

Sexual size dimorphism in anurans

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Several hypotheses have been proposed to explain the direction and extent of sexual size dimorphism in anurans (in which males are usually smaller than females) as a result of sexual selection. Here, we present an analysis to test the hypothesis that sexual dimorphism in anurans is largely a function of differences between the sexes in life-history strategies. Morphological and demographic data for anurans were collected from the literature, and the mean size and age in each sex were calculated for 51 populations, across 30 species and eight genera. Comparisons across 14 *Rana* species, eight *Bufo* species and across the genera showed a highly significant relationship between size dimorphism, measured using the female–male size ratio, and mean female–male age difference. A comparison of a subset of 17 of these species for which phylogenetic information was available, using the method of independent contrasts, yielded a similar result. These results indicate that most of the variation in size dimorphism in the anura can be explained in terms of differences in the age structure between the sexes in breeding populations. If sexual selection has an effect on size dimorphism in anurans, it is likely to be only a secondary one.

Keywords: size dimorphism; anurans; age; life history

1. INTRODUCTION

Females are larger than males in 90% of anuran species (Shine 1979). Several attempts have been made to explain this pattern of size dimorphism as a consequence of sexual selection. Shine (1979) suggested that males are larger than females in anuran species in which males engage in physical combat with one another. His methodology was criticized by Halliday & Verrell (1986), who considered his allocation of species into ‘combat’ and ‘non-combat’ groups to be inaccurate, and further by Halliday (1987), on the grounds that it is invalid to compare these categories of species without taking phylogeny into account (Felsenstein 1985). Woolbright (1983) proposed another model to explain sexual dimorphism, based on three assumptions: (i) sexual selection favours large males; (ii) sexual selection for increased male size is greater in species with longer breeding seasons; and (iii) energetic constraints on male body size depend on the relative duration of the breeding as opposed to the growth season. However, none of these appears to be correct (Sullivan 1984). Woolbright (1985) countered by claiming that existing data were insufficient either to affirm or to reject these assumptions. Arak (1988) developed a model based on counteracting selective pressures from natural selection for optimal body size, and sexual selection for large body size in male and female anurans. He tested this model successfully for nine species of anurans, and found a significant relationship between sexual dimorphism in body size and the difference between male and female selection gradients (Lande & Arnold 1983). Thus, males were smallest relative to females in species in which the reproductive selection gradients for males were lowest relative to the reproductive selection gradients for females. Although it explains most of the variation in the extent of sexual dimorphism between species, Arak’s model fails to

account for the direction of sexual dimorphism. Both Woolbright’s (1985) and Arak’s (1988) models, however, fail to address the issue of the non-independence of data points on account of systematic bias (Felsenstein 1985).

The approach by Arak (1988) was the first to incorporate demographic factors, although these are not specified. As size dimorphism will be the result of ‘the difference between the sum of all the selective pressures affecting the size of the female and the sum of those affecting the size of the male’ (Ralls 1976, p. 259), differences in life-history strategies between the sexes (Halliday & Verrell 1986) are likely to affect it. Sex differences in age at first breeding and longevity, in particular, are likely to be important determinants of both the direction and the extent of size dimorphism.

Over the past 20 years, skeletochronology has been widely used in studies of anuran populations, as it has proved to be a reliable determinant of the individual age of amphibians (e.g. Hemelaar 1988; Kusano *et al.* 1995a). The method is based on the presence of lines of arrested growth (LAGs) recorded in cross-sections of long bones (Halliday & Verrell 1988; Castanet & Smirina 1990), the annual periodicity of which has been demonstrated in several temperate (Smirina 1972; Hemelaar & Van Gelder 1980), desert (Sullivan & Fernandez 1999) and tropical anuran species (Guarino *et al.* 1998; Khonsue *et al.* 2000). The enumeration of LAGs in anuran phalanges has since been used to assess age, age at sexual maturity and longevity, and allows for the collection of demographic information on anuran populations much more rapidly than mark–recapture methods (Halliday & Verrell 1988), so that much more data are now available about demographic parameters in natural populations.

The aim of this study was to use the life-history data collected (with one exception; Briggs & Storm 1970) from skeletochronological studies of wild anuran populations to test whether the size ratio of males: females can be explained by differences between the sexes in the mean age at which they breed. In doing so, we make use of the

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comparative method (Felsenstein 1985; Garland *et al.* 1992) to control for the non-independence of data points caused by systematic bias.

2. METHODS

Demographic and morphological data on mean age and size for both sexes were collected from published studies of 51 breeding anuran populations, across 30 species and eight genera (table 1). The two genera with the largest number of species were *Bufo* ($n = 8$) and *Rana* ($n = 14$). When data were available for different years for the same population, the mean values for the population were calculated as algebraic means of values for each year, weighted by the sample size, so as to minimize the weight of years with small sample sizes; in cases where data were available for different populations of the same species, mean values for the species were calculated as algebraic means of population values, regardless of the sample size. The mean female–male size ratio (SSD) and the mean female–male age difference (MAD) were calculated for each species. These two variables were correlated across the eight genera, across the eight *Bufo* species and across the 14 *Rana* species, for which we also performed a linear regression after testing the data to make sure they were normally distributed. Values for the genera were calculated as algebraic means of species values.

As this simplistic approach of comparative studies has been widely criticized for over-estimating the independence of individual species' data points (Felsenstein 1985; Pagel & Harvey 1989), we used, in addition, the comparative method of independent contrasts described by Felsenstein (1985) and reviewed by Garland *et al.* (1992). The entire dataset could not be used, because phylogenetic relationships among 13 taxa were unresolved. We used Case's (1978) phylogeny for *Rana*, Graybeal's (1997) phylogeny for *Bufo* and the phylogeny of Hay *et al.* (1995) for the higher nodes of the anuran tree. As those trees do not all display the same information about branch lengths, they were first set arbitrarily as suggested by Pagel (1992), and mean size and age in both sexes for ancestral nodes were calculated as the algebraic mean of the two closest lower nodes, according to Felsenstein's (1985) method. With 17 species at the tips of this reconstructed tree, 16 ($17 - 1$) SSD and MAD pairs of contrasts could be computed for pairs of nodes sharing an immediate common ancestor, and then re-scaled and analysed as suggested by Garland *et al.* (1992) and Diaz-Uriarte & Garland (1996). Computer simulations by Diaz-Uriarte & Garland (1996) have shown that Felsenstein's (1985) method yields acceptable type I error rates under Brownian motion, but inflates rates under other models. However, re-scaling branch lengths decreases the rates of type I error, and the maximum type I error rate never exceeds twice the nominal p value at 0.05. All tests were performed using SPSS v. 11.0 software.

3. RESULTS

SSD was positively correlated with MAD across the 14 *Rana* species (Spearman's rank correlation coefficient: $r_s = 0.678$, $p = 0.004$), across the eight *Bufo* species ($r_s = 0.881$, $p = 0.002$) and across the eight genera ($r_s = 0.810$, $p = 0.007$). All tests are one-tailed tests. Plots of SSD as a function of MAD are shown in figure 1. As SSD had a normal distribution (one-sample Kolmogorov–Smirnov two-tailed test: $Z = 0.438$, $p = 0.991$), as did mean age (one-sample Kolmogorov–Smirnov two-tailed

test: $Z = 0.641$, $p = 0.806$), we were able to perform a linear regression with SSD as the dependent variable and MAD as the independent variable, which also indicated a highly significant relationship across the 14 *Rana* species ($r^2 = 0.647$, $p = 0.001$). The residuals showed no heteroscedasticity, having a normal distribution (one-sample Kolmogorov–Smirnov two-tailed test: $Z = 0.735$, $p = 0.652$), and displayed no significant relationship when plotted as a function of the predicted SSD values (Spearman's rank correlation coefficient: $r_s = -0.073$, two-tailed $p = 0.805$).

The set of comparisons obtained from the phylogenetic tree (figure 2) was analysed as suggested by Garland *et al.* (1992) and Diaz-Uriarte & Garland (1996). As SSD and MAD standardized contrasts were negatively correlated with their standard deviations, branch lengths were re-scaled in order to minimize the correlation. The new set of SSD and MAD contrasts showed no significant correlation with their standard deviations (Spearman's rank correlation coefficient: $r_s = 0.060$ and $r_s = -0.077$, respectively; two-tailed $p = 0.824$ and $p = 0.777$, respectively) and had a bivariate normal distribution (one-sample Kolmogorov–Smirnov two-tailed test on SSD and MAD contrasts: $Z = 0.822$ and $Z = 0.623$, respectively; $p = 0.508$ and $p = 0.740$, respectively). A regression forced through the origin (figure 3) yielded significant results ($r^2 = 0.570$, $p < 0.001$), where r^2 measures the proportion of the variability in the dependent variable about the origin that is explained by the regression, and thus differs from r^2 for models that include a constant. Residuals showed no heteroscedasticity (Spearman's rank correlation coefficient between residuals and predicted SSD values: $r_s = 0.124$, two-tailed $p = 0.649$) and were normally distributed (one-sample Kolmogorov–Smirnov two-tailed test: $Z = 0.481$, $p = 0.975$), indicating that the regression is reliable. Removing the outlier (point B4; see figure 3) did not change any result significantly (regression forced through the origin: $r^2 = 0.529$, $p = 0.001$). Diaz-Uriarte & Garland (1996) suggest one degree of freedom should be subtracted for each transformation on branch lengths. The correlation coefficients of regressions (with or without the outlier) remain highly significant even when either one or two degrees of freedom is/are subtracted ($p < 0.005$ in both cases).

4. DISCUSSION

Comparisons across species and genera using standard techniques of correlation and regression as well as the comparative analysis indicate a highly significant correlation between SSD and MAD in anurans. Thus, in the species we have considered, SSD can be explained in terms of sex differences in the age structure of breeding populations. Whereas former studies have focused on differences in sexual selection between species, our results indicate that age differences between breeding males and females appear to have a major influence on the extent of dimorphism. Female anuran fecundity appears to be correlated with body size in all anuran species in which this phenomenon has been investigated, and, as anurans display indeterminate growth (Halliday & Verrell 1988), this could be expected to lead to faster growth rates and delayed reproduction in females. If females delay reproduction, one would expect them to live longer, both

Table 1. Species, location, mean size and age for both sexes and references of published papers for the 51 anuran populations considered in this study.

species	population	mean length (mm)		mean age (years)		reference(s)
		male	female	male	female	
<i>Bufo alvarius</i>	Arizona, USA	117.8	125	2.78	2.33	Sullivan & Fernandez (1999)
<i>Bufo cognatus</i>	Arizona, USA	70.4	70	3.19	3.25	
	Arizona, USA	64	73.6	2.5	3.38	
<i>Bufo punctatus</i>	Arizona, USA	52	59.2	2.27	2	
<i>Bufo bufo</i>	Netherlands	52.86	64.85	4.31	5.28	Hemelaar (1988)
	Germany	56.71	68.52	4.3	5.43	
	France	68.84	87.38	5.24	6.8	
	Norway	58.92	72.13	7.32	8.84	
	Switzerland	62.48	73.91	8.56	9.96	
<i>Bufo bufo</i>	mid-Wales, UK	57.29	69.5	3.39	4.8	Gittins <i>et al.</i> (1982)
<i>Bufo americanus</i>	Virginia, USA	64.8	82.3	3.11	4	Kalb & Zug (1990)
<i>Bufo americanus</i>	Illinois, USA	64.32	71.48	2.58	3.49	Acker <i>et al.</i> (1986)
<i>Bufo pardalis</i>	South Africa	96.06	110.67	1.88	3.17	Cherry & Françillon-Vieillot (1992)
<i>Bufo achalensis</i>	Argentina	60.71	53.37	5.36	4.38	Sinsch <i>et al.</i> (2001)
<i>Bufo pentoni</i>	Sénégal	58.7	64.2	3.88	3.91	Françillon <i>et al.</i> (1984)
<i>Mantidactylus microtympanum</i>	Madagascar	74.7	94.1	4.1	4.9	Guarino <i>et al.</i> (1998)
<i>Scaphiopus couchii</i>	Arizona, USA	52.4	50.4	2.13	2.33	Sullivan & Fernandez (1999)
<i>Hyla arborea</i>	southern Germany	43.07	44.35	3.08	3.26	Friedl & Klump (1997)
<i>Hyla crucifer</i>	Maryland, USA	26.46	28.4	2.58	2.8	Lykens & Forester (1987)
<i>Xenopus laevis</i>	south Wales, UK	59.9	63.3	3.71	3.87	Measey (2001)
<i>Alytes obstetricans</i>	Spain	41.74	49.69	2.34	3.68	Marquez <i>et al.</i> (1997)
<i>Alytes cisternasii</i>	Spain	35.79	38.58	2.43	3.15	
<i>Pelobates fuscus</i>	France	45.87	53.89	3.57	4.56	Eggert & Guyétant (1999); Eggert (2000)
<i>Rana catesbeiana</i>	Canada	105.3	113.2	4.41	5.25	Shirose <i>et al.</i> (1993)
<i>Rana septentrionalis</i>	Québec, Canada	61.1	67.9	2.19	2.42	Leclair & Laurin (1996)
	Québec, Canada	52.6	58.6	1.3	1.7	
<i>Rana iberica</i>	lowland, Spain	36.93	43.53	2.26	2.53	Esteban & Sanchiz (2000)
	mountain, Spain	41.33	48.75	3.04	3.37	
<i>Rana subaquavocalis</i>	Arizona, USA	84.85	104.84	4.73	6.1	Platz <i>et al.</i> (1997)
<i>Rana sakuraii</i>	Japan	44.9	48.8	3.25	3.45	Kusano <i>et al.</i> (1995b)
<i>Rana sylvatica</i>	Québec, Canada	43.6	48.8	2.49	2.76	Sagor <i>et al.</i> (1998)
<i>Rana sylvatica</i>	high altitude, Virginia, USA	55.3	64.4	2.89	3.56	Berven (1982)
	lowland, Maryland, USA	41.7	47.7	1.16	1.99	
<i>Rana sylvatica</i>	Québec, Canada	43.6	49.3	2.82	3.22	Bastien & Leclair (1992)
<i>Rana luteiventris</i>	Nevada, USA	54	57	1.7	2	Reaser (2000)
<i>Rana cascadae</i>	Oregon, USA	44.3	39.8	1.99	1.51	Briggs & Storm (1970)
<i>Rana perezi</i>	Spain	52	65.6	2.32	3.54	Esteban <i>et al.</i> (1996)
<i>Rana temporaria</i>	Ireland	62.17	66.62	2.9	3.26	Gibbons & McCarthy (1984)
<i>Rana temporaria</i>	east France	61.14	64.52	3.13	3.06	Augert & Joly (1993)
	east France	55.98	57.41	2.82	2.85	
<i>Rana temporaria</i>	Swiss Alps, altitude 650 m	73.7	81.6	4.38	4.72	Ryser (1988)
	Swiss Alps, altitude 1930 m	74.6	80.6	6.6	8.3	Ryser (1996)
<i>Rana temporaria</i>	French Alps, altitude 2300 m	77.8	83.6	8.33	8.38	Miaud <i>et al.</i> (1999)
<i>Rana rugosa</i>	Gondoike, Japan	41.2	53.2	1.52	2.24	Khonsue <i>et al.</i> (2001b)
	Iwakura, Japan	41.4	53.4	1.78	2.07	
	Kiyotaki, Japan	43.1	57.4	1.89	2.52	
<i>Rana nigrovittata</i>	Thailand	50.6	45.3	3.7	3.29	Khonsue <i>et al.</i> (2000)
<i>Rana nigromaculata</i>	Katata, Japan	63.6	75.9	3.27	4.1	Khonsue <i>et al.</i> (2001a)
	Shizuhara, Japan	66.7	76.3	3.42	4.08	
<i>Rana tagoi tagoi</i>	Ichinosawa, Japan	42.2	44.2	2.9	3.2	Kusano <i>et al.</i> (1995a)
	Kamiange, Japan	41.7	42.2	2.7	3.2	

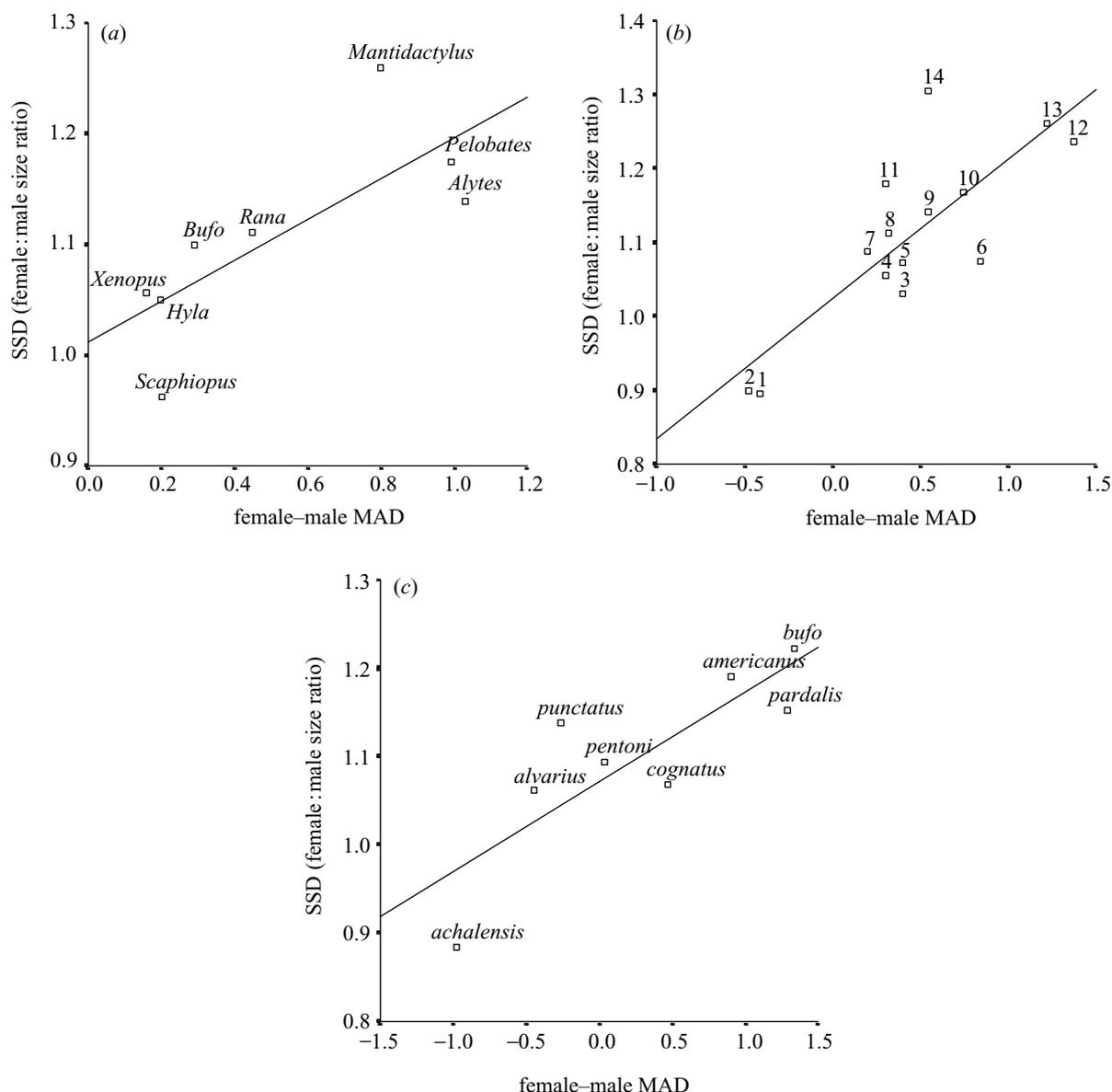


Figure 1. SSD (female–male size ratio) as a function of female–male mean age difference (MAD) in (a) eight anuran genera; (b) 14 *Rana* species; and (c) eight *Bufo* species. The numbers in (b) refer to: *R. nigrovittata* (1); *R. cascadae* (2); *R. tagoi tagoi* (3); *R. luteiventris* (4); *R. temporaria* (5); *R. catesbeiana* (6); *R. sakuraii* (7); *R. septentrionalis* (8); *R. sylvatica* (9); *R. nigromaculata* (10); *R. iberica* (11); *R. subaquavocalis* (12); *R. perezii* (13); and *R. rugosa* (14).

because of energetic investment in reproduction and because it is usually during breeding that they are particularly vulnerable to predation. In the minority of species (*Bufo achalensis*, *Rana cascadae*, *R. nigrovittata* and *Scaphiopus couchii*) in which females are smaller than males, in all cases except *S. couchii* males are the older sex, indicating that delayed maturity in males in these cases is related to size dimorphism. More generally, any factor affecting the demographic characteristics of one sex appears to influence size dimorphism, as this reflects sex differences in age structure. Sexual selection for body size is one such factor: where increased male body size is an important determinant of male mating success, males should not be expected to forego growth in order to breed earlier than females.

Some reservations may apply to our methodology. First, population age structure in anurans has often been shown to be unstable (e.g. Augert & Joly 1993; Friedl & Klump

1997; Sullivan & Fernandez 1999), so that mean age and size for both sexes may vary considerably between years in the same population. In some cases our data were based on only a single year. The age of frogs is, in most cases, given as a number of LAGs, and skeletochronological assessment of an individual's age can be problematic because of resorption of the first lines (Hemelaar 1981) and the presence of double or false lines (Frañillon & Pascal 1986). However, if there is systematic bias in ageing individuals, it should affect male and female age in the same way, in which case considering MAD should remove any such bias. Both potential sources of error, mainly linked to natural and experimental constraints, are, therefore, likely to constitute only random noise, and should not have systematically biased our results.

Results of regressions and correlations across a group of species (figure 1*b,c*) should be handled cautiously as species' data points cannot be assumed to be statistically

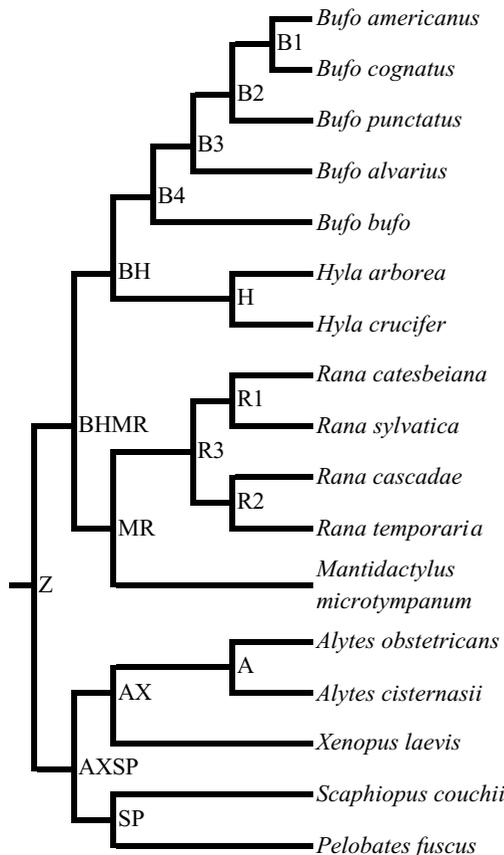


Figure 2. The phylogenetic tree of the anura used in the comparative analysis, after Case (1978); Hay *et al.* (1995) and Graybeal (1997).

independent (Felsenstein 1985; Pagel 1992) and, indeed, computer simulations have indicated a higher type I error rate using this method compared with other comparative methods (Martins & Garland 1991; Diaz-Uriarte & Garland 1996). Concerning the generic comparisons (figure 1a), using mean values of variables of the species within each genera implies a simultaneous radiation pattern of phylogeny from the genera node to species, which is, of course, very unlikely, but has the advantage of allowing us to incorporate all our data in the calculation. Making across-genera comparisons and thus treating them as independent points implies a similar branching pattern and may result in the same type of errors. However, as pointed out by Harvey & Pagel (1991), conclusions from generic comparisons should not be considered as worthless, provided the data do not depend on a cluster of points that share an immediate common ancestor, which is not the case in the anuran genera we considered (Hay *et al.* 1995).

We can assume that the species for which we have data were randomly chosen among all anuran species, or at least do not display a systematic bias in terms of SSD or age structure, as only one of these studies contained an explicit reference to size dimorphism (Marquez *et al.* 1997). Although the number of species considered (17 in the phylogenetic analysis and 30 in the analysis across and within genera) represents only a tiny proportion of anuran diversity, our results indicate that SSD in the anura can largely be explained in terms of age differences between the sexes.

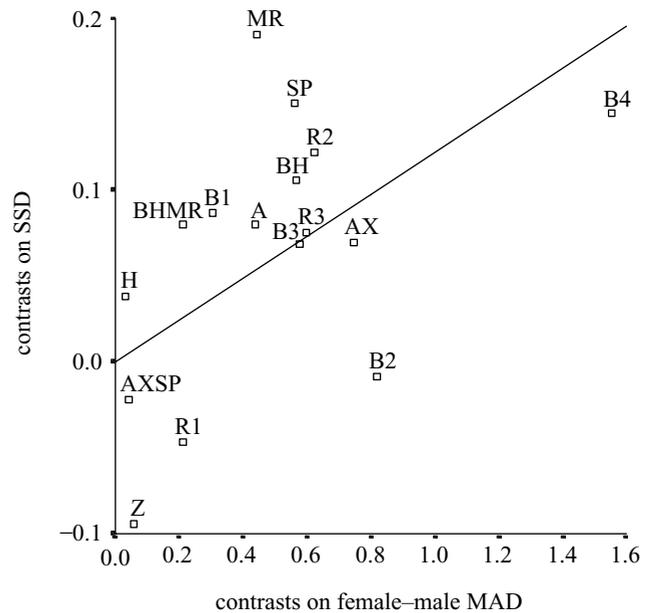


Figure 3. SSD (female-male size ratio) contrasts plotted against female-male mean age difference (MAD) contrasts calculated from the phylogenetic tree in figure 2, using the method of independent comparisons (Felsenstein 1985; Garland *et al.* 1992). The letters refer to the node in figure 2 immediately ancestral to the taxa used in each comparison. The line is a linear regression through the origin ($r^2 = 0.570$; $p < 0.001$).

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