais cores de comprimentos de onda curtos (azul/UV) e longos (amarelo-a-vermelho), em ambos os sexos, e adicionalmente possuindo uma maior diferença acromática, em machos, e um bico mais ornamentado (maior conteúdo em carotenóides), em fêmeas. Estes resultados sugerem que indivíduos de espécies que vivem em bandos interagem uns com os outros mais, o que pode aumentar a oportunidade para a seleção sexual e para a evolução da ornamentação. Outras variáveis ecológicas e sociais aparecem associadas com características de cor ornamental individuais, mas os seus efeitos não são tão fortes ou consistentes. A forte relação entre gregariedade e ornamentação sexual poderá ser o resultado da grande variação de sistemas socias, entre espécies da família Estrildidae.

Palavras-chave: Estrildidae, cor ornamental, seleção sexual, especiação, especiação ecológica.

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Abbreviations

PC – Principal Component

PCA – Principal Component Analysis

PGLS – Phylogenetic Generalized Least Squares

UV – Ultraviolet

Introduction

Sexual selection is a component of natural selection driven by variation in mating or fertilization success or social competition signals (West-Eberhard 1983; Andersson 1994; Ritchie 2007; Seddon et al. 2013). Sexual selection explains the evolution of ornaments and other secondary sexual characters. These secondary sexual traits are usually more developed in males, because males typically have variation in mating success (e.g. Andersson 1994). But females also often express sexual ornamentation, either due to selection on females (e.g. related with female-female competition; Burns 1998; Amundsen 2000) or due to correlated evolution with male phenotypes (e.g. Cardoso and Mota 2010). The differences between male and female sexual ornamentation, within the same species, can be caused or maintained by different selective pressures among the sexes (Badyaev and Hill 2003).

Sexually-selected traits such as ornamentation tend to evolve rapidly and lead to differences between closely related taxa (e.g. West-Eberhard 1983; Civetta and Singh 1998; Panhuis et al. 2001), especially in geographically separated populations (Servedio and Burger 2014). Because sexual ornamentation is involved in species recognition and mate choice, divergence in ornamentation may contribute to reproductive isolation and further evolutionary divergence, among species. Therefore, it has been hypothesized that sexual selection promotes reproductive isolation and, thus, increases the species-richness of taxonomic groups (e.g. Barraclough et al. 1995; Moller and Cuervo 1998; Seddon et al. 2013).

Although sexual selection has for long been suggested to promote speciation, comparative studies have found mixed support for the predictions that more strength of sexual selection should be associated with increased speciation or higher species-richness (papers supporting/partially supporting the hypothesis: Barraclough et al. 1995; Mitra et al. 1996; Moller and Cuervo 1998; Owens et al. 1999; Arnqvist et al. 2000; Katzourakis et al. 2001; Stuart-Fox and Owens 2003; Seddon et al. 2008; Hugall and Stuart-Fox 2012; Seddon et al. 2013. papers not supporting/partially not supporting the hypothesis: Mooers and Møller 1996; Gage et al. 2002; Morrow et al. 2003; Isaac et al. 2005; Phillimore et al. 2006; Cardoso and Mota 2008; Rabosky and Matute 2013; Huang and Rabosky 2014; Servedio and Burger 2014. reviewed in: Ritchie 2007; Kraaijeveld et al. 2011). For example, in birds, one of the most studied taxonomic groups in this respect, one of the largest-scale comparative study so far, demonstrated

effects of ecological traits on species richness, but was not able to find an effect of sexual selection (Phillimore et al. 2006).

An argument that has rarely been considered by researchers is that the hypothesised relation between strength of sexual selection and speciation is indirect and may at times be reversed (Cardoso and Mota 2008). Sexual selection should cause the evolution of ornamentation, and then the divergence in ornamentation among populations, should promote reproductive isolation and speciation. Since divergence in ornamentation could occur either by gains or losses of ornamentation, it may be that both increased and decreased strength of sexual selection (leading to ornament gains and losses, respectively) promote reproductive isolation. In fact, the evolutionary dynamics of sexual ornamentation is characterized by frequent gains and losses (e.g. Kimball et al. 2001; Wiens 2001; Ödeen and Björklund 2003). I hypothesise that in clades that are overall little ornamented (which experience weak sexual selection), increasing the strength of sexual selection should result in more changes in ornamentation (because sexual selection is needed for ornaments to evolve in the first place; left part of Figure 1). But in clades where ornamentation is already

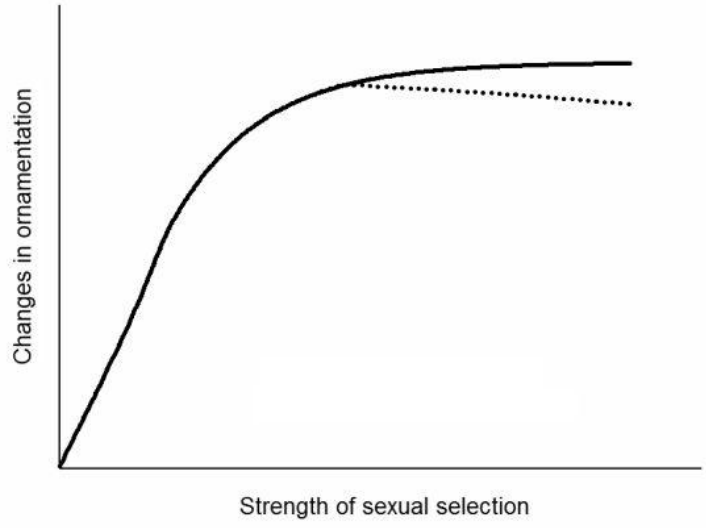

Figure 1. Hypothetical relation between the strength of sexual selection and evolutionary changes in ornamentation. The left part of the graph corresponds to taxa experiencing weak sexual selection and which are, consequently, little ornamented. It is likely that such taxa conform to the classic hypothesis that stronger sexual selection increases the amount of evolutionary changes in ornamentation. The right part of the graph corresponds to taxa under strong sexual selection and where, consequently, sexual ornamentation is widespread. It is unlikely that for those taxa the amount of evolutionary changes in ornamentation should keep increasing with the strength of sexual selection, because the rate of phenotypic evolution eventually reaches a maximum. It may even be that the rate of phenotypic evolution decreases under very strong sexual selection (dashed line) because alternation of ornamental gains and losses becomes rare.

widespread (e.g. in bird taxa, which experience strong sexual selection) further increasing sexual selection probably does not indefinitely result in more frequent changes in ornamentation (right part of Figure 1). It is even possible that under very strong sexual selection the rate of phenotypic evolution in ornamentation actually decreases, because there is no alternation of gains and losses happening (dashed line in Figure 1). Yet another reason by which strong sexual selection may act against speciation is the possibility that, upon secondary contact, sexual preferences introgresses among incipient species and destroys reproductive isolation (Servedio and Burger 2014). These reasons might explain why past studies failed to show that cladogenesis increases in taxa under stronger sexual selection.

One of the aims of this thesis is to test for relations between sexual selection and speciation, but going beyond the classic hypothesis that stronger sexual selection should cause more speciation. With this goal, I studied the evolution of ornamental coloration in one of the largest avian families, the Estrildidae finches (see below). In addition to testing if stronger sexual selection (as evaluated by the extent and intensity of ornamental coloration) promotes speciation, I also tested the hypothesis that changes in ornamentation (whether increases or decreases) are associated with speciation (Cardoso and Mota 2008). The latter hypothesis predicts that phenotypic divergence in ornamentation is proportional to the quantity of speciation events separating different species, rather than to the amount of time separating species (Mooers et al. 1999). I tested this prediction with likelihood tests comparing alternative models of phenotypic evolution (Mooers et al. 1999) for ornamental coloration, across the family Estrildidae.

Another aim of the thesis is to investigate causes for the evolution of sexual ornamentation, to gain a more complete picture of how sexually-selected ornamentation influence speciation. Sexual selection and ornamentation can be affected by various socio-ecological factors (e.g. Boughman 2002; Candolin and Heuschele 2008; Maan and Seehausen 2011; Baldassarre et al. 2013), including habitat properties and social organization. Therefore, ecological speciation could be mediated by sexual selection if, for example, colonizing new habitats precipitates divergence in sexually-selected traits that then contribute to reproductive isolation, between the ecologically differentiated populations (e.g. Schluter 2001; Rundle and Nosil 2005; Schluter 2009; Vonlanthen et al. 2012). With the above goal, I tested whether a set of ecological and social traits, which have been predicted to influence sexual selection, are associated with differences in the extent or intensity of colour ornamentation across the family Estrildidae. These traits include, for example, gregariousness and migration, which were proposed to increase the strength of sexual

selection and have in some cases been found associated with more ornamented species (gregariousness: Baker and Parker 1979; West-Eberhard 1983; Cuervo and Møller 1999. migration: Fitzpatrick 1994, 1998; Spottiswoode and Møller 2004; Albrecht et al. 2007; Cardoso et al. 2012); or also vegetation density, which may affect the conspicuousness of different colours and, thus, the evolution of ornamentation (McNaught and Owens 2002). The family Estrildidae includes species with various types of ecologies, namely with regards to sociality (from solitary species to year-round gregarious; Clement et al. 1993), making it a good study system to test for socio-ecological correlates of sexual ornamentation.

Estrildid finches and colour ornamentation

Birds are one of the vertebrate taxa with more ornamental coloration. Colour ornamentation in birds is very useful for studies of sexual selection, because of the great diversity across avian species, even among closely related species, and because bird colour ornamentation can diverge rapidly (e.g. Omland and Lanyon 2000; Milá et al. 2007; Kiere et al. 2009).

Here I studied colour ornamentation in estrildid finches, one of the largest and fastest radiations of songbirds (Jetz et al. 2012) and which contain striking diversity in patterns and colours of plumage ornamentation. The family Estrildidae (order: Passeriformes) comprises about 135-140 recognized finch species, which occur naturally across Africa, Arabia, South-eastern Asia, Pacific Islands and Australia, and have a large diversity in pigmentation patterns, as colours of plumage ornamentation, as well as some variation in bill colour ornamentation (Clement et al. 1993). Different estrildid species can live from open habitats (e.g. desert) to closed habitats (e.g. forests) and at different altitudes (from sea level to 3500 meters); furthermore, most species are granivorous, who forage at different heights, and are frequently gregarious and wanders, however in all these traits differences between species exist (Clement et al. 1993). This family includes the zebra finch (*Taeniopygia guttata*) which is an important model species for behavioural ecology and other fields, enhancing the scientific relevance of research conducted in this group.

Ornamental coloration result from two different mechanisms: pigments (chemical compounds that make colour, absorbing selective and specific wavelengths; Bleiweiss 2005), such as carotenoids and melanins, and structural coloration (Owens and Hartley 1998; Vorobyev et al. 1998; Badyaev and Hill 2000; Griffith et al. 2006;

Price 2006; Roulin and Ducrest 2013) often responsible for blue and ultraviolet (UV) colours in birds (Prum et al. 2003). In addition to the human-visible colours, these ultraviolet colours can be important in avian communication, because birds have a fourth optical cone which can perceive some of the ultraviolet portion (> ca. 320 nm) of the electromagnetic spectrum (e.g. Bennett and Cuthill 1994; Maier 1994; Bowmaker et al. 1997; Cuthill et al. 2000). As individuals or species may differ in ultraviolet coloration, it is important to consider these colours in avian studies.

In what concerns pigment-based coloration, carotenoid pigments are responsible for most of the red, orange and yellow colours of birds, i.e. the long-wavelength colours (e.g. Brush 1990; Price 2006; Pérez-Rodríguez 2008; Roulin and Ducrest 2013), and in conjunction with structural colour they may also influence shorter-wavelength colours such as blue, violet and ultraviolet (Völker 1953 in Price 2006). Carotenoids cannot be synthesised by animals and are instead obtained from the diet (e.g. Brush 1990; Britton 1995; Griffith et al. 2006; Roulin and Ducrest 2013). Melanin pigments are even more common than carotenoids in bird coloration, and are responsible for black, grey, brown and rufous coloration (e.g. Price 2006; Roulin and Ducrest 2013), and occasionally contribute to dark green and dark yellow (Jawor and Breitwisch 2003). These pigments are synthesized by animals, and so do not need to be acquired from the diet (e.g. Griffith et al. 2006; Price 2006; Roulin and Ducrest 2013).

Because of these different mechanisms subjacent to the different colours, and also because of differences in colour detectability, in different environments (Endler 1992; Schluter and Price 1993), sexual selection may act differently on each ornamental colour. For example, carotenoids need to be obtained from the diet and, therefore, carotenoid-based colours are thought as good indicators of nutritional status and, in some taxa, sexual selection appears stronger on carotenoid coloration than on melanin coloration (Hill 1996; Badyaev and Hill 2000). Conversely, melanin-based coloration has often been related to social interactions and social status (e.g. Hill and Brawner 1998; Price 2006). Therefore, especially when investigating causes for the evolution of sexual ornamentation, it may be advisable to assess to different colours, as these may respond to different ecological or social factors. Most colour ornamentation in estrildids is located on the plumage, but there are also several species with conspicuously coloured red bills, which appear to be, at least in part, also due to carotenoid pigments (Rosenthal et al. 2012). Bill coloration, as plumage coloration, has also been found to indicate individual condition, mainly in males, and may influence female mate choice (Murphy et al. 2009; Rosenthal et al. 2012). Unlike plumage coloration, which is set at the moment of the moult, the bill is a keratinized,

living tissue, and its coloration can change with reflecting physiological condition changes (e.g. Leclaire et al. 2011; Rosenthal et al. 2012).

Goals summary

In this work I address two main issues, one on speciation and another on ecological correlates of sexual ornamentation, using the ornamental colours of estrildid finches as the study system. First, I asked if ornamental coloration is related with speciation, and tested both the classic prediction that speciation should increase with increasing strength of sexual selection (and thus increasing ornamentation), and the alternative prediction that evolutionary changes in ornamentation (irrespective of those being increases or decreases) should be associated with speciation. In the second part of the work I searched for social and ecological factors that predict the extent or intensity of ornamental coloration, across the family Estrildidae.

Material and Methods

Morphometric and colour measurements

Taxa

I measured coloration and morphology on skins of 135 species of Estrildidae family (according to the taxa classification of Clement et al. (1993) and/or proposed by M. D. Sorenson (personal communication)) available at the ornithological collection of the Natural History Museum of London (appendix Table A1). When available, the nominal subspecies was chosen for measurements (exceptions are *Parmoptila woodhousei ansorgei*, *Parmoptila rubrifrons jamesoni* and *Erythrura hyperthura intermedia*, due to lack of skins of the nominal species). Here I also considered as species those subspecies (as per the classification in Clement et al. (1993)) when they appear polyphyletic with the nominal (sub)species group in the phylogeny of Sorenson (per. comm.). For each taxa I measured up to 3 adult skins of each sex, depending on the availability of well conserved skins, sexed in the label, and chose skins based on their quality of conservation. When there were not enough sexed specimens, I sexed them by their plumage coloration based in the descriptions in Clement et al. (1993).

Morphometrics

I obtained, for each skin, morphometric measures of 5 body parts: tarsus length (from the notch between the tibia and tarsus to the end of the last undivided scale), bill length (from anterior edge of nostrils to tip of upper mandible), bill depth (in the plane of the nostril perpendicular to inter-mandibular plan), tail length (from the tip of the longest feather to the point of entry into the body at the base of the central feather) and wing length (distance from the carpal joint to the longest primary of the unflattened wing). All measurements were taken with a calliper to the nearest 0.05 mm, and $\log_{10}(x)$ transformed to quantify proportional differences in size among species. To obtain species values more robust to atypical individuals or to measurement error, rather than simply calculating simple averages for each taxon and sex, I first excluded the measurement most dissimilar to the mean of the three individuals, for each taxon and sex, and then averaged only the other two. In cases where less than three individuals were measured, then I simply averaged the measurements available.

From these morphometric measurements, I calculated three variables that summarize differences in size and shape across species: body size was computed as

the score of the first Principal Component (PC), from a Principal Component Analysis (PCA), on all morphological dimensions measured (59% and 62% variance explained, for males and females respectively; all trait loadings > 0.45); bill shape was computed as the difference between the log-transformed bill length and bill depth; and wing-to-tarsus ratio was computed as the difference between the log-transformed values of wing and tarsus.

Extent of ornamental coloration

To compare the extent of plumage colours among species, I took 3 photographs (dorsal, ventral and lateral) from each skin with a 10MP digital camera (Canon digital iXus 85 IS) 23 cm high on a tripod, pointing down to the skin on a metric scale background (Figure 2). I defined the following ornamental colour categories: yellow-to-red, green, blue, and homogeneous black. Additionally, rufous, brown, grey or white were considered ornamental if plain (i.e. not mottled or disrupted by other pigmentation pattern) and/or contrasting with the duller background colour of the bird; mottled colours and counter-shading white (i.e. white colour in the ventral, the less illuminated part of the body, which reduces perceived contrast under the sunlight; Thayer 1896; Tankus and Yeshurun 2009) were not considered ornamental. From the digital photographs I measured the extent of each ornamental colour category dorsally (from the dorsal photos), ventrally (from the ventral photos), and on the head and wing (from the lateral photos). The extent of dorsal, ventral and wing colour were measured along the bird's longitudinal axis, which captures most of the variation in colour extent in

Figure 2. Example of the photographs made. The photos were made with skins above a graph paper for posterior measure, in GIMP 2.6.8 software.

these body parts. For the case of ventral parts of the body, it was common that ornamental coloration was only present on the flanks or across the ventral width for some extent and then only on the flanks; I noted these cases also. In the head, where there could be thin or wide colour patches (e.g. stripe or masks), I measured the maximum extent of colour along two dimensions: parallel and perpendicular to the axis of the bill. From these photographs I also measured head width (measured from the base of the bill, parallel to the bill line, to the most distal head point) and length of the wing (measured from the most proximal point of the wing to the tip of the wing), the ventral and the dorsal parts of the body (measured from the base of the bill to infra-caudal plumage, or to supra-caudal plumage, respectively). As before, for each of those measurements I calculated mean values per species and sex, by first excluding

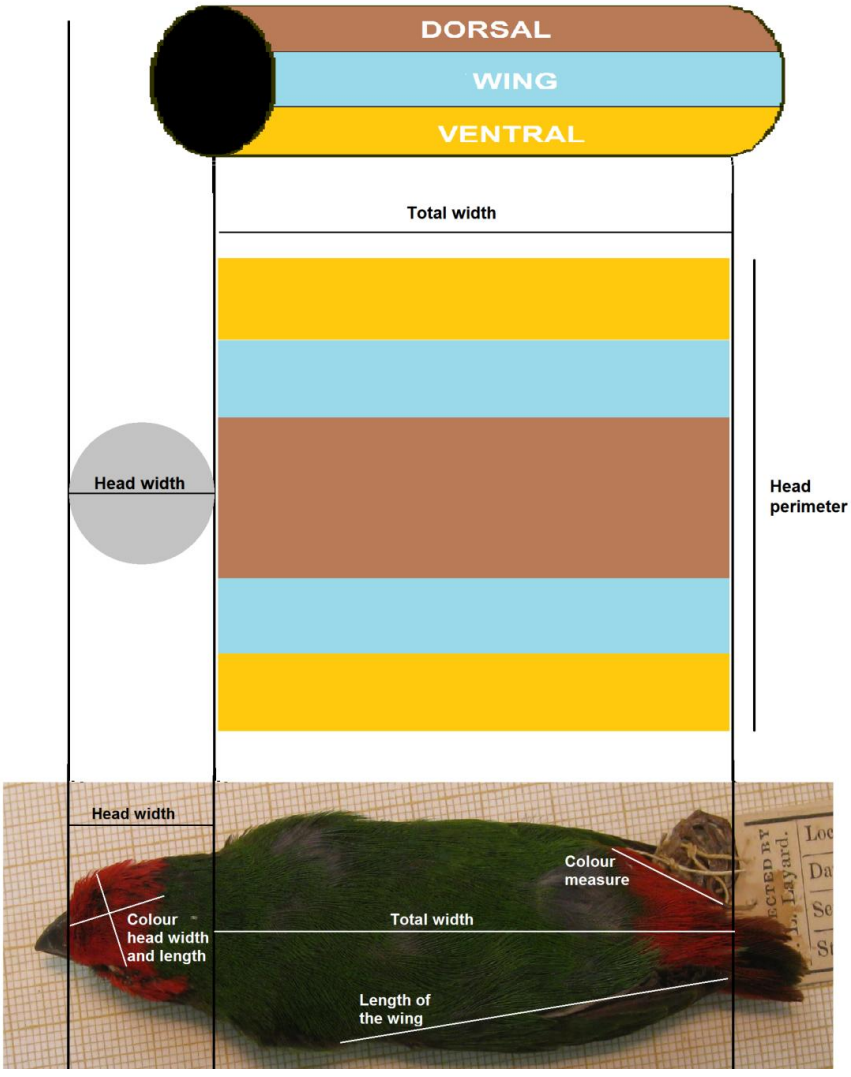

Figure 3. Model of calculation of the overall extent of ornamental coloration, in birds.

the measurement most dissimilar to the mean of the three individuals (when three individuals were measured for a taxon and sex), and then averaging the remaining measurements. With these mean values, I computed an index for the extent of ornamental coloration for each species and sex. First, I made an approximated estimate of the proportion of ornamental coloured areas in the head, wings, dorsal and ventral parts of the body. The proportion of ornamental colour on the head was computed as the area of an ellipse with length and width equal to the two linear measurements taken for the colour patch, divided by the area of a sphere with diameter equal to the head width. The proportion of ornamental colour on the wings, dorsal or ventral parts of the body was computed as the extent of ornamental colour divided by the length of the wing, ventral or dorsal part of the body, respectively. For ventral ornamental coloration, the estimate was multiplied by 0.5 when ornamental coloration was present only on the flanks, or multiplied by ¾ when ornamental coloration was present only on the flanks for part of its extent. Second, I constructed a simplistic model to integrate the relative areas of ornamental coloration in these body parts: the head area was modelled as the area of a sphere with diameter equal to the head width, as measured from photographs; the dorsal area, ventral area and joint area of the two wings were each modelled as 1/3 the area of a cylinder with diameter equal to the measured head diameter, and length equal to the measured dorsal length (Figure 3).

Table 1. Colour ornamental variables, considered for analyses, and its description and calculation.

Colour ornamental variables	Description
Maximum achromatic difference	Resulted from the difference between the maximum and minimum brightness value
Maximum colour saturation	Maximum saturation value (colour saturation; perceived saturation irrespective of hue and brightness)
Mean colour saturation	Mean saturation value (colour saturation; perceived saturation irrespective of hue and brightness)
Extent of ornamental coloration	Sum of the proportion of each ornamental colour (yellow-to-red, green, blue and black), in all regions, of an individual
Bill colour	Coded from literature
Minimum PC2	Minimum PC2 value of an individual; it represents yellow-to-red coloration (long-wavelength colours)
Maximum PC2	Maximum PC2 value of an individual; it represents UV/blue coloration (short-wavelength colours)

The index for the extent of ornamental colour was the sum of the proportions of ornamental coloured areas (yellow-to-red, green, blue and black) for the four body parts, divided by total area of the four body parts (Table 1). This is a rough estimate of the extent of ornamental colour across the entire body that, nevertheless, captures well the variation among species (range 0.000 to 0.932; appendix Table A1).

Plumage coloration

I used spectrophotometry to measure plumage colour in 6 body parts: crown (including forehead), throat (including chin), back (including mantle), belly (including breast and flanks), tail (including rump and uppertail-coverts) and wing (wing coverts, secondaries and scapulars; see Figure 4). In each of these parts I measured the main ornamental colour (see above) or, if the body part was not ornamented, the dominant colour. I took an additional measurement of colour in the mask (ear-coverts and lores; see Figure 4) when its ornamental colour was different from the crown and throat, and took a second colour measurement in the belly when there was an additional colour in this body part that had not been measured previously (e.g. because it is not ornamental). Colour reflectance was measured with an Ocean Optics usb4000 spectrophotometer coupled to a PX-2 xenon light source. Measurements were taken perpendicularly to the feathers' surface, and were calibrate with a Micropack WS-1-SL white standard and a black velvet cloth, before measuring each taxon. For each body part, two independent measurements were made, after relocating the probe to account for possible heterogeneity of coloration.

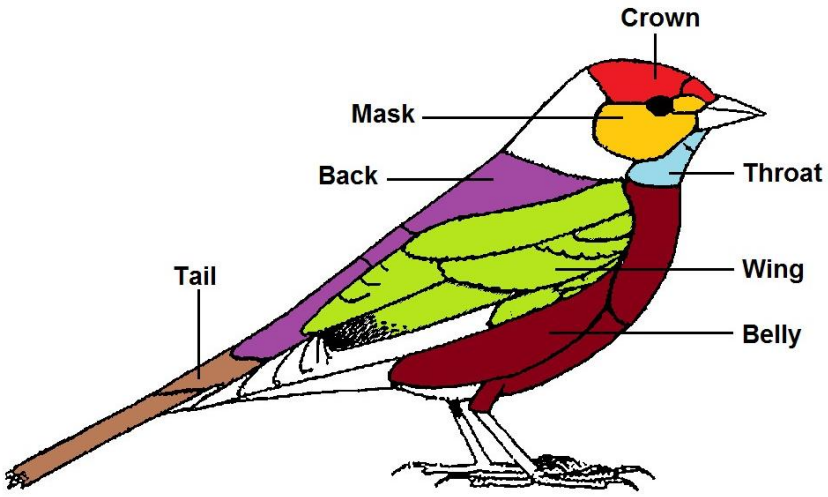

Figure 4. Body parts of the colour measures made in each individuals (adapted from Clement et al. (1993)). Each of the different section, considered for the spetrophotometric measures, have a different colour, with the correspondent section name.

Spectral data were quantified using two main approaches: 1- Principal Component Analysis (PCA) was used to obtain summary metrics (Principal Components, PC) that distinguish colours of different hues (e.g. short-wavelength vs. long-wavelengths colours; Montgomerie 2006; Armenta et al. 2008); these metrics were used for data quality control and to test for ecological correlates of the evolution of different ornamental colours. 2- Models based on animal vision were used to quantify colour saturation as perceived by animals, across all colour hues (Stoddard and Prum 2008; Maia et al. 2013). I also quantified brightness differences between colours directly from the spectra. I explain these procedures in turn.

To perform a PCA using all reflectance spectra from all species, I first corrected negative reflectance values to zero (near zero reflectance might be read as slightly negative due to measurement error), and computed the average of the $\log_{10}(x+1)$ transformed reflectance for each bin of 20 nm wavelength, from 320 nm to 700 nm (the bird-visible light wavelengths, including the ultraviolet; e.g. Burkhardt 1989; Eaton and Lanyon 2003; Armenta et al. 2008); the mean reflectance for each 20 nm-bin were then used as input variable in the PCA. The reason why I log-transformed reflectance data (except when applying visual models, which already incorporate a log-transformation within their algorithms; Vorobyev et al. 1998) was because reflectance ratios are more meaningful biologically from the perspective of colour perception (animal vision discriminate better at low than high reflectance; Vorobyev et al. 1998) and pigment-based colour production (the relation between pigment concentration and light reflectance generally takes the form of an exponential decay; e.g. Sims and Gamon 2002). It is advisable that reflectance data is screened for outliers, which could be due to light contamination during spectrophotometry (Montgomerie 2006). I used the scores on PC1, PC2 and PC3 (which explained 99% of total variation) for this, by identifying pairs of measurements of the same individual and body part that differed by more than 2 standard deviations (standard deviation of the entire set of measurements for each PC), and deleting the spectrum with the most dissimilar measurement by comparison to spectra of the same body part, in other individuals of the same species and sex; 44 spectra (0.49% of total) were deleted. Then the PCA analysis was repeated without those spectra (eigenvalues and traits loadings similar to the ones described above), and visual models described below also did not use those spectra.

The final PCA returned two main PCs which together explained 94% of the variation. PC1 explained 85% of total variation and, as is typical in this type of analysis (e.g. Mays et al. 2004; Montgomerie 2006; Armenta et al. 2008), had strong positive loadings on all wavelengths (Figure 5). It thus indicates the overall brightness of colour and, as intended, removes this variation from the data so that the next PC

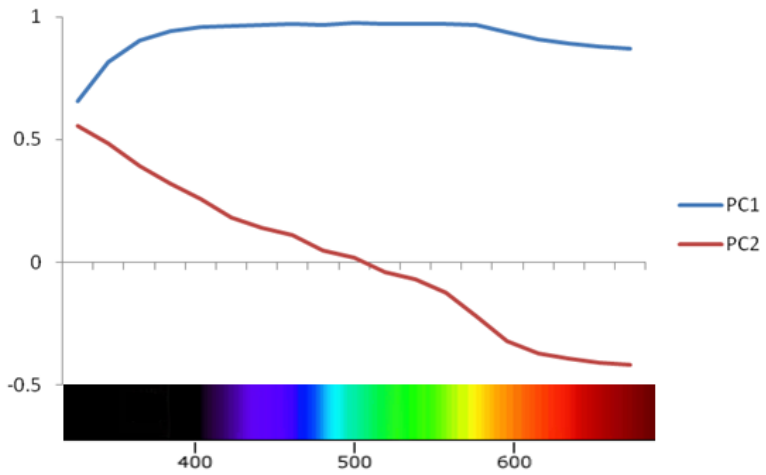

Figure 5. Trait loadings of the original reflectance variables (i.e. reflectance on each 20 nm-bin intervals of wavelengths) on the two main PCs from a PCA.

quantifies the main differences in colour, independently of brightness. PC2 explained 9% of variation (or, equivalently, 60% of the remaining colour variation, after removing differences in brightness), and had positive loadings from 320 nm to 500 nm (UV and blue) and negative loadings from 500 nm to 700 nm (green-to-red; Figure 5). PC2 thus reflects short vs. long-wavelength colour, and I used PC2 scores as a metric of colour saturation in the short-wavelengths (high PC2 scores) or long-wavelengths (low PC2 scores).

Estrildid ornamentation comprises many different colours, and I used avian visual models to obtain a metric of colour saturation applicable to, and comparable across, all colours. I used models of perception in the tetrahedral colour space (Figure 6), based on the relative stimulation of each of the four cones of birds (Endler and Mielke 2005; Montgomerie 2006), as implemented in the software pavo (Maia et al. 2013), to compute the statistic *r* (r.vec in pavo software; Maia et al. 2013). *r* (hereafter, colour saturation) is computed as the euclidean distance from the achromatic centre of the colour space, and quantifies the perceived colour saturation independently of differences in hue or brightness (Stoddard and Prum 2008). Prior to these calculations, reflectance lower than 1% were trimmed up to 1% because, since visual models function on a ratio scale, even small measurement error on the low-reflectance range can strongly affect results.

Overall brightness of colour (b_2 variable in pavo software; Maia et al. 2013) was calculated as the mean $\log_{10}$ reflectance across the bird-visible wavelengths (320 to 700 nm). As above, here I used spectra where the very low reflectance had been trimmed to 1% (or, equivalently, to 0 $\log_{10}$ reflectance).

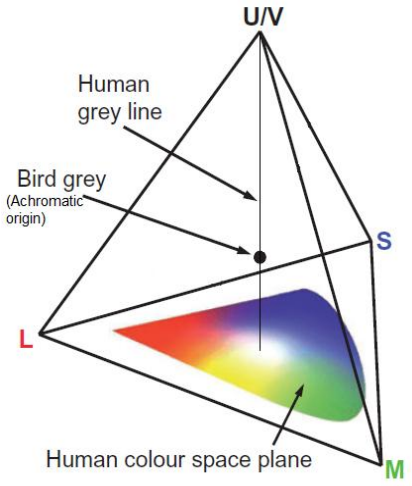

Figure 6. Tetrahedral colour space, adapted from Goldsmith (1990) and Endler and Mielke (2005). Visual models are based in the relative stimulation of each of the four bird cones (L, S, M, and U/V).

I calculated mean values, per body region, of the same individual, after excluding the outliers (see above). Then, as before, for each of those measurements (PC2 scores, colour saturation and brightness of each body part) I calculated mean values, per species and sex, after excluding the measurement most dissimilar in the three individuals of the same species and sex (when three individuals were measured for a taxon and sex). Then, across the several body parts of each species and sex, I computed maximum PC2 score (the maximum colour saturation at short-wavelengths, UV/blue), minimum PC2 score (the maximum colour saturation at long-wavelengths, yellow-to-red), mean colour saturation, maximum colour saturation, and maximum achromatic difference among colour patches (maximum pair-wise difference in brightness between colour patches; Table 1).

Bill colour

Bill coloration cannot be measured from museum specimens, because it is a dynamic trait (Rosenthal et al. 2012) and fades after death. Thus, I simply categorized bill colour based on the illustrations and descriptions of Clement et al. (1993), considering red bills to be ornamental (scored 1) and other colours (black, brown, yellow or whitish) to be non-ornamental (scored 0). Intermediate scores (scored 0.5) were used for species with a mixture of the two categories (Table 1; appendix Table A1).

Ecological and social data

I obtained ecological information on each species to understand which selective factors modulate the evolution of ornamentation. The data were collected primarily from Clement et al. (1993) and, for missing values, were complemented with information of Payne (2010), except for habitat information which was only collected from Clement et al. (1993), and breeding and nestling information which were collected only from Payne (2010). For each species, I classified vegetal density, altitude distribution, commonness, gregariousness, diet and feeding local, migration movements, breeding and nestling ecology. Information on most of these variables was reduced into ordered categories for regression analyses. In cases when more than one information is described, for a species, the values are averaged (except for information referred to as "occasional" or "rarely" in the literature, which was not considered; appendix Table A2). Ecological variables are summarized in Table 2 and are described next.

Table 2. Summary of ecological and social indexes.

Ecological and Social dimensions	Variables	Categories
Habitat	Vegetation density	Open (1), semiclosed with low vegetation (2), semiclosed with high vegetation (3), closed (4)
	Mean altitude	--
	Range altitude	--
Commonness	Commonness	Rare and uncommon (1), locally common and seasonally common (2), common (3)
Movements	Migration	Sedentary (1), nomadic / wanders (2), partially migratory (3), migratory (4)
Social system	Gregariousness	Alone / single (0), pairs (1), small groups / family parties (2) larger groups / flocks (3)
Feeding	Diet	Insects, fruits, eggs, plants, nectar and algae (0), seeds and grains (1)
	Feeding height mean	Ground (1), vegetation / bushes (2) and in trees (3)
	Feeding height range	--
Breeding	Length of breeding season	--
	Clutch size	--
	Incubation period	--
	Nestling period	--
Nest vulnerability	Nest height	Ground (1), bushes (2), trees (3)
	Parasitized species	Not parasitized (0), parasitized (1)

The vegetation density of the habitats may influence the evolution of ornamentation; for example, species in tropical closed habitats have less sexual dichromatism (Price 1996), and species who live in closed habitats in average have longer-wavelength colour hue (McNaught and Owens 2002). I classified *vegetation density* of the typical habitats, using the same categorical scale as in Hu and Cardoso (2009), as open habitats (scored 1; e.g. stone and semi-arid desert, gorges and rocky hills, spinifex, dunes, open country, cultivated areas in towns, savanna, dry sandy plains and wadis, parks, paddy-fields, cane-fields, rice fields, villages, cultivation, rushes, grassland, saltflats, tall grass), semiclosed with low vegetation (scored 2; defined as habitats with fields of low vegetation, e.g. bushes, thickets, scrubs, thornscrub, patches of reeds, tamarisk, reed-beds, thornbush thickets, cane grass, swamps, damp thickets, rank vegetation bamboo, mangroves, reeds near water, coastal scrub, marshes), semiclosed with high vegetation (scored 3; defined as habitats with fields of high vegetation, e.g. forest edges and clearings, acacias, grassy areas with trees, lowland grassland, woodland), and closed (scored 4; defined as habitats with dense and closed vegetation, e.g. forest, lowland secondary-forest undergrowth, creepers in mountain forest, tangled thickets of mountain forest, mature rainforest).

The altitude of habitats strongly influences ecology (e.g. climate, seasonality, breeding length and synchrony), and it has been related to sexual ornamentation in some avian species (Badyaev 1997a). Also, the breadth of altitudes at which a species occurs is indicative of ecological generalism, and ecological generalism has been related to ornamentation across species (Badyaev and Ghalambor 1998; Tobias and Seddon 2009; Östman and Stuart-Fox 2011; Cardoso et al. 2012). I used information on the minimum and maximum altitude, at which each species occurs, to calculate its *mean altitude* (average of minimum and maximum) and *altitudinal range* (maximum minus minimum).

Species can be common or rare, and it has been discussed whether ornamentation and sexual selection contribute to the rarity of species and consequently to their risk of extinction (e.g. McLain et al. 1995; Bro-Jørgensen 2014). I categorised *commonness* of each species based on whether they are described as rare or uncommon (scored 1), locally or seasonally common (scored 2), and common (scored 3).

Migratory bird species are, on average, more ornamented and experience stronger sexual selection (Fitzpatrick 1994, 1998; Spottiswoode and Møller 2004; Albrecht et al. 2007; Cardoso et al. 2012), which could be due to mate choice based on arrival dates at the breeding grounds (Spottiswoode et al. 2006) or to increased

variance in male genetic quality (Fitzpatrick 1994, 1998). I assessed the extent of *migration* in each species by categorizing it as sedentary (scored 1), nomadic or wander (scored 2), partially migratory (scored 3), and migratory (scored 4).

The social system on which a species live should strongly affect sexual selection, and gregarious species have been described as more colourful and ornamented (Baker and Parker 1979; West-Eberhard 1983; Cuervo and Møller 1999). I computed a *gregariousness* categorical variable based on each species description as occurring alone or single (scored 0), in pairs (scored 1), in small groups or family parties (scored 2) and in larger groups or flocks (scored 3).

I noted whether the *diet* of each species was granivorous or included other items; seeds have the lowest carotenoid content of the foods used by estrildids, and low carotenoid content of the diet has been related to lower carotenoid-based plumage coloration (yellow-to-red) across species (Olson and Owens 2005). It was noted whether the food items described as commonly used by a species include seed and grains (scored 1) or other, more carotenoid-rich foods, such as insects, fruits, eggs, plants, nectar and/or algae (scored 0).

I noted whether each species forages on the ground (scored 1), on vegetation or bushes (scored 2) and in trees (scored 3). I used the mean of these height categories to score each species *foraging height mean*, because higher foraging height (e.g. in bushes or trees canopies) can allow birds to hide more easily and be less exposed to predation. I used the *range of foraging heights* (maximum minus minimum) as an additional measure of ecological generalism, because ecological generalism has been related to ornamentation across species (see above).

I noted the *length of the breeding season* (the maximum number of months on which breeding is described for a population of a species) because shorter breeding seasons imply greater breeding synchrony among individuals, which in birds can increase the opportunity for extra-pair paternity and, consequently, the strength of sexual selection (Albrecht et al. 2007; Hammers et al. 2009).

Some reproductive investment indexes can be associated with parental care. Species with more ornamented males show higher levels of parental care, because male ornamentation is a signal of good quality and of the ability to provide offspring (“good parent hypothesis”; e.g. Germain et al. 2010; Gladbach et al. 2010). However, more ornamented male species can also provide less parental care, either to invest their energy in their selves, so that females can mate with more attractive males and produce high-quality offspring (“differential allocation hypothesis”; e.g. Badyaev and Hill 2002), or to be able to pursuit extra mating opportunities (“trade-off hypothesis”; e.g. Badyaev 1997b; Mitchell et al. 2007). I took information on three aspects of

reproductive investment: *clutch size* (number of eggs per clutch), length of the *incubation period* (the time, in days, incubating a clutch of eggs) and of the *nestling period* (the time, in days, caring for young in the nest).

The vulnerability of nests to predation can constrain the evolution of conspicuous colour ornamentation, especially in the sex that incubates. For example, species that have more elevated nests (which are less vulnerable to predation or to bird parasitism), or less exposed nests, are on average more ornamented (Martin and Badyaev 1996; Cuervo and Møller 1999; Badyaev and Hill 2003). I classified *nest height* as on the ground (scored 1; defined as species who make their nests on, or near, the ground, or over water), on bushes (scored 2; defined as species who make their nest in bushes, or similar vegetation, e.g. thickets, shrubs, herbs, near streams, creepers, grass, thornbush, tall grass, ferns, reeds, paddy grasses, dense vegetation and spinifex), and in trees (scored 3; defined as species who make their nests in trees, in branches of trees, in the canopy, or in small trees). Information of nest location on human settlements was ignored. The nests of some estrildid species are also *parasitized by brood parasites*. I noted whether each species is described as parasitized by brood parasites (scored 1) or not (scored 0).

Analyses

As the basis for phylogenetic comparisons, I used the mitochondrial DNA (mtDNA) phylogeny of Sorenson (per. comm.), comprising all extant estrildid species. This tree is based on a partioned analysis of mtDNA gene regions and codon positions, and estimates branch lengths proportionally to time (i.e. chronogram). For species with more than one sample in the phylogeny only one was kept: if all samples of a species form a monophyletic clade, then an arbitrary sample was kept; when samples of a species form a non-monophyletic group, then the nominal subspecies was retained (if there was more than one sample of the nominal subspecies and forming a non-monophyletic group, then I retained the sample branching off earlier). The final phylogenetic tree contains the 135 species in our dataset measurements (132 species for male data and 123 species for female data).

I estimated the phylogenetic signal of each colour or morphometric traits as the parameter lambda (λ; Pagel 1999), separately for males (132 species) and females (123 species); the parameter λ can vary between 0 (differences in phenotype between

species are not related with phylogenetic differences) and 1 (differences in phenotype are exactly proportional to phylogenetic differences).

Relation between speciation and ornamentation

To test the classic hypothesis that "sexual selection promotes speciation", I used the method described in Freckleton et al. (2008): I computed the number of speciation events since the root of the phylogenetic tree (i.e. the number of nodes between the root and the tip) for each species, and tested if it is related to ornamental coloration with a Phylogenetic Generalized Least Squares (PGLS) regression (Pagel 1999), using one colour trait as dependent variable and the number of nodes as the predictor. Additionally, I tested if the terminal branch length for each species was related to ornamental coloration with a PGLS regression, using a colour trait as dependent variable and the terminal branch lengths as the predictor. The colour traits used in this analysis were the overall extent of ornamental colour, maximum and mean colour saturation, brightness contrast, and bill colour (Table 1); I tested, for each colour trait, male coloration (132 species) and female coloration (123 species), separately.

To test the alternative hypothesis that changes in ornamentation (whichever changes: increases, decreases, etc.) promote speciation, I used Mooers et al. (1999) test of speciational evolution, which estimates maximum likelihoods for different models of phenotypic evolution. When speciational evolution is supported relative to gradual evolution this means one of two things: 1- the trait has a punctuated mode of evolution associated with speciation; or 2- the trait may evolve gradually but it promotes speciation, creating a correlation between the extent of phenotypic evolution and speciation (Rabosky 2012). Both cases indicate an involvement of ornamental evolution in speciation. Speciational evolution was modelled using a phylogenetic tree with all branch lengths equal (i.e. the predicted phenotypic change is proportional to the number of nodes in each lineage), and gradual evolution was modelled using the same phylogenetic tree with the original branch lengths (i.e. the predicted phenotypic change is proportional to time). I report the likelihoods of these models relative to a non-historical model, modelled as a star phylogeny, which represents the absence of phylogenetic signal in the data (i.e. predicted phenotypic change is not related to phylogeny).

The ornamental phenotypes studied were also the extent of ornamental colour, mean and maximum colour saturation, brightness contrast and bill colour (Table 1), for both male coloration (132 species) and female coloration (123 species). I also ran an overall model, with the most significant PCs of a PCA with all the colour ornamental variables, used in the analysis (extent, saturation, brightness and bill measures), both

for males and females (PCA returns 2 PCs with eigenvalues higher than 1, which explained 79% of total variation). In all cases, phylogenetic trees (for Mooers et al. (1999) method) were unrooted and, when phenotypes comprised values lower than zero, the minimum phenotype was summed to all species in order to avoid negative values (Mooers et al. 1999). For comparison, I also ran these analyses for morphology: body size, bill shape, and wing-to-tarsus ratio.

Social and ecological correlates of ornamentation

I tested for social and ecological correlates of ornamental colour across species in two steps: first, I ran PGLS regressions with each of the social or ecological trait candidates, as a single predictor of the colour trait of interest, for males and females, separately (appendix Table A3, A4, respectively); then, I selected the candidate traits that had suggestive associations with that colour trait ($P < 0.1$) for inclusion in a single PGLS multiple regression. The goal of this two-step procedure is to avoid excessively reducing sample size: there are missing values for each of the different candidate traits, such that running the PGLS multiple regression with all candidate traits would reduce sample size to less than half the species in the colour dataset; by first selecting those candidate traits showing suggestive associations with colour, I still include all relevant ecological and social traits while retaining a larger sample size of species. Analyses were made separately for male and female coloration, and I used either the chronogram or the speciational phylogeny, depending on the results of the previous section supporting gradual or speciational evolution, for each ornamental colour trait. Sample sizes were different between the analyses of each ornamental trait, but were never less than 86, so I can analyse with confidence each result, because all have a good statistical power.

The colour traits used in these analyses were the same as in the previous section: extent of ornamental colour, mean and maximum colour saturation, brightness contrast and bill colour (Table 1). As a follow-up, I also analysed the maximum and minimum PC2 scores (colour saturation in the UV/blue or yellow-to-red range, respectively; Table 1) to help understand if ecological correlates of saturation are specifically due to short- or long-wavelength colours (UV/blue vs. yellow-to-red).

I tested for possible relation between predictors, which may assess problems of multicollinearity; I ran correlations, to verify if any value of Person correlation was higher than 0.6 (none Pearson correlation was higher than 0.6; results not shown), calculated in SPSS 20 (SPSS inc., Chicago, IL, USA). Graphic representations, without controlling for phylogeny, were made for all the significant values of the analyses, in order to control for possible outliers who could biased the regression results.

For λ estimates and all PGLS regressions described above, I used the software BayesTraits (Pagel and Meade, available from http://www.evolution.rdg.ac.uk). PGLS regressions also estimated the degree of phylogenetic signal in the regression model (λ) to adjust the phylogenetic correction accordingly (Freckleton et al. 2002), and standardized variables were used to obtain standardized regression coefficients. Estimates of maximum likelihood for different evolutionary models were made with the program CONTML of PHYLIP (Felsenstein 1993) modified by Mooers et al. (1999).

Results

Relation between speciation and ornamentation

Phylogenetic signal was high for all ornamental colour traits, both in males ($0.60 < \lambda < 0.96$) and females ($0.58 < \lambda < 1.00$) (Table 3). Furthermore, phylogenetic signals for morphological traits were also high for males (λ=0.84 for body size; λ=1.00 for bill shape; λ=0.87 for wing-to-tarsus ratio) and females (λ=0.85, 0.97 and 0.81, respectively).

None of the ornamental traits studied, in either sex, was related to the number of speciation events along the phylogeny or to the terminal branch lengths (Table 3). Thus, I found no evidence that more ornamented species speciate more or, on average, that they have speciated more recently. In all cases effect sizes were small (absolute values of standardized PGLS regression coefficients, $|\beta_{st}| < 0.18$; Table 3).

Table 3. Phylogenetic signal (λ) of each ornamental colour trait, and results of PGLS regressions relating ornamental traits with terminal branch lengths or with the quantity of speciation events, along the phylogeny.

		Terminal branch lengths	**Speciation events**
	λ	**β_{st} (P ; λ)**	**β_{st} (P ; λ)**
Maximum colour saturation			
Males	0.78	0.05 (0.65 ; 0.78)	-0.02 (0.86 ; 0.78)
Females	0.68	0.09 (0.39 ; 0.68)	< 0.01 (1.00 ; 0.68)
Mean colour saturation			
Males	0.87	0.13 (0.25 ; 0.87)	0.024 (0.86 ; 0.87)
Females	0.58	0.05 (0.66 ; 0.59)	-0.01 (0.91 ; 0.59)
Achromatic difference			
Males	0.60	-0.04 (0.69 ; 0.60)	0.02 (0.83 ; 0.60)
Females	0.62	0.07 (0.46 ; 0.62)	-0.14 (0.24 ; 0.62)
Extent of ornamental colour			
Males	0.73	0.01 (0.88 ; 0.73)	0.03 (0.78 ; 0.72)
Females	0.77	-0.01 (0.91 ; 0.77)	0.17 (0.17 ; 0.76)
Bill colour			
Males	0.96	0.07 (0.56 ; 0.96)	-0.17 (0.16 ; 1.00)
Females	1.00	0.03 (0.84 ; 1.00)	-0.07 (0.64 ; 1.00)

N = 132 species for males and 123 species for females.

Most of the ornamental traits (mean and maximum colour saturation, achromatic difference, and extent of ornamental coloration) fitted the model of speciational evolution significantly better than gradual evolution (i.e. log-likelihood differences were larger than 2; Figure 7). Bill colour, on the contrary, fitted significantly

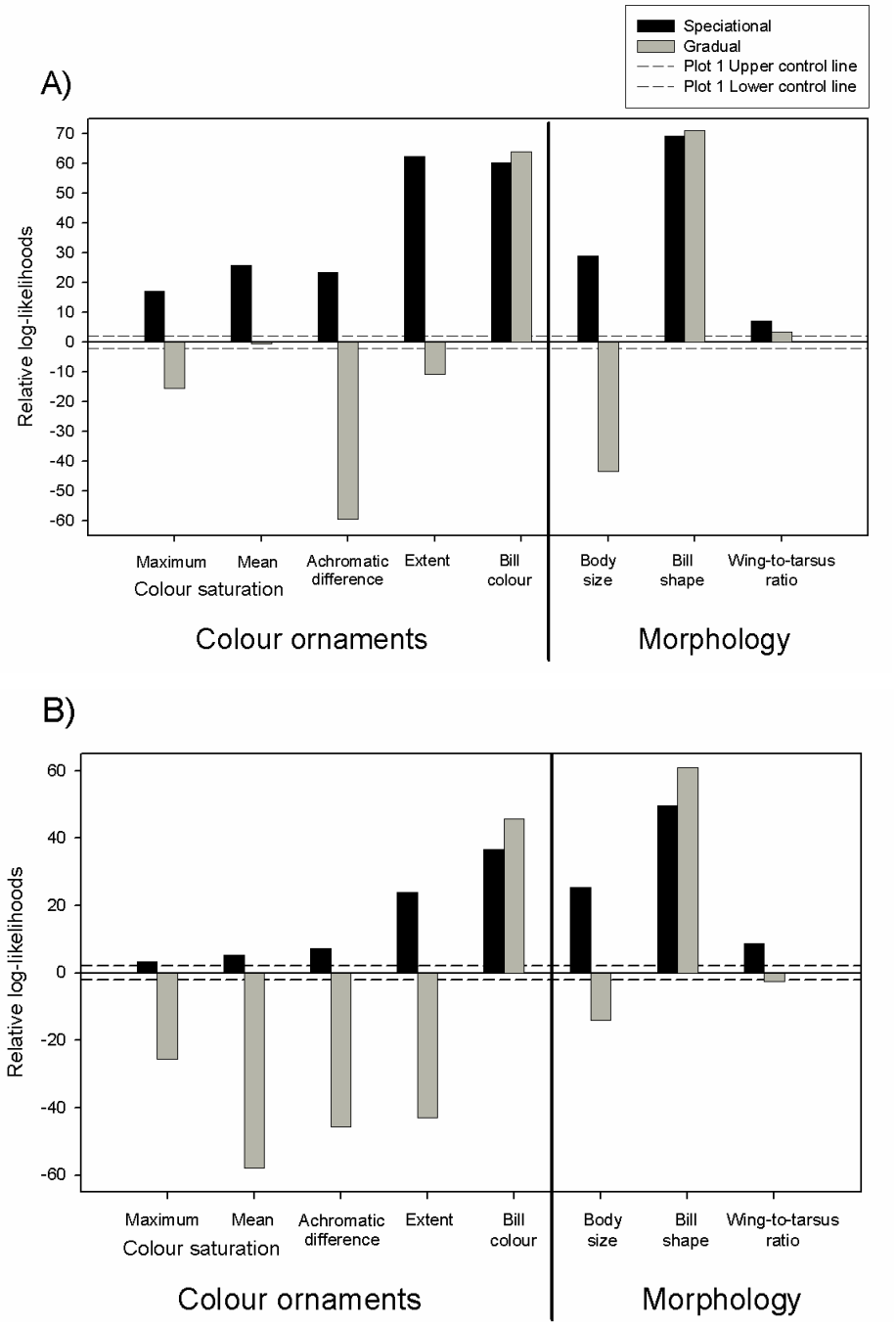

Figure 7. Log-likelihoods of models of evolutionary change for (A) male or (B) female ornamental and morphological traits in relation to a non-historical model (star tree model). Dashed horizontal lines indicate threshold for significant differences (2 log-likelihood differences) relative to the non-historical model. Differences between speciational and gradual models were significant in all cases (log-likelihood difference > 2) except for male bill shape (log-likelihood difference = 1.94).

better gradual than speciational evolution (Figure 7). These results were stronger for male ornamentation (Figure 7A), but also significant for females (Figure 7B). While the fit to speciational evolution was better than to non-historical model in all ornamental traits, for some traits, the fit to gradual evolution, was significantly worse than to the non-historical model (Figure 7). Appendix Table A5 shows the log-likelihood values, for each sex, of the overall model including analyses of colour PCs, which also support speciational evolution.

Among morphological traits, body size and wing-to-tarsus ratio fitted better speciational evolution than gradual evolution, and bill shape fitted significantly better gradual than speciational evolution (Figure 7). These results were significant for both sexes, except for males bill shape (log-likelihood difference = 1.94; Figure 7).

Social and ecological correlates of ornamentation

Table 4 shows the results of the final PGLS multiple regression models, relating ornamental colour traits of males to candidate ecological and social predictors.

Maximum and mean saturation had a positive significant relation both with gregariousness (Table 4, Figure 8a,b), which means that species who live in flocks and groups have a more saturated plumage than solitary species. This result was confirmed analysing saturation of short- (blue/UV) and long-wavelength (yellow-to-red) colours separately (maximum and minimum PC2 scores, respectively), which means that on average flock-living species have both more UV/blue and more yellow-to-red plumage colour saturation (Table 4, Figure 8d,e). These analyses also revealed significant relations of maximum blue/UV saturation with clutch size and of maximum yellow-to-red saturation with vegetation density: species with higher number of eggs per clutch have more UV/blue plumage content, while species that live in more closed habitats have more yellow-to-red plumage (Table 4). The maximum achromatic plumage differences were also positively related with gregariousness (Table 4, Figure 8c) and clutch size (Table 4). Extent of ornamental coloration in males was marginally positively related to incubation period, and bill colour of males was not significantly related to any of the candidate social and ecological predictors (Table 4).

Table 5 shows identical analyses on the ornamental colour traits of females. Maximum and mean chromatic saturation were not related to gregariousness, and relations with other predictors were not significant either (Table 5). Nonetheless, when analysing saturation of short- and long-wavelength colours separately there were some

Table 4. Results, for males, of PGLS multiple regressions† of each ornamental colour variable on predictor ecological and social significant variables for each trait.

		Maximum saturation	Mean saturation	Achromatic difference	Extent	Bill colour	Maximum PC2*	Minimum PC2*
MALES	**Vegetation density**							**-0.23 (0.02)**
	Range altitude	0.12 (0.23)						
	Gregariousness	**0.26 (0.03)**	**0.24 (<0.01)**	**0.29 (<0.01)**			**0.26 (<0.01)**	**-0.21 (0.02)**
	Diet					0.10 (0.12)		
	Clutch size			**0.25 (0.02)**			**0.23 (0.02)**	
	Incubation period			-0.06 (0.47)	**0.16 (0.05)**		-0.07 (0.41)	
	Nest height			-0.09 (0.19)			-0.08 (0.27)	
	Parasitized species					0.08 (0.35)		
	Model λ (Model N)	0.89 (86)	1.00 (129)	0.63 (97)	0.91 (108)	1.00 (131)	0.63 (97)	0.85 (129)

Standardized partial regression coefficients are out of parentheses; P-values are given in parentheses. Significant effects in bold.

* Higher maximum PC2 scores indicate more short-wavelength (blue/UV) colour saturation, and lower minimum PC2 scores indicate more long-wavelength (yellow-to-red) colour saturation.

† PGLS regressions were made with the phylogenetic tree who revealed to be the best fitting model for each ecological trait (speciational tree for all the traits except bill colour for which is used the gradual model tree; Figure 7); for minimum and maximum PC2, speciational model tree was used (minimum PC2 log likelihood differences with the null model was 6.25 for speciational model and –48.01 for gradual model; and maximum PC2 log likelihood differences with the null model was 30.81 for speciational model and –24.66 for gradual model).

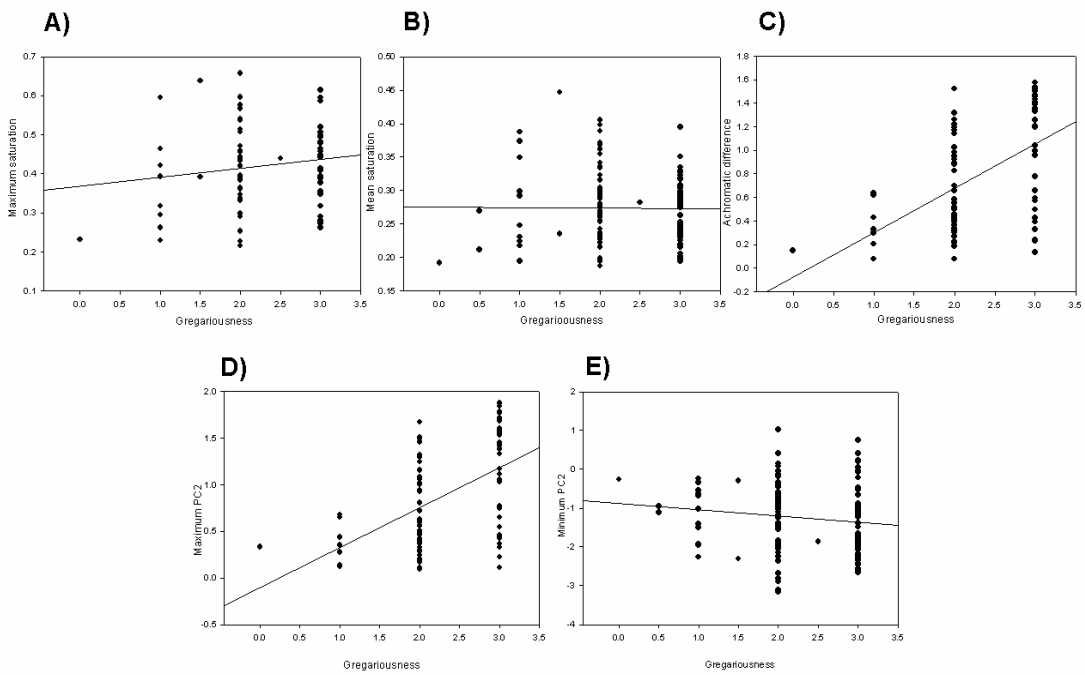

Figure 8. Relationship between gregariousness and the different ornamental traits which were chosen to be analysed, for males. (A) relationship between gregariousness and maximum saturation. (B) relationship between gregariousness and mean saturation. (C) relationship between gregariousness and achromatic difference. (D) relationship between gregariousness and maximum PC2 value. (E) relationship between gregariousness and minimum PC2 value.

significant associations with ecological predictors: species with higher maximum short-wavelength saturation (blue/UV) were more common, while species with higher maximum long-wavelength saturation (yellow-to-red) were rarer and more migratory (Table 5). Maximum achromatic difference in females was positively related to clutch size and length of the breeding season (Table 5), and ornamental bill colour of females was positively related to gregariousness (Table 5, Figure 9).

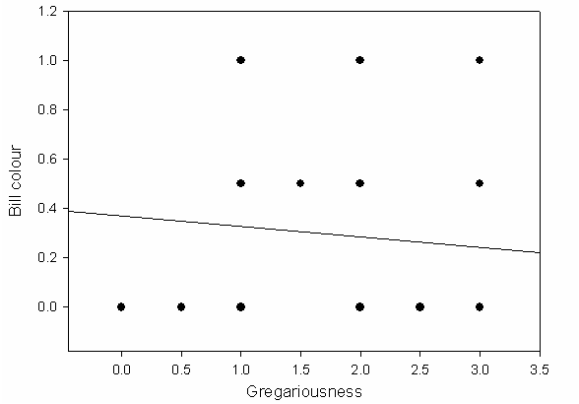

Figure 9. Relationship between gregariousness and bill colour, for females.

Table 5. Results, for females, of PGLS multiple regressions† of each ornamental colour variable on predictor ecological and social significant variables for each trait.

		Maximum saturation	Mean saturation	Achromatic difference	Extent	Bill colour	Maximum PC2*	Minimum PC2*
FEMALES	**Commonness**						**0.19 (0.04)**	**0.21 (0.02)**
	Migration							**-0.18 (0.05)**
	Gregariousness			0.15 (0.08)	-0.14 (0.10)	**0.15 (0.04)**	0.18 (0.10)	
	Feeding Height Mean		-0.17 (0.07)	-0.01 (0.93)	0.13 (0.11)			
	Feeding Height Range						-0.12 (0.30)	
	Breeding season			**0.18 (0.03)**			0.16 (0.08)	
	Clutch size			**0.30 (<0.01)**		0.11 (0.11)		
	Incubation period	0.20 (0.06)		-0.06 (0.50)				
	Model λ (Model N)	0.45 (102)	0.73 (116)	0.69 (94)	0.87 (114)	1.00 (110)	0.51 (103)	0.42 (114)

Standardized partial regression coefficients are out of parentheses; P-values are given in parentheses. Significant effects in bold.

* Higher max PC2 scores indicate more short-wavelength (blue/UV) colour saturation, and lower min PC2 scores indicate more long-wavelength (yellow-to-red) colour saturation.

† PGLS regressions were made with the phylogenetic tree who revealed to be the best fitting model for each ecological trait (speciational tree for all the traits except bill colour for which is used the gradual model tree; Figure 7); for minimum and maximum PC2 gradual model tree was used (minimum PC2 log likelihood differences with the null model was -8.13 for speciational model and –39.48 for gradual model; and maximum PC2 log likelihood differences with the null model was -9.91 for speciational model and –34.50 for gradual model; in both traits the models were worse than the null model so gradual model will be used because is the best representation of the reality).

Discussion

I found that ornamental coloration in the family Estrildidae fits a speciational model of evolution better than a gradual model, in both sexes, for chromatic colour saturation (mean and maximum colour saturation), achromatic colour contrasts and the extent of ornamental colour; only bill colour fitted gradual evolution better. The same was true for some, but not all, nonornamental morphological traits (only for body size and wing-to-tarsus ratio). This relation between ornamental changes and speciation appears not to be directional, as I found no evidence for more ornamented species to have higher speciation rates or to have diverged more recently. So, the present results indicate that, in the Estrildidae, changes in colour ornamentation are related with speciation, but not in a directional way, meaning that either increases or decreases in ornamentation are associated with speciation.

Furthermore, this comparative study found that ornamental coloration is related to some of the ecological and social traits of estrildid species, both in males and females. The trait most strongly related with colour was gregariousness, with more gregarious species being, on average, more ornamented. There were also some suggestive relations between other ecological conditions or indexes of reproductive investment and some coloration traits.

Relation between speciation and ornamentation

Comparative methods informed by phylogeny can assess whether and how speciation is related to sexually-selected signals. The classic hypothesis on this issue proposes that sexual selection promotes speciation, in a directional way, that is, stronger sexual selection leads to more speciation (e.g. Barraclough et al. 1995; Moller and Cuervo 1998; Arnqvist et al. 2000; Seddon et al. 2008; Seddon et al. 2013). An alternative hypothesis proposes that changes in ornamentation (whichever changes: increases, decreases, etc.) promote speciation, not necessarily in a directional way, so a relation between stronger sexual selection and increase in speciation is not predicted (e.g. Morrow et al. 2003; Phillimore et al. 2006; Cardoso and Mota 2008; Huang and Rabosky 2014; Servedio and Burger 2014).

Results show that most ornamental coloration traits (maximum and mean saturation, maximum achromatic difference and overall colour extent, with exception of

the bill coloration) fit a speciational model of evolution better than a gradual model, in both sexes. Support for a speciational model of evolution indicate one of two scenarios: first, ornamental traits may have had a punctuated mode of evolution (i.e. periods of stasis alternating with periods of rapid evolution) with the periods of rapid evolution associated with speciation events; or, second, these traits may have evolved more gradually but with phenotypic changes promoting speciation, and thus creating a correlation between the extent of phenotypic evolution and speciation (Mooers et al. 1999; Rabosky 2012). Either case indicates an association between changes in colour ornamentation and speciation, meaning that ornamental coloration either promotes speciation or changes as its consequence.

Although I found that most of the ornamental traits evolve through a speciational pattern, I found no evidence for directionality in the relation between these ornamental evolutionary changes and speciation. In fact, results did not show a relation between the degree of colour ornamentation and the terminal branch lengths or the number of speciation events, in either sex, which means that more ornamented species do not have higher rates of speciation. Because analyses had a desirable sample size (over 120 species; Freckleton et al. 2008) and consequently a very good statistical power, these negative results are strong evidence against the classic hypothesis that stronger sexual selection (as evaluated by the degree of ornamentation) increases speciation.

Therefore, in estrildid finches, it appears that it is not sexual selection per se that promotes speciation. Instead, evolutionary changes in colour ornamentation are associated with speciation, irrespective of these changes being increases or decreases in ornamentation. Evolutionary changes comprise both increases and decreases (or gains and losses) in ornamentation (e.g. Kimball et al. 2001; Wiens 2001), and many of the evolutionary changes in ornamentation appear to be losses or reductions (Wiens 2001). These losses or reductions, should not be exclusively due to sexual selection, and may even be due to reduction or absence of sexual selection. Thus, while the results indicate an association of sexual ornamentation with speciation, more ornamented lineages do not speciate more, contrary to the prediction of the classic hypothesis that increased sexual selection would promote speciation. This may help explain the conflicting results of past comparative studies on the relation between sexual selection and speciation (e.g. Barraclough et al. 1995; Mooers and Møller 1996; Arnqvist et al. 2000; Phillimore et al. 2006; Kraaijeveld et al. 2011; Seddon et al. 2013; Huang and Rabosky 2014; Servedio and Burger 2014). Past work relating the strength of sexual selection to speciation may have greatly underestimated the importance of sexually-selected ornamentation in speciation. The methods and results in this study with estrildid finches are similar to a previous paper in *Carduelis* finches (Cardoso and

Mota 2008), and both support the hypothesis that changes in ornamentation, not strength of sexual selection, promote speciation. This study, however, has a much higher statistical power, and therefore its negative result on the classic “sexual selection promotes speciation” hypothesis is more convincing.

The involvement of ornamental changes in speciation could be either due to changes in ornamentation causing speciation or being a consequence of speciation. For example, ornamental plumage evolution by reinforcement selection or reproductive character displacement would cause sexual selection and ornament evolution during the speciation event (Coyne and Orr 1998; Tobias et al. 2014), but divergence in ornaments could also be facilitated after speciation by drift in female preferences when reproductive isolation already took place. In the former case, changes in ornaments would increase speciation by creating reproductive isolation before populations become ecologically differentiated, and, in the latter case, changes in ornaments would still contribute to prevent gene flow in populations already ecologically differentiated. Therefore, changes likely contribute to reproductive isolation even if they happen after the speciation process is already under way.

As referred above, speciational evolution of most ornamentation trait was supported both for males and females. In the literature it is predicted that male coloration is more important for speciation and accelerates the evolution of reproductive isolation, because females are generally the sex that chooses mates (e.g. Andersson 1994). In line with this, the support for speciational over gradual evolution was slightly stronger for male ornamentation. But female ornamentation also showed a speciational pattern, possibly because male and female ornamentation is similar in many estrildid species.

I did not expect that morphological traits (body size and wing-to-tarsus ratio) evolved with a speciational pattern, because these traits are not expected to create reproductive isolation. Instead, my result probably means that speciation facilitated subsequent divergence on morphological traits. Nonetheless, some traits (bill shape and bill colour) fitted significantly better a gradual model of evolution, ensuring that there was no problem with the analyses that would bias results against regular gradual evolution.

Social and ecological correlates of ornamentation

Sexual selection, in both sexes, may be influenced by several ecological and social conditions, whose variation will lead to changes in ornamental coloration. In the present study, some of the relations between ecology and ornamentation were according to previous predictions in the literature. Males and females results were different, at some extent, and it is worth to note that some results on male ornamentation were stronger than on female's, which may be due to the fact that, for some estrildid species, males have more colourful plumage.

Gregariousness was the socio-ecological trait with the most interesting results. The social system of a species should strongly affect sexual selection, and it is expected that gregarious species have more colourful and ornamented plumage (Baker and Parker 1979; West-Eberhard 1983; Cuervo and Møller 1999). My results support this prediction. I found that, for males, more gregarious species (who live in larger groups or flocks) have more saturated plumage, and also more short- (blue/UV) and long-wavelength (yellow-to-red) plumage colour saturation. Furthermore, in males, more flock-living species revealed to have higher maximum achromatic difference and, in females, to have a more ornamented coloration in the bill (with more carotenoid-content). Social competition might be stronger in species that live in flocks or groups due to more frequent interactions of individuals, of the same or different sexes, in the search for food or in assessing potential mates (West-Eberhard 1983). Social competition, in which individuals interact with conspecific rivals to gain access to resources (West-Eberhard 1983), can lead to reproductive competition (Alexander 1974) in the search for mates, and so morphology and ornaments (such as coloration) will often evolve rapidly, leading to exaggeration (West-Eberhard 1983). So stronger social selection (which implies more variance in reproductive success due to social competition) will originate more complex and exaggerated signals, which increases sexual selection degree (West-Eberhard 1983). Additionally, flock-living birds should be more protected from predators, due to their numbers and coloration and to the vigilance of flock members (Baker and Parker 1979), such that the ornamentation costs should be lower in these species. Past studies relating coloration to gregarious condition are few and not strong; Baker and Parker (1979) showed an increase in ornamentation, of all birds' body part, in more gregarious birds, and Cuervo and Møller (1999) also found an overall, but not significant, tendency for more ornamental bird species to be more flock-living. My results show more convincing evidence for this relationship between gregariousness and sexual ornamentation.

Some ecological and social traits noted in the literature to influence bird plumage coloration, namely the altitude of the habitats (Badyaev 1997a), the diet (Olson and Owens 2005), the foraging heights (Badyaev and Ghalambor 1998; Tobias and Seddon 2009; Östman and Stuart-Fox 2011; Cardoso et al. 2012), the nestling period (e.g. Badyaev and Hill 2002; Mitchell et al. 2007; Germain et al. 2010), the nest height and the parasitism by brood parasites (Martin and Badyaev 1996; Cuervo and Møller 1999; Badyaev and Hill 2003), did not shown significant relations with the coloration of estrildids. Perhaps these social and ecological traits are not important for the evolution of coloration in estrildid finches, or maybe they do not have enough variability across species to explain differences in ornamentation. Nonetheless, other few ecological variables show some suggestive relations with individual coloration traits, which I discuss next. Note, though, that these additional results were not as strong or consistent across ornamental traits as those found for gregariousness, despite the analyses, as referred, had a good sample size (over 80 species) and consequently a good statistical power.

My results suggest that in species with larger clutches (which imply more parental care), males have an higher UV/blue content (short-wavelength plumage), and both sexes present an higher maximum achromatic difference; additionally, males with more ornamental coloration extent showed a small, but not significant, tendency to have higher incubation periods (involving more parental care). Clutch size and incubation period, as referred before, are indicative of reproductive investment, which in turn was suggested to influence male ornamentation through 3 different hypotheses: “good parent hypothesis”, “differential allocation hypothesis and “trade-off hypothesis” (see material and methods). Both of my results provide support to “good parent hypothesis” which predicts that, because more ornamented males provide better parental care, selection for male ornamentation as a parental signal should be stronger in species with higher reproductive investment (Germain et al. 2010; Gladbach et al. 2010). The alternative hypotheses predict the opposite association that more ornamented species provide less parental care (Badyaev 1997b; Badyaev and Hill 2002; Mitchell et al. 2007).

Estrildid species that are more migratory had higher long-wavelengths (yellow-to-red) colour content, but only in females. Males of migratory species are predicted to be more ornamented (Fitzpatrick 1994, 1998; Spottiswoode and Møller 2004; Albrecht et al. 2007; Cardoso et al. 2012), due to increased genetic variance (Fitzpatrick 1994, 1998) or because the time of arrival is an honest signal of male quality (subjected to sexual selection by female choice), being associated with higher rates of extra-pair opportunity (Spottiswoode and Møller 2004; Albrecht et al. 2007), and so males of

species with costlier migrations should experience a stronger sexual selection (Spottiswoode and Møller 2004); towards this prediction, my results found for females, what it is expected and predicted to occur in males.

Results show that estrildid species with longer breeding seasons have higher maximum achromatic difference, in females. I used the length of the breeding season as an index of breeding synchrony, among individuals. It is predicted that males of more synchronous bird species (with shorter breeding seasons) have more opportunity for extra-pair paternity and, consequently, increasing sexual selection strength (Albrecht et al. 2007; Hammers et al. 2009), and so are more ornamented. For estrildid species I did not found this correlation in males, but my results reveal an opposite relation for more ornamented females to have less breeding synchrony (larger breeding seasons).

Estrildid species in more closed habitats had higher long-wavelength saturation content, in males, meaning that have more yellow-to-red plumage, which is in agreement with the prediction that species living in more closed habitats should experience stronger sexual selection, particularly on longer-wavelengths colour hue (McNaught and Owens 2002). Different habitats are associated with different light exposition, and red and orange coloration are predicted to appear in species who live in closed habitats because the environment light spectrum, in these habitats, are rich in long-wavelengths colours, so signals, in this range, will contrast more with the surrounding vegetation (Endler 1993; McNaught and Owens 2002).

More common estrildid species showed higher blue/UV content but rare species showed higher yellow-to-red content, in females, which indicates that species with higher long-wavelengths and less short-wavelengths plumage content tend to be rarer, and consequently, to have an higher extinction risk. In passerids, this association of plumage with increased risk of extinction has been reported before (McLain et al. 1995). Bird species under strong sexual selection (and consequently with more ornamented plumage) are referred as more vulnerable to extinction (McLain et al. 1995). My results support, for females, the prediction that sexual selection increases the risk of extinction suggested in few past studies (e.g. McLain et al. 1995; Bro-Jørgensen 2014).

Conclusion

I conclude that evolutionary changes in ornamental coloration, such as colour saturation, maximum achromatic difference and colour extent, are associated with speciation in Estrildidae, and therefore changes in sexual ornamentation likely promote speciation. But there was no evidence for a directional pattern of increased colour ornamentation promoting speciation, which suggests that stronger sexual selection could not lead to more reproductive isolation, and consequently, nether to higher speciation rate. Together, these indicate that diverging ornamentation, rather than strength of sexual selection, is implicated in speciation, which helps explain conflicting results in the literature regarding the classic hypothesis that stronger sexual selection promotes speciation. Thus, I suggest that differences in cladogenesis among Estrildidae taxa can maybe be explained by evolutionary lability of ornaments, caused by ornamental gains as well as ornamental losses, with the latter clearly not related to stronger intensity of sexual selection. Past work relating strength of sexual selection to speciation may have strongly underestimated the importance of sexually-selected ornamentation in speciation.

I also conclude that, among a large set of social and ecological traits, ornamental coloration of Estrildidae is mainly related to the degree of gregariousness. Across the species in this family there is great variation in social systems, from solitary species or species where individuals gather in pairs, to species that live in large flocks year-round (Clement et al. 1993). This may explain why the relation between social system and sexual ornamentation (West-Eberhard 1983) appears more important here than in other bird groups (Baker and Parker 1979; Cuervo and Møller 1999). Additionally, some variables involved in reproductive investment explain, to some extent, variation of individual ornamental coloration traits, but those effects were not as strong or consistent among the coloration traits as that of gregariousness.

References

Albrecht, T., J. Schnitzer, J. Kreisinger, A. Exnerová, J. Bryja, and P. Munclinger. 2007. Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines. Behavioral Ecology 18:477-486.

Alexander, R. D. 1974. The evolution of social behavior. Annual review of ecology and systematics 5:325-383.

Amundsen, T. 2000. Why are female birds ornamented? Trends in Ecology & Evolution 15:149-155.

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

Armenta, J. K., P. O. Dunn, and L. A. Whittingham. 2008. Quantifying avian sexual dichromatism: a comparison of methods. Journal of Experimental Biology 211:2423-2430.

Arnqvist, G., M. Edvardsson, U. Friberg, and T. Nilsson. 2000. Sexual conflict promotes speciation in insects. Proceedings of the National Academy of Sciences 97:10460-10464.

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

Badyaev, A. V. 1997b. Covariation between life history and sexually selected traits: an example with cardueline finches. Oikos 80:128-138.

Badyaev, A. V., and C. K. Ghalambor. 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., and G. E. Hill. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. Biological Journal of the Linnean Society 69:153-172.

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

Badyaev, A. V., and G. E. Hill. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annual Review of Ecology, Evolution & Systematics 34:27-49.

Baker, R. R., and G. Parker. 1979. The evolution of bird coloration. Philosophical transactions of the Royal Society of London B 287:63-130.

Baldassarre, D. T., H. A. Thomassen, J. Karubian, and M. S. Webster. 2013. The role of ecological variation in driving divergence of sexual and non-sexual traits in the red-backed fairy-wren (*Malurus melanocephalus*). BMC evolutionary biology 13:75.

Barraclough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine birds. Proceedings of the Royal Society of London B 259:211-215.

Bennett, A., and I. Cuthill. 1994. Ultraviolet vision in birds: what is its function? Vision research 34:1471-1478.

Bleiweiss, R. 2005. Variation in ultraviolet reflectance by carotenoid-bearing feathers of tanagers (Thraupini: Emberizinae: Passeriformes). Biological Journal of the Linnean Society 84:243-257.

Boughman, J. W. 2002. How sensory drive can promote speciation. Trends in Ecology & Evolution 17:571-577.

Bowmaker, J., L. Heath, S. Wilkie, and D. Hunt. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. Vision research 37:2183-2194.

Britton, G. 1995. Structure and properties of carotenoids in relation to function. The FASEB Journal 9:1551-1558.

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

Brush, A. H. 1990. Metabolism of carotenoid pigments in birds. The FASEB Journal 4:2969-2977.

Burkhardt, D. 1989. UV vision: a bird's eye view of feathers. Journal of Comparative Physiology A 164:787-796.

Burns, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. Evolution 52:1219-1224.

Candolin, U., and J. Heuschele. 2008. Is sexual selection beneficial during adaptation to environmental change? Trends in Ecology & Evolution 23:446-452.

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

Cardoso, G. C., and P. G. Mota. 2008. Speciational Evolution of Coloration in the Genus Carduelis. Evolution 62:753-762.

Cardoso, G. C., and P. G. Mota. 2010. Evolution of female carotenoid coloration by sexual constraint in Carduelis finches. BMC evolutionary biology 10:82.

Civetta, A., and R. S. Singh. 1998. Sex and speciation: genetic architecture and evolutionary potential of sexual versus nonsexual traits in the sibling species of the Drosophila melanogaster complex. Evolution 52:1080-1092.

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

Coyne, J. A., and H. A. Orr. 1998. The evolutionary genetics of speciation. Philosophical Transactions of the Royal Society of London B 353:287-305.

Cuervo, J., and A. Møller. 1999. Ecology and evolution of extravagant feather ornaments. Journal of evolutionary biology 12:986-998.

Cuthill, I. C., J. C. Partridge, A. T. D. Bennett, S. C. Church, N. S. Hart, and S. Hunt. 2000. Ultraviolet vision in birds. Advances in the Study of Behavior 29:159-214.

Eaton, M. D., and S. M. Lanyon. 2003. The ubiquity of avian ultraviolet plumage reflectance. Proceedings of the Royal Society of London B 270:1721-1726.

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

Endler, J. A. 1993. The color of light in forests and its implications. Ecological monographs 63:1-27.

Endler, J. A., and P. W. Mielke. 2005. Comparing entire colour patterns as birds see them. Biological Journal of the Linnean Society 86:405-431.

Felsenstein, J. 1993. PHYLIP (Phylogeny Inference Package). version 3.0. Seattle.

Fitzpatrick, S. 1994. Colourful migratory birds: evidence for a mechanism other than parasite resistance for the maintenance of 'good genes' sexual selection. Proceedings of the Royal Society of London B 257:155-160.

Fitzpatrick, S. 1998. Intraspecific variation in wing length and male plumage coloration with migratory behaviour in continental and island populations. Journal of avian biology 29:248-256.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. The American naturalist 160:712-726.

Freckleton, R. P., A. B. Phillimore, and M. Pagel. 2008. Relating traits to diversification: a simple test. The American naturalist 172:102-115.

Gage, M. J., G. A. Parker, S. Nylin, and C. Wiklund. 2002. Sexual selection and speciation in mammals, butterflies and spiders. Proceedings of the Royal Society of London B 269:2309-2316.

Germain, R. R., M. W. Reudink, P. P. Marra, and L. M. Ratcliffe. 2010. Carotenoid-based male plumage predicts parental investment in the American Redstart. Wilson Journal of Ornithology 122:318-325.

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

Goldsmith, T. H. 1990. Optimization, constraint, and history in the evolution of eyes. Quarterly Review of Biology:281-322.

Griffith, S. C., T. H. Parker, and V. A. Olson. 2006. Melanin-versus carotenoid-based sexual signals: is the difference really so black and red? Animal Behaviour 71:749-763.

Hammers, M., N. von Engelhardt, N. E. Langmore, J. Komdeur, S. C. Griffith, and M. J. Magrath. 2009. Mate-guarding intensity increases with breeding synchrony in the colonial fairy martin, *Petrochelidon ariel*. Animal Behaviour 78:661-669.

Hill, G. E. 1996. Redness as a measure of the production cost of ornamental coloration. Ethology Ecology & Evolution 8:157-175.

Hill, G. E., and W. R. Brawner. 1998. Melanin–based plumage coloration in the house finch is unaffected by coccidial infection. Proceedings of the Royal Society of London B 265:1105-1109.

Hu, Y., and G. C. Cardoso. 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? Behavioral Ecology 20:1268-1273.

Huang, H., and D. L. Rabosky. 2014. Sexual selection and diversification: reexamining the correlation between dichromatism and speciation rate in birds. The American naturalist. 184:E101-E114.

Hugall, A. F., and D. Stuart-Fox. 2012. Accelerated speciation in colour-polymorphic birds. Nature 485:631-634.

Isaac, N. J., K. E. Jones, J. L. Gittleman, and A. Purvis. 2005. Correlates of species richness in mammals: body size, life history, and ecology. The American naturalist 165:600-607.

Jawor, J. M., and R. Breitwisch. 2003. Melanin ornaments, honesty, and sexual selection. The Auk 120:249-265.

Jetz, W., G. Thomas, J. Joy, K. Hartmann, and A. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444-448.

Katzourakis, A., A. Purvis, S. Azmeh, G. Rotheray, and F. Gilbert. 2001. Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. Journal of evolutionary biology 14:219-227.

Kiere, L. M., C. M. Hofmann, J. Jordan Price, T. W. Cronin, and K. E. Omland. 2009. Discrete evolutionary color changes in caciques suggest different modes of carotenoid evolution between closely related taxa. Journal of Avian Biology 40:605-613.

Kimball, R. T., E. L. Braun, J. D. Ligon, V. Lucchini, and E. Randi. 2001. A molecular phylogeny of the peacock-pheasants (Galliformes: *Polyplectron* spp.) indicates loss and reduction of ornamental traits and display behaviours. Biological Journal of the Linnean Society 73:187-198.

Kraaijeveld, K., F. J. Kraaijeveld-Smit, and M. E. Maan. 2011. Sexual selection and speciation: the comparative evidence revisited. Biological Reviews 86:367-377.

Leclaire, S., J. White, E. Arnoux, B. Faivre, N. Vetter, S. A. Hatch, and E. Danchin. 2011. Integument coloration signals reproductive success, heterozygosity, and antioxidant levels in chick-rearing black-legged kittiwakes. Die Naturwissenschaften 98:773-782.

Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection and speciation. Ecology Letters 14:591-602.

Maia, R., C. M. Eliason, P.P. Bitton, S. M. Doucet, M. D. Shawkey, and A. Tatem. 2013. pavo: an R package for the analysis, visualization and organization of spectral data. Methods in Ecology and Evolution 4:906-913.

Maier, E. 1994. Ultraviolet vision in a passeriform bird: from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. Vision research 34:1415-1418.

Martin, T. E., and A. V. Badyaev. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. Evolution 50:2454-2460.

Mays Jr, H. L., K. J. McGraw, G. Ritchison, S. Cooper, V. Rush, and R. S. Parker. 2004. Sexual dichromatism in the yellow-breasted chat *Icteria virens*: spectrophotometric analysis and biochemical basis. Journal of Avian Biology 35:125-134.

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

McNaught, M. K., and I. P. Owens. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? Journal of evolutionary biology 15:505-514.

Milá, B., T. B. Smith, and R. K. Wayne. 2007. Speciation and rapid phenotypic differentiation in the yellow-rumped warbler *Dendroica coronata* complex. Molecular Ecology 16:159-173.

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

Mitra, S., H. Landel, and S. Pruett-Jones. 1996. Species richness covaries with mating system in birds. The Auk 113:544-551.

Moller, A., and J. Cuervo. 1998. Speciation and feather ornamentation in birds. Evolution 52:859-869.

Montgomerie, R. 2006. Analyzing colors. Pp. 90-147 *in* G. E. Hill, and K. McGraw, eds. Bird coloration: volume 1, mechanisms and measurements. Harvard University Press, Boston MA.

Mooers, A. Ø., and A. P. Møller. 1996. Colonial breeding and speciation in birds. Evolutionary Ecology 10:375-385.

Mooers, A. Ø., S. M. Vamosi, and D. Schluter. 1999. Using phylogenies to test macroevolutionary hypotheses of trait evolution in cranes (Gruinae). The American naturalist 154:249-259.

Morrow, E. H., T. E. Pitcher, and G. Arnqvist. 2003. No evidence that sexual selection is an 'engine of speciation' in birds. Ecology Letters 6:228-234.

Murphy, T. G., M. F. Rosenthal, R. Montgomerie, and K. A. Tarvin. 2009. Female American goldfinches use carotenoid-based bill coloration to signal status. Behavioral Ecology 20:1348-1355.

Ödeen, A., and M. Björklund. 2003. Dynamics in the evolution of sexual traits: losses and gains, radiation and convergence in yellow wagtails (*Motacilla flava*). Molecular Ecology 12:2113-2130.

Olson, V. A., and I. P. F. Owens. 2005. Interspecific variation in the use of carotenoid-based coloration in birds: diet, life history and phylogeny. Journal of evolutionary biology 18:1534-1546.

Omland, K. E., and S. M. Lanyon. 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. Evolution 54:2119-2133.

Östman, Ö., and D. Stuart-Fox. 2011. Sexual selection is positively associated with ecological generalism among agamid lizards. Journal of evolutionary biology 24:733-740.

Owens, I. P., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? Proceedings of the Royal Society of London B 266:933-939.

Owens, I. P., and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society B 265:397-407.

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

Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza. 2001. Sexual selection and speciation. Trends in Ecology & Evolution 16:364-371.

Payne, R. 2010. Family Estrildidae (Waxbills) *in* J. del Hoyo, A. Elliott, and D. A. Christie, eds. Handbook of the Birds of the World - Weavers to New World Warblers. Lynx Edicions.

Pérez-Rodríguez, L. 2008. Carotenoid-based ornamentation as a dynamic but consistent individual trait. Behavioral Ecology and Sociobiology 62:995-1005.

Phillimore, A. B., R. P. Freckleton, C. D. L. Orme, and I. P. Owens. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. The American naturalist 168:220-229.

Price, J. J. 1996. An Association of Habitat with Color Dimorphism in Finches. The Auk 113:256-257.

Price, T. D. 2006. Phenotypic plasticity, sexual selection and the evolution of colour patterns. Journal of Experimental Biology 209:2368-2376.

Prum, R. O., S. Andersson, R. H. Torres, and T. Grubb. 2003. Coherent scattering of ultraviolet light by avian feather barbs. The Auk 120:163-170.

Rabosky, D. L. 2012. Positive correlation between diversification rates and phenotypic evolvability can mimic punctuated equilibrium on molecular phylogenies. Evolution 66:2622-2627.

Rabosky, D. L., and D. R. Matute. 2013. Macroevolutionary speciation rates are decoupled from the evolution of intrinsic reproductive isolation in *Drosophila* and birds. Proceedings of the National Academy of Sciences 110:15354-15359.

Ritchie, M. G. 2007. Sexual Selection and Speciation. Annual Review of Ecology, Evolution, and Systematics 38:79-102.

Rosenthal, M. F., T. G. Murphy, N. Darling, and K. A. Tarvin. 2012. Ornamental bill color rapidly signals changing condition. Journal of Avian Biology 43:553-564.

Roulin, A., and A. L. Ducrest. 2013. Genetics of colouration in birds. Seminars in cell & developmental biology 24:594-608.

Rundle, H. D., and P. Nosil. 2005. Ecological speciation. Ecology letters 8:336-352.

Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology & Evolution 16:372-380.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323:737-741.

Schluter, D., and T. Price. 1993. Honesty, perception and population divergence in sexually selected traits. Proceedings of the Royal Society of London B 253:117-122.

Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. MacGregor, D. R. Rubenstein, J. A. C. Uy, J. T. Weir, L. A. Whittingham, and R. J. Safran. 2013. Sexual selection accelerates signal evolution during speciation in birds. Proceedings of the Royal Society B 280:20131065.

Seddon, N., R. M. Merrill, and J. A. Tobias. 2008. Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. The American naturalist 171:620-631.

Servedio, M. R., and R. Burger. 2014. The counterintuitive role of sexual selection in species maintenance and speciation. Proceedings of the National Academy of Sciences of the United States of America 111:8113-8118.

Sims, D. A., and J. A. Gamon. 2002. Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. Remote sensing of environment 81:337-354.

Spottiswoode, C., and A. P. Møller. 2004. Extrapair paternity, migration, and breeding synchrony in birds. Behavioral Ecology 15:41-57.

Spottiswoode, C. N., A. P. Tøttrup, and T. Coppack. 2006. Sexual selection predicts advancement of avian spring migration in response to climate change. Proceedings of the Royal Society B 273:3023-3029.

Stoddard, M. C., and R. O. Prum. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. The American naturalist 171:755-776.

Stuart-Fox, D., and I. P. F. Owens. 2003. Species richness in agamid lizards: chance, body size, sexual selection or ecology? Journal of evolutionary biology 16:659-669.

Tankus, A., and Y. Yeshurun. 2009. Computer vision, camouflage breaking and countershading. Philosophical Transactions of the Royal Society B 364:529-536.

Thayer, A. H. 1896. The Law Which Underlies Protective Coloration. The Auk 13:124-129.

Tobias, J., and N. Seddon. 2009. Sexual selection and ecological generalism are correlated in antbirds. Journal of evolutionary biology 22:623-636.

Tobias, J. A., C. K. Cornwallis, E. P. Derryberry, S. Claramunt, R. T. Brumfield, and N. Seddon. 2014. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. Nature 506:359-363.

Völker, O. 1953. Das Farbkleid der Flaumfußtauben (Ptilinopodinae). Journal of Ornithology 94:263-273.

Vonlanthen, P., D. Bittner, A. G. Hudson, K. A. Young, R. Muller, B. Lundsgaard-Hansen, D. Roy, S. Di Piazza, C. R. Largiader, and O. Seehausen. 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. Nature 482:357-362.

Vorobyev, M., D. Osorio, A. Bennett, N. Marshall, and I. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. Journal of Comparative Physiology A 183:621-633.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58:155-183.

Wiens, J. J. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. Trends in Ecology & Evolution 16:517-523.

Appendix

- Table A1 to A5.

Table A1. Morphology and coloration traits for the measured estrildid species, for both males and females (when available).

		Morphology traits			Coloration traits						
Species	**Sex**	**PC1 Body dimension (bd)**	**Bill shape (bs)**	**Wing / Tarsus ratio (wtr)**	**Maximum achromatic difference (max achr diff)**	**Maximum colour saturation (max col sat)**	**Mean colour saturation (mean col sat)**	**Maximum PC2 (max pc2)**	**Minimum PC2 (min pc2)**	**Extent of ornamental coloration (eoc)**	**Bill colour (bc)**
Parmoptila woodhousei	m	-1.02	2.58	3.48	0.58	0.49	0.32	0.19	-2.82	0.011	0
Parmoptila woodhousei	f	-1.05	2.26	3.78	0.70	0.44	0.29	-0.12	-3.17	0.000	0
Parmoptila rubifrons	m	-0.88	2.33	3.69	0.45	0.57	0.34	-0.17	-3.11	0.023	0
Parmoptila rubifrons	f	-0.68	2.41	3.66	1.07	0.34	0.23	-0.24	-1.59	0.000	0
Nigrita fusconota	m	-1.36	2.10	4.01	1.53	0.26	0.22	2.18	-1.03	0.140	0
Nigrita fusconota	f	-1.27	2.06	4.06	1.66	0.24	0.21	2.25	-0.62	0.167	0
Nigrita bicolor	m	-0.62	1.62	4.06	0.08	0.23	0.19	0.76	-0.24	0.000	0
Nigrita bicolor	f	-0.68	1.52	4.20	0.14	0.27	0.21	-0.03	-1.32	0.000	0
Nigrita luteifrons	m	-0.56	1.49	4.11	1.13	0.32	0.21	0.48	-1.11	0.298	0
Nigrita luteifrons	f	-0.69	1.50	4.17	0.98	0.28	0.22	0.42	-0.78	0.016	0
Nigrita canicapilla	m	1.08	1.63	4.40	0.15	0.23	0.19	0.56	-0.26	0.575	0
Nigrita canicapilla	f	1.04	1.63	4.36	0.60	0.25	0.19	0.26	-0.39	0.586	0
Nesocharis shelleyi	m	-1.85	1.75	3.30	0.69	0.35	0.23	0.62	-0.99	0.690	0
Nesocharis shelleyi	f	-1.60	1.71	3.22	0.44	0.39	0.23	0.56	-1.07	0.594	0
Nesocharis ansorgei	m	-0.69	1.06	3.72	0.75	0.38	0.24	1.53	-0.78	0.656	0
Nesocharis capistrata	m	0.18	1.25	3.36	0.64	0.39	0.25	0.57	-0.68	0.572	0
Nesocharis capistrata	f	0.43	1.28	3.44	0.73	0.40	0.24	0.77	-0.89	0.545	0
Pytilia phoenicoptera	m	-0.09	1.55	3.92	0.30	0.35	0.29	0.12	-1.04	0.312	0
Pytilia phoenicoptera	f	-0.20	1.48	4.10	0.61	0.46	0.31	0.45	-1.55	0.316	0
Pytilia phoenicoptera lineata	m	0.07	1.55	4.03	0.32	0.38	0.27	0.24	-1.18	0.341	1
Pytilia hypogrammica	m	-0.13	1.62	3.60	0.20	0.49	0.35	0.00	-1.50	0.268	0
Pytilia hypogrammica	f	-0.16	1.63	3.49	0.48	0.40	0.30	0.26	-1.05	0.213	0
Pytilia afra	m	-0.42	1.39	3.77	0.49	0.49	0.39	-0.35	-1.92	0.759	1
Pytilia afra	f	0.01	1.47	4.32	0.72	0.41	0.29	-0.13	-1.08	0.389	1
Pytilia melba	m	0.52	1.68	3.67	0.43	0.66	0.40	-0.24	-3.17	0.592	1
Pytilia melba	f	0.27	1.52	3.83	0.37	0.28	0.24	0.10	-0.70	0.529	1
Mandingoa nitidula	m	-0.79	1.29	3.77	0.70	0.43	0.27	0.86	-1.89	0.714	0.5
Mandingoa nitidula	f	-1.14	1.32	3.73	1.03	0.42	0.27	0.49	-1.66	0.648	0.5
Cryptospiza reichenovii	m	0.19	1.30	3.11	0.66	0.60	0.29	0.65	-2.25	0.665	0
Cryptospiza reichenovii	f	0.13	1.35	3.08	0.37	0.32	0.22	0.28	-0.77	0.571	0
Cryptospiza salvadorii	m	0.44	1.27	3.62	0.32	0.32	0.23	0.64	-1.01	0.570	0

Species	Sex	bd	bs	wtr	max achr diff	max col sat	mean col sat	max pc2	min pc2	eoc	bc
Cryptospiza salvadorii	f	0.10	1.31	3.50	0.85	0.39	0.25	0.80	-0.68	0.675	0
Cryptospiza jacksoni	m	0.93	1.33	2.74	0.10	0.26	0.22	0.68	-0.55	0.443	
Cryptospiza jacksoni	f	0.92	1.43	3.10	0.33	0.45	0.28	1.02	-1.25	0.439	
Cryptospiza shelleyi	m	1.71	1.27	3.02	0.44	0.42	0.30	0.33	-1.95	0.591	1
Pyrenestes sanguineus	m	1.74	0.86	3.32	0.32	0.58	0.40	0.84	-2.15	0.310	
Pyrenestes sanguineus	f	1.92	1.02	3.24	0.18	0.43	0.32	0.88	-0.82	0.316	
Pyrenestes ostrinus	m	2.21	0.96	3.27	0.36	0.54	0.37	1.63	-1.18	0.923	0
Pyrenestes ostrinus	f	2.18	0.83	3.23	0.33	0.56	0.36	1.42	-0.83	0.266	0
Pyrenestes minor	m	0.93	0.81	3.88	0.33	0.60	0.39	0.82	-1.92	0.256	0
Pyrenestes minor	f	1.08	0.97	3.23	0.35	0.52	0.33	0.21	-1.81	0.159	0
Spermophaga poliogenys	m	2.38	1.03	3.14	0.35	0.64	0.45	0.77	-2.31	0.821	0.5
Spermophaga poliogenys	f	1.95	1.15	3.33	0.62	0.62	0.39	1.21	-2.35	0.126	0.5
Spermophaga haematina	m	2.72	1.07	2.93	0.39	0.58	0.30	0.75	-1.54	0.809	0.5
Spermophaga haematina	f	2.88	1.22	3.06	0.60	0.60	0.31	0.44	-1.63	0.676	0.5
Spermophaga haematina pustulata	m	2.64	1.12	3.26	0.46	0.63	0.39	0.44	-2.36	0.836	0.5
Spermophaga haematina pustulata	f	2.64	1.13	3.17	0.47	0.54	0.34	0.96	-1.82	0.395	0.5
Spermophaga ruficapilla	m	3.07	1.00	3.36	0.32	0.57	0.35	0.35	-1.98	0.709	0.5
Spermophaga ruficapilla	f	2.68	1.06	3.20	0.34	0.55	0.34	0.49	-1.49	0.222	0.5
Clytospiza montieri	m	0.84	1.54	3.71	0.54	0.44	0.29	1.07	-0.89	0.075	0
Clytospiza montieri	f	0.90	1.31	3.61	1.04	0.38	0.26	1.06	-0.88	0.055	0
Hypargos margaritatus	m	0.11	1.32	3.46	0.40	0.44	0.26	0.60	-0.94	0.309	0
Hypargos margaritatus	f	0.02	1.20	3.28	0.63	0.29	0.26	0.54	-0.31	0.040	0
Hypargos niveoguttatus	m	0.91	1.39	3.44	0.36	0.39	0.25	1.10	-0.74	0.227	0
Hypargos niveoguttatus	f	0.76	1.36	3.52	0.73	0.53	0.30	0.87	-1.71	0.116	0
Euschistospiza dybowskii	m	-0.01	1.30	3.61	0.08	0.22	0.19	0.55	-0.47	0.539	0
Euschistospiza dybowskii	f	0.00	1.46	3.57	0.26	0.26	0.22	0.52	-0.50	0.327	0
Euschistospiza cinereovinacea	m	-0.05	1.26	3.37	0.11	0.23	0.20	0.80	-0.04	0.306	0
Euschistospiza cinereovinacea	f	0.17	1.33	3.34	0.08	0.21	0.19	0.80	-0.04	0.302	0
Lagonosticta rara	m	-0.39	1.30	3.43	0.19	0.38	0.23	1.00	-0.33	0.745	0.5
Lagonosticta rara	f	-0.26	1.26	3.49	0.19	0.36	0.24	0.91	-0.25	0.734	0.5
Lagonosticta rufopicta	m	-0.74	1.25	3.30	0.43	0.43	0.32	0.58	-0.47	0.252	0.5
Lagonosticta rufopicta	f	-0.80	1.22	3.72	0.44	0.40	0.27	0.97	-0.45	0.230	0.5
Lagonosticta nitidula	m	-0.15	1.18	3.77	0.22	0.33	0.23	0.73	-0.18	0.136	0.5
Lagonosticta nitidula	f	-0.33	1.17	3.39	0.24	0.33	0.23	0.94	0.26	0.109	0.5
Lagonosticta senegala	m	-1.06	1.10	4.28	0.27	0.51	0.34	0.37	-0.73	0.460	0.5
Lagonosticta senegala	f	-1.14	1.19	3.85	0.70	0.38	0.29	0.72	-1.15	0.566	0.5
Lagonosticta rubricata	m	-0.57	1.48	3.36	0.30	0.45	0.30	0.62	-1.04	0.789	0.5
Lagonosticta rubricata	f	-0.29	1.41	3.58	0.37	0.49	0.30	0.68	-1.53	0.863	0.5
Lagonosticta landanae	m	-0.82	1.29	3.41	0.35	0.52	0.32	0.91	-1.11	0.694	

Species	Sex	bd	bs	wtr	max achr diff	max col sat	mean col sat	max pc2	min pc2	eoc	bc
Lagonosticta landanae	f	-0.88	1.21	3.93	0.55	0.42	0.28	0.77	-0.77	0.590	
Lagonosticta rhodopareia	m	-0.91	1.40	3.66	0.42	0.44	0.29	0.56	-1.85	0.391	0
Lagonosticta rhodopareia	f	-0.55	1.43	3.46	0.63	0.61	0.32	0.53	-2.20	0.333	0
Lagonosticta larvata	m	-0.02	1.46	3.82	0.34	0.39	0.25	0.47	-0.36	0.429	
Lagonosticta larvata	f	-0.67	1.45	3.68	0.58	0.45	0.29	0.86	-1.90	0.498	
Lagonosticta rhodopareia virata	m	-0.29	1.61	3.29	0.45	0.44	0.29	0.06	-1.19	0.316	
Lagonosticta rhodopareia virata	f	-0.21	1.54	3.59	0.35	0.43	0.26	0.78	-1.09	0.344	
Uraeginthus angolensis	m	-0.56	1.57	3.61	0.45	0.25	0.20	2.74	1.02	0.301	0
Uraeginthus angolensis	f	-0.54	1.43	3.88	0.59	0.25	0.20	2.41	1.43	0.261	0
Uraeginthus bengalus	m	-0.40	1.38	3.78	0.55	0.47	0.24	2.56	-0.66	0.269	0.5
Uraeginthus bengalus	f	-0.51	1.52	3.74	0.59	0.25	0.22	1.88	0.80	0.271	0.5
Uraeginthus cyanocephala	m	-0.13	1.44	4.42	0.88	0.22	0.20	2.31	0.14	0.416	1
Uraeginthus cyanocephala	f	-0.14	1.30	3.76	1.01	0.35	0.26	1.69	-0.68	0.312	1
Uraeginthus granatina	m	0.56	1.58	3.81	0.43	0.36	0.22	2.26	-0.64	0.170	1
Uraeginthus granatina	f	0.70	1.33	3.31	0.75	0.42	0.27	1.18	-1.02	0.087	1
Uraeginthus ianthinogaster	m	1.14	1.16	3.47	0.37	0.30	0.19	2.18	-0.41	0.257	1
Uraeginthus ianthinogaster	f	0.71	1.32	3.43	0.74	0.45	0.28	2.13	-1.60	0.057	1
Estrilda caerulescens	m	-0.37	1.52	3.78	1.14	0.36	0.24	0.47	-1.38	0.221	0
Estrilda caerulescens	f	-0.43	1.40	3.67	1.04	0.28	0.24	0.80	-0.92	0.236	0
Estrilda perreini	m	-0.40	1.28	3.82	0.61	0.29	0.22	0.91	-0.34	0.106	0
Estrilda perreini	f	-0.34	1.41	3.66	0.70	0.34	0.23	0.89	-0.19	0.080	0
Estrilda thomensis	m	-0.86	1.50	3.94	1.45	0.28	0.24	2.82	-0.90	0.177	
Estrilda thomensis	f	-0.71	1.29	4.26	0.91	0.47	0.30	1.03	-1.06	0.161	
Estrilda melanotis	m	-1.36	1.31	3.69	0.98	0.54	0.26	1.00	-1.45	0.523	0.5
Estrilda melanotis	f	-1.00	1.32	3.69	1.12	0.53	0.28	0.09	-0.98	0.424	0.5
Estrilda melanotis bocagei	m	-1.70	1.28	3.75	0.82	0.42	0.26	0.74	-1.83	0.600	0.5
Estrilda melanotis bocagei	f	-1.84	1.19	3.99	1.21	0.39	0.27	1.65	-0.81	0.513	0.5
Estrilda paludicola	m	-1.06	1.20	3.42	1.26	0.34	0.26	0.49	-0.84	0.053	1
Estrilda paludicola	f	-0.94	1.07	3.39	1.19	0.32	0.23	0.35	-0.76	0.062	1
Estrilda paludicola ochrogaster	m	-1.04	1.19	3.68	1.31	0.39	0.28	0.82	-0.20	0.354	1
Estrilda paludicola ochrogaster	f	-1.03	1.16	3.56	1.36	0.35	0.26	1.71	-0.39	0.353	1
Estrilda paludicola bengelensis	m	-1.08	1.08	3.58	1.32	0.44	0.27	1.41	-0.97	0.364	1
Estrilda paludicola bengelensis	f	-0.79	1.08	3.45	1.32	0.38	0.26	1.72	0.55	0.359	1
Estrilda poliopareia	m	-0.91	1.04	3.44	1.22	0.45	0.31	0.09	-2.36	0.086	1
Estrilda poliopareia	f	-0.90	1.00	3.34	1.08	0.41	0.29	0.23	-1.21	0.073	1
Estrilda melpoda	m	-0.96	1.04	3.44	1.22	0.59	0.33	1.31	-2.90	0.114	1
Estrilda melpoda	f	-1.00	1.23	3.26	0.91	0.45	0.28	0.87	-1.35	0.123	1
Estrilda rhodopyga	m	-0.79	1.36	3.62	0.95	0.43	0.30	-0.07	-1.55	0.152	0.5
Estrilda rhodopyga	f	-1.10	1.39	3.71	0.78	0.43	0.30	0.56	-1.53	0.136	0.5

Species	Sex	bd	bs	wtr	max achr diff	max col sat	mean col sat	max pc2	min pc2	eoc	bc
Estrilda rufibarba	m	-1.04	1.32	3.80	1.40	0.49	0.27	0.22	-1.23	0.070	0.5
Estrilda rufibarba	f	-0.86	1.25	4.01	1.15	0.40	0.25	0.60	-0.87	0.067	0.5
Estrilda melanotis quartinia	m	-1.26	1.39	3.82	1.19	0.50	0.29	1.39	-2.44	0.542	0
Estrilda melanotis quartinia	f	-1.22	1.19	3.44	1.12	0.45	0.28	1.53	-1.04	0.577	0
Estrilda troglodytes	m	-1.38	1.19	4.16	1.17	0.54	0.30	0.49	-0.88	0.209	1
Estrilda troglodytes	f	-1.30	1.26	3.96	0.97	0.44	0.28	0.70	-0.90	0.178	1
Estrilda astrild	m	-0.65	1.12	3.73	1.00	0.61	0.33	0.59	-1.83	0.063	1
Estrilda astrild	f	-0.15	1.14	3.28	0.94	0.63	0.34	0.74	-2.06	0.085	1
Estrilda nonnula	m	-0.75	1.18	3.54	1.39	0.45	0.25	1.29	-1.03	0.195	0.5
Estrilda nonnula	f	-0.51	1.13	3.26	1.29	0.34	0.23	1.40	-0.52	0.155	0.5
Estrilda atricapilla	m	-1.01	1.15	3.45	0.96	0.52	0.29	1.34	-0.48	0.205	0.5
Estrilda atricapilla	f	-0.93	1.14	3.21	0.82	0.54	0.27	1.85	0.08	0.207	0.5
Estrilda erythronotos	m	-0.09	1.45	3.78	0.13	0.35	0.24	0.50	-0.89	0.306	0
Estrilda erythronotos	f	-0.02	1.38	3.62	0.29	0.28	0.22	0.71	-0.68	0.278	0
Estrilda erythronotos charmosyna	m	-0.50	1.29	3.83	0.91	0.52	0.30	0.78	-1.18	0.125	
Estrilda erythronotos charmosyna	f	-0.32	1.32	3.76	1.11	0.41	0.26	0.93	-0.52	0.126	
Amandava amandava	m	-1.04	1.32	3.61	0.23	0.46	0.29	0.49	-1.40	0.214	0.5
Amandava amandava	f	-1.10	1.30	3.93	0.87	0.43	0.26	0.87	-2.46	0.150	0.5
Amandava formosa	m	-0.74	1.42	3.45	1.22	0.36	0.26	0.94	-0.60	0.719	1
Amandava formosa	f	-0.78	1.54	3.32	1.45	0.36	0.25	1.39	0.39	0.713	1
Amandava subflava	m	-2.45	1.40	3.67	0.65	0.57	0.34	-0.11	-1.97	0.560	0.5
Amandava subflava	f	-2.06	1.24	3.67	0.92	0.45	0.28	0.65	-1.56	0.583	0.5
Ortygospiza atricollis	m	-0.74	1.16	3.60	0.21	0.39	0.22	0.65	-0.75	0.099	1
Ortygospiza atricollis	f	-1.25	1.12	3.71	0.29	0.46	0.24	0.74	-2.10	0.000	1
Ortygospiza gabonensis	m	-1.84	1.00	3.53	0.37	0.38	0.23	0.73	-1.04	0.049	1
Ortygospiza gabonensis	f	-1.21	1.02	3.47	0.77	0.36	0.24	0.68	-0.94	0.000	1
Ortygospiza locustella	m	-1.65	0.89	3.42	0.42	0.54	0.41	0.74	-0.81	0.426	0.5
Ortygospiza locustella	f	-1.68	0.89	3.17	1.07	0.43	0.28	0.96	-0.76	0.207	0.5
Aegintha temporalis	m	-0.19	1.15	3.82	1.02	0.51	0.30	0.95	-1.25	0.491	0.5
Aegintha temporalis	f	-0.20	1.16	3.82	0.80	0.51	0.32	1.12	-1.11	0.504	0.5
Emblema picta	m	0.21	1.82	3.96	0.29	0.60	0.37	0.17	-2.26	0.383	0.5
Emblema picta	f	0.06	1.79	4.21	0.31	0.54	0.27	0.54	-1.89	0.073	0.5
Emblema bella	m	0.72	1.21	3.46	0.44	0.58	0.27	0.45	-2.05	0.243	1
Emblema bella	f	0.93	1.25	3.50	0.27	0.52	0.27	0.74	-1.56	0.244	1
Emblema oculata	m	0.66	1.21	3.24	0.50	0.51	0.29	0.81	-1.52	0.219	1
Emblema oculata	f	0.38	1.16	3.82	0.37	0.44	0.27	0.34	-1.11	0.225	1
Emblema guttata	m	0.90	1.11	4.23	1.39	0.51	0.25	0.81	-1.66	0.224	1
Emblema guttata	f	0.71	1.10	4.07	1.42	0.60	0.28	1.77	-1.55	0.231	1
Oreostruthus fuliginosus	m	1.49	0.97	3.11	0.31	0.46	0.29	0.49	-1.41	0.108	1

Species	Sex	bd	bs	wtr	max achr diff	max col sat	mean col sat	max pc2	min pc2	eoc	bc
Neochmia phaeton	m	0.40	1.07	3.73	0.19	0.40	0.28	1.36	0.08	0.776	0.5
Neochmia phaeton	f	0.43	1.19	3.67	0.34	0.47	0.29	0.53	-1.05	0.483	0.5
Neochmia ruficauda	m	-0.37	1.07	3.74	1.19	0.57	0.36	1.28	-1.40	0.718	1
Neochmia ruficauda	f	-0.17	1.14	3.60	0.83	0.44	0.29	0.47	-1.06	0.690	1
Poephila guttata	m	-0.87	1.14	3.99	1.33	0.46	0.28	1.28	-2.24	0.001	1
Poephila guttata	f	-0.82	1.08	4.09	1.20	0.34	0.23	1.04	-1.43	0.001	1
Poephila guttata castanotis	m	-0.20	1.13	3.91	1.45	0.49	0.29	0.94	-1.49	0.001	1
Poephila guttata castanotis	f	-0.43	1.15	4.40	1.33	0.31	0.25	1.22	-0.60	0.002	1
Poephila bichenovii	m	-0.67	0.98	4.03	1.54	0.26	0.23	2.25	0.41	0.121	0
Poephila bichenovii	f	-1.21	1.01	4.19	1.25	0.29	0.25	1.38	0.01	0.116	0
Poephila personata	m	0.65	1.12	4.25	0.89	0.41	0.30	0.79	-1.22	0.046	0
Poephila personata	f	0.64	1.11	3.99	1.43	0.37	0.26	1.10	-0.39	0.039	0
Poephila acuticauda	m	0.98	1.23	4.29	1.47	0.40	0.26	0.96	-0.54	0.089	0
Poephila acuticauda	f	0.87	1.21	4.29	1.68	0.38	0.25	2.82	-0.86	0.082	0
Poephila cincta	m	0.01	1.08	3.99	1.26	0.45	0.28	0.98	-1.39	0.091	0
Poephila cincta	f	0.10	1.24	4.06	1.37	0.46	0.28	1.08	-1.59	0.090	0
Erythrura hyperythra	m	-0.38	1.19	3.67	0.52	0.47	0.28	0.68	-1.94	0.663	0
Erythrura hyperythra	f	-0.25	1.17	3.94	0.86	0.48	0.27	0.36	-1.66	0.553	0
Erythrura prasina	m	0.64	1.33	4.25	0.66	0.59	0.33	0.86	-2.66	0.780	0
Erythrura prasina	f	0.60	1.30	4.50	0.70	0.44	0.27	0.74	-2.97	0.558	0
Erythrura viridifacies	m	0.08	1.26	4.60	0.26	0.47	0.27	0.60	-0.96	0.769	0
Erythrura tricolor	m	-0.25	1.19	3.44	0.22	0.39	0.22	1.10	-0.60	0.855	0
Erythrura trichroa	m	0.32	1.12	3.75	0.22	0.36	0.23	1.41	0.41	0.880	0
Erythrura trichroa	f	0.77	1.08	3.49	0.25	0.42	0.22	1.52	0.37	0.900	0
Erythrura papuana	m	1.87	1.12	3.59	0.26	0.44	0.23	0.40	-0.72	0.932	0
Erythrura papuana	f	1.76	1.14	3.65	0.38	0.35	0.25	0.77	-0.55	0.865	0
Erythrura coloria	m	0.10	1.06	3.43	0.24	0.39	0.24	0.80	-0.29	0.848	0
Erythrura psittacea	m	0.65	1.07	3.32	0.42	0.60	0.37	0.90	-2.24	0.896	0
Erythrura psittacea	f	0.41	1.06	3.32	0.52	0.61	0.36	0.37	-2.69	0.862	0
Erythrura cyanovirens pealii	m	0.13	1.12	3.82	0.38	0.53	0.30	0.88	-1.75	0.826	
Erythrura cyanovirens pealii	f	0.44	1.05	3.64	0.28	0.42	0.25	0.86	-0.46	0.872	
Erythrura cyanovirens	m	0.94	1.19	3.91	0.24	0.46	0.25	1.21	-1.11	0.915	0
Erythrura cyanovirens	f	1.07	1.14	3.65	0.13	0.27	0.21	1.67	0.77	0.828	0
Erythrura cyanovirens regia	m	1.11	1.09	3.78	0.33	0.61	0.30	0.99	-1.80	0.856	0
Erythrura cyanovirens regia	f	1.13	1.02	3.74	0.36	0.62	0.30	0.82	-2.72	0.814	0
Erythrura kleinschmidti	f	2.02	1.53	3.06	0.34	0.57	0.26	1.00	-2.04	0.845	0
Chloebia gouldiae	m	0.61	1.22	4.57	1.14	0.56	0.32	1.13	-2.37	0.761	0
Chloebia gouldiae	f	0.73	1.10	4.72	1.25	0.43	0.25	0.90	-1.65	0.725	0
Aidemosyne modesta	m	-0.05	1.05	4.24	0.78	0.32	0.22	0.99	-0.04	0.063	0

Species	Sex	bd	bs	wtr	max achr diff	max col sat	mean col sat	max pc2	min pc2	eoc	bc
Aidemosyne modesta	f	0.07	1.08	4.12	1.05	0.34	0.23	1.14	-0.34	0.002	0
Lonchura cantans	m	-0.34	1.01	4.71	1.25	0.41	0.28	0.95	-2.29	0.060	0
Lonchura cantans	f	0.07	1.17	3.94	1.46	0.40	0.27	1.21	-1.69	0.063	0
Lonchura malabarica	m	-0.25	1.15	4.24	1.54	0.27	0.23	0.92	-1.11	0.000	0
Lonchura malabarica	f	-0.27	1.13	4.30	1.48	0.30	0.25	0.48	-0.66	0.000	0
Lonchura griseicapilla	m	0.68	0.86	4.70	1.36	0.45	0.30	0.46	-1.98	0.000	0
Lonchura griseicapilla	f	1.06	0.84	4.71	1.08	0.45	0.29	0.55	-2.31	0.000	0
Lonchura nana	m	0.23	0.96	3.69	0.69	0.35	0.22	1.61	-0.22	0.029	0
Lonchura nana	f	0.33	0.97	3.63	0.51	0.41	0.25	1.59	-0.60	0.042	0
Lonchura cucullata	m	-1.54	1.14	4.22	1.33	0.26	0.19	1.17	0.75	0.032	0
Lonchura cucullata	f	-1.38	0.92	4.30	1.22	0.30	0.21	1.35	0.33	0.045	0
Lonchura bicolor	m	-1.25	1.07	4.24	1.50	0.28	0.20	0.94	0.19	0.709	0
Lonchura bicolor	f	-1.38	1.08	4.06	1.61	0.25	0.19	1.58	0.50	0.677	0
Lonchura fringilloides	m	-0.68	1.22	4.32	1.57	0.32	0.20	1.02	0.24	0.251	0
Lonchura fringilloides	f	-0.44	1.24	4.02	1.33	0.32	0.20	0.75	-1.64	0.275	0
Lonchura striata	m	1.50	1.05	4.02	1.20	0.35	0.23	0.51	-1.73	0.000	0
Lonchura striata	f	1.51	1.19	3.78	1.26	0.31	0.22	0.92	-1.18	0.000	0
Lonchura leucogastroides	m	-0.11	0.97	3.73	1.51	0.28	0.22	0.58	0.04	0.060	0
Lonchura leucogastroides	f	0.14	1.12	3.60	1.36	0.30	0.20	0.91	-0.60	0.057	0
Lonchura fuscans	m	-0.67	0.99	3.78	0.06	0.18	0.18	1.01	0.17	0.074	0
Lonchura fuscans	f	-0.41	0.97	3.79	0.12	0.22	0.19	1.14	0.34	0.111	0
Lonchura molucca	m	-0.15	1.05	3.81	0.58	0.29	0.23	0.98	-0.13	0.183	0
Lonchura molucca	f	-0.17	1.08	3.78	0.57	0.33	0.22	1.28	-0.70	0.161	0
Lonchura punctulata	m	-0.46	1.23	4.28	1.52	0.39	0.24	0.84	-1.05	0.000	0
Lonchura punctulata	f	-0.36	1.14	3.78	1.61	0.39	0.26	1.07	-0.39	0.000	0
Lonchura kelaarti	m	0.33	1.18	4.08	0.50	0.36	0.23	0.98	-1.22	0.050	0
Lonchura kelaarti	f	0.39	1.12	4.15	0.63	0.37	0.24	0.51	-0.71	0.061	0
Lonchura leucogastra	m	0.16	1.00	3.71	1.03	0.39	0.24	0.80	-1.23	0.021	0
Lonchura leucogastra	f	0.54	0.99	4.05	1.10	0.41	0.24	0.91	-1.31	0.013	0
Lonchura tristissima	m	-0.67	1.01	3.70	0.91	0.38	0.22	1.00	-1.89	0.000	0
Lonchura tristissima	f	-0.63	1.02	3.81	0.71	0.40	0.23	0.65	-1.21	0.000	0
Lonchura leucosticta	f	-0.64	1.08	3.76	1.00	0.37	0.26	0.92	-1.13	0.000	0
Lonchura quinticolor	m	-0.56	1.04	3.83	1.52	0.51	0.27	0.84	-2.68	0.000	0
Lonchura malacca	m	0.31	1.00	3.53	1.43	0.27	0.21	0.68	-0.09	0.440	0
Lonchura malacca	f	-0.64	1.01	3.55	1.10	0.34	0.23	0.99	-1.17	0.417	0
Lonchura malacca ferruginosa	m	0.48	0.98	3.41	1.04	0.29	0.21	0.79	-1.01	0.218	
Lonchura malacca ferruginosa	f	0.47	1.04	3.82	1.13	0.31	0.21	1.06	-0.69	0.252	
Lonchura maja	m	0.13	0.99	3.49	1.34	0.39	0.25	1.02	-0.96	0.235	0
Lonchura maja	f	0.11	1.04	3.71	1.37	0.37	0.26	1.12	-0.64	0.225	0

Species	Sex	bd	bs	wtr	max achr diff	max col sat	mean col sat	max pc2	min pc2	eoc	bc
Lonchura pallida	m	0.09	1.00	3.52	1.26	0.44	0.28	0.35	-1.86	0.085	0
Lonchura pallida	f	0.14	1.06	3.68	1.10	0.46	0.33	1.00	-1.26	0.065	0
Lonchura grandis	?	0.26	0.97	3.21	0.39	0.50	0.35	0.49	-2.20	0.416	0
Lonchura caniceps	?	0.78	1.03	3.67	0.75	0.51	0.29	1.18	-2.19	0.088	0
Lonchura nevermanni	m	-0.81	0.94	3.32	0.40	0.46	0.28	0.92	-1.54	0.036	0
Lonchura spectabilis	m	0.14	1.00	3.40	1.41	0.48	0.25	0.83	-2.34	0.245	0
Lonchura spectabilis	f	-0.67	0.96	3.40	1.36	0.40	0.25	0.58	-1.42	0.252	0
Lonchura forbesi	m	-0.26	1.10	3.30	0.45	0.48	0.31	0.69	-2.05	0.269	0
Lonchura hunsteini	m	0.50	0.95	3.33	0.46	0.52	0.24	0.94	-2.64	0.827	0
Lonchura hunsteini	f	-0.20	1.04	3.29	0.28	0.44	0.23	0.89	-2.06	0.802	0
Lonchura flaviprymna	m	-0.41	1.01	3.47	1.35	0.45	0.32	0.51	-1.96	0.000	0
Lonchura castaneothorax	m	0.46	1.10	3.47	1.39	0.44	0.31	0.80	-2.27	0.000	0
Lonchura stygia	f	-0.66	1.06	3.81	0.51	0.41	0.22	1.04	-1.47	0.821	0
Lonchura monticola	?	0.32	1.05	3.47	1.31	0.41	0.26	0.36	-2.59	0.167	0
Lonchura melaena	m	0.99	0.94	3.86	0.45	0.48	0.28	1.00	-2.57	0.649	0
Lonchura melaena	f	1.06	1.01	3.41	0.64	0.54	0.29	0.39	-2.52	0.669	0
Lonchura pectoralis	m	1.02	1.27	4.04	0.92	0.39	0.23	0.89	-0.92	0.057	0
Lonchura pectoralis	f	1.23	1.23	4.12	0.99	0.39	0.24	0.36	-1.34	0.052	0
Padda fuscata	m	0.73	1.18	3.71	1.52	0.28	0.22	0.82	-0.36	0.076	0
Padda fuscata	f	0.64	1.19	3.73	1.48	0.30	0.23	0.90	-0.81	0.097	0
Padda oryzivora	m	1.52	1.16	3.91	1.51	0.36	0.23	0.94	-0.67	0.152	0
Padda oryzivora	f	1.28	1.09	3.92	1.59	0.35	0.23	1.00	-0.26	0.158	0
Amandina erythrocephala	m	2.31	0.98	4.74	0.59	0.59	0.32	0.42	-2.08	0.143	0
Amandina erythrocephala	f	2.33	1.00	4.62	1.15	0.33	0.26	0.38	-1.00	0.000	0
Amandina fasciata	m	1.52	1.04	4.27	0.57	0.60	0.33	0.34	-2.47	0.025	0
Amandina fasciata	f	1.68	1.16	3.75	0.72	0.37	0.31	-0.19	-2.04	0.000	0

Table A2. Scores of the ecology and social variables for the measured estrildid species. Within the same species, males and females information are the same.

	Habitat			Commonness	Social system	Feeding			Movements	Breeding				Nest Vulnerability	
Species	Vegetation density (vd)	Range altitude (ra)	Mean altitude (ma)	Commonness (c)	Gregariousness (g)	Feeding height mean (fhm)	Feeding heigth range (fhr)	Diet (d)	Migration (m)	Length of breeding season (lbs)	Clutch size (cs)	Incubation period (ip)	Nestling period (np)	Nest height (nh)	Parasitized species (ps)
Parmoptila woodhousei	4			1	2	2	2	0	2	12	3.5	12		3	0
Parmoptila rubifrons	3.5	1100	1250	1	2	1.5	1	0		2				2	0
Nigrita fusconota	2.5	700	1050	2.5	1			0	2	4	4.5				0
Nigrita bicolor	2.5	1100	1250	2.5	1			0	2	3	3.5	12.5	19	3	0
Nigrita luteifrons	2.5			2.5	0.5			0	1	5	4			2.5	0
Nigrita canicapilla	3.5	1500	1500	2	0	2.5	1	1	1	7	4.5	12.5		3	0
Nesocharis shelleyi	2	900	1650	2	2	2		0.5	1.5	4	3				0
Nesocharis ansorgei	3	970	1485	2	2	2	2	1	1	8	2.5				0
Nesocharis capistrata	2.5	1200	1200	2	1	2	2	0.5	1	3	4	15.5	21.5	2.5	0
Pytilia phoenicoptera	2.5			1.5	1	1	1	1	3	6	3.5	14	20	2	1
Pytilia phoenicoptera lineata		1050	1275						1.5						0
Pytilia hypogrammica	1.5			2	1	1	1	0.5	1	4	3.5	13	21	2.5	1
Pytilia afra	2	1650	1650	1.5	3	1	1	1	2	6	4	13	21	2.5	1
Pytilia melba	2.5	1400	800	2.5	2	2	2	1	2	8	4	12.5	21	2.5	1
Mandingoa nitidula	2.5	2400	2400	1	2	1.5	1	0.5	1.5	5	4.5	13	22	2	0
Cryptospiza reichenovii	3.5	1100	1550	2.5	2	1	1	1	1	3	4.5	13.5	21	2	0
Cryptospiza salvadorii	4	1500	2250	2	1	1.5	1	1		2	4	15	20.5	2	0
Cryptospiza jacksoni	3	1650	2375	3	1	1	1	1	1	3	2			3	0
Cryptospiza shelleyi	4	1850	2475	1	1	1	1	1	1						0
Pyrenestes sanguineus	3			1	2	1	1	1	1	1	3.5	16	24	3	0
Pyrenestes ostrinus	1.5	1020	1190	2	2	1.5	1	1	1	8	4	16	24	2.5	0
Pyrenestes minor	3	1075	1262.5	1.5	1	1.5	1	1	1	4	3	14	21.5	1	0

Species	vd	ra	ma	c	g	fhm	fhr	d	m	lbs	cs	ip	np	nh	ps
Spermophaga poliogenys	4	1400	1400	1	1.5	1	1	1	1	7	3			3	0
Spermophaga haematina	2.5			2	2	1.5	1	1	1	5	4	15	21.5	2	0
Spermophaga haematina pustulata	2.5			2	2	1.5	1	1	1	5	4	15	21.5	2	0
Spermophaga ruficapilla	2.5	2400	2400	1.5	2	1.5	1	1	1	7	2.5	17.5	20	3	0
Clytospiza montieri	2			1.5	2	1	1	1	1						0
Hypargos margaritatus	2.5			2.5	2	1.5	1	1	1	1	4	13	20.5	3	1
Hypargos niveoguttatus	2.3	750	875	2.5	2	1	1	1	1	5	4.5	13.5	21	2	1
Euschistospiza dybowskii	2.5			1.5	2	1	1	1	1	2	5	13.5	19	1.5	1
Euschistospiza cinereovinacea	2	300	1650	2	2	1	1	0.5	1	2	3	13	21		0
Lagonosticta rara	1.5			2.5	2	1	1	1	1	5	3.5	13.5	19	2.5	1
Lagonosticta rufopicta	1.5			2.5	3	1	1	1	1	5	4.5	13.5	18	3	1
Lagonosticta nitidula	3	1800	1800	2.5	2	1	1	1	1	7	4	13.5	18.5	3	1
Lagonosticta senegala	2.5	1200	1600	3	2	1	1	1	2	12	4	11.5	18.5	2.5	1
Lagonosticta rubricata	2	2110	2110	2.5	2	1	1	1	2	7	4.5	13	21	2.5	1
Lagonosticta landanae	2			2.5	2	1	1	1							0
Lagonosticta rhodopareia	2.5	450	1575	2.5	2	1.5	1	1	1	7	4	12.5	17.5	2	1
Lagonosticta larvata	2	1700	1700	2	2	1	1	1	2	3	3.5	11.5	18	2	1
Lagonosticta rhodopareia virata	1.5			1.5	2	1	1	1	1	6	3.5	12	19	2	1
Uraeginthus angolensis	2	1400	1400	3	2	1	1	1	2	7	4	13.5	18	2.5	1
Uraeginthus bengalus	2	1800	900	3	2	1	1	1	2	9	4	13.5	17.5	2.5	1
Uraeginthus cyanocephala	1.5	750	625	2	2	1	1	1	2	8	5	13.5	18	3	1
Uraeginthus granatina	2.5			3	1	1	1	1	2	8	3.5	14	17	2	1
Uraeginthus ianthinogaster	3	1600	800	2.5	2	1	1	1	2	7	4	13.5	17		1
Estrilda caerulescens	1.5			2.5	2	1.5	1	1	1	2	5	11.5	19	2	1
Estrilda perreini	2.5	1890	1005	1	1	2.5	1	1	1	6	3.5	12	19.5	2.5	1
Estrilda thomensis	2.5			2	2	2.5	1	1	2	2	3.5	13	19		0
Estrilda melanotis	2.5	2400	1200	2.5	2			1	1.5	8	4.5	12.5	20	2	1
Estrilda melanotis bocagei	3	2400	1200	3	2			1	1	8	4.5	12.5	20	2	1
Estrilda paludicola	2	900	1650	2.5	2	1.5	1	1	2	5	5	12.5	20	2	1
Estrilda paludicola ochrogaster	2	900	1650	2.5	2	1.5	1	1	2	5	5	12.5	20	2	1
Estrilda paludicola bengelensis	2	900	1650	2.5	2	1.5	1	1	2	5	5	12.5	20	2	1
Estrilda poliopareia	3.5			1		2	2	1	2	2					1
Estrilda melpoda	2			2.5	2	1.5	1	1	2	7	5	11	20.5	1	1
Estrilda rhodopyga	2	1650	1650	2.5	2	1.5	1	1	2	3	4	13	18	1	1
Estrilda rufibarba	1.5	1950	1225	1.5	3	1	1	1	1.5						0
Estrilda melanotis quartinia	3	2100	1950	2	3	1	1	1		5	4.5	13.5	21.5	2.5	1

Species	vd	ra	ma	c	g	fhm	fhr	d	m	lbs	cs	ip	np	nh	ps
Estrilda troglodytes	2			2	2	1.5	1	1	1.5	6	4.5	11.5	18.5	1.5	1
Estrilda astrild	1.5	1000	1000	3	3	1.5	1	1		8	5	12	18	1.5	1
Estrilda nonnula	3	2000	1500	2.5	3	1.5	1	1	1	8	4.5	13	19	2.5	0
Estrilda atricapilla	3	3050	3050	2.5	3	1	1	1	1	4	4.5	12	19	2	0
Estrilda erythronotos	2	1000	1000	2.5	3	1.5	1	1	1.5	7	4.5	12	21	3	1
Estrilda erythronotos charmosyna	2	1000	1000		3	1.5	1	1	1.5	7	4.5	12	21	3	1
Amandava amandava	2.5	1500	1500	2.5	3	1.5	1	1	3	7	5	12		2	0
Amandava formosa	2			2	2	1	1	1	1	9	5.5	11.5		2	0
Amandava subflava	1.5	2000	2000	1.5	2	1.5	1	1	2.5	6	5	13.5	20	2	0
Ortygospiza atricollis	1.5	1200	2100	2.5	2	1	1	1	2	5	5	14	20	2	1
Ortygospiza gabonensis	2	1500	1500	2	2	1	1	1	2						0
Ortygospiza locustella	2	1050	1475	1.5	2	1	1	1	2	5	4			2	0
Aegintha temporalis	3.5			2.5	2	1.5	1	1	1.5	9	5	14	21	2	0
Emblema picta	1			1.5	1	1	1	1	1.5	10	4	13.5	23	1	0
Emblema bella	3	1500	1500	1.5	2	1.5	1	1	1.5	5	4.5	15	26	2.5	0
Emblema oculata	3			1	2	1.5	1	1	1	4	4.5	14	22.5	2	0
Emblema guttata	2.7			1.5	3	1	1	1	1	10	4.5	14	22	2.5	0
Oreostruthus fuliginosus	3.5	1580	2990	1	1	1.5	1	1	1					3	0
Neochmia phaeton	2.5			2.5	2	1.5	1	1	1.5	9	5	14	21	3.5	0
Neochmia ruficauda	1.5			2.5	2	1.5	1	1	1	5	4.5	13.5	21	2	0
Poephila guttata	2	2300	1150	3	3	1.5	1	1	1.5	6	5	12.5	17.5	2.5	0
Poephila guttata castanotis	2.5	2300	1150	3	3	1.5	1	1	1.5	8	5	12.5	17.5	2.5	0
Poephila bichenovii	2			2.5	3	1.5	1	1	1.5	6	4.5	11.5	19	2	0
Poephila personata	3			2.5	2	1	1	1	1.5	9	4.5	14	21.5	2	0
Poephila acuticauda	2.5			3	3	1	1	1	1	6	4.5	13.5	21	2.5	0
Poephila cincta	2			2	3	1	1	1	1	5	5	13	21.5	3	0
Erythrura hyperythra	3.5	2000	2000	1	2	1	1	1	1.5	2	5	13.5	24	2.5	0
Erythrura prasina	3.5	1500	1500	2	3	1	1	1	2.5	8	5	13	21	2.5	0
Erythrura viridifacies	2.5		1000	1	0.5	1.5	1	1	1.5	2	3.5	14			0
Erythrura tricolor	2.5	1400	1400		2	1.5	1	1			5	14		3	0
Erythrura trichroa	2.7	2000	2000	2	2	1.5	1	1	1.5	6	4.5	13	21	2	0
Erythrura papuana	4	1700	1750	1	2	3	3	1	1						0
Erythrura coloria	3	450	1375	1	1.5	1.5	1	1	1	3	2	14	22		0
Erythrura psittacea	2			3	2	1.5	1	0.5	1	2	5	13	20	3	0
Erythrura cyanovirens pealii	2			1.5	3	2.5	1	1		5	3.5	13.5	19.5	3	0
Erythrura cyanovirens	2.5			1.5	3	2.5	1	1		5	3.5	13.5	19.5	3	0

Species	vd	ra	ma	c	g	fhm	fhr	d	m	lbs	cs	ip	np	nh	ps
Erythrura cyanovirens regia	4			1.5	3	2.5	1	1	2	5	3.5	13.5	19.5	3	0
Erythrura kleinschmidti	4	915	915	2	2	2	2	0.5	1					2.5	0
Chloebia gouldiae	2.5			2	2	2	2	1	2	5	6	14.5	21.5	0	0
Aidemosyne modesta	2			2	3	1	1	1	2.5	9	4	12	21	2	0
Lonchura cantans	2	2000	2000	2	3	1	1	1	2	7	4.5	12	21	2.5	1
Lonchura malabarica	2	600	600	2.5	3	1.5	1	1	2.5	4	5.5	13	22	3	0
Lonchura griseicapilla	2			2	3	1	1	1	1.5		4.5	13.5	22.5	3	0
Lonchura nana	2	2000	1000	2.5	3	1.5	1	1	1	11	5.5		21	2.5	0
Lonchura cucullata	2	2150	1075	3	3	1.5	1	1	2	9	6	14	20	1.7	0
Lonchura bicolor	2	1500	1500	2.5	3	1.5	1	1	1.5	9	4.5	14	18.5	2.5	0
Lonchura fringilloides	2.5	1000	1000	1.5	3	2	2	1	1.5	6	5	13.5	21	2.5	0
Lonchura striata	2	1800	1800	2.5	3	1.5	1	1	1	8	4.5	14	23	2.5	0
Lonchura leucogastroides	1.5	1500	750	2	3	1.5	1	1	1	12	5	13	19	2.5	0
Lonchura fuscans	2	500	250	3		1.5	1	1	1	5	5	14	21.5	2.5	0
Lonchura molucca	1.5	1000	500	2.5	2	1.5	1	1	1	4	4.5	15.5	19.5	2.5	0
Lonchura punctulata	2	2000	1000	2.5	3	1.5	1	1	1	8	4.5	14	18.5	2.5	0
Lonchura kelaarti	2	1500	1350	2	2	1.5	1	1	3	7	6			3.5	0
Lonchura leucogastra	2.5	700	700	2	3			1	1.5	6	5	15	20	3	0
Lonchura tristissima	3	1700	1700	2	3	1.5	1	1	1	2		14		3	0
Lonchura leucosticta	2			2.5	2	1.5	1	1	1						0
Lonchura quinticolor	2	1600	800	1.5	2	1.5	1	1	1	5	5.5	15	21	2	0
Lonchura malacca	2	1500	750	2	3	1	1	1	1.5	12	4.5	12.5	21	2	0
Lonchura malacca ferruginosa	1.5	1500	750	2	3	2	2	1	1	7	5.5	13.5	21	2	0
Lonchura maja	1.5	1500	750	2.5	3	1.5	1	1	1	9	5	12.5	21	2	0
Lonchura pallida	1.5	1400	700	3	2.5	1	1	1	1	12	5	15	21		0
Lonchura grandis	1.5	600	300	1.5	3	1.5	1	1		4	4.5	14	21	2.5	0
Lonchura caniceps	2	2200	1100	2.5	3	1.5	1	1	2	7	5			2.5	0
Lonchura nevermanni	1.5	1800	1800	2.5	2	1	1	1	1		4.5	13	21	2	0
Lonchura spectabilis	1.5	2500	2500	2.5	3	1	1	1	1	12	4.5	14.5	19.5	2	0
Lonchura forbesi	1	1000	500	2	3			1	1	1					0
Lonchura hunsteini	1			2	3			1	1						0
Lonchura flaviprymna	2			2	3	2	2	1	1.5	4	4.5	13	21	2	0
Lonchura castaneothorax	1.5	1200	1200	2.5	3	1.5	1	1	2	5	5	13.5	17.5	2	0
Lonchura stygia	1.5			2	3	1.5	1	1	1		5	15	22	2	0
Lonchura monticola	1.5	1200	3300	3	3	1.5	1	1	1	3				3	0
Lonchura melaena	2	1200	1200	2.5	3	1	1	1	2	2	3.5				0

Species	vd	ra	ma	c	g	fhm	fhr	d	m	lbs	cs	ip	np	nh	ps
Lonchura pectoralis	2			1.5	2	1.5	1	1	2	4	5	13	21	2	0
Padda fuscata	1.5			2	2	1	1	1	1	2	5	14.5	31.5		0
Padda oryzivora	2	1500	1500	1	3	1.5	1	0.5	1	5	5.5	13.5	34	2	0
Amandina erythrocephala	2			3	3	1	1	1	2	10	5	14	20	3	0
Amandina fasciata	2.5	1500	1500	2.5	3	1	1	1	1.5	4	5	12.5	24	1.7	0

Table A3. Results of exploratory PGLS pair-wise regressions of each ornamental colour trait on an ecological or social candidate predictor, for males.

		Maximum saturation	Mean saturation	Achromatic difference	Extent	Bill colour	Maximum PC2	Minimum PC2	N*
MALES	**Vegetation density**	0.07 (0.41) †	-0.04 (0.48)	-0.10 (0.24)	-0.08 (0.24)	0.01 (0.88)	-0.11 (0.20)	**-0.24 (0.01)**	131
	Range altitude	**0.18 (0.08)**	0.04 (0.62)	0.08 (0.35)	0.04 (0.63)	-0.01 (0.86)	0.07 (0.44)	-0.09 (0.39)	88
	Mean altitude	0.05 (0.64)	0.05 (0.59)	-0.08 (0.37)	0.13 (0.11)	-0.01 (0.86)	-0.05 (0.56)	-0.12 (0.26)	89
	Commonness	0.01 (0.92)	-0.04 (0.47)	0.08 (0.22)	-0.01 (0.93)	-0.01 (0.76)	0.07 (0.30)	0.10 (0.17)	129
	Migration	0.01 (0.91)	0.04 (0.61)	-0.03 (0.71)	-0.09 (0.20)	-0.01 (0.88)	-0.02 (0.78)	-0.10 (0.27)	123
	Gregariousness	**0.18 (0.04)**	**0.24 (<0.01)**	**0.27 (<0.01)**	-0.04 (0.62)	0.06 (0.24)	**0.24 (<0.01)**	**-0.20 (0.03)**	129
	Diet	-0.04 (0.66)	-0.07 (0.45)	-0.06 (0.47)	0.12 (0.13)	**0.10 (0.10)**	-0.05 (0.52)	0.08 (0.42)	131
	Feeding Height Mean	-0.09 (0.30)	-0.08 (0.28)	-0.01 (0.89)	0.06 (0.36)	<0.01 (0.85)	<0.01 (0.98)	0.04 (0.70)	123
	Feeding Height Range	0.05 (0.49)	0.01 (0.61)	0.08 (0.23)	0.02 (0.78)	<0.01 (0.98)	0.07 (0.25)	-0.11 (0.17)	122
	Breeding season	0.10 (0.20)	0.03 (0.71)	0.11 (0.13)	0.08 (0.19)	0.04 (0.33)	0.10 (0.17)	0.02 (0.77)	120
	Clutch size	0.05 (0.59)	<0.01 (1.00)	**0.27 (<0.01)**	0.06 (0.42)	0.08 (0.13)	**0.24 (0.01)**	-0.07 (0.48)	118
	Incubation period	-0.06 (0.59)	-0.06 (0.50)	**-0.14 (0.10)**	**0.16 (0.05)**	-0.03 (0.57)	**-0.14 (0.09)**	<-0.01 (0.99)	108
	Nestling period	0.13 (0.26)	0.12 (0.23)	-0.02 (0.85)	0.09 (0.33)	-0.01 (0.93)	-0.03 (0.74)	-0.13 (0.24)	102
	Nest height	-0.11 (0.20)	-0.04 (0.63)	**-0.14 (0.05)**	0.05 (0.47)	0.04 (0.53)	**-0.12 (0.08)**	0.07 (0.45)	109
	Parasitized species	0.01 (0.94)	0.19 (0.11)	-0.05 (0.61)	0.02 (0.83)	**-0.15 (0.08)**	-0.05 (0.62)	-0.08 (0.45)	132

* Number of species with data for the corresponding ecological or social trait.

† Standardized partial regression coefficients (β) are given and, in parentheses, P-values. In bold are cases with P < 0.1, the threshold used to include predictor variables in the final model.

Table A4. Results of exploratory PGLS pair-wise regressions of each ornamental colour trait on an ecological or social candidate predictor, for females.

		Maximum saturation	Mean saturation	Achromatic difference	Extent	Bill colour	Maximum PC2	Minimum PC2	N*
FEMALES	**Vegetation density**	0.13 (0.17) †	0.13 (0.17)	-0.04 (0.66)	-0.04 (0.63)	<-0.01 (0.92)	-0.06 (0.54)	-0.14 (0.12)	123
	Range altitude	0.09 (0.40)	0.05 (0.64)	0.10 (0.34)	<0.01 (1.00)	-0.01 (0.80)	0.11 (0.34)	0.10 (0.37)	79
	Mean altitude	0.12 (0.29)	-0.01 (0.96)	-0.01 (0.91)	0.12 (0.18)	-0.02 (0.64)	-0.13 (0.27)	-0.13 (0.25)	79
	Commonness	-0.07 (0.37)	-0.01 (0.91)	0.02 (0.81)	-0.01 (0.92)	<-0.01 (0.99)	**0.27 (<0.01)**	**0.16 (0.07)**	122
	Migration	0.01 (0.89)	0.06 (0.50)	0.06 (0.48)	-0.12 (0.13)	0.02 (0.60)	-0.07 (0.46)	**-0.19 (0.04)**	115
	Gregariousness	-0.03 (0.78)	<-0.01 (0.98)	**0.20 (0.03)**	**-0.15 (0.10)**	**0.12 (0.06)**	**0.18 (0.10)**	-0.06 (0.52)	121
	Diet	0.01 (0.94)	0.02 (0.82)	0.02 (0.84)	0.08 (0.38)	0.10 (0.12)	0.15 (0.15)	0.12 (0.17)	123
	Feeding Height Mean	-0.15 (0.12)	**-0.17 (0.07)**	**-0.16 (0.06)**	**0.15 (0.05)**	0.01 (0.79)	-0.15 (0.12)	0.03 (0.74)	116
	Feeding Height Range	-0.06 (0.45)	-0.08 (0.33)	-0.03 (0.72)	0.08 (0.21)	<0.01 (0.95)	**-0.13 (0.10)**	-0.09 (0.37)	115
	Breeding season	0.07 (0.43)	0.05 (0.55)	**0.16 (0.06)**	-0.01 (0.86)	0.04 (0.32)	**0.21 (0.03)**	0.07 (0.46)	113
	Clutch size	-0.12 (0.26)	-0.11 (0.29)	**0.33 (<0.01)**	0.12 (0.18)	**0.14 (0.05)**	0.10 (0.38)	0.08 (0.40)	111
	Incubation period	**0.20 (0.06)**	0.09 (0.42)	**-0.21 (0.03)**	0.12 (0.21)	-0.03 (0.57)	0.03 (0.76)	-0.04 (0.66)	102
	Nestling period	0.06 (0.62)	0.08 (0.46)	-0.02 (0.82)	0.12 (0.21)	-0.01 (0.89)	-0.18 (0.11)	-0.11 (0.29)	98
	Nest height	-0.05 (0.57)	0.05 (0.53)	-0.13 (0.12)	-0.07 (0.36)	0.03 (0.60)	0.04 (0.67)	0.05 (0.62)	107
	Parasitized species	-0.01 (0.91)	0.02 (0.88)	-0.02 (0.86)	<-0.01 (0.98)	0.10 (0.25)	0.08 (0.49)	0.14 (0.13)	123

* Number of species with data for the corresponding ecological or social trait.

† Standardized partial regression coefficients (β) are given and, in parentheses, P-values. In bold are cases with P < 0.1, the threshold used to include predictor variables in the final model.

Table A5. Log-likelihood values for overall model, for both males and females, which include analyses of colour PCs.

	Gradual	Speciation	Null
Males overall model	-186.9996	-68.46268 *	-151.6411
Females overall model	-198.3483	-85.85322 *	-126.6697

* Best log-likelihood value, highlighting best model fitting for overall models.