

Species richness in agamid lizards: chance, body size, sexual selection or ecology?

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Abstract

Why does species richness vary so greatly across lineages? Traditionally, variation in species richness has been attributed to deterministic processes, although it is equally plausible that it may result from purely stochastic processes. We show that, based on the best available phylogenetic hypothesis, the pattern of cladogenesis among agamid lizards is not consistent with a random model, with some lineages having more species, and others fewer species, than expected by chance. We then use phylogenetic comparative methods to test six types of deterministic explanation for variation in species richness: body size, life history, sexual selection, ecological generalism, range size and latitude. Of eight variables we tested, only sexual size dimorphism and sexual dichromatism predicted species richness. Increases in species richness are associated with increases in sexual dichromatism but reductions in sexual size dimorphism. Consistent with recent comparative studies, we find no evidence that species richness is associated with small body size or high fecundity. Equally, we find no evidence that species richness covaries with ecological generalism, latitude or range size.

Introduction

'Where many species of a genus have been formed through variation, circumstances have been favourable for variation; and hence we might expect that the circumstances would generally be still favourable to variation...The larger genera thus tend to become larger; and throughout nature, the forms of life which are now dominant tend to become still more dominant by leaving many modified and dominant descendants.' (Darwin, 1859, pp. 110–113)

Darwin (1859) was among the first to suggest that some groups of organisms contain disproportionately large numbers of species, and that the unusual species richness of these groups may be because of characteristics of either the organisms or their environment. The search for explanations for observed patterns of species richness

has generated much speculation as to the underlying processes influencing rates of speciation (e.g. Simpson, 1953; Mayr, 1963; MacArthur *et al.*, 1966). Traditionally, differences between lineages in species richness have been explained by invoking aspects of the intrinsic biology of the organisms themselves, such as body size or generation time. However, as pointed out by Raup *et al.* (1973), it is equally plausible that variation in the distribution of species richness among higher taxa may also result from purely stochastic processes. This realization, coupled with new null models of cladogenesis and the availability of large and more complete phylogenies, has led to a surge of interest in identifying general factors that make some lineages more likely to diversify and others reach an evolutionary dead end (e.g. Dial & Marzluff, 1989; Nee *et al.*, 1992; Guyer & Slowinski, 1993; Ricklefs & Renner, 1994; Nee *et al.*, 1996; Rosenzweig, 1997; Barraclough *et al.*, 1998; Owens *et al.*, 1999; Katzourakis *et al.*, 2001; Gage *et al.*, 2002).

The overall aim of this study is to investigate six types of explanations that have been proposed to explain patterns of species richness. The first type of explanation

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is that variation in species richness is due to chance (Raup *et al.*, 1973). The second type of explanation, the body size hypothesis, proposes that smaller species are more likely to diversify, because smaller species require fewer resources and can partition the environment more finely (Stanley, 1973; van Valen, 1973; May, 1986). The third type of explanation is that variation in species richness is associated with variation in life-history traits. The life-history hypothesis suggests that organisms with greater reproductive outputs and/or shorter generation times may evolve faster and/or may be less likely to go extinct. Higher intrinsic rates of increase (r) may allow species to adapt quickly to new niches (increased speciation) and recover rapidly from environmental perturbations (reduced extinction) (Stanley, 1979; Marzluff & Dial, 1991). The fourth type of explanation is that variation in species richness is associated with variation in the intensity of sexual selection. The sexual selection hypothesis is supported by substantial theoretical and experimental evidence that sexual selection may promote diversification through divergence in female mate preferences, leading ultimately to reproductive isolation between populations (reviewed in West-Eberhard, 1983; Barraclough *et al.*, 1995; Carson, 1997; Houde, 1997; Payne & Krakauer, 1997; Saetre *et al.*, 1997; Price, 1998). The fifth type of explanation is that species richness is associated with ecological factors such as degree of habitat generalism. Several authors have suggested that habitat generalists may be more likely to colonize new regions or experience population subdivision because of biogeographical barriers, both of which may lead to increased speciation (Simpson, 1953; Mayr, 1963; Rosenzweig, 1995). However, if speciation events are associated with ecological character displacement, sibling species may partition ecological niches more finely, resulting in a higher frequency of habitat specialists (MacArthur *et al.*, 1966; Schluter, 1996). Finally, biogeographical parameters such as geographical range size and latitude have been proposed as correlates of species richness. The range size hypothesis suggests that species with larger range sizes should have greater opportunity for range fragmentation because of geographical barriers or alternatively, greater opportunity to colonize new ecological niches (Rosenzweig, 1995; Gaston & Blackburn, 1997). Because speciation events should be associated with a splitting of range sizes, species belonging to lineages with higher rates of cladogenesis are expected to have smaller mean range sizes (Rosenzweig, 1995; Gaston & Blackburn, 1997). Rates of diversification may also vary with latitude, the expectation being that they increase towards the equator (Rosenzweig, 1995).

To date, the majority of comparative tests of correlates of species richness have been on birds and mammals because biological data for these taxa are the most readily available (but see Mitter *et al.*, 1988; Ricklefs & Renner, 1994; Katzourakis *et al.*, 2001; Gage *et al.*, 2002; Orme *et al.*, 2002). Furthermore, most studies have only

examined one of these hypotheses; yet it is most likely that diversification rates in any given taxon are influenced by several factors, some of which may be correlated (but see Owens *et al.*, 1999; Katzourakis *et al.*, 2001; Bennett & Owens, 2002). The relative importance of different factors and their generality across different taxonomic groups therefore remains to be determined. Here, we use comparative methods and a recently available molecular phylogeny of the lizard family Agamidae to test competing hypotheses about correlates of diversification. The Agamidae is an old-world distributed family of lizards that comprises over 350 species. As generally conspicuous members of the herpetofauna, they are relatively well-studied. Most importantly, they are highly variable in morphological, life-history and ecological characteristics, unlike some other major squamate lineages. For example, the Agamidae includes such diverse groups as the flying lizards (*Draco*), the chamaeleon-like horned lizards (*Ceratophora*), the ant-specialist thorny devil (*Moloch*) and the large, semi-aquatic, sail-fin lizards (*Hydrosaurus*). For these reasons, agamid lizards represent a good reptilian group with which to test for correlates of species richness.

Methods

Phylogeny

We based our analyses primarily on a recent molecular phylogeny of the Agamidae based on 1434 nucleotides from three protein-coding mitochondrial genes (ND1, ND2 and COI) and intervening tRNA genes (Macey *et al.*, 2000). The phylogeny is near complete, and includes one or more representatives of 36 of 49 currently recognized agamid genera. Of the 13 genera not represented, most are poorly known monotypic taxa. The list of currently recognized genera and their associated species richness is from the EMBL reptile database (<http://www.embl-heidelberg.de/uetz/LivingReptiles.html>), based on Barts & Wilms (1997). Three monotypic genera listed in the EMBL reptile database were not included in the complete phylogeny used for our analyses. The existence and status of *Paracalotes* and *Coryphophylax* is uncertain and the genus *Oreodeira* is a junior synonym of the African species *Agama agama* (Moody, 1988).

At least three genera in Macey *et al.*'s phylogeny are not monophyletic. The genus *Physignathus* contains only two species and is paraphyletic (Fig. 1). The two species were treated as two separate genera in our analyses as *P. cocincinus* is the basal member of the entire Australopapuan clade, so a generic reclassification based on monophyly of *Physignathus* is not sensible. The genus *Japalura* contains two widely divergent groups, which we also treat as two separate genera in our analyses. These groups can be classified according to geographical

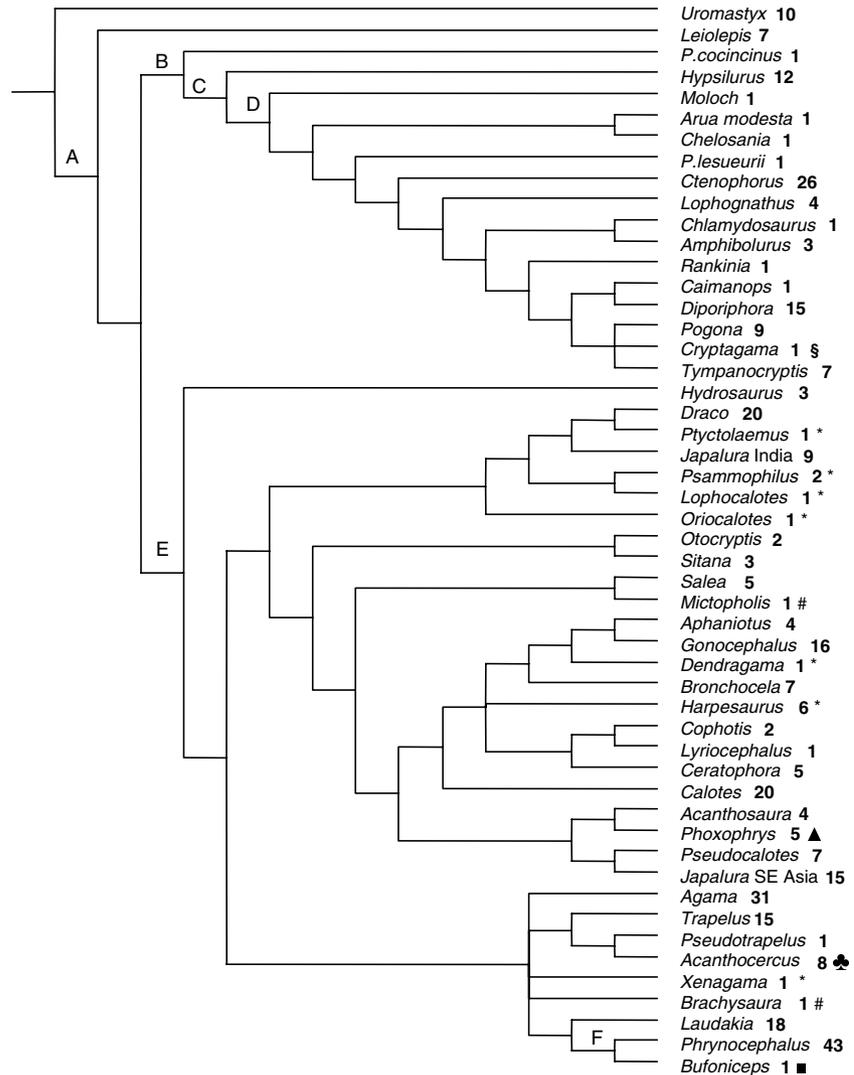


Fig. 1 Complete phylogeny of agamid genera used for comparative analysis of correlates of species richness. The topology is based on the phylogeny of Macey *et al.* (2000) and Melville *et al.* (2001) for the Australo-papuan clade. Species richness for each genus is given in bold next to each taxon name. Letters indicate nodes that are significantly imbalanced according to the Slowinski–Guyer test. Symbols indicate genera not included in Macey *et al.*'s original phylogeny, inserted based on alternative sources. The placement of *Laudakia* is based on the topology of Macey *et al.* (2000) when weakly supported branches are collapsed. *Moody (1980); #Smith (1935); Das (1996); §Storr (1981); Witten (1984); ▲Honda *et al.* (2000); ♣Joger (1991); ■Arnold (1992).

affinity: members of the *J. splendida* group (comprising 14 species) occur in east Asia, whereas members of *Japalura variegata* group (comprising nine species) occur principally in south Asia. The third genus that may not be monophyletic is the widely distributed genus *Laudakia*. However, bootstrap support for the paraphyly of *Laudakia* is weak (relevant branches have <30% bootstrap support). In addition, species within *Laudakia* are not easily divisible according to either morphology or geography. For these reasons, we have retained current members of the genus *Laudakia* within a single group for our analyses.

For the Australo-papuan clade within Macey *et al.*'s larger agamid phylogeny, we use the topology of Melville *et al.* (2001) because it is based on the same characters but represents a more complete dataset. Melville *et al.*'s (2001) phylogeny of the Australo-papuan clade and the large Australian genus *Ctenophorus* indicates that the

genus *Rankinia* is also not monophyletic. Melville *et al.* (2001) suggest including *R. adelaidensis* and *R. chapmani* in the genus *Ctenophorus* and retaining the name *Rankinia* for *R. diemensis* alone. We follow this generic classification in our analyses.

Missing taxa may greatly affect the calculation of independent contrasts (Harvey & Pagel, 1991; Blackburn & Gaston, 1998). Therefore, following previous comparative studies (e.g. Katzourakis *et al.*, 2001), we inserted missing taxa based on other available morphological and molecular phylogenetic information (Smith, 1935; Moody, 1980; Storr, 1981; Witten, 1984; Joger, 1991; Arnold, 1992; Das, 1996; Honda *et al.*, 2000). Where different sources differed in their placement of genera, we took the conservative approach of collapsing branches into polytomies. This complete phylogeny has 45 nodes of 50 possible nodes for a fully bifurcating tree (Fig. 1).

Tree imbalance

To assess whether the topology of the Agamid tree could have been produced by a random branching process, we used two different measures of tree imbalance. Both measures test for a significant deviation from patterns of species richness expected under a Markovian null model, in which all lineages have an equal net probability of splitting at any point in time (Raup *et al.*, 1973). The first method we used was Slowinski & Guyer's (1989) test of imbalance for each bifurcation. Under this test, a bifurcation can only be significantly imbalanced if it subtends 40 or more species, so we applied this test only to nodes meeting this criterion. Second, we used Purvis *et al.*'s (2002) correction of Fusco & Cronk (1995) measure of tree imbalance. Fusco and Cronk's method measures the imbalance of the overall tree structure rather than of particular nodes. The method compares the distribution of an imbalance measure, I , for all nodes, to the expected distribution under a Markovian model. Fusco and Cronk's method has the advantage of being applicable to phylogenies containing polytomies. Purvis *et al.*'s correction ensures that imbalance, I' , is independent of the number of species within a node (Purvis *et al.*, 2002). The median of the distribution of imbalance I' values is compared with the expected median of 0.5 using a Wilcoxon signed-ranks test (Purvis *et al.*, 2002). Because we do not have a robust time line to our phylogeny, we cannot ensure that terminal taxa are of the same age (Avisé & Johns, 1999). As such differences in age can significantly affect imbalance patterns unless species numbers are considered (Katzourakis *et al.*, 2001), we included the species richness of each genus in both tests. Both measures of imbalance were calculated using the program *mesa* (Agapow & Purvis, in prep., available from <http://www.agapow.net/software/mesa/>).

Data

We compiled a database of morphological, life history, ecological and geographical information for as many agamid species as possible from the literature (see Appendix 1 for literature sources). Literature-derived information was supplemented with information obtained from museum specimens (Appendix 2). Where possible, five individuals of each sex, for each species were examined. Average values for each genus were derived from as many species for which data were available (Table 1). Genus average values were log transformed prior to analysis. For variables with 0 values the transformation was $\log(x + 1)$. The dataset used for all analyses is given in Appendix 3. In total, we collected data on five indices that have been predicted to be linked to variation in species richness: body size, life history, sexual selection, ecological generalism and biogeography.

Body size was measured in millimetres as the mean snout-vent length (SVL) of males and females combined.

Table 1 Proportion of species per genus for which data was available for each variable.

Variable	Number of genera	Mean proportion of species per genus \pm SD
Body size	48	0.77 \pm 0.25
Clutch size	40	0.57 \pm 0.32
Size dimorphism	43	0.61 \pm 0.28
Color dimorphism	37	0.56 \pm 0.33
Ornament dimorphism	49	0.79 \pm 0.24
Habitat generalism	48	0.69 \pm 0.30
Latitudinal midpoint	48	0.70 \pm 0.31
Range size	46	0.70 \pm 0.31

Where data for only one sex was available, or where sex was not specified, we used this value instead. Where data was available for more than one population we used the mean value.

Variation in life history was measured in terms of modal clutch size. Where a range of clutch sizes was given, we used a value halfway between the extremes. Data on number of clutches per year and longevity were not available for the majority of species so we were unable to derive measures of yearly or lifetime reproductive output. Data on age at first reproduction or generation time were also too poor to include in the analysis.

We used three indices of the intensity of sexual selection. The first measure was sexual size dimorphism (SSD), calculated as the percentage difference between mean male and female SVLs, where the male was larger. Much of the size data used for this index was obtained from museum specimens (Appendix 2). If the female was larger, the species was given a SSD value of 0 because processes other than sexual selection are more likely to be responsible for larger female than male size (reviewed in Shine, 1989). The second measure was the extent of sexual dichromatism, which was a count of the number of body regions for which the sexes were dichromatic, ranging from 0 to 11. The 11 body regions used were: crown, lateral region of the head, throat, chest, ventral region, anterior dorsal, posterior dorsal, flanks, forelimbs, hindlimbs and tail. Body regions were scored as dichromatic only if they differed in colour (hue), not merely intensity. The third measure of the intensity of sexual selection is the degree of dimorphism in ornament, which was a weighted index based on a count of dimorphic physical features (ornaments). If the ornament was present in both sexes, but relatively larger in the male, it was given a value of 1. If only the male possessed the ornament, it was given a value of 2. Total ornament dimorphism was calculated as the sum of the values for seven ornament types, and thus ranged between 0 and 14. The seven categories of ornament were: nape crest/spines; dorsal crest/spines; tail crest/spines; enlarged cheeks; gular pouch; rostral appendage; supra-ocular spines/ridges. Both dichromatism and

ornament dimorphism were scored from a combination of photographs and species descriptions. Where there was documented geographical variation in any of the above morphological variables, we took the maximum value. For instance, if one population of species *x* was dichromatic for the lateral head region in one population, but not another, that body region was classed as dichromatic.

An index of ecological generalism was derived based on a count of the number of discrete habitat types occupied by each species across its entire geographical range. The 14 habitat categories used were as follows: (1) rock-outcrops/crevice dwelling, (2) riparian, (3) montane cloud forest, (4) primary rainforest, (5) secondary rainforest, (6) forest edges/ecotones, (7) stony desert, (8) sandy desert, (9) semi-desert/savanna, (10) arid acacia woodlands, (11) open woodlands, (12) seasonally dry (monsoon) forest, (13) seasonally dry wetlands, (14) heath/dunes/coastal, (15) human-inhabited/highly disturbed. Although most species occupy more than one of these habitat types, occupation of one type of habitat does not necessarily entail occupation of any of the other habitats. Therefore, the habitat categories are effectively discrete and a simple count may be used as a surrogate for habitat generalism at the macroecological scale of analysis. Other studies have examined diet, or a surrogate for diet, as a measure of ecological generalism (e.g. Katzourakis *et al.*, 2001). However, most agamid species are insectivorous, consuming a wide variety of arthropod prey types, so this variable is not informative for our analysis.

The biogeographical variables that we used were the latitudinal midpoint for the species range to test whether species richness is associated with latitude. We also calculated approximate range size by mapping ranges onto a global 1° grid and calculating area of the resulting polygon, in thousands of square kilometres, using the GIS program ArcView. Approximate ranges were mapped using information from point range maps, shaded distribution maps and detailed range descriptions. We did not use data where descriptions of sex differences, habitat or distribution were vague. For example, if the distribution was described as Iran, Afghanistan and Pakistan, or habitat was described simply as 'rainforest', such information was not used.

Comparative analysis

We used phylogenetically independent contrasts for all statistical tests because closely related taxa are often more similar to one another than expected by chance alone (Harvey & Pagel, 1991). First, we examined possible correlations between predictor variables, using univariate regression through the origin, based on independent contrasts for each pair of predictor variables generated in CAIC (Purvis & Rambaut, 1995). Because many of the predictor variables were intercorrelated, we subsequently used a multiple regression model to test for associations

between the predictor variables and species richness. In this multiple regression model, we used a backwards model selection procedure whereby all variables are initially included within the model and at each step, the variable contributing least to variance reduction is dropped until only significant variables remain (see Purvis *et al.*, 2000). The criterion for remaining within the model was set at $P = 0.1$ significance level and again the model was forced through the origin. The multiple regression model was based on independent contrasts for each variable, calculated using the software MacroCAIC (Agapow & Isaac, 2002), which is specifically designed for comparative analyses of correlates of species richness. In this analysis, branches were assumed to be of equal length. Simulation studies have shown that, in the absence of independent branch length information, setting branches to equal lengths yields acceptable type I error rates for larger sample sizes, and performs better than branch lengths estimated using alternative methods (e.g. algorithms based on tree topology) (Ackerly, 2000).

Results

Tree imbalance

The distribution of species richness among genera within the Agamidae (Fig. 2) is not consistent with the Markovian null model of cladogenesis. According to the Slowinski–Guyer test, six of the 19 bifurcating nodes subtending more than 40 species were significantly imbalanced (Table 2). This was significantly more than expected by chance (binomial test: $P < 0.001$) (Katzourakis *et al.*, 2001). However, four of these significant nodes are nested and therefore not independent. If these four nested nodes are treated as one, so that only three of 19 possible nodes are considered significant according to the Slowinski–Guyer test, this is still significantly more than expected by chance ($P < 0.05$).

The Fusco–Cronk measure of tree imbalance (Fusco & Cronk, 1995; Purvis *et al.*, 2002) also rejects the Markovian model. With species richness included, the median

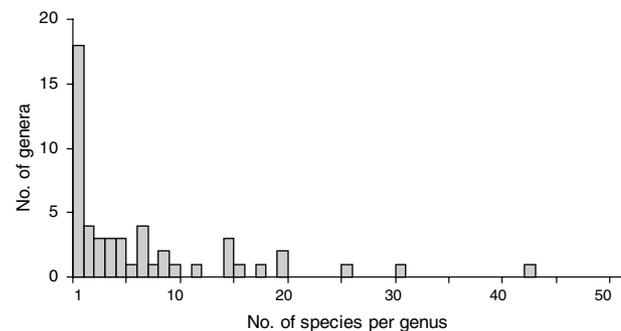


Fig. 2 Frequency histogram of the number of species per genus within the Agamidae.

Table 2 Nodes in the complete phylogeny that are significantly imbalanced according to the Slowinski–Guyer tests and Fusco–Cronk measure of imbalance for each of those nodes. The code refers to the position of the node on the phylogeny (Fig. 1).

Node	Code	Larger clade	Smaller clade	I_w
<i>Leiolepis</i> vs. sister clade	A	345	7	0.997
<i>P. cocincinus</i> vs. sister clade	B	84	1	1
<i>Moloch</i> vs. sister clade	C	71	1	0.986
<i>P. lesueuri</i> vs. sister clade	D	68	1	1
<i>Hydrosaurus</i> vs. sister clade	E	257	3	0.996
<i>Phrynocephalus</i> vs. <i>Bufo</i> clade	F	43	1	0.977

imbalance I for the 39 bifurcating nodes within the complete phylogeny was 0.85, which is significantly greater than the expected median value of 0.5 (Wilcoxon signed-ranks test: $W = 190.5$, $P < 0.005$). This result is also true for Macey *et al.*'s molecular phylogeny ($n = 35$, median = 0.72, $W = 200$, $P = 0.05$).

Correlates of species richness

There were significant associations between many of the predictor variables (Table 3). Size was significantly correlated with clutch size, size dimorphism, ornament dimorphism and habitat. Clutch size was significantly correlated with the latter three variables. Size dimorphism was significantly correlated with range size, in addition to size, ornament dimorphism, clutch size and habitat. Finally, dichromatism was significantly correlated with latitude and range size. The nonindependence of predictor variables emphasizes the need to incorporate multiple variables into tests of correlates of species richness, rather than examining each variable independently as has been carried out in most previous studies.

Using a backwards stepwise multiple regression model, we found that only two variables explained a significant portion of the variance in species richness: sexual dichromatism and SSD ($n = 26$, $F = 4.03$, $P < 0.03$). This model explained 25% ($r^2 = 0.251$) of the total variation and the variables SSD and sexual dichromatism

Table 4 Results of the multiple regression model testing for associations between predictor variables and species richness, controlling for phylogeny.

	Partial r^2	Coefficient	t	P -value
(a) Variables included in final model				
Size dimorphism	0.128	-3.36	2.68	0.013
Dichromatism	0.123	6.52	2.00	0.056
(b) Variables excluded from final model				
SVL	<0.001	-1.05	0.02	0.886
Ornament	0.001	-0.84	0.04	0.836
Range size	0.018	-0.99	0.58	0.455
Latitude	0.051	-4.69	1.69	0.208
Clutch size	0.037	4.49	1.19	0.288
Habitat generalism	0.032	-3.72	1.01	0.325

The regression model is based on independent contrasts from MacroCAIC and is forced through the origin. A backwards stepwise procedure was used for the model. SVL refers to body size (snout-vent length), 'ornament' refers to dimorphism in morphological ornamentation.

were significant, or marginally so ($P = 0.0135$ and $P < 0.0565$ for SSD and dichromatism, respectively, Table 4). The slopes for these variables indicate a negative relationship between species richness and SSD, but a positive relationship between species richness and dichromatism. No other variable entered the final model or explained a significant portion of variance in univariate models of species richness.

Discussion

Our results indicate that the distribution of species richness among genera of Agamid lizards is inconsistent with the distribution expected from a Markovian model of random cladogenesis. The best available phylogenetic tree for agamids contains more nodes that are significantly imbalanced according to the Slowinski–Guyer test than expected by chance alone. In addition, the overall tree has a significantly imbalanced branching structure according to the Fusco–Cronk test. This suggests that

	SVL	Clutch size	Size dimorphism	Ornament	Dichromatism	Habitat	Latitude	Range size
SVL	–	<0.001	<0.001	<0.001	0.47	<0.01	0.86	0.54
Clutch size	0.39	–	<0.001	0.03	0.20	<0.001	<0.001	0.84
Size dimorphism	0.43	0.32	–	<0.01	0.09	0.02	0.08	0.46
Ornament	0.39	0.12	0.23	–	0.55	<0.01	0.25	0.79
Dichromatism	0.02	0.06	0.09	0.01	–	0.99	0.01	0.03
Habitat	0.17	0.30	0.16	0.16	0.00	–	0.16	0.39
Latitude	<0.001	0.27	0.08	0.03	0.18	0.05	–	0.70
Range size	0.01	0.001	0.02	<0.01	0.15	0.02	<0.01	–

Figures below the diagonal show R^2 values, whereas figures above the diagonal show P -values above. n ranges between 27 and 40. SVL refers to body size (snout-vent length), 'ornament' refers to dimorphism in morphological ornamentation, 'habitat' refers to habitat generalism.

Table 3 Associations among predictor variables, controlling for phylogeny. Regression models are based on independent contrasts from CAIC and are forced through the origin.

deterministic, rather than purely stochastic processes, may influence net rates of cladogenesis in the Agamidae. Similar tests have consistently shown that the distribution of species or subspecies amongst higher taxa tends to be highly skewed and significantly different to that expected by chance for a broad range of taxa, including plants, invertebrates and many vertebrate groups (Dial & Marzluff, 1989; Guyer & Slowinski, 1991; Ricklefs & Renner, 1994; Purvis *et al.*, 1995; Owens *et al.*, 1999; Katzourakis *et al.*, 2001). It is this nonrandom distribution of species richness that suggests to us that it is worthwhile searching for general deterministic processes that influence rates of speciation and extinction.

Sexual selection and species richness

Of the eight variables we tested, only SSD and sexual dichromatism predicted species richness. Increases in species richness are associated with increases in sexual dichromatism but decreases in SSD. We interpret these results to suggest that sexual selection may influence the net rate of cladogenesis in agamid lizards. Several previous phylogenetic comparative studies have found associations between species richness and surrogates for the strength of sexual selection. Mating system, feather ornamentation, and plumage dichromatism have all been shown to be associated with species richness in birds (Barraclough *et al.*, 1995; Mitra *et al.*, 1996; Moller & Cuervo, 1998; Owens *et al.*, 1999). Evidence for the latter is particularly convincing and consistent between different studies (Barraclough *et al.*, 1995; Owens *et al.*, 1999). These results have been interpreted as strong evidence that divergence in female preferences drives speciation in birds. However, apart from birds, phylogenetic comparative evidence for the role of sexual selection in promoting diversification is available for very few other taxa.

Theoretical evidence that sexual selection may increase rates of diversification suggests the most likely mechanism is divergence in female mate preferences and consequent reproductive isolation between populations (Lande, 1981; Price & Schluter, 1993; Turner & Burrows, 1995; Payne & Krakauer, 1997; van Doorn *et al.*, 1998; Higashi *et al.*, 1999; Seehausen & van Alphen, 1999; Kirkpatrick & Ravigne, 2002). Although the evidence for female choice in lizards is at best equivocal (Olsson & Madsen, 1998), many lizard taxa display striking sexual dichromatism and males of many species possess ornaments such as rostral horns, dewlaps, gular sacs and crests. This is particularly true of agamids, chamaeleons and their new-world sister group, the iguanids. This has led to the suggestion that the dominant mechanism of sexual selection in lizards is male competition (Stamps, 1983; West-Eberhard, 1983; Tokarz, 1995). Colour patches may be used as badges of status among males and have been shown to affect the outcome of male contests in some lizard species (reviewed in Olsson & Madsen, 1998). Although the theoretical and empirical evidence is

weaker, sexual selection via the mechanism of male competition may also promote divergence and ultimately speciation (West-Eberhard, 1983). For instance, it is thought that in some taxa active female choice plays a relatively minor role in determining the pattern of mating and that variation in reproductive success is largely the result of male–male aggression (reviewed in Andersson, 1994). Under this scenario it is plausible that local-adaptation in the traits employed in male–male combat may lead to allopatric speciation without the need for active species recognition. Therefore, it is also possible that the relationship between species richness and dichromatism in agamids reflects the action of sexual selection through the mechanism of male competition.

Another possibility is that the extent of dichromatism reflects selection for inter-specific, rather than intra-specific signalling functions. Selection for specific mate recognition (Paterson, 1993) is expected to maximize interspecific differences in coloration, where species occur in sympatry (Ratcliffe & Grant, 1983). If selection for species recognition is more important in males, perhaps because of selection to minimize costly territorial conflicts among males, a by-product may be greater sexual dichromatism (Losos, 1985; Macedonia *et al.*, 1994; Macedonia & Stamps, 1994). Because there is likely to be a higher probability of closely related species occurring in sympatry for species rich than species poor lineages, selection for species recognition could account for the relationship between species richness and dichromatism observed in agamids. Empirical evidence suggests that colour is important for species recognition in *Anolis*, one of the most species rich genera of lizards (e.g. Williams, 1977; Losos, 1985; Macedonia *et al.*, 1994; Macedonia & Stamps, 1994).

The negative correlation between SSD and species richness is more difficult to interpret. Why might members of species rich groups be highly dichromatic, but less dimorphic? Owens & Hartley (1998) have shown that whereas dichromatism is associated with the frequency of extra-pair paternity, size dimorphism is associated with social mating system (social polygamy) and sex differences in parental care in birds. These authors suggested that the difference they observed reflected different evolutionary mechanisms: whereas dichromatism reflects cryptic female choice, size dimorphism reflects intra-sexual competition, which may not be a good indicator of the strength of sexual selection (Owens & Hartley, 1998). Notably, SSD is not correlated with species richness in birds, mammals, butterflies or spiders (Owens *et al.*, 1999; Gage *et al.*, 2002). This suggests that in these taxa at least, it is intersexual selection (mate choice), rather than intrasexual selection (male–male competition) that is implicated in origin of variation in species richness.

In the case of agamid lizards the available evidence does indeed indicate that SSD is determined largely by factors other than mate choice. For instance, there is

evidence that size dimorphism may be associated with territoriality, social polygyny and male–male competition in lizards (Stamps, 1983; Olsson & Madsen, 1998). Size dimorphism in lizards is also known to reflect ecological factors, such as resource partitioning (Shine, 1989; Perez-Mellado & De la Riva, 1993; Magurran, 1998). In contrast, there is little experimental evidence that, in lizards, body size is used in a cue during mate choice (reviewed in Olsson & Madsen, 1998). Thus, we cautiously suggest that the negative association between species richness and size dimorphism reported here may reflect mechanisms other than intersexual selection (female choice). Instead, we suggest that it most likely that the association between SSD and species richness is a manifestation of a mechanism other than intersexual selection, such as resource partitioning. That observed differences may be because of a correlation with another unknown variable is a problem common to all phylogenetic comparative studies (Price, 1997; Martins, 2000). The biological significance of the relationship between SSD and species richness, and the possible mechanisms involved, warrants further investigation, particularly at the species-level scale of analysis.

Body size and life history

We found no evidence that species richness is associated with body size or life history. Although the body-size hypothesis has been tested more often than any other explanation for patterns of species richness, the majority of phylogenetic comparative tests have similarly failed to show that body size is related to species richness at the family level or below (Dial & Marzluff, 1988; Nee *et al.*, 1992; Gittleman & Purvis, 1998; Gardezi & Da Silva, 1999; Owens *et al.*, 1999; Katzourakis *et al.*, 2001; Orme *et al.*, 2002). It is probable that a linear relationship between body size and species richness may only hold at higher taxonomic levels. At lower taxonomic levels, there is evidence that the more speciose lineages are those with intermediate body sizes rather than those at either extreme of the size spectrum (Hutchinson & MacArthur, 1959; Dial & Marzluff, 1988; Rosenzweig, 1995). Indeed, in an analysis applying advanced phylogenetic methods to a large range of taxonomic groups, Orme *et al.* (2002) consistently found no association between body size and species richness at the species level.

Although we found no evidence for a relationship between clutch-size and species richness, it is possible that other life-history traits influence speciation rates. Life-history traits used in studies of species richness vary greatly. Marzluff & Dial (1991) found evidence that species richness is associated with short generation time, measured as age at first reproduction. However, they found no correlation with fecundity, although conclusions from their results are restricted to higher taxonomic groups (birds and mammals) and tempered by limited

taxonomic sampling. Owens *et al.* (1999) similarly found no relationship between clutch size and species richness among avian families and Katzourakis *et al.* (2001) found no relationship between species richness and ovariole number in hoverflies. Given this weight of evidence and the results of the present study, it appears likely that, in general, fecundity does not influence speciation rates. Whether short generation time is a general correlate of species richness at different taxonomic levels remains to be determined.

Ecological and biogeographical factors

We also found no evidence to support the hypotheses that ecological or biogeographical factors may influence rates of speciation. Such factors have often been invoked to explain patterns of species richness (e.g. MacArthur *et al.*, 1966). However, the mechanisms involved have seldom been clearly articulated and this has resulted in a lack of clear predictions. Phylogenetic comparative evidence for an association between species richness and ecological generalism or range size is similarly equivocal. Although some studies have found a positive relationship between degree of ecological generalism and species richness (Ricklefs & Renner, 1994; Owens *et al.*, 1999; Katzourakis *et al.*, 2001), specialist adaptations have also been shown to be associated with species richness (e.g. phytophagy in insects, Mitter *et al.*, 1988). However, there is little evidence for a relationship between species richness and range size (Gaston & Blackburn, 1997). Our results for agamid lizards suggest that higher speciation rates are associated with neither habitat generalism, nor range size. These results support the view that the evolutionary history of geographical patterns of speciation is likely to be masked by post-speciational changes in range size, given that this trait appears to be particularly labile and not heritable in the same way as intrinsic biological traits of organisms (Gaston & Blackburn, 1997). At any single snapshot in time, higher taxa are likely to consist of both wide-ranging generalists, which have colonized new habitats and regions in the past, as well as habitat specialists and species with small geographical ranges that have become isolated and speciated, perhaps through a process of ecological character displacement. It may be more informative, therefore, to examine biogeographical factors at the species level (see Barraclough *et al.*, 1998; Barraclough & Vogler, 2000).

Methodological issues

There are limits to the inferences that can be drawn from phylogenetic comparative studies of processes influencing net rates of cladogenesis. Some of these limitations are general to the comparative method, whereas others are specific to this study. The most important general limitation is that phylogenetic correlations alone cannot

unambiguously identify a causal relationship. Our discussion of the relationship between sexual selection and speciation must, therefore, remain somewhat speculative. Having said that, it would not be trivial to obtain direct experimental evidence on the role of sexual selection in speciation, so it is likely that this sort of comparative analysis will remain the best evidence available for some time (Bennett & Owens, 2002).

Turning now to the limitations of this study, the first is that any conclusions are necessarily dependent on the accuracy of the phylogenetic hypothesis used. In addition, although branch length information was available for Macey *et al.*'s molecular phylogeny, insertion of missing taxa necessitated the use of equal branch lengths and the punctuational model of evolution assumed by this method may be inappropriate for some characters (e.g. see Gaston & Blackburn, 1997). Therefore, results could conceivably differ given a better-resolved phylogeny with branch lengths. A second limitation of this particular study is that there may be biases in taxon sampling when using species-level information to obtain genus-average values (Blackburn & Gaston, 1998). However, sampling biases in the present study are likely to be small, relative to other macroecological studies, in which a few well known taxa or sister group pairs are often used to make inferences on a much broader range of taxa. A third limitation of this study is that the indices of sexual selection and habitat specificity are necessarily coarse, given the available data and scale of analysis. Much noise is likely to be associated with most of the variables used. However, if noise within the dataset is distributed randomly, it is likely to obscure patterns. Results most likely indicate patterns that are detectable despite, rather than because of, the relatively coarse data and scale of analysis. It is nevertheless possible that error is distributed nonrandomly within the data. Having said this, macroecological studies such as ours have identified many interesting, and often unexpected, patterns of diversity, despite the limitations of available phylogenetic and biological information (Nee *et al.*, 1996; Purvis, 1996; Barraclough *et al.*, 1998).

In summary, this study provides the first evidence that sexual dichromatism correlates with species richness in nonavian taxa. Sexual dichromatism may be a useful indicator of the strength of sexual selection, or selection for visual signals. In addition, possible sex differences in ecology, inferred from the relationship with SSD, may influence speciation or extinction rates in this group. Finally, results reported here add to the growing evidence, now available for a broad range of taxa, that body size, fecundity and range size are not generally associated with species richness at lower taxonomic levels, once phylogenetic relationships have been taken into account. This is despite the prevalence of these types of explanation for nonrandom patterns of species richness in the literature.

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