

Sexual selection and speciation: the comparative evidence revisited

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(Received 22 December 2009; revised 18 June 2010; accepted 23 June 2010)

ABSTRACT

The spectacular diversity in sexually selected traits in the animal kingdom has inspired the hypothesis that sexual selection can promote species divergence. In recent years, several studies have attempted to test this idea by correlating species richness with estimates of sexual selection across phylogenies. These studies have yielded mixed results and it remains unclear whether the comparative evidence can be taken as generally supportive. Here, we conduct a meta-analysis of the comparative evidence and find a small but significant positive overall correlation between sexual selection and speciation rate. However, we also find that effect size estimates are influenced by methodological choices. Analyses that included deeper phylogenetic nodes yielded weaker correlations, and different proxies for sexual selection showed different relationships with species richness. We discuss the biological and methodological implications of these findings. We argue that progress requires more representative sampling and justification of chosen proxies for sexual selection and speciation rate, as well as more mechanistic approaches.

Key words: diversification, species richness, sexual dimorphism, mating system, meta-analysis, phylogeny.

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I. INTRODUCTION: SEXUAL SELECTION AND SPECIATION

Sexual selection has long been thought to be an important contributing factor to the spectacular diversity in species richness among groups of animals (Darwin, 1859; West-Eberhard, 1983; Panhuis *et al.*, 2001; Ritchie, 2007). This idea is intuitively appealing for two reasons. First, sexually selected traits affect mating patterns and their divergence

could thus immediately reduce interbreeding between incipient species. Second, sexually selected traits tend to show high levels of variation and may diverge relatively fast (West-Eberhard, 1983; Civetta & Singh, 1998). Despite this potential, and the recent research effort directed at testing its predictions, the hypothesis has remained controversial.

Sexual selection may contribute to species richness in various ways. In geographically isolated populations, sexual selection may initiate independent episodes of male-female

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coevolution, resulting in divergence of both the male trait and female preference (Lande, 1981). Unequivocal evidence for divergent male-female coevolution is hard to come by, but several studies have reported observations consistent with such a scenario: rapid evolution of seemingly arbitrary population or species differences in sexually selected traits. For example, allopatric populations of the jumping spider *Habronattus pugillis* in Arizona differ strikingly in both visual and seismic male courtship signals, mediating (partial) reproductive isolation (Masta & Maddison, 2002; Elias *et al.*, 2006). Likewise, populations of the Vogelkop bowerbird *Amblyornis inornatus* in the mountains of Irian Jaya are characterised by distinct bower architectures and associated female preferences, despite only minor genetic differentiation (Uy & Borgia, 2000). Additional evidence comes from studies of sexually antagonistic coevolution. For example, the rapid evolution of reproductive proteins among insects and mammals has been proposed to result from divergent sexual conflict (Rice, 1998; Swanson & Vacquier, 2002).

To some extent, sexual coevolution may proceed independently from ecological conditions. However, sexual traits and preferences are often subject to natural selection, setting the stage for ecologically driven divergence in sexual communication. It is well established, for example, that vegetation structure and ambient noise exert selection on bird song (Slabbekoorn & Smith, 2002) and that fish colours adapt to variation in underwater light environments (Boughman, 2001; Fuller, 2002; Seehausen *et al.*, 2008). Ecological adaptation may also lead to signal divergence as a by-product: dietary specialization changes beak morphology in Darwin's finches, causing changes in song characteristics that may affect mating patterns (Podos, 2001).

Irrespective of the involvement of ecological selection, the hypothesis that sexual selection can drive speciation predicts that any variation in sexual communication can ultimately give rise to pre-mating isolation.

II. EVALUATING THE COMPARATIVE EVIDENCE

One often-used approach to test the role of sexual selection in speciation is comparing patterns of species richness across taxa. If divergent sexual selection promotes speciation, taxa in which sexual selection is important should be relatively species-rich. Indeed, the first notion that sexual selection influences speciation came from comparative evidence. Darwin himself observed that genera with elaborate sexual displays were more species-rich (Darwin, 1871) than those without. After more than a century of relative silence, West-Eberhardt (1983) published an influential paper centred around a similar argument. Starting with Barraclough, Harvey & Nee (1995), the hypothesis was addressed using more formal comparative analyses in a phylogenetic context.

The method of phylogenetically explicit comparative analysis has evolved in recent years. Taking into account possible

effects of common descent, the initial studies used sister-group comparisons. Subsequently, the introduction of new statistical methods allowed more comprehensive analyses, in which not only the most recent diversification events were incorporated, but also deeper phylogenetic nodes (Agapow & Isaac, 2002; Isaac *et al.*, 2003). In contrast to sister-group analysis, incorporating deeper phylogenetic nodes requires assumptions about the model of trait evolution. Most studies assume gradual Brownian trait evolution, although this has been criticised (Freckleton & Harvey, 2006).

Because neither speciation rate nor the strength of sexual selection can practically be measured in large groups of related organisms, comparative studies are forced to use proxies for these parameters. Speciation rate is usually estimated by the number of extant species in a clade (family or genus). In actual fact, the number of extant species per clade measures net diversification rate (the balance of speciation and extinction), and only when time is controlled for in the analysis. The latter can be done by comparing sister groups, which by definition have had an equal amount of time to accumulate species, or by incorporating phylogenetic information. The importance of sexual selection in a given taxon is estimated using a variety of proxies, such as genital size, mating system and dichromatism (colour differences between the sexes). The choice of sexual selection proxy is not trivial, since different traits may reflect different aspects of sexual selection. For example, variation in mating systems may predict the opportunity for mate selectivity, whereas variation in sexual dichromatism may reflect the evolutionary lability of sexual signals. If mate selectivity and signal evolvability affect speciation processes in different ways, then these proxies are not equivalent. One goal of this review is to evaluate the consequences of using different proxies in analyses of speciation patterns.

Ongoing comparative work has generated a body of literature presenting correlative evidence for the relationship between sexual selection and speciation. Some of these studies find strong support for the hypothesis, while others fail to find a pattern (see Table 1). This means that the overall message is currently ambiguous, which allows authors to cite selectively from the available literature. Here, we conduct a meta-analysis of all comparative studies addressing the hypothesis that sexual selection promotes speciation. We estimate an overall effect size (the strength of the relationship between sexual selection and species richness) to provide a quantitative background to the claims and counter-claims that have been made. We estimate the degree to which this overall effect size is affected by publication bias. In addition, we investigate possible explanations for the conflicting results in the comparative literature. In particular, we evaluate how methodological choices influence the findings. As indicated above, analyses may or may not include relatively deep phylogenetic nodes. We also assess whether the different sexual selection proxies yield different results. By evaluating these differences, we hope to inspire more judicious analyses that may further clarify the mechanisms underlying the relationship between sexual selection and species richness.

Table 1. Studies used in the analysis. Test statistics marked with * were calculated from the published data

Taxon (broad)	Taxon (narrow)	Sexual selection proxy	Speciation rate proxy	Phylogenetic nodes incorporated	<i>N</i> (contrasts)	Test statistic	<i>r</i>	Interpretation	Reference
Birds	all birds	mating system	sister-group species number	tips only	14	$P = 0.0725$	0.389	supportive	Mitra <i>et al.</i> (1996)
Birds	all birds	dichromatism	sister-group species number	tips only	68	$r = 0.181^*$	0.181	supportive	Møller & Cuervo (1998)
Birds	all birds	dichromatism	sister-group subspecies number	tips only	68	$r = 0.169^*$	0.169	supportive	Møller & Cuervo (1998)
Birds	all birds	mating system	sister-group species number	tips only	66	$r = -0.138^*$	-0.138	supportive	Møller & Cuervo (1998)
Birds	all birds	mating system	sister-group subspecies number	tips only	66	$r = -0.087^*$	-0.087	supportive	Møller & Cuervo (1998)
Birds	all birds	colonial breeding	sister-group species number	tips only	175	$r = 0.127$	0.101	not supportive	Moors & Møller (1996)
Birds	all birds	size dimorphism	RRD	all nodes	133	$t = -0.79$	-0.069	not supportive	Morrow <i>et al.</i> (2003)
birds	all birds	dichromatism	RRD	all nodes	180	$t = -0.43$	-0.032	not supportive	Morrow <i>et al.</i> (2003)
birds	all birds	testis size	RRD	all nodes	178	$t = 0.38$	0.029	not supportive	Morrow <i>et al.</i> (2003)
birds	all birds	mating system	sister-group species number	tips only	10	$P = 0.62$	0.096	supportive	Owens <i>et al.</i> (1999)
birds	all birds	size dimorphism	sister-group species number	tips only	23	$P = 0.34$	0.086	supportive	Owens <i>et al.</i> (1999)
birds	all birds	dichromatism	sister-group species number	tips only	22	$P = 0.03$	0.401	supportive	Owens <i>et al.</i> (1999)
birds	all birds	dichromatism	speciation rate	all nodes	133	$r^2 = 0.01$	-0.1	not supportive	Phillimore <i>et al.</i> (2006)
birds	antbirds	dichromatism	sister-group species number	tips only	16	$P = 0.033$	0.46	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song pitch and bandwidth	sister-group species number	tips only	17	$P = 0.184$	0.218	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song note types, pace and number	sister-group species number	tips only	17	$P = 0.023$	0.484	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	dichromatism	sister-group subspecies number	tips only	16	$P = 0.004$	0.663	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song pitch and bandwidth	sister-group subspecies number	tips only	17	$P = 0.386$	0.07	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song note types, pace and number	sister-group subspecies number	tips only	17	$P = 0.048$	0.404	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	dichromatism	PDI species	all nodes	51	$t = 2.51$	0.335	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song pitch and bandwidth	PDI species	all nodes	51	$t = 1.33$	0.185	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song note types, pace and number	PDI species	all nodes	51	$t = -0.45$	-0.064	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	dichromatism	PDI subspecies	all nodes	51	$t = 4.21$	0.512	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song pitch and bandwidth	PDI subspecies	all nodes	51	$t = -0.33$	-0.047	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song note types, pace and number	PDI subspecies	all nodes	51	$t = 0.25$	0.035	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	dichromatism	RRD species	all nodes	51	$t = 2.56$	0.34	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song pitch and bandwidth	RRD species	all nodes	51	$t = 0.98$	-0.137	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song note types, pace and number	RRD species	all nodes	51	$t = -0.47$	-0.066	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	dichromatism	RRD subspecies	all nodes	51	$t = 4.39$	0.528	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song pitch and bandwidth	RRD subspecies	all nodes	51	$t = -0.46$	-0.065	supportive	Seddon <i>et al.</i> (2008)
birds	antbirds	song note types, pace and number	RRD subspecies	all nodes	51	$t = 0.29$	0.041	supportive	Seddon <i>et al.</i> (2008)

Table 1. (Cont.)

Taxon (broad)	Taxon (narrow)	Sexual selection proxy	Speciation rate proxy	Phylogenetic nodes incorporated	N (contrasts)	Test statistic	r	Interpretation	Reference
birds	<i>Carduelis</i> spp.	plumage colouration	speciation events per lineage	all nodes	23	$r < 0.21$	0.21	not supportive	Cardoso & Mota (2008)
birds	<i>Carduelis</i> spp.	plumage colouration	terminal branch length	all nodes	23	$r < 0.21$	0.21	not supportive	Cardoso & Mota (2008)
birds	passerines	dichromatism	sister-group species number	tips only	31	$P = 0.05$	0.343	supportive	Barracough <i>et al.</i> (1995)
birds	passerines	dichromatism	subspecies number	all nodes	199	$F = 0.06$	0.0187	not supportive	Sol <i>et al.</i> (2005)
birds	raptors	dichromatism	PDI	all nodes	53	$r = 0.298$	0.298	ambiguous	Kruger (2008)
birds	raptors	mating system	PDI	all nodes	53	$r = 0.348$	0.348	ambiguous	Kruger (2008)
birds	raptors	size dimorphism	PDI	all nodes	53	$r = 0.058$	0.058	ambiguous	Kruger (2008)
fish	goodeid fish	fin shape dimorphism	time to speciation	all nodes	16	sign test 10/16*	0.187	not supportive	Ritchie <i>et al.</i> (2007)
fish	ray-finned fish	composite	sister-group species number	tips only	9	$P = 0.02$	0.685	supportive	Mank (2007)
insects	all insects	mating system	sister-group species number	tips only	25	$t = 2.45$	0.447	supportive	Arngqvist <i>et al.</i> (2000)
insects	Anisoptera	dichromatism	sister-group species number	tips only	8	$P = 0.05$	0.623	supportive	Misof (2002)
insects	butterflies	size dimorphism	species number per genus	tips only	105	$r^2 = 0.004$	0.063	not supportive	Gage <i>et al.</i> (2002)
insects	butterflies	spermatophore count	species number per genus	tips only	53	$r^2 = 0.027$	0.148	not supportive	Gage <i>et al.</i> (2002)
insects	hoverflies	spermathecal width	contrasts in species number	all nodes	41	$t = 1.30$	0.201	supportive	Katzourakis <i>et al.</i> (2001)
insects	hoverflies	testis length	contrasts in species number	all nodes	40	$t = 1.07$	0.169	supportive	Katzourakis <i>et al.</i> (2001)
mammals	all mammals	size dimorphism	contrasts in species number	all nodes	40	$r^2 = 0.002$	0.045	not supportive	Gage <i>et al.</i> (2002)
mammals	all mammals	testes mass	contrasts in species number	all nodes	6	$r^2 = 0.14$	0.374	not supportive	Gage <i>et al.</i> (2002)
mammals	all mammals	size dimorphism	RRD	all nodes	302	$r = 0.006$	0.006	not supportive	Isaac <i>et al.</i> (2005)
mammals	all mammals	size dimorphism	RRD	all nodes	69	$r < 0.001$	0.001	not supportive	Isaac <i>et al.</i> (2005)
mammals	primates	size dimorphism	PDI	all nodes	72	$t = 1.67$	-0.194	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	canine dimorphism	PDI	all nodes	41	$t = 1.13$	-0.176	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	sexual swellings	PDI	all nodes	5	$t = 0.32$	-0.158	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	dichromatism	PDI	all nodes	5	$t = 2.03$	-0.712	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	bright genitalia	PDI	all nodes	7	$t = 1.64$	-0.556	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	size dimorphism	RRD	all nodes	72	$t = 1.60$	-0.187	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	canine dimorphism	RRD	all nodes	41	$t = 1.11$	-0.173	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	sexual swellings	RRD	all nodes	5	$t = 0.53$	-0.256	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	dichromatism	RRD	all nodes	5	$t = 2.06$	-0.718	not supportive	Nunn <i>et al.</i> (2004)
mammals	primates	bright genitalia	RRD	all nodes	7	$t = 1.61$	-0.549	not supportive	Nunn <i>et al.</i> (2004)
reptiles	agamid lizards	size dimorphism	contrasts in species number	all nodes	43	$r^2 = 0.128$	-0.358	supportive	Stuart-Fox & Owens (2003)
reptiles	agamid lizards	dichromatism	contrasts in species number	all nodes	37	$r^2 = 0.123$	0.351	supportive	Stuart-Fox & Owens (2003)
reptiles	agamid lizards	ornament	contrasts in species number	all nodes	49	$r^2 = 0.001$	-0.032	supportive	Stuart-Fox & Owens (2003)
spiders	all spiders	size dimorphism	species number per genus	tips only	130	$r^2 = 0.006$	0.077	not supportive	Gage <i>et al.</i> (2002)

RRD: Relative Rate Difference, PDI: Proportional Dominance Index.

III. DATASET

We searched for primary papers using the *ISI Web of Science* (key words ‘sexual selection’, ‘speciation’, ‘comparative’, ‘mate choice’, ‘diversification’, ‘cladogenesis’, ‘species richness’ and ‘phylogenetic’; February 2010) and consulting the reference lists of relevant papers. This yielded a data set of 20 papers reporting a total of 64 correlations between (what the authors considered to be) proxies for sexual selection and speciation rate (Table 1). We used different approaches to account for non-independence of data points: we calculated weighted means, eliminated taxonomic overlap, and fitted linear mixed-effects models. When studies reported estimates with and without outliers, we used the estimate including the outliers. One paper (Gage *et al.*, 2002) included estimates for three different clades (spiders, insects and mammals), which we treated as separate studies (resulting in a total $N = 22$ studies). From each study, we extracted a Pearson’s correlation coefficient r as our measure of effect size. If the source paper did not report r , we transformed the published statistic into r using the Statistical Calculator in the dedicated meta-analytical software MetaWin (Rosenberg, Adams & Gurevitch, 2000). We consider an estimate statistically significant when its 95% confidence intervals exclude zero.

IV. OVERALL EFFECT SIZE

To estimate overall effect size, we first converted all r values to z using Fisher’s z -transformation and calculated the variance for each z based on the associated sample size [$v_z = 1/(N - 3)$]. Using the MetaWin version 2 (Rosenberg *et al.*, 2000) to fit a random-effects model, we found a mean Fisher’s z of 0.092 (95% CI 0.04–0.15, $N = 64$), corresponding to a mean r of 0.092. This model treats each data point as if it was sampled from a separate population of effect sizes. It does not take into account that some studies reported multiple estimates or that there was taxonomic overlap among studies (e.g. some studies incorporate all birds, while others use only specific groups of birds, such as raptors or passerines). As one way to account for this, we calculated weighted means for each of the 22 studies and eliminated taxonomic overlap. We first selected the lowest taxonomic rank (e.g. raptors instead of all birds) which maximised the number of studies. For this dataset, a MetaWin random effects model yielded a mean Fisher’s z of 0.107 (95% CI -0.002–0.216, $N = 10$), corresponding to a mean r of 0.107. Because selecting only the lowest taxonomic rank may bias the estimate (see below), we also conducted an analysis in which we selected only the highest taxonomic rank available (e.g. all birds instead of raptors). For this dataset, the model yielded a mean Fisher’s z of 0.092 (95% CI -0.091–0.274, $N = 6$), corresponding to a mean r of 0.092. As both these approaches discard more than half of the data, we finally constructed a linear mixed-effect model that included all data points ($N = 64$) and included study ($N = 22$) as a random effect, using R version 2.9.2 (R Development Core Team,

2009). The raw r values were used as the dependent variable. This model yielded a mean r of 0.14 (95% CI 0.04–0.24). Weighting the data points by sample size resulted in a lower value (mean $r = 0.07$, 95% CI 0.006–0.14). Thus, the different approaches produced effect size estimates between 0.07 and 0.14 with confidence intervals that excluded zero in most cases. We interpret this as support for the hypothesis that sexual selection contributes to speciation.

V. PUBLICATION BIAS?

If studies with negative results are less likely to be published, the positive overall effect size may be inflated. In the absence of a universally accepted method (Møller & Jennions, 2001), we used three approaches to estimate publication bias, based on our sample of 64 data points.

First, we visually examined a plot of effect size against sample size. Fig. 1 reveals a paucity of data points in the lower left (low sample size and low effect size), consistent with publication bias. However, the R_0 and L_0 estimators of the ‘trim and fill’ method proposed by Duval & Tweedie (2000) did not indicate a significant number of missing studies. This method is based on the assumption that publication bias leads to under-representation of large negative effect sizes with small sample sizes (i.e. the points in the lower left corner of Fig. 1). In our sample of studies, the most extreme effect sizes were actually negative.

Second, we calculated a Spearman rank correlation between standardized effect size and sample size. When the true effect size is small and publication bias favours significant results, a negative correlation is expected (Begg & Mazumdar, 1994). For our sample, this correlation was not significant ($r_s = -0.23$ $P = 0.07$).

Third, we calculated the ‘fail-safe’ number, which estimates the number of null results that would need to be published to change a significant result into a non-significant

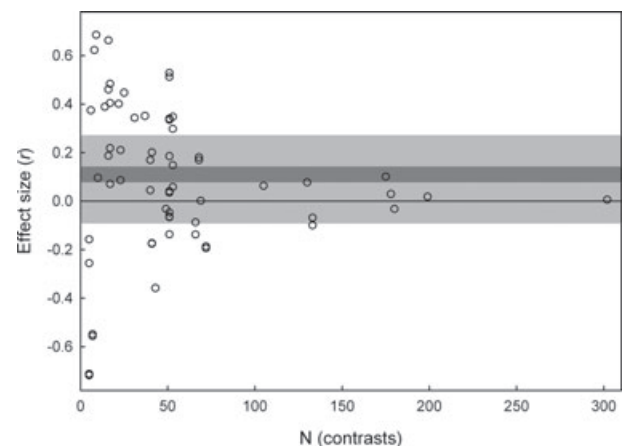


Fig. 1. Funnel plot of effect size against sample size. The dark grey area indicates the range of overall effect size estimates derived from statistical analysis, the light grey area covers the corresponding 95% confidence intervals (for details see text).

result (Møller & Jennions, 2001; Rosenthal, 1991). A fail-safe number of $5K + 10$ or greater is considered to provide evidence of a robust average effect size, where K is the number of data points in the sample (Møller & Jennions, 2001). At $\alpha = 0.05$, we found a fail-safe number of 413.8, which is substantially higher than this cut-off ($5 \times 64 + 10 = 330$). Thus, a relatively large number of new null effects would need to be published to cancel out the small positive effect size that we found.

Together, these analyses suggest that negative results are not severely under-represented in the literature. This is not unexpected, because from the moment of its resurrection (Barracough *et al.*, 1995; Lande, 1981; West-Eberhard, 1983), arguments both for and against the hypothesis that sexual selection promotes speciation have attracted attention (see e.g. the highly cited critical review by Price, 1998). Some additional analysis confirms this impression. Based on the authors' own assessment, we characterized each of the comparative studies as either 'supporting' or 'rejecting' a role of sexual selection in speciation [$N_{\text{support}} = 10$, $N_{\text{reject}} = 9$; the study of Kruger (2008) presented a neutral conclusion and was omitted from this analysis, see Table 1]. We then tested whether the former were published in journals with higher impact factors, which would be indicative of publication bias favouring supportive evidence. We found no difference: $IF_{\text{support}} = 3.8 \pm 0.8$ S.E.M., $IF_{\text{reject}} = 3.9 \pm 0.3$ S.E.M., $t = 0.12$, d.f. = 11.2, $P = 0.91$. Likewise, we found no difference in the number of citations to each study in the two years following publication (4.1 ± 1.1 S.E.M. *versus* 3.7 ± 0.8 S.E.M., $t = -0.24$, d.f. = 16.4, $P = 0.82$). Thus, studies that fail to support the hypothesis, or that present significantly negative correlations, do not appear to face greater difficulties in reaching an audience.

VI. TAXONOMY

It is likely that the effects of sexual selection on species richness differ among taxa. Sexual selection will interact with taxon-level variation in ecology, life-history, body size, dispersal ability, range size, clade age and extinction rate (e.g. see Barracough, Vogler & Harvey, 1998; Seddon, Merrill & Tobias, 2008). In our dataset, effect size did not differ significantly among taxa (likelihood ratio = 8.83, d.f. = 5, $P = 0.12$, Fig. 2). However, the uneven taxonomic distribution reduces confidence in this conclusion: with the exception of birds, the taxa in our sample are represented by only one or a few studies.

A related issue is whether the signature of sexual selection on speciation changes with taxonomic level. It has been suggested that the effects of sexual selection on speciation might be most pronounced in the initial stages of divergence (e.g. Ritchie *et al.*, 2007; Seddon *et al.*, 2008). This is because sexual selection may promote divergence in traits that immediately affect reproductive isolation, such as mating signals and preferences. However, divergence in these traits does not necessarily contribute to long-term persistence of the new species. If sexual selection increases species turnover, its effect would be more difficult to detect at deeper phylogenetic nodes, because extinct species are not included in the estimate for speciation rate. As illustrated in Fig. 3, the true influence of sexual selection on the process of speciation is reflected accurately by recently diverged clades, but its influence is severely underestimated in clades that diverged a long time ago.

Methodological variation in the way in which comparative analyses estimate speciation rate allows preliminary

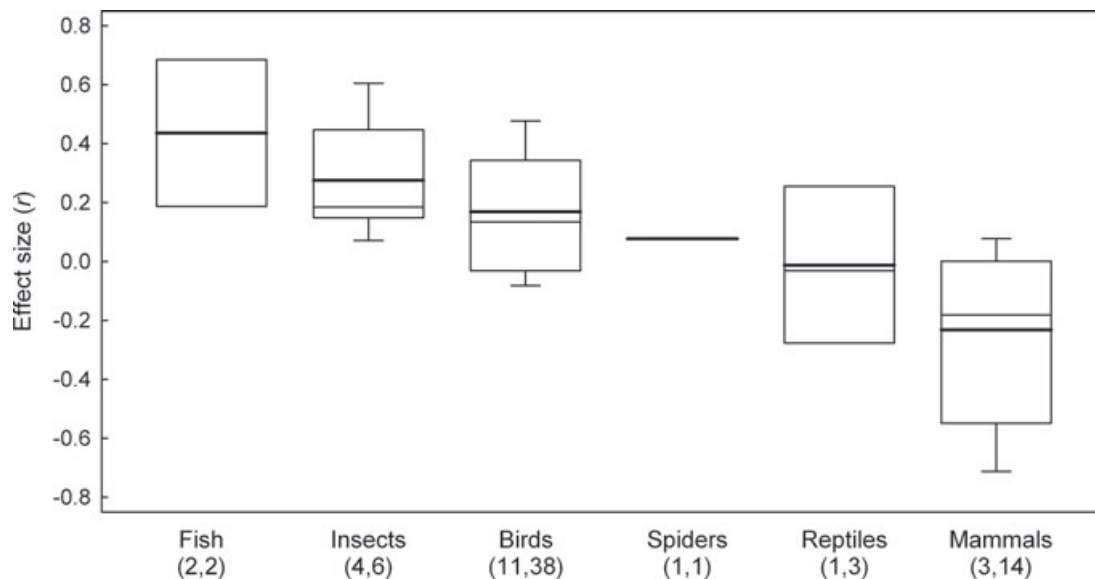


Fig. 2. Boxplot showing variation in effect size among taxonomic groups. Boxes indicate 25–75th percentiles, intercepted by the median (thin line) and mean (thick line). Whiskers indicate 10–90th percentiles. For each taxon, the number of studies and the number of effect size estimates are given in parentheses.

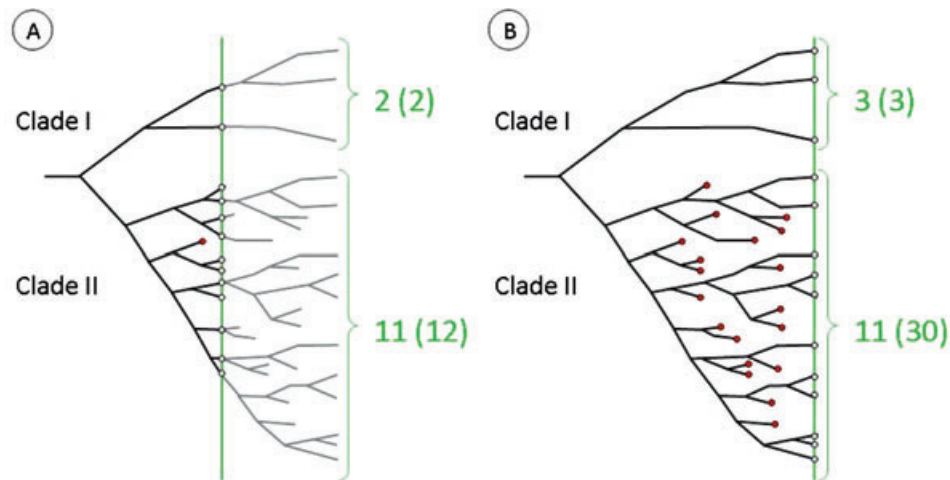


Fig. 3. The effect of differences in species turnover on estimates of species richness at shallow *versus* deep phylogenetic nodes. In this hypothetical example, sexual selection generates many new species in clade II, but not in clade I. Many of these new species go extinct (merging between species—not illustrated—would have the same effect). **(A)** When the comparison is made at a time (vertical line) when the two clades have split recently and few species have gone extinct, the number of extant species (first number in each pair) is similar to the true number of species generated (number in parentheses) in each clade. This situation is representative of sister-group comparisons, provided the sister clades are closely related. **(B)** When the comparison is made a long time after the divergence between the two clades, many species have gone extinct in clade II, which are not counted. This leads to a large discrepancy between the estimate for species richness (11) and the true number of species generated (30) in clade II. This situation is representative for comparisons at deep phylogenetic nodes.

assessment of this effect. Some studies compare extant (sub)species numbers between closely related genera or families and thus take into account only the most shallow nodes of phylogenetic trees. Other studies estimate speciation rate throughout phylogenies that often include multiple families, an approach that also incorporates deeper nodes in the tree. If the diversifying effect of sexual selection is most apparent at lower taxonomic levels, we would expect methods that incorporate deeper phylogenetic nodes to yield smaller effect sizes from those that do not. We tested this prediction using a linear mixed-effect model with study as random effect and sample size as weights. We found that, indeed, effect sizes based on speciation rate estimates from phylogenies are lower than those obtained from sister-group comparisons (likelihood ratio = 5.95, d.f. = 1, $P = 0.01$, Fig. 4). This can be further illustrated by the studies on bird speciation included in our analysis (Fig. 5). Studies that only compare sister groups consistently have larger effect sizes and smaller sample sizes than studies that also incorporate deeper phylogenetic nodes.

Thus, while indirect, the evidence suggests that the signature of sexual selection in patterns of diversification depends on phylogenetic depth. Our analysis indicates that sexual selection is important early in the speciation process but that it does not contribute to further divergence after speciation. A similar effect was detected by Phillimore *et al.* (2006). This study, together with Morrow, Pitcher & Arnqvist (2003), used whole-phylogeny speciation rate estimation and failed to reproduce the previously reported associations between sexual dichromatism and speciation rate in birds,

that were based on species richness at the tips of a phylogeny (Barracough *et al.*, 1995; Owens, Bennett & Harvey, 1999).

Not surprisingly, young radiations and incipient sister species are often viewed as ideal research subjects to study ‘speciation in action’ (Ritchie, 2007; Seddon *et al.*, 2008). However, species evolve after speciation and traits that are only weakly involved in speciation may continue to diverge. The processes involved in the early speciation stages (e.g. sexual selection) may be systematically different from those that contribute to species survival (e.g. ecological differentiation). If so, looking only at young species will give us a biased understanding of the factors underlying current species diversity. We note that this argument is different from the idea that vertebrate speciation is characterized by the sequential involvement of different selective pressures (Danley & Kocher, 2001; Strelman & Danley, 2003). The scenario of distinct ‘stages’ of radiation suggests that ecological specialization comes first and sexual selection operates only later (Strelman & Danley, 2003). By contrast, we hypothesize that sexual selection may continuously generate new species, but the extent to which these persist as distinct lineages depends on additional factors, such as ecological differentiation and spatial isolation (*cf.* Sauer & Hausdorf, 2009).

We hope that future studies will address these issues quantitatively, for example by presenting results separately for different phylogenetic levels and evaluating potential differences statistically (e.g. see Seddon *et al.*, 2008). Such studies can inform us about the biological significance of this pattern, especially if they include both young and

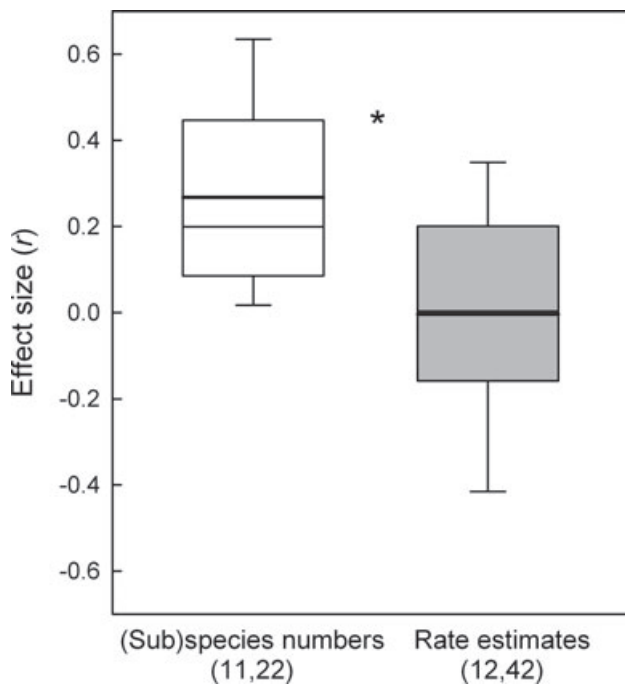


Fig. 4. Boxplot showing the difference in mean effect size between studies that use (sub)species number per genus or family *versus* studies that also incorporate deeper phylogenetic nodes. Boxes indicate 25–75th percentiles, intercepted by the median (thin line) and mean (thick line). Whiskers indicate 10–90th percentiles. The number of studies and the number of effect size estimates are given in parentheses (one study used both approaches: Seddon, Merrill & Tobias, 2008). *Indicates a significant difference between the two groups of studies ($P = 0.01$).

old speciation events and incorporate both sexually and ecologically selected traits.

VII. MEASURING SEXUAL SELECTION

The studies in our sample use 18 different measures of sexual selection (Table 1), a number too high to allow meaningful statistical analysis. Moreover, sexual selection proxies are confounded with taxonomy—most fish don't have spermatheca and insects don't have canines. The proxies for sexual selection can thus not easily be lumped into meaningful larger categories.

Nevertheless, analysis reveals significant differences in effect size among the three sexual selection proxies that were used in several studies, namely sexual dichromatism (11 studies), mating system (five) and sexual size dimorphism (nine). A linear mixed-effect model with study as random effect and sample size as weights showed that effect sizes differ significantly between these proxies (likelihood ratio = 7.49, d.f. = 1, $P = 0.02$, Fig. 6). This was not confounded by taxonomy, as there was no significant taxonomic effect in

this subset of the data (likelihood ratio = 4.47, d.f. = 1, $P = 0.35$).

Probably, different proxies represent different components of sexual selection. Authors of comparative studies often argue that their chosen proxy represents the 'strength' of sexual selection. However, the hypothesised diversifying effect of sexual selection may in fact consist of two distinct components: sexual trait evolution and effects of mate selectivity.

First, sexual selection can generate changes in sexual signals, thereby promoting variation and preventing mate recognition between diverging populations. However, this 'trait lability' (Cardoso & Mota, 2008) is influenced by other factors as well, such as (sex differences in) niche use (Shine, 1989), exposure to predation (Martin & Badyaev, 1996), and genetic and developmental constraints. Possibly, the weak relationship between species richness and sexual size dimorphism (see Fig. 6) can be explained by strong ecological selection on body size. Furthermore, sexual dimorphism may be driven by male-male competition, a component of sexual selection that may have a weaker effect on speciation rate than mate choice (Emlen, 2008). This implies that measures relying on trait lability (such as sexual dimorphism and signal elaboration) may represent the 'net' effect of different sources of selection in generating trait diversity, rather than the 'strength' of sexual selection *per se*. In addition, estimates of sexual dimorphism are typically biased towards phenotypic variation that is conspicuous to human observers (Ritchie, 2007). When sexual selection and sexual conflict generate variation in traits that are not so easily observed and quantified (e.g. male seminal fluid proteins), the contribution of sexual selection to diversification may be underestimated. Human perceptual biases may also affect estimates of speciation rates: the tradition of discriminating and describing species on the basis of sexually dimorphic traits increases species numbers in taxa with large or colourful ornaments (Panhuis *et al.*, 2001). However, the latter problem is not an issue in the comparative studies considered here, all of which used phylogenies based on genetic markers.

Second, isolating effects of sexual selection can be due to mate selectivity: high levels of choosiness within populations may coincide with an increased probability of mate rejection between populations. In comparison with trait lability, variation in choosiness may be a better estimate for the 'strength' of sexual selection, and to some extent, differences in mating systems may represent this variation. We have to keep in mind, however, that even in monogamous taxa, strong sexual selection can be generated by mutual mate choice, desertion, extra-pair paternity and competition over limited breeding opportunities (Kraaijeveld, Kraaijeveld-Smit & Komdeur, 2007). In addition, there may be indirect associations between mating systems and species richness. For example, strong reproductive skew decreases effective population size, facilitating divergence through genetic drift as well as increasing extinction risk.

We acknowledge that these problems, some of which have been raised before, are not easily resolved. For example,

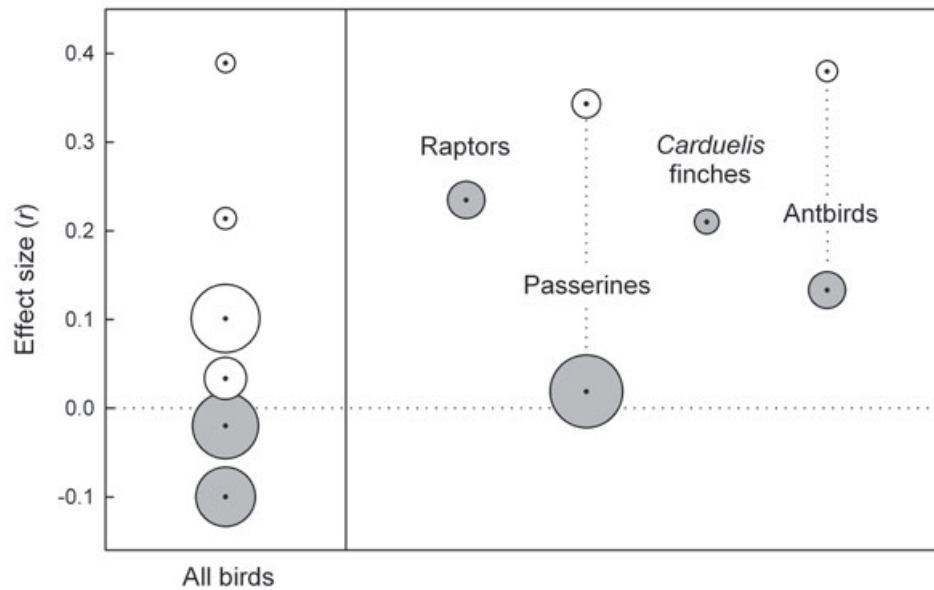


Fig. 5. The relationship between taxonomic level and effect size, illustrated by studies on birds. Studies at lower taxonomic levels tend to have smaller sample sizes (indicated by the symbol size) and larger effect sizes. Open symbols indicate studies that estimate speciation rate by (sub)species counts; grey symbols indicate studies that incorporate deeper phylogenetic nodes.

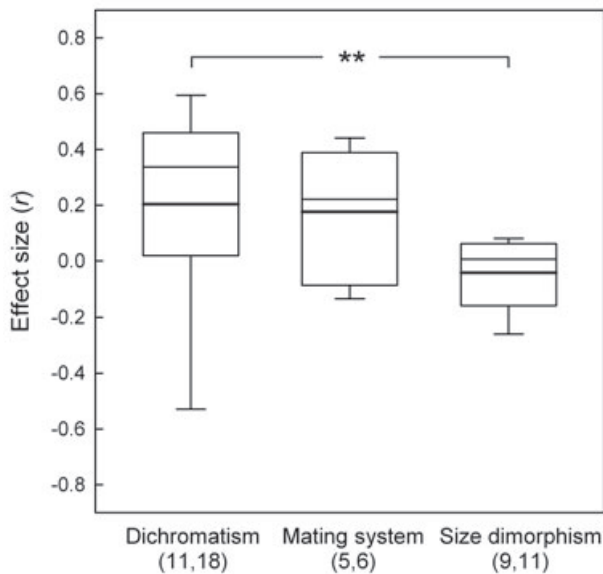


Fig. 6. Boxplot showing the variation in effect size among the three sexual selection proxies for which multiple studies provided estimates. Boxes indicate 25–75th percentiles, intercepted by the median (thin line) and mean (thick line). Whiskers indicate 10–90th percentiles. The number of studies and the number of effect size estimates are given in parentheses. **Indicates a significant difference between dichromatism and size dimorphism ($P < 0.01$).

measuring sexual selection directly in a large number of taxa may not be feasible. We do, however, suggest that authors of future comparative studies provide more justification for the proxies used than is currently conventional.

VIII. CONCLUSIONS

- (1) Our analysis of the comparative evidence reveals a small but positive overall effect of sexual selection on speciation rate.
- (2) Our analysis further suggests that the signature of sexual selection in diversification processes may fade with time.
- (3) We find significant differences between alternative measures of sexual selection that cannot be explained by taxonomy, indicating that some components of sexual selection may have a stronger influence on speciation rate than others.
- (4) We suggest that future comparative analyses incorporate new taxa, different sources of selection, geographic data, and carefully selected proxies for sexual selection and speciation rate.
- (5) Comparative studies in additional (non-bird) taxa could establish whether the relationship between sexual selection and speciation differs among taxa.
- (6) The signature of sexual selection on species richness at deep and shallow phylogenetic nodes requires additional study. The interaction between sexual selection and ecological adaptation is of particular relevance here. When sexual selection accelerates ecological adaptation, it may contribute not only to the origin but also the maintenance of species. Furthermore, ecological segregation is likely to increase selection for species recognition and assortative mating. To detect and understand such interactions better, future comparative studies could incorporate several measures of both natural

and sexual selection (e.g. see Isaac *et al.*, 2005; Owens *et al.*, 1999; Phillimore *et al.*, 2006).

- (7) Another potentially important interaction emerges from geography: distribution patterns will influence diversification processes. While the effects of sexual selection in strictly allopatric divergence may be relatively straightforward, geneflow in parapatry or sympatry may either inhibit divergence through genetic homogenization, or accelerate it through character displacement and reinforcement. To address these questions with comparative methods, analyses should incorporate species ranges or dispersal distances (e.g. Martin, Montgomerie & Loughheed, in press).
- (8) Obviously, there are limits to the applicability and explanatory power of comparative approaches. Comparative studies require well-resolved phylogenies, using very complete sampling (Barracough & Nee, 2001). Any phylogeny is subject to debate and even widely accepted phylogenies can turn out to be wrong with the accumulation of new molecular data. Further, analyses often rely on the assumption that extinction rate was either zero or constant. This is particularly problematic given the indications that sexual selection can increase extinction rate (Kokko & Brooks, 2003; Promislow, Montgomerie & Martin, 1994; Tanaka, 1996), which could obscure increased speciation rates in sexually selected species. Ongoing methodological developments may resolve this problem to some extent (Barracough & Nee, 2001). New approaches to phylogenetic analysis, such as generalized least squares, can account for models of trait evolution other than Brownian and explore different estimates for speciation rate (e.g. Thomas, Freckleton & Székely, 2006).
- (9) Finally, comparative studies detect patterns, potentially leaving mechanistic questions unanswered. For example, the question whether sexual selection alone can drive speciation, in the absence of ecological differentiation, may be better addressed in experimental studies. Yet, with a more systematic incorporation of ecological parameters, as well as more representative sampling, comparative studies can bring us closer to quantifying the contribution of sexual selection to diversification.

IX. ACKNOWLEDGEMENTS

We thank Hans Slabbekoorn and Russ Lande for comments and discussion; and the Netherlands Foundation for Scientific Research (NWO) for financial support.

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