

Sexual dimorphism explains residual variance around the survival-reproduction tradeoff in lizards: Implications for sexual conflict over life-history evolution*

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The tradeoff between survival and reproduction is a central feature of life-history variation, but few studies have sought to explain why females of some species exhibit relatively lower survival than expected for a given level of reproductive effort (RE). Intralocus sexual conflict theory proposes that sex differences in selection on survival and RE may, by virtue of shared genes underlying these components of fitness, prevent females from optimizing this life-history tradeoff. To test this hypothesis, we used a phylogenetically based comparative analysis of published estimates for mean annual survival and RE from females of **82 lizard species** to (1) characterize the tradeoff between survival and reproduction and (2) test whether variation around this tradeoff is explained by sexual size dimorphism (SSD), a potential proxy for sexual conflict over life-history traits. Across species, we found a strong negative correlation between mean annual survival and RE, confirming this classic life-history tradeoff. Although residual variance around this tradeoff is unrelated to the absolute magnitude of SSD, it is strongly related to the direction of SSD. Specifically, we found that females have lower survival than expected for a given level of RE in female-larger species, whereas they have higher survival than expected in male-larger species. Given that female-larger SSD is thought to reflect selection for increased fecundity, our results suggest that intralocus sexual conflict may be particularly likely to constrain female life-history evolution in situations where increased RE is favored, but the phenotypes that facilitate this increase (e.g., body size) are constrained by antagonistic selection on males.

KEY WORDS: cost of reproduction, intralocus sexual conflict, life-history tradeoff, phylogenetic comparative method, sexual size dimorphism.

Species with high annual reproductive effort (RE) are generally short lived, whereas those with low annual RE are typically long lived (Tinkle 1969; Promislow and Harvey 1990; Shine and Schwarzkopf 1992; Sæther and Bakke 2000). Given that selection should favor both high survival and high reproductive output, this negative correlation is generally interpreted as evidence for an inherent tradeoff between survival and reproduction (Partridge and Harvey 1988; Reznick et al. 2000). This tradeoff is founda-

tional to life-history theory (Williams 1966; Stearns 1989; Roff 1993) and has proven useful for exploring the basic question of why some species have long lifespans while others are short lived (Williams 1966; Schaffer 1974; Reznick 1985; Roff and Fairbairn 2007). Previous phylogenetic comparative analyses have documented this tradeoff between species means for annual survival or longevity and RE across groups as diverse as insects, mammals, fish, and reptiles (Read and Harvey 1989; Gunderson 1997; Jervis et al. 2001; Jervis et al. 2007), but few have gone on to ask why females of many species exhibit lower survival than expected for a given level of RE. One potentially general answer to this question could be that the divergent reproductive

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strategies of males and females often lead to the evolution of an intermediate life history that represents a suboptimal compromise for females (Wedell et al. 2006; Bonduriansky et al. 2008; Maklakov and Lummaa 2013). Indeed, recent empirical work suggests that intralocus sexual conflict may help explain variation in life-history traits that is not fully explained by classic life-history theory (Harano et al. 2010; Lewis et al. 2011; Berg and Maklakov 2012).

Intralocus sexual conflict occurs when females and males have different fitness optima for traits with a genetic basis that is shared by both sexes (Bonduriansky and Chenoweth 2009). If selection favors different resolutions to the tradeoff between survival and reproduction in each sex, and if the traits that influence survival and reproduction have a genetic basis that is shared by both sexes, then intralocus sexual conflict may prevent one or both sexes from optimizing the tradeoff between survival and reproduction (Holland and Rice 1999; Maklakov et al. 2007; Bonduriansky et al. 2008; Berger et al. 2016). For example, males of many polygynous species are expected to prioritize mating success at the expense of survival, resulting in a relatively “fast” life-history strategy that favors investment in aggressive behaviors and exaggerated weapons or ornaments over immunity and self-maintenance (Vinogradov 1998; Rolff 2002; Bonduriansky et al. 2008). By contrast, females are generally predicted to maximize their lifetime fitness with a relatively “slow” life-history strategy that balances current RE against survival and future reproduction (Rolff et al. 2005; Bonduriansky et al. 2008). Therefore, selection for a “live fast, die young” strategy in males may, by virtue of any shared genetic basis for longevity and self-maintenance, inhibit females of polygynous species from attaining optimal levels of survival for a given level of annual RE (Lande 1980; Promislow 2003; Maklakov and Lummaa 2013; Adler and Bonduriansky 2014). Nonetheless, it is still an open question whether selection on males influences how females resolve the tradeoff between survival and reproduction (Lessells 2012; Pennell and Morrow 2013).

To address this question, we compiled a dataset containing published estimates of mean annual survival and mean annual RE of adult females from wild lizard populations. We selected lizards because previous studies on this lineage have documented tradeoffs between individual RE and annual survival within species (Landwer 1994; Sorci et al. 1996; Cox and Calsbeek 2010; Cox et al. 2010; Cox et al. 2014) and between mean RE and annual survival across species (Tinkle 1969; Clobert et al. 1998). First, we used phylogenetically based statistical methods to test for the expected life-history tradeoff between species means for annual survival and annual RE (Fig. 1A). Next, to test the hypothesis that intralocus sexual conflict prevents females from maximizing survival for a given level of RE, we asked whether residual variance around this tradeoff is related to sexual size

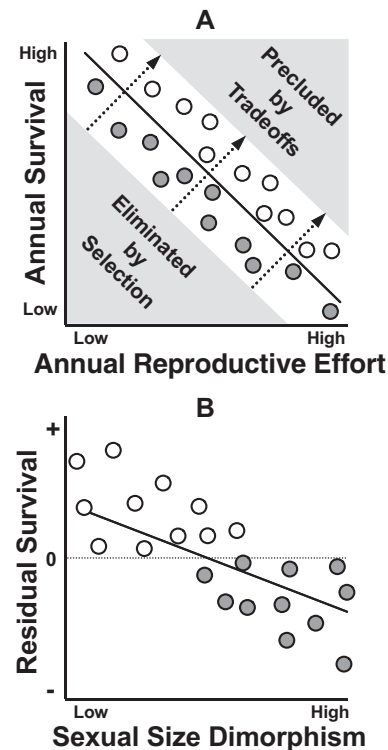


Figure 1. Conceptual diagrams illustrating our predictions. Each point represents an individual species. (A) The line of best fit (solid line) illustrates the average resolution of the tradeoff between survival and reproduction in light of intralocus sexual conflict. The shaded area in the upper right represents combinations of annual survival and annual reproductive effort that are precluded by tradeoffs. The shaded area in the lower left represents low fitness combinations expected to be eliminated by selection. The dashed arrows represent the general direction of selection, which pushes species toward higher survival and reproductive effort. Species with low survival for a given level of reproductive effort (grey symbols) fall below the line of best fit whereas those with relatively high survival (white symbols) fall above. (B) If the magnitude of SSD is a general proxy for overall sexual conflict, we predict that females of species with high SSD will exhibit lower annual survival than expected for their annual reproductive effort.

dimorphism (SSD). There are several ways in which SSD may serve as a proxy for intralocus sexual conflict. Evidence across species suggests that sex differences in selection, the ultimate driver of sexual conflict, may be stronger for sexually dimorphic traits than for traits which do not differ between sexes (Cox and Calsbeek 2009). Given the general importance of body size with respect to ecology, physiology, and life history, the extent to which males and females differ in size may broadly reflect the extent to which selection favors sex differences in other traits (Badyaev 2002; Blanckenhorn 2005), thereby, providing an index of overall sexual conflict across a variety of phenotypes. In particular, SSD is likely indicative of sexual conflict over life history

because body size is intimately tied to canonical life-history traits such as growth rate, size at maturation, fecundity, and longevity (Roff 1986; Roff 1993; Klingenberg and Spence 1997; Webb and Freckleton 2007; Lewis et al. 2011). If the degree of SSD represents the overall magnitude of past or current sexual conflict over life-history traits, we would predict that females of species with high SSD should exhibit lower levels of annual survival than expected for their level of annual RE, irrespective of the direction (male- or female-biased) of SSD (Fig. 1B). However, the direction of SSD may also be important, given that male-biased SSD in lizards (and other taxa) is thought to result from intrasexual selection on male size, whereas female-biased SSD is viewed as the result of fecundity selection on female size (Cox et al. 2003; Cox et al. 2007). Therefore, we also tested whether the direction of SSD predicts whether females experience relatively higher or lower levels of survival than expected for a given level of RE.

Methods

COMPARATIVE DATASET

We reviewed published studies of lizard demography and reproduction to compile a dataset with estimates of four parameters for each species: SSD, snout-vent length (SVL), annual RE of adult females, and annual survival probability of adult females (Supporting Information Table S1). Our dataset includes 82 lizard species from 15 families.

Estimates of SSD used in our analyses are taken directly from reviews by Cox et al. (2003, 2007) for 73 of the species in our dataset. Following Cox et al. (2007), we quantified SSD with an index calculated using snout-vent length:

$$\text{SSD} = \frac{\text{Mean SVL of larger sex}}{\text{Mean SVL of smaller sex}} - 1$$

When using a directional index of SSD, we followed convention by expressing this value as positive in female-larger species and negative in male-larger species (Lovich and Gibbons 1992).

Our estimates of mean adult-female SVL were taken from the same source as our estimate of SSD whenever available (70 of 82 species) and from other sources when this was not possible.

Meiri et al. (2012) listed a value of RE as “specific productivity” for all species in our dataset, and when possible we used the mean of that value, and the calculated value from other sources, as RE in our analyses. We calculated annual RE as:

$$\text{RE} = \frac{\text{Mean clutch mass}}{\text{Mean female mass}} \times \text{Number of clutches per year}$$

In cases, where the values in Meiri et al. (2012) differed by more than a factor of 1.5 from other sources, the values from Meiri et al. (2012) were not used. We favored the calculated values from other sources because they were derived from direct

measurements of relative clutch mass rather than from indirect measurements of SVL that were converted to values for relative clutch mass based on family specific conversions of SVL to mass (Meiri et al. 2012).

Estimates of survival were obtained primarily from values published in two reviews (Clobert et al. 1998; Charnov et al. 2007) and supplemented with species-specific studies when values were not included in those reviews (Supporting Information Appendix S1). When multiple sources were available, we used the mean annual survival across sources. For annual species in which individuals rarely survived for longer than one year ($n = 6$), we assigned a nonzero value of 0.01 for annual survival following Clobert et al. (1998). Field estimates of life-history parameters are expected to have limited precision, but are not generally expected to suffer from low accuracy or bias (Krebs 1989; Charnov et al. 2007). Although some comparative studies of life-history evolution have used lifespan rather than annual survival rate (Jervis et al. 2001, 2007), we chose annual survival because (1) this metric is more widely reported in the literature, (2) previous studies have documented tradeoffs between reproduction and annual survival both within and across lizard species, and (3) annual survival is preferable to lifespan for comparative studies of life-history covariation because estimates of lifespan are more sensitive to initial sample size, study duration, and sampling intensity (Krementz et al. 1989).

NONPHYLOGENETIC ANALYSES

To test the prediction of a tradeoff between survival and reproduction, we regressed mean annual survival for each species on mean annual RE. To test the hypothesis that intralocus sexual conflict explains residual variation in survival, we regressed the residuals from that regression (i.e., residual survival) on SSD, our proxy for sexual conflict. We did this with three different measures of SSD. We first used the absolute value of SSD to test the prediction that the overall extent to which selection has favored different phenotypes, irrespective of which sex has evolved to be larger, is associated with lower female survival than would be expected for a given level of RE (Fig. 1B). However, if the causes and/or resolution of sexual conflict differ between male- and female-larger species, then using the absolute value of SSD may be inappropriate. This could occur, for example, if female-biased SSD generally results from fecundity selection on females, whereas male-biased SSD arises primarily from sexual selection on males (Cox et al. 2003, 2007). Considering this, we next used a directional index of SSD to test whether continuous variation in the direction and magnitude of SSD (from female- to male-biased) is associated with residual survival of females. Finally, we also used a multivariate approach that did not rely on the creation of a residual survival variable. To do this, we used multiple regression of annual survival on annual RE, female body size (SVL), and

Table 1. Estimates of phylogenetic signal (Blomberg's K and Pagel's λ) are significantly greater than zero for each of the five traits measured in this study.

Trait	Blomberg's K	P value	Pagel's λ	P value
Annual survival	0.48	<0.01	0.87	<0.01
Annual reproductive effort	0.41	<0.01	0.72	<0.01
Residual survival	0.39	<0.01	0.71	<0.01
Sexual size dimorphism	0.42	<0.01	0.50	<0.01
Snout-vent length	0.61	<0.01	0.84	<0.01

our quantitative, directional measure of SSD. We included SVL in the model as a covariate because of the established positive relationship between body size and annual survival, as well as the tendency (Rensch's Rule) for SSD to increase with body size in taxa, which males are the larger sex (Abouheif and Fairbairn 1997).

PHYLOGENETIC ANALYSES

We carried out phylogenetically based comparative analyses in R (R Core Team 2013) using a published phylogeny for lizards and snakes (Pyron et al. 2013). We trimmed this large phylogeny to remove those species not included in our dataset using Analysis of Phylogenetics and Evolution (APE) and Geiger (Paradis et al. 2004; Harmon et al. 2007). Five species in our dataset were not found in the phylogeny (*Anolis nebulosus*, *Anolis tropidolepis*, *Japalura swinhonis*, *Morethia boulengeri*, and *Trachylepis buetneri*). To retain these data, we placed these species on the phylogeny at tips occupied by closely related species (*Anolis conspersus*, *Anolis auratus*, *Japalura polygonata*, *Morethia butleri*, and *Trachylepis perrotetii*). We tested for phylogenetic signal by using Picante and Phytools to calculate Blomberg's K and Pagel's λ for each trait (Blomberg et al. 2003; Kembel et al. 2010; Revell 2012). A value of $K > 0$ indicates some phylogenetic signal for a given trait and $K = 1$ indicates that phylogenetic signal is equivalent to what is expected under a Brownian motion model of character evolution (Blomberg et al. 2003). A value of $\lambda = 0$ indicates no phylogenetic signal and $\lambda = 1$ indicates that variance in traits across the phylogeny matches the expectation under Brownian motion (Pagel 1999). We detected significant phylogenetic signal in annual survival, annual RE, residual survival, SSD, and body size of females, with values of K ranging from 0.39 to 0.61 and values of λ ranging from 0.50 to 0.87 (Table 1). Therefore, we tested each hypothesis described above using additional, phylogenetically based comparative methods.

We computed phylogenetically independent contrasts for annual survival, RE, residual survival, and SSD by using the pic function in APE (Felsenstein 1985; Paradis et al. 2004). To test for a tradeoff between survival and reproduction, we regressed contrasts of survival on contrasts of RE. To test the hypothesis that sexual conflict explains residual variation in survival around this tradeoff, we regressed the contrasts of residual survival on the contrasts of SSD. Both of these models were ordinary least squares regressions forced through the origin (Garland et al. 1992). Similar to our nonphylogenetic analyses, we also ran a complimentary multivariate analysis using Phylogenetic Generalized Least-Squares (PGLS) multiple regression in Comparative Analyses of Phylogenetics and Evolution in R (CAPER) with annual survival as a response variable and directional SSD, annual RE, and mean SVL of females as independent variables (Orme 2013).

Results

NONPHYLOGENETIC ANALYSES

As predicted by life-history theory, we found a strong negative relationship between mean annual survival and mean annual RE of females ($r = 0.61$; $P < 0.001$; Fig. 2A). Contrary to our prediction based on sexual conflict, residual survival from this regression is not correlated with the absolute magnitude of SSD ($r = 0.18$; $P = 0.10$). However, residual survival is strongly correlated with the directional index of SSD, such that female survival tends to be higher than expected based on RE for male-larger species and lower than expected for female-larger species ($r = 0.41$; $P < 0.001$; Fig. 3A). Similarly, multiple regression showed that annual survival decreases with increasing annual RE ($F_{1,78} = 36.00$; $P < 0.001$) and decreases as directional SSD shifts from male- to female-larger ($F_{1,78} = 4.63$; $P = 0.03$), even when controlling for the overall increase in annual survival with body size ($F_{1,78} = 23.14$; $P < 0.001$).

PHYLOGENETIC ANALYSES

All of the results described above remained significant when taking phylogeny into account. The strong negative relationship between annual survival and RE remained significant when using phylogenetically independent contrasts ($r = 0.45$; $P < 0.001$; Fig. 2B). Likewise, independent contrasts revealed that evolutionary shifts from male- to female-larger SSD are accompanied by evolutionary shifts toward lower values of survival than predicted for a given level of reproductive investment ($r = 0.28$; $P < 0.01$; Fig. 3C). Similarly, PGLS multiple regression showed that annual survival decreases with RE ($t = -5.90$; $P < 0.001$), decreases with the degree of female bias in SSD ($t = -2.08$; $P = 0.04$), and increases with female body size ($t = 3.82$; $P < 0.001$).

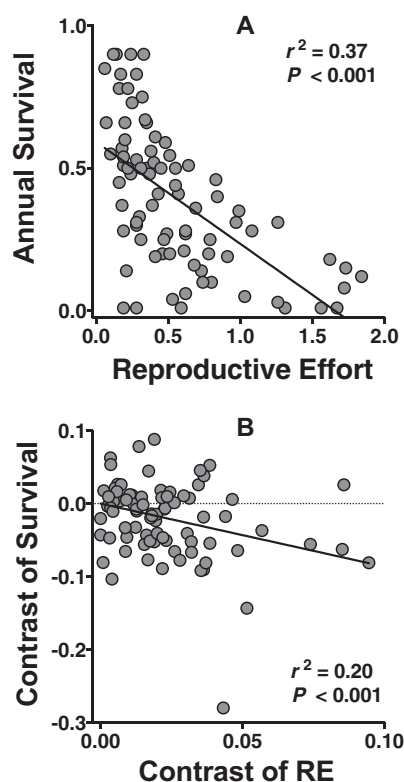


Figure 2. (A) Across 82 lizard species, mean annual survival of adult females decreases as mean annual reproductive effort increases. Statistics and line of best fit are from ordinary least-squares regression. Annual reproductive effort is the mean mass of eggs or offspring produced per year, divided by the mean body mass of adult females. (B) This tradeoff is also observed when using phylogenetically independent contrasts of annual survival and annual reproductive effort, such that inferred evolutionary increases in reproductive effort are associated with evolutionary decreases in annual survival. Contrasts have been “positivized” and the least-squares regression line has been forced through the origin following Garland et al. (1992).

Discussion

Annual survival probability decreases sharply with mean annual RE of adult females across the 82 lizard species in our dataset, even when accounting for variance due to phylogeny and body size. This result provides one of the clearest interspecific demonstrations of this fundamental life-history tradeoff in any taxonomic group (Williams 1966; Tinkle 1969; Linden and Møller 1989; Gunderson 1997; De Paepe and Taddei 2006). Additionally, we found that residual variance around this life-history tradeoff is related to the direction of SSD, suggesting that patterns of sex-specific selection may influence the extent to which females can optimize the tradeoff between RE and survival. Specifically, we found that females of species in which *females* are the larger sex have relatively *lower* probability of survival than expected for their level of RE, whereas females of species in which *males* are

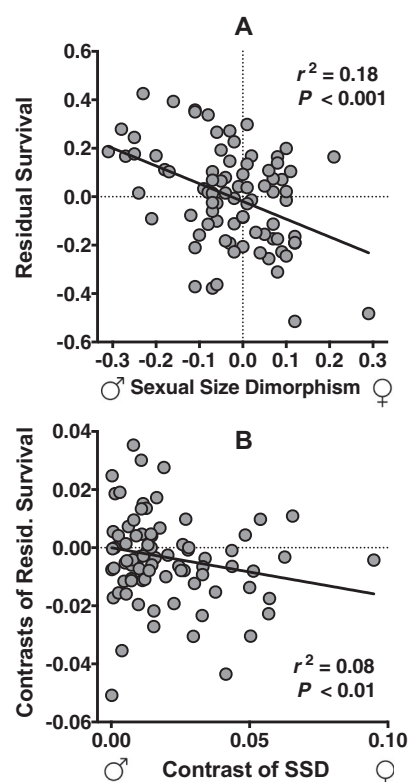


Figure 3. (A) Across the range of sexual size dimorphism (SSD), male-larger species have higher residual survival than female-larger species. Statistics and line of best fit are from least-squares regression. (B) When accounting for phylogeny with independent contrasts of residual survival and SSD, evolutionary shifts toward female-larger SSD tend to be accompanied by evolutionary decreases in residual survival. Contrasts have been “positivized” and the least-squares regression line has been forced through the origin following Garland et al. (1992). These negative relationships were still found when accounting for body size with a PGLS multiple regression.

the larger sex have relatively *higher* survival than expected for their level of RE. Below, we characterize the tradeoff between annual survival and RE in lizards, evaluate interpretations for the observed relationship between residual survival and SSD, and discuss their implications for the hypothesis that intralocus sexual conflict can constrain females from optimizing the tradeoff between survival and reproduction (Bonduriansky et al. 2008; Maklakov and Lummaa 2013).

In our dataset, most species fall along an axis running from high survival and low RE to low survival and high RE (Fig. 2). Annual RE explains roughly one third of the variance in mean annual survival (Fig. 2A), and phylogenetically independent contrasts for annual RE explain one fifth of the variance in contrasts for annual survival (Fig. 2B). It is perhaps not surprising that the majority of variance in survival is left unexplained by RE, given that field estimates of survival and RE are often highly variable across years or among populations of a species. For example,

estimates of annual survival in the ornate tree lizard, *Urosaurus ornatus*, range from 0.11 to 0.56 across five populations, while estimates of the number of clutches per year range from 1.5 to 3.5 (Charnov et al. 2007; Supporting Information Appendix S1). Perhaps because of the inherent difficulty in estimating these life-history parameters and the large number of possible explanatory factors, residual variance around the tradeoff between survival and reproduction is often dismissed as measurement error, for which no further explanation is required. Instead, we propose that some of this residual variance may reflect ongoing intralocus sexual conflict over life-history traits. Viewed this way, costs of reproduction impose a fitness ceiling against which species with the highest values of residual survival are pushing, and the line of best fit represents the average resolution of the tradeoff in light of sexual conflict (Fig. 1A). The absence of lizard life histories in the upper right quadrant of Figure 2A supports the theoretical expectation that combinations of high RE and high survival (i.e., “Darwinian demons” [Law 1979]) are unattainable. By contrast, many species fall in the lower left quadrant of Figure 2A and exhibit combinations of low RE and low survival that should be eliminated by selection, raising the question of why these suboptimal life histories occur.

We found that species exhibiting these low-fitness combinations also tend to be those in which females are the larger sex, which is at least partially consistent with the idea that the sexual conflict constrains life-history evolution. To evaluate this possibility, it helps to consider how a relatively indirect proxy, such as SSD, might actually reflect different forms of sexual conflict. If the degree of SSD, which likely indicates sex differences in the optima for life-history traits (Roff 1986; Lewis et al. 2011), is broadly indicative of the extent of sexual conflict over other traits and loci (Badyaev 2002), then any residual variance around the survival-reproduction tradeoff that is due to sexual conflict should correlate with the overall magnitude of SSD. Our results show that this is clearly not the case. Instead, we found higher residual survival of females in male-larger species and lower residual survival of females in female-larger species, raising the question of how male-larger SSD differs from female-larger SSD. In lizards and other reptiles, phylogenetic comparative analyses show that male-larger SSD is related to sexual selection for large male size, whereas female-larger SSD is related to fecundity selection for large female size, and the observed level of SSD in any given species presumably reflects a combination of these and other factors (Cox et al. 2003, 2007). Therefore, our analyses suggest that sexual conflict may be particularly likely to constrain females from optimizing the survival-reproduction tradeoff in situations where selection favors increased RE in females, but the evolution of phenotypes that facilitate this increase in ways that also maintain expected levels of survival (e.g., larger body size) is constrained by antagonistic selection in males.

By contrast, our results do not provide any support for the idea that females experience suboptimal levels of survival (for a given level of RE) simply due to increased sexual selection for large male size. Instead, females of species with male-larger SSD apparently come the closest to optimizing the tradeoff between survival and reproduction (Fig. 3). This could indicate the general absence of sexual conflict over survival and reproductive investment in these species, or it could reflect a beneficial effect of strong sexual selection on males. For example, strong sexual selection is predicted to efficiently remove deleterious mutations, many of which would also influence survival (Agrawal 2001; Siller 2001; Radwan 2004; Whitlock & Agrawal 2009; Connallon et al. 2019). Therefore, strong sexual selection for large male size, as represented by male-larger SSD, may indirectly improve survival by reducing mutation load, thereby, indirectly allowing females to optimize the tradeoff between survival and reproduction.

Another possibility is that the association between high female survival and male-larger SSD that we observed is actually driven by a permissive effect of the former on the latter. For example, Promislow et al. (1992) found a positive correlation between female survival and the brightness of male plumage in birds and proposed that bright plumage, which is expected to come with an additional mortality cost for males, will only evolve when baseline survival probability is high for a species. If the aspects of mating systems that favor male-biased SSD are also associated with high survival costs for males (e.g., due to intense sexual competition, increased exposure to predators, or energetic costs of rapid growth), then perhaps male-larger SSD only evolves when survival rates are relatively high for a given level of RE. This explanation differs from our initial hypothesis in that annual survival of the species would be constraining the evolution of male-larger SSD, rather than selection on males constraining the evolution of female life history. Finally, some apparently suboptimal combinations of survival and RE may be explained by idiosyncratic or lineage-specific constraints due to environment, genetics, lifestyle, or morphology (Shine 1992). In any case, the distribution of life histories in Figure 2A strongly suggests that inherent tradeoffs impose a strict upper limit on annual survival and reproduction, but that some apparently suboptimal combinations of low survival and reproduction do persist, whether due to intralocus sexual conflict or other factors.

Our data are also consistent with a model for the evolution of lifetime RE developed by Charnov et al. (2007). Their model, based on metabolic theory, predicts an approximate lifetime RE of 1.4 times the mass of an adult female and has general predictive power across taxa. For example, when lifetime reproductive data from 54 lizard species and 40 mammal species were analyzed separately, mean lifetime RE in these groups was found to be 1.43 and 1.41, respectively (Charnov et al. 2007). Our analyses, which used annual rather than lifetime RE, found that the line

of best fit for the tradeoff between survival and reproduction yields a maximal predicted annual RE (i.e., where annual survival reaches 0) of 1.63, slightly above the theoretical lifetime RE of 1.4 predicted by Charnov et al. (2007). Only seven of 82 species in our dataset exceeded an annual RE of 1.4, and all were annual or nearly annual species with survival probabilities less than 0.18 (Fig. 2A; Supporting Information Table S1).

Our results illustrate a pronounced tradeoff between annual survival and RE across lizard species. As predicted by life-history theory, combinations of high survival and high RE are not observed in wild lizard populations. However, many species appear to exhibit suboptimal combinations of relatively low survival and low RE that should, all else equal, be eliminated by natural selection. Intralocus sexual conflict over body size and associated life-history traits provides a potential explanation for the persistence of these suboptimal fitness combinations, and one that is at least partially consistent with our data. As SSD shifts from male- to female-larger, the annual survival of females tends to fall further below the level expected based on their annual RE. Given that female-larger SSD is related to fecundity selection for large female size, this result suggests that sex differences in selection may be particularly likely to hinder an optimal resolution of the survival-reproduction tradeoff in situations where fecundity selection is strong. Due to the correlative nature of our data and the imperfect association between SSD and intralocus sexual conflict, this pattern is best viewed as a promising hypothesis for further exploration rather than a direct demonstration of sexual conflict shaping life-history evolution.

AUTHOR CONTRIBUTIONS

AMR conceived of the presented ideas and wrote the first draft of the manuscript. AMR and RMC developed the ideas and hypothesis tests. AMR and WJE collected data from the literature and performed analyses. All authors discussed results and contributed to the final manuscript.

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DATA ARCHIVING

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p3f31c1>.

LITERATURE CITED

Abouheif, E., and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *Am. Nat.* 149:540–562.

- Adler, M. I., and R. Bonduriansky. 2014. Sexual conflict, life span, and aging. *Cold Spring Harb. Perspect. Biol.* 6:a017566.
- Agrawal, A. F. 2001. Sexual selection and the maintenance of sexual reproduction. *Nature* 411:692.
- Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends Ecol. Evol.* 17:369–378.
- Berg, E. C., and A. A. Maklakov. 2012. Sexes suffer from suboptimal lifespan because of genetic conflict in a seed beetle. *Proc. Royal Soc. London B: Biol. Sci.* 279:4296–4302.
- Berger, D., I. Martinossi-Allibert, K. Grieshop, M. I. Lind, A. A. Maklakov, and G. Arnqvist. 2016. Intralocus sexual conflict and the tragedy of the commons in seed beetles. *Am. Nat.* 188:E98–E112.
- Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology* 111:977–1016.
- Blomberg, S. P., T. Garland Jr, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.
- Bonduriansky, R., and S. F. Chenoweth. 2009. Intralocus sexual conflict. *Trends Ecol. Evol.* 24:280–288.
- Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol.* 22:443–453.
- Charnov, E. L., R. Warne, and M. Moses. 2007. Lifetime reproductive effort. *Am. Nat.* 170:E129–E142.
- Clobert, J., T. Garland, and R. Barbault. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *Journal of Evolutionary Biology* 11:329–364.
- Connallon, T., and G. Matthews. 2019. Cross-sex genetic correlations for fitness and fitness components: connecting theoretical predictions to empirical patterns. *Evolution* 3:254–262.
- Cox, R. M., M. A. Butler, and H. B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Pp: 38–49. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford Univ. Press, Oxford, U.K.
- Cox, R. M., and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. *Am. Nat.* 173:176–187.
- . 2010. Severe costs of reproduction persist in *Anolis* lizards despite the evolution of a single-egg clutch. *Evolution* 64:1321–1330.
- Cox, R. M., M. B. Lovern, and R. Calsbeek. 2014. Experimentally decoupling reproductive investment from energy storage to test the functional basis of a life-history trade-off. *J. Anim. Ecol.* 83:888–898.
- Cox, R. M., E. U. Parker, D. M. Cheney, A. L. Liebl, L. B. Martin, and R. Calsbeek. 2010. Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. *Funct. Ecol.* 24:1262–1269.
- Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57:1653–1669.
- De Paepe, M. and F. Taddei. 2006. Viruses' life history: towards a mechanistic basis of a trade-off between survival and reproduction among phages. *PLoS Biol.* 4:e193.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41:18–32.
- Gunderson, D. R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can. J. Fish. Aquat. Sci.* 54:990–998.

- Harano, T., K. Okada, S. Nakayama, T. Miyatake, and D. J. Hosken. 2010. Intralocus sexual conflict unresolved by sex-limited trait expression. *Curr. Biol.* 20:2036–2039.
- Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2007. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Holland, B., and W. R. Rice. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl. Acad. Sci.* 96:5083–5088.
- Jervis, M. A., C. L. Boggs, and P. N. Ferns. 2007. Egg maturation strategy and survival trade-offs in holometabolous insects: a comparative approach. *Biol. J. Linn. Soc.* 90:293–302.
- Jervis, M. A., G. E. Heimpel, P. N. Ferns, J. A. Harvey, and N. A. Kidd. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J. Anim. Ecol.* 70:442–458.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: r tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Klingenberg, C. P., and J. Spence. 1997. On the role of body size for life-history evolution. *Ecol. Entomol.* 22:55–68.
- Krebs, C. J. 1989. *Ecological methodology*. Harper & Row, New York, NY.
- Krementz, David G., John R. Sauer, and James D. Nichols. 1989. Model-based estimates of annual survival rate are preferable to observed maximum lifespan statistics for use in comparative life-history studies. *Oikos* 56:203–208.
- Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292–305.
- Landwer, A. J. 1994. Manipulation of egg production reveals costs of reproduction in the tree lizard (*Urosaurus ornatus*). *Oecologia* 100:243–249.
- Law, R. 1979. Optimal life histories under age-specific predation. *Am. Nat.* 114:399–417.
- Lessells, K. 2012. *Sexual conflict*. Wiley Online Library, Hoboken, NJ.
- Lewis, Z., N. Wedell, and J. Hunt. 2011. Evidence for strong intralocus sexual conflict in the Indian meal moth, *Plodia interpunctella*. *Evolution* 65:2085–2097.
- Linden, M., and A. P. Møller. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* 4:367–371.
- Lovich, J. E., and J. W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Develop. Aging* 56:269–281.
- Maklakov, A. A., C. Fricke, and G. Arnqvist. 2007. Sexual selection affects lifespan and aging in the seed beetle. *Aging Cell* 6:739–744.
- Maklakov, A. A., and V. Lummaa. 2013. Evolution of sex differences in lifespan and aging: causes and constraints. *Bioessays* 35:717–724.
- Meiri, S., J. H. Brown, and R. M. Sibly. 2012. The ecology of lizard reproductive output. *Global Ecology and Biogeography* 21:592–602.
- Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R Package Version 5:1–36.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Partridge, L., and P. H. Harvey. 1988. The ecological context of life history evolution. *Science* 241:1449–1455.
- Pennell, T. M., and E. H. Morrow. 2013. Two sexes, one genome: the evolutionary dynamics of intralocus sexual conflict. *Ecol. Evol.* 3:1819–1834.
- Promislow, D. 2003. Mate choice, sexual conflict, and evolution of senescence. *Behav. Genet.* 33:191–201.
- Promislow, D. E., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. *J. Zool.* 220:417–437.
- Promislow, D. E., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. *Proc. Royal Soc. Lond. B: Biological Sci.* 250:143–150.
- Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* 13:93.
- Radwan, J. 2004. Effectiveness of sexual selection in removing mutations induced with ionizing radiation. *Ecology Letters* 7:1149–1154.
- Read, A. F., and P. H. Harvey. 1989. Life history differences among the Eutherian radiations. *J. Zool.* 219:329–353.
- Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3:217–223.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44:257–267.
- Reznick, D., L. Nunney, and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol. Evol.* 15:421–425.
- Roff, D. 1993. *Evolution of life histories: theory and analysis*. Springer Science & Business Media, Springer, Berlin, Germany.
- Roff, D., and D. Fairbairn. 2007. The evolution of trade-offs: where are we? *J. Evol. Biol.* 20:433–447.
- Roff, D. A. 1986. Predicting body size with life history models. *Bioscience* 36:316–323.
- Rolff, J. 2002. Bateman's principle and immunity. *Proc. Royal Soc. Lond. B: Biol. Sci.* 269:867–872.
- Rolff, J., S. A. Armitage, and D. W. Coltman. 2005. Genetic constraints and sexual dimorphism in immune defense. *Evolution* 59:1844–1850.
- Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. *Am. Nat.* 108:783–790.
- Shine, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* 46:828–833.
- Shine, R., and L. Schwarzkopf. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46:62–75.
- Siller, S. 2001. Sexual selection and the maintenance of sex. *Nature* 411:689.
- Sorci, G., J. Clobert, and Y. Michalakakis. 1996. Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos* 76:121–130.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Funct. Ecol.* 3:259–268.
- Team, R. C. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Am. Nat.* 103:501–516.
- Vinogradov, A. E. 1998. Male reproductive strategy and decreased longevity. *Acta Biotheor.* 46:157–160.
- Webb, T. J., and R. P. Freckleton. 2007. Only half right: species with female-biased sexual size dimorphism consistently break Rensch's rule. *PLoS One* 2:e897.
- Wedell, N., C. Kvarnemo, and T. Tregenza. 2006. Sexual conflict and life histories. *Anim. Behav.* 71:999–1011.
- Whitlock, M. C., and A. F. Agrawal. 2009. Purging the genome with sexual selection: reducing mutation load through selection on males. *Evolution* 63:569–582.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100:687–690.

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Supporting Information

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

Supplemental Figure S1. Phylogenetic hypothesis used in this study, based on Pyron et al. (2013), illustrating relationships among 82 lizard species representing 15 families.

Supplemental Appendix S1. Literature-review dataset used for comparative analyses.

Appendix S2. References for Appendix S1.