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Sexual selection is positively associated with ecological generalism among agamid lizards

Ö. ÖSTMAN* & D. STUART-FOX†

*Department of Ecology & Genetics/Population Biology, Norbyvägen, Uppsala, Sweden
†Department of Zoology, The University of Melbourne, Parkville, Victoria, Australia

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Abstract

Natural and sexual selection shape the evolution of species but the interplay between them is poorly understood. Two phylogenetic studies on birds have suggested that species with greater sexual dichromatism have a broader habitat use. We show that in agamid lizards, species with more elaborate secondary sexual traits are also ecologically more opportunistic. Species with greater dimorphism in head size and ornamentation have greater altitudinal range and broader habitat use, respectively, and species with greater sexual dichromatism have wider microhabitat use. Body size was positively associated with sexual and ecological generalism, but associations between ecological and sexual traits remained after accounting for body size. We suggest that sexual and natural selection may be linked either because sexual selection can promote generalism at the population level by favouring 'good genes', or because higher population densities may be associated with both stronger sexual selection and broader resource use.

Introduction

There are two basic modes of selection, natural and sexual, that are both important for the evolution of species and speciation (Darwin, 1859, 1871; Mayr, 1963; Andersson, 1994). The association between sexual and natural selection is, however, poorly understood. For example, in theory, the direction of the relationship between the strength of sexual selection and the degree of ecological generalism can differ. The high cost of sexual ornaments in species with strong sexual selection may result in reduced population growth rate and greater sensitivity to environmental stress, predators or parasites (Lande, 1980; Grafen, 1990; Kirkpatrick & Ryan, 1991). Reduced viability may, in turn, result in reduced ecological plasticity, which may be manifested as narrow resource use, small populations and higher extinction probabilities (e.g. McLain *et al.*, 1995, 1999; Doherty *et al.*, 2003). Evidence for this hypothesis is based on studies showing that environmental stress influences the expression of secondary sexual characters among individuals within species (e.g. Møller, 1989; Parsons, 1995) and comparative studies showing a positive relationship between sexual selection and extinction risk among species (Morrow & Pitcher, 2003). If sexual and natural selection act in concert, a runaway co-evolutionary process between ecological specialisation and ornament evolution can be expected (van Doorn *et al.*, 2009). Elaborate sexual ornaments may then reflect local adaptations of individuals resulting in both local adaptation and reproductive isolation. Such a co-evolutionary process would also result in specialist species having more elaborate sexual ornaments. On the other hand, sexual selection promotes proliferation of 'good genes' or purging of deleterious genes in a population (Proulx, 1999, 2002; Lorch *et al.*, 2003; Rankin & Arnqvist, 2008). Strong sexual selection may therefore increase a species' ability to be ecologically plastic and have a broad environmental tolerance (Proulx, 1999). Thus, different evolutionary processes are expected to lead to opposite relationships between the strength of sexual selection and the degree of ecological generalism among species.

Correspondence: Örjan Östman, Department of Ecology & Genetics/
Population Biology, Norbyvägen 18 D, 752 36 Uppsala, Sweden.
Tel.: +46 18 471 26 80; fax: +46 18 471 64 84;
e-mail: orjan.ostman@ebc.uu.se

There may also be indirect interactions between sexual and natural selection if they are both dependent on a third factor, for example, physiological or morphological differences between species (Badyaev & Ghalambor, 1998; Tobias & Seddon, 2009). In many clades, species with large body size are ecologically more diverse than smaller species because of a greater propensity to move between habitats (Hambäck *et al.*, 2007; Griffiths, 2010) and diet shifts between different size classes (De Mott *et al.*, 2010; Griffiths, 2010). Although there is no reason to expect the strength of sexual selection to vary systematically across a body size gradient, Rensch's rule suggests that sexual size dimorphism should increase with increasing body size because of sexual selection acting on male body size and weaker correlational selection on female size (Rensch, 1960; Fairbairn, 1997; Szekely *et al.*, 2004). Consequently, we may observe a correlation between ecological generalism and proxies for sexual selection, such as sexual size dimorphism, because both are correlated with body size. Another confounding factor may be that generalist species (species with a large geographical distribution or that occupy several habitat types) tend to have higher local population densities than specialist species (Brown, 1984; Borregaard & Rahbek, 2010). The reason for this pattern is not well understood (Borregaard & Rahbek, 2010), but high population density could also increase competition for mates, especially in territorial species (Sharp & Agrawal, 2008; Tobias & Seddon, 2009). Variance in reproductive success may therefore increase with increasing population density, potentially resulting in stronger selection for elaborate secondary sexual ornaments. Thus, species with high densities may be more likely to use different resources and experience strong sexual selection causing a positive association between ecological generalism and intensity of sexual selection.

Despite the plethora of hypotheses predicting associations between degree of sexual selection and degree of ecological generalism, few empirical studies have examined this relationship across species. The two among-species comparative studies that we are aware of, Badyaev & Ghalambor (1998) and Tobias & Seddon (2009), both suggest that there is a positive association between the strength of sexual selection (degree of sexual dichromatism) and habitat breadth among cardueline finches (Carduelinae) and antbirds (Thamnophilidae) respectively. These studies only used one or two indices each for strength of sexual selection (plumage dichromatism and song structure) and degree of ecological generalism (altitudinal range and habitat breadth). Clearly, empirical studies of a broader range of taxa, using a range of measures of ecological traits, are required to resolve whether sexual selection is positively or negatively associated with ecological generalism.

To broaden our understanding of the empirical relationship between the strength of sexual selection and degree of ecological generalism, we conducted a phylogenetic comparative analysis using a large lizard clade (Family: Agamidae) and four different measures of both sexual selection and ecological generalism. Agamid lizards are an 'old world' distributed family found in Africa, Asia, Europe and Australasia comprising over 350 currently described species. They show substantial variation in ornamentation, colouration, degree of sexual dimorphism and ecological traits, making them ideal for such a study. For instance, many species have conspicuous colour patches on their throats, heads and sides, and possess a variety of sexual ornaments such as fleshy rostral protrusions, spines, crests and dewlaps (throat 'fans'). Experimental evidence from lizards suggests that these traits are sexually selected (reviewed in Olsson & Madsen, 1998; Whiting *et al.*, 2003). Agamid lizards also occupy a broad range of habitats ranging from salt pans, rocky and sandy deserts, and open woodlands through to montane and lowland primary rainforest (Manthey & Schuster, 1996). Hence, species vary in their microhabitat use (e.g. rock crevices, sandy substrates, grass tussocks, trees etc.) and altitudinal range. Consequently, we used several measures of ecological generalism, namely, altitudinal range, number of broad habitat types occupied, range size and microhabitat use, of which the latter two have not been used in comparative studies of the relationship between sexual and natural selection. These different proxies for the degree of ecological generalism allow us to study associations between sexual selection and both tolerance to different environments (number of habitats, range size, altitudinal range) and resource use (number of microhabitats, number of habitats). As a proxy of the strength of sexual selection, we used degree of sexual dichromatism (extent of colour differences between the sexes) and sexual ornament dimorphism (degree of difference in morphological ornamentation between the sexes) as well as head and body-size dimorphism. However, body size in itself is associated with both sexual dimorphism and habitat use in agamid lizards (Stuart-Fox & Ord, 2004), and we therefore included average body size of both sexes as a covariate in the models as differences in body size between species otherwise may confound the relationship between ecological and sexual traits.

Methods

We use a data set on agamid lizards (Stuart-Fox & Owens, 2003; Stuart-Fox & Ord, 2004; Ord & Stuart-Fox, 2006) that contains information on morphology, habitat use and geographical information for 259 species of agamid lizards. We use the composite phylogeny for the agamid family from Ord & Stuart-Fox (2006), based primarily on mt-DNA studies (Macey *et al.*, 2000; McGuire & Heang, 2001; Schulte *et al.*, 2002, 2003; Pang *et al.*, 2003), with the placement of the few species not represented in any phylogeny determined according to Moody's (1980) morphological classification or left as polytomies within their respective genera (see Ord & Stuart-Fox, 2006 for details). Phylogenies of some clades could also be confirmed by more recent molecular studies (Doughty *et al.*, 2007; Hugall *et al.*, 2008; Shoo *et al.*, 2008; Melville *et al.*, 2009). Because the general resolution of the phylogenetic tree was too low to estimate branch lengths in most clades, all branch lengths were set to one. The exception was for clusters of species with unknown or uncertain phylogenetic relationships, represented as polytomies in the tree. We randomly resolved these polytomies by setting internal branch lengths to 0.0001 in Mesquite 2.72 (Maddison & Maddison, 2009).

As a proxy of the strength of sexual selection, we here use sex differences in body size, head size and secondary sexual characters. Previous studies of agamid lizards have used sexual dimorphism in body and head dimensions as an index for the strength of sexual selection (Stuart-Fox & Owens, 2003; Stuart-Fox & Ord, 2004), because experimental studies have shown these to be good indicators of the strength of intra-sexual selection (the primary selective force in lizards) (e.g. Anderson & Vitt, 1990; Olsson, 1992; Kratochvil & Frynta, 2002; Lopez *et al.*, 2002; Perry *et al.*, 2004). However, sexual dimorphism in body and head size may potentially also be driven by natural selection (Shine, 1989); so, we also used sexual dichromatism and sexual dimorphism in secondary sexual morphological ornaments as additional proxies for the strength of sexual selection. In lizards, sexual dimorphism in colouration and ornamentation have been shown to be influenced by both intra- and inter-sexual selection (Thompson & Moore, 1991; Baird *et al.*, 1997; Anderholm *et al.*, 2004). Thus, we used four different estimates of the strength of sexual selection in a species. (i) Degree of dimorphism in ornamentation between the sexes (*Ornament dimorphism*, $N = 240$; N – refers to the number of species for which there was available information) was scored as a weighted index based on the count of dimorphic physical features, with 0 = ornament similar in both sexes; 1 = present in both sexes, but larger in the male and 2 = only present in males. Total ornament dimorphism was then calculated as the sum of the values for seven ornament types (nape crest/spines, dorsal crest/spines, tail crest/spines, enlarged cheeks, gular pouch, rostral appendage and supra-ocular spines/ridges) and thus ranged between 0 and 14. (ii) Degree of dichromatic differences between sexes (*Dichromatism*, $N = 155$) was scored as a conservative index of difference in colouration between the sexes. Specifically, each body region was scored as dichromatic (1) or not (0). These scores were then summed over 11 body regions [crown, lateral region of the head, throat, chest, ventral region, anterior dorsal, posterior dorsal, flanks (dorso-lateral region), forelimbs, hindlimbs and tail]. (iii) Sexual head dimorphism [*Head size dimorphism (HSD)*, $N = 108$] is an index of head morphology based on difference in head size between the sexes. This index was the PC-scores from the first axis of a principal components analysis (PCA) on the percentage differences in head width and head depth between the sexes [(male head size/female head size-1) × 100]. The correlation coefficient between the PC-axis and percentage differences was $r = 0.88$ for both head depth and head width. Finally, (iv) we used the percentage difference in snout-to-vent length (SVL) between the sexes as an estimate of *sexual size dimorphism* [*SSD*, (male SVL/female SVL-1) × 100, $N = 159$].

We used four estimates of degree of ecological generalism: (i) The number of distinct habitat types a species occurs in (*Habitats*, $N = 176$ of which 124 species occurred in more than one habitat). The 16 habitats were rocky outcrops, riparian zones, mountane cloud forest, primary rainforest, secondary (regrowth) rainforest, forest edges, stony desert, sandy desert, semi-desert, savannah/grasslands, arid acacia woodland, open woodland, disturbed habitats, monsoon scrub, seasonally dry wetlands, and heath/coastal vegetation. (ii) The number of microhabitats or substrates a species uses within habitats (*Microhabitats*, $N = 205$ of which 127 species occurred in more than one microhabitat). These were ground (apart from sand and rock substrates), rocks, sand, fallen timber, grass tussocks, shrubs, trees and semi-aquatic. Finally, (iii) we used the geographical range of each species (*Range*, $N = 170$) as the logarithm of the estimated range size in square kilometres (see Stuart-Fox & Owens, 2003 for detailed methods) and altitudinal range (*AltRange*, $N = 93$) as the logarithm of the maximum minus the minimum recorded altitude. To account for differences in mean body size between species, we used the logarithm of the average snout-to-vent length of both sexes for each species (*SVL*, $N = 240$) as a covariate in models.

Statistical procedure

To test whether there was an association between sexual dimorphism and degree of ecological generalism, we constructed phylogenetic generalized least square regression models (PGLS) using REGRESSIONV2 (Lavin *et al.*, 2008). Because species share a common evolutionary history, more closely related species may be phenotypically more similar than expected by chance (Harvey & Pagel, 1991). To account for this correlation among species, we used Pagel's λ-transformation of the phylogenetic variance–covariance matrix. We also tested other λ-transformations [i.e. OU-transformation, ACDC-transformation, and Martins λ – transformation (using the APE-package in R)], but Pagel's transformation generally resulted in the lowest Aikake's information criteria of the models and we therefore only present results using Pagel's transformation for calculating λ. That means that the evolution of characters could best be described as a Brownian motion, where a low λ (close to zero) indicates a weak phylogenetic signal, that is, a character is not conserved within clades, and a high λ (close to one) indicates a strong phylogenetic signal, that is, a character is conserved within clades.

First, we did pair-wise PGLS regressions between all traits used to assess the correlations between individual pairs of traits and assess potential for co-linearity. Then, for each of the sexual dimorphism traits, we did PGLS multiple regressions with all four ecological characters as explanatory variables and vice versa. Body size was included as a covariate in all regressions as previous studies have shown a relationship between body size and both morphological and ecological traits (Stuart-Fox & Owens, 2003). In contrast to previous studies (Badyaev & Ghalambor, 1998; Tobias & Seddon, 2009), which have only used ecological characters as the response variables, we also test for the reciprocal association. Because the correlation structure within clades can vary between different traits, PGLS model fit can vary depending on which character is the response variable and which is explanatory variable (i.e. the models A = B and B = A may not produce identical model fits). Explanatory variables were removed in a backward manner to increase sample size until we obtained a final model with only explanatory variables with $P < 0.1$. To check that the final model was not sensitive to sample size, we re-introduced all eliminated variables one at the time to the model but removed them again if $P > 0.1$ to make sure a variable was not eliminated because of a low subsample. When there were two or more explanatory variables left in the final model, we standardized these explanatory variables (mean = 0, variance = 1) and re-ran the regression to calculate the regression slope coefficients of the standardized variables as a measure of effect size of each individual explanatory variable, i.e. a variable with considerably higher regression slope coefficient had a considerably larger 'effect' on the response variable. Because we used multiple regression tests for the same general null hypothesis, we applied sequential Bonferroni correction to overall model P values (Rice, 1989). We did this separately for the four models with ecological variables as dependent variables and the four models with sexual selection variables as dependent variables because the reciprocal models were only included for studying quantitative differences, not hypothesis testing.

Results

Pair-wise PGLS associations between traits were generally positive, or showed no associations at all (Table 1). Our estimates of ecological generalism were all inter-correlated except between *Microhabitats* and *AltRange*, whereas only *Dichromatism* and *Head size dimorphism* were correlated among the secondary sexual traits (Table 1). The correlation coefficients (i.e. R^2 values) were, however, modest to low (Table 1), and therefore, the different variables in the multiple regression models were only weakly colinear. A number of traits were associated with body size, namely microhabitat use, habitat breadth, range size, sexual dimorphism in ornaments and sexual size dimorphism, but again R^2 values were modest (Table 1).

The final models from the PGLS multiple regressions between differences in sexual secondary traits between sexes and degree of ecological generalism are presented in Table 2. There were positive associations between degree of dimorphism in head shape and altitudinal range, the degree of sexual dichromatism and number of microhabitats used, and sexual dimorphism in ornamentation and habitat breadth, respectively. These relationships were consistent regardless of whether ecological variables or indices of sexual selection were considered the explanatory variable. R^2 values were modest but of similar magnitude to previous studies (e.g. Tobias & Seddon, 2009). Body size was positively associated with three of the four estimates of degree of ecological generalism (not *AltRange*) and two of the four estimates

Table 1 R^2-values from pair-wise phylogenetic least-square regressions between the different traits using Pagel's lambda-transformation. The variable in the header row is the response variable and the variable in the first column the explanatory variable in the PGLS:s. A negative sign in brackets denotes a negative association.

	Micro-habitats	Habitats	Range	AltRange	Ornaments	Dichromatism	HSD	SSD
Microhabitats		0.07***	0.03*	< 0.01	0.02*	0.04*	0.03	0.05*
Habitats	0.07***		0.07**	0.11**	0.08***	0.02	0.04	0.04*
Range	0.04*	0.09***		0.11**	< 0.01(–)	0.04*	0.02	0.03
AltRange	< 0.01	0.10**	0.09**		0.02	0.01	0.09*	< 0.01 (–)
Ornaments	0.015	0.07***	< 0.01	0.02		< 0.01	0.02	0.04*
Dichromatism	0.04*	0.01	0.02	< 0.01	< 0.01		0.14**	0.02
HSD	< 0.01	< 0.01	0.03	0.09*	0.03	0.06*		< 0.01
SSD	0.05*	0.05*	0.03	< 0.01(–)	0.04*	< 0.01	0.03	
SVL	0.06***	0.05**	0.06**	< 0.01	0.06***	< 0.01	0.02	0.09***

*$P < 0.01$, **$P < 0.01$, ***$P < 0.001$. All significant associations were positive.

AltRange, altitudinal range; Range, range size; Ornaments, ornament dimorphism; HSD, head size dimorphism; SSD, sexual size dimorphism – see Methods for definition; PGLS, phylogenetic generalized least square; SVL, snout-to-vent length.

Table 2 Results from multiple phylogentic generalised least-square regressions (PGLS) between degree of ecological generalism and degree of sexual differences in secondary sexual traits using Pagel's lambda-transformation.

Dependent variable	Explanatory variable	$\beta \pm$ SE	t	P	P_{model}/P_{crit}	N	λ	R^2	Effect size
Microhabitats	*SVL*	0.61 ± 0.18	3.4	< 0.001	< 0.001/0.013	133	0.70	0.12	0.24 ± 0.062
	Dichromatism	0.075 ± 0.031	2.4	0.01					0.19 ± 0.073
Habitats	*SVL*	0.55 ± 0.27	2.0	0.05	< 0.001/0.017	171	0.90	0.09	0.23 ± 0.011
	Ornaments	0.18 ± 0.065	2.7	0.008					0.30 ± 0.10
Range	*SVL*	0.96 ± 0.29	3.3	0.002	0.002/0.025	158	0.31	0.06	0.4 ± 012
AltRange	*HSD*	0.24 ± 0.12	2.1	0.04	0.04/0.05	44	0.01	0.09	2.4 ± 1.1
Ornaments	*SVL*	1.02 ± 0.28	3.7	< 0.001	< 0.001/0.013	171	0.65	0.15	0.42 ± 0.12
	Habitats	0.27 ± 0.084	3.2	0.002					0.34 ± 0.11
SSD	*SVL*	12.2 ± 3.07	4.0	< 0.001	< 0.001/0.017	158	0.50	0.09	5.0 ± 1.3
Dichromatism	*Microhabitat*	0.50 ± 0.22	2.3	0.02	0.002/0.025	138	0.87	0.04	0.44 ± 0.19
HSD	*AltRange*	0.38 ± 0.18	2.1	0.04	0.04/0.05	44	0.01	0.09	0.29 ± 0.14

'$\beta \pm$ SE' is the slope and standard error of the slope between two traits, 't' is t-value and 'P' the associated P-value. 'P_{model}/P_{crit}' shows the P-value of the model and the critical P-value from the sequential Bonferroni correction ($\alpha/[1 + k - i]$, where $\alpha = 0.05$, $k = 4$, and i = order of test 1–4), 'N' is the number of species included, 'λ' is Pagel's lambda transformation using REML, 'R^2' is the full model's R^2, and 'Effect size' is a relative estimate of the effect of explanatory variables on the response variable.

AltRange, altitudinal range; *Range*, range size; *Ornaments*, ornament dimorphism; *HSD*, head size dimorphism; *SSD*, sexual size dimorphism – see Methods for definition; SVL, snout-to-vent length.

of strength of sexual selection (*Sexual Size Dimorphism* and *Ornaments*; Table 2). The results were qualitatively unchanged after application of sequential Bonferroni correction to overall model P-values (Table 2).

Discussion

Our results suggest that agamid species with greater sexual dimorphism are more likely to be ecological generalists, consistent with previous studies on birds (Badyaev & Ghalambor, 1998; Tobias & Seddon, 2009). These earlier studies only considered associations between broad measures of ecological generalism, namely altitudinal range and habitat use, and measures of sexual selection. Our study supports their findings, with head size dimorphism showing a positive association with altitudinal range and sexual dimorphism in ornamentation increasing with increasing habitat breadth. The association between head size dimorphism and altitudinal range in particular suggests that the strength of sexual selection is associated with greater physiological tolerances, because altitudinal range is likely to be associated with physiological tolerance, especially in ectotherms (Sinervo *et al*., 2010). In addition, we found a positive association between sexual dichromatism and finer scale resource use (microhabitat breadth), which has not been examined in previous studies. However, further studies are required in a broader range of taxa to test whether this association between sexual traits and fine scale resource use reflects a more general pattern.

There are at least two general mechanisms that may generate a positive relationship between the strength of sexual selection and the degree of ecological generalism. This relationship may arise directly because strong sexual selection results in the proliferation of 'good genes' and purging of deleterious genes (e.g. Proulx, 1999, 2002) causing these species to be more viable and more ecologically variable. Alternatively, the positive relationships may be an indirect consequence of a third variable, for example population density, which is believed to increase both strength of sexual selection (e.g. Sharp & Agrawal, 2008) and degree of ecological generalism (e.g. Borregaard & Rahbek, 2010). Tobias & Seddon (2009) argue that the positive effects of sexual selection (via spread of 'good genes' or purging of 'genetic load') may be more evident in species without highly elaborate ornamentation or dichromatism because these species do not carry such a high burden of energetic investment in ornamentation. Results from previous studies, however, do not support this hypothesis as sexual dimorphism in ornamentation is highly correlated with degree of both male and female ornamentation in agamid lizards (Stuart-Fox & Ord, 2004). Although both sexes are likely to pay energetic and perhaps predation and foraging costs for secondary sexual ornaments and colouration, our results suggest that agamid species that are both more sexually dimorphic in ornamentation and highly ornamented can still reproduce in a broader range of habitats. Our data, however, do not allow us to distinguish whether the same individuals can reproduce in different habitats because of plasticity or whether different individuals are adapted to different habitats.

We found a positive association between body size and both ecological generalism and elaboration of sexual ornaments; large species were more likely to have a broader microhabitat use, occur in different distinct habitat types and have a large geographical range, but larger species were also more likely to show large differences in body ornamentation and greater size differences between the sexes. This may reflect stronger sexual selection in larger species, weaker correlational selection on female size in larger species (Fairbairn, 1997; Szekely *et al.*, 2004), decreased constraints on ornament evolution for larger species, or even an observational bias (e.g. we are more likely to identify ornaments on a large individual than a small one). Regardless, body size does not completely confound the relationship between ecological and sexual traits. The effect size of body size was similar to the effect size of habitat breadth or sexual dichromatism when these were explanatory variables. Thus, although body size was related to both degree of sexual selection and degree of ecological generalism, there was still a clear positive association between them when correcting for body size.

It has been shown for several taxa that species richness is higher in genera with apparently strong sexual selection (Owens *et al.*, 1999; Seddon *et al.*, 2008), including agamid lizards (Stuart-Fox & Owens, 2003). Hence, speciation seems to be faster or extinction slower in clades with more pronounced sexual selection. The positive association between strength of sexual selection and degree of ecological generalism, however, suggests that the high speciation rates of clades with strong sexual selection may also be dependent on ecological processes. Janz *et al.* (2006) suggested that speciation of butterflies was highly contingent on the occurrence of host plant generalists. That is, most speciation events stem from generalist species. Consequently, the occurrence of ecological generalism, or generalist traits, may be very important for speciation, a view supported by both theory and data from other organisms (e.g. van Doorn *et al.*, 2009; Labonne & Hendry, 2010). Thus, even when sexual selection rather than natural selection drives speciation, it may nevertheless be facilitated by ecological generalism.

Previous studies have considered the ecological variables to be the dependent variable because they specifically set out to test the traditional hypothesis that increased sexual selection is associated with reduced ecological tolerance. However, given the complex nature of possible interactions between sexual and natural selection, it is equally possible that natural selection promotes sexual selection. For this reason, we did not assume that one type of variable was the explanatory variable and constructed models with ecological and sexual dimorphism variables as both the dependent and explanatory variables. However, our results were consistent regardless of which type of variable was considered to be dependent or explanatory and therefore do not depend on any prior assumptions about causality between ecological and sexual traits.

Overall, our results are consistent with previous comparative studies which (i) fail to support the traditional view of a trade-off between sexual selection and ecological generalism and (ii) instead indicate a positive association between the two. By identifying such a general pattern among species, this study will help to focus attention of empiricists on hypotheses explaining how sexual selection and ecological generalism may be linked. However, as this is a broad comparative study, we are unable to identify the direction of causality or the specific mechanisms involved. Moreover, as with all studies of this kind, the data are coarse proxies for ecological and evolutionary processes. However, if error is randomly distributed across the data set, the patterns we identify will be evident despite the coarse data and scale of analysis (Stuart-Fox & Owens, 2003). It is possible that error is distributed nonrandomly owing to bias in taxon sampling and systematic bias in quantification of sexual and ecological traits across the family (e.g. owing to bias in the taxa that have been studied because of their geographical location). Despite these potential sources of error, we note that the variables we used are based on previously published data and methods (e.g. Owens & Bennett, 1994; Stuart-Fox & Owens, 2003; Stuart-Fox & Ord, 2004; Tobias & Seddon, 2009), which have identified a range of biological patterns, consistent with theoretical predictions.

In summary, we identified broad associations between sexual dimorphism and habitat breadth, microhabitat use or altitudinal range in Agamid lizards via a phylogenetic comparative approach. There are at least two main mechanisms that could produce a positive relationship between the strength of sexual selection and ecological generalism. First, strong sexual selection based on 'good genes' models can promote beneficial alleles and purge deleterious alleles. Second, if generalist species are more common, they may occur at higher population densities and therefore experience stronger sexual selection. That is, stronger sexual selection may be an indirect consequence of the commonly observed abundance and range/occupancy relationship. Thus, our study supports the view that a variety of processes can promote synergy between natural and sexual selection leading to a positive association between primarily naturally and sexually selected traits.

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