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Sexual selection, speciation, and constraints on geographical range overlap in birds

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Abstract

The role of sexual selection as a driver of speciation remains unresolved, not least because we lack a clear empirical understanding of its influence on different phases of the speciation process. Here, using data from 1306 recent avian speciation events, we show that plumage dichromatism (a proxy for sexual selection) does not predict diversification rates, but instead explains the rate at which young lineages achieve geographical range overlap. Importantly, this effect is only significant when range overlap is narrow (<20%). These findings are consistent with a 'differential fusion' model wherein sexual selection reduces rates of fusion among lineages undergoing secondary contact, facilitating parapatry or limited coexistence, whereas more extensive sympatry is contingent on additional factors such as ecological differentiation. Our results provide a more mechanistic explanation for why sexual selection appears to drive early stages of speciation while playing a seemingly limited role in determining broad-scale patterns of diversification.

Key-words: Differential fusion, plumage dichromatism, sexual selection, speciation, species coexistence, sympatry

Introduction

Speciation in animals is often viewed as a cyclical process beginning with divergence in allopatry and ending with coexistence in sympatry once the evolution of reproductive isolation permits the overlap of geographic ranges (Dobzhansky 1937; Mayr 1942). The concept of a 'speciation cycle' (Grant and Grant 2008; Price 2008) provides a unifying framework for understanding how lineage diversification gives rise to broad-scale patterns of species richness over space and time, first by generating new lineages with non-overlapping ranges, and second by regulating the capacity of such lineages to co-occur in ecological communities. The rates at which these stages of the cycle are completed are fundamental to the build-up of diversity and potentially influenced by a combination of ecology and sexual selection (Grant and Grant 2008; Price 2008). However, while the importance of ecology in driving or constraining speciation cycles is becoming increasingly well understood (e.g. Pigot and Tobias 2013; Price et al. 2014), the role of sexual selection remains unclear (Ritchie 2007; Kraaijeveld et al. 2011; Butlin et al. 2012).

Because of its propensity to stimulate the rapid evolution of phenotypic traits, sexual selection has long been recognised as a positive diversifying force (Darwin 1871; West-Eberhard 1983; Andersson 1994; Panhuis et al. 2001). In particular, by driving the evolution of traits involved in mate choice and species recognition (Lande 1981; Seddon et al. 2013), sexual selection could accelerate progression through stages of the speciation cycle, firstly by generating substantial reproductive isolation between lineages diverging in allopatry (Price 1998; Panhuis et al. 2001), and secondly by maintaining and/or strengthening isolating barriers when species ranges expand into sympatry (Gröning and Hochkirch 2008; Hudson and Price 2014; Weber and Strauss 2016). Despite these expectations, empirical support for a general coupling between sexual selection and diversification rates is surprisingly weak, and highly inconsistent both within and among taxonomic groups (Kraaijeveld et al. 2011). For instance, most comparative work has focused on birds, where the correlation between proxies of sexual selection and speciation rates are sometimes positive (Barraclough et al. 1995; Owens et al. 1999; Seddon et al. 2008) but just as often not (Morrow et al. 2003; Phillimore et al. 2006; Huang and Rabosky 2014).

Compared with rates of speciation, the connection between sexual selection and the establishment of geographic range overlap has received far less attention. This is partly because sexual selection (in isolation) seems unlikely to facilitate substantial range overlap because it tends to produce allospecies with divergent mating signals yet similar morphology, leaving in place the ecological barriers to co-existence associated with niche similarity and interspecific competition (Price 1998). However, an alternative view is that sexual selection may accelerate the initial establishment of range overlap by maintaining and/or strengthening reproductive isolation, thereby allowing young lineages to avoid 'fusion' following secondary contact (Noor 1999). Indeed, theoretical studies (e.g. van Doorn et al. 2009; M'Gonigle et al. 2012) suggest that sexual selection may play a general role in reducing the costs associated with reproductive interference (Gröning and Hochkirch 2008; Weber and Strauss 2016) thus facilitating more extensive sympatry between young lineages. However, direct comparative tests of these ideas are lacking, and the extent to which sexual selection promotes (or impedes) range overlap among species is unknown (Price 2008).

Uncertainty over the role of sexual selection in speciation processes is also exacerbated by the variable results generated by different methodological approaches. For instance, studies testing the link between sexual selection and diversification using comparisons among deeper (i.e. older) phylogenetic nodes, such as those between genera and families, tend to yield weaker effects (Kraaijeveld et al. 2011). This suggests that the signature of sexual selection in diversification processes may fade over time (Kraaijeveld et al. 2011), possibly due to the confounding effect of extinction over longer evolutionary timescales (Rabosky 2010) and/or fluctuations in the strength of sexual selection as clade diversification progresses (Wiens 2001; Badyaev and Hill 2003; Price and Eaton 2014). Regardless of the underlying explanation, it seems plausible that clade-based studies comparing across deep timescales (e.g. Morrow et al. 2003; Phillimore et al. 2006; Huang and Rabosky 2014) may underestimate the role of sexual selection in speciation (Kraaijeveld et al. 2011).

To address these issues, we estimated the association between sexual selection and speciation processes across a global sample of avian sister species, representing the most recent divergence events culminating in full species. By focusing only on sister species (pairs of lineages which are each other's closest extant relatives), our approach minimises the difficulties associated with inferring the geographic, phenotypic, and evolutionary history of taxa descended from deeper phylogenetic nodes (Losos 2011), and maximises the power to detect an accurate signal of sexual selection on speciation (Seddon et al. 2013). Using two independent datasets, we employ phylogenetic modelling approaches (Weir and Schluter 2007; Pigot and Tobias 2013) to test the effects of sexual selection on both stages of the speciation cycle, first by studying links to rates of speciation (and extinction), and secondly by assessing the relationship between sexual selection and rates of transition from allopatry to sympatry.

If sexual selection accelerates the formation of new species (prediction 1), we expect sister pairs experiencing strong sexual selection to be associated with (i) more recent divergence times (i.e. younger evolutionary age), and (ii) faster rates of speciation. Similarly, if sexual selection plays an important role in facilitating range overlap among close relatives, we expect sister pairs experiencing strong sexual selection to be associated with (i) accelerated rates of transition from allopatric to parapatric/sympatric distributions, and (ii) for this effect to remain after accounting for other potentially important factors (e.g. geographical realm, latitude, body size, dispersal). Birds provide an ideal system in which to conduct these tests as they are a well-studied group with comprehensive data on phylogeny, ecology and biogeography, and because avian plumage dichromatism—the difference in colouration of males and females of the same species—is a relatively robust and commonly used proxy for the degree of sexual selection (Owens and Hartley 1998; Dunn et al. 2001; Dale et al. 2015; Dunn et al. 2015).

Materials and methods

SISTER SPECIES DATASETS

We generated two datasets of avian sister species pairs. First, we assembled a dataset of passerine sister pairs for which we could collect detailed data on dichromatism using spectrophotometric measurements of plumage colouration from museum specimens. Second, we used the Jetz et al. (2012) time-calibrated phylogenies combined with human (visual) scores of dichromatism to provide data for a larger set of sister pairs sampled from across the avian radiation. The resulting datasets contained 144 and 1306 sister pairs, respectively, and are referred to throughout as dataset 1 and dataset 2, respectively. See Appendix S1 for full details of methods, data and data sources.

QUANTIFYING SEXUAL DICHROMATISM

We quantified sexual dichromatism in two ways. First, for the 144 pairs of passerine bird species in dataset 1, we measured sexual dichromatism objectively using measurements of plumage colour collected using a spectrophotometer. Second, as it was not feasible to obtain spectrophotometric measures of plumage colour for thousands of species, for all the species in dataset 2, including replicate trees (total species = 5681; see Appendix S1), we scored sexual dichromatism from handbook illustrations (del Hoyo et al. 1992–2011). In both cases, a low dichromatism score indicates similar colouration in both sexes (monochromatism) with higher values indicating greater degree of dichromatism. See Appendix S1 for full details of the methods used to quantify dichromatism.

A key assumption underlying our analyses is that sexual dichromatism is a valid proxy for the intensity of sexual selection in birds. Evidence supporting this comes from a number of broad-scale studies that reveal strong positive relationships between dichromatism and other indices of sexual selection such as testes size, the degree of polygyny and the frequency of extra-pair paternity (Owens and Hartley 1998; Dunn et al. 2001; Dale et al. 2015; Dunn et al. 2015). As a consequence, dichromatism is widely used as a standard proxy for sexual selection in birds (e.g. Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Sol et al. 2005; Phillimore et al. 2006; Krüger 2008; Seddon et al. 2008; Bloch 2015), as well as other taxa including lizards (e.g. Stuart-Fox and Owens 2003), insects (e.g. Misof 2002) and fish (e.g. Wagner et al. 2012). We note, however, that the use of sexual dichromatism as a proxy for sexual selection is subject to a number of important caveats. For example, sexual dichromatism and sexual selection are likely to be only partially correlated, not least because other mechanisms can influence patterns of sex-differences in plumage colouration, such as natural selection for female crypsis in species with female-only incubation (Badyaev and Hill 2003) or social selection on females to signal quality in the context of male mate choice or female-female competition (Tobias et al. 2012). In addition, sexual dichromatism may only provide a lower bound estimate of the overall intensity of sexual selection. This is because of potential trade-offs between signalling modalities (Darwin 1871), where investment in one signalling modality (e.g. visual signals) constrains elaboration in another (e.g. acoustic signals). While it would therefore be preferable to compare direct measures of sexual selection from detailed studies of behaviour or reproduction, these estimates are lacking for large numbers of species. Thus, we conclude that dichromatism is the best proxy currently available for the purposes of broad-scale comparative analyses, and also that our analysis is likely to underestimate the effects of sexual selection on rates of diversification and range overlap, rather than exaggerate them.

QUANTIFYING RANGE OVERLAP

Sister pairs were assigned to range overlap categories based on current spatial overlap of species breeding distributions. To quantify range overlap we used range map polygons provided by BirdLife International and NatureServe (2015) and calculated percentage range overlap within sister pairs as the area of overlap between species divided by the area of the smaller species' range (Pigot and Tobias 2013; Tobias et al. 2014; Pigot and Tobias 2015; Pigot et al. 2016). We then used these values to assign sister pairs to range overlap categories using two different approaches. Following previous studies (Pigot and Tobias 2013, 2015; Pigot et al. 2016), pairs were initially categorized as either allopatric or sympatric under a range of overlap thresholds to define sympatry (>0%, >5% >10%, >20%, >30%, >40%, >50%, >60%, >70%, >80%). As results based on this approach suggested that dichromatism was primarily correlated with instances of moderate but not substantial range overlap (see below), we then employed a second approach by introducing a third category (parapatry) to distinguish instances of narrow (<20%) range overlap between species that are distinct from cases of more extensive, range-wide sympatry. In this second approach, we categorized pairs as either allopatric, parapatric or sympatric using three alternative combinations of overlap thresholds to define allopatry (<0%, <5%, <10%), parapatry (>0-20%, >5-25%, >10-30%) and sympatry (>20%, >25%, >30%). We note that one additional benefit of considering increasingly stringent definitions of parapatry/sympatry is that we were able to control for the possibility that erroneous overlap estimates caused by mapping errors (Hurlbert and Jetz 2007) could influence our results. In total, we quantified levels of range overlap for 140 (97%) in dataset 1, and 1306 (100%) pairs in dataset 2 (Fig. S1).

ADDITIONAL PREDICTORS OF SYMPATRY RATE

Several factors have the potential to confound tests of the link between sexual selection and sympatry through shared correlations with plumage dichromatism and sympatry rate. For instance, dichromatism has been linked to high breeding latitude, migratory behavior and territoriality (Badyaev and Hill 2003; Tobias et al. 2012) and all three variables are known to correlate with sympatry rate in birds, presumably through their associations with organism vagility (Weir and Price 2011; Pigot and Tobias 2015). Similarly, body size correlates with plumage dichromatism in passerines (Dale et al. 2015) and could also influence sympatry rate through correlated effects on dispersal ability, range size and habitat partitioning. Furthermore, at very broad scales, tests of the link between sexual selection and sympatry rate could also be hampered by idiosyncratic differences among taxonomic groups (Huang and Rabosky 2014) or geographic regions (Pigot et al. 2016). Thus, in addition to plumage dichromatism, we also quantified (i) latitude, (ii) level of migratory behaviour, (iii) level of territoriality, (iv) body size, (v) taxonomy (non-passerine/passerine) and (vi) geographic region, for each sister pair in dataset 2 (see Appendix S1). To aid comparison of effect sizes, all continuous variables were centered and rescaled prior to analysis.

ESTIMATING RATES OF SPECIATION AND EXTINCTION

To assess the link between sexual selection and rates of speciation and extinction, we fitted a set of birth-death models to our datasets of sister pair ages (Weir and Schluter 2007; Seddon et al. 2013). In these models, observed sister pair ages are compared to probability distributions of sister pair ages generated by simulating a large number of phylogenetic trees under a range of different values of speciation and extinction rate. Each parameter combination produces a distribution with a unique mean and shape—where the phylogenetic signals of the speciation and extinction rates are contained in the mean and shape of the distribution, respectively—making it possible to estimate recent rates of speciation and extinction using only information for extant species (Weir and Schluter 2007). In our models, rates of speciation and extinction were allowed to vary linearly with increasing extent of sexual dichromatism, and the approach estimated the combination of speciation rates, extinction rates and lag-time to species recognition most likely to yield the distribution of species' ages observed in the sample. The lag time adjustment prunes out nodes from phylogenetic trees if they are younger than a focal lag time drawn at random from an exponential distribution and is intended to correct for the fact that empirical phylogenies typically lack nodes representing intraspecific splits between taxa not currently recognised as separate species. Probability distributions of sister pair ages were simulated under a birth-death model using a wide range of parameter values (see Appendix S1).

We compared the fit of a two-parameter model in which all sister pairs had a single rate of speciation and extinction, to models that allowed speciation rate and/or extinction rate to change linearly with increasing dichromatism (i.e. three or four parameter models with one or two slopes and two intercepts, respectively). All models estimated a single lag time parameter (i.e. one additional parameter), which for simplicity was assumed not to vary with increasing sexual dichromatism (Seddon et al. 2013). To infer the significance of slope estimates we used likelihood ratio tests (LRTs) and ΔAICc scores interpreted with reference to the results of simulations tests designed to control for elevated rates of Type I error (see below). To provide an alternative test of the link between sexual dichromatism and diversification, we also used PGLS models (implemented in the 'caper' R package; Orme et al. 2013) to assess the raw relationship between dichromatism and sister pair age.

ESTIMATING RATES OF PARAPATRY/SYMPATRY

To test the link between sexual selection and rates of geographic range overlap, we used a modeling approach based on continuous time multi-state Markov models (Pigot and Tobias 2013, 2015; Pigot et al. 2016). In this approach, each sister pair contributes two observations: the geographic state at the time of population divergence and that of the present day. Here we assume that sister species originated in allopatry (first observation) based on substantial evidence that allopatric speciation is the predominant mode of speciation across all organisms (Coyne and Orr 2004) and especially for birds (Phillimore et al. 2008; Price 2008). We considered two model types with alternative sets of possible states for present day distributions. In the first, pairs could take one of two possible secondary states, either allopatric and sympatric. In the second this was extended to three possible secondary states, either allopatric, parapatric or sympatric (see above). Separately for both datasets 1 and 2, we used maximum likelihood to estimate the rate (per million years; [Myr]) at which species pairs transition from either allopatry to sympatry (model 1) or allopatry to parapatry and parapatry to sympatry (model 2). For simplicity, we modelled this as a one-way process in which transitions from allopatry to sympatry (via parapatry) are irreversible. A detailed description of the modeling approach can be found in (Pigot and Tobias 2013).

We compared the fit of constant-rate models, in which the transition rates are equal across species pairs (accounting for age), to variable-rate models that allow sympatry rate to vary in accordance with one or more covariates. The significance of any co-variation between dichromatism and transition rates was assessed using ΔAICc scores interpreted with reference to the results of simulations tests (see below). All models were implemented in R using the msm library (Jackson 2011).

SIMULATION TESTS

The statistical significance of parameter estimates may be overestimated if models are biased towards the inference of 'false positives' (i.e. have inflated Type I error rates). To determine when our null (i.e. constant-rate) models can be confidently rejected, we used the distribution of

ΔAICc values derived from fits to simulated datasets to identify critical values required to maintain a Type I error rate of α = 0.05 (Rabosky 2006; Lawson and Weir 2014). We simulated 100 null datasets for each dichromatism dataset using BM models of trait evolution fit to pair-level trees, and then tested both constant- and variable-rate models. By simulating data under the null hypothesis of rate-constancy, we can confidently reject the constant-rate model (with a Type I error rate ≤ 0.05) if the ΔAICc for a particular parameter is greater than the appropriate critical value (Rabosky 2006). Critical values correspond to the 95th percentile of the null ΔAICc distribution and values vary depending on the model and parameter in question (Table S2).

Results

SEXUAL SELECTION AND RECENT RATES OF SPECIATION AND EXTINCTION

Using the observed distributions of sister pair ages in our datasets (Fig. 1), we fitted models estimating the relationship between speciation and extinction rates and sexual dichromatism. In dataset 1, based on spectrophotometric measurements of dichromatism (n = 144 pairs; Fig. S1a), the full model estimated a positive slope between speciation rate and dichromatism (Table 1). Likewise, in dataset 2, based on human scores of dichromatism (n = 1306 pairs; Fig. S1b), the full model also estimated a positive slope between speciation rate and dichromatism (Table 1). However, support for variable rates of speciation was lower than the corresponding critical ΔAICc values for both datasets (see Table S2), meaning the null hypothesis of equal speciation rates across the dichromatism gradient could not be rejected. Similarly, in terms of extinction, we also found little evidence that extinction rates vary significantly in line with dichromatism in either of our datasets (Table 1). Analyses based on 100 replicate trees produced comparable results (Table S3). The conclusion of minimal differences in diversification rates among monochromatic and dichromatic species is further supported by the observation that sister pair age was uncorrelated with levels of dichromatism in both data cases (Fig. 1, Table S4). Thus, overall we found little support for the idea that sexual selection significantly elevates rates of lineage formation.

RATES OF TRANSITION INTO PARAPATRY/SYMPATRY

In support of the hypothesis that sexual selection facilitates secondary contact between closely related bird species, we found positive associations between dichromatism and the rate at which sister species achieve geographic range overlap. First, by categorizing pairs as either allopatric or sympatric, we found robust support for positive associations between dichromatism and sympatry rate in both dataset 1 and 2 when using relaxed definitions of sympatry (i.e. range overlap thresholds 0-20%; Table S5). However, under more stringent definitions of sympatry (i.e. range overlap thresholds 30-80%), there were no significant associations between dichromatism and the rate at which sister pairs achieve sympatry (Table S5). Second, using an alternative approach in which pairs were categorized as allopatric, parapatric or sympatric, we found robust support in both datasets 1 and 2 for a positive relationship between dichromatism and the rate at which sister species achieve narrow (i.e. parapatric) but not extensive (i.e. sympatric) geographic range overlap (Table 2; Fig. 2). Dichromatic sister species are inferred to become parapatric 2-4 times faster than monochromatic sisters (Table 2, Fig. 2a,c). In contrast, in both datasets dichromatism did not significantly predict the rate at which sister species transition from parapatric distributions to more extensive levels of sympatry (Table 2, Fig. 2b,d). In all cases, results were similar when we re-ran our analyses on 100 replicate trees (Table S6 and S7).

Furthermore, focusing on dataset 2, we found that the positive association between dichromatism and fast transitions to (narrow) geographic range overlap could not be explained by correlations with potentially confounding variables. Based on relaxed definitions of sympatry (i.e. <20% overlap = sympatry), we found strong evidence for associations between territoriality, body mass and geographical realm in explaining sympatry rates across birds (Table S8), suggesting that differences in levels of competition and dispersal ability among species, and/or niche availability within biomes, contributes to explaining variation in sympatry rate among bird species. Yet, none of these effects accounted for the significant association between sympatry rate and dichromatism (Table S8). Likewise, distinguishing between transitions from allopatry to parapatry, and parapatry to sympatry, we found comparable results: dichromatism remained an important predictor or transition rates to parapatry but not sympatry (Table S9).

Discussion

Using plumage dichromatism as a proxy for the intensity of sexual selection, we tested two separate hypotheses linking sexual selection to the outcome of speciation cycles in birds. Our results reveal that, even when focusing on recent speciation events (i.e. sister species), there is little evidence linking variation in levels of plumage dichromatism to differences in divergence times or rates of speciation (and extinction) across lineages. However, sexual selection had a significant role in facilitating the early stages of range overlap between close relatives. These findings suggest that sexual selection plays a limited role in driving diversification rates, even within recently diverged taxa, but can help to explain transitions to stable secondary contact.

The lack of a significant positive association between sexual selection and speciation rates across avian sister pairs corroborates the findings of previous studies testing this relationship in taxa descended from deeper phylogenetic nodes (Morrow et al. 2003; Phillimore et al. 2006; Huang and Rabosky 2014). In these previous studies, the failure to detect a signature of sexual selection may have occurred simply because the analyses focused on longer evolutionary timescales. For instance, if extinction were biased towards sexually selected taxa, many of the speciation events generated by sexual selection would be lost over time, thus becoming harder to detect in comparisons among older extant lineages (Kraaijeveld et al. 2011).

Similarly, the intensity of sexual selection likely fluctuates over time (Wiens 2001) and thus there may be a disconnect between present day levels of selection (as measured through our dichromatism scores) and those occurring during the speciation processes that initially gave rise to the study lineages. Such disconnects almost certainly increase in scale and frequency over time since speciation, meaning that the inclusion of deeper phylogenetic nodes may increase uncertainty and thus mask any effect of sexual selection on the speciation process. Thus, although it has become increasingly clear that no 'universal' relationship between sexual selection and speciation rate exists at the scale of higher taxa (e.g. genera and families), previous comparative studies left open the possibility that sexual selection is a stronger driver of speciation in recently diverged taxa (Kraaijeveld et al. 2011). Our study addresses this question directly, and yet we still find no relationship between sexual selection and recent speciation rates estimated from avian sister pairs. This finding supports the growing consensus that, for birds at least, sexual selection plays a limited role in driving diversification irrespective of evolutionary timescale (Huang and Rabosky 2014).

The weak association between sexual selection and speciation rates at the level of sister species has several potential explanations. One is that the effect of sexual selection on diversification may produce phenotypically divergent but short-lived 'ephemeral species' (Rosenblum et al. 2012) that are difficult to detect empirically. However, this seems unlikely given that new species are often described on the basis of differences in sexually selected traits (Ritchie 2007). An alternative explanation is that the rate at which new species form is more strongly controlled by other factors besides sexual selection, including the rate of ecological or genetic differentiation (Sobel et al. 2010), and thus that sexual selection plays a limited role in driving the evolution of new species (Price 1998; Servedio and Bürger 2014). It can be argued, for example, that sexual selection is episodic and highly contingent on other factors, such as resource availability and local changes in population density or predation risk (e.g. Irwin 2000; Johnson and Lanyon 2000), thus weakening its effects on diversification and longer-term evolutionary change. Finally—and perhaps more plausibly—if sexual selection contributes to the evolution of reproductive isolation, it seems likely to do so in allopatry/parapatry without giving rise to the type of differences that facilitate coexistence in sympatry, thus delaying the completion of speciation cycles.

We tested this possibility by assessing whether sexual selection was associated with rates of transition to sympatry or merely to parapatry, finding strong support for the hypothesis that sexual selection plays a role in shaping patterns of geographic range overlap in birds. Specifically, we found that dichromatism was positively correlated with the rate at which sister species became parapatric (i.e. only narrowly sympatric), such that highly dichromatic sister pairs achieved parapatry 2-4 times faster than more monochromatic sister pairs. This positive effect on range overlap rate was consistent across two independent dichromatism datasets that differed in taxonomic scope and the method used to quantify dichromatism. Although this relationship has not previously been directly assessed, compatible findings have been reported in particular avian clades, including the waterfowl (Anseriformes) and New World warblers (Parulidae), where dichromatism (and bright male plumage) is associated with increased sympatric diversity among closely related species (Figuerola and Green 2000; Pfennig and Hurlbert 2012). An alternative possibility is that dichromatism (our proxy for sexual selection) co-varies with a variety of ecological, behavioural and biogeographic factors (Badyaev and Hill 2003; Dale et al. 2015; Dunn et al. 2015), many of which could explain correlations between dichromatism and rates of range overlap. However, we found no support for this idea when we included a suite of such variables (latitude, migration, territoriality, body size and geographic realm) in our models, as none explained the key association. We conclude that the link between dichromatism and rates of achieving parapatry is not attributable to shared correlations with confounding factors.

A positive correlation between dichromatism and rates of achieving narrow range overlap may arise because sexual selection reduces the likelihood of young lineages collapsing back into single species following the onset of secondary contact. Termed ‘differential fusion’, this hypothesis predicts that only species with strong mating discrimination (i.e. pre-mating isolation) persist after secondary contact, while populations lacking such discrimination frequently fuse through hybridisation and gene flow (Noor 1999). Differential fusion does not necessarily rely on sexual selection influencing the underlying rate at which lineages come into contact, but merely accelerating the evolution of traits important for pre-mating isolation (Seddon et al. 2013) and thus increasing the likelihood of remaining distinct following secondary contact (Edwards et al. 2005; Hudson and Price 2014). The pattern we detect of reduced average waiting times to parapatry in dichromatic lineages may therefore be produced by elevated rates of fusion in young monochromatic lineages after secondary contact. Coyne and Orr (1989) argued against the importance of differential fusion for understanding speciation in *Drosophila*, but recent work examining patterns of mating signal divergence and range overlap in birds (Martin et al. 2010; Delmore et al. 2015; Martin et al. 2015) suggests that differential fusion may play a more important role than currently appreciated.

Differential fusion is relevant to secondary contact in parapatric lineages with narrow range overlap, but wider spatial overlap between incipient lineages is theoretically less dependent on reproductive isolation. In this case, our results clearly indicate that the positive influence of sexual selection does not result in more extensive levels of sympatry. In particular, we found that transition rates from allopatry (or parapatry) to more substantial levels of range overlap (i.e. 30-80%) were unrelated to levels of dichromatism across pairs, and that this lack of an effect was similar for both dichromatism datasets. The most likely explanation for this pattern is that, while divergent sexual selection may generate sufficient reproductive isolation between lineages to prevent complete fusion, sister species must still overcome ecological barriers to sympatry, such as niche similarity and resource competition, which are likely to represent particularly important barriers to range expansions among close relatives (Pigot and Tobias 2013; Price et al. 2014). Thus, while sexual selection appears to promote the initial establishment of contact and minor overlap between species ranges, our results are consistent with the view that ecological rather than sexual interactions are more important in determining transitions to more extensive levels of species co-existence (Sobel et al. 2010).

Geographic range expansion is a necessary step for repeated rounds of speciation, and the large amount of time required to establish sympatry with close relatives likely places a severe limit on the rate of on-going speciation (Price 2008; Weir and Price 2011). By failing to facilitate transitions to extensive sympatry among sister species, sexual selection (in isolation) is unlikely to promote the type of large-scale range expansion required for repeated progression through the speciation cycle, especially within mature, species rich, continental radiations. Our findings therefore provide a novel explanation for the generally weak (or nonexistent) effect of sexual selection on speciation rates. By playing only a limited role in allowing lineages to overcome barriers to continued diversification imposed by competition with related species, sexual selection soon comes up against the constraints of ecological competition. Thus, the best opportunity for rapid and sustained species diversification is likely to occur in situations where ecological opportunity and sexual selection coincide (Wagner et al. 2012).

Taken together, our results add a further dimension to the well-established view that biotic interactions limit range expansion and species co-existence (MacArthur 1972; Diamond 1975) by providing comparative evidence that the initial stages of range overlap are likely to be constrained by fitness costs associated with sexual as well as ecological interactions between species (Gröning and Hochkirch 2008; Weber and Strauss 2016). Thus, while sexual selection may accelerate the establishment of (narrow) range overlap among sister species, it plays a more limited role in driving the formation of new lineages or promoting the type of large-scale range expansions required for repeated rounds of speciation. Our study therefore provides a more mechanistic explanation for the general observation that sexual selection (in isolation) plays a seemingly limited role in explaining broad-scale patterns of diversification (Kraaijeveld et al. 2011).

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Supporting information

Additional supporting information may be found in Appendix S1:

Includes supplementary methods, figures (S1) and tables (S1-S9).

Figure and table captions

Figure 1. The relationship between pair age and sexual dichromatism across avian sister pairs based on (a) spectrophotometric and (b) human estimates of dichromatism (n = 144 pairs in dataset 1, and 1306 pairs in dataset 2, respectively).

Figure 2. The effect of dichromatism on rates of transition from allopatry to parapatry (a,c) and parapatry to sympatry (b,d) based on spectrophotometric (a,b) and visual (c,d) estimates of dichromatism in avian sister pairs (n = 140 pairs in dataset 1, and 1306 pairs in dataset 2, respectively). Plotted rate estimates are mean values (solid line) with 95% confidence intervals (grey shading) using range overlap thresholds of <5%, 5-25% and >25% to categorise species as allopatric, parapatric and sympatric, respectively. Asterisks (*) denote significant ($\alpha = 0.05$) effects (see Table S2).

Table 1. Estimates of speciation and extinction rates across gradients of increasing sexual dichromatism.

Table 2. Models of the relationship between parapatry and sympatry rate and sexual dichromatism across sister pairs of birds using alternative range overlap thresholds to assign parapatry and sympatry.

Supplementary figure and table captions

Figure S1. Plot showing the variation in evolutionary age, extent of range overlap and level of sexual dichromatism across avian sister species pairs with respect to the underlying phylogeny. In (a) dichromatism is estimated for a set of passerine sister pairs using spectrophotometric measurements of plumage (dataset 1; n = 144 species pairs), whereas in (b) estimates are based on human scores of dichromatism for a broader sample of passerine and non-passerine pairs (dataset 2; n = 1306 species pairs).

Table S1. Principal component (PC) loadings and importance values for reflectance measurements of plumage colour (n = 61920) collapsed into 20nm bins.

Table S2. Critical ΔAICc values for models testing the association between diversification and parapatry/sympatry rates and dichromatism across alternative sister pair datasets.

Table S3. Median parameter values of speciation and extinction rates across gradients of increasing sexual dichromatism estimated using datasets of avian sister pairs (n = 1283 – 1321) sampled from 100 posterior trees.

Table S4. PGLS models of the relationship between age and sexual dichromatism across avian sister pairs.

Table S5. Models of the relationship between sympatry rate and sexual dichromatism across sister pairs of birds under alternative range overlap thresholds used to assign sympatry.

Table S6. Median parameter values for the relationship between sympatry rate and sexual dichromatism (under alternative range overlap thresholds) using datasets of avian sister pairs (n = 1283 – 1321) sampled from 100 posterior trees.

Table S7. Median parameter values for the relationships between parapatry and sympatry rate and sexual dichromatism (under alternative range overlap thresholds) using datasets of avian sister pairs (n = 1283 – 1321) sampled from 100 posterior trees.

Table S8. Multi-predictor model of variation in sympatry rate among sister pairs of birds (dataset 2; n = 1306) using alternative range overlap thresholds to define sympatry.

Table S9. Multi-predictor model of variation in parapatry and sympatry rate among sister pairs of birds (dataset 2; n = 1306) using alternative range overlap thresholds (%; parapatry / sympatry).

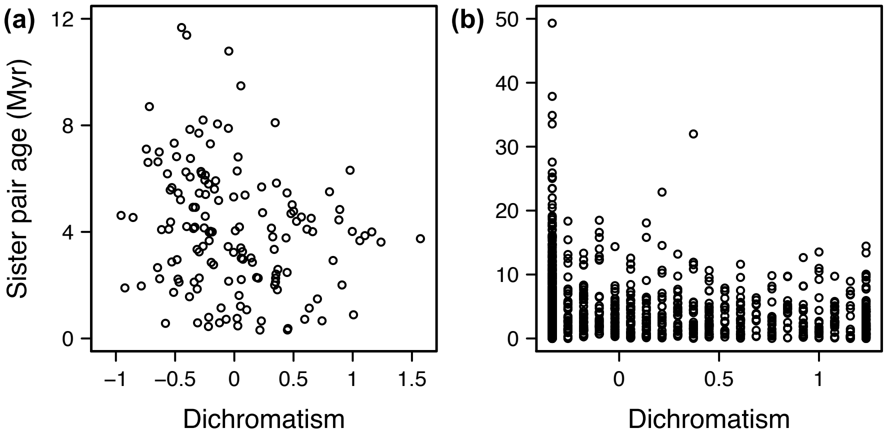

Figure 1. The relationship between pair age and sexual dichromatism across avian sister pairs based on (a) spectrophotometric and (b) human estimates of dichromatism (n = 144 pairs in dataset 1, and 1306 pairs in dataset 2, respectively)

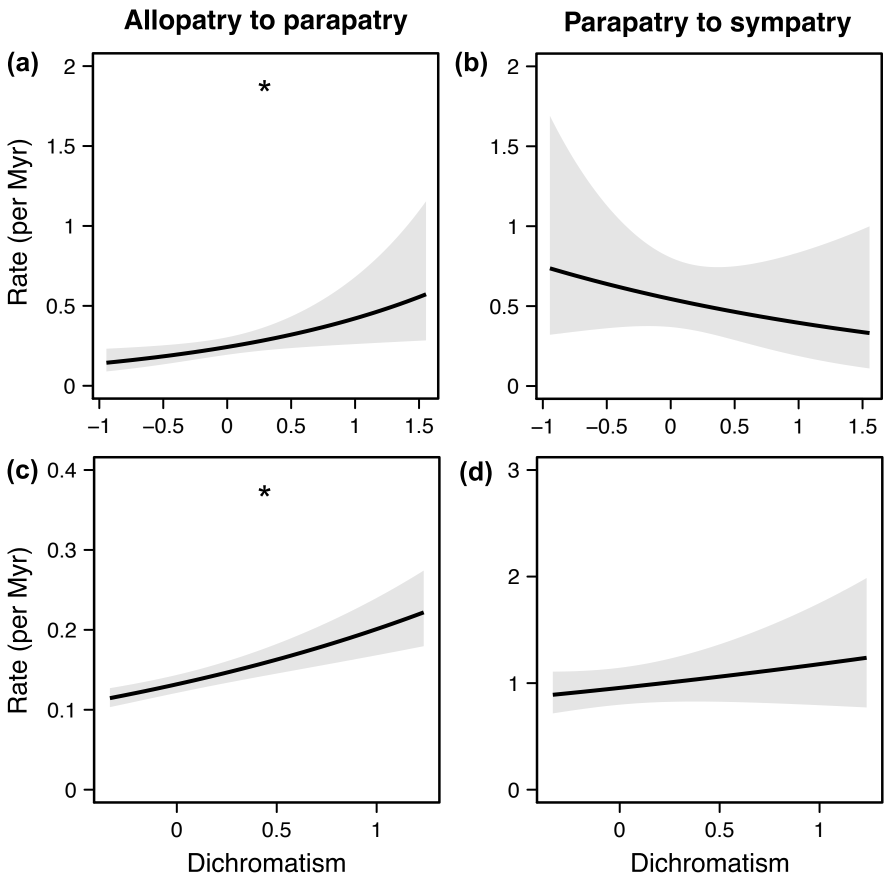

Figure 2. The effect of dichromatism on rates of transition from allopatry to parapatry (a,c) and parapatry to sympatry (b,d) based on spectrophotometric (a,b) and visual (c,d) estimates of dichromatism in avian sister pairs (n = 140 pairs in dataset 1, and 1306 pairs in dataset 2, respectively). Plotted rate estimates are mean values (solid line) with 95% confidence intervals (grey shading) using range overlap thresholds of <5%, 5-25% and >25% to categorise species as allopatric, parapatric and sympatric, respectively. Asterisks (*) denote significant ($\alpha = 0.05$) effects (see Table S2).

Table 1. Estimates of speciation and extinction rates across gradients of increasing sexual dichromatism.

Parameter	**Estimate**	**ΔAICc**
Dataset 1		
Speciation intercept	0.06	–
Speciation slope	0.19	3.69
Extinction intercept	0.00	–
Extinction slope	0.01	–2.12
Dataset 2		
Speciation intercept	0.08	–
Speciation slope	0.03	11.19
Extinction intercept	0.01	–
Extinction slope	0.02	–2.84

ΔAICc values quantify the improvement in model fit (positive values) compared to constant-rate models in which the focal slope parameter(s) were constrained to be zero. In each case, support for slope parameters was non-significant when compared to critical ΔAICc values derived from simulated datasets (see Table S2).

Table 2. Models of the relationship between parapatry and sympatry rate and sexual dichromatism across sister pairs of birds using alternative range overlap thresholds to assign parapatry and sympatry.

Thresholds (%; para/sym)	*N* (allo/para/sym)	Parameter	Hazard ratio [95% CI]	ΔAICc
Dataset 1				
0-20 / >20	43 / 33 / 64	ap	1.85 [1.96, 2.85]	5.58*
		ps	1.00 [0.52, 1.92]	–2.09
5-15 / >25	54 / 31 / 55	ap	1.74 [1.13, 2.68]	4.06*
		ps	0.73 [0.36, 1.48]	–1.28
10-30 / >30	60 / 32 / 48	ap	1.80 [1.15, 2.81]	4.31*
		ps	0.86 [0.43, 1.75]	–1.92
Dataset 2				
0-20 / >20	600 / 283 / 423	ap	1.45 [1.25, 1.68]	20.60*
		ps	1.55 [1.16, 2.08]	6.90
5-15 / >25	750 / 163 / 393	ap	1.53 [1.30, 1.80]	22.35*
		ps	1.23 [0.86, 1.76]	–0.63
10-30 / >30	804 / 134 / 386	ap	1.49 [1.26, 1.77]	17.64*
		ps	1.17 [0.79, 1.74]	–1.35

Hazard ratios refer to the ratio of transition rates per unit change in dichromatism. To aid comparison, dichromatism values were standardised prior to analysis. ΔAICc values quantify the improvement in model fit (positive values) compared to constant-rate models. Asterisks (*) denote significant ($\alpha = 0.05$) ΔAICc values compared to null expectations. allo = allopatric; para = parapatric; sym = sympatric; ap = allopatry to paraptry; ps = parapatry to sympatry.

SUPPLEMENTARY MATERIAL

APPENDIX S1

Supplementary methods

Supplementary figures (S1) and tables (S1-S9)

APPENDIX S1

SUPPLEMENTARY METHODS

Compiling sister species datasets

We generated two datasets of avian sister species pairs. First, we assembled a dataset of passerine sister pairs for which we could collect detailed data on plumage colouration using spectrophotometric measurements. To do this, we compiled a list of sister pairs from published phylogenetic trees of passerine families or genera generated using mtDNA. We only included trees in which (i) > 70% of taxa had been sampled, and (ii) node support was high, with either posterior probability > 95% or ML bootstrap support > 70%. When several phylogenies were presented in a paper, we only selected sister species resolved in all trees. When nodal support varied with the method of phylogenetic reconstruction, ML bootstrap values took precedence. We assumed that consensus trees and trees based on concatenated molecular datasets provided the most reliable source of phylogenetic information and thus, whenever possible, we assessed nodal support based on the values given in these trees. Sister pair ages were generated by building a time-calibrated phylogenetic tree using multiple mitochondrial cytochrome (cyt) *b* sequences per species (where possible; see below). The resulting dataset contained 144 species pairs and is referred to as dataset 1 throughout.

Second, to assess the links between speciation, sympatry and sexual selection on a broader scale, we assembled data for a larger set of sister pairs sampled from across the avian radiation (including non-passerines). Following previous analyses (Pigot et al. 2016), sister pairs and their divergence times (My) were extracted from the Jetz et al. (2012) time-calibrated phylogenies, using the Hackett et al. (2008) backbone topology and focusing on trees containing only those species represented by genetic data (n = 6,670). Using a random sample of 100 trees, we generated a single MCC tree with median node heights and extracted sister pairs from across the tree, excluding pairs containing pelagic species with poorly defined breeding distributions (n = 69) and pairs from poorly sampled genera (sampling <70%; n = 723), which are unlikely to represent true sister species (Pigot et al. 2016). The resulting dataset contained 1306 sister species pairs. We report the results produced using pairs sampled from the MCC tree, but as these results are subject to phylogenetic uncertainty, we re-ran our analyses on pairs extracted from each of the 100 sampled trees and also report median values across all replicate trees. Aside from differences in sample size and taxonomic scope, this larger dataset was comparable to the first, except that it included many species for which we were unable to obtain spectrophotometric measurements of colour. Thus, for all species included in all replicate trees, we quantified dichromatism using human visual estimates of sex-differences in colouration based on illustrations (see below). We refer to this larger dataset as dataset 2 throughout the text.

Estimating passerine-only sister species ages

To build a time-calibrated tree for passerine-only sister species, we searched GenBank for available cyt-*b* sequences, excluding those <400 bp in length and all sequences that were excessively divergent from other conspecific sequences, which are likely to represent nuclear copies of the cyt-*b* gene (i.e. ‘numts’). For species represented by multiple sequences, we pruned out those sequences originating from similar localities/subspecies that had identical (or extremely similar) sequence identity. For the remaining species in the dataset we included a single representative cyt *b* sequence and where a choice of sequences was available for a given species, we chose the longest. The resulting dataset contained 288 bird species (i.e. 144 sister species pairs) represented by 556 cyt-*b* sequences, with 86/288 species represented by more than one sequence. We aligned the chosen sequences using MAFFT (Katoh et al. 2002) and built the phylogeny with BEAST v1.7.4 (Drummond et al. 2012) using an uncorrelated lognormal relaxed-clock model with a Yule prior on branch lengths and a GTR-gamma model set to a mean rate of 1.05% sequence evolution per lineage per million years (Weir and Schluter 2008). As cyt-*b* is inappropriate for inferring deeper phylogenetic relationships, we used backbone constraints to define *a priori* all the known species pairs and genera in our sample. We conducted four runs (each 20 million generations sampled every 5000 generations) and combined the samples from each run after first checking for convergence and removing the first 25% as burn in. To produce a dated phylogeny, we generated a maximum clade credibility (MCC) tree using TREEANNOTATOR (Drummond et al. 2012), with node ages equal to the median age across all posterior trees.

Quantifying sexual dichromatism

Spectrophotometric measurements of dichromatism

For the 144 pairs of passerine bird species in our smaller dataset, we quantified sexual dichromatism objectively using measurements of plumage colour collected using a spectrophotometer. By using colour data derived from a spectrophotometer, this allows us to assess the links between plumage dichromatism and speciation/sympatry whilst avoiding the problems associated with human misrepresentation of avian colour (Cuthill et al. 1999). All spectrophotometer measurements were collected using an Ocean Optics (Dunedin, Florida) USB2000 spectrophotometer and a PX-2-pulsed Xenon light source with the spectrophotometer probe at 90^{o}

to the feather’s surface. Measurements were standardized to a WS-1 white standard, considered to reflect more than 98% of light with 250–1500 nm wavelength.

To measure plumage colouration, we took five replicate spectrophotometric measurements at six body regions (crown, throat, belly, wing coverts, back and tail) from three male and three female adult specimens of each species (where possible) in full breeding plumage. For each reflectance reading, the reflectance data were averaged into 19 bins covering 20 nm of the spectrum between 320 and 700 nm, the approximate visible spectrum of most avian species (Hart 2001). Reflectance scores are highly correlated at similar wavelengths, so we used principal components analysis (PCA) to collapse reflectance values into fewer independent axes of variation capable of summarising spectrum shape (Endler 1990; Cuthill et al. 1999). Some previous comparative studies (e.g. Stoddard and Prum 2008) have instead modelled the spectral sensitivity of the avian eye but this involves making assumptions about colour perception in numerous species for which data on spectral sensitivity are lacking (Borges et al. 2015). We note that our PCA analysis is a widely-used procedure for handling spectral data (Endler and Théry 1996; Bennett et al. 1997; Hunt et al. 1999; Macedonia 2001; Stein and Uy 2006; Seddon et al. 2013; Dunn et al. 2015), and previous studies comparing the outputs with those of visual models have yielded qualitatively similar estimates of colour and dichromatism (Armenta et al. 2008; Stoddard and Prum 2008) and dichromatism (Armenta et al. 2008). We used the first three PCs, which together explained over 99% of the variance spectrum shape (Table S1) and broadly correspond to variation in brightness (PC1), chroma/hue (PC2 and PC3) across spectra. To calculate dichromatism we averaged replicate measurements within a patch for each sex and then summed the Euclidean distances between male and female scores for each patch (Seddon et al. 2013). A dichromatism score of zero indicates identical colouration in both sexes (monochromatism) with higher positive values indicating greater degree of dichromatism. To improve normality, dichromatism scores were log-transformed. Finally, to calculate pair-level scores, we used the average score of both species.

Human scores of dichromatism

It is not yet feasible to obtain spectrophotometric measures of plumage colour for thousands of species, so for all species in dataset 2 (n = 5681, including all species occurring in replicate trees) we scored sexual dichromatism from handbook illustrations (del Hoyo et al. 1992–2011). Specifically, we used standard methodology (Owens and Bennett 1994; Owens and Hartley 1998) to score the difference in plumage coloration between the sexes over five body regions (head, nape-rump-back, throat-belly, tail, and wings) for each species in our sample. Each region was scored separately using three scores: 0, no difference between the sexes; 1, difference between the sexes only in shade or intensity of color; 2, difference in colour or pattern between the sexes. The dichromatism scores for all five body regions were then summed to give species-specific scores of plumage dichromatism on a scale from 0 (monochromatic) to 10 (maximum dichromatism). Unlike spectrophotometric scores of dichromatism, our human scores of dichromatism were not log-transformed because of issues associated with the log-transformation of count data (O'Hara and Kotze 2010). As before, pair-level scores were calculated by taking the average score of both species.

Human observers may underestimate the extent of sexual dichromatism in birds because of an inability to perceive signals in ultraviolet wavelengths (Cuthill et al. 1999). Nevertheless, among the species common to both datasets (n = 281), spectrophotometric and human-derived estimates of dichromatism were highly correlated (Spearman's $r = 0.69$, $P < 0.001$), adding to a growing body of evidence that human scores can provide useful estimates of plumage dichromatism (Armenta et al. 2008; Seddon et al. 2010). Furthermore, our results were similar irrespective of whether spectrophotometric or human visual estimates of dichromatism were used, suggesting that our conclusions are robust to the particular approach used to quantify dichromatism.

Additional predictors of geographic range overlap

Latitude. Species' latitudinal centroids were estimated using the R package PBSmapping. Following previous studies (e.g. Weir and Schluter 2007), we then used average (absolute) centroid values to estimate the midpoint latitudinal position of sister pairs.

Migration and territoriality. Following previous studies (Salisbury et al. 2012; Pigot and Tobias 2015; Cooney et al. 2016), we used descriptions in *The Handbook of the Birds of the World* series (del Hoyo et al. 1992–2011) to score species according to levels of migratory tendency (1 = sedentary, 2 = short-distance migrants, 3 = long-distance migrants) and territoriality (1 = permanent year-round territoriality, 2 = seasonal or weak territoriality, 3 = non-territorial). For both variables, we then used the mean score of species within each pair to provide a simple index capturing the relative level of migratory behavior or territoriality in a sister pair. For further details and justification of traits and scoring method see Pigot and Tobias (2015).

Body size. Body mass values were extracted from 'EltonTraits 1.0' (Wilman et al. 2014) and log-transformed before taking the average for each sister pair.

Geographic realm. Each sister pair was unambiguously assigned to a particular geographic realm (Africa, Eurasia, Oceania, North America, South America) based on the dominant geographic position of their breeding range distributions.

Simulating birth-death trees

Birth-death trees with lag time correction were simulated using the R package TreeSim (Stadler 2011) and custom code. For dataset 1, trees were simulated for 15 time units (max sister pair age =

11.7 My) using speciation rate values ranging from 0 to 0.15 in 0.01 intervals, and from 0.15 to 0.90 in 0.05 intervals. For speciation rates ≤ 0.4, simulated extinction fractions ranged from 0, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 0.95, 0.99. For speciation rates > 0.4, the same extinction rates were used provided net diversification rate (speciation – extinction) < 0.45. For dataset 2, trees were simulated for 50 time units (max sister pair age = 49.3 My) using similar parameter values except that for speciation rates > 0.15, the same extinction rates were used provided net diversification rate ≤ 0.15. This type of restriction was necessary for computational reasons given the excessively large tree sizes, but should not bias our likelihood search because such trees are unrealistically large. For each set speciation and extinction rates, 21 values of lag time were used (0, 0.1, 0.2…1.9, 2). For each set of sister pair age distributions, the probability density function was obtained using the LOCFIT package in R, and the probability of given pair age equals the probability density at the corresponding point in the simulated distribution. For a given set of slope and intercept parameters describing the change in speciation and extinction rates with increasing dichromatism, the likelihood was obtained by multiplying the probabilities of each sister species age, derived from the appropriate simulated distribution. More details of the simulation approach and model fitting can be found in Weir and Schluter (2007) and Seddon et al. (2013).

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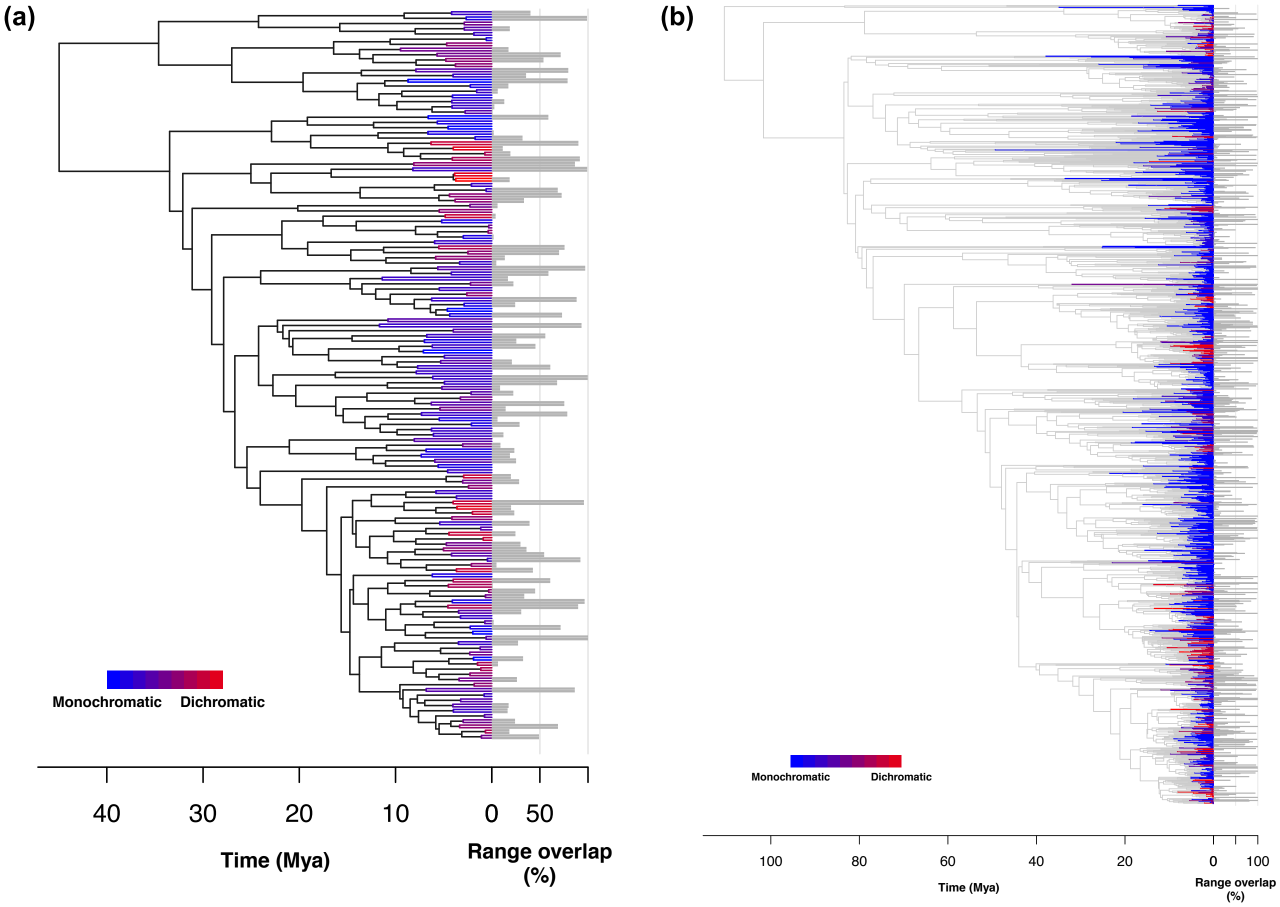

Figure S1. Plot showing the variation in evolutionary age, extent of range overlap and level of sexual dichromatism across avian sister species pairs with respect to the underlying phylogeny. In (a) dichromatism is estimated for a set of passerine sister pairs using spectrophotometric measurements of plumage (dataset 1; n = 144 species pairs), whereas in (b) estimates are based on human scores of dichromatism for a broader sample of passerine and non-passerine pairs (dataset 2; n = 1306 species pairs).

Table S1. Principal component (PC) loadings and importance values for reflectance measurements of plumage colour (n = 61920) collapsed into 20nm bins.

Wavelength bin (nm)	**PC1**	**PC2**	**PC3**
320-340	0.21	0.26	–0.54
340-360	0.22	0.23	–0.43
360-380	0.23	0.23	–0.29
380-400	0.23	0.25	–0.09
400-420	0.23	0.26	0.09
420-440	0.23	0.25	0.22
440-460	0.23	0.23	0.31
460-480	0.23	0.20	0.36
480-500	0.23	0.15	0.35
500-520	0.24	0.03	0.15
520-540	0.24	–0.08	0.00
540-560	0.24	–0.14	–0.03
560-580	0.24	–0.19	–0.03
580-600	0.23	–0.23	–0.04
600-620	0.23	–0.26	–0.03
620-640	0.23	–0.28	–0.03
640-660	0.22	–0.29	–0.02
660-680	0.22	–0.30	–0.02
680-700	0.22	–0.31	–0.01
Standard deviation	4.04	1.43	0.67
Proportion of variance	0.86	0.11	0.02
Cumulative proportion	0.86	0.97	0.99

Table S2. Critical ΔAICc values for models testing the association between diversification and parapatry/sympatry rates and dichromatism across alternative sister pair datasets.

	Dataset 1	**Dataset 2**
Parameter	**Critical ΔAICc**	**Critical ΔAICc**
Diversification models		
Speciation rate	3.66	18.05
Extinction rate	–1.42	3.37
Allopatry / sympatry models		
Sympatry rate (>0%)	1.80	8.32
Sympatry rate (>5%)	1.87	8.45
Sympatry rate (>10%)	2.55	8.03
Sympatry rate (>20%)	3.26	8.63
Sympatry rate (>30%)	4.13	9.04
Sympatry rate (>40%)	1.86	8.21
Sympatry rate (>50%)	0.68	7.90
Sympatry rate (>60%)	0.78	4.57
Sympatry rate (>70%)	1.05	3.07
Sympatry rate (>80%)	1.35	4.26
Allopatry / parapatry / sympatry models		
Parapatry rate (0-20%)	1.86	10.47
Parapatry rate (5-25%)	2.27	8.36
Parapatry rate (10-30%)	3.07	9.63
Sympatry rate (>20%)	4.04	11.84
Sympatry rate (>25%)	3.13	8.61
Sympatry rate (>30%)	3.09	7.10

Values correspond to the 95th percentile ($\alpha = 0.05$) of the null distribution of ΔAICc values generated by fitting models to simulated datasets (n = 100; see Methods). Net slope refers to the slope of net diversification rates (i.e. speciation rate – extinction rate).

Table S3. Median parameter values of speciation and extinction rates across gradients of increasing sexual dichromatism estimated using datasets of avian sister pairs (n = 1283 – 1321) sampled from 100 posterior trees.

Parameter	**Estimate**	**ΔAICc**
Speciation intercept	0.07	–
Speciation slope	0.03	12.33
Extinction intercept	0.02	–
Extinction slope	–0.10	–1.15
Net intercept	0.06	–
Net slope	0.04	16.43

Dichromatism values were re-scaled (0-1) prior to model fitting. ΔAICc values quantify the improvement in model fit (positive values) compared to constant-rate models in which the focal slope parameter(s) were constrained to be zero.

Table S4. PGLS models of the relationship between age and sexual dichromatism across avian sister pairs.

Term	**Estimate**	**SE**	***t***	***P***
Dataset 1				
Intercept	4.568	0.924	4.943	<0.001
Dichromatism	–0.631	0.405	–1.559	0.121
Dataset 2				
Intercept	14.491	4.456	3.252	0.001
Dichromatism	0.312	0.197	1.592	0.112

Spec dataset: R^2 = 0.01; Pagel's λ = 0.76. Human dataset: R^2 < 0.01; Pagel's λ = 1.00.

Table S5. Models of the relationship between sympatry rate and sexual dichromatism across sister pairs of birds under alternative range overlap thresholds used to assign sympatry.

Threshold (%)	***N* (allo/sym)**	**Hazard ratio [95% CI]**	**ΔAICc**
Dataset 1			
>0	43 / 97	1.86 [1.19, 2.92]	5.39*
>5	54 / 86	1.78 [1.14, 2.78]	4.27*
>10	60 / 80	1.81 [1.14, 2.85]	4.22*
>20	76 / 64	1.41 [0.87, 2.28]	–0.19
>30	92 / 48	1.28 [0.73, 2.23]	–1.33
>40	100 / 40	1.38 [0.75, 2.51]	–1.01
>50	105 / 35	1.23 [0.64, 2.37]	–1.68
>60	110 / 30	1.40 [0.70, 2.79]	–1.18
>70	116 / 24	1.30 [0.59, 2.85]	–1.64
>80	125 / 15	1.47 [0.56, 3.88]	–1.46
Dataset 2			
>0	600 / 706	1..38 [1.19, 1.60]	14.95*
>5	750 / 556	1.53 [1.30, 1.80]	22.29*
>10	804 / 502	1.50 [1.27, 1.78]	18.09*
>20	883 / 423	1.44 [1.20, 1.74]	11.87*
>30	938 / 368	1.42 [1.16, 1.73]	8.88
>40	994 / 312	1.35 [1.09, 1.68]	4.88
>50	1035 / 271	1.44 [1.15, 1.82]	6.94
>60	1075 / 231	1.36 [1.06, 1.75]	3.40
>70	1112 / 194	1.27 [0.96, 1.68]	0.69
>80	1150 / 156	1.18 [0.86, 1.62]	–1.05

Hazard ratios refer to the ratio of transition rates per unit change in dichromatism. To aid comparison, dichromatism values were standardised prior to analysis. ΔAICc values quantify the improvement in model fit (positive values) compared to constant-rate models. Asterisks (*) denote significant (α = 0.05) ΔAICc values compared to null expectations. allo = allopatric; sym = sympatric.

Table S6. Median parameter values for the relationship between sympatry rate and sexual dichromatism (under alternative range overlap thresholds) using datasets of avian sister pairs (n = 1283 – 1321) sampled from 100 posterior trees.

Threshold	Hazard ratio [95% CI]	ΔAICc
0	1.43 [1.23, 1.66]	18.31*
5	1.53 [1.29, 1.80]	21.31*
10	1.50 [1.27, 1.78]	17.99*
20	1.43 [1.18, 1.73]	10.71*
30	1.37 [1.12, 1.68]	6.57
40	1.31 [1.05, 1.64]	3.37
50	1.39 [1.09, 1.76]	4.74
60	1.31 [1.01, 1.70]	2.03
70	1.22 [0.91, 1.63]	–0.32
80	1.12 [0.81, 1.57]	–1.56

Hazard ratios refer to the ratio of transition rates per unit change in dichromatism. ΔAICc values quantify the relative improvement in model fit (positive ΔAICc values) compared to constant-rate models. Asterisks (*) denote significant (α = 0.05) ΔAICc values compared to null expectations.

Table S7. Median parameter values for the relationships between parapatry and sympatry rate and sexual dichromatism (under alternative range overlap thresholds) using datasets of avian sister pairs (n = 1283 – 1321) sampled from 100 posterior trees.

Thresholds (%; para/sym)	***N* (allo/para/ sym)**	**Parameter**	**Hazard ratio [95% CI]**	**ΔAICc**
0-20 / >20	607 / 280 / 434	ap	1.48 [1.27, 1.71]	22.40*
		ps	1.41 [1.05, 1.89]	3.28
5-15 / >25	755 / 166 / 400	ap	1.51 [1.29, 1.78]	20.99*
		ps	1.14 [0.79, 1.64]	–1.53
10-30 / >30	811 / 136 / 374	ap	1.49 [1.25, 1.77]	16.99*
		ps	1.04 [0.70, 1.54]	–1.85

Hazard ratios refer to the ratio of transition rates per unit change in dichromatism. To aid comparison, dichromatism values were standardised prior to analysis. ΔAICc values quantify the improvement in model fit (positive values) compared to constant-rate models. Asterisks (*) denote significant (α = 0.05) ΔAICc values compared to null expectations. allo = allopatric; para = parapatric; sym = sympatric; ap = allopatry to paraptry; ps = parapatry to sympatry.

Table S8. Multi-predictor model of variation in sympatry rate among sister pairs of birds (dataset 2; n = 1306) using alternative range overlap thresholds to define sympatry.

	>0%		**>10%**		**>20%**	
Term	**Hazard ratio**	**ΔAICc**	**Hazard ratio**	**ΔAICc**	**Hazard ratio**	**ΔAICc**
Dichromatism	1.25 [1.07, 1.46]	5.56	1.34 [1.18, 1.60]	7.56	1.29 [1.06, 1.57]	4.19
Migration	1.20 [0.95, 1.51]	0.31	1.19 [0.91, 1.54]	–0.41	1.17 [0.89, 1.56]	–0.80
Territoriality	1.33 [1.12, 1.58]	8.54	1.49 [1.22, 1.82]	13.05	1.55 [1.25, 1.92]	13.64
Latitude	1.11 [0.87, 1.42]	–1.36	1.17 [0.88, 1.55]	–0.92	1.23 [0.91, 1.66]	–0.22
Body mass	0.75 [0.61, 0.92]	5.73	0.73 [0.58, 0.92]	5.01	0.84 [0.66, 1.08]	–0.16
Pass/non-pass: Pass	1.21 [0.98, 1.49]	1.01	1.26 [0.98, 1.61]	1.34	1.35 [1.03, 1.77]	2.79
Continent: Eurasia	1.09 [0.85, 1.41]	18.28	1.01 [0.75, 1.36]	12.63	1.05 [0.76, 1.46]	10.68
Continent: North America	1.11 [0.82, 1.49]	–	1.11 [0.78, 1.58]	–	1.15 [0.78, 1.70]	–
Continent: Oceania	1.37 [0.94, 1.99]	–	1.78 [1.19, 2.68]	–	1.95 [1.27, 3.01]	–
Continent: South America	1.69 [1.33, 2.14]	–	1.55 [1.18, 2.05]	–	1.57 [1.16, 2.13]	–

Hazard ratios [95% CI] refer to the ratio of transition rates per unit change in predictor variable. ΔAICc values quantify the relative change in model fit when the focal variable was included in the model compared to when it was excluded (positive values imply improvement). Reference categories: Pass/non-pass = non-Passeriformes; Continent = Africa.

Table S9. Multi-predictor model of variation in parapatry and sympatry rate among sister pairs of birds (dataset 2; n = 1306) using alternative range overlap thresholds (%; parapatry / sympatry).

		0-20 / >20		5-25 / >25		10-30 / >30	
Parameter	**Term**	**Hazard ratio**	**ΔAICc**	**Hazard ratio**	**ΔAICc**	**Hazard ratio**	**ΔAICc**
ap	Dichromatism	1.30 [1.11, 1.51]	8.41	1.34 [1.13, 1.59]	9.05	1.32 [1.11, 1.58]	7.10
	Migration	1.17 [0.93, 1.47]	–0.23	1.20 [0.94, 1.54]	0.06	1.19 [0.91, 1.54]	–0.41
	Territoriality	1.35 [1.14, 1.60]	10.18	1.52 [1.26, 1.85]	17.11	1.50 [1.23, 1.83]	13.82
	Latitude	1.16 [0.91, 1.48]	–0.58	1.17 [0.90, 1.54]	–0.59	1.17 [0.88, 1.55]	–0.84
	Body mass	0.73 [0.60, 0.89]	7.91	0.74 [0.60, 0.92]	5.21	0.76 [0.60, 0.95]	3.64
	Pass/non-pass: Pass	1.23 [1.00, 1.52]	1.77	1.28 [1.01, 1.61]	2.32	1.31 [1.03, 1.68]	2.89
	Continent: Eurasia	1.03 [0.80, 1.32]	20.56	1.11 [0.83, 1.47]	14.35	1.00 [0.74, 1.34]	13.1
	Continent: N. America	1.12 [0.83, 1.50]	–	1.12 [0.80, 1.57]	–	1.11 [0.78, 1.58]	–
	Continent: Oceania	1.36 [0.94, 1.97]	–	1.84 [1.25, 2.73]	–	1.79 [1.20, 2.68]	–
	Continent: S. America	1.67 [1.32, 2.11]	–	1.61 [1.24, 2.11]	–	1.54 [1.17, 2.03]	–
ps	Dichromatism	1.41 [1.05, 1.89]	3.24	1.61 [0.81, 1.66]	–1.35	1.13 [0.77, 1.67]	–1.65
	Migration	1.15 [0.76, 1.75]	–1.58	0.98 [0.60, 1.60]	–2.03	1.05 [0.62, 1.79]	–2.00
	Territoriality	2.17 [1.59, 2.97]	21.93	1.63 [1.09, 2.42]	3.64	2.30 [1.48, 3.58]	11.77
	Latitude	1.59 [1.02, 2.50]	2.01	1.40 [0.81, 2.43]	–0.59	1.38 [0.77, 2.50]	–0.86
	Body mass	1.38 [0.94, 2.02]	0.71	1.59 [1.00, 2.53]	1.89	1.68 [1.01, 2.80]	1.92
	Pass/non-pass: Pass	1.52 [1.05, 2.22]	2.77	1.45 [0.90, 2.33]	0.29	1.72 [1.01, 2.94]	1.91
	Continent: Eurasia	0.84 [0.53, 1.32]	10.12	0.61 [0.33, 1.12]	5.45	0.52 [0.27, 0.99]	4.34
	Continent: N. America	1.30 [0.73, 2.32]	–	1.40 [0.63, 3.09]	–	0.97 [0.42, 2.26]	–
	Continent: Oceania	3.21 [1.38, 7.47]	–	1.79 [0.68, 4.75]	–	1.72 [0.61, 4.86]	–
	Continent: S. America	1.44 [0.94, 2.19]	–	1.08 [0.61, 1.90]	–	1.03 [0.56, 1.91]	–

Hazard ratios [95% CI] refer to the ratio of transition rates per unit change in predictor variable. ΔAICc values quantify the relative change in model fit when the focal variable was included in the model compared to when it was excluded (positive values imply improvement). Reference categories: Pass/non-pass = non-Passeriformes; Continent = Africa. ap = allopatry to paraptry; ps = parapatry to sympatry.