LETTER

Accelerated speciation in colour-polymorphic birds

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Colour polymorphism exemplifies extreme morphological diversity within populations[1,2]. It is taxonomically widespread but generally rare. Theory suggests that where colour polymorphism does occur, processes generating and maintaining it can promote speciation but the generality of this claim is unclear[1]. Here we confirm, using species-level molecular phylogenies for five families of non-passerine birds, that colour polymorphism is associated with accelerated speciation rates in the three groups in which polymorphism is most prevalent. In all five groups, colour polymorphism is lost at a significantly greater rate than it is gained. Thus, the general rarity and phylogenetic dispersion of colour polymorphism is accounted for by a combination of higher speciation rate and higher transition rate from polymorphism to monomorphism, consistent with theoretical models where speciation is driven by fixation of one or more morphs[3]. This is corroborated by evidence from a species-level molecular phylogeny of passerines, incorporating 4,128 (66.5%) extant species, that polymorphic species tend to be younger than monomorphic species. Our results provide empirical support for the general proposition, dating from classical evolutionary theory[2,4–6], that colour polymorphism can increase speciation rates.

The study of colour-polymorphic species has been crucial for the development of evolutionary theory[5–7]. Polymorphic systems provide critical insights into processes generating and maintaining genetic and phenotypic diversity within species[2,4,8]. Theoretical arguments[1,3,9] and recent mathematical models[10–12] suggest that colour polymorphism can also promote the generation of new species (speciation), although the role of polymorphism in speciation remains highly controversial[1]. One reason is that the definition of polymorphism as the presence of discrete, genetically determined forms within an interbreeding population[2] has often been thought to imply that speciation occurs in sympatry; that is, in the absence of geographic isolation. This mode of speciation has traditionally been thought to occur rarely, if at all[13], but recent empirical support comes from polymorphic systems[14–16]. Moreover, polymorphism may have an important role in speciation under much less restrictive conditions than required under the sympatric speciation model[1,17], generating much recent theoretical and empirical interest in the role of colour polymorphism in speciation[1,9,17–19]. Despite specific cases linking colour polymorphism to rapid phenotypic evolution and speciation[1,18], the acceleration of speciation rates as a result of colour polymorphism has not been demonstrated in any group.

We tested whether colour polymorphism is associated with relatively rapid, recent speciation in birds, the group with the most comprehensive data on taxonomy, molecular phylogeny and prevalence of colour polymorphism. We compared speciation rates, calculated using a generalized binary-state speciation and extinction model (BiSSE)[20,21], for colour-polymorphic and colour-monomorphic species within five groups with a relatively high proportion of polymorphic species and sufficient sequence data (Supplementary Table 1 and Supplementary Fig. 1): Accipitridae (hawks, eagles, kites and Old World vultures), Striginae and Surniinae combined (two sub-families of owls), Caprimulgidae (nightjars), Falconidae (falcons) and Phasianidae (pheasants). The five groups contain <7% of bird species but 47% of colour-polymorphic species. The phylogenies were constructed using

a supermatrix approach[22] from GenBank sequence data accumulated over one-quarter of a century (Supplementary Methods, Supplementary Tables 3, 5–7, Supplementary Figs 3–7 and Supplementary Data).

In the three groups in which colour polymorphism is most prevalent, both in terms of absolute numbers (>20) and in proportion of polymorphic species (>20%), colour polymorphism is associated with higher speciation rate (Fig. 1). In the Accipitridae, one of the two major families of diurnal birds of prey, speciation rates are almost three-times higher for polymorphic species (likelihood ratio test (LRT), $P < 0.0001$; Fig. 1), a pattern driven particularly by the buteonine hawks and buzzards ($P < 0.0001$). Similarly, speciation rates are 2 to 4 times higher for polymorphic species in owls and nightjars, respectively (Fig. 1). In owls, the pattern is driven primarily by one subfamily, the Surniinae (12 colour-polymorphic species out of 39 species; LRT, $P = 0.007$; Supplementary Table 2). Of the groups we tested, falcons had the smallest number of polymorphic species (9 colour-polymorphic species out of 65 species), which showed only a weak trend towards having a higher speciation rate, reflected in the bimodal posterior probability distribution of speciation rates for the polymorphic state (Fig. 1; LRT, $P = 0.58$). In the pheasants (15 colour-polymorphic species out of 181 species), we found the opposite trend to the birds of prey (Accipitridae, Striginae and Surniinae, Caprimulgidae
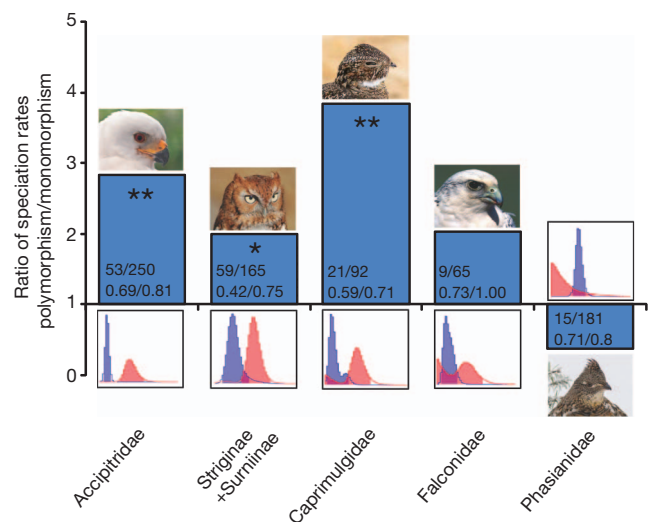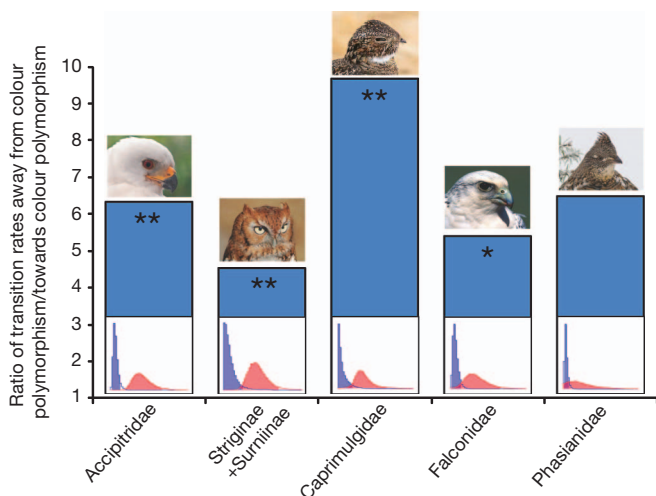

Figure 1 | Speciation rate (λ_1/λ_0) ratio from Bayesian Diversitree analyses. Values >1 indicate higher speciation rates for the colour-polymorphic state. *$P \leq 0.05$; **$P \leq 0.01$ for likelihood ratio tests (LRTs) comparing a model with two different speciation rates versus one with equal rates. Numbers on each bar are the colour-polymorphic taxa/total number of taxa (above) and sampling fractions for polymorphic/monomorphic species. Diversitree posterior distributions are shown with blue indicating monomorphic and red indicating polymorphic. Images are representative polymorphic species: grey goshawk, *Accipiter novaehollandiae* (photo: Á. Lumnitzer); eastern screech owl, *Megascops asio* (photo: J. Whitlock); Antillean nighthawk, *Chordeiles gundlachii* (photo: M. Landestoy); gyrfalcon, *Falco rusticolus* (http://www.animalspedia.com/wallpaper/Piercing-Stare---Gyrfalcon/); and ruffed grouse, *Bonasa umbellus* (photo: J. Pons).

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and Falconidae), with speciation rates slightly higher for the mono-morphic state (LRT, $P = 0.16$; Fig. 1). In all cases, the Bayesian posterior probabilities are qualitatively the same as the LRT results (Supplementary Table 2).

Different processes contributing to the generation, maintenance and loss of polymorphism[1] may operate in different groups and affect speciation rates in different ways. In the birds of prey, in which we find an association between colour polymorphism and higher speciation rates, polymorphic species tend to have larger geographic ranges than monomorphic species, live in more spatially and temporally hetero-geneous environments, occupy more diverse environments and have activity patterns spanning day and night[24]. In other words, colour polymorphism tends to be associated with diverse ecological condi-tions. Furthermore, in the four families of birds of prey, colour poly-morphism is sex-limited (restricted to one sex) in fewer species than expected by chance (13 sex-limited species out of 142 colour-polymorphic species; null expectation = 0.195 (ref. 23); binomial test, $P = 0.006$) whereas colour polymorphism tends to be sex-limited more often than expected by chance in the pheasants (7 sex-limited species out of 15 colour-polymorphic species; binomial test, $P = 0.015$). These observations support the view that ecologically based divergent selec-tion, including the special case of disruptive selection favouring extreme phenotypes over intermediates within a population, is probably important for colour-polymorphism-associated speciation in the birds of prey. By contrast, there is no indication that the higher speciation rates are associated with sexual selection in these groups (at least as indicated by sex-limited polymorphism). Whether sexual selection has a role in the maintenance of polymorphism in the pheasants requires empirical testing.

The general rarity of colour polymorphism can be explained by the loss of polymorphism through the fixation of a morph; or alternatively, by polymorphic species having substantially higher extinction rates. We find no evidence for the latter but across all five groups the tran-sition rate from polymorphism to monomorphism estimated from BiSSE models is greater than the reverse (Fig. 2) and is of similar magnitude to the speciation rate for the colour-polymorphic state (Supplementary Table 2). LRTs of transition rates are significant (Fig. 2) and similar to the Bayesian posterior probabilities, with the exception of the pheasants for which $P = 0.406$ for the LRT but the Bayesian posterior is 0.042 (Supplementary Table 2). The relatively
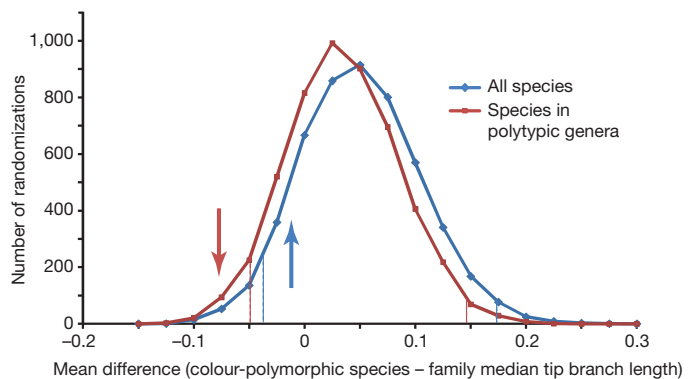
high transition rate away from colour polymorphism is not simply an artefact of the low frequency of polymorphism, as the two variables are not correlated (coefficient of correlation (r) = 0.361; $P = 0.551$). The relatively high rate of shifts from polymorphism to monomorphism is consistent with speciation events often entailing fixation of a morph in one or more descendant lineages. In all five families, the majority of speciation events involving colour polymorphism also involve a trans-ition, as inferred from a posteriori simulations using the BiSSE parameters (Accipitridae, 0.61; Striginae and Surniinae, 0.55; Caprimulgidae, 0.53; Falconidae, 0.78; Phasianidae, 0.67), consistent with the observed phylogenetic dispersion of colour polymorphism (Supplementary Table 2). This pattern is underscored by phylogenetic studies in other groups showing that colour polymorphism is repeat-edly lost[18,25,26], and by the widespread tendency towards fixation of discrete phenotypes more generally[3].

The rarity and phylogenetically scattered nature of colour poly-morphism is apparent in the remaining birds. For instance, 23% of all known colour-polymorphic species are within the Passeriformes, yet polymorphic species represent only 1.2% of passerines (75 colour-polymorphic species out of 6,213 species) and are distributed across 58 genera in 30 families. This level of phylogenetic scatter pre-vents reliable estimation of speciation rates for the polymorphic state (and hence use of the BiSSE model). However, if colour polymorphism accelerates speciation, divergence between extant colour-polymorphic species and their sister lineages should be relatively more recent. That is, colour-polymorphic species should have shorter terminal branches in the phylogeny. This pattern is evident in the four families of birds of prey, in which tip branch lengths are 12–38% shorter for polymorphic than monomorphic species, but 19% longer in the pheasants in which polymorphism is not associated with higher speciation rates (Sup-plementary Table 2).

To assess the generality of our findings, we tested the prediction that colour-polymorphic species should be relatively younger in the Passeriformes, the largest order of birds including more than half of all bird species. We constructed a species-level phylogeny of this group from DNA sequence data (with branch lengths proportional to time) incorporating 4,128 (66.5%) of extant species (Supplementary Methods, Supplementary Tables 4–7, Supplementary Fig. 2 and Sup-plementary Data). The phylogeny includes 67 (89%) of the poly-morphic species, of which 59 belong to polytypic genera and 8 belong to monotypic genera. The frequency that 67 randomly chosen species have shorter branch lengths than those observed for colour-polymorphic species is 0.074 (5,000 randomizations; Fig. 3). Monotypic genera

Figure 2 | Ratio of transition rates (q_{10}/q_{01}) between states from Bayesian Diversitree analyses. Values >1 indicate a higher transition rate from polymorphic to monomorphic than the converse. *$P \leq 0.05$; **$P \leq 0.01$ for LRTs comparing a model with two different transition rates versus one with equal rates. Diversitree posterior distributions of transition rates away from polymorphism are shown with blue indicating monomorphic and red indicating polymorphic. Images and credits as in Fig. 1.

Figure 3 | Randomization tests of relative tip branch lengths for passerine species. Mean difference between the tip branch length of 67 randomly chosen species and the median tip branch length for members of the relevant family. Lines show the distribution from 5,000 randomizations. Blue line shows all species and red line shows species belonging to polytypic genera (that is, excluding monotypic genera). Arrows indicate the observed value for colour-polymorphic species; both are in the left tail of the distribution, indicating that tip branch lengths of colour-polymorphic species tend to be shorter than monomorphic species. Dotted lines indicate 95% confidence intervals.

represent distinctive lineages that have experienced little speciation and/or high extinction. High levels of extinction will obscure patterns of speciation[27] and excluding monotypic genera recovers a much stronger signal (randomization test, $P = 0.004$). Thus, consistent with the birds of prey, polymorphism within passerines is associated with relatively recent speciation (younger extant species). Also consistent with the birds of prey, the pattern is not driven by species with sex-limited polymorphism; it remains when species with sex-limited polymorphism[23] are excluded (all species/polytypic genera only: $n = 46/41$; $P = 0.106/0.008$), despite the reduced sample size. By contrast, exclusion of species with a cline in morph frequencies associated with habitat variation[23] substantially weakens the signal (all species/ polytypic genera only: $n = 48/42$; $P = 0.214/0.078$).

The tendency for polymorphic species to speciate more rapidly and to give rise to monomorphic daughter species is predicted by theory[1,17]. Polymorphism in coloration is often associated with differences in suites of correlated traits (for example, morphology, physiology, behaviour and life history) due to correlational or epistatic selection or shared developmental pathways[9,17]. These different trait combinations may allow populations to persist in spatially and temporally variable environments and facilitate range expansion and/or successful colonization or founder events[17], all of which could increase the probability of speciation[28]. In colour-polymorphic species with large geographic ranges, for example, parapatric speciation may occur at the ends of a ratio cline in morph frequencies[2,29]. This may be moderately common; among colour-polymorphic birds, at least 20% show a cline in the relative frequency of morphs[23]. If colour polymorphism facilitates the evolution of geographic colour variants, this could lead to taxonomic oversplitting and inflated speciation rates. However, geographic colour variation is a well-known indicator of incipient speciation[28]. Thus, the observed accelerated speciation probably reflects biogeographic and evolutionary processes associated with colour polymorphism rather than systematic biases.

More generally, the existence of correlated traits, with underlying co-adapted gene complexes, can promote speciation when processes maintaining colour polymorphism, such as frequency-dependent selection or balancing selection, are destabilized in populations in which morphs are gained or lost[3]. The change in selective environment leads to a breakdown of co-adapted gene complexes, which could result in speciation despite ongoing gene flow when new trait combinations evolve[3,8,9,29]. Colour polymorphism may also occur where populations come into secondary contact after diverging in coloration in allopatry[30] or when colour forms are under disruptive selection associated with different microhabitats[1,30]. In both cases, colour polymorphism may represent incomplete speciation (transient polymorphism[4]) and under certain conditions (for example, when accompanied by selection against hybrids and/or assortative mating) the speciation process will culminate in the evolution of monomorphic daughter species[1,30]. In sum, a combination of ecological, geographic and genetic processes may accelerate speciation in colour-polymorphic species; our data provide empirical confirmation of a link between colour polymorphism and relatively rapid, recent speciation.

METHODS SUMMARY

We tested whether colour polymorphism is associated with speciation rate in the Accipitridae, Striginae and Surniinae, Caprimulgidae, Falconidae and Phasianidae. We also tested whether colour-polymorphic species tend to have diverged more recently in the Passeriformes. The data set included 232 (70%) known colour-polymorphic bird species. We used GenBank sequence data and a supermatrix approach to reconstruct robust molecular phylogenies for each of these groups (Supplementary Information).

We assessed the relationship between colour polymorphism and speciation rates using the BiSSE[21] method with modifications allowing for incomplete sampling and incorporating a Bayesian Markov chain Monte Carlo (MCMC) method of assessing parameter space[20], implemented in the R-package Diversitree (versions 0.6-1 and 0.7-6). The method describes diversification across a phylogeny in terms speciation rate (λ) extinction rate (μ) and transition rate (q)

between binary states, here colour polymorphic (state 1) and monomorphic (state 0). We included sampling fraction for both states based on the International Ornithological Congress (IOC) 2.4-defined taxonomy and accounted for phylogenetic uncertainty by doing the Bayesian analysis on a random sample of 50 BEAST trees.

For the analysis of passerines, we computed the difference between the tip branch length of each polymorphic species and the median tip branch length of all species within the same family. To test whether this difference could be expected by chance, we performed 5,000 randomizations comparing the difference between 67 randomly chosen species and their matching family median value. We repeated randomization tests (1) excluding species where the genus or the family sampling was <50%; (2) for oscines only; (3) including only the families containing one or more colour-polymorphic species. In all cases the results were qualitatively unchanged: all taxa, $n = 67/59$, randomization $P = 0.074/0.004$ (all/polytypic only); >50% sampling, $n = 53/46$, $P = 0.059/0.002$; oscines, $n = 66/59$, $P = 0.085/0.004$; and colour-polymorphic families: $n = 67/59$, $P = 0.085/0.007$.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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METHODS

We used the list of bird species known to exhibit true colour polymorphism from ref. 23. Colour-polymorphic species are defined as discrete colour variants within interbreeding populations so as not to confound polymorphism with geographic colour variation. We defined all species and higher level taxonomy according to the International Ornithological Congress IOC 2.4 species list (http://www.worldbirdnames.org/index.html) and ref. 31. To be conservative, we subsumed all categories below the rank of species into the IOC species category.

Taxon sampling. We restricted our analysis to the species rank (to minimize potential taxonomic bias) and to phylogenetically coherent groups that were well sampled in terms of available sequence data and contained a relatively high proportion of colour-polymorphic species. This resulted in the choice of five groups for species-level diversification analyses: Accipitridae, Striginae and Surniinae combined, Caprimulgidae, Falconidae and Phasianidae. The five groups contain 157 (47%) of colour-polymorphic taxa. We also investigated the relative age (tip branch lengths) of colour-polymorphic species in the Passeriformes, which includes 23% of colour-polymorphic species (75 out of 6,213 passerine species). Including the passerines, these groups contain 232 (70%) of known colour-polymorphic bird species. Further details are provided in Supplementary Information.

Phylogeny reconstruction. We downloaded all sequence data from GenBank via the NCBI website (http://www.ncbi.nlm.nih.gov). Nomenclature in ref. 23 and GenBank accessions was reconciled with the IOC 2.4 list with the help of the Avibase world bird database (http://avibase.bsc-eoc.org/avibase.jsp), Wikipedia and the Internet Bird Collection (http://ibc.lynxeds.com).

We maximized the number of species within the phylogenies by using the now widely used supermatrix approach[22]. All supermatrices contained substantial amounts of common data enabling robust phylogenetic inference and estimation of branch lengths[22,32,33]. Overall, the phylogenies are robust, with ≥70% of nodes having maximum likelihood bootstrap >70% and MCMC posterior probability >0.90; for passerines >60% of nodes have bootstrap >70% in the genus and species level trees (Supplementary Methods, Supplementary Tables 3–7 and Supplementary Figs 3–7).

Speciation rate analyses. To test for an association between colour polymorphism and speciation rate, we used binary-state speciation and extinction (BiSSE)[21] with modifications allowing for incomplete sampling and incorporating a Bayesian MCMC method of assessing parameter space[20], implemented in the R-package Diversitree 0.6-1 and 0.7-6 (ref. 20). The method describes diversification across a phylogeny in terms of six parameters: speciation rate (λ_1 and λ_0), extinction rate (μ_1 and μ_0) and transition rate between states (from 1 to 0, q_{10}; and from 0 to 1, q_{01}). Here the binary states are colour-polymorphic (state 1) and not colour-polymorphic (state 0). The MCMC analyses followed the procedure outlined in the Diversitree manual and R help file (http://cran.r-project.org/web/packages/diversitree) using an exponential prior $1/(2r)$, optimized step size (w), and started using maximum likelihood optimized parameter values. Analyses of single trees used 20,000 step MCMC. We included sampling fraction for both states based on the IOC 2.4-defined taxonomy and accounted for phylogenetic uncertainty using the pooled results of 1,000 step MCMC for each of 50 randomly sampled BEAST trees. All cases gave parameter effective samples sizes >200 and a burn-in period was not required.

We focused on speciation rate rather than net diversification rate (speciation rate – extinction rate: $r = \lambda - \mu$) because we were specifically interested in the effect of colour polymorphism on speciation rates and because of limitations in estimating extinction rate in extant phylogenies[27,34,35]. In this particular case, the empirically estimated extinction rate values are mostly low or very low; therefore net diversification rate (r) estimates are similar to speciation rate (λ) estimates and in all cases the ratio of net diversification rate shows the same trend as that of speciation rate (not shown). We also recorded the transition rate results, focusing on the ratio of the transition rate away from the colour-polymorphic state to the transition rate towards the colour-polymorphic state (q_{10}/q_{01}). An estimate of the proportion of colour-polymorphic speciation associated with fixation of a polymorphism can be inferred from the BiSSE model parameters using simulations. These were calculated as the proportion of colour-polymorphic nodes that have

either one or both descendant lineages losing colour polymorphism before they speciate (or end in a terminal taxon including extinctions), based on a set of simulations totalling 1,000 nodes. From these simulations, we can gain an indication of the proportion of all speciations that involve a colour-polymorphic parent lineage (Accipitridae, 0.45; Striginae and Surniinae, 0.46; Caprimulgidae, 0.58; Falconidae, 0.29; and Phasianidae, 0.03). For the birds of prey these proportions are higher than the frequency of polymorphic species because colour polymorphism has a higher speciation rate but most colour-polymorphic speciations give rise to monomorphic species. Thus, in our models the overall proportion of colour-polymorphic species remains relatively constant.

Although the assumption of the BiSSE model that speciation and character state changes are not correlated could potentially result in overestimation of relative transition rates, our results are corroborated by simple comparison of tip branch lengths and by maximum parsimony analysis showing limited phylogenetic clustering and frequent state changes (Supplementary Table 2).

As a statistical measure we recorded the number of individual MCMC samples where colour-polymorphic speciation rate ≤ non-colour-polymorphic rate; similarly for transition rate. In addition, we present maximum likelihood results and likelihood ratio tests (LRT) of the difference between the full unconstrained six-parameter model and a five-parameter model with the speciation or transition rates constrained to be equal.

For the analysis of passerines, we compared the difference between the tip branch length of each colour-polymorphic species to the median tip branch length of all species within the same family. This analysis assumes that the most recent common ancestor of most colour-polymorphic species and their closest relative were also polymorphic. Although rapid gain/loss of colour polymorphism will weaken the association between colour polymorphism and speciation it should not confound it. Using families allows a reasonable sample size for determining a median value but avoids comparing very disparate lineages, and only needs relative divergences to be comparable within families rather than across the whole tree. In addition, almost all families are monophyletic (whereas ∼10% of genera probably are not). Median values are appropriate as phylogenies tend to be asymmetrical and hence branch length distributions skewed. Monotypic genera are by definition distinct, and will tend to have relatively long tip branches (nearly twice as long: t-test, $P < 0.0001$). Owing to these peculiarities we conducted analyses with and without colour-polymorphic species comprising monotypic genera.

To test whether the observed difference in tip branch length could be expected by chance, we performed 5,000 randomizations comparing the difference between 67 randomly chosen species and their matching family median value. We repeated analyses excluding species with sex-limited polymorphism or associated with morphoclines and multiple habitats based on data from ref. 23. Incomplete sampling may affect results; as we use tip branch lengths and family median values, the critical comparison is how well genera containing colour-polymorphic species are sampled compared to the other genera in the family. In this regard, the percentage sampling is relatively even: 78/81 (all) and 75/71 (polytypic). To assess the robustness of our results, we conducted the following additional analyses: (1) excluding species where the genus or the family sampling was <50%; (2) oscines only; (3) including only the families containing one or more colour-polymorphic species. In all cases the results were qualitatively unchanged: all taxa, $n = 67/59$, randomization $P = 0.074/0.004$ (all/polytypic only); >50% sampling, $n = 53/46$, $P = 0.059/0.002$; oscines, $n = 66/59$, $P = 0.085/0.004$; and colour-polymorphic families, $n = 67/59$, $P = 0.085/0.007$.

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