

## LETTER

# 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 co-existence, 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.

### Keywords

Differential fusion, plumage dichromatism, sexual selection, speciation, species co-existence, sympatry.

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## INTRODUCTION

Speciation in animals is often viewed as a cyclical process beginning with divergence in allopatry and ending with co-existence 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 & 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 & Grant 2008; Price 2008). However, while the importance of ecology in driving or constraining speciation cycles is becoming increasingly well understood (e.g. Pigot & 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, first by generating substantial reproductive isolation between lineages diverging in allopatry (Price 1998; Panhuis *et al.* 2001), and second by maintaining and/or strengthening isolating barriers when species ranges expand into sympatry (Gröning & Hochkirch 2008; Hudson & Price 2014; Weber & 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 is 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 & 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

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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 & Hochkirch 2008; Weber & 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 & Hill 2003; Price & 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 & 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 & Schluter 2007; Pigot & 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 second 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 (1) more recent divergence times (i.e. younger evolutionary age), and (2) 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 (1) accelerated rates of transition from allopatric to parapatric/sympatric distributions, and (2) 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 & Hartley 1998; Dunn *et al.* 2001, 2015; Dale *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 & Hartley 1998; Dunn *et al.* 2001, 2015; Dale *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 & 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 & 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 & Tobias 2013, 2015; Tobias *et al.* 2014; 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 & Tobias 2013, 2015; Pigot *et al.* 2016), pairs were initially categorised 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 categorised 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 & 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 behaviour and territoriality (Badyaev & 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 & Price 2011; Pigot & 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 & Rabosky 2014) or geographic regions (Pigot *et al.* 2016). Thus, in addition to plumage dichromatism, we also quantified (1) latitude, (2) level of migratory behaviour, (3) level of territoriality, (4) body size, (5) taxonomy (non-passerine/passerine) and (6) geographic region, for each sister pair in dataset 2 (see Appendix S1). To aid comparison of effect sizes, all continuous variables were centred 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 & 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 & 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  $\Delta\text{AICc}$  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 modelling approach based on continuous time multi-state Markov models (Pigot & 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 & 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 modelling approach can be found in (Pigot & 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  $\Delta\text{AICc}$  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  $\Delta\text{AICc}$  values derived from fits to simulated datasets to identify critical values required to maintain a Type I error rate of  $\alpha = 0.05$  (Rabosky 2006; Lawson & 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  $\leq 0.05$ ) if the  $\Delta\text{AICc}$  for a particular parameter is greater than the appropriate critical value (Rabosky 2006). Critical values correspond to the 95th percentile of the null  $\Delta\text{AICc}$  distribution and values vary depending on the model and parameter in question (Table S2).

## RESULTS

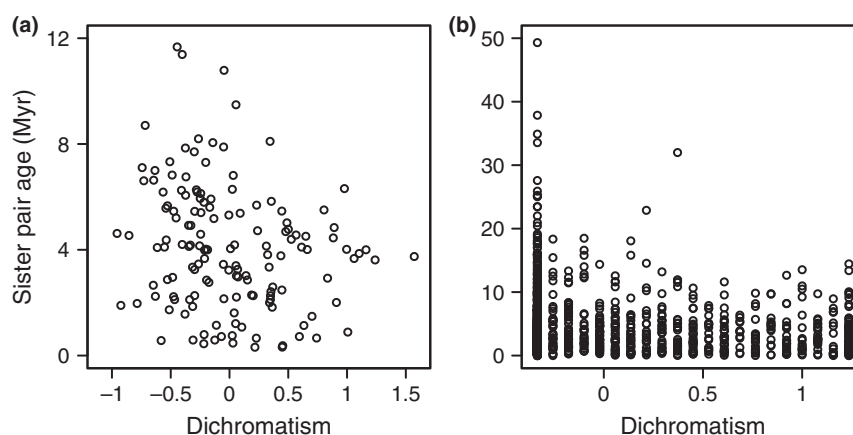
### Sexual selection and recent rates of speciation and extinction

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  $\Delta\text{AICc}$  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 categorising 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. all species pairs with  $>0$ –20% range overlap treated as sympatric; 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 categorised 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 and 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 and 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



**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).

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

Parameter	Estimate	$\Delta$ AICc
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

$\Delta$ AICc 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  $\Delta$ AICc values derived from simulated datasets (see Table S2).

transitions to (narrow) geographic range overlap could not be explained by correlations with potentially confounding variables. Based on relaxed definitions of sympatry (i.e. species pairs with  $>0$ –20% range overlap treated as sympatric), 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, contribute 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 of 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

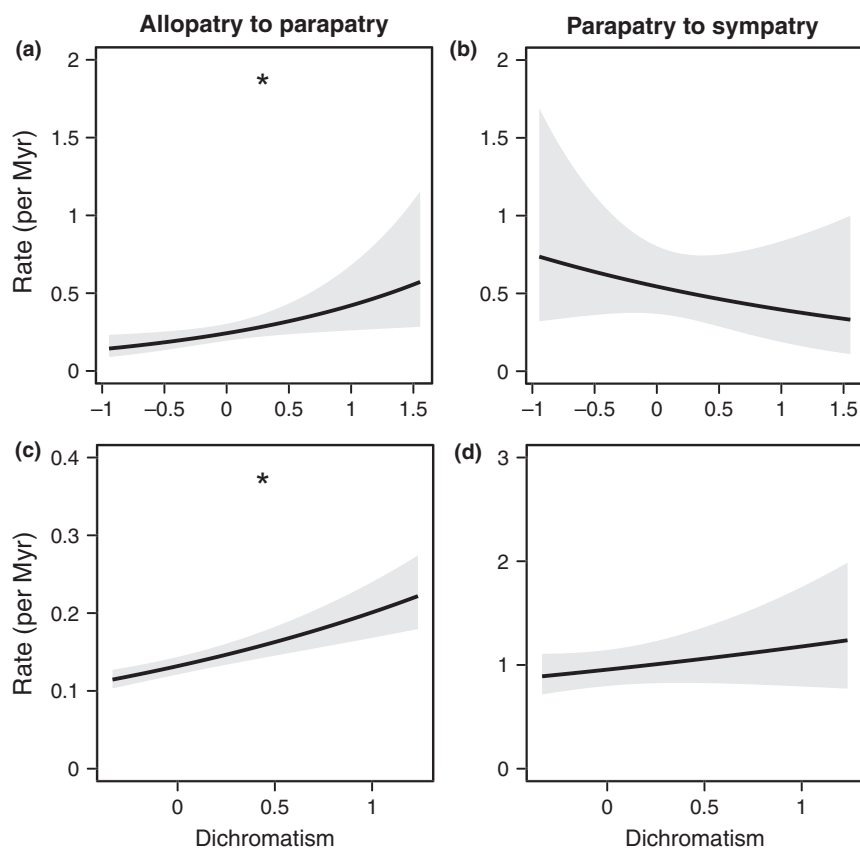
**Table 2** Models of the relationship between parapatry and sympatry rate and sexual dichromatism across sister pairs of birds using alternative range overlap thresholds to assign parapatry and sympatry

Thresholds (%; para/sym)	$N$ (allo/para/sym)	Parameter	Hazard ratio [95% CI]	$\Delta$ AICc
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.  $\Delta$ AICc values quantify the improvement in model fit (positive values) compared to constant-rate models. Asterisks (\*) denote significant ( $\alpha = 0.05$ )  $\Delta$ AICc values compared to null expectations. allo = allopatric; para = parapatric; sym = sympatric; ap = allopatry to parapatry; ps = parapatry to sympatry.

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



**Figure 2** The effect of dichromatism on rates of transition from allopatry to parapatry (a and c) and parapatry to sympatry (b and d) based on spectrophotometric (a and b) and visual (c and 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).

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 & 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 time-scales. For instance, if extinction was 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 & 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 & 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 & 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 co-existence 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 & Green 2000; Pfenig & 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 & 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 & 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, 2015; Delmore *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 & 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 & 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 non-existent) 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 & Hochkirch 2008; Weber & 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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## AUTHOR CONTRIBUTIONS

All authors developed the conceptual framework. C.R.C. collected data and conducted the analyses. C.R.C., J.A.T. and N.S. wrote the manuscript, with input from all authors.

## REFERENCES

- Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.
- Badyaev, A.V. & Hill, G.E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Evol. Syst.*, 34, 27–49.
- Barracough, T.G., Harvey, P.H. & Nee, S. (1995). Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. London Ser. B*, 259, 211–215.
- Bloch, N.I. (2015). Evolution of opsin expression in birds driven by sexual selection and habitat. *Proc. R. Soc. London Ser. B*, 282, 20142321.
- Butlin, R., Debelle, A., Kerth, C., Snook, R.R., Beukeboom, L.W., Castillo Cajas, R.F. *et al.* (2012). What do we need to know about speciation?. *Trends Ecol. Evol.*, 27, 27–39.
- Coyne, J.A. & Orr, H.A. (1989). Patterns of speciation in *Drosophila*. *Evolution*, 43, 362–381.
- Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinauer, Sunderland, MA.
- Dale, J., Dey, C.J., Delhey, K., Kempnaers, B. & Valcu, M. (2015). The effects of life history and sexual selection on male and female plumage colouration. *Nature*, 527, 367–370.
- Darwin, C.R. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray, London, UK.
- Delmore, K.E., Kenyon, H.L., Germain, R.R. & Irwin, D.E. (2015). Phenotypic divergence during speciation is inversely associated with differences in seasonal migration. *Proc. R. Soc. London Ser. B*, 282, 20151921.
- Diamond, J.M. (1975). Assembly of species communities. In *Ecology and Evolution of Communities* (eds Cody, M.L., Diamond, J.M.). Harvard University Press, Cambridge, MA, pp. 342–444.
- Dobzhansky, T. (1937). *Genetics and the Origin of Species*. Columbia University Press, New York, NY.
- van Doorn, G.S., Edelaar, P. & Weissing, F.J. (2009). On the origin of species by natural and sexual selection. *Science*, 326, 1704–1707.
- Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, 55, 161–175.
- Dunn, P.O., Armenta, J.K. & Whittingham, L.A. (2015). Natural and sexual selection act on different axes of variation in avian plumage color. *Sci. Advances*, 1, e1400155.
- Edwards, S.V., Kingan, S.B., Calkins, J.D., Balakrishnan, C.N., Jennings, W.B., Swanson, W.J. *et al.* (2005). Speciation in birds: genes, geography, and sexual selection. *Proc. Natl Acad. Sci. USA*, 102, 6550–6557.
- Figuerola, J. & Green, A.J. (2000). The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.*, 14, 701–710.
- Grant, P.R. & Grant, B.R. (2008). *How and Why Species Multiply: the Radiation of Darwin's Finches*. Princeton University Press, Princeton, NJ.
- Gröning, J. & Hochkirch, A. (2008). Reproductive interference between animal species. *Q. Rev. Biol.*, 83, 257–282.
- del Hoyo, J., Elliott, A., Sargatal, J. & Christie, D.A. 1992–2011. *The Handbook of the Birds of the World, vols 1–16*. Lynx Edicions, Barcelona.
- Huang, H. & Rabosky, D.L. (2014). Sexual selection and diversification: reexamining the correlation between dichromatism and speciation rate in birds. *Am. Nat.*, 184, E101–E114.
- Hudson, E.J. & Price, T.D. (2014). Pervasive reinforcement and the role of sexual selection in biological speciation. *J. Hered.*, 105, 821–833.
- Hurlbert, A.H. & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl Acad. Sci. USA*, 104, 13384–13389.
- Irwin, D.E. (2000). Song variation in an avian ring species. *Evolution*, 54, 998–1010.
- Jackson, C.H. (2011). Multi-state models for panel data: the msm package for R. *J. Stat. Softw.*, 38, 1–28.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448.
- Johnson, K.P. & Lanyon, S.M. (2000). Evolutionary changes in color patches of blackbirds are associated with marsh nesting. *Behav. Ecol.*, 11, 515–519.
- Kraaijeveld, K., Kraaijeveld-Smit, F.J.L. & Maan, M.E. (2011). Sexual selection and speciation: the comparative evidence revisited. *Biol. Rev. Camb. Philos. Soc.*, 86, 367–377.
- Krüger, O. (2008). Engines of speciation: a comparative study in birds of prey. *J. Evol. Biol.*, 21, 861–872.
- Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA*, 78, 3721–3725.
- Lawson, A.M. & Weir, J.T. (2014). Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecol. Lett.*, 17, 1427–1436.
- Losos, J.B. (2011). Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *Am. Nat.*, 177, 709–727.
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distributions of Species*. Harper and Row, New York, NY.
- Martin, P.R., Montgomerie, R. & Loughheed, S.C. (2010). Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution*, 64, 336–347.
- Martin, P.R., Montgomerie, R. & Loughheed, S.C. (2015). Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *Am. Nat.*, 185, 443–451.
- Mayr, E. (1942). *Systematics and the Origin of Species*. Cambridge University Press, New York, NY.
- M'Gonigle, L.K., Mazzucco, R., Otto, S.P. & Dieckmann, U. (2012). Sexual selection enables long-term coexistence despite ecological equivalence. *Nature*, 484, 506–509.
- Misof, B. (2002). Diversity of Anisoptera (Odonata): inferring speciation processes from patterns of morphological diversity. *Zoology*, 105, 355–365.
- Morrow, E.H., Pitcher, T.E. & Arnqvist, G. (2003). No evidence that sexual selection is an 'engine of speciation' in birds. *Ecol. Lett.*, 6, 228–234.
- Noor, M.A.F. (1999). Reinforcement and other consequences of sympatry. *Heredity*, 83, 503–508.
- Orme, C.D.L., Freckleton, R.P., Thomas, G.H., Petzoldt, T., Fritz, S.A., Isaac, N. *et al.* 2013. Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. <http://CRAN.R-project.org/package=caper>.



- Owens, I.P.F. & Hartley, I.R. (1998). Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. London Ser. B*, 265, 397–407.
- Owens, I.P.F., Bennett, P.M. & Harvey, P.H. (1999). Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. London Ser. B*, 266, 933–939.
- Panhuis, T.M., Butlin, R., Zuk, M. & Tregenza, T. (2001). Sexual selection and speciation. *Trends Ecol. Evol.*, 16, 364–371.
- Pfennig, K.S. & Hurlbert, A.H. (2012). Heterospecific interactions and the proliferation of sexually dimorphic traits. *Curr. Zool.*, 58, 453–462.
- Phillimore, A.B., Freckleton, R.P., Orme, C.D.L. & Owens, I.P.F. (2006). Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat.*, 168, 220–229.
- Phillimore, A.B., Orme, C.D.L., Thomas, G.H., Blackburn, T.M., Bennett, P.M., Gaston, K.J. *et al.* (2008). Sympatric speciation in birds is rare: insights from range data and simulations. *Am. Nat.*, 171, 646–657.
- Pigot, A.L. & Tobias, J.A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecol. Lett.*, 16, 330–338.
- Pigot, A.L. & Tobias, J.A. (2015). Dispersal and the transition to sympatry in vertebrates. *Proc. R. Soc. London Ser. B*, 282, 20141929.
- Pigot, A.L., Tobias, J.A. & Jetz, W. (2016). Energetic constraints on species coexistence in birds. *PLoS Biol.*, 14, e1002407.
- Price, T. (1998). Sexual selection and natural selection in bird speciation. *Philos. Trans. R. Soc. London Ser. B*, 353, 251–260.
- Price, T.D. (2008). *Speciation in Birds*. Roberts and Co., Greenwood Village CO.
- Price, J.J. & Eaton, M.D. (2014). Reconstructing the evolution of sexual dichromatism: current color diversity does not reflect past rates of male and female change. *Evolution*, 68, 2026–2037.
- Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P. *et al.* (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, 509, 222–225.
- Rabosky, D.L. (2006). Likelihood methods for detecting temporal shifts in diversification rates. *Evolution*, 60, 1152–1164.
- Rabosky, D.L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution*, 64, 1816–1824.
- Ritchie, M.G. (2007). Sexual selection and speciation. *Annu. Rev. Ecol. Syst.*, 38, 79–102.
- Rosenblum, E.B., Sarver, B.A.J., Brown, J.W., Des Roches, S., Hardwick, K.M., Hether, T.D. *et al.* (2012). Goldilocks meets Santa Rosalia: an ephemeral speciation model explains patterns of diversification across time scales. *Evol. Biol.*, 39, 255–261.
- Seddon, N., Merrill, R.M. & Tobias, J.A. (2008). Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *Am. Nat.*, 171, 620–631.
- Seddon, N., Botero, C.A., Tobias, J.A., Dunn, P.O., Macgregor, H.E., Rubenstein, D.R. *et al.* (2013). Sexual selection accelerates signal evolution during speciation in birds. *Proc. R. Soc. London Ser. B*, 280, 20131065.
- Servedio, M.R. & Bürger, R. (2014). The counterintuitive role of sexual selection in species maintenance and speciation. *Proc. Natl Acad. Sci. USA*, 111, 8113–8118.
- Sobel, J.M., Chen, G.F., Watt, L.R. & Schemske, D.W. (2010). The biology of speciation. *Evolution*, 64, 295–315.
- Sol, D., Stirling, D.G. & Lefebvre, L. (2005). Behavioural drive or behavioural inhibition in evolution: subspecific diversification in Holarctic passerines. *Evolution*, 59, 2669–2677.
- Stuart-Fox, D. & Owens, I.P.F. (2003). Species richness in agamid lizards: chance, body size, sexual selection or ecology? *J. Evol. Biol.*, 16, 659–669.
- Tobias, J.A., Montgomerie, R. & Lyon, B.E. (2012). The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philos. Trans. R. Soc. London Ser. B*, 367, 2274–2293.
- Tobias, J.A., Cornwallis, C.K., Derryberry, E.P., Claramunt, S., Brumfield, R.T. & Seddon, N. (2014). Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, 506, 359–363.
- Wagner, C.E., Harmon, L.J. & Seehausen, O. (2012). Ecological opportunity and sexual selection together predict adaptive radiation. *Nature*, 487, 366–370.
- Weber, M.G. & Strauss, S.Y. (2016). Coexistence in close relatives: beyond competition and reproductive isolation in sister taxa. *Annu. Rev. Ecol. Syst.*, 47, 359–381.
- Weir, J.T. & Price, T.D. (2011). Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *Am. Nat.*, 177, 462–469.
- Weir, J.T. & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, 315, 1574–1576.
- West-Eberhard, M.J. (1983). Sexual selection, social competition, and speciation. *Q. Rev. Biol.*, 58, 155–183.
- Wiens, J.J. (2001). Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends Ecol. Evol.*, 16, 517–523.

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