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

3
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33

34 **Abstract**

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

47

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

50

51

52 **Introduction**

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

65 Because of its propensity to stimulate the rapid evolution of phenotypic traits, sexual
66 selection has long been recognised as a positive diversifying force (Darwin 1871; West-
67 Eberhard 1983; Andersson 1994; Panhuis et al. 2001). In particular, by driving the evolution of
68 traits involved in mate choice and species recognition (Lande 1981; Seddon et al. 2013), sexual
69 selection could accelerate progression through stages of the speciation cycle, firstly by
70 generating substantial reproductive isolation between lineages diverging in allopatry (Price 1998;
71 Panhuis et al. 2001), and secondly by maintaining and/or strengthening isolating barriers when
72 species ranges expand into sympatry (Gröning and Hochkirch 2008; Hudson and Price 2014;
73 Weber and Strauss 2016). Despite these expectations, empirical support for a general coupling
74 between sexual selection and diversification rates is surprisingly weak, and highly inconsistent
75 both within and among taxonomic groups (Kraaijeveld et al. 2011). For instance, most
76 comparative work has focused on birds, where the correlation between proxies of sexual
77 selection and speciation rates are sometimes positive (Barraclough et al. 1995; Owens et al.
78 1999; Seddon et al. 2008) but just as often not (Morrow et al. 2003; Phillimore et al. 2006;
79 Huang and Rabosky 2014).

80 Compared with rates of speciation, the connection between sexual selection and the
81 establishment of geographic range overlap has received far less attention. This is partly because
82 sexual selection (in isolation) seems unlikely to facilitate substantial range overlap because it
83 tends to produce allospecies with divergent mating signals yet similar morphology, leaving in
84 place the ecological barriers to co-existence associated with niche similarity and interspecific
85 competition (Price 1998). However, an alternative view is that sexual selection may accelerate
86 the initial establishment of range overlap by maintaining and/or strengthening reproductive
87 isolation, thereby allowing young lineages to avoid 'fusion' following secondary contact (Noor
88 1999). Indeed, theoretical studies (e.g. van Doorn et al. 2009; M'Gonigle et al. 2012) suggest

89 that sexual selection may play a general role in reducing the costs associated with reproductive
90 interference (Gröning and Hochkirch 2008; Weber and Strauss 2016) thus facilitating more
91 extensive sympatry between young lineages. However, direct comparative tests of these ideas
92 are lacking, and the extent to which sexual selection promotes (or impedes) range overlap
93 among species is unknown (Price 2008).

94 Uncertainty over the role of sexual selection in speciation processes is also exacerbated
95 by the variable results generated by different methodological approaches. For instance, studies
96 testing the link between sexual selection and diversification using comparisons among deeper
97 (i.e. older) phylogenetic nodes, such as those between genera and families, tend to yield weaker
98 effects (Kraaijeveld et al. 2011). This suggests that the signature of sexual selection in
99 diversification processes may fade over time (Kraaijeveld et al. 2011), possibly due to the
100 confounding effect of extinction over longer evolutionary timescales (Rabosky 2010) and/or
101 fluctuations in the strength of sexual selection as clade diversification progresses (Wiens 2001;
102 Badyaev and Hill 2003; Price and Eaton 2014). Regardless of the underlying explanation, it
103 seems plausible that clade-based studies comparing across deep timescales (e.g. Morrow et al.
104 2003; Phillimore et al. 2006; Huang and Rabosky 2014) may underestimate the role of sexual
105 selection in speciation (Kraaijeveld et al. 2011).

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

117 If sexual selection accelerates the formation of new species (prediction 1), we expect
118 sister pairs experiencing strong sexual selection to be associated with (i) more recent
119 divergence times (i.e. younger evolutionary age), and (ii) faster rates of speciation. Similarly, if
120 sexual selection plays an important role in facilitating range overlap among close relatives, we
121 expect sister pairs experiencing strong sexual selection to be associated with (i) accelerated
122 rates of transition from allopatric to parapatric/sympatric distributions, and (ii) for this effect to
123 remain after accounting for other potentially important factors (e.g. geographical realm, latitude,
124 body size, dispersal). Birds provide an ideal system in which to conduct these tests as they are a
125 well-studied group with comprehensive data on phylogeny, ecology and biogeography, and

126 because avian plumage dichromatism—the difference in colouration of males and females of the
127 same species—is a relatively robust and commonly used proxy for the degree of sexual
128 selection (Owens and Hartley 1998; Dunn et al. 2001; Dale et al. 2015; Dunn et al. 2015).

129

130 **Materials and methods**

131 SISTER SPECIES DATASETS

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

140

141 QUANTIFYING SEXUAL DICHROMATISM

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

151 A key assumption underlying our analyses is that sexual dichromatism is a valid proxy for
152 the intensity of sexual selection in birds. Evidence supporting this comes from a number of
153 broad-scale studies that reveal strong positive relationships between dichromatism and other
154 indices of sexual selection such as testes size, the degree of polygyny and the frequency of
155 extra-pair paternity (Owens and Hartley 1998; Dunn et al. 2001; Dale et al. 2015; Dunn et al.
156 2015). As a consequence, dichromatism is widely used as a standard proxy for sexual selection
157 in birds (e.g. Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Sol et al. 2005;
158 Phillimore et al. 2006; Krüger 2008; Seddon et al. 2008; Bloch 2015), as well as other taxa
159 including lizards (e.g. Stuart-Fox and Owens 2003), insects (e.g. Misof 2002) and fish (e.g.
160 Wagner et al. 2012). We note, however, that the use of sexual dichromatism as a proxy for
161 sexual selection is subject to a number of important caveats. For example, sexual dichromatism
162 and sexual selection are likely to be only partially correlated, not least because other

163 mechanisms can influence patterns of sex-differences in plumage colouration, such as natural
164 selection for female crypsis in species with female-only incubation (Badyaev and Hill 2003) or
165 social selection on females to signal quality in the context of male mate choice or female-female
166 competition (Tobias et al. 2012). In addition, sexual dichromatism may only provide a lower
167 bound estimate of the overall intensity of sexual selection. This is because of potential trade-offs
168 between signalling modalities (Darwin 1871), where investment in one signalling modality (e.g.
169 visual signals) constrains elaboration in another (e.g. acoustic signals). While it would therefore
170 be preferable to compare direct measures of sexual selection from detailed studies of behaviour
171 or reproduction, these estimates are lacking for large numbers of species. Thus, we conclude
172 that dichromatism is the best proxy currently available for the purposes of broad-scale
173 comparative analyses, and also that our analysis is likely to underestimate the effects of sexual
174 selection on rates of diversification and range overlap, rather than exaggerate them.

175

176 QUANTIFYING RANGE OVERLAP

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

197

198 ADDITIONAL PREDICTORS OF SYMPATRY RATE

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

214

215 ESTIMATING RATES OF SPECIATION AND EXTINCTION

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

233 We compared the fit of a two-parameter model in which all sister pairs had a single rate
234 of speciation and extinction, to models that allowed speciation rate and/or extinction rate to
235 change linearly with increasing dichromatism (i.e. three or four parameter models with one or

236 two slopes and two intercepts, respectively). All models estimated a single lag time parameter
237 (i.e. one additional parameter), which for simplicity was assumed not to vary with increasing
238 sexual dichromatism (Seddon et al. 2013). To infer the significance of slope estimates we used
239 likelihood ratio tests (LRTs) and ΔAICc scores interpreted with reference to the results of
240 simulations tests designed to control for elevated rates of Type I error (see below). To provide
241 an alternative test of the link between sexual dichromatism and diversification, we also used
242 PGLS models (implemented in the 'caper' R package; Orme et al. 2013) to assess the raw
243 relationship between dichromatism and sister pair age.

244

245 ESTIMATING RATES OF PARAPATRY/SYMPATRY

246 To test the link between sexual selection and rates of geographic range overlap, we used a
247 modeling approach based on continuous time multi-state Markov models (Pigot and Tobias
248 2013, 2015; Pigot et al. 2016). In this approach, each sister pair contributes two observations:
249 the geographic state at the time of population divergence and that of the present day. Here we
250 assume that sister species originated in allopatry (first observation) based on substantial
251 evidence that allopatric speciation is the predominant mode of speciation across all organisms
252 (Coyne and Orr 2004) and especially for birds (Phillimore et al. 2008; Price 2008). We
253 considered two model types with alternative sets of possible states for present day distributions.
254 In the first, pairs could take one of two possible secondary states, either allopatric and sympatric.
255 In the second this was extended to three possible secondary states, either allopatric, parapatric
256 or sympatric (see above). Separately for both datasets 1 and 2, we used maximum likelihood to
257 estimate the rate (per million years; [Myr]) at which species pairs transition from either allopatry
258 to sympatry (model 1) or allopatry to parapatry and parapatry to sympatry (model 2). For
259 simplicity, we modelled this as a one-way process in which transitions from allopatry to sympatry
260 (via parapatry) are irreversible. A detailed description of the modeling approach can be found in
261 (Pigot and Tobias 2013).

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

268

269 SIMULATION TESTS

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

273 ΔAICc values derived from fits to simulated datasets to identify critical values required to
274 maintain a Type I error rate of $\alpha = 0.05$ (Rabosky 2006; Lawson and Weir 2014). We simulated
275 100 null datasets for each dichromatism dataset using BM models of trait evolution fit to pair-
276 level trees, and then tested both constant- and variable-rate models. By simulating data under
277 the null hypothesis of rate-constancy, we can confidently reject the constant-rate model (with a
278 Type I error rate ≤ 0.05) if the ΔAICc for a particular parameter is greater than the appropriate
279 critical value (Rabosky 2006). Critical values correspond to the 95th percentile of the null ΔAICc
280 distribution and values vary depending on the model and parameter in question (Table S2).

281

282 **Results**

283 SEXUAL SELECTION AND RECENT RATES OF SPECIATION AND EXTINCTION

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

300

301 RATES OF TRANSITION INTO PARAPATRY/SYMPATRY

302 In support of the hypothesis that sexual selection facilitates secondary contact between closely
303 related bird species, we found positive associations between dichromatism and the rate at which
304 sister species achieve geographic range overlap. First, by categorizing pairs as either allopatric
305 or sympatric, we found robust support for positive associations between dichromatism and
306 sympatry rate in both dataset 1 and 2 when using relaxed definitions of sympatry (i.e. range
307 overlap thresholds 0-20%; Table S5). However, under more stringent definitions of sympatry (i.e.
308 range overlap thresholds 30-80%), there were no significant associations between dichromatism
309 and the rate at which sister pairs achieve sympatry (Table S5). Second, using an alternative

310 approach in which pairs were categorized as allopatric, parapatric or sympatric, we found robust
311 support in both datasets 1 and 2 for a positive relationship between dichromatism and the rate at
312 which sister species achieve narrow (i.e. parapatric) but not extensive (i.e. sympatric)
313 geographic range overlap (Table 2; Fig. 2). Dichromatic sister species are inferred to become
314 parapatric 2-4 times faster than monochromatic sisters (Table 2, Fig. 2a,c). In contrast,
315 dichromatism did not significantly predict the rate at which sister species transition from
316 parapatric distributions to more extensive levels of sympatry (Table 2, Fig. 2b,d). In all cases,
317 results were similar when we re-ran our analyses on 100 replicate trees (Table S6 and S7).

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

329

330 **Discussion**

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

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

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

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

377 We tested this possibility by assessing whether sexual selection was associated with
378 rates of transition to sympatry or merely to parapatry, finding strong support for the hypothesis
379 that sexual selection plays a role in shaping patterns of geographic range overlap in birds.
380 Specifically, we found that dichromatism was positively correlated with the rate at which sister
381 species became parapatric (i.e. only narrowly sympatric), such that highly dichromatic sister
382 pairs achieved parapatry 2-4 times faster than more monochromatic sister pairs. This positive
383 effect on range overlap rate was consistent across two independent dichromatism datasets that

384 differed in taxonomic scope and the method used to quantify dichromatism. Although this
385 relationship has not previously been directly assessed, compatible findings have been reported
386 in particular avian clades, including the waterfowl (Anseriformes) and New World warblers
387 (Parulidae), where dichromatism (and bright male plumage) is associated with increased
388 sympatric diversity among closely related species (Figuerola and Green 2000; Pfennig and
389 Hurlbert 2012). An alternative possibility is that dichromatism (our proxy for sexual selection) co-
390 varies with a variety of ecological, behavioural and biogeographic factors (Badyaev and Hill
391 2003; Dale et al. 2015; Dunn et al. 2015), many of which could explain correlations between
392 dichromatism and rates of range overlap. However, we found no support for this idea when we
393 included a suite of such variables (latitude, migration, territoriality, body size and geographic
394 realm) in our models, as none explained the key association. We conclude that the link between
395 dichromatism and rates of achieving parapatry is not attributable to shared correlations with
396 confounding factors.

397 A positive correlation between dichromatism and rates of achieving narrow range overlap
398 may arise because sexual selection reduces the likelihood of young lineages collapsing back
399 into single species following the onset of secondary contact. Termed ‘differential fusion’, this
400 hypothesis predicts that only species with strong mating discrimination (i.e. pre-mating isolation)
401 persist after secondary contact, while populations lacking such discrimination frequently fuse
402 through hybridisation and gene flow (Noor 1999). Differential fusion does not necessarily rely on
403 sexual selection influencing the underlying rate at which lineages come into contact, but merely
404 accelerating the evolution of traits important for pre-mating isolation (Seddon et al. 2013) and
405 thus increasing the likelihood of remaining distinct following secondary contact (Edwards et al.
406 2005; Hudson and Price 2014). The pattern we detect of reduced average waiting times to
407 parapatry in dichromatic lineages may therefore be produced by elevated rates of fusion in
408 young monochromatic lineages after secondary contact. Coyne and Orr (1989) argued against
409 the importance of differential fusion for understanding speciation in *Drosophila*, but recent work
410 examining patterns of mating signal divergence and range overlap in birds (Martin et al. 2010;
411 Delmore et al. 2015; Martin et al. 2015) suggests that differential fusion may play a more
412 important role than currently appreciated.

413 Differential fusion is relevant to secondary contact in parapatric lineages with narrow
414 range overlap, but wider spatial overlap between incipient lineages is theoretically less
415 dependent on reproductive isolation. In this case, our results clearly indicate that the positive
416 influence of sexual selection does not result in more extensive levels of sympatry. In particular,
417 we found that transition rates from allopatry (or parapatry) to more substantial levels of range
418 overlap (i.e. 30-80%) were unrelated to levels of dichromatism across pairs. The most likely
419 explanation for this pattern is that, while divergent sexual selection may generate sufficient
420 reproductive isolation between lineages to prevent complete fusion, sister species must still

421 overcome ecological barriers to sympatry, such as niche similarity and resource competition,
422 which are likely to represent particularly important barriers to range expansions among close
423 relatives (Pigot and Tobias 2013; Price et al. 2014). Thus, while sexual selection appears to
424 promote the initial establishment of contact and minor overlap between species ranges, our
425 results are consistent with the view that ecological rather than sexual interactions are more
426 important in determining transitions to more extensive levels of species co-existence (Sobel et
427 al. 2010).

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

440 Taken together, our results add a further dimension to the well-established view that
441 biotic interactions limit range expansion and species co-existence (MacArthur 1972; Diamond
442 1975) by providing comparative evidence that the initial stages of range overlap are likely to be
443 constrained by fitness costs associated with sexual as well as ecological interactions between
444 species (Gröning and Hochkirch 2008; Weber and Strauss 2016). Thus, while sexual selection
445 may accelerate the establishment of (narrow) range overlap among sister species, it plays a
446 more limited role in driving the formation of new lineages or promoting the type of large-scale
447 range expansions required for repeated rounds of speciation. Our study therefore provides a
448 more mechanistic explanation for the general observation that sexual selection (in isolation)
449 plays a seemingly limited role in explaining broad-scale patterns of diversification (Kraaijeveld et
450 al. 2011).

451

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459

460 **References**

- 461 Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton.
- 462 Badyaev, A. V. and G. E. Hill. 2003. Avian sexual dichromatism in relation to phylogeny and ecology.
463 *Annu. Rev. Ecol. Evol. Syst.* 34:27-49.
- 464 Barraclough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in
465 passerine birds. *Proc. R. Soc. London Ser. B* 259:211-215.
- 466 Bloch, N. I. 2015. Evolution of opsin expression in birds driven by sexual selection and habitat. *Proc.*
467 *R. Soc. London Ser. B* 282:20142321.
- 468 Butlin, R., A. DeBelle, C. Kerth, R. R. Snook, L. W. Beukeboom, R. F. Castillo Cajas, W. Diao, M. E. Maan,
469 S. Paolucci, F. J. Weissing, L. van de Zande, A. Hoikkala, E. Geuverink, J. Jennings, M. Kankare,
470 K. E. Knott, V. I. Tyukmaeva, C. Zoumadakis, M. G. Ritchie, D. Barker, E. Immonen, M.
471 Kirkpatrick, M. Noor, C. Macias Garcia, T. Schmitt, and M. Schilthuizen. 2012. What do we
472 need to know about speciation? *Trends Ecol. Evol.* 27:27-39.
- 473 Coyne, J. A. and H. A. Orr. 2004. Speciation. Sinauer, Sunderland, MA.
- 474 Dale, J., C. J. Dey, K. Delhey, B. Kempnaers, and M. Valcu. 2015. The effects of life history and sexual
475 selection on male and female plumage colouration. *Nature* 527:367-370.
- 476 Darwin, C. R. 1871. The descent of man, and selection in relation to sex. John Murray, London, UK.
- 477 del Hoyo, J., A. Elliott, J. Sargatal, and D. A. Christie. 1992–2011. The Handbook of the Birds of the
478 World, vols 1-16. Lynx Edicions, Barcelona.
- 479 Delmore, K. E., H. L. Kenyon, R. R. Germain, and D. E. Irwin. 2015. Phenotypic divergence during
480 speciation is inversely associated with differences in seasonal migration. *Proc. R. Soc.*
481 *London Ser. B* 282:20151921.
- 482 Diamond, J. M. 1975. Assembly of species communities *in* M. L. Cody, and J. M. Diamond, eds. *Ecology*
483 *and Evolution of Communities*. Harvard University Press, Cambridge, MA.
- 484 Dobzhansky, T. 1937. Genetics and the origin of species. Columbia University Press, New York, NY.
- 485 Dunn, P. O., J. K. Armenta, and L. A. Whittingham. 2015. Natural and sexual selection act on different
486 axes of variation in avian plumage color. *Science Advances* 1:e1400155.
- 487 Dunn, P. O., L. A. Whittingham, and T. E. Pitcher. 2001. Mating systems, sperm competition, and the
488 evolution of sexual dimorphism in birds. *Evolution* 55:161-175.
- 489 Edwards, S. V., S. B. Kingan, J. D. Calkins, C. N. Balakrishnan, W. B. Jennings, W. J. Swanson, and M. D.
490 Sorenson. 2005. Speciation in birds: genes, geography, and sexual selection. *Proc. Natl. Acad.*
491 *Sci. U.S.A.* 102:6550-6557.
- 492 Figuerola, J. and A. J. Green. 2000. The evolution of sexual dimorphism in relation to mating
493 patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.* 14:701-
494 710.
- 495 Grant, P. R. and B. R. Grant. 2008. How and why species multiply: the radiation of Darwin's finches.
496 Princeton University Press, Princeton, NJ.
- 497 Gröning, J. and A. Hochkirch. 2008. Reproductive interference between animal species. *Q. Rev. Biol.*
498 83:257-282.
- 499 Huang, H. and D. L. Rabosky. 2014. Sexual selection and diversification: reexamining the correlation
500 between dichromatism and speciation rate in birds. *Am. Nat.* 184:E101-E114.
- 501 Hudson, E. J. and T. D. Price. 2014. Pervasive reinforcement and the role of sexual selection in
502 biological speciation. *J. Hered.* 105:821-833.
- 503 Hurlbert, A. H. and W. Jetz. 2007. Species richness, hotspots, and the scale dependence of range
504 maps in ecology and conservation. *Proc. Natl. Acad. Sci. U.S.A.* 104:13384-13389.
- 505 Irwin, D. E. 2000. Song variation in an avian ring species. *Evolution* 54:998-1010.
- 506 Jackson, C. H. 2011. Multi-state models for panel data: the msm package for R. *Journal of Statistical*
507 *Software* 38:1-28.

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

510 Johnson, K. P. and S. M. Lanyon. 2000. Evolutionary changes in color patches of blackbirds are
511 associated with marsh nesting. *Behav. Ecol.* 11:515-519.

512 Kraaijeveld, K., F. J. L. Kraaijeveld-Smit, and M. E. Maan. 2011. Sexual selection and speciation: the
513 comparative evidence revisited. *Biol. Rev. Camb. Philos. Soc.* 86:367-377.

514 Krüger, O. 2008. Engines of speciation: a comparative study in birds of prey. *J. Evol. Biol.* 21:861-
515 872.

516 Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci.*
517 U.S.A. 78:3721-3725.

518 Lawson, A. M. and J. T. Weir. 2014. Latitudinal gradients in climatic-niche evolution accelerate trait
519 evolution at high latitudes. *Ecol. Lett.* 17:1427-1436.

520 Losos, J. B. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative
521 biology. *Am. Nat.* 177:709-727.

522 M'Gonigle, L. K., R. Mazzucco, S. P. Otto, and U. Dieckmann. 2012. Sexual selection enables long-term
523 coexistence despite ecological equivalence. *Nature* 484:506-509.

524 MacArthur, R. H. 1972. *Geographical ecology: patterns in the distributions of species.* Harper and
525 Row, New York, NY.

526 Martin, P. R., R. Montgomerie, and S. C. Loughheed. 2010. Rapid sympatry explains greater color
527 pattern divergence in high latitude birds. *Evolution* 64:336-347.

528 Martin, P. R., R. Montgomerie, and S. C. Loughheed. 2015. Color patterns of closely related bird species
529 are more divergent at intermediate levels of breeding-range sympatry. *Am. Nat.* 185:443-
530 451.

531 Mayr, E. 1942. *Systematics and the origin of species.* Cambridge University Press, New York, NY.

532 Misof, B. 2002. Diversity of Anisoptera (Odonata): inferring speciation processes from patterns of
533 morphological diversity. *Zoology* 105:355-365.

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

536 Noor, M. A. F. 1999. Reinforcement and other consequences of sympatry. *Heredity* 83:503-508.

537 Orme, C. D. L., R. P. Freckleton, G. H. Thomas, T. Petzoldt, S. A. Fritz, N. Isaac, and W. D. Pearse. 2013.
538 *Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2.*
539 <http://CRAN.R-project.org/package=caper>.

540 Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life
541 history, sexual selection or ecology? *Proc. R. Soc. London Ser. B* 266:933-939.

542 Owens, I. P. F. and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different
543 forms of dimorphism? *Proc. R. Soc. London Ser. B* 265:397-407.

544 Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza. 2001. Sexual selection and speciation. *Trends Ecol.*
545 *Evol.* 16:364-371.

546 Pfennig, K. S. and A. H. Hurlbert. 2012. Heterospecific interactions and the proliferation of sexually
547 dimorphic traits. *Current Zoology* 58:453-462.

548 Phillimore, A. B., R. P. Freckleton, C. D. L. Orme, and I. P. F. Owens. 2006. Ecology predicts large-scale
549 patterns of phylogenetic diversification in birds. *Am. Nat.* 168:220-229.

550 Phillimore, A. B., C. D. L. Orme, G. H. Thomas, T. M. Blackburn, P. M. Bennett, K. J. Gaston, and I. P. F.
551 Owens. 2008. Sympatric speciation in birds is rare: insights from range data and
552 simulations. *Am. Nat.* 171:646-657.

553 Pigot, A. L. and J. A. Tobias. 2013. Species interactions constrain geographic range expansion over
554 evolutionary time. *Ecol. Lett.* 16:330-338.

555 Pigot, A. L. and J. A. Tobias. 2015. Dispersal and the transition to sympatry in vertebrates. *Proc. R.*
556 *Soc. London Ser. B* 282:20141929.

557 Pigot, A. L., J. A. Tobias, and W. Jetz. 2016. Energetic constraints on species coexistence in birds. *PLoS*
558 *Biol.* 14:e1002407.

559 Price, J. J. and M. D. Eaton. 2014. Reconstructing the evolution of sexual dichromatism: current color
560 diversity does not reflect past rates of male and female change. *Evolution* 68:2026-2037.

561 Price, T. 1998. Sexual selection and natural selection in bird speciation. *Philos. Trans. R. Soc. London*
562 *Ser. B* 353:251-260.

563 Price, T. D. 2008. *Speciation in birds*. Roberts and Co., Greenwood Village, CO.

564 Price, T. D., D. M. Hooper, C. D. Buchanan, U. S. Johannsson, D. T. Tietze, P. Alström, U. Olsson, M.
565 Ghosh-Harihar, F. Ishtiaq, S. K. Gupta, J. Martens, B. Harr, P. Singh, and D. Mohan. 2014. Niche
566 filling slows the diversification of Himalayan songbirds. *Nature* 509:222-225.

567 Rabosky, D. L. 2006. Likelihood methods for detecting temporal shifts in diversification rates.
568 *Evolution* 60:1152-1164.

569 Rabosky, D. L. 2010. Extinction rates should not be estimated from molecular phylogenies. *Evolution*
570 64:1816-1824.

571 Ritchie, M. G. 2007. Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.* 38:79-102.

572 Rosenblum, E. B., B. A. J. Sarver, J. W. Brown, S. Des Roches, K. M. Hardwick, T. D. Hether, J. M.
573 Eastman, M. W. Pennell, and L. J. Harmon. 2012. Goldilocks meets Santa Rosalia: an
574 ephemeral speciation model explains patterns of diversification across time scales.
575 *Evolutionary Biology* 39:255-261.

576 Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. Macgregor, D. R. Rubenstein, J. A. Uy, J. T. Weir,
577 L. A. Whittingham, and R. J. Safran. 2013. Sexual selection accelerates signal evolution during
578 speciation in birds. *Proc. R. Soc. London Ser. B* 280:20131065.

579 Seddon, N., R. M. Merrill, and J. A. Tobias. 2008. Sexually selected traits predict patterns of species
580 richness in a diverse clade of suboscine birds. *Am. Nat.* 171:620-631.

581 Servedio, M. R. and R. Bürger. 2014. The counterintuitive role of sexual selection in species
582 maintenance and speciation. *Proc. Natl. Acad. Sci. U.S.A.* 111:8113-8118.

583 Sobel, J. M., G. F. Chen, L. R. Watt, and D. W. Schemske. 2010. The biology of speciation. *Evolution*
584 64:295-315.

585 Sol, D., D. G. Stirling, and L. Lefebvre. 2005. Behavioural drive or behavioural inhibition in evolution:
586 subspecific diversification in Holarctic passerines. *Evolution* 59:2669-2677.

587 Stuart-Fox, D. and I. P. F. Owens. 2003. Species richness in agamid lizards: chance, body size, sexual
588 selection or ecology? *J. Evol. Biol.* 16:659-669.

589 Tobias, J. A., C. K. Cornwallis, E. P. Derryberry, S. Claramunt, R. T. Brumfield, and N. Seddon. 2014.
590 Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*
591 506:359-363.

592 Tobias, J. A., R. Montgomerie, and B. E. Lyon. 2012. The evolution of female ornaments and
593 weaponry: social selection, sexual selection and ecological competition. *Philos. Trans. R. Soc.*
594 *London Ser. B* 367:2274-2293.

595 van Doorn, G. S., P. Edelaar, and F. J. Weissing. 2009. On the origin of species by natural and sexual
596 selection. *Science* 326:1704-1707.

597 Wagner, C. E., L. J. Harmon, and O. Seehausen. 2012. Ecological opportunity and sexual selection
598 together predict adaptive radiation. *Nature* 487:366-370.

599 Weber, M. G. and S. Y. Strauss. 2016. Coexistence in close relatives: beyond competition and
600 reproductive isolation in sister taxa. *Annu. Rev. Ecol. Evol. Syst.* 47:359-381.

601 Weir, J. T. and T. D. Price. 2011. Limits to speciation inferred from times to secondary sympatry and
602 ages of hybridizing species along a latitudinal gradient. *Am. Nat.* 177:462-469.

603 Weir, J. T. and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of
604 birds and mammals. *Science* 315:1574-1576.

605 West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 58:155-
606 183.

607 Wiens, J. J. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends*
608 *Ecol. Evol.* 16:517-523.

609

610

611 **Supporting information**

612

613 Additional supporting information may be found in Appendix S1:

614

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

616

617

618 **Figure and table captions**

619

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

623

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

631

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

634

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

638

639

640 **Supplementary figure and table captions**

641

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

648

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

651

652 **Table S2.** Critical $\Delta AICc$ values for models testing the association between diversification and
653 parapatry/sympatry rates and dichromatism across alternative sister pair datasets.

654

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

658

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

661

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

664

665 **Table S6.** Median parameter values for the relationship between sympatry rate and sexual
666 dichromatism (under alternative range overlap thresholds) using datasets of avian sister pairs (n
667 = 1283 – 1321) sampled from 100 posterior trees.

668

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

672

673 **Table S8.** Multi-predictor model of variation in sympatry rate among sister pairs of birds (dataset
674 2; n = 1306) using alternative range overlap thresholds to define sympatry.

675

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

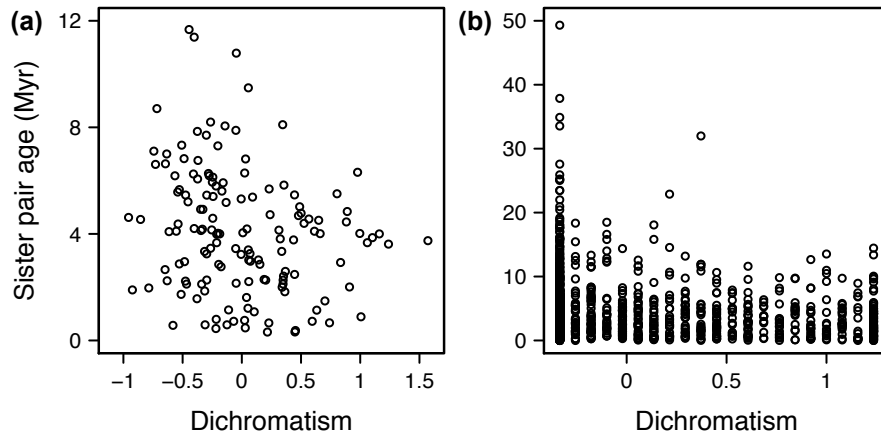


Figure 1. The relationship between pair age and sexual dichromatism across avian sister pairs based on (a) spectrophotometric and (b) human estimates of dichromatism (n = 144 pairs in dataset 1, and 1306 pairs in dataset 2, respectively)

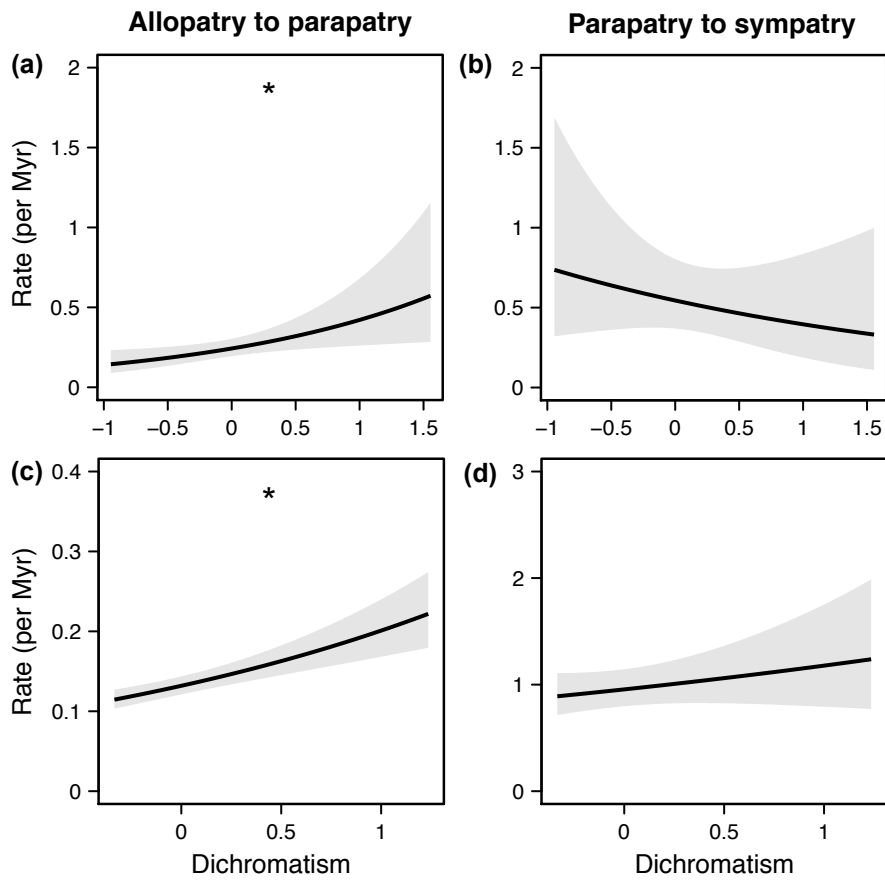


Figure 2. The effect of dichromatism on rates of transition from allopatry to parapatry (a,c) and parapatry to sympatry (b,d) based on spectrophotometric (a,b) and visual (c,d) estimates of dichromatism in avian sister pairs ($n = 140$ pairs in dataset 1, and 1306 pairs in dataset 2, respectively). Plotted 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
<i>Dataset 1</i>		
Speciation intercept	0.06	–
Speciation slope	0.19	3.69
Extinction intercept	0.00	–
Extinction slope	0.01	–2.12
<i>Dataset 2</i>		
Speciation intercept	0.08	–
Speciation slope	0.03	11.19
Extinction intercept	0.01	–
Extinction slope	0.02	–2.84

Δ 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 Δ AICc 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]	Δ AICc
<i>Dataset 1</i>				
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
<i>Dataset 2</i>				
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. Δ AICc values quantify the improvement in model fit (positive values) compared to constant-rate models. Asterisks (*) denote significant ($\alpha = 0.05$) Δ AICc values compared to null expectations. allo = allopatric; para = parapatric; sym = sympatric; ap = allopatry to parapatry; ps = parapatry to sympatry.