

Influence of microhabitat, fecundity, and parental care on the evolution of sexual size dimorphism in Caribbean *Eleutherodactylus* frogs

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Received December 30, 2021

Accepted August 29, 2022

Rensch's rule suggests that sexual size dimorphism (SSD) increases with species size when males are the larger sex, whereas it decreases when females are the larger sex. However, the process responsible for this pattern remains obscure. SSD can result from sexual selection, such as intrasexual competition for access to mates, or from natural selection, due to resource partitioning or fecundity selection. We studied SSD in Caribbean *Eleutherodactylus* frogs using phylogenetic comparative methods to investigate the influence of microhabitat, fecundity, and parental care. Our results show that in Caribbean *Eleutherodactylus* females tend to be larger and, contrary to Rensch's rule, dimorphism increases with species size. SSD was not related to microhabitat use. However, SSD was positively correlated with fecundity, mediated by a greater increase in female size. SSD was also influenced by parental care, suggesting that male care promotes larger male size and reduces the female bias in SSD. As suggested for other anurans, female-biased SSD in Caribbean *Eleutherodactylus* results from fecundity selection, although the magnitude is countered by increased male size in species with paternal care. Our results highlight the importance of considering various selective forces that may act in concert to influence the evolution of SSD.

KEY WORDS: *Eleutherodactylus*, fecundity selection, frogs, parental care, Rensch's rule, sexual dimorphism.

Sexual dimorphism, that is, phenotypic differences between the sexes of the same species beyond their reproductive organs, has long intrigued evolutionary biologists. The pervasive occurrence of marked, and often extravagant, sexually dimorphic traits even complicated the drafting of the emerging theory of evolution by natural selection, leading Darwin to introduce the concept of sexual selection in his masterpiece (Darwin 1859). The concept of sexual selection was then more extensively developed in his book "The Descent of Man, and Selection in Relation to Sex" (Darwin 1871), devoted to explaining the persistence of these traits that seemed to represent an obstacle to the survival of individuals.

Sexual size dimorphism (SSD) is possibly the most ubiquitous kind of sexual dimorphism and the one that has attracted most attention, probably because it can be easily measured and compared between species. Studies across several animal groups led to the observation of a general pattern, with larger males compared to females (SSD biased toward males) in most birds, mammals, and lizards, and larger females than males (SSD biased toward females) in invertebrates, fish, amphibians, turtles, and snakes (Fairbairn et al. 2007), although with numerous exceptions (e.g., Stephens and Wiens 2009; Nali et al. 2014; Brandt et al. 2016). In the mid-20th century, the German biologist

Bernhard Rensch proposed an allometric rule in relation to SSD (Rensch, 1950, 1959), later known as Rensch's rule, which proposes a positive association between SSD and body size in taxa where males are the larger sex (hyperallometry) and a negative relationship in groups where females are larger (hypoallometry; Abouheif and Fairbairn 1997; Fairbairn 1997). Although these predictions may seem independent, both could be the result of male body size evolving faster than female body size, resulting in a positive allometry (i.e., larger males in large bodied species, but smaller males in small-bodied species: Fairbairn 2012; De Lisle and Rowe 2013). However, tests of Rensch's rule have produced ambiguous results (Abouheif and Fairbairn 1997; Fairbairn et al. 2007). Most studies support the prediction of Rensch's rule when SSD is male biased (Webb and Freckleton 2007; Stephens and Wiens 2009), although with notable exceptions (Martínez et al. 2014; García-Navas et al. 2016). However, the pattern does not seem to hold when females are the larger sex (Head 1995; Tubaro and Bertelli 2003; Webb and Freckleton 2007; Stephens and Wiens 2009; Liao et al. 2013b; Nali et al. 2014), although some studies support it (Stuart-Fox 2009).

Investigating the origin of SSD has proven to be an even greater challenge. Sexual selection, as proposed by Darwin, has been found to be associated with SSD in comparative analyses across different taxa (reviewed in Fairbairn et al. 2007); however, it is not the only explanation. As noted early on by Wallace (1889), natural selection can also lead to SSD, for example, because of resource partitioning between the sexes (Krüger 2005; Krüger et al. 2014), due to fecundity selection acting on females (Andersson 1994; Fairbairn 2013), or to division of parental care duties (Houston and McNamara 2002; Mank et al. 2005). Sexual selection, particularly competition between males, is often cited as a driver of male-biased SSD in mammals, birds, and lizards (Cox et al. 2007; Dale et al. 2007; Lindenfors et al. 2007; Székely et al. 2007), whereas selection for increased fecundity is generally seen as an important explanation of the biased SSD pattern toward females in other animals (Cox et al. 2007; Foellmer and Moya-Laraño 2007; Kupfer 2007; Stephens and Wiens 2009), but other factors also influence SSD across taxa (Fairbairn et al. 2007). Although rarely included in analyses of factors influencing the evolution of SSD (but see Mank et al. 2005; Han and Fu 2013; Monroe and Alonzo 2014), parental care patterns may play an important role. Strong sexual selection acting on males is proposed to select against investment in care (Queller 1997; Gonzalez-Voyer et al. 2008; Kokko and Jennions 2008), whereas high female investment into egg production may limit their ability to also provide care (Gross and Sargent 1985). Ultimately, SSD is likely the result of a combination of selective forces and/or evolutionary constraints as well as different evolutionary rates of male

and female size. This is the reason why the effect of any alleged cause for the dimorphism must be investigated separately for each sex (Blanckenhorn 2005; Fairbairn et al. 2007; Carranza 2009), and when indicated and possible, both sexual selection and natural selection should be considered simultaneously (Krüger et al. 2014; Littleford-Colquhoun et al. 2019).

Direct-developing frogs of the genus *Eleutherodactylus* (Dumeril and Bibron 1841), or rain frogs, include about 200 species (Frost 2021) distributed from southern United States to northern Central America (Belize and Guatemala), and across the Caribbean islands, where the largest diversity of the genus is found (167 species). The elevated species richness of the Caribbean islands was recently found to be the result of replicate radiations on the islands accompanied by ecomorphological diversification and convergence (Dugo-Cota et al. 2019). Caribbean rain frogs have striking variation in size, including one of the smallest tetrapods in the world, the 10 mm *Eleutherodactylus iberia* (Estrada and Hedges 1996), and at the other extreme the more than 124 mm *Eleutherodactylus zeus* (García 2012). They inhabit very diverse microhabitats, including leaf litter, rocky areas, river courses, tree canopies, the interior of caves, or in terrestrial and arboreal bromeliads, which are associated with specific phenotypic differences (Díaz and Cádiz 2008; Henderson and Powell 2009; Dugo-Cota et al. 2019). They also show important differences in fecundity, ranging from one to more than 100 eggs per clutch (Henderson and Powell 2009), and various types of parental care (Townsend 1996; Wells 2007). This later feature is relatively exceptional, even among amphibians, and seems associated to terrestrial reproduction (Vági et al. 2019). Despite the staggering diversity of *Eleutherodactylus* frogs, few studies to date have addressed SSD and its causes in this group, except for Woolbright's (1989) work with *E. coqui*. Further, previous studies on SSD across frogs included only a few *Eleutherodactylus* species (i.e., 20 species included in Monroe and Alonzo [2014] and Monroe et al. [2015], four and three species in Han and Fu [2013] and Nali et al. [2014], respectively).

We used modern phylogenetic comparative methods to determine whether SSD follows Rensch's rule, whether SSD patterns are due to faster evolution of body size in males or females, and analyzed the ultimate drivers of SSD patterns across species of Caribbean *Eleutherodactylus* frogs. We analyzed (1) whether some microhabitats promote size differences among the sexes; (2) the fecundity selection hypothesis, which suggests that greater female size is associated with greater fertility; and (3) the effect of parental care, considering both paternal and maternal care, favoring different sizes between the sexes resulting from their role in offspring care.

Materials and Methods

SEXING AND MEASUREMENT OF SPECIMENS

We examined 1662 male and female adult *Eleutherodactylus* frogs conserved in 16 institutions from the United States, Cuba, Dominican Republic, and Mexico. On average, 23 specimens were measured per species for 139 species, which represents 83% of the species described in this genus for Caribbean *Eleutherodactylus* (Frost 2021). The sexing of specimens was performed by identifying secondary sexual characters such as vocal sacs and/or vocal slits, external observation of the presence of developed oviducts and/or eggs, or dissection for direct observation of the gonads. We measured snout-vent length (SVL) for all specimens using a Mitutoyo digital caliper (Model: 500–172) to the nearest 0.01 mm. The sexing and measurement of specimens was performed by a single investigator (AD-C) to avoid potential observer biases. Details on the number of specimens measured for each species and sex are shown in Table S1.

SEXUAL SIZE DIMORPHISM

SSD in size was calculated from the average SVL for each sex. The “Two-step ratio” index proposed by Smith (1999) was used as reformulated by Lovich and Gibbons (1992):

- if $\delta > \text{♀}$: $SSDi = SVL_{\delta} / SVL_{\text{♀}}$,
- if $\text{♀} > \delta$: $SSDi = 2 - SVL_{\text{♀}} / SVL_{\delta}$,

where $SSDi$ is the SSD index, and SVL_{δ} and $SVL_{\text{♀}}$ are the average SVL for adult males and females, respectively, of a given species. This $SSDi$ is linear, symmetrical, and intuitive, with positive values when females are not more than twice as large as the males, as was the case in our study. A value of $SSDi = 1$ indicates that males and females are equal in size, $SSDi < 1$ indicates that females are larger, and $SSDi > 1$ indicates that males are larger. At the same time, a value of $SSDi = 0.7$ would show that females were 30% larger than males, whereas an $SSDi = 1.3$ would imply that males were 30% larger. Table S2 shows the average values of SVL for males and females of each species and the corresponding $SSDi$.

ECOLOGICAL AND REPRODUCTIVE TRAITS

The classification of the species into 10 microhabitat types (aquatic, arboreal, bromeliculous, cavernicolous, fossorial, leaf-litter, petriculous, riparian, semiarboreal, and terrestrial), based on the habitat use and behavior of each species, was taken from a previous compilation (Dugo-Cota et al. 2019). In addition, we compiled information on the fecundity of 89 of the species from the literature: size of the clutches, number of eggs in the oviducts, or number of juveniles (Table S3). We chose to use the maximum value of those described in the literature, being cautious to avoid considering multiple clutches, of one or several females,

as has been recorded to occur in Caribbean *Eleutherodactylus* (Henderson and Powell 2009; Ríos-López et al. 2016; Alfonso et al. 2017). Similarly, we also compiled literature information on parental care for 40 species, classifying care into five categories: maternal, paternal, biparental, uncertain (no caring sex specified), or absent (Table S3). Parental care categories are inevitably somewhat contentious as it is unclear how many observations are sufficient to determine with certainty that care is uniparental or absent. Induction is inevitably fraught with uncertainty. Parental care was thus considered absent for a given species when researchers consider that the knowledge is sufficient to judge such behavior as absent in a given species. Therefore, we only categorized species as presenting no parental care when explicitly described as such.

COMPARATIVE PHYLOGENETIC METHODS

Observations from closely related species cannot be considered statistically independent because they share a common evolutionary history and therefore tend to resemble each other (Felsenstein 1985). To account for this, we used the most complete phylogeny available for the group (Dugo-Cota et al. 2019) and calculated the phylogenetic signal of $SSDi$ and all predictors using the K (Blomberg et al. 2003) and λ statistics (Pagel 1999) as implemented in the *phytools* package (Revell 2012). We found a significant phylogenetic signal in all cases ($P < 0.001$, see Table S4), justifying the use of comparative phylogenetic methods in downstream analyses. For each analysis, species with missing data were excluded from the phylogeny.

Following Fairbairn and Preziosi (1994), the evaluation of Rensch’s rule was carried out with phylogenetic regression analysis of \ln -transformed SVL data (for males and females) using the *ppls* function of the R package *caper* (Orme et al. 2018). This approach allowed us to avoid regressing the size of either sex on $SSDi$, which is statistically nonindependent from the body sizes of either sex. We used the size of the males as the dependent variable and that of the females as the independent one. A slope of $b > 1$ indicates that the data fit Rensch’s rule, where male size increases faster than female size in larger species. A slope of $b < 1$ would be contrary to Rensch’s rule, because female size would increase faster than male size in larger species (Fairbairn and Preziosi 1994; Fig. 1). To verify that the slope was significantly different from 1, corresponding to the null hypothesis of an isometric relationship, a phylogenetic RMA (reduced major axis) regression was performed using the *phyl.RMA* function of the *phytools* package (Revell 2012). Although the statistical relationship between male and female SVL can be better explained by a correlation test, we opted for this approach to incorporate nonindependence due to shared ancestry, as well measurement error in the independent variable.

To compare rates of evolution of male and female body sizes, which could provide information about whether SSD

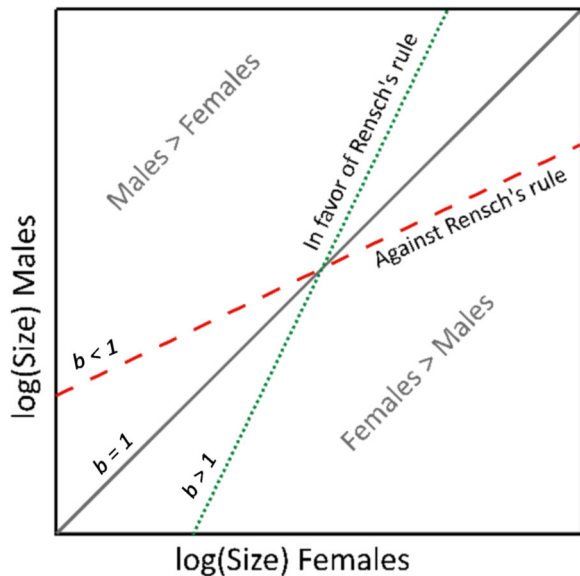


Figure 1. Potential allometric relationships between the size of males and females. The solid line indicates an isometric relationship ($b = 1$), the dotted line a relationship consistent with Rensch's rule ($b > 1$), and the dashed line against it ($b < 1$).

results from changes in sizes of males or females, we used the maximum likelihood method of Adams (2013). This method considers within-species variation in the estimates of evolutionary rates by incorporating the standard deviation of the measurements of each species to produce more precise estimates, as high within-species variation suggests there is a burst of phenotypic evolution at the tips of the branches of the tree. Furthermore, this method shows more desirable statistical properties than the methods based on phylogenetically independent contrasts (Felsenstein 1985, Adams 2013).

We assessed the possible differential response of the sexes to similar selective pressures by evaluating the relationship between $SSDi$, and male and female sizes taking microhabitat into account. The association with microhabitats was evaluated by means of an ANOVA using the RRPP method (Collyer and Adams 2018), a randomization procedure of residuals by permutation that results in a higher statistical power than phylogenetic ANOVAs in highly aggregated groups in the phylogeny (Adams and Collyer 2018), as is the case of microhabitats (groups of closely related species often use the same microhabitat). The analyses were performed with 1000 permutations using the RRPP package (Collyer and Adams 2018).

The effect of fecundity selection was assessed by analyzing the association between $SSDi$ and clutch size using the *ppls* function of the *caper* package (Orme et al. 2018) with a maximum likelihood estimate of the λ parameter as an estimate of phylogenetic signal in the residuals (Rohlf 2006; Revell 2010). The association between fecundity and the size of females and males

was also evaluated, as male size could also have an indirect effect on female fecundity.

To assess the effect of parental care on SSD and the size of each of the sexes, we used the RRPP method (Collyer and Adams 2018) considering paternal, maternal, biparental, and the absence of care. Despite collecting information for 40 species, the sample size for these analyses was 37 because for three of the species we had no information regarding the sex responsible for parental care (*Eleutherodactylus audanti*, *Eleutherodactylus melacara*, and *Eleutherodactylus zugii*).

The visual representations of the evolution of SSD and the size of males and females on the phylogeny were made with the *contMap* function of the *phytools* package (Revell 2012), which reconstructs the evolution of a continuous trait estimating the ancestral values via maximum likelihood. All the analyses were carried out in R 4.0.2 (R Core Team 2018).

Results

SSD IN CARIBBEAN *Eleutherodactylus*

Most of the 139 *Eleutherodactylus* species analyzed showed a clearly female-biased SSD, with an average $SSDi$ value of 0.75 (females 25% larger than males) ranging from 0.16 in *Eleutherodactylus oxyrhynchus* to 1.1 in *Eleutherodactylus hedricki* (females 84% larger than males and males 10% larger than females, respectively; Table S2). However, for the only species for which our measurements suggested that males were larger than females (*E. hedricki*), literature data show a much less pronounced male-biased dimorphism (maximum sizes recorded for each sex, $SSDi = 1.01$; Joglar 1998).

RENSCH'S RULE

Male and female sizes were positively correlated, as expected, and male size explained a significant proportion of the variation in female size ($R^2_{adj.} = 0.862$, $F_{(1,137)} = 860$, $b = 0.857$, standard error [SE] = 0.029, $\lambda = 0.347$, $P < 0.001$; Fig. 2). The estimated slope of the regression was significantly different from an isometric relationship (RMA phylogenetic regression, $P = 0.045$). Contrary to Rensch's rule, the relationship between male and female size was hypoallometric (see Fig. 1), indicating that female size increases faster than male size. Thus, SSD becomes increasingly female biased as species size increases. In agreement with these results, the rate of evolution for female body size was significantly higher than that for male body size (σ^2 for females = 0.024 [95% CI = 0.023–0.024] vs. σ^2 for males = 0.021 [95% CI = 0.020–0.021], Likelihood ratio test (LRT) = 572.646, $P < 0.001$) (Fig. 3).

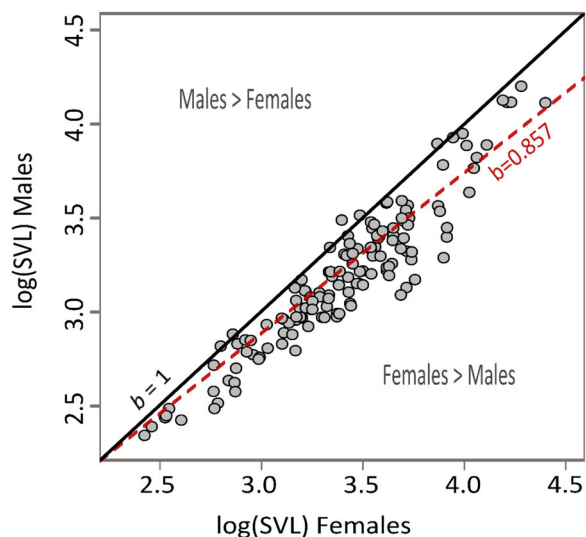


Figure 2. Allometric relationship between the size of males and females in Caribbean *Eleutherodactylus*. The solid line indicates a hypothetical isometric relationship. Male and female sizes are highly correlated ($R^2_{\text{adj.}} = 0.862$, $F_{(1,137)} = 860$, $b = 0.857$, $SE = 0.029$, $\lambda = 0.347$, $P < 0.001$). For almost all species, females are larger than males. The dashed line represents the slope calculated from the phylogenetic regression: $b = 0.857$ is significantly different from an isometric relationship $b = 1$ (phylogenetic regression of RMA, $P = 0.045$). The pattern of dimorphism is contrary to the prediction of Rensch's rule (see Fig. 1), increasing $SSDi$ toward females as the species size increases.

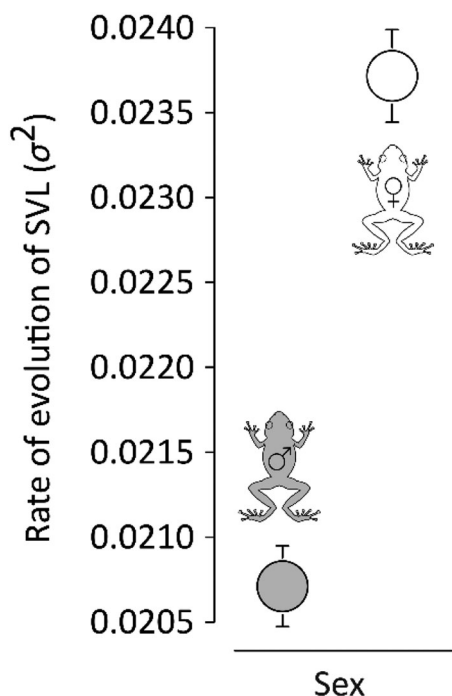


Figure 3. Estimated rate of evolution for male and female sizes. Female size evolves at a higher rate than male size (LRT = 572.646, $P < 0.001$).

MICROHABITATS

The phylogenetic ANOVA using the *RRPP* method showed no significant difference in $SSDi$ between microhabitats ($F_{(9,129)} = 0.480$, $R^2_{\text{adj.}} = 0.032$, $Z = -1.191$, $P = 0.882$; Fig. 4). However, we found significant differences when considering separately the size of males ($F_{(9,129)} = 5.275$, $R^2_{\text{adj.}} = 0.269$, $Z = 4.152$, $P = 0.001$) and females ($F_{(9,129)} = 2.733$, $R^2_{\text{adj.}} = 0.160$, $Z = 2.178$, $P = 0.02$), suggesting that the different microhabitats are associated with different species sizes (see also Dugo-Cota et al. 2019), but that the two sexes vary similarly across microhabitats. Leaf litter species were particularly small, for both males and females, whereas fossorial and cavernicolous species tended to be larger than species from other microhabitats.

FECONDITY

We found a significant negative association between $SSDi$ and fecundity ($R^2_{\text{adj.}} = 0.082$, $F_{(1,84)} = 8.565$, $b = -0.049$, $SE = 0.017$, $\lambda = 0.788$, $P < 0.001$), indicating that in species with larger clutch sizes $SSDi$ is more biased toward larger females (Fig. 5). At the same time, fecundity is positively associated with the size of males ($R^2_{\text{adj.}} = 0.405$, $F_{(1,84)} = 58.78$, $b = 0.202$, $SE = 0.026$, $\lambda = 0.858$, $P < 0.001$) and females ($R^2_{\text{adj.}} = 0.457$, $F_{(1,84)} = 72.56$, $b = 0.226$, $SE = 0.026$, $\lambda = 0.923$, $P < 0.001$). The observed pattern of SSD toward larger females could be a result of the steeper slope in the relationship between SSD and female size, although the slope is not significantly different from that for males (b for females = 0.226 ± 0.026 vs. b for males = 0.202 ± 0.026 ; Fig. 6).

PARENTAL CARE

Among the 40 *Eleutherodactylus* species for which information on the type of parental care was available, both sexes provided care (biparental) in four species (10%), for 11 species (27.5%) only the female provided care (maternal), for 20 species (50%) only the male provided care (paternal), for three species (7.5%) parental care was observed, but the sex of the caring parent was not specified (parental), and for two species (5%) parental care was considered to be absent. These data suggest that paternal care is common among Caribbean *Eleutherodactylus*. Absence of parental care in some species should be interpreted with caution due to limitations in research effort, a critical aspect to confirm the absence of a certain behavior.

Phylogenetic ANOVAs suggested that parental care was associated with $SSDi$ ($F_{(3,33)} = 4.559$, $R^2_{\text{adj.}} = 0.293$, $Z = 1.837$, $P = 0.01$). Note that species with parental care for which the sex of the carer was not specified were excluded from the analyses. According to post hoc tests, species with paternal care showed significantly decreased SSD (male size is closer to the female size, i.e., $SSDi$ closer to 1; Fig. 7) than in those with maternal care ($Z = 3.492$, $P = 0.004$) or species with biparental care

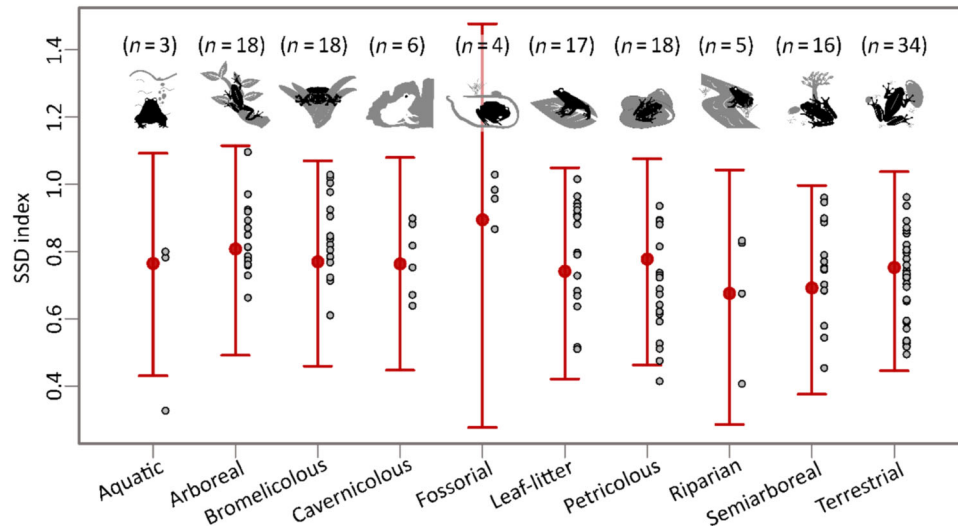


Figure 4. *SSDi*, mean size, and estimated range (IC-95%) in each microhabitat according to a phylogenetic ANOVA using the *RRPP* method. No significant differences were observed between microhabitats. The striking amplitude of the confidence interval for fossorial species, in clear contrast to the observed range of *SSDi* (0.867–1.029), is due to the monophyly of the group.

($Z = 2.257$, $P = 0.022$). This pattern seems to be due to the larger size of males that take care of their offspring and not to changes in the size of females, as indicated by the marginally significant results of the pairwise comparison of the mean male size for species with paternal care versus maternal care ($Z = 1.628$, $P = 0.073$). No relationship was observed between type of care and the size of females.

Discussion

FEMALE BIAS IN SSD INCREASES WITH SPECIES SIZE

The SSD pattern observed in Caribbean *Eleutherodactylus* coincides with that usually found in other anurans (Han and Fu 2013; Nali et al. 2014), with females on average 30% larger than males. However, there is considerable variation across species, with females ranging from being similar in size to up to 84% larger than males. In fact, *Eleutherodactylus* is remarkable in the degree and variation in the size dimorphism. Indeed, although females were at least 23% larger than males ($SSDi < 0.77$) in merely 29% of the 613 amphibian species studied by Nali et al. (2014), this occurred in 63% of Caribbean *Eleutherodactylus* species (Fig. 8). Furthermore, our measure of size is based on SVL, a one-dimensional magnitude. The differences between the sexes will thus be much larger when three-dimensional measurements such as mass and volume are considered, because mass has an exponential relationship with length. The magnitude of the dimorphism present in *Eleutherodactylus* is well exemplified by the photographs included in Figure 5, which show amplexus of *Eleutherodactylus etheridgei* and *Eleutherodactylus planirostris*, with *SSDi* estimates of 0.82 and 0.74, respectively, that is, females around 20%

and 25% larger than males, although the actual differences in body size are evidently larger.

Our results also indicate that, as in most anurans (Liao et al. 2013b; Nali et al. 2014), Caribbean *Eleutherodactylus* do not comply with Rensch's rule (although see Han and Fu 2013). In fact, our analyses revealed a pattern opposite to that predicted by Rensch's rule, because the relative size of females increased in relation to the size of males as species became larger. This is in stark contrast with the nearly isometric relationship found by Nali et al. (2014) across amphibians, and by Liao et al. (2013) in species from the Chinese province of Sichuan. To the best of our knowledge, patterns contrary to those predicted by Rensch's rule in anurans have only been detected in intraspecific studies (Liao and Chen 2012; Liao et al. 2015). However, across species patterns contrary to Rensch's rule are not exceptional in other groups of animals. Indeed, a review of over 1200 bird species found that species where females are the larger sex do not follow Rensch's rule (Webb and Freckleton 2007). A similar pattern occurs in arthropods and fish (Blackenhorn et al. 2007, Webb and Freckleton 2007, Guillermo-Ferreira et al. 2014). Nonetheless, the factors responsible for patterns *contra*-Rensch's rule are often unknown, and it has been suggested that they may be taxon specific (Webb and Freckleton 2007), highlighting the importance of investigating potential explanations.

DRIVERS OF SSD IN *Eleutherodactylus*

The female-biased SSD and pattern contrary to Rensch's rule in *Eleutherodactylus* is likely the result of a greater rate of evolution of body size for females compared to males (see Fig. 3). The greater rate of evolution in female size suggests stronger selection

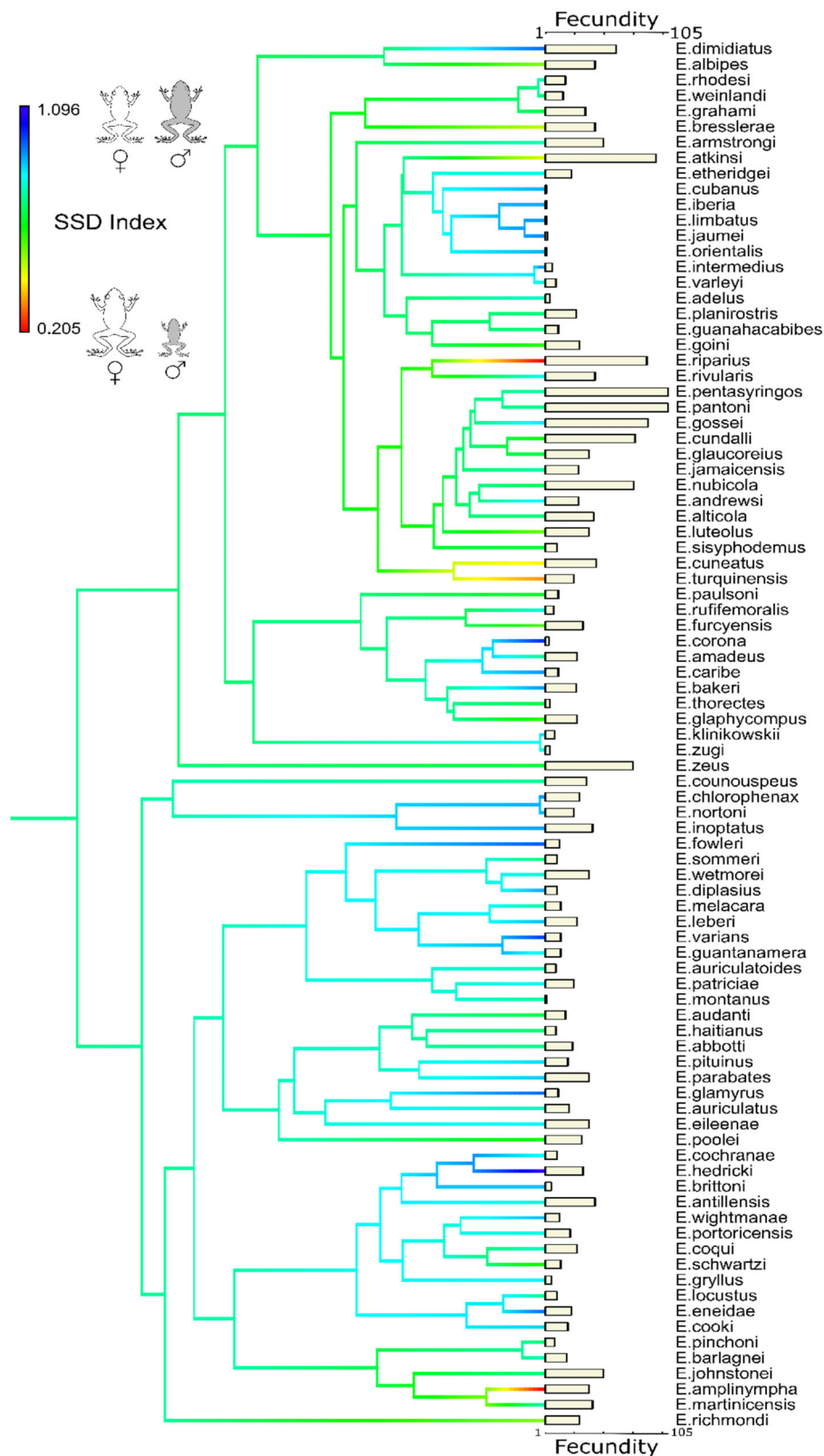


Figure 5. Evolution of SSD_i in relation to fecundity. The phylogenetic regression shows a negative correlation between SSD_i and fecundity ($R^2_{adj} = 0.082$, $F_{(1,84)} = 8.565$, $b = -0.049$, $SE = 0.017$, $\lambda = 0.788$, $P < 0.001$), that is, species with larger clutches tend to have higher SSD_i . This could be due to the strong positive correlation between fecundity and female size (see Fig. 6). The pictures show amplexus for two species, (a) *Eleutherodactylus etheridgei* (photo by AR) and (b) *Eleutherodactylus planirostris* (photo by ADC), to illustrate some examples of SSD.

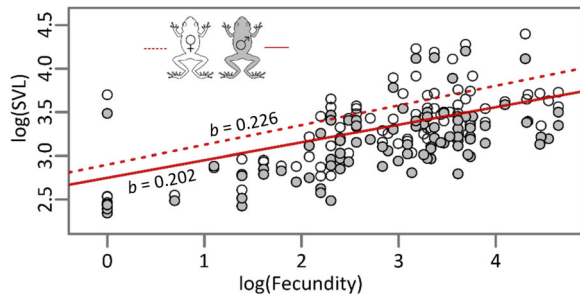


Figure 6. Relationship between fecundity and the size of males and females. The solid line shows the slope of the phylogenetic regression between male size (grey dots) and fecundity ($R^2_{\text{adj}} = 0.405$, $F_{(1,84)} = 58.78$, $b = 0.202$, $SE = 0.026$, $\lambda = 0.858$, $P < 0.001$), whereas the dashed line represents the slope for females ($R^2_{\text{adj}} = 0.457$, $F_{(1,84)} = 72.56$, $b = 0.226$, $SE = 0.026$, $\lambda = 0.923$, $P < 0.001$). The difference between the slopes results in a negative relationship between $SSDi$ and fecundity (see Fig. 5), which could possibly be due to a larger increase with female size, although the slopes for males and females are not significantly different.

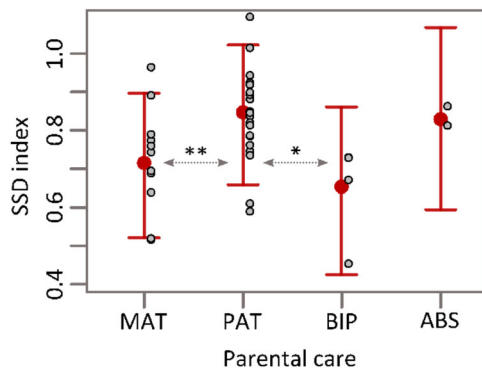


Figure 7. Mean and 95% CI of $SSDi$ according to the type of parental care. Parental care is associated with $SSDi$ ($F_{(3,33)} = 4.559$, $R^2_{\text{adj}} = 0.293$, $Z = 1.837$, $P = 0.01$). The pairwise comparison shows significant differences between species with paternal and maternal care ($Z = 3.492$, $P = 0.004$) or paternal and biparental care ($Z = 2.257$, $P = 0.022$), with a lower $SSDi$ biased towards females ($SSDi$ closer to 1) in the species with paternal care.

on female size than on male size (Shine 1979; Andersson 1994; De Lisle and Rowe 2013). However, in theory, the same pattern could also result from evolutionary constraints limiting the size of males while enabling greater lability to female size, or stabilizing selection acting on male size.

FECUNDITY SELECTION

Our results indicate that female-biased $SSDi$ in *Eleutherodactylus* is associated with greater fecundity, which in turn suggests that, at least in part, female-biased $SSDi$ results from selection for increased fertility (see Fig 5). This hypothesis, already advanced by Darwin (1871), proposes that larger females could lay

a greater number of eggs, which would be strongly favored by natural selection (Fairbairn et al. 2007). Furthermore, female-biased $SSDi$ could be exacerbated by sexual selection if males exhibit a preference based on female size, although as far as we know there are no data supporting this possibility. Fecundity was positively correlated with average female size across species (see Fig 6), a relationship that has also been observed at an intraspecific level in *Eleutherodactylus atkinsi* (Alfonso et al. 2017). Fecundity was also positively correlated, to a lesser extent, with the size of males.

The hypothesis suggesting that selection for fecundity may have contributed to female-biased $SSDi$ has received empirical support from several groups of organisms, such as lizards (Cox et al. 2003), snakes (Shine 1994), turtles (Stephens and Wiens 2009), or spiders (Head 1995), although in some cases the authors only found a significant correlation between fecundity and female size but not $SSDi$ (Fairbairn and Shine 1993; García-Navas et al. 2016). In frogs, Monroe et al. (2015) did not detect any significant relationship between fecundity and $SSDi$, despite finding a strong relationship between fecundity and female size in a species sample that included 18 *Eleutherodactylus* species. The inclusion of four different clades of frogs (*Dendrobates*, *Eleutherodactylus*, *Hyla*, and *Rana*, the latter more phylogenetically distant; Pyron and Wiens 2011) suggests that the detected patterns could have been driven by the most abundantly sampled group, rather than representing truly overarching patterns, common across distantly related groups. Nali et al. (2014) also found a relationship between fecundity and female size but did not test the relationship with $SSDi$. In contrast, the fecundity hypothesis is supported by Han and Fu (2013), which also included some *Eleutherodactylus* species, although fewer than Monroe et al. (2015). These somewhat contrasting results highlight the need to not only look for broad patterns in macroevolutionary studies, but also test whether subsamples of species from different higher taxa show different patterns. Samples of species, with varying representation from different groups, can obscure group-specific idiosyncrasies.

PARENTAL CARE

Our results suggest that parental care also influences $SSDi$ in *Eleutherodactylus* (Fig 7). In species with exclusive male care of clutches (paternal care), males tend to be larger, reducing the degree of female bias in $SSDi$. Paternal care is frequent in the genus (observed in 50% of the species for which we had information) and could be a compensatory mechanism for the enormous effort made by females to produce large clutches of eggs (Gross and Sargent 1985; Kokko and Jennions 2008; Monroe and Alonzo 2014; Delia et al. 2017). Females could increase their size to produce more eggs, freeing themselves from the offspring care that would be done by the males. An extensive analysis of parental

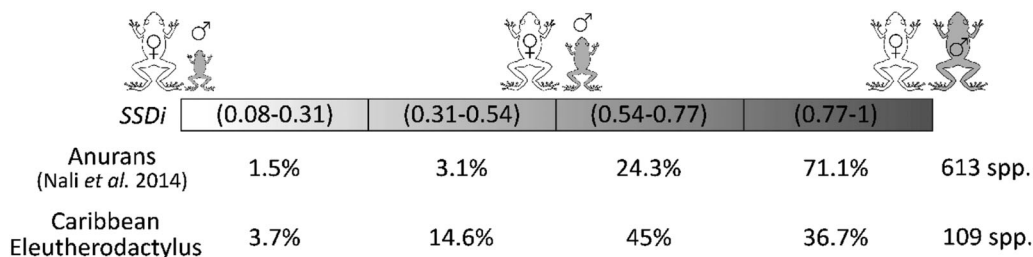


Figure 8. Distribution of SSD-biased toward females—across anurans and Caribbean *Eleutherodactylus*. The sketches represent the relationship between the size of males (in gray) and females (in white) along the scale. *SSDi* values were grouped into four classes as in Nali et al. (2014).

care in anurans (Vági et al. 2019) also showed an association between small clutches (of large eggs) and paternal care.

The association between parental care and SSD is a result of the relatively larger size of the males that take exclusive care of their offspring, which reduces the magnitude of the size difference between males and females. Paternal activities that have been described for the genus include the protection of eggs against desiccation, the proliferation of fungi, or predation (Joglar 1998; Henderson and Powell 2009). Experimental removal of males from clutches reduced reproductive success in one *Eleutherodactylus* species due to greater desiccation or cannibalism of eggs (Townsend et al. 1984). Larger males could incubate better the clutch, defend the nest more efficiently against predators, or simply provide care during a protracted period of time if size is associated with larger fat reserves, because they would not need to leave the nest to feed as frequently (Han and Fu 2013). Monroe and Alonzo (2014) did not detect a correlation between the type of parental care and SSD, as opposed to Han and Fu (2013). The latter observed a negative relationship between paternal care and SSD, but they did not assess whether this was a result of the size of males, females, or both. Vági et al. (2019) found that paternal care was associated with male-biased SSD across anurans, which is consistent with our results, although perhaps mitigated by the selective pressure for fecundity in *Eleutherodactylus* females.

ABSENCE OF RELATIONSHIP WITH MICROHABITATS

We did not find any differences in SSD between microhabitats (Fig. 4), contrary to what has been found in *Anolis* lizards in Puerto Rico and Jamaica, which did present habitat-specific SSD (Butler et al. 2000). Species size differed across microhabitats, but the size of males and females behaved similarly. For example, in leaf-litter dwelling species, both males and females were small in size. This suggests that SSD patterns were not the outcome of differential selective pressures or different evolutionary constrictions acting on the sexes among microhabitats. Several studies suggest that habitat use can influence SSD (Shine 1989; Fairbairn et al. 2007); however, this has been empirically

tested in just a few occasions (in turtles, Ceballos et al. 2013; in *Anolis* lizards, Butler et al. 2000; in deer, Geist and Bayer 1988; and in rodents, García-Navas et al. 2016). As far as we know, the only analysis on anurans that evaluated the influence of habitat did not observe differences in SSD between terrestrial, arboreal, aquatic, or semiaquatic species (Liao et al. 2013a). However, it would be interesting to assess whether spatial or trophic niche segregation between males and females, regardless of microhabitat, could influence SSD. For example, males spend a lot of time in exposed places while calling, having to feed there, whereas females would not be as constrained (Kupfer 2007). Some studies have shown different patterns of habitat use between the sexes in *Eleutherodactylus*, specifically in *Eleutherodactylus antillensis* and *Eleutherodactylus cooki* (Joglar 1998), but we lack information for sufficient species to allow proper analyses.

Conclusions

Caribbean *Eleutherodactylus* show female-biased SSD with a pattern of increasingly larger dimorphism with increased species size, contrary to the expectations derived from Rensch's rule. Female-biased SSD seems to be, at least in part, the result of selection for larger female size, which results in higher rates of phenotypic evolution of size in females, compared to males, and is likely associated with increased fecundity. The bias toward larger females, however, is reduced in species with paternal care, where males become larger in relation to females. The separate analysis of both sexes offers a unique and more comprehensive interpretation of the dynamics of SSD. Thus, SSD can be the result of forces acting in opposite directions and can be driven by natural selection. However, our data do not allow us to formally investigate the role of sexual selection.

Our results contrast with those of previous work that included diverse groups of anurans (including *Eleutherodactylus*). Stephens and Wiens (2009) already warned that including groups with very different evolutionary histories in a single analysis can lead to confusing or contradictory results and can mask the true relationship between SSD and diverse factors. In addition,

our results also show the importance of not only investigating SSD but also evaluating, at the same time, the putative impact of different selective forces on the body size of males and females separately, to assess the ultimate causes of sexual dimorphism (Blanckenhorn 2005; Fairbairn et al. 2007).

De Lisle and Rowe (2015) suggest that the evolution of SSD biased toward females in amphibians is associated with high speciation and low extinction rate. The authors suggest that the independent evolution of the sexes underlying the existence of the SSD would allow adaptation of both sexes to their respective optimum, favoring diversification and reducing the possibility of extinction. Thus, sexual dimorphism may have played an important role in the extraordinary diversity of Caribbean *Eleutherodactylus* resulting from replicated adaptive radiations (Dugo-Cota et al. 2019), as suggested by Butler et al. (2007) for *Anolis* lizards and Wagner et al. (2012) for cichlids. Increasing knowledge about the natural history of males and females *Eleutherodactylus* and their dimorphism may be essential to understand the origin of their extraordinary diversity.

AUTHOR CONTRIBUTIONS

AGV, CV, and AD-C conceived and designed the study. AD-C collected the data with input from AR. AD-C analyzed the data with input from AGV. AD-C wrote the first draft of the manuscript with substantial contributions from all co-authors.

ACKNOWLEDGMENTS

We would like to sincerely thank curators from all museums that we visited for data collection. Different museums granted permission for the study their scientific collections (see Table S1) and curators and personnel provided valuable support for this work. Initial versions of this manuscript were discussed with the members of the Conservation and Evolutionary Genetics Group at the Estación Biológica de Doñana (EBD-CSIC; Seville, Spain). We thank E. Ávila Luna for logistic support. This study was supported by projects CGL2013-47547-P and CGL2016-75227-P of the Ministry of Economy, Industry and Competitiveness of the Government of Spain to CV and by a PAPIIT-UNAM research grant (IA201716) to AG-V. AD-C received a predoctoral fellowship (BES-2011-050123) and three grants for short stays abroad (EEBB-I-13-06648, EEBB-I-14-08498, and EEBB-I-15-09410) from the Spanish Government. Computing time was provided by Doñana ICTS-RBD.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

All data are provided as Supporting Information.

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Associate Editor: R. M. Tinghitella
Handling Editor: T. Chapman

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Measured *Eleutherodactylus* specimens by species and sex.

Tabla S2. Mean snout-vent length by species and sex, and estimated sexual size dimorphism index (SSDi).

Table S3. Microhabitat, fecundity and parental care by species.

Table S4. Phylogenetic signal of sexual size dimorphism index (SSDi), males and females snout-vent length (SVL) and fecundity.