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Sexual selection and sex ratios in *Anolis* lizards

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Abstract

Biased sex ratios, or unequal numbers of males and females in a population, can alter the intensity of sexual selection by enhancing competition for mates, and thus may affect the evolution of reproductive strategies. Studies of sex ratio variation across a clade provide an opportunity to examine the morphological or behavioral consequences of different levels of sexual selection. We examined sex ratio variation, using phylogenetic comparative methods, across a diverse clade of terrestrial vertebrates, the *Anolis* lizards. Across a sample of 14 species in 21 localities, we found remarkable bidirectional variation in sex ratios across the *Anolis* clade: males are more common in some populations and females in others. However, we find no evidence that sex ratio bias is associated with sexual size dimorphism, a proxy for sexual selection. Nor do we find an association of sex ratio bias with ecological niches (i.e. ecomorphs), which vary in sexual selection pressures and mating systems. The observed inter-specific variation in sex ratio suggests that a balance of different, possibly opposing, factors, including sex-specific dispersal and mortality rates, may play a role in determining population sex ratio.

Introduction

The population sex ratio reflects both the distribution and availability of potential mates, and thus affects sexual selection within a species (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996). Skew in adult sex ratio often corresponds with differences in the variation in average reproductive success within each sex (Emlen & Oring, 1977; Donald, 2007). If the sexes differ in their variance in reproductive success, divergent mating strategies for each sex are favored; this phenomenon is exemplified by polygynous mating systems, in which females discriminate between possible mates, while males compete for access to mating opportunities (Trivers, 1972; Emlen & Oring, 1977; Kokko & Jennions, 2008).

Variation in adult sex ratio can be observed across geographically distinct populations within a single species, while the sex ratio of a single population can also change across multiple generations. If such changes in sex ratio are persistent across multiple generations in their bias toward a single sex, they can lead to alterations in patterns of sexual selection within a population, modifying the intensity of both inter-sexual and intra-sexual selection. This phenomenon of increased sexual selection due to sex ratio bias has been observed across multiple taxa in both natural populations and experimental manipulations: within-sex competition and mate selection strategies respond to changes in sex ratio skew in plants (Sanderson *et al.*, 2016), insects (Linklater *et al.*, 2007), amphibians (Pröhl, 2002; Jones, Arguello & Arnold, 2004), fish (Grant, Bryant & Soos, 1995; Mills & Reynolds, 2003), birds (Pruett-Jones & Lewis, 1990) and mammals (Mitani, Gros-Louis & Richards, 1996). Studying the causes and consequences of biased sex ratios may therefore uncover a framework for the evolution of mating systems, and by extension, reflect the strength of sexual selection in different species (Emlen & Oring, 1977; Pipoly *et al.*, 2015). Specifically, if one sex is limited in a population, the other, more common, sex is expected to compete more for mating opportunities and thus be under stronger sexual selection (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996; Jones *et al.*, 2004; Kokko & Jennions, 2008). Despite the important role that sex ratio may play in mating systems and patterns of sexual selection, the consequences of variation in sex ratio among diverse members of a clade remain unclear (Pipoly *et al.*, 2015).

Here, we report variation in sex ratios across and within species using a diverse clade of reptiles: lizards in the genus *Anolis*. Anoles are well-known for their ecological niche diversification, and species vary in territoriality, sexual dimorphism and mating systems (reviewed in Losos, 2009). Greater Antillean anole species are grouped into six main ecological niches, or ecomorphs (trunk-crown, trunk-ground, trunk, grass-bush, twig and crown-giant), that have independently evolved multiple times on different islands (Williams, 1972; Losos *et al.*, 1998). These ecomorphs are also characterized by different degrees of sexual size dimorphism (Butler, Schoener & Losos, 2000; Butler, Sawyer & Losos, 2007), a measure that often corresponds to the degree of sexual selection in a lineage (Andersson, 1994; Mitani *et al.*, 1996). We would therefore expect that a population will exhibit a bias in sexual size dimorphism toward the more common sex, as a result of increased sexual selection pressure. In addition, as both sexual size dimorphism and mating systems diverge between ecomorphs, we expect an association between biased sex ratios and ecomorph class. To date, this hypothesis has not been examined, and few comparative data are available on anole sex ratios. Understanding these correlations between sex ratio and sexual selection provides additional information on whether biased sex ratios, and the opportunity they provide for sexual selection, can influence the evolution and divergence of anole species.

We examined sex ratios of 14 species of *Anolis* lizards in 21 localities. These species occupy four different islands and four ecomorph types in the Caribbean, with one species in mainland North America. For six of these species, we also examined the sex ratio in multiple localities to determine the extent of intra-specific variation in sex ratio. Our aims were (1) to quantify sex ratios in species across the *Anolis* clade and determine if these ratios varied across species, (2) to test the hypothesis that sex ratios converge by ecomorph class or level of sexual dimorphism and (3) to examine the level of sex ratio variation within a species.

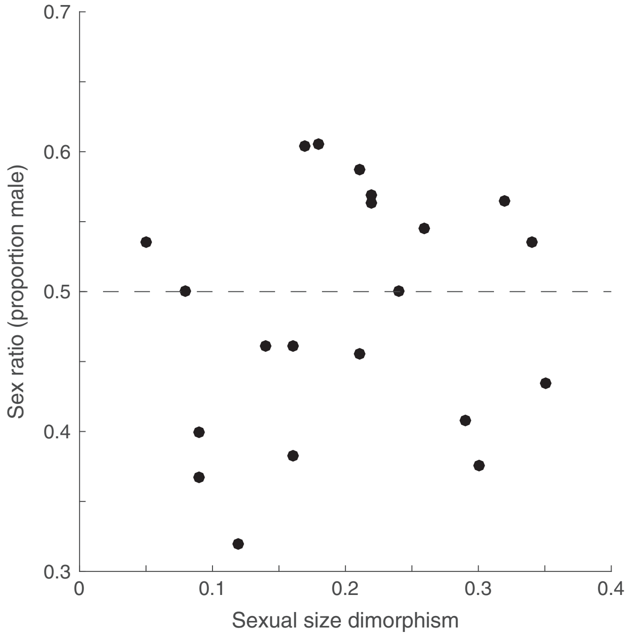

Figure 1 Sex ratio versus sexual size dimorphism. Sex ratio is represented as the proportion of males among adults in the population, while sexual size dimorphism was calculated dividing the average SVL of the larger sex by the average SVL of the smaller sex, and subtracting 1 for each population. Each circle represents 1 of the 21 localities sampled in this study. The dashed line represents an equal sex ratio of 0.5. We found no relationship between sexual size dimorphism and sex ratio across the 21 localities (PGLS: adjusted $R^2 = -0.08$, $P = 0.86$).

Materials and methods

We chose four sites on Jamaica, Puerto Rico, Dominican Republic and South Bimini, Bahamas, with each study site containing multiple anole species. We also chose a site in southeast Texas to sample multiple localities of the North American mainland anole, *Anolis carolinensis*, as a comparison to the island populations. All anole species have male heterogametic sex determination and so their sex ratios at conception will not be directly affected by different environments (Gamble *et al.*, 2014). At each site, we set up two or three 500–1000 m^2 plots and captured every individual found within each plot. In cases where we set-up paired plots to determine variation in sex ratios within a species (Dominican Republic and Jamaica), we chose two localities that were similar in species richness, population density, habitat availability and levels of direct sunlight to minimize environmental variation between the plots. In this way, we determined the level of sex ratio variation between localities without confounding habitat differences. At our mainland site, we sampled three localities from a single forested area that differed in microhabitat type. Additional details on the study plots are available in Johnson, Revell & Losos (2010) and Dill *et al.* (2013).

Every individual within a plot was captured and permanently tagged with beads sewn into the tail (Fisher & Muth, 1989) or temporarily marked with bee marking tags (Johnson, 2005). We recorded snout–vent length (SVL) and sex for each individual, and released it at its site of capture for subsequent behavioral observations over the next several weeks. The sex of each individual was determined by a combination of everting the hemipenes of males, palpating large eggs in the abdomens of females and visual inspections of dewlap size in species with sexually dimorphic dewlaps. We tagged any new anoles entering the plots during the observation period to include all available individuals of each sex within our observed area. By continuously observing each plot for multiple weeks, we censused the entire anole population within a given area, and accurately estimated the sex ratio of a population. We calculated sex ratios as the proportion of males among adults in the population, where 0.5 indicated an equal sex ratio. All plots were observed at approximately the same time of year (May–early July) in summer, during the height of the mating season (Losos, 2009; Johnson *et al.*, 2010).

Because we had two or three localities for six species in our dataset, we performed all analyses including both localities, and included each locality from the species individually (i.e. without its paired population) to determine whether the duplicate locality had an effect on our results. No results changed significantly under this treatment, and so all results are reported with both localities of each species included for analysis.

We performed chi-squared tests on each species or locality to determine whether they deviated significantly from our null expectation of a 1:1 (i.e. 0.5) sex ratio (Table 1). We used Fisher's test of combined probabilities on these results to

Table 1 Sex ratios across *Anolis*

	Ecomorph	Population size	Males	Females	Sex ratio	*P* value	SSD (category)	SSD (SVL)
Jamaica								
A. valencienni	TW	87	32	55	0.37	0.01	Low	0.09
A. lineatopus (1)	TG	103	58	45	0.56	0.20	High	0.22
A. lineatopus (2)	TG	72	41	31	0.57	0.24	High	0.22
A. grahami (1)	TC	79	36	43	0.46	0.43	High	0.21
A. grahami (2)	TC	54	27	27	0.50	1.00	High	0.24
Bimini								
A. angusticeps	TW	48	29	19	0.60	0.15	Low	0.17
A. sagrei	TG	43	23	20	0.53	0.65	High	0.34
A. smargadinus	TC	38	23	15	0.61	0.19	High	0.18
Dominican Republic								
A. baharucoensis	GB	52	24	28	0.46	0.58	Low	0.16
A. olssoni	GB	43	23	20	0.53	0.65	Low	0.05
A. cybotes (1)	TG	46	27	19	0.59	0.24	High	0.21
A. cybotes (2)	TG	44	24	20	0.55	0.55	High	0.26
A. coelestinus (1)	TC	32	12	20	0.38	0.16	High	0.30
A. coelestinus (2)	TC	46	26	20	0.57	0.38	High	0.32
Puerto Rico								
A. krugi (1)	GB	36	18	18	0.50	1.00	Low	0.08
A. krugi (2)	GB	50	16	34	0.32	0.01	Low	0.12
A. cristatellus	TG	81	33	48	0.41	0.10	High	0.29
A. gundlachi	TG	115	50	65	0.43	0.16	High	0.35
United States								
A. carolinensis (1)	TC	39	18	21	0.46	0.63	High	0.14
A. carolinensis (2)	TC	50	20	30	0.40	0.16	High	0.09
A. carolinensis (3)	TC	60	23	37	0.38	0.07	High	0.16

All sex ratios reported from a survey of 21 *Anolis* localities. Ecomorph categories have been abbreviated as follows: TW (twig), TG (trunk-ground), TC (trunk-crown), GB (grass-bush). Sex ratios are the proportion of males among adults in the population. SSD indicates sexual size dimorphism; SSD category classifications are taken from Butler *et al.* (2000), while SSD (SVL) was calculated within each locality by dividing the average snout-vent length of males by the average snout-vent length of females and subtracting 1 within each study locality. *P* values reported are the results of a chi-squared test against a null hypothesis of an equal number of males and females in the population (see Materials and Methods).

determine whether the overall sex ratios of all of the anole species differed from 1:1. We also tested for significant differences between our paired localities using Welsh's two-sample *t* test. Across all populations, the mean number of males was 28 (range = 12–58) and the mean number of females was 30 (range = 15–65).

We sampled lizards from four ecomorphs: trunk-ground, trunk-crown, grass-bush and twig anole species. We tested for association between ecomorph class and sex ratio with phylogenetic ANOVA using the geiger package (Harmon *et al.*, 2008) in R (R Development Core Team, 2014). We determined whether there was phylogenetic signal in sex ratio using Blomberg's *K* and Pagel's lambda, calculated using the phytools package (Revell, 2012) in R. Because anole ecomorph classes fall into two categories of sexual size dimorphism (trunk-ground and trunk-crown species are highly sexually size dimorphic, whereas grass-bush and twig species are not; Butler *et al.*, 2000), we grouped species into high and low sexual dimorphism categories to examine the association between sex ratio and sexual selection, using phylogenetic ANOVA. We also tested for effects of locality and island on population sex ratio using phylogenetic ANOVA. We calculated the specific sexual size dimorphism of each species or locality by dividing the average SVL of the larger sex by the average SVL of the smaller sex, and subtracting 1 (Lovich & Gibbons, 1992), although males were the larger sex in all our populations. We conducted a regression using a phylogenetic generalized least squares (PGLS) regression analysis, using the caper package (Freckleton, Harvey & Pagel, 2002) in R, to determine whether the sexual size dimorphism of a population was associated with the sex ratio of that population (Butler *et al.*, 2000). All phylogenetic analyses were performed with average sex ratios for each species, and using the squamate phylogeny in Pyron, Burbrink & Wiens (2013) pruned to include only the species in this study.

Results

We found a range of sex ratios across species and localities (Fig. 1), from a female bias of 0.32 (*Anolis krugi*) to a male bias of 0.61 (*Anolis smaragdinus*), with an average sex ratio of 0.48 (Table 1). While sex ratios varied substantially among species, only two populations diverged significantly ($P < 0.05$) from an expected 1:1 sex ratio (Table 1; *Anolis valencienni* and *Anolis krugi* (2), $P = 0.01$), both with an excess of females relative to males. Fisher's test of combined probabilities was significant when we included all of our populations ($P = 0.016$), suggesting that females are more common than males in anole populations, but not when we removed the *Anolis valencienni* and the second *Anolis krugi* locality ($P = 0.18$). We also tested for differences in sex ratio between our paired anole localities within a single species, but found no significant differences. We found no relationship between population size and the degree of sex ratio bias in that population ($R^2 = 0.04$).

We found no evidence that ecomorph categories varied in sex ratio (phylogenetic ANOVA, $F_{3,10} = 0.09$, $P = 0.96$), or that sex ratio differed between the high and low sexual size dimorphism ecomorph classes (phylogenetic ANOVA: $F_{1,12} = 0.23$, $P = 0.60$). We also found no evidence that the sexual size dimorphism of a species, based on male to female SVL measurements, was related to its sex ratio (PGLS: adjusted $R^2 = -0.08$, $P = 0.86$; Fig. 1). Finally, there was no effect of locality (phylogenetic ANOVA: $F_{6,7} = 2.2$, $P = 0.31$) or island (phylogenetic ANOVA: $F_{4,9} = 3.5$, $P = 0.19$) on sex ratio, and no phylogenetic signal in sex ratio ($\lambda = 6.61$ e-05; $K = 0.66$, $P = 0.71$).

Discussion

We find a range of both male- and female-biased sex ratios across anole species, from 0.32 (about one male to every two females) to 0.61 (about three males to every two females). Our results fall within those of previous studies on adult sex ratios in anoles, which have reported values as low as 0.31 and as high as 0.76 (*Anolis sagrei*; Schoener & Schoener, 1980). If stable over time, this level of variation is likely to have a large impact on intra-sexual competition for mates and the selection strategies of the rare sex, which could lead to the establishment of different mating systems (Emlen & Oring, 1977; Donald, 2007).

Despite the variation in sex ratio that we observed among species, only two of 21 sex ratios significantly diverged from our null expectations of an equal number of males and females. The extremely female-skewed sex ratio of *Anolis valencienni* (0.37) is surprising, as it is a twig anole species with very low sexual dimorphism (Hicks & Trivers, 1983; Butler *et al.*, 2000). This species is cryptic and arboreal, which can make detection and capture of individuals difficult; female *A. valencienni* also perch lower in trees than males on average (Johnson, 2007), and so our ability to detect males (from the ground) may have been compromised if they were using the highest available perches. However, our extended behavioral observations of our study population and our success at capturing every individual we saw, regardless of sex, does provide support for our reported sex ratio. In addition, the other cryptic and arboreal twig anole species in our dataset, *Anolis angusticeps*, has a male-biased sex ratio, suggesting that any capture bias in these species was limited.

Remarkably, previous behavioral work on *Anolis valencienni* reported almost no territoriality or sex-specific resource competition, a rare observation in anoles (Hicks & Trivers, 1983). This behavioral information suggests that males should not undergo increased mortality compared to females within this species, as they likely suffer no additional costs of territory or resource defense. Because the costs of survival and reproduction should be more similar for both sexes in this species compared to species with a higher degree of polygyny, we would predict an approximately equal adult sex ratio in this species (Hicks & Trivers, 1983; Andersson, 1994). Our results may indicate greater variability in mating pattern or reproductive costs than previously inferred in this species, or the presence of sex-specific effects on dispersal or mortality.

Anolis krugi, the other species with a significantly biased sex ratio (0.32) in one of the two studied localities, also has an extremely female-biased sex ratio and low sexual size dimorphism, yet we have no reason to believe that our detection and capture of this species was sex biased as the result of their habitat use. However, the paired *Anolis krugi* locality does not show any skew in sex ratio. This may indicate that sex ratio is primarily influenced by highly localized population dynamics rather than species-level factors. In general, the highly skewed sex ratios we observed may indicate that the factors influencing sex ratio in anole populations are more complex than simple sex-specific differential mortality. This conclusion is further supported by the lack of a relationship across species between sex ratio and both the degree of sexual size dimorphism or ecomorph.

While we find variation in sex ratio between and within anole species, this variation could be attributed to random fluctuations around a true population sex ratio of 1:1 (Williams, 1979). Although we did obtain large sample sizes for some species, the sample size for most species is relatively low and so we may lack power to detect statistically significant skew in sex ratio. The variance of the binomial distribution of our statistical tests is greatest at the mean, and therefore skew from an equal sex ratio is intrinsically difficult to detect. Assuming a true underlying sex ratio of 0.4 (or 0.6), we would need population sizes of *c.* 780 lizards to detect a significant skew away from equality 80% of the time. Population sizes this large will be difficult to find for many anole species, and may simply not exist for many others. Thus, the differences in sex ratio we report may have biological meaning, even though this dataset cannot show statistically significant sex ratio skew. Indeed, detecting significant sex ratio skew may not be possible for a wide range of vertebrates with low population sizes if the sex ratio bias is not extreme. The biological meaning of biased sex ratios should therefore be assessed separately from whether this skew is statistically significant (Donald, 2007). This issue is especially critical in threatened or declining populations, where high levels of sex ratio bias may have dire effects on conservation efforts (Donald, 2007).

If sex ratio variation is real and maintained over time, the number of available mates for males and females is dramatically different, favoring different reproductive strategies for each sex (Emlen & Oring, 1977). In anoles, this variation could promote migration between populations, especially sex-biased dispersal of individuals between populations in search of potential mates. In addition, anoles may be able to bias the sex of their offspring; strong sex ratio skew may provide a selective advantage to individuals who can produce offspring of the less frequent sex (Fisher, 1930; Cox *et al.*, 2011). Ideally, further observations of sex ratio in anoles with large sample sizes across multiple years will clarify whether this pattern of variation has a biological basis. Our intra-specific sex ratio comparisons also illustrate potential flaws in the use of adult sex ratios as representative of species, given the high level of variation in sex ratio we observe between nearly identical localities (Pipoly *et al.*, 2015); measurements of adult sex ratios between and within anole species may indicate whether species in this clade can be accurately characterized by a single sex ratio. We present the strengths and limitations of our study of sex ratios here to demonstrate the potential power of our approach for future studies of sex ratios of species in highly variable environments; this is especially true when strong intra-population sex ratio differences are suspected. Sex ratios across populations and clades may provide more information on sex-specific causes of mortality or dispersal, along with suggesting the potential for divergence in mating systems within and between species and confirming theoretical predictions on the prevalence of sex ratio skew.

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