Evolutionary ecology of separate sexes:
Causes and consequences of sex differences in morphology, behavior, and life history

Aaron Michael Reedy
Villa Park, Illinois

Bachelor of Arts, Southern Illinois University, 1999

A Dissertation presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Doctor of Philosophy

Department of Biology

University of Virginia
May, 2018

ABSTRACT

As a consequence of anisogamy, females and males are expected to have sex-specific optima for morphological, behavioral and life history traits. Selection acting differently on the same traits in both sexes has pushed towards these sex-specific optima and driven the evolution of sex differences in morphology, reproductive strategy, behavior, and life history. The great diversity in sexual dimorphism that has evolved across species is a testament to the effects of independent evolution of males and females. However, despite the assumption of sex-specific evolutionary dynamics, many phenomena central to evolutionary ecology, such as costs of reproduction, aggressive interactions, selection, and life-history evolution, have often been studied with a focus limited to a single sex. The lack of between-sex comparisons of these phenomena has left outstanding questions as to how often the same evolutionary dynamics are operating in both sexes and how sex differences in selection may shape the evolutionary trajectories of separate sexes within a species. In Chapters 1-3 of this dissertation, I test theoretical predictions related to costs of reproduction, aggressive behavior, and selection with approaches that make direct comparisons between females and males using experimental manipulations, behavioral assays, and mark-recapture methods in wild populations of brown anole lizards (*Anolis sagrei*). In Chapter 1, I use an experimental manipulation of reproductive investment to show that, despite their dramatically different forms of reproductive investment, females and males pay comparable costs of reproduction in the common currencies of energy storage and parasitism. In Chapter 2, I test the assumption that males are categorically more aggressive than females in territorial polygynous species and find no sex difference in the likelihood that males or females will attack a territorial intruder and that females actually have a shortened latency to attack as compared to males. In Chapter 3, I test the hypothesis that sexually antagonistic selection develops over ontogeny and find that natural selection on body size is similar for females and males during the earliest part of the juvenile life stage, but that selection on body size diverges coincident with the onset of sexual maturity. In Chapter 4, I test across 82 lizard species for evolutionary consequences of sex-specific selection acting on life-history traits in the context of intralocus sexual conflict. Chapter 4, both provides a clear demonstration of the tradeoff between survival and reproduction and shows that sexual conflict can shape life history evolution by demonstrating a correlation between sexual size dimorphism and residual variation in survival around the central life-history tradeoff. Specifically, I find that the degree of sexual size dimorphism correlates with residual survival such that female-larger species have lower survival than would be predicted by reproductive effort, while male-larger species tend to have greater levels of annual survival than would be predicted by reproductive effort.

DEDICATION

This work is dedicated to Benjamin and Cordelia. I will never be able to separate the memories of this work from those of your earliest days. I will always remember both fondly.

ACKNOWLEDGEMENTS

I gratefully acknowledge the support that I received from Sarah Morgan Reedy, my wife and partner for the whole of my adult life. She is has contributed to everything worthwhile that I have managed to achieve and this dissertation is no exception. It was her trust that gave me the confidence to take on this PhD that initiated so many changes in our lives all at once. In the midst of starting a family, moving across the country, and changing careers, she never doubted that I would succeed. That confidence helped me to silence my own doubts at times. I thank her for the countless things that she has done to support my professional efforts all while raising our two beautiful children to be kind, curious, and brave human beings. I'm not sure if I could have done this without her, but I'm certain that I wouldn't have wanted to. I am forever grateful.

My academic advisor, Robert Cox, played an active role in my growth as a scientist over the last six years. Bob aided my progress in many areas and specifically improved how I formulate research questions, defend ideas, write competitive grants, talk science and give talks, visually communicate ideas, and pull the interesting story out of a dataset. He did this largely by example and by always treating me as a colleague. Perhaps more than anything else it was the high expectations that he sets for himself and his colleagues that improved the quality of my own work. Allowing me to contribute to the ideas and the writing in his NSF CAREER proposal showed me what it takes to get wins in the big leagues and prepared me to succeed in our competitive field. He always put me in a position to succeed. I couldn't have had a better mentor.

My grad school experience would not have been the same without my labmate and academic sister, Ariel Kahrl. She conveys a joy for the science life that is contagious and she is one heck of a lizard catcher. Working with her to mentor undergraduates in field biology is one of the greatest memories I will keep from my graduate school experience. She was a constant and positive force in the lab for my first five years of graduate school and I will always feel lucky that our time in the Cox Lab overlapped.

I would like to thank Christian Cox for his mentorship early in my graduate studies. His reading of my first manuscripts and grant proposals helped to build my skills as a professional thinker. He helped to indoctrinate me into the critical culture of science but was encouraging always. I am eternally appreciative of his willingness to put reading and commenting on my work towards the top of his to-do list.

I would like to thank Dan Warner for serving as an informal pre-doctoral mentor to me as I developed my science hobby during the summers when I was teaching high school biology. Dan provided invaluable advice on choosing a lab for grad school. His willingness to collaborate on research with a high school biology teacher eventually led to my dissertation project. I look forward to years of continued collaborations with Dan.

I would like to thank my brother John H. Reedy Jr. for the frequent conversations and his interest in my work. I greatly appreciate his ability to talk about anything and everything while reminding me that the work was interesting even when I was lost in the minutiae.

Having worked in high school science education in my previous career, I recognize the contributions to an advanced degree that are made long before a student arrives in graduate school. I would like to thank my parents John and Carre Reedy for the work they put in early in my life to ensure that I could pursue opportunities through education and for always being my cheerleaders. I would like to acknowledge the role that my godmother, Jill Pettibone, played in nurturing my identity as a young scientist by giving so many generous and thoughtful science-themed gifts and experiences throughout my childhood. Additionally, her relative proximity to Charlottesville and willingness to visit led her to become family to Sarah and our children during this time while I pursued a graduate education so far from our extended families.

I would like to thank the dedicated and talented undergraduates who assisted with my work. Albert Chung, Will Evans, Cara Giordano and Matt Kustra all made individual

contributions to my work at different points. I would not have produced the same quality or volume of work without their help. I look forward to following their inevitable future successes.

I would like to acknowledge the support of the UVa EEBio community, especially my committee, Butch Brodie, Alan Bergland, Dave Carr and Debbie Roach. I also wish to thank the members of the Brodie and Cox labs and others who gave feedback on my ideas over the years, especially Malcolm Augat, Karen Barnard-Kubow, Rachana Bhave, Robin Costello, Mike Hague, Amanda Hanninen, Lisa Mitchem, Heidi Seears, Brian Sanderson, Gabriela Toledo, Tyler Wittman, Cory Weller, and Corlett Wood.

I want to thank the Jefferson Scholar Foundation for their support and deep commitment to my career development. Their financial support has meant so much to me and my family, much of the writing of this dissertation was done at the Fellows Center, and their support through the Exploratory Fund has allowed me to embark on a future pursuing my professional interests in science and education. I am especially grateful to my benefactors, James H. and Elizabeth W. Wright.

Financial support for this dissertation was provided by a NSF Doctoral Dissertation Improvement Grant, an NSF CAREER award to Robert Cox, the Chicago Herpetological Society, and the Jefferson Scholars Foundation.

TABLE OF CONTENTS

INTRODUCTION

As a consequence of anisogamy, female and male evolutionary interests will diverge as each sex evolves towards a sex-specific strategy for achieving fitness (Trivers 1972a; Dawkins and Carlisle 1976; Parker 1979). Females produce a relatively small number of relatively large eggs, while males produce a large number of relatively small sperm (Parker 1982; Bulmer and Parker 2002). The sexes will be selected to achieve fitness in different ways that maximize individual fitness given their respective sex-specific strategies (Chapman et al. 2003). This sex difference in reproductive strategies has ultimately driven the array of sexual dimorphism in morphology and life history that we see across all taxa (Kodric-Brown and Brown 1987; Levitan 1996; Schärer et al. 2012). These divergent interests of the sexes have also set the stage for frequent evolutionary conflicts of interest for females and males of the same species when selection acts differently on each sex for traits that share the same genetic basis in both sexes. Such intralocus sexual conflict has wide ranging consequences and can constrain the independent evolution of one or both sexes (Bonduriansky and Chenoweth 2009). In this dissertation, I explore sex differences in costs of reproduction, aggressive interactions, natural selection, and their potential consequence for life-history evolution. In these studies, I employ experimental manipulations, behavioral assays, and mark-recapture methods in wild populations of brown anole lizards (*Anolis sagrei*). In addition to these field studies, I use comparative methods with existing data collected across lizard species to test predictions about the consequences of sexual conflict on the evolutionary trajectories of females.

Costs of reproduction in both sexes

Despite different forms and schedules of reproductive investment, theory predicts that average total lifetime reproductive investment will be equal for males and females because mean reproductive success should be the same for both sexes provided that the sex ratio at birth is balanced (Fisher 1930b; Queller 1997a). The form of reproductive investment for each sex will be dictated by the species-specific mating system and reproductive roles, but in general female reproductive investment takes the form of energetic provisioning of offspring and variation in fitness is closely tied to variation in fecundity and offspring quality (Clutton-Brock 1988). For males, variance in mating success is typically higher and reproductive investment takes the form of traits that allow an individual to increase mating opportunities (Wade 1979; Jones et al. 2002a). While it is generally well understood that reproductive investment comes in different forms for females and males, much less is known about sex-specific forms of costs of reproduction (Cox 2014c). Costs of reproduction have a long history of being studied in a single sex. For females, this has often been achieved via manipulating reproductive effort with brood manipulations or controlling the number of matings (Allander 1997; Wigby and Chapman 2005; Christe et al. 2011). Specifically in *Anolis sagrei,* surgical manipulations have been used to remove ovaries, directly eliminating reproductive investment for females, and costs of reproduction were shown in the currencies of survival, energy storage, and immune function (Cox and Calsbeek 2010b; Cox et al. 2010). In males, studies of costs of reproduction have often focused on costs of sexual selection, ornaments and weaponry used in courtship (Magnhagen 1991; Grether 1997; Moore and Wilson 2002; McCullough and Emlen 2013). These costs have more frequently been approached as costs, unique to males, arising from investment in competition for mates. However, direct comparisons between female and male costs of reproduction within a species have rarely been made (Kotiaho and Simmons 2003a; Fedorka et al. 2004; Dugas et al. 2015a). In part, this is due to the difficulty in measuring and manipulating reproductive investment for males. This is also partly due to sex differences in the timing of reproductive investment and identifying costs where identical measurements can be made in both sexes (Cox 2014c). This single-sex focus has prevented us from asking to what extent costs of reproduction in females and costs of sexual selection in males are actually equivalent. Directly comparing costs of reproduction between the sexes and integrating the concepts of costs from life history and sexual selection is an approach that could allow for an understanding of how sex differences in reproductive investment shape life-history evolution of both sexes when the reproductive strategies of males and females differ greatly.

In Chapter 1, I directly compare costs of reproduction between males and females in the common currencies of energy storage, immune function and parasites by surgically eliminating reproduction for male and female *A. sagrei* in a wild population. This experimental manipulation in the wild showed that, in the currencies of energy storage and parasite infections, males and females paid comparable costs of reproduction over the course of a single breeding season. These results suggest that despite dramatic sex differences in the form of reproductive investment and a high degree of sexual dimorphism, males and females can pay similar costs of reproduction in currencies that are common to both sexes. This work highlights that an integrated approach to simultaneously measuring costs of reproduction in both sexes is possible and can inform an understanding of life history evolution that incorporates sex differences in reproductive investment.

Comparing intrasexual aggression between the sexes

Females and males of many species use aggressive behaviors when competing with same-sex individuals of their species for resources within a home range or defended territory (Stamps 1977b; Wolff 1993; Spence and Smith 2005; Gill et al. 2007). The fitness costs and benefits of aggressive interactions are likely to differ between sexes due to sex differences in the forms of reproductive investment and the sex-specific way that fitness is achieved (Cain and Ketterson 2013). Because each offspring requires a parent of each sex, individuals only compete for reproductive success with individuals of the same sex and this can intensify intrasexual aggressive-interactions even when the resource being competed for is not direct access to mates. However, some of the most studied aggressive interactions are male-male combat over direct access to mates (Clutton-Brock et al. 1979; Schuett 1997; McElligott et al. 2001). In many species that frequently engage in male-male combat, weaponry has evolved and males frequently use aggressive behavioral display to assess competitors and avoid physical conflict when potential costs (i.e. risk of injury, energetic expenditure) outweigh the likely benefits (McElligott et al. 1998; López and Martín 2001). Although females are known to engage in aggressive interactions with same sex competitors, it is generally not known whether or to what extent females employ aggressive behavioral display to mitigate physical conflict with competitors (Cain and Ketterson 2013). Between-sex comparisons of aggressive interactions and display behaviors for territorial species are extremely rare.

In Chapter 2, I directly compare female-female and male-male aggressive interactions in *A. sagrei,* a polygynous species that exhibits territorial aggression. This comparison was done by staging same-sex territorial intrusions in the field and conducting behavioral observations. In accordance with a priori predictions, males did make greater use of behavioral display before escalating conflicts to physical attack. This is consistent with the hypothesis that males, which experience a greater risk of injury during combat due to a pronounced sexual dimorphism in jaw strength, will use display to avoid combat that is likely to be costly. However, somewhat surprisingly, there was no sex difference in the probability that a territorial intrusion would end in a physical attack. Females were just as likely as males to attack an intruder and they did so more quickly following intrusion. These results challenge the notion that males are categorically more aggressive than females in territorial polygynous species.

Intralocus sexual conflict

Selection frequently acts differently on the same traits for females and males of the same sex (Cox and Calsbeek 2009). If the genetic basis for those traits is shared between the sexes, then this sexually antagonistic selection will pull the genome in two different directions. The shared genome will then prevent one or both sexes from reaching their sex-specific optima for traits over which this intralocus sexual conflict exists (Van Doorn 2009; Harano et al. 2010). Even in situations where selection is not pulling in opposite directions per se, any between-sex differences in the fitness surfaces of traits with a shared genetic basis can hamper the independent evolution of the sexes (Bonduriansky and Chenoweth 2009). Although this conflict was well described by theoreticians more than 30 years ago and conceived of well before that, it has only been in the last two decades that we have seen a serious expansion of empirical research testing predictions which stem from this theory (Trivers 1972a; Dawkins and Carlisle 1976; Parker 1979; Bonduriansky and Chenoweth 2009). Pioneering work at the outset of this recent empirical interest in intralocus sexual conflict framed the conflict as "ontogenetic sexual conflict" because it demonstrated that the same genomes produced high fitness (as measured by viability) female and male *Drosophila* during the juvenile life stage, but that at the adult life stage the genomes which produced the highest fitness (via reproductive success) for males produced the lowest fitness for females and vice-versa (Chippindale et al. 2001). This work was interpreted as evidence that sexual conflict develops over ontogeny as the evolutionary interests of females and males diverge. Despite this compelling evidence and the significance of the idea that sexual conflict develops over ontogeny to the evolutionary dynamics of sexual conflict, this idea has not been thoroughly explored during this period of great interest by empiricists in sexual conflict.

In Chapter 3, I test the prediction that sexually antagonistic selection develops over ontogeny. This test was done by estimating natural (viability) selection on body size of juveniles in a wild *A. sagrei* population for multiple episodes of selection across a three-year period. I directly tested for sexually antagonistic selection with sex-by-trait interactions for both linear and quadratic selection. Additionally, I pooled data across all three years of study to visualize the fitness surfaces for both sexes to facilitate between-sex comparisons across the young-of-the-year cohort. I found a pattern of selection that is the same for females and males during the earliest part of the juvenile life stage, when large body size is strongly favored in both sexes. However, for juveniles that grow large enough to approach sexual maturity in same season in which they hatched, fitness surfaces strongly diverge as selection acts strongly against the largest young-of-the-year females in the population while the probability of survival remains consistently high for the largest males in this age cohort.

Sexual conflict over life history

The tradeoff between reproduction and survival is the cornerstone of life history theory (Williams 1966; Stearns 1989; Roff et al. 2006). This tradeoff has been demonstrated among species and has been instrumental in answering the basic question of why some species have long lifespans and others are short lived. This tradeoff has also been described within species through manipulations of reproduction and through negative correlations between reproduction and survival that have been detected within natural variation among individuals (Nur 1984; Brooks 2000; Koivula et al. 2003; Cox and Calsbeek 2010a; Cox et al. 2010; Hegemann et al. 2013). However, it has only been relatively recently that the role that intralocus sexual conflict may play in the resolution of this tradeoff has been considered (Bonduriansky et al. 2008; Maklakov and Lummaa 2013). Mounting experimental evidence shows that females and males have different sex-specific optima for the balance that is struck between investment in reproduction and survival and in the optimal lifespan for maximizing fitness (Maklakov et al. 2007; Lewis et al. 2011; Lind et al. 2015; Berger et al. 2016). This leads to sexual conflict over lifespan that is predicted to persist even with the evolution of sexual dimorphism due in part to the pleiotropic nature of life-history traits (Bonduriansky et al. 2008). Much of the study of life-history tradeoffs between survival and reproduction has focused on females, and comparative methods have demonstrated negative correlations between survival and reproduction across species using data from females (Read and Harvey 1989a; Jervis et al. 2007). However, residual variation around that tradeoff has typically been treated as error variance. The role that intralocus sexual conflict may play in explaining variation in the resolution of the tradeoff between reproduction and survival has been proposed but has not yet been tested across species (Bonduriansky et al. 2008; Maklakov and Lummaa 2013).

In Chapter 4, I test for a negative correlation between female annual survival and reproductive effort across lizards. I then test whether intralocus sexual conflict plays a role in the resolution of that tradeoff by testing for a correlation between sexual size dimorphism (SSD) and the residual variation in survival around the tradeoff between survival and reproduction. I find evidence that clearly demonstrates the tradeoff between survival and reproduction. I also find that residual variation is correlated with a directional index of SSD, such that residual survival decreases for species along an axis that runs from male-larger to female-larger species. This result suggests that intralocus sexual conflict inhibits the evolution of life history traits in females.

References

Allander, K. 1997. Reproductive investment and parasite susceptibility in the great tit. Functional Ecology 11:358-364.

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. The American Naturalist 188:E98-E112.

Bonduriansky, R. and S. F. Chenoweth. 2009. Intralocus sexual conflict. Trends in ecology & evolution 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. Functional ecology 22:443-453.

Brooks, R. 2000. Negative genetic correlation between male sexual attractiveness and survival. Nature 406:67.

Bulmer, M. and G. Parker. 2002. The evolution of anisogamy: a game-theoretic approach. Proceedings of the Royal Society of London B: Biological Sciences 269:2381-2388.

Cain, K. E. and E. D. Ketterson. 2013. Costs and benefits of competitive traits in females: aggression, maternal care and reproductive success. PLoS One 8:e77816.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends in Ecology & Evolution 18:41-47.

Chippindale, A. K., J. R. Gibson, and W. R. Rice. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in Drosophila. Proceedings of the National Academy of Sciences 98:1671-1675.

Christe, P., O. Glaizot, N. Strepparava, G. Devevey, and L. Fumagalli. 2011. Twofold cost of reproduction: an increase in parental effort leads to higher malarial parasitaemia and to a decrease in resistance to oxidative stress. Proceedings of the Royal Society of London B: Biological Sciences:rspb20111546.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press.

Clutton-Brock, T. H., S. Albon, R. Gibson, and F. E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus L.). Animal behaviour 27:211-225.

Cox, R. M. 2014. Integrating costs of reproduction between the sexes. Integrative Organismal Biology:153-168.

Cox, R. M. and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. The American Naturalist 173:176-187.

Cox, R. M. and R. Calsbeek. 2010. Severe sosts of reproduction persist in Anolis lizards despite the evolutio of a single-egg clutch. Evolution 64:1321-1330.

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. Functional Ecology 24:1262-1269.

Dawkins, R. and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131.

Dugas, M. B., C. N. Wamelink, and C. L. Richards-Zawacki. 2015. Both sexes pay a cost of reproduction in a frog with biparental care. Biological journal of the Linnean Society 115:211-218.

Fedorka, K. M., M. Zuk, and T. A. Mousseau. 2004. Immune suppression and the cost of reproduction in the ground cricket, Allonemobius socius. Evolution 58:2478-2485.

Fisher, R. A. 1930. The genetical theory of natural selection: a complete variorum edition. Oxford University Press.

Gill, S. A., E. D. Alfson, and M. Hau. 2007. Context matters: female aggression and testosterone in a year-round territorial neotropical songbird (Thryothorus leucotis). Proceedings of the Royal Society of London B: Biological Sciences 274:2187-2194.

Grether, G. F. 1997. Survival cost of an intrasexually selected ornament in a damselfly. Proceedings of the Royal Society of London B: Biological Sciences 264:207-210.

Harano, T., K. Okada, S. Nakayama, T. Miyatake, and D. J. Hosken. 2010. Intralocus sexual conflict unresolved by sex-limited trait expression. Current Biology 20:2036-2039.

Hegemann, A., K. D. Matson, H. Flinks, and B. I. Tieleman. 2013. Offspring pay sooner, parents pay later: experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. Frontiers in zoology 10:77.

Jervis, M. A., C. L. Boggs, and P. N. Ferns. 2007. Egg maturation strategy and survival trade-offs in holometabolous insects: a comparative approach. Biological Journal of the Linnean Society 90:293-302.

Jones, A. G., J. R. Arguello, and S. J. Arnold. 2002. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough–skinned newt. Proceedings of the Royal Society of London B: Biological Sciences 269:2533-2539.

Kodric-Brown, A. and J. H. Brown. 1987. Anisogamy, sexual selection, and the evolution and maintenance of sex. Evolutionary Ecology 1:95-105.

Koivula, M., E. Koskela, T. Mappes, and T. A. Oksanen. 2003. Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. Ecology 84:398-405.

Kotiaho, J. S. and L. W. Simmons. 2003. Longevity cost of reproduction for males but no longevity cost of mating or courtship for females in the male-dimorphic dung beetle Onthophagus binodis. Journal of Insect Physiology 49:817-822.

Levitan, D. R. 1996. Effects of gamete traits on fertilization in the sea and the evolution of sexual dimorphism. Nature 382:153.

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.

Lind, M. I., M. K. Zwoinska, S. Meurling, H. Carlsson, and A. A. Maklakov. 2015. Sex-specific tradeoffs with growth and fitness following life-span extension by rapamycin in an outcrossing nematode, Caenorhabditis remanei. Journals of Gerontology Series A: Biomedical Sciences and Medical Sciences 71:882-890.

López, P. and J. Martín. 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards, Podarcis hispanica. Behavioral Ecology and Sociobiology 49:111-116.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends in Ecology & Evolution 6:183-186.

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.

McCullough, E. L. and D. J. Emlen. 2013. Evaluating the costs of a sexually selected weapon: big horns at a small price. Animal Behaviour 86:977-985.

McElligott, A. G., M. P. Gammell, H. C. Harty, D. R. Paini, D. T. Murphy, J. T. Walsh, and T. J. Hayden. 2001. Sexual size dimorphism in fallow deer (Dama dama): do larger, heavier males gain greater mating success? Behavioral Ecology and Sociobiology 49:266-272.

McElligott, A. G., V. Mattiangeli, S. Mattiello, M. Verga, C. A. Reynolds, and T. J. Hayden. 1998. Fighting tactics of fallow bucks (Dama dama, Cervidae): reducing the risks of serious conflict. Ethology 104:789-803.

Moore, S. L. and K. Wilson. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. Science 297:2015-2018.

Nur, N. 1984. The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. The Journal of Animal Ecology:479-496.

Parker, G. 1979. Sexual selection and sexual conflict. Sexual selection and reproductive competition in insects 123:166.

Parker, G. A. 1982. Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. Journal of Theoretical Biology 96:281-294.

Queller, D. C. 1997. Why do females care more than males? Proceedings of the Royal Society of London B: Biological Sciences 264:1555-1557.

Read, A. and P. H. Harvey. 1989. Life history differences among the eutherian radiations. Journal of Zoology 219:329-353.

Roff, D. A., E. Heibo, and L. Vøllestad. 2006. The importance of growth and mortality costs in the evolution of the optimal life history. Journal of Evolutionary Biology 19:1920-1930.

Schärer, L., L. Rowe, and G. Arnqvist. 2012. Anisogamy, chance and the evolution of sex roles. Trends in Ecology & Evolution 27:260-264.

Schuett, G. W. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. Animal Behaviour 54:213-224.

Spence, R. and C. Smith. 2005. Male territoriality mediates density and sex ratio effects on oviposition in the zebrafish, Danio rerio. Animal Behaviour 69:1317-1323.

Stamps, J. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional ecology 3:259-268.

Trivers, R. 1972. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), Sexual selection and the descent of man. Chicago# Aldine.

Van Doorn, G. S. 2009. Intralocus sexual conflict. Annals of the New York Academy of Sciences 1168:52-71.

Wade, M. J. 1979. Sexual selection and variance in reproductive success. The American Naturalist 114:742-747.

Wigby, S. and T. Chapman. 2005. Sex peptide causes mating costs in female Drosophila melanogaster. Current Biology 15:316-321.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist 100:687-690.

Wolff, J. O. 1993. Why are female small mammals territorial? Oikos:364-370.

Chapter One:

Both sexes suffer increased parasitism and reduced energy storage as costs of reproduction in the brown anole, *Anolis sagrei*

As published: Reedy, A.M., C.L. Cox, A. K. Chung, W.J. Evans, and R.M Cox. 2016. Both sexes suffer increased parasitism and reduced energy storage as costs of reproduction in the brown anole, *Anolis sagrei*. *Biological Journal of the Linnean Society* 117(3), 516-527.

ABSTRACT

Sexual selection theory proposes that males suffer reduced immune function and increased parasitism as costs of expressing sexual signals. Life history theory proposes that females suffer the same costs due to inherent tradeoffs between reproduction and self-maintenance. Mechanistically, each theory invokes an energetic tradeoff, but few experiments have directly compared these costs of reproduction between the sexes due to fundamental sex differences in the nature of reproductive investment and a tendency for each theory to focus on a single sex. To test whether males and females experience comparable costs of reproduction in terms of energetics, immune function, and parasitism, we used gonadectomy to eliminate most aspects of reproductive investment in wild brown anole lizards (*Anolis sagrei*) of both sexes. We compared these non-reproductive males and females to intact, reproductive controls with respect to stored energy (fat bodies), immune function (swelling response to phytohemagglutinin), and the prevalence and intensity of infection by four types of parasite (gastric nematodes, intestinal nematodes, fecal coccidia, and ectoparasitic mites). Gonadectomized anoles experienced dramatic increases in fat storage that were accompanied by decreases in the prevalence of intestinal nematodes and in the intensity of coccidia infection. These costs of reproduction were comparable between males and females, but neither sex exhibited the predicted increase in immune function following gonadectomy. Our results suggest that, despite fundamental sex differences in the nature of reproductive investment, both male and female anoles experience similar costs of reproduction with respect to energy storage and some aspects of parasitism.

INTRODUCTION

Due to fundamental differences in their reproductive biology, males and females invest resources in different aspects of reproduction (Trivers 1972b; Clutton-Brock and Parker 1992; Rolff 2002; Maklakov and Lummaa 2013). Males of many species maximize their reproductive success by increasing their mating opportunities, so they often invest heavily in ornaments, weaponry, mate searching, courtship, and territory defense (Bateman 1948; Jones et al. 2002b; Bonduriansky et al. 2008). Females are limited by the time and energy required to provision an embryo, so they are inherently predisposed to allocate resources to vitellogenesis, egg or embryo production, and parental care (Queller 1997b; Kokko and Jennions 2008). Despite these fundamental sex differences, total reproductive investment is predicted to be equal for males and females when the adult sex ratio is equal. This is because, at the population level, each sex is engaged in intrasexual competition for the same overall fitness benefit: half of the genes that will be passed on to the next generation (Fisher 1930a; Queller 1997b). However, this prediction is often difficult to assess in wild populations because of inherent sex differences in the nature and seasonal timing of reproductive investment (Cox 2014a). Consequently, the costs associated with reproduction are rarely considered simultaneously in both sexes (Queller 1997b; Bonduriansky et al. 2008; Chu and Lee 2012).

One reason for this lack of integration between sexes stems from the historical separation of sexual selection theory, which has focused on costs of reproduction that enforce honest signaling in males (Zahavi 1975; Folstad and Karter 1992), and life history theory, which grew from an interest in costs that structure the evolution of demography and population growth via female reproduction (Cole 1954; Gadgil and Bossert 1970). This distinction can be illustrated by considering immunosuppression and parasitism as proximate costs of reproduction (Cox 2014). As an extension of sexual selection theory, the immunocompetence handicap hypothesis (ICHH) predicts that male vertebrates should suffer increased parasitism due to the immunosuppressive effects of androgens that coordinate the expression of secondary sex traits, which serve as honest indicators of health and quality (Folstad and Karter 1992). Although males exhibit lower immune function and higher parasite loads than females in some taxa (Moore and Wilson 2002; Nunn et al. 2009), the reverse is true in others (McCurdy et al. 1998), and general tests for male-biased parasitism and immunosuppression yield equivocal results (Roberts et al. 2004). One reason may be that reproductive females, like males, also experience costs of reduced immune function and increased parasitism (Nordling et al. 1998; Ardia et al. 2003; French et al. 2007; Cox et al. 2010; McKean and Lazzaro 2011). Life history theory assumes that such physiological costs structure the evolutionary tradeoff between reproduction and survival (Rose and Charlesworth 1981), and reduced immunocompetence in females is thought to result from energetic tradeoffs between reproduction and self-maintenance (Sheldon and Verlhust 1996; Martin et al. 2003; Martin et al. 2011). These energetic tradeoffs provide a mechanism that is common to both sexes, because the immunosuppressive effects of androgens invoked by the ICHH are thought to derive from their role in coordinating energy allocation between reproduction and immune defense (Wedekind and Folstad 1994; Cox 2014a). Therefore, both sexes are predicted to face pronounced energy allocation tradeoffs during reproduction, which could result in similar costs with respect to reduced immune function and increased parasitism. However, the extent to which these costs are comparable between the sexes is generally unknown.

Experimental manipulations of reproductive investment are often necessary to provide conclusive evidence for proximate costs of reproduction (Reznick 1992; Landwer 1994; Cox 2006). However, experiments can be complicated by the fact that reproductive investment occurs at different times, involves different aspects of reproduction, and incorporates different regulatory pathways in each sex (Cox 2014a). As a simplified example, male vertebrates tend to incur large respiratory (i.e., metabolic) costs related to androgen-mediated courtship, mate-searching, and territory defense at the outset of the breeding season, whereas female vertebrates tend to incur large production (i.e., biosynthetic) costs related to estrogen- and progesterone-mediated provisioning of eggs and embryos later in the season (Michener and Locklear 1990; Hoffman et al. 2008; Cox 2014a). Experimental comparisons of reproductive costs are therefore most straightforward in situations where the timing and nature of reproductive investment are closely aligned for males and females. For example, in birds with biparental care, brood manipulations (egg removals and additions) have demonstrated that loss of body mass and increased parasitism are costs incurred by one or both sexes during offspring provisioning (Allander 1997; Velando and Alonso-Alvarez 2003; Christe et al. 2012). However, brood manipulations only address a single aspect of reproductive investment, and their generality is unclear beyond the relatively small proportion of species that provide biparental care (Cox 2014a). Other studies have directly compared the costs of reproduction between the sexes by manipulating mating frequency or the duration of exposure to mates (Kotiaho and Simmons 2003b; Fedorka et al. 2004; Dugas et al.

2015b), but the costs associated solely with mating likely represent different fractions of total reproductive investment for each sex. An ideal approach would manipulate total reproductive investment and directly compare the magnitude of its associated costs between the sexes.

One way to experimentally assess the total cost of reproduction is to eliminate most aspects of reproductive investment via gonadectomy. In female brown anole lizards (*Anolis sagrei*) this method has been used to demonstrate pronounced costs of reproduction with respect to growth, body condition, energy storage, hematocrit, immune function, and survival (Cox and Calsbeek 2010a; Cox et al. 2010; Cox et al. 2014b). In principle, castration can also be used to eliminate direct costs of gamete production in males and to reduce or eliminate other indirect costs due to androgen-mediated behavior and physiology. Castration of males abolishes some reproductive and territorial behaviors completely, and reduces the frequency or elevates the stimulus threshold necessary for others (Barfield et al. 1972; Arnold 1975; Adkins 1977; Harding et al. 1983; Tokarz 1986; Tokarz et al. 2002). In this study, we used gonadectomy to reduce or eliminate most aspects of reproductive investment in a wild population of brown anoles. We then directly tested whether males and females experience similar costs of reproduction with respect to energy storage (wet mass of fat bodies), immune function (swelling response to a novel antigen, phytohemagglutinin), and the prevalence (percentage of infected individuals) and intensity (number of parasites per infected individual) of infection by four different parasites: gastric nematodes (Physalopteridae), intestinal nematodes (Atractidae), fecal coccidia (Eimeriidae), and ectoparasitic mites (Trombiculidae). We predicted that reduction of reproductive investment via gonadectomy would increase energy storage and immune response while decreasing the prevalence and/or intensity of parasites in both sexes. In accordance with the general prediction that overall reproductive investment of males and females should be equivalent, we predicted that treatment effects would be similar in both sexes (Rolff 2002; Bonduriansky et al. 2008).

MATERIAL AND METHODS

Study Species

The brown anole (*Anolis sagrei*) is a sexually dimorphic lizard that is native to Cuba and The Bahamas. Adult males from the closed island population that we studied at Regatta Point on Great Exuma in The Bahamas (23°30'N, 75°45'W) average 32% larger than females in terms of snout-vent length (SVL) and 150% larger in terms of mass (Cox and Calsbeek 2010c). Males fight and display to establish territories encompassing multiple females, and their seasonal reproductive investment extends approximately from the onset of testicular recrudescence and elevated testosterone levels in February through the cessation of mating around September (Tokarz 1985, 1998; Tokarz et al. 1998). Females repeatedly produce single-egg clutches approximately every 10 days from April to as late as October, with follicular maturation and ovulation continuously alternating between right and left ovaries (Lee et al. 1989a; Cox and Calsbeek 2010a). Genetic analyses reveal a high incidence of multiple paternity across successive eggs produced by individual females (Calsbeek et al. 2007), such that both sexes are polygamous. Because opportunities for fertilization are continuously available and females are constantly gravid, the overall timing of reproductive investment in this species is broadly similar between sexes across most of the lengthy breeding season.

Experimental Design and Surgical Procedures

We used a hand-held noose to capture 220 female and 120 male *A. sagrei* adults early in the reproductive season (May 23 – June 4), well after the onset of mating activity (Feb-Mar) and shortly after the onset of regular oviposition (Apr-May), but 4-5 months prior to the cessation of mating activity and oviposition (Sep-Oct). We measured snout-vent length (SVL, nearest 1 mm) and body mass (nearest 0.01 g) for each lizard. We then marked each animal with a unique toe clip and randomly assigned it to one of two treatment groups: (1) bilateral gonadectomy (GDX: removal of both ovaries or testes, *n* =110 females, 60 males), or (2) control surgery (gonads manipulated but left intact, *n* = 110 females, 60 males). During surgery, we confirmed that all experimental animals were in reproductive condition, as determined by enlarged testes with visible seminiferous tubules or enlarged ovaries with vitellogeneic follicles. We followed published surgical protocols (Cox et al. 2009b; Cox and Calsbeek 2010a; Cox et al. 2010; Cox et al. 2014b) that began with administration of local anesthesia and analgesia (2-4 μl injection of 0.25% bupivacaine HCl, Hospira Inc., Lake Forest, IL). We then immobilized animals with a 5–8 min exposure to 4ºC and conducted surgeries atop a chemical ice pack with a slighlty thawed boundary layer. For all surgeries, we made a single 5–8 mm ventral incision into the coelomic cavity, then ligated, ablated, and cauterized each gonad for the gonadectomy treatment. For control surgeries, we briefly exteriorized the gonads and returned them to the body cavity intact. We closed incisions with VetClose™ cyanoacrylate surgical glue (Butler Schein Animal Health, Dublin, OH). We allowed animals to recover overnight in individual containers, then released each animal at its exact site of capture the following day.

We returned to Regatta Point 10 weeks later (August 6–15) to recapture 50 of 120 males (17 GDX; 33 control) and 51 of 220 females (23 GDX; 28 control), which were used to assess sex and treatment effects on energy storage, immune function, and parasite loads (see below). Although we have previously documented increased survival of GDX females, relative to controls, in a nearby population (Cox & Calsbeek, 2010a; Cox et al., 2010), we did not detect any treatment effect on female survival in the present study (logistic regression: $\chi^2 = 0.41$, $P = 0.52$), and survival rates of both GDX and control females (21% and 25%, respectively) were at the low end of natural variation across six previous years at Regatta Point (mean 33%, range 17-46%). By contrast, survival of control males (55%) was significantly higher than that of GDX males (28%) in the present study (logistic regression: $\chi^2 = 9.31$, $P < 0.01$), and higher than in any of nine previous years of study on unmanipulated males at Regatta Point (mean 38%, range 24-46%), whereas survival of GDX males was within the lower range of natural variation across previous years. Consequently, we found a significant sex difference in survival in the present study (logistic regression: $\chi^2 = 11.36$, $P < 0.001$), driven primarily by the atypically high survival of control males ($\chi^2 = 3.56$, $P = 0.059$), as well as an overall treatment effect on survival ($\chi^2 = 7.46$, $P < 0.01$). Because this treatment effect was in the opposite direction predicted from previous studies of GDX and control females (Cox & Calsbeek, 2010a; Cox et al., 2010), we do not interpret these results in the context of survival costs of reproduction. It is unclear whether this indicates that our GDX procedure itself detrimentally impacted the survival of males, that survival of control males was atypically high by chance, or both. Consequently, we focus on inferring costs of reproduction from measures of energy storage, immune function, and parasite levels of recaptured animals.

Energy Storage

Anoles and other lizards store energy in paired, abdominal fat bodies (Derickson 1976). This energy is used for gonadal recrudescence, egg provisioning, and nutrition during periods of low food availability (Chapman and Chapman 1964; Sexton et al. 1971; Lin 1979). The size of these fat bodies cycles seasonally in anoles, increasing as reproductive activity decreases toward the end of the breeding season (Licht and Gorman 1970). Analysis of stomach contents at multiple time points throughout the year suggests that, rather than being driven by patterns of food intake, changes in the mass of fat bodies are instead driven by reproductive activity, as stored energy is mobilized to fuel reproduction (Lee et al. 1989a). Though the fat bodies are not the sole sites of fat storage, they are a useful index of energetic savings associated with the cessation or elimination of reproduction (Cox et al. 2010; Cox et al. 2014b). To assess the energetic cost of reproduction, we compared the wet mass of abdominal fat bodies dissected from a subset of recaptured males and females in each treatment (n = 23 total: 6 GDX males, 5 control males; 7 GDX females, 5 control females).

Immune Function

We assayed immune function by measuring the localized swelling response to challenge with a novel antigen, phytohemagglutinin (PHA), for a subset of recaptured individuals (n = 65 total: 10 GDX males, 22 control males; 12 GDX females, 21 control females). Injection of PHA induces both innate and acquired immune defenses (Kennedy and Nager 2006), including the influx of lymphocytes, heterophils, thrombocytes, basophils, and macrophages, which manifests as localized swelling at the site of injection (Martin et al. 2006). The extent of localized swelling in response to PHA is typically interpreted as a measure of immunocompetence, with greater swelling indicative of a more robust immune response (Goto et al. 1978; Smits et al. 1999, Calsbeek et al. 2008; but see Kennedy and Nager 2006). We used a dial caliper to measure the thickness of each animal's right hind foot to the nearest 0.1 mm between the first and fifth digits, then subcutaneously injected 0.1 mg PHA (Sigma-Aldrich Inc., St Louis, MO, USA), dissolved in 0.01 ml phosphate-buffered saline, at this same location. We measured the thickness of the foot again 24 h after injection of PHA and calculated the proportional increase in the thickness of the foot as the difference between initial and final thickness divided by initial thickness. We used the mean of three consecutive measurements per individual at each time point in our analysis.

Parasite Infection

We used a hand lens to count external mite parasites (Trombiculidae) on a subset of recaptured individuals (n = 80 total: 15 GDX males, 24 control males; 19 GDX females, 22 control females). We then held all animals for 24 h in sanitized plastic containers to collect a fecal sample for later quantification of coccidian oocysts (n = 55 individuals provided fecal samples: 8 GDX males, 19 control males; 11 GDX females, 17 control females). We measured the wet mass of each fecal sample and stored it in 1 ml of

10% formalin. We later placed each fecal sample into a Fecalyzer (EVSCO Pharmaceuticals, NJ, USA) with 8 ml of Fecasol (Vétoquinol, TX, USA), ground each fecal sample into solution, and added additional Fecasol (~7 ml) until a meniscus formed on the top of the tube. We then placed a coverslip on the meniscus and let each sample stand for 17 min to allow oocysts to float to the surface before transferring the coverslip to a clean microscope slide for examination at 100x magnification. We recorded the number of coccidian oocysts on the entire coverslip for each individual and expressed this number per mg of feces. We identified all oocysts as belonging to Eimeriidae, a family of intracellular protozoan parasites within the Coccidia subclass of the phylum Apicomplexa. Coccidians induce cell damage in their hosts, but the degree to which they can be considered pathogenic in wild reptiles is largely unknown (Greiner 2003).

To quantify both intestinal and gastric nematodes, we dissected the gastrointestinal tracts from the same subset of individuals that we euthanized to assess fat storage (*n* = 23 total: 6 GDX males, 5 control males; 7 GDX females, 5 control females). We stored the entire gastrointestinal tract in 10% formalin, then sectioned lower gastrointestinal tracts into 1-cm pieces and counted the total number of rectal nematodes (Atractidae) in all sections under a dissection scope. Atractid nematodes are viviparous, undergo direct development in the lower intestine of their host, and have a venereal mode of transmission between individual hosts (Norval et al. 2011; Langford et al. 2013). For the same subset of animals, we dissected the stomach and counted all visible nematodes (Physalopteridae). Physalopterids parasitize all vertebrate classes and their attachment to gastric mucosa can cause inflammation and excessive mucus production (Levine 1968; Goldberg and Bursey 1989).

Statistical Analyses

To test for effects of sex and reproductive investment on energy storage, we used ANOVA with mass-specific fat mass (fat mass / (body mass - fat mass)) as the response variable and main effects of sex and treatment with a sex-by-treatment interaction. To test for effects of reproductive investment on immune function, we used ANOVA with proportional swelling response to PHA ((final thickness – initial thickness) / initial thickness) as the response variable and main effects of sex and treatment with a sex-by-treatment interaction. To account for scaling of fat mass or swelling response with body mass, we also performed ANCOVA with either absolute fat mass or swelling as the response variable, treatment as the main effect, and body mass as a covariate. We conducted these analyses separately within each sex because males and females do not overlap in the covariate (body mass). To compare the prevalence of infection by each parasite (i.e., the proportion of lizards infected) between sexes and treatment groups, we used nominal logistic models with presence of each parasite type (0 or 1) as the response variable, sex and treatment as main effects, and a sex-by-treatment interaction. Because parasite count data were non-normally distributed, we used generalized linear models to compare the intensity of infection by each parasite (i.e., number of parasites per infected individual) between sexes and treatment groups (Alexander 2012) with untransformed parasite counts (O'Hara & Kotze 2010) as the response variable, fitted with a Poisson distribution and an over-dispersion parameter estimated as the Pearson chi-square value divided by degrees of freedom. For each of these models, we tested for effects of sex, treatment, and their interaction.

RESULTS

Energy storage and immune function

Experimental reduction of reproductive investment via gonadectomy dramatically increased the wet mass of fat bodies (Fig. 1a; treatment: $F_{1,19} = 21.99$, $P < 0.001$). The treatment effect did not differ between sexes (sex x treatment: $F_{1,19} = 0.08$, $P = 0.78$) and there was no overall sex difference in fat storage per unit body mass (sex: $F_{1,19} = 0.61$, $P = 0.44$). Separate models that included body mass as a covariate also showed that treatment reduced fat body mass for both sexes (females: $F_{1,11} = 14.77$, $P < 0.005$; males: $F_{1,10} = 24.98$, $P < 0.005$). Swelling response to PHA did not differ as a function of sex (Fig. 1b; $F_{1,65} = 0.67$, $P = 0.42$), treatment ($F_{1,65} = 0.06$, $P = 0.81$), or their interaction ($F_{1,65} < 0.01$, $P = 0.98$). Separate analyses with body mass included as a covariate also indicated no treatment effect on swelling response to PHA for either sex (females: $F_{1,32} = 2.58$, $P = 0.12$; males: $F_{1,31} = 0.39$, $P = 0.54$)

Prevalence and intensity of parasite infection

Experimental reduction of reproductive investment via gonadectomy resulted in a significant decrease in the prevalence (presence or absence) of atractid nematodes in the intestine, but did not impact the prevalence of physalopterid nematodes in the stomach, eimeriid coccidia in the feces, or trombiculid mites on the ectoderm (Fig. 2, Table 1). Males and females did not differ in the prevalence of infection by atractid nematodes, physalopterid nematodes, eimeriid oocysts, or trombiculid mites (Fig. 2; Table 1).

Treatment effects on the prevalence of infection did not differ by sex for any class of parasite (Fig. 2, Table 1).

Experimental reduction of reproductive investment via gonadectomy resulted in a significant decrease in the intensity of infection (parasites per infected host) by eimeriid coccidia, but it did not impact the intensity of infection by physalopterid nematodes, atractid nematodes, or trombiculid mites (Fig. 3, Table 1). Infected males had a greater number of mites than infected females (Fig. 3, Table 1), but we did not detect any other sex differences in the intensity of infection, nor did treatment effects on the intensity of infection differ by sex for any class of parasite (Fig. 3, Table 1).

DISCUSSION

Reproductive investment is predicted to be equivalent in males and females because, at the population level, average reproductive success should be equal for each sex when the adult sex ratio is balanced (Fisher 1930a; Queller 1997b). Hence, each sex stands to gain comparable genetic benefits from reproduction. Whether this means that the myriad costs of reproduction should also tend to be similar in each sex is less clear, particularly when these costs are measured in units (e.g., stored energy, intensity of parasitism) that do not translate directly into fitness (Cox 2014). In the present study, we found comparable costs of reproduction in each sex with respect to energy storage and several measures of parasite infection, which we view as broadly consistent with the prediction that both sexes should invest similarly in reproduction. In female brown anoles, gonadectomy has previously been used to demonstrate physiological costs of reproduction including reduced energy storage, immune function, and parasite tolerance (Cox et al. 2010; Cox and Calsbeek 2011). Our experiment extends those results by demonstrating that males also experience similar costs of reproduction. Despite dramatic differences in the behavioral and physiological basis of reproductive investment in each sex, males and females experienced costs of reproduction that were comparable with respect to energy storage and parasite load, though we note that small sample sizes reduced the power of our statistical tests for sex-by-treatment interactions for several parasites (Table 1). An additional caveat to our study is that our experimental design limited our assessment of costs of reproduction to animals that survived to be recaptured, which could complicate our inferences about treatment effects if, for example, individuals with particularly high or low levels of energy storage or parasitism were more likely to survive in one treatment group than another.

The similar increase in the mass of fat bodies for both sexes following gonadectomy suggests that, for both male and female brown anoles, the energy invested in reproduction is diverted from storage over the course of the breeding season. However, given the divergent reproductive strategies of each sex, different mechanisms likely underlie these otherwise comparable energetic responses. For females, the biosynthetic demands of provisioning eggs are likely to drive the total cost of reproduction. The mass of a single egg is typically close to 10% of the body mass of an adult female brown anole, and individual females repeatedly lay single eggs approximately once every 10 days. Across a six-month breeding season, a female anole may therefore have a total reproductive output far exceeding its own body mass (Andrews and Rand 1974a). Removal of the ovaries eliminates this large biosynthetic cost and likely results in a substantial energetic savings. However, we cannot rule out additional, non-exclusive explanations, such as an increase in the abdominal space available for food and fat storage, direct effects of ovarian hormones on fat storage and metabolism, or indirect effects of ovarian hormones on behaviors that influence energy acquisition and/or expenditure (Cox et al. 2010). Although we cannot rigorously address most of these possibilities, GDX and control females do not differ in their aggressive responses to staged territorial intrusions by females, nor does exogenous estradiol (which may be reduced by GDX) have any discernable effect on display behavior in captive females (Cox et al. 2014; E. Parker, N. Brown, R. Cox, and R. Calsbeek, unpublished data).

For male anoles, competitive interactions with other males and the associated metabolic costs of activity and territory defense are likely to contribute heavily to the overall cost of reproduction. Male anoles are highly aggressive towards each other and engage in frequent displays and occasional combat throughout their lengthy breeding season (Evans 1938; Stamps 1977a; Jenssen et al. 1995). Surgical and chemical castration of male anoles abolishes some aggressive behaviors while reducing the frequency others (Tokarz 1986, 1995; Tokarz et al. 2002; Cox et al. 2009b), and these behavioral aspects of male reproductive investment have demonstrable metabolic costs in other lizards (Marler et al. 1995; Cox et al. 2005). Mechanistically, many of these energetic effects are likely mediated by a reduction in circulating levels of androgens such as testosterone, which we have previously confirmed as a consequence of our gonadectomy procedure (Cox and John-Alder 2005; Cox et al. 2005; Cox et al. 2009b). These effects could occur directly, given that testosterone reduces body fat in many vertebrate species (Ketterson et al. 1991; Cox et al. 2014a), or indirectly due to the elimination of androgen-mediated behaviors with energetic costs (Marler et al. 1995; Cox et al. 2005). As in the case of females, we cannot rule out additional, non-exclusive explanations for increased energy storage in gonadectomized males, such as an increase in the abdominal space available for food and fat storage (the testes comprise a substantial portion of the coelomic cavity during the breeding season) or the energetic costs associated with maintaining enlarged testes and supporting spermatogenesis. Indeed, one advantage of gonadectomy is that it provides a holistic assessment of the summed contributions of all of these aspects of reproductive investment in each sex.

Irrespective of the exact causative factors underlying the energetic costs of reproduction, our results are consistent with the idea that reproductive anoles have less energy available for functions such as immune defense, which may leave reproductive anoles of either sex vulnerable to parasites if there is an energetic cost associated with parasite defense. Reduced immune defense against parasites and pathogens is frequently implicated as a cost of reproductive investment mediating the ubiquitous tradeoff between reproduction and survival (Gustafsson et al. 1997; Lochmiller and Deerenberg 2000; Norris and Evans 2000; Harshman and Zera 2007). Contrary to previous work in this species, we did not detect compromised immune function (reduced swelling response to PHA) as a cost of reproduction (Cox et al. 2010; Cox and Calsbeek 2011), potentially because our sample sizes were relatively small and the PHA assay is subject to considerable measurement error (Smits et al. 1999). Despite this, we observed reductions in the prevalence or intensity of parasite infection for two of the four parasite types that we quantified (atractid nematodes, eimeriid oocysts), which builds on previous studies of lizards demonstrating that GDX decreases ectoparasite loads in male striped plateau lizards (Cox and John-Alder 2007) and female brown anoles (Cox et al., 2010). The fact that, in our study, this treatment effect was seen for some endoparasites, but not for ectoparasites, is consistent with the ideas that immune responses to parasites can be highly specific and achieved by a variety of underlying mechanisms (Vass et al. 1993; Schmid-Hempel and Ebert 2003), and that different modes of defense can vary in the costs that they impose on the host (Coustau and Chevillon 2000; Rigby et al. 2002). The decrease in the prevalence of atractid nematodes that we observed in non-reproductive males and females also highlights the importance of sexually transmitted parasites as a frequently overlooked cost of reproduction (Hurst et al. 1995; Lockhart et al. 1996). To the extent that castration may have eliminated or reduced the frequency of copulation, castrated animals may have been sheltered from continued reinfection by atractid nematodes (Langford et al. 2013). Although few sexually transmitted parasites are studied in wild populations, animals with high degrees of promiscuity and overlapping generations are particularly likely to harbor such parasites (Webberley et al. 2004). Although we found that gonadectomy increased energy storage and reduced infection by some parasites, we cannot conclusively determine the causality in this relationship. The reduced energy stores of reproductive individuals could leave them more vulnerable to parasitism or, alternatively, reproduction could directly lead to higher levels of parasitism (e.g., exposure to sexually transmitted nematodes), thereby placing greater demands on the immune system and, in turn, reducing energy stores. Although gonadectomy had no effect on immune function as measured in our study with the PHA assay, the relationship between immunocompetence and host-parasite interactions is highly complex, and we caution against a simplistic interpretation of our data evidence against a relationship between immune function and parasite loads (Owen and Clayton 2007). Regardless of any causal links that may exist between reduced energy storage and increased parasite loads, our results show that both occur as costs of reproduction for male and female brown anoles. This is broadly consistent with the theoretical prediction that total reproductive investment should be comparable for males and females, and it supports the emerging view that males and females share many of the same costs of reproduction (Fedorka et al. 2004; Paukku and Kotiaho 2005; Penn and Smith 2007; Hoffman et al. 2008; Cox 2014a; Dugas et al. 2015b). Our study also presents a new experimental framework for directly comparing costs of reproduction between sexes by using the same measures of cost and manipulations of total reproductive investment over the same period of time.

Acknowledgements

We thank R. Calsbeek and A. Kahrl for assistance with fieldwork, N. Bottomley for permission to work at Regatta Point, and B. Falk and C. McAllister for assistance with parasite identification. We thank C. Alencar, M. Augat, E.D. Brodie III, R. Costello, H. Donald-Cannon, M. Hague, A. Hanninen, B. Sanderson, and C. Wood for comments on an early version of this manuscript. Additionally, we thank three anonymous reviewers for their helpful comments. Research was conducted under permits from The Bahamas Environment, Science and Technology (BEST) Commission and Ministry of Agriculture and with approval from the Animal Care and Use Committee of the University of Virginia (protocol 3896). This project was supported by startup funding from the University of Virginia to RMC.

References

Adkins, E. K. 1977. Effects of diverse androgens on the sexual behavior and morphology of castrated male quail. Horm. Behav. 8:201-207.

Alexander, N. 2012. Review: analysis of parasite and other skewed counts. Tropical Medicine & International Health 17:684-693.

Allander, K. 1997. Reproductive investment and parasite susceptibility in the great tit. Funct. Ecol. 11:358-364.

Andrews, R. and A. S. Rand. 1974. Reproductive effort in anoline lizards. Ecology 55:1317-1327.

Ardia, D. R., K. A. Schat, and D. W. Winkler. 2003. Reproductive effort reduces long-term immune function in breeding tree-swallows (*Tachycineta bicolor*). Proc. Roy. Soc. B 270:1679-1683.

Arnold, A. P. 1975. The effects of castration and androgen replacement on song, courtship, and aggression in zebra finches (*Poephila guttata*). J. Exp. Zool. 191:309-325.

Barfield, R., D. Busch, and K. Wallen. 1972. Gonadal influence on agonistic behavior in the male domestic rat. Horm. Behav. 3:247-259.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2:349-368.

Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. Functional ecology 22:443-453.

Calsbeek, R., C. Bonneaud, S. Prabhu, N. Manoukis, and T. B. Smith. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards. Evol. Ecol. Res. 9:495.

Calsbeek, R., C. Bonneaud, and T. B. Smith. 2008. Differential fitness effects of immunocompetence and neighbourhood density in alternative female lizard morphs. J. Anim. Ecol. 77:103-109.

Chapman, B. and R. Chapman. 1964. Observations on the biology of the lizard *Agama agama* in Ghana. Proceedings of the Zoological Society of London 143:121-132.

Christe, P., O. Glaizot, N. Strepparava, G. Devevey, and L. Fumagalli. 2012. Twofold cost of reproduction: an increase in parental effort leads to higher malarial parasitaemia and to a decrease in resistance to oxidative stress. Proc. Roy. Soc. B 279:1142-1149.

Chu, C. Y. C. and R. D. Lee. 2012. Sexual dimorphism and sexual selection: a unified economic analysis. Theor. Popul. Biol. 82:335-363.

Clutton-Brock, T. H. and G. A. Parker. 1992. Potential reproductive rates and the operation of sexual selection. Q. Rev. Biol. 67:437-456.

Cole, L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29:103-137.

Coustau, C. and C. Chevillon. 2000. Resistance to xenobiotics and parasites: can we count the cost? Trends Ecol. Evol. 15:378-383.

Cox, C. L., A. F. Hanninen, A. M. Reedy, and R. M. Cox. 2014a. Female anoles retain responsiveness to testosterone despite the evolution of androgen-mediated sexual dimorphism. Funct. Ecol. 29:758-769.

Cox, R. and R. Calsbeek. 2011. An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. J. Evol. Biol. 24:343-353.

Cox, R. M. 2006. A test of the reproductive cost hypothesis for sexual size dimorphism in Yarrow's Spiny Lizard, *Sceloporus jarrovii*. J. Anim. Ecol. 75:1361-1369.

Cox, R. M. 2014. Integrating costs of reproduction between the sexes *in* L. B. Martin, Woods L.B., Ghalambor C., ed. Integrative Organismal Biology. Wiley Scientific.

Cox, R. M. and R. Calsbeek. 2010a. Severe costs of reproduction persist in Anolis lizards despite the evolution of a single-egg clutch. Evolution 64:1321-1330.

Cox, R. M. and R. Calsbeek. 2010b. Sex-specific selection and intraspecific variation in sexual size dimorphism Evolution 64:798-809.

Cox, R. M. and H. B. John-Alder. 2005. Testosterone has opposite effects on male growth in lizards (*Sceloporus spp*.) with opposite patterns of sexual size dimorphism. J. Exp. Biol. 208:4679-4687.

Cox, R. M. and H. B. John-Alder. 2007. Increased mite parasitism as a cost of testosterone in male striped plateau lizards *Sceloporus virgatus*. Funct. Ecol. 21:327-334.

Cox, R. M., M. B. Lovern, and R. Calsbeek. 2014b. 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. Functional Ecology 24:1262-1269.

Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2005. Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. Physiol. Biochem. Zool. 78:531-545.

Cox, R. M., D. S. Stenquist, J. P. Henningsen, and R. Calsbeek. 2009. Manipulating testosterone to assess links between behavior, morphology, and performance in the brown anole *Anolis sagrei*. Physiol. Biochem. Zool. 82:686-698.

Derickson, W. K. 1976. Lipid storage and utilization in reptiles. Am. Zool. 16:711-723.

Dugas, M. B., C. N. Wamelink, and C. L. Richards-Zawacki. 2015. Both sexes pay a cost of reproduction in a frog with biparental care. Biol. J. Linn. Soc.

Evans, L. T. 1938. Cuban field studies on territoriality of the lizard *Anolis sagrei*. J. Comp. Psychol. 25:97.

Fedorka, K. M., M. Zuk, and T. A. Mousseau. 2004. Immune suppression and the cost of reproduction in the ground cricket, Allonemobius socius. Evolution 58:2478-2485.

Fisher, R. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Folstad, I. and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139:603-622.

French, S. S., D. F. DeNardo, and M. C. Moore. 2007. Trade-offs between the reproductive and immune systems: facultative responses to resources or obligate responses to reproduction? Am. Nat. 170:79-89.

Gadgil, M. and W. H. Bossert. 1970. Life historical consequences of natural selection. Am. Nat. 104:1-24.

Goldberg, S. R. and C. R. Bursey. 1989. *Physaloptera retusa* (Nematoda, Physalopteridae) in naturally infected sagebrush lizards, *Sceloporus graciosus* (Iguanidae). J. Wildl. Dis. 25:425-429.

Goto, N., H. Kodama, K. Okada, and Y. Fujimoto. 1978. Suppression of phytohemagglutinin skin response in thymectomized chickens. Poult. Sci. 57:246-250.

Greiner, E. C. 2003. Coccidiosis in reptiles. Pp. 49-56 *in* Elsevier, ed. Semin. Avian. Exot. Pet.

Gustafsson, L., D. Nordling, M. Andersson, B. Sheldon, and A. Qvarnström. 1997. Infectious diseases, reproductive effort and the cost of reproduction in birds. Pp. 53-61 *in* W. D. Hamilton, and J. C. Howard, eds. Infection, Polymorphism and Evolution. Springer, New York.

Harding, C. F., K. Sheridan, and M. J. Walters. 1983. Hormonal specificity and activation of sexual behavior in male zebra finches. Horm. Behav. 17:111-133.

Harshman, L. G. and A. J. Zera. 2007. The cost of reproduction: the devil in the details. Trends Ecol. Evol. 22:80-86.

Hoffman, C. L., A. V. Ruiz-Lambides, E. Davila, E. Maldonado, M. S. Gerald, and D. Maestripieri. 2008. Sex differences in survival costs of reproduction in a promiscuous primate. Behav. Ecol. Sociobiol. 62:1711-1718.

Hurst, G. D., R. G. Sharpe, A. H. Broomfield, L. E. Walker, T. M. Majerus, I. A. Zakharov, and M. E. Majerus. 1995. Sexually transmitted disease in a promiscuous insect, *Adalia bipunctata*. Ecol. Entomol. 20:230-236.

Jenssen, T. A., N. Greenberg, and K. A. Hovde. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. Herpetol. Monogr. 9:41-62.

Jones, A. G., J. R. Arguello, and S. J. Arnold. 2002. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough–skinned newt. Proc. Roy. Soc. B 269:2533-2539.

Kennedy, M. W. and R. G. Nager. 2006. The perils and prospects of using phytohaemagglutinin in evolutionary ecology. Trends Ecol. Evol. 21:653-655.

Ketterson, E. D., V. Nolan Jr, L. Wolf, C. Ziegenfus, A. M. Dufty Jr, G. F. Ball, and T. S. Johnsen. 1991. Testosterone and avian life histories: the effect of experimentally elevated testosterone on corticosterone and body mass in dark-eyed juncos. Horm. Behav. 25:489-503.

Kokko, H. and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. J. Evol. Biol. 21:919-948.

Kotiaho, J. S. and L. W. Simmons. 2003. Longevity cost of reproduction for males but no longevity cost of mating or courtship for females in the male-dimorphic dung beetle, *Onthophagus binodis*. J. Insect Physiol. 49:817-822.

Landwer, A. 1994. Manipulation of egg production reveals costs of reproduction in the tree lizard (*Urosaurus ornatus*). Oecologia 100:243-249.

Langford, G. J., B. A. Willobee, and L. F. Isidoro. 2013. Transmission, Host Specificity, and Seasonal Occurrence of *Cyrtosomum penneri* (Nematoda: Atractidae) in Lizards from Florida. J. Parasitol. 99:241-246.

Lee, J. C., D. Clayton, S. Eisenstein, and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 4:930-937.

Levine, N. D. 1968. Nematode parasites of domestic animals and of man. Burgess Pub. Co, Minneapolis.

Licht, P. and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. University of California Press.

Lin, E. J. 1979. Fatbody and liver cycles in two tropical lizards *Chamaeleo hohneli* and *Chamaeleo jacksoni* (Reptilia, Lacertilia, Chamaeleonidae). J. Herpetol. 13:113-117.

Lochmiller, R. L. and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? Oikos 88:87-98.

Lockhart, A. B., P. H. Thrall, and J. Antonovics. 1996. Sexually transmitted diseases in animals: ecological and evolutionary implications. Biol. Rev. 71:415-471.

Maklakov, A. A. and V. Lummaa. 2013. Evolution of sex differences in lifespan and aging: causes and constraints. Bioessays 35:717-724.

Marler, C. A., G. Walsberg, M. L. White, M. Moore, and C. Marler. 1995. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. Behav. Ecol. Sociobiol. 37:225-231.

Martin, L. B., D. M. Hawley, and D. R. Ardia. 2011. An introduction to ecological immunology. Funct. Ecol. 25:1-4.

Martin, L. B., A. Scheuerlein, and M. Wikelski. 2003. Immune activity elevates energy expenditure of house sparrows: a link between direct and indirect costs? Proc. Roy. Soc. Lond. B 270:153-158.

McCurdy, D. G., D. Shutler, A. Mullie, and M. R. Forbes. 1998. Sex-biased parasitism of avian hosts: relations to blood parasite taxon and mating system. Oikos 82:303-312.

McKean, K. A. and B. P. Lazzaro. 2011. The costs of immunity and the evolution of immunological defense mechanisms. Pp. 299-310 *in* T. Flatt, and A. Heyland, eds. Mechanisms of Life History Evolution. Oxford University Press, Oxford, UK.

Michener, G. R. and L. Locklear. 1990. Differential costs of reproductive effort for male and female Richardson's ground squirrels. Ecology:855-868.

Moore, S. L. and K. Wilson. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. Science 297:2015-2018.

Nordling, D., M. Andersson, S. Zohari, and L. Gustafsson. 1998. Reproductive effort reduces specific immune response and parasite resistance. Proc. Roy. Soc. B 265:1291-1298.

Norris, K. and M. R. Evans. 2000. Ecological immunology: life history trade-offs and immune defense in birds. Behav. Ecol. 11:19-26.

Norval, G., C. R. Bursey, S. R. Goldberg, J.-J. Mao, and K. Slater. 2011. Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei* (Squamata: Polychrotidae), in southwestern Taiwan. Pac. Sci. 65:383-390.

Nunn, C. L., P. Lindenfors, E. R. Pursall, and J. Rolff. 2009. On sexual dimorphism in immune function. Philos. T. Roy. Soc. B 364:61-69.

Owen, J. P. and D. H. Clayton. 2007. Where are the parasites in the PHA response? Trends Ecol. Evol. 22:228-229.

Paukku, S. and J. S. Kotiaho. 2005. Cost of reproduction in Callosobruchus maculatus: effects of mating on male longevity and the effect of male mating status on female longevity. J. Insect Physiol. 51:1220-1226.

Penn, D. J. and K. R. Smith. 2007. Differential fitness costs of reproduction between the sexes. Proceedings of the National Academy of Sciences 104:553-558.

Queller, D. C. 1997. Why do females care more than males? Proc. Roy. Soc. B 264:1555-1557.

Reznick, D. 1992. Measuring the costs of reproduction. Trends Ecol. Evol. 7:42-45.

Rigby, M. C., R. F. Hechinger, and L. Stevens. 2002. Why should parasite resistance be costly? Trends Parasitol. 18:116-120.

Roberts, M. L., K. L. Buchanan, and M. R. Evans. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. Anim. Behav. 68:227-239.

Rolff, J. 2002. Bateman's principle and immunity. Proc. Roy. Soc. B 269:867-872.

Rose, M. R. and B. Charlesworth. 1981. Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. Genetics 97:173-186.

Schmid-Hempel, P. and D. Ebert. 2003. On the evolutionary ecology of specific immune defence. Trends Ecol. Evol. 18:27-32.

Sexton, O. J., E. P. Ortleb, L. M. Hathaway, R. E. Ballinger, and P. Licht. 1971. Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. Ecology 52:202-215.

Sheldon, B. C. and S. Verlhust. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends Ecol. Evol. 11:317-321.

Smits, J., G. R. Bortolotti, and J. L. Tella. 1999. Simplifying the phytohaemagglutinin skin-testing technique in studies of avian immunocompetence. Funct. Ecol. 13:567-572.

Stamps, J. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Tokarz, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Anim. Behav. 33:746-753.

Tokarz, R. R. 1986. Hormonal regulation of male reproductive behavior in the lizard *Anolis sagrei*: A test of the aromatization hypothesis. Horm. Behav. 20:364-377.

Tokarz, R. R. 1995. Importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*: an experimental test. Anim. Behav. 49:661-669.

Tokarz, R. R. 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. Herpetologica 54:388-394.

Tokarz, R. R., S. McMann, L. Seitz, and H. B. John-Alder. 1998. Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (*Anolis sagrei*). Physiol. Zool. 71:139-146.

Tokarz, R. R., S. McMann, L. C. Smith, and H. John-Alder. 2002. Effects of Testosterone Treatment and Season on the Frequency of Dewlap Extensions during Male–Male Interactions in the Lizard *Anolis sagrei*. Horm. Behav. 41:70-79.

Trivers, R. 1972. Parental investment and sexual selection. Pp. 136-179. *in* B. Campbell, ed. Sexual Selection and the Descent of Man, 1871-1971. Aldine-Atherton, Chicago

Vass, E., A. J. Nappi, and Y. Carton. 1993. Comparative study of immune competence and host susceptibility in *Drosophila melanogaster* parasitized by *Leptopilina boulardi* and *Asobara tabida*. J. Parasitol. 79:106-112.

Velando, A. and C. Alonso-Alvarez. 2003. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. J. Anim. Ecol. 72:846-856.

Webberley, K. M., G. D. Hurst, R. W. Husband, J. Schulenburg, J. J. Sloggett, V. Isham, J. Buszko, and M. E. Majerus. 2004. Host reproduction and a sexually transmitted disease: causes and consequences of *Coccipolipus hippodamiae* distribution on coccinellid beetles. J. Anim. Ecol. 73:1-10.

Wedekind, C. and I. Folstad. 1994. Adaptive or nonadaptive immunosuppression by sex hormones? Am. Nat. 143:936-938.

Zahavi, A. 1975. Mate selection - a selection for a handicap. J. Theor. Biol. 53:205-214.

Tables and Figures

Table 1

		Prevalence (+/−)			Intensity (number)		
Parasite family	Model effect	d.f.	χ^2	*P*	d.f.	χ^2	*P*
Atractidae	Sex	19	0.01	0.99	15	2.83	0.09
	Treatment		**4.51**	**0.038**		0.45	0.50
	Sex*Treatment		0.01	0.99		1.22	0.27
Physalopteridae	Sex	19	2.07	0.15	15	1.35	0.24
	Treatment		1.47	0.23		0.56	0.46
	Sex*Treatment		2.46	0.10		0.01	0.99
Eimeriidae	Sex	51	0.98	0.32	40	2.04	0.15
	Treatment		0.01	0.96		**4.26**	**0.039**
	Sex*Treatment		0.10	0.76		0.38	0.54
Trombiculidae	Sex	80	2.21	0.14	7	**4.50**	**0.034**
	Treatment		0.82	0.36		0.02	0.87
	Sex*Treatment		0.01	0.09		0.02	0.87

Table 1. Summary of statistical tests for effects of host sex, reproductive treatment, and their interaction on the prevalence (presence or absence) and intensity (number) of four parasites. Significant ($P < 0.05$) effects are shown in bold.

Figure 1

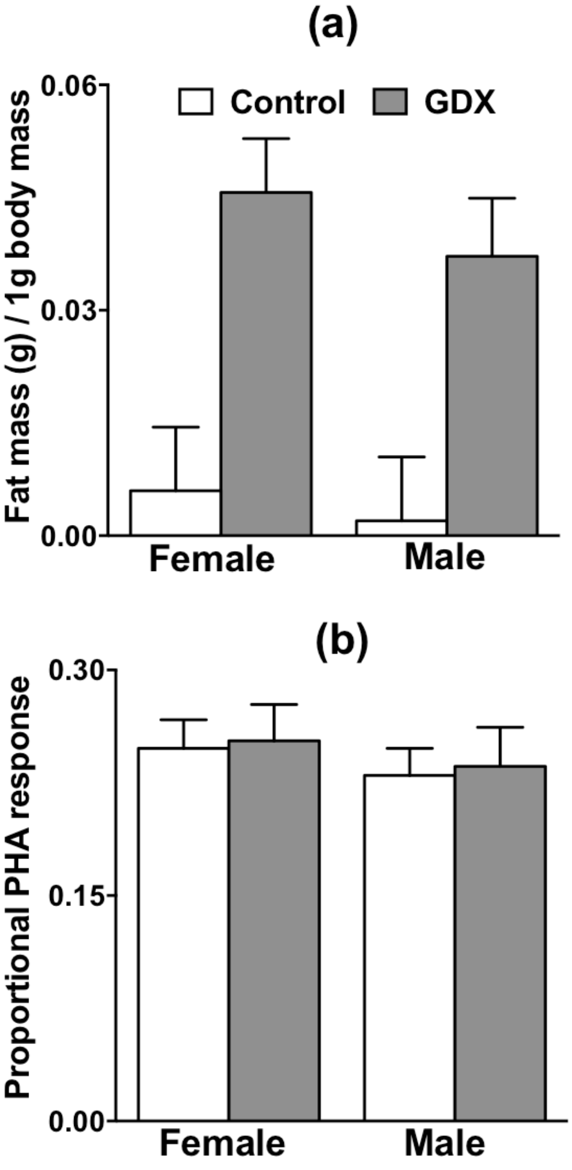


Figure 1. Gonadectomy (GDX) dramatically increased energy storage (wet mass of fat bodies) for both sexes (a). Gonadectomy did not affect immune response to PHA, which was measured as the proportional increase in the thickness of the foot from pre- to post-treatment with PHA (b). All data are means (±SE).

Figure 2

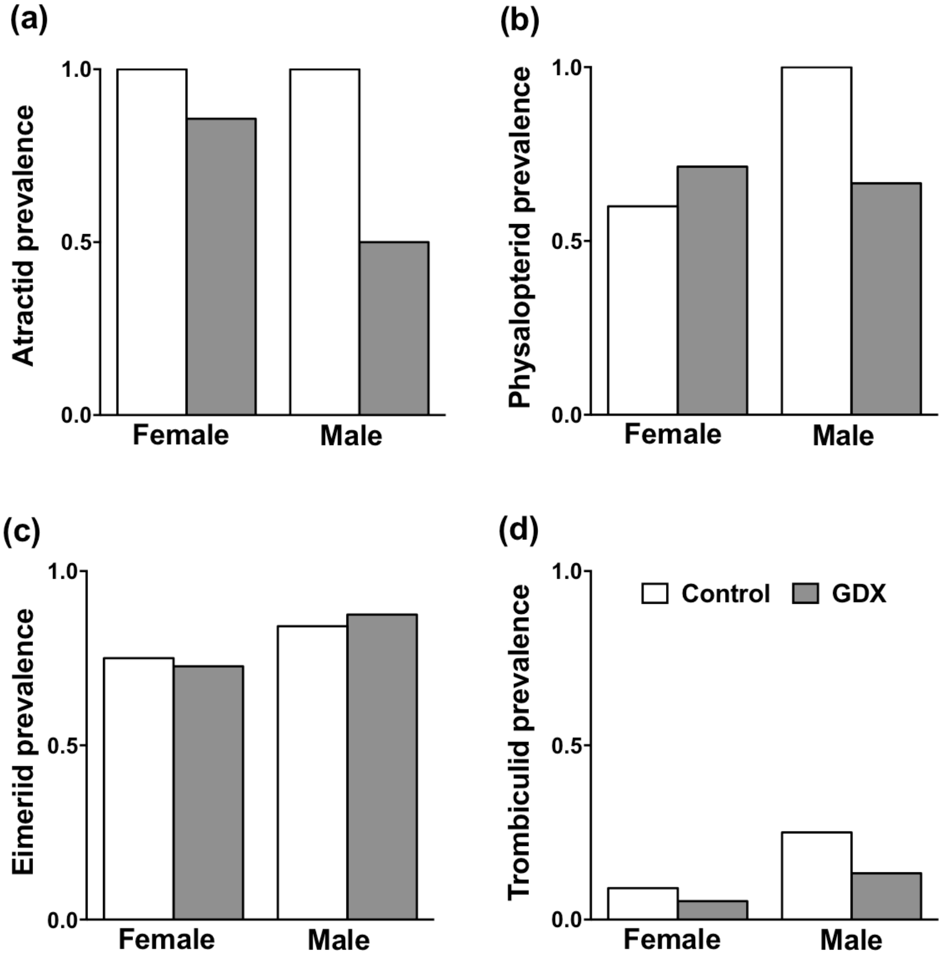


Figure 2. Gonadectomy (GDX) reduced the prevalence of infection by atractid nematodes for individuals of both sexes (a). Treatment did not affect the prevalence of physalopterid nematodes (b), eimeriid coccidia (c), or trombiculid mites (d).

Figure 3

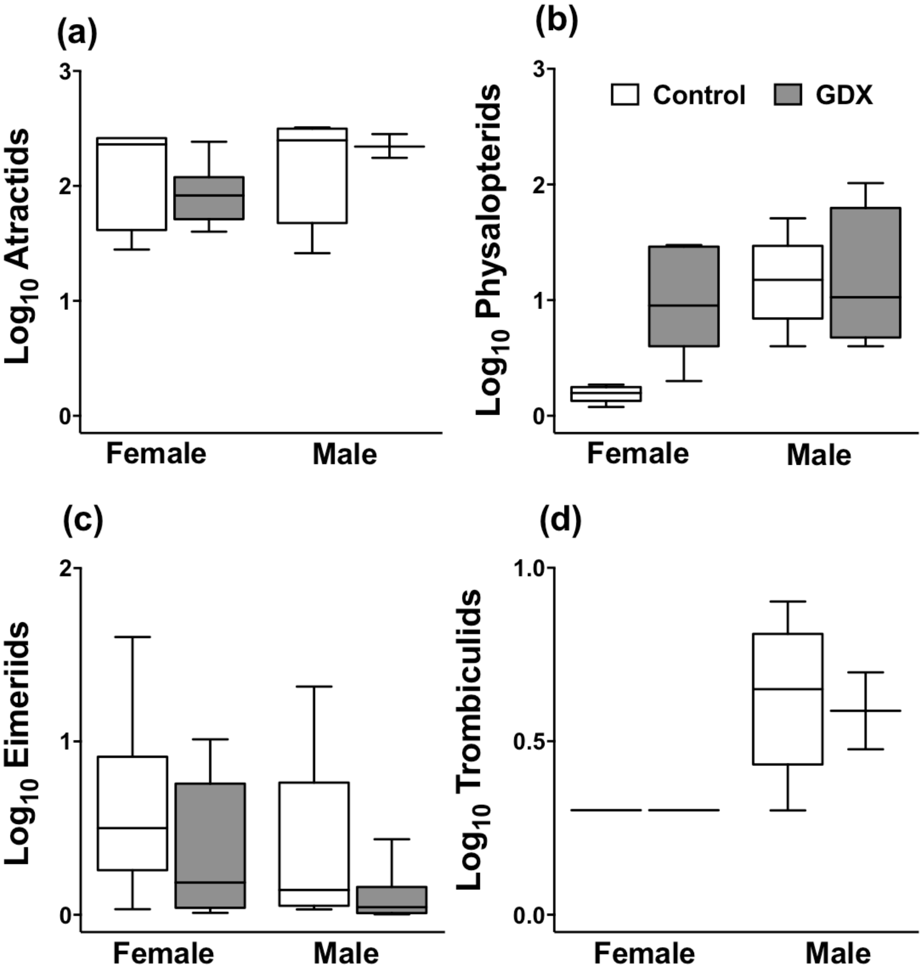


Figure 3. Treatment had no effect on the intensity of infection by atractid nematodes (a) or physalopterid nematodes (b). Gonadectomy (GDX) reduced the number of eimeriid oocysts for infected individuals of both sexes (c). Treatment had no effect on the number of trombiculid mite parasites. However, infected males had more mites than did infected females (d). Because the distributions of parasite counts are non-normal, all data are expressed as medians (bar) with 25%-75% interquartiles (box) and the total range (whiskers).

Chapter Two:

Female anoles display less but attack more quickly than males in response to territorial intrusions

---

As published: Reedy, A.M., B.D. Pope, N.M. Kiriazis, C.L. Giordano, C.L. Sams, D.A. Warner, and R.M. Cox. 2017. Female anoles display less but attack more quickly than males in response to territorial intrusions. *Behavioral Ecology*. 28(5): 1323-1328.

Abstract

Fighting to defend a territory can be costly due to the risk of injury associated with physical combat. Therefore, many species rely on displays that allow individuals to assess one another, avoid escalation, and mitigate the costs of physical conflict. Most studies of territorial aggression have been conducted in the context of male-male competition, and although females of many species are also aggressive, direct comparisons of male-male and female-female aggression are rare. Consequently, the relative extent to which males and females of territorial species use behavioral displays and physical aggression to mediate intrasexual competition is generally unknown. To address this question, we experimentally introduced same-sex intruders onto the territories of male and female brown anole lizards (*Anolis sagrei*). We found that, although males were slightly more likely to attack an intruder than were females, males also allowed a greater amount of time to elapse before escalating to an attack, relative to females. Males also exhibited more aggressive display behaviors (dewlap extensions, push-ups, and head-bobs) prior to engaging in a physical attack. These results are consistent with the idea that, due to a potentially greater risk of injury, males may attempt to avoid escalating to physical conflict. The high rates of attack and low latency to attack that we observed for interactions between females also run counter to the general assumption that males are categorically more aggressive in territorial, polygynous species characterized by extreme male-biased sexual size dimorphism.

Introduction

Competition among males often involves fighting with weapons such as antlers, horns, claws, and jaws (Clutton-Brock 1982; Moczek and Emlen 2000; Gvozdík and Damme 2003; Pratt et al. 2003). Such weapons render fighting dangerous because they can inflict serious and even fatal injuries (Jakobsson et al. 1995; Neat et al. 1998; Watson and Field 2004). Consequently, males often use behavioral displays to avoid escalation to physical aggression, particularly when the potential combatants are mismatched in size or fighting ability (McElligott et al. 1998; López and Martín 2001; Logue et al. 2010). Females of many species also interact aggressively when competing for resources such as food, nest sites, and reproductive opportunities (Slagsvold and Lifjeld 1994; Sandell and Smith 1997; Pruetz and Isbell 2000; Clutton-Brock 2007). However, the extent to which females use behavioral displays to mediate intrasexual aggression is largely unknown (Edwards and Lailvaux 2013; Cain and Rosvall 2014).

Theory predicts that escalation to physical combat occurs when the probable benefits of fighting outweigh the expected costs to an individual (Smith and Parker 1976; Clutton-Brock et al. 1979). Given that the nature and magnitude of these costs and benefits likely differs between males and females owing to differences in their reproductive strategies, it is expected that the sexes will also differ in their use of behavioral displays and/or physical aggression to resolve intrasexual competition. However, due to a historical focus on male-male aggression and its associated behaviors, relatively few studies have directly asked whether the frequency of physical aggression and associated behavioral repertoires differs between conspecific males and females (Foote 1990; Albert et al. 1992; Grant and Foam 2002; Arnott and Elwood 2009). To address this question, we conducted an experiment in free-living brown anole lizards (*Anolis sagrei*), a species in which intrasexual aggression has been observed in both sexes (Evans 1938; Edwards and Lailvaux 2013), but heretofore studied primarily in males (but see Driessens et al. 2014). We experimentally quantified and compared the behavioral repertoires of adult males and females when confronted with a novel intruder of the same sex by introducing tethered stimulus animals onto the territories of resident anoles (Vinegar 1972; Cooper Jr 1999),

Anolis sagrei is found at population densities of nearly 1 lizard/m^2 and frequently engages in social interactions (Schoener and Schoener 1980). Both sexes are territorial, but males are 2-3 times more massive than females (Cox and Calsbeek 2010c) and typically hold larger territories from which they aggressively exclude other males, and within which females hold smaller territories overlapping those of other females (Schoener and Schoener 1982; Jenssen and Nunez 1998; Paterson 2002). Individuals frequently engage in social displays (Tokarz 1985; Tokarz and Beck 1987), and both sexes communicate with a similar repertoire of visual signals, including head-bobs, push-ups, and extensions of the dewlap, a brightly colored flap of skin that extends from the throat (Orrell and Jenssen 2003; Simon 2007). However, *A. sagrei* males tend to use these behavioral displays to a greater degree than females in a variety of social contexts (Driessens et al. 2014). Male anoles frequently engage in fights that involve biting and can result in serious injuries, but less is known about female aggression (Greenberg and Noble 1944; McMann 1993; Stamps and Krishnan 1997; Stamps and Krishnan 1998; Jenssen et al. 2000). Successful territory defense is likely to confer fitness benefits for both sexes through increased mating success for males and increased food availability to support egg production for females (Trivers 1976; Stamps 1977b). Therefore, we predicted that males and females would both respond aggressively towards territorial intruders. Because males have more powerful jaws capable of inflicting serious injury and more conspicuous displays, (i.e., 10-fold larger dewlaps, dorsal and nuchal crests that are absent in females), we predicted that males would be more likely than females to use these elaborate displays, but also show a greater latency than females to escalate to a physical attack (Edwards and Lailvaux 2013; Driessens et al. 2014). The latter prediction runs counter to the simplistic expectation that males of a polygynous, territorial species with extreme male-biased sexual size dimorphism should generally exhibit a greater propensity toward physical aggression, relative to females.

Methods

We conducted our experiment on two spoil islands within the Guana Tolomoto Matanzas Estuarine Research Reserve in northern Florida (29° 63' N, 81° 21' W). We conducted all behavioral observations between 9:00 and 18:00 from July 29 to August 2, 2015. This period is during the middle of the lengthy reproductive season, which spans from approximately March to October in other Florida populations of *A. sagrei* (Lee et al. 1989b). At the time of our study, females are expected to be producing eggs at near peak levels and males have enlarged testes and elevated plasma testosterone levels (Lee et al., 1989; Tokarz et al., 1998).

We staged a total of 85 territorial intrusions by introducing a tethered stimulus male onto the territory of a focal male (*n* = 43 individual focal males), or a tethered stimulus female onto the territory of a focal female (*n* = 42 individual focal females). We use the term “territory” with the reasonable assumption that focal individuals (which were alert, visually conspicuous, and stationary when first encountered) were challenged on their actual territories. For each introduction, we used a stimulus animal collected that same day from the other island, thereby ensuring that the focal animal had never previously encountered the stimulus animal. We measured each stimulus animal for snout-vent length (SVL, nearest mm) and body mass (nearest 0.01 g), deployed it for up to 3 successive trials, then released it on the same day at its location of capture on its home island. Prior to release, we gave each stimulus animal a paint mark on its dorsum to prevent its inadvertent use in a subsequent trial.

We tethered the stimulus animal to a 3-m telescoping fishing pole with a 1-m length of braided fishing line (Spiderwire 30lb test, Pure Fishing, SC, USA), then gently placed it within 1 m of an otherwise undisturbed focal animal of the same sex. We attempted to place each stimulus animal at the same perch height as the focal animal. If this was not possible due to the spatial configuration of available perches, we placed the stimulus animal slightly below, but never above, the focal animal. After introducing the stimulus animal, the observer set the fishing pole on the ground, backed away to a distance of 10 m, and conducted a focal observation through binoculars. Each trial lasted 15 min or until (1) physical contact occurred between the focal and stimulus animals, or (2) the focal animal fled. During each trial, we recorded in sequence for the focal animal: (1) any movement towards or away from the stimulus animal, (2) each extension of the dewlap, and (3) each head-bob (vertical nodding of the head) or push-up (elevation of the anterior portion of the body using the forelimbs). For analysis, we combined head-bobs and push-ups into a single category of behavior due to difficulty discerning between the two in some trials, particularly for females. We recorded the end time of each trial and categorized its outcome depending on whether the focal animal attacked (charged the intruder and initiated physical contact), fled (left the vicinity and ceased interacting with the intruder), or reached the end of the 15-min period without attacking or fleeing. We excluded trials in which the focal animal interacted with an individual other than the stimulus animal. At the end of a trial, we captured the focal individual, measured its SVL and body mass, and painted a unique numeral on its flank to avoid unknowingly testing the same focal animal in multiple trials.

Lizards lack a corpus callosum integrating right and left hemispheres of the brain, and can therefore exhibit a bias toward increased aggression when viewing rivals from their left field of view, reflecting lateralization of aggressive behavior controlled by the right hemisphere of the brain (Deckel 1995; Hews and Worthington 2002; Hews et al. 2004). For this reason, we alternated the field of view (right or left) into which the stimulus animal was introduced at the beginning of each trial. During each trial, we recorded all changes in field of view and classified each individual behavior (dewlap extension, head-bob, push-up, attack) according to the field of view through which the focal animal was observing the intruder at the time when that behavior was expressed. We found no effect of field of view on any aspect of aggression, including probability of attack, latency to attack, and the frequency of display behaviors, irrespective of whether we separated or combined males and females for analysis (Supplemental Material, Table S1). Consequently, we did not consider field of view in any subsequent analyses testing for sex differences in behavioral responses.

Statistical Methods

To test for a sex difference in the probability of attack, we used logistic regression with the outcome of each trial (1 = attack, 0 = flee or time out) as the response variable and sex as the main effect. To test for a sex difference in the latency to attack, we restricted our analysis to the subset of trials that ended in attack (37 of 43 male; 29 of 42 female) and used generalized linear models with latency to attack (time in seconds) as the dependent variable and sex as the main effect. To test for sex differences in the number of behaviors preceding an attack, we conducted similar analyses using counts of dewlap extensions, head-bobs + push-ups, or total behaviors (dewlap extensions + head-bobs + push-ups) as dependent variables. Because any differences in count data could potentially be explained by differences in the length of trials due to differences in the latency to attack, we also conducted analogous tests for sex differences in the rate (behaviors per minute) of each behavior. Latency to attack, behavioral counts, and behavioral rates were not normally distributed, so we used generalized linear models with a Poisson distribution, a log link, and an overdispersion parameter estimated as the chi-square value divided by the degrees of freedom.

Because body size can affect aggressive interactions in anoles, we ran separate iterations of each of our models including both body size (SVL) of the focal animal and the difference in body size between focal and stimulus individuals (SVL focal – SVL stimulus) as covariates. To make male and female measures of body size equivalent for inclusion in the same model, SVL was standardized to a mean of zero and converted to units of standard deviation. Additionally, we also tested for effects of body size (SVL and mass) or body size difference on the probability of attack, latency to attack, or on the number and rate of display behaviors (Supplemental Material, Tables S2-S5).

Because temperature can influence the behavior of ectotherms, we tested for effects of time of day on aggressive behaviors. Time of day was found to have no effect on probability of attack ($X^2 = 2.35$; $P = 0.13$), latency to attack ($F_{1,64} = 0.02$; $P = 0.88$), rate of display behaviors ($F_{1,67} = 1.16$; $P = 0.28$), or number of display behaviors ($F_{1,83} = 1.07$; $P = 0.30$). Therefore, we do not include time of day in any of our analyses.

Results

Sex difference in frequency of attack

Most trials (66 of 85; 77.6%) ended in an attack of the intruder by the focal animal within 15 min (Fig. 1). The remaining trials ended with the focal animal fleeing (10 of 85; 11.8%) or with 15 min elapsing without the focal animal fleeing or attacking (9 of 85; 10.6%). In all trials scored as attacks, the focal animal charged, bit, or initiated physical contact with the stimulus animal. We never observed the stimulus animal attacking the focal animal. Although a greater percentage of male-male trials ended in attack (37 of 43; 86%) than did female-female trials (29 of 42; 69%), this difference was marginally non-significant ($\chi^2 = 3.60$; $P = 0.058$; Fig. 1A). This difference remained non-significant when including a covariate for the body size of the focal animal ($\chi^2 = 2.08$; $P = 0.15$) or for the difference in size between focal and stimulus animals ($\chi^2 = 2.11$; $P = 0.15$).

Sex difference in latency to attack

Across both sexes, trials that concluded with an attack usually (53 of 66; 80%) ended in less than 5 min. When a trial did end in attack, females displayed a much shorter latency to attack (median/mean: 104/119 sec) than did males (median/mean: 186/226 sec), and this difference was highly significant ($\chi^2 = 9.63$; $P = 0.002$; Fig. 1B). This sex difference remained significant when including a covariate for the body size of the focal animal ($\chi^2 = 12.35$; $P < 0.001$) or for the difference in size between focal and stimulus animals ($\chi^2 = 12.62$; $P < 0.001$).

Nearly half (48%) of the attacks by resident females occurred within 90 seconds of our staged territorial intrusions, and nearly all (97%) of the attacks by females occurred within 5 minutes. By contrast, less than a third (30%) of attacks by males occurred within 90 seconds, and only two thirds (68%) of the attacks by males occurred within the first 5 minutes.

Sex difference in display behavior preceding attack

For trials that ended in attack, females performed display behaviors in 23 of 29 trials while males displayed in 34 of 37 trials. In these trials that ended in attack, females performed fewer head-bob and push-up behaviors ($\chi^2 = 12.95$; $P < 0.001$; Fig. 2A), fewer dewlap extensions ($\chi^2 = 22.86$; P < 0.001; Fig. 2C) and fewer total display behaviors (dewlap extensions + head-bobs + push-ups) than did males prior to attacking the intruding stimulus animal ($\chi^2 = 23.53$; $P < 0.001$; Fig. 2E). When body size of the focal animal was included in these models as a covariate, sex differences remained similar for head-bobs and push-up behaviors ($\chi^2 = 12.75$; $P < 0.001$), dewlap extensions ($\chi^2 = 17.39$; $P < 0.001$), and total behaviors ($\chi^2 = 21.20$; $P < 0.001$). When the difference in body size between focal and stimulus animals was used as the covariate, sex differences also remained similar for head-bobs and push-ups ($\chi^2 = 11.70$; $P < 0.001$), dewlap extensions ($\chi^2 = 18.75$; $P < 0.001$) and total behaviors ($\chi^2 = 19.45$; $P < 0.001$).

When these data were expressed as rates of behavior rather than numbers of behaviors, females also exhibited lower rates of head-bobs and push-ups ($\chi^2 = 5.48$; $P = 0.019$; Fig 2B), dewlap extensions ($\chi^2 = 32.29$; $P < 0.001$; Fig 2D) and total display behaviors ($\chi^2 = 9.24$; $P = 0.002$; Fig 2F). Again, these results were qualitatively similar when body size of the focal individual was included as a covariate; females exhibited lower rates of head-bobs and push-ups ($\chi^2 = 11.70$; $P < 0.001$), dewlap extensions ($\chi^2 = 18.15$; $P < 0.001$), and total display behaviors ($\chi^2 = 19.45$; $P < 0.001$). When the difference in body size between focal and stimulus animals was the covariate, results remained significant for effects of sex on head-bobs and push-ups ($\chi^2 = 6.12$; $P = 0.012$), dewlap extensions ($\chi^2 = 21.77$; $P < 0.001$), and total display behaviors ($\chi^2 = 7.82$; $P = 0.002$).

Discussion

Our experimental introductions revealed that both male and female brown anoles use a combination of visual displays and physical attacks to defend their territories against same-sex intruders. Although male-male interactions were slightly more likely to result in physical attacks (86%) than were female-female interactions (69%), this difference was not significant, such that most trials in each sex culminated in an attack of the novel intruder. However, males did exhibit an increased latency to attack, which was accompanied by an increased rate and duration of signaling using dewlap extensions, head-bobs, and push-ups. Although females also signaled to intruders using these same behaviors, notably head-bobs, they tended to instigate physical attacks more quickly and with less behavioral preamble than males. These results are consistent with the hypothesis that male anoles, which sometimes engage in prolonged and costly fights involving wrestling and harmful biting with their enlarged jaws (Cooper 1977; Lailvaux and Irschick 2007), have an expanded morphological and behavioral repertoire (e.g., enlarged dewlap, dewlap extensions) which they use as a primary response to territorial intrusion before resorting to physical attacks. More broadly, our results are consistent with a game-theory view of animal combat, which predicts that individuals will benefit from assessing the ability of rivals and avoiding dangerous contests when costs are likely to outweigh benefits (Emlen 2008). Although this view has often been applied to male contests involving weaponry, it is equally applicable to predictions about female behavior even if sex differences dictate that the potential costs and benefits will be different than in a male contest.

Our results are noteworthy in demonstrating that female anoles attack more quickly and with less visual signaling than males. Nearly all (97%) of the attacks by resident females occurred within 5 minutes of a territorial intrusion. By contrast, only two thirds (68%) of the attacks by males occurred within the first 5 minutes. These data are consistent with the idea that the risk of intense combat and serious injury may be relatively lower for females, lessening their reliance on elaborate behavioral displays to avoid physical aggression (Stamps 1977). Reports of prolonged combat involving wrestling and biting are generally restricted to male anoles (Vanhooydonck et al. 2005) and males of many *Anolis* species have larger jaws that are capable of exerting greater bite force than those of females (Herrel et al. 2006; Herrel et al. 2007). In *Anolis sagrei,* males produce a bite force that is more than 400% greater than that produced by females, and it is not clear whether females generally create enough bite force to inflict significant injuries (Edwards and Lailvaux 2013). The presumably lower risk of injury in female-female combat may therefore explain why females in our study were quicker to attack a same-sex intruder. The fitness benefits of successful territory defense are likely greater in male anoles (e.g., increased mating opportunities and reproductive success) than in female anoles (e.g., preferred basking or retreat sites, access to prey), given the elaborate behavioral displays of males and their propensity to engage in prolonged wresting and biting (Jenssen et al. 2000). However, the fact that females in our study quickly and consistently defended their territories against intruding females implies that territory defense confers fitness benefits in both sexes. These results add to the expanding body of work demonstrating that strong predictions about female-female aggression can often be made when its costs and benefits are considered together (Rosvall 2011; Cain and Ketterson 2013).

Female-female aggression has been documented in several *Anolis* species, but it is generally unknown how frequently females fight in the wild. The relative frequency with which females in our study engaged in intrasexual aggression suggests that, by some metrics (e.g., frequency of and latency to attack), females of polygynous species can be as aggressive as males in territorial defense. It is conceivable that rates of aggression in our study may have been artificially high because stimulus animals were tethered and unable to avoid escalation, and because they were novel intruders without any prior history of social interactions with the focal individuals. The "dear enemy" phenomenon suggests that, for many animal species, fighting between neighbors decreases after dominance or territorial boundaries are established (Fisher 1954; Jaeger 1981). This has been shown in lizards generally and anoles specifically (Qualls and Jaeger 1991; Fox and Baird 1992; Paterson and McMann 2004). This decrease in fighting between neighbors could be particularly important for female anoles because their territories tend to overlap one another more than those of males overlap one another (Jenssen and Nunez 1998). Our focal animals may have been much more likely to escalate conflicts against these novel intruders than they would have been against a familiar intruder from a neighboring territory. However, each of these explanations apply similarly to males and females, so any upward bias in aggression under our experimental design is unlikely to account for the sex differences we observed. An additional caveat to our experiment is that we directly compared males and females in their use of a behavioral repertoire that is shared by both sexes, but it is possible that the signals we measured are not equivalent for each sex. Although push-ups and head-bobs have the same amplitude in males and females of other anole species (Jenssen et al. 2000), the dewlap itself is sexually dimorphic in *A. sagrei* (8-10x larger in males; Cox et al. 2015) and in many other anoles (Harrison and Poe 2012). The larger dewlap of males implies a greater functional significance relative to females, and likely allows for signaling across greater distances (Jenssen et al. 2000). Despite any sex differences in use of and information conveyed by behavioral displays, our data clearly show that *A. sagrei* females provide fewer displays before escalating to physical conflict.

Collectively, our data show that both male and female brown anoles typically respond to same-sex territorial intruders with behavioral displays and overt physical aggression. Although males exhibited significantly more aggressive behavioral displays prior to attack, they were not significantly more likely to attack intruders than were females, and females were significantly quicker than males to attack an intruder. These results are broadly consistent with the hypothesis that females will escalate to physical conflict more quickly because the risk of injury is relatively low, though further study is required to test this hypothesis directly. Taken together, our results run counter to the assumption that males are categorically more aggressive than females in territorial, polygynous species characterized by male-biased sexual size dimorphism.

Acknowledgements

We thank Mountain Lake Biological Station for hosting the Evolution Education Teacher Workshop where this experiment was designed. This study was conducted under a research permit from the Guana Tolomato Matanzas National Estuarine Research Reserve and approval of the University of Virginia Animal Care and Use Committee (protocol 3896). This project was funded by a National Science Foundation CAREER award (DEB-1453089 to RMC). Thanks to M. Augat, R. Bhave, E. Brodie III, R. Costello, M. Hague, A. Kahrl, H. Seears, G. Toledo, and T. Wittman for comments on an early draft of this manuscript.

References

Albert D, Jonik R, Walsh M, 1992. Hormone-dependent aggression in male and female rats: experiential, hormonal, and neural foundations. Neuroscience & Biobehavioral Reviews 16:177-192.

Arnott G, Elwood RW, 2009. Gender differences in aggressive behaviour in convict cichlids. Animal behaviour 78:1221-1227.

Cain KE, Ketterson ED, 2013. Costs and benefits of competitive traits in females: aggression, maternal care and reproductive success. PLoS One 8:e77816.

Cain KE, Rosvall KA, 2014. Next steps for understanding the selective relevance of female-female competition. Frontiers in Ecology and Evolution 2:32.

Clutton-Brock T, 1982. The functions of antlers. Behaviour 79:108-124.

Clutton-Brock T, 2007. Sexual selection in males and females. Science 318:1882-1885.

Clutton-Brock TH, Albon S, Gibson R, Guinness FE, 1979. The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus L.). Animal Behaviour 27:211-225.

Cooper Jr WE, 1999. Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, Eumeces laticeps. Behavioral Ecology and Sociobiology 47:54-59.

Cooper WE, 1977. Information analysis of agonistic behavioral sequences in male iguanid lizards, Anolis carolinensis. Copeia 1977:721-735.

Cox CL, Hanninen AF, Reedy AM, Cox RM, 2015. Female anoles retain responsiveness to testosterone despite the evolution of androgen‐mediated sexual dimorphism. Functional Ecology 29:758-767.

Cox RM, Calsbeek R, 2010. Sex-specific selection and intraspecific variation in sexual size dimorphism. Evolution 64:798-809.

Deckel AW, 1995. Laterality of aggressive responses in Anolis. Journal of Experimental Zoology 272:194-200.

Driessens T, Vanhooydonck B, Van Damme R, 2014. Deterring predators, daunting opponents or drawing partners? Signaling rates across diverse contexts in the lizard Anolis sagrei. Behavioral ecology and sociobiology 68:173-184.

Edwards JR, Lailvaux SP, 2013. Do interspecific interactions between females drive shifts in habitat use? A test using the lizards Anolis carolinensis and A. sagrei. Biological Journal of the Linnean Society 110:843-851.

Emlen DJ, 2008. The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics 39:387-413.

Evans LT, 1938. Cuban field studies on territoriality of the lizard Anolis sagrei. Journal of Comparative Psychology 25:97.

Fisher J, 1954. Evolution and bird sociality. Evolution as a Process 71:83.

Foote CJ, 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. Behaviour 115:283-314.

Fox SF, Baird TA, 1992. The dear enemy phenomenon in the collared lizard, Crotaphytus collaris, with a cautionary note on experimental methodology. Animal Behaviour 44:780-782.

Grant JW, Foam PE, 2002. Effect of operational sex ratio on female female versus male male competitive aggression. Canadian Journal of Zoology 80:2242-2246.

Greenberg B, Noble GK, 1944. Social behavior of the American chameleon (Anolis carolinensis Voigt). Physiological Zoology 17:392-439.

Gvozdík L, Damme R, 2003. Evolutionary maintenance of sexual dimorphism in head size in the lizard Zootoca vivipara: a test of two hypotheses. Journal of Zoology 259:7-13.

Harrison A, Poe S, 2012. Evolution of an ornament, the dewlap, in females of the lizard genus Anolis. Biological Journal of the Linnean Society 106:191-201.

Herrel A, Joachim R, Vanhooydonck B, Irschick DJ, 2006. Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard Anolis lineatopus. Biological Journal of the Linnean Society 89:443-454.

Herrel A, McBrayer LD, Larson PM, 2007. Functional basis for sexual differences in bite force in the lizard Anolis carolinensis. Biological Journal of the Linnean Society 91:111-119.

Hews DK, Castellano M, Hara E, 2004. Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. Animal Behaviour 68:1201-1207.

Hews DK, Worthington RA, 2002. Fighting from the right side of the brain: left visual field preference during aggression in free-ranging male tree lizards (Urosaurus ornatus). Brain, Behavior and Evolution 58:356-361.

Jaeger RG, 1981. Dear enemy recognition and the costs of aggression between salamanders. American Naturalist 117:962-974.

Jakobsson S, Brick O, Kullberg C, 1995. Escalated fighting behaviour incurs increased predation risk. Animal Behaviour 49:235-239.

Jenssen TA, Nunez SC, 1998. Spatial and breeding relationships of the lizard, Anolis carolinensis: evidence of intrasexual selection. Behaviour 1998:981-1003.

Jenssen TA, Orrell KS, Lovern MB, Ross S, 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, Anolis carolinensis. Copeia 2000:140-149.

Lailvaux SP, Irschick DJ, 2007. The evolution of performance - based male fighting ability in Caribbean Anolis lizards. The American Naturalist 170:573-586.

Lee JC, Clayton D, Eisenstein S, Perez I, 1989. The reproductive cycle of Anolis sagrei in southern Florida. Copeia:930-937.

Logue D, Abiola I, Rains D, Bailey N, Zuk M, Cade W, 2010. Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song. Proceedings of the Royal Society of London B: Biological Sciences 277:2571-2575.

López P, Martín J, 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards, Podarcis hispanica. Behavioral Ecology and Sociobiology 49:111-116.

McElligott AG, Mattiangeli V, Mattiello S, Verga M, Reynolds CA, Hayden TJ, 1998. Fighting tactics of fallow bucks (Dama dama, Cervidae): reducing the risks of serious conflict. Ethology 104:789-803.

McMann S, 1993. Contextual signalling and the structure of dyadic encounters in Anolis carolinensis. Animal Behaviour 46:657-668.

Moczek AP, Emlen DJ, 2000. Male horn dimorphism in the scarab beetle, Onthophagus taurus: do alternative reproductive tactics favour alternative phenotypes? Animal behaviour 59:459-466.

Neat FC, Taylor AC, Huntingford FA, 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Animal Behaviour 55:875-882.

Orrell KS, Jenssen TA, 2003. Heterosexual signalling by the lizard Anolis carolinensis, with intersexual comparisons across contexts. Behaviour 140:603-634.

Paterson AV, 2002. Effects of an individual's removal on space use and behavior in territorial neighborhoods of brown anoles (Anolis sagrei). Herpetologica 58:382-393.

Paterson AV, McMann S, 2004. Differential headbob displays toward neighbors and nonneighbors in the territorial lizard Anolis sagrei. Journal of Herpetology 38:288-291.

Pratt AE, McLain DK, Lathrop GR, 2003. The assessment game in sand fiddler crab contests for breeding burrows. Animal Behaviour 65:945-955.

Pruetz JD, Isbell LA, 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (Chlorocebus aethiops) and patas monkeys (Erythrocebus patas) living in simple habitats. Behavioral Ecology and Sociobiology 49:38-47.

Qualls CP, Jaeger RG, 1991. Dear enemy recognition in Anolis carolinenis. Journal of Herpetology 25:361-363.

Rosvall KA, 2011. Maintenance of variation in sexually selected traits in females: a case study using intrasexual aggression in tree swallows Tachycineta bicolor. Journal of Avian Biology 42:454-462.

Sandell MI, Smith HG, 1997. Female aggression in the European starling during the breeding season. Animal Behaviour 53:13-23.

Schoener TW, Schoener A, 1980. Densities, sex ratios, and population structure in four species of Bahamian Anolis lizards. The Journal of Animal Ecology 1980:19-53.

Schoener TW, Schoener A, 1982. Intraspecific Variation in Home‐Range Size in Some Anolis Lizards. Ecology 63:809-823.

Simon VB, 2007. Not all signals are equal: male brown anole lizards (Anolis sagrei) selectively decrease pushup frequency following a simulated predatory attack. Ethology 113:793-801.

Slagsvold T, Lifjeld JT, 1994. Polygyny in birds: the role of competition between females for male parental care. American Naturalist 143:59-94.

Smith JM, Parker GA, 1976. The logic of asymmetric contests. Animal behaviour 24:159-175.

Stamps J, 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Stamps J, Krishnan V, 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Animal Behaviour 55:461-472.

Stamps JA, Krishnan V, 1997. Functions of fights in territory establishment. The American Naturalist 150:393-405.

Tokarz RR, 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (Anolis sagrei). Animal Behaviour 33:746-753.

Tokarz RR, Beck JW, 1987. Behaviour of the suspected lizard competitors Anolis sagrei and Anolis carolinensis: an experimental test for behavioural interference. Animal Behaviour 35:722-734.

Tokarz RR, McMann S, Seitz L, John-Alder H, 1998. Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (Anolis sagrei). Physiological Zoology 71:139-146.

Trivers RL, 1976. Sexual selection and resource-accruing abilities in Anolis garmani. Evolution 1976:253-269.

Vanhooydonck B, Herrel A, Van Damme R, Irschick D, 2005. Does dewlap size predict male bite performance in Jamaican Anolis lizards? Functional Ecology 19:38-42.

Vinegar MB, 1972. The function of breeding coloration in the lizard, Sceloporus virgatus. Copeia 1972:660-664.

Watson PJ, Field SA, 2004. Costs increase as ritualized fighting progresses within and between phases in the sierra dome spider, Neriene litigiosa. Animal Behaviour 68:473-482.

Figures

Figure 1

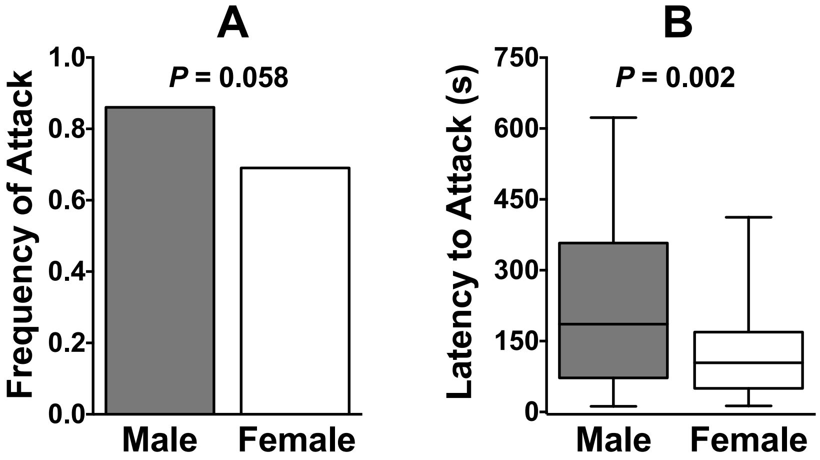


Figure 1. Sex differences in (A) frequency of attack, and (B) latency to attack between focal males and females challenged with a same-sex territorial intruder. (A) Proportion of trials that ended in attack of the intruding animal, shown separately for *n* = 43 and 42 focal males and females, respectively. (B) Median (bar), 25-75% interquartiles (box), and 5-95% percentiles (whiskers) for elapsed time until attack in the subset of trials that ended in attack. See text for statistical details.

Figure 2

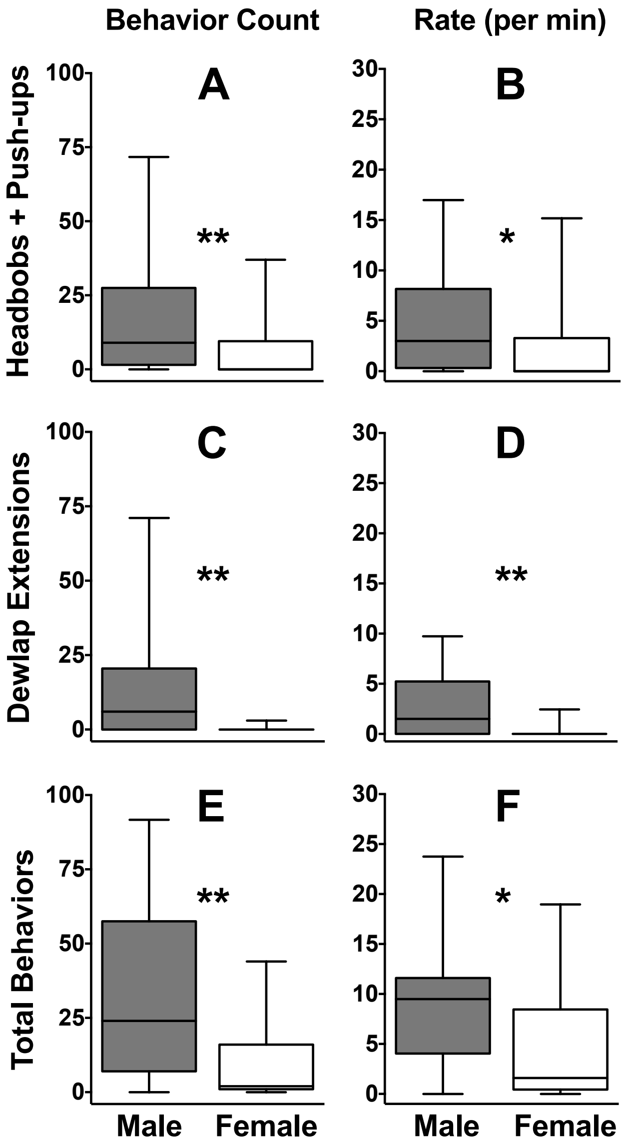


Figure 2. Sex differences in the number (A-C, left column) and rate (D-F, right column) of aggressive behaviors for trials that ended in attack of the same-sex terriorial intruder. Data are medians (bar), 25-75% interquartiles (box), and 5-95% percentiles (whiskers). Total behaviors (lower panels) represent the sum of behavioral categories reported separately in the upper and middle panels. ** $P < 0.001$; * $P < 0.02$. See text for statistical details.

Supplementary Tables

Supplemental Materials

Table S1

Behavioral characteristic	Mean left ± SE	Mean right ± SE	df	Test statistic	*P*
Sexes Combined					
Attack probability (initial FOV)	0.72 ± 0.06	0.85 ± 0.07	83	$\chi^2 = 1.98$	0.16
Attack probability (final FOV)	0.83 ± 0.06	0.72 ± 0.07	82	$\chi^2 = 1.38$	0.24
Time (s) to attack (initial FOV)	178 ± 26	186 ± 29	64	$\chi^2 = 0.03$	0.85
Time (s) to attack (final FOV)	168 ± 25	201 ± 31	64	$\chi^2 = 0.68$	0.41
Number of behaviors	13.79 ± 2.48	11.8 ± 2.44	84	$t = -0.58$	0.57
Males					
Attack probability (initial FOV)	0.83 ± 0.08	0.90 ± 0.07	41	$\chi^2 = 0.39$	0.53
Attack probability (final FOV)	0.91 ± 0.06	0.84 ± 0.09	40	$\chi^2 = 0.43$	0.51
Time (s) to attack (initial FOV)	240 ± 43	223 ± 43	35	$\chi^2 = 0.08$	0.78
Time (s) to attack (final FOV)	214 ± 35	254 ± 52	35	$\chi^2 = 0.43$	0.51
Number of behaviors	19.6 ± 4.16	18.8 ± 4.24	41	$t = -0.12$	0.90
Females					
Attack probability (initial FOV)	0.63 ± 0.09	0.80 ± 0.11	41	$\chi^2 = 1.37$	0.24
Attack probability (final FOV)	0.76 ± 0.09	0.59 ± 0.12	41	$\chi^2 = 1.38$	0.24
Time (s) to attack (initial FOV)	109 ± 24	133 ± 24	28	$\chi^2 = 0.43$	0.51
Time (s) to attack (final FOV)	120 ± 22	117 ± 28	28	$\chi^2 = 0.01$	0.94
Number of behaviors	7.9 ± 2.37	4.64 ± 1.85	41	$t = -1.22$	0.23

Table S1. Tests for field of view (FOV) preference. Attack probability tests for the effect of field of view (both initial FOV to start the trial and the final FOV in the trial) on the probability that a trial would end in an attack and was tested using logistic regression. Time to attack tests for the effect of field of view (both the initial FOV to start the trial and the final FOV just prior to attack) on the duration of the trial for those that ended in an attack and was tested for using generalized linear models fitted with a Poisson distribution and an over-dispersion parameter estimated as the chi-square value divided by the degrees of freedom. Tests for numbers of behaviors compared the number of total behaviors each focal animal performed while viewing the intruder from the left and right FOVs and were done using paired t-tests. Mean left and right display the mean for each FOV individually.

Table S2

Behavioral characteristic	df	Chi-square	*P* value
Males			
Attack probability	26	0.70	0.40
Latency to attack	24	3.52	0.06
Number of behaviors	26	0.14	0.70
Rate of behaviors	24	3.02	0.08
Females			
Attack probability	25	0.88	0.35
Latency to attack	19	0.43	0.51
Number of behaviors	25	0.13	0.71
Rate of behaviors	20	0.60	0.44

Table S2. Tests for effects of focal-animal size (SVL) on behavioral outcomes. Attack probability tests for an effect of SVL on the probability that a trial ended in attack and was tested using a logistic regression. All other tests used generalized linear models fitted with a Poisson distribution and an over-dispersion parameter estimated as the chi-square value divided by the degrees of freedom. Latency to attack tested for an effect of SVL on time to trial end only for trials that ended in attack. Number of behaviors tested for an effect of SVL on the total number of behaviors observed during a trial. Rate of behaviors tested for an effect of SVL on the rate of behaviors observed (number of behaviors/duration (s) of trial). Tests were conducted only within a single sex because of the non-overlapping values of SVL between the sexes.

Table S3

Behavioral characteristic	df	Chi-square	P value
Males			
Attack probability	26	0.02	0.90
Latency to attack	24	1.53	0.22
Number of behaviors	26	0.03	0.86
Rate of behaviors	24	1.26	0.26
Females			
Attack probability	25	0.60	0.44
Latency to attack	19	0.39	0.53
Number of behaviors	25	0.02	0.90
Rate of behaviors	20	0.67	0.41

Table S3. Tests for effects of focal-animal mass (g) on behavioral outcomes. Attack probability tests for an effect of mass on the probability that a trial ended in attack and was tested using a logistic regression. All other tests used generalized linear models fitted with a Poisson distribution and an over-dispersion parameter estimated as the chi-square value divided by the degrees of freedom. Latency to attack tested for an effect of mass on time to trial end only for trials that ended in attack. Number of behaviors tested for an effect of mass on the total number of behaviors observed during a trial. Rate of behaviors tested for an effect of mass on the rate of behaviors observed (number of behaviors/duration (s) of trial). Tests were conducted only within a single sex because of the non-overlapping values of mass between the sexes.

Table S4

Behavioral characteristic	df	Test statistic	P value
Sexes Combined			
Attack probability	52	$\chi^2 = 0.22$	0.62
Latency to attack	44	$\chi^2 = 0.04$	0.85
Number of behaviors	52	$t = 0.44$	0.66
Rate of behaviors	45	$\chi^2 = -0.40$	0.69
Males			
Attack probability	26	$\chi^2 = 0.01$	0.94
Latency to attack	24	$\chi^2 = 0.25$	0.62
Number of behaviors	26	$\chi^2 = 0.15$	0.69
Rate of behaviors	24	$\chi^2 = 0.87$	0.35
Females			
Attack probability	25	$\chi^2 = 0.88$	0.35
Latency to attack	19	$\chi^2 = 1.35$	0.25
Number of behaviors	25	$\chi^2 = 1.52$	0.22
Rate of behaviors	20	$\chi^2 = 0.28$	0.60

Table S4. Tests for effects of the difference in length between focal and stimulus animals ($SVL_{focal} – SVL_{stimulus}$) on behavioral outcomes. Attack probability tests for an effect of SVL difference on the probability that a trial ended in attack and was tested using a logistic regression. All other tests used generalized linear models fitted with a Poisson distribution and an over-dispersion parameter estimated as the chi-square value divided by the degrees of freedom. Latency to attack tested for an effect of SVL difference on time to trial end only for trials that ended in attack. Number of behaviors tested for an effect of SVL difference on the total number of behaviors observed during a trial. Rate of behaviors tested for an effect of SVL difference on the rate of behaviors observed (number of behaviors/duration (s) of trial).

Table S5

Behavioral characteristic	df	Test statistic	P value
Sexes Combined			
Probability of attack	52	0.10	0.75
Latency to attack	44	0.06	0.80
Number of behaviors	52	0.00	0.98
Rate of behaviors	45	0.99	0.32
Males			
Probability of attack	24	0.86	0.35
Latency to attack	24	0.04	0.85
Number of behaviors	26	0.01	0.90
Rate of behaviors	24	0.75	0.39
Females			
Probability of attack	20	0.81	0.37
Latency to attack	19	3.25	0.07
Number of behaviors	25	0.49	0.49
Rate of behaviors	20	1.83	0.18

Table S5. Tests for effects of the difference in mass between focal and stimulus animals ($\text{Mass}_{\text{focal}} - \text{Mass}_{\text{stimulus}}$) on behavioral outcomes. Attack probability tests for an effect of mass difference on the probability that a trial ended in attack and was tested using a logistic regression. All other tests used generalized linear models fitted with a Poisson distribution and an over-dispersion parameter estimated as the chi-square value divided by the degrees of freedom. Latency to attack tested for an effect of mass difference on time to trial end only for trials that ended in attack. Number of behaviors tested for an effect of mass difference on the total number of behaviors observed during a trial. Rate of behaviors tested for an effect of mass difference on the rate of behaviors observed (number of behaviors/duration (s) of trial).

Chapter Three:

Sexually antagonistic natural selection on body size emerges during sexual maturation while selection acts against rapid growth rate in the brown anole, *Anolis sagrei*

Formatted as a coauthored manuscript: Reedy, A.M., A. F. Kahrl, H.A. Seears, D.A. Warner, and R.M. Cox

Abstract

Females and males inherently differ in their reproductive strategies and thus sexually antagonistic selection is expected to push the sexes towards different optima on the fitness landscape. Studies of natural and sexual selection in wild populations show that sexually antagonistic selection is common at the adult life-stage, but few studies have explored how this conflict emerges during ontogeny, despite the initial framing of intralocus sexual conflict as "ontogenetic" sexual conflict. Here, we use a system in which previous work has demonstrated sexually antagonistic natural selection on adult body size to trace the emergence of this sexual antagonism across ontogeny using a detailed characterization of the changing fitness surface for body size in females and males from hatching to maturation. We used mark-recapture in a closed island population of brown anole lizards (*Anolis sagrei)* over a three-year period to track the survival of 4,609 unique young-of-the-year individuals. We estimated selection on body size and growth rate for these individuals across multiple episodes during their first ten months of life and characterized sex-specific fitness surfaces for body size from hatching to sexual maturation. We find evidence that selection on body size is sexually concordant during the earliest ontogenetic stages, when large body size is favored in both sexes, but becomes sexually antagonistic as the sexes approach maturity. Specifically, selection on body size among the largest females in the young-of-the year age class becomes negative as smaller body size is favored among the largest females. Conversely, in males there is no such decline in survival among the largest individuals. Despite selection for large body size in both sexes at the earliest stages of life, we found selection against rapid growth rates in both sexes. We interpret our results as support for the predictions that

sexually antagonistic selection develops gradually over ontogeny and that growth trades off against survival.

Introduction

The evolutionary interests of females and males will never be fully aligned (Wedell et al. 2006; Schärer et al. 2012). Consequently, natural selection often acts antagonistically on traits as it pushes females and males towards different optima on the fitness landscape and drives intralocus sexual conflict (Parker 1979; Lande 1980; Chapman et al. 2003; Pischedda and Chippindale 2006; Bonduriansky and Chenoweth 2009). Sexual dimorphism indicates at least a partial resolution of sexual conflict over some traits (Cox and Calsbeek 2009). However, even in species where sexual dimorphism is pronounced at the adult life stage, the sexes are often phenotypically indistinguishable at the earliest life stages (Badyaev 2002; Connallon and Clark 2014). For these species, each ontogenetic stage comes with the potential for sexual antagonism as selection acts on two sexes that start life with essentially a shared phenotype, but are faced with different fitness landscapes (Badyaev 2002). This continual potential for sexual conflict over ontogeny is predicted to be greatest for highly integrated traits such as body size, because pleiotropy limits the degree to which sex-specific expression can resolve conflict (Badyaev 2002). Foundational work on intralocus sexual conflict highlighted the potential for sexually antagonistic selection to manifest over ontogeny, but as the empirical study of sexual conflict has grown, natural systems in which to test the idea that sexual conflict increases over ontogeny have not been forthcoming (Chippindale et al. 2001; Rice and Chippindale 2001).

Since the early focus on ontogenetic sexual conflict, studies of intralocus sexual conflict have rapidly expanded to test for conflict in the lab and field (Brommer et al. 2007; Foerster et al. 2007; Mank 2008; Delcourt et al. 2009; Berger et al. 2014; Berger et al. 2016). Despite this increase in studies of sexual conflict, the frequency with which intralocus sexual conflict occurs in natural systems and which traits and components of fitness drive it in those systems remain largely open questions (Long and Rice 2007; Maklakov et al. 2008; Bonduriansky and Chenoweth 2009). Furthermore, despite the early focus of the development of conflict over ontogeny, tests of intralocus sexual conflict across different life stages remain scarce and it remains generally unknown whether sexually antagonistic selection occurs at the juvenile life stage prior to the onset of sexual maturity (Prasad et al. 2006; Cox and Calsbeek 2009).

It has only been relatively recently that studies of selection in the wild have been conducted with the explicit goal of identifying sexually antagonistic selection and, as a result, we generally do not know how similar or dissimilar the fitness surfaces are for males and females (Cox and Calsbeek 2009; Innocenti and Morrow 2010; Tarka et al. 2013). Additionally, the nature of temporal variation in selection can make forming general conclusions about how a typical female or male fitness surface may differ fraught with difficulty (Siepielski et al. 2009; Schoener 2011; Gotanda and Hendry 2014; Ercit 2016). This challenge is not easily overcome, and forming general conclusions about sex differences in selection will require long term study of populations across many episodes of selection (Clutton-Brock and Sheldon 2010).

To test the hypothesis that intralocus sexual conflict develops over ontogeny, we conducted three years of mark-recapture study on a closed island population of brown anoles (*Anolis sagrei)* and measured natural selection on body size separately for female and male young-of-the-year individuals throughout their first 10 months of life. In this species, because adult females repeatedly lay a single egg every 7-10 days throughout a 6-8 month breeding season, new hatchlings emerge continuously from late May through October. This results in a highly age-structured population within the young-of-the-year cohort. As these juveniles mature, the largest individuals with the earliest hatch dates attain sexual maturity within the same summer in which they hatched, and by the following year, all surviving individuals reach the adult life stage. This highly age-structured population presents the opportunity to test for sexually antagonistic selection at different points during development. To characterize sexually antagonistic selection at a fine developmental scale over early ontogeny, we partitioned data from juveniles into narrow size classes and estimated natural selection on body size separately for males and females within these size classes. As a complementary approach, we visualized non-linear fitness surfaces for the highly age-structured young-of-the-year cohort over multiple episodes of selection. In accordance with the hypothesis that intralocus sexual conflict is an ontogenetic conflict, we predict that sexually antagonistic selection on body size will develop gradually over ontogeny (Chippindale et al. 2001; Badyaev 2002). Specifically, we predict that directional selection on body size will increasingly favor large body size and become stronger in males as compared to females (Cox and Calsbeek 2010c).

Because growth rate contributes greatly to juvenile body size as measured at any time point in early life, estimates of selection on juvenile body size can be potentially confounded by selection on growth rate. Additionally, growth rate is frequently tied to sex-specific reproductive strategies that are thought to be the ultimate drivers of sexually antagonistic selection (Bonduriansky et al. 2008). In many species, rapid growth rate has demonstrated costs, even when adult fitness is enhanced by large body size (Gotthard et al. 1994; Weimerskirch et al. 2000). In females specifically, growth rate frequently has been tied to reproductive tactics where early maturity trades off against lifespan (Hutchings 1993; Metcalfe and Monaghan 2003). For these reasons, we test for a potential tradeoff between growth rate and survival by testing whether rapid growth rate during the late summer trades off against overwinter survival. We predict that although large body size is typically favored for animals during early ontogeny, growth rate will trade off with survival resulting in natural selection against rapid growth.

Materials and Methods

Species and Study Site

Anolis sagrei is a small, semi-arboreal lizard which exhibits pronounced sexual size dimorphism; on average, adult males in our study population are 25% larger than adult females in terms of snout-vent length (SVL) and more than twice as large by mass. Female anoles are capable of laying a single egg every 7-10 days throughout the breeding season, which in Florida lasts from May through October (Andrews and Rand 1974b; Lee et al. 1989b). Males and females do not differ in size at hatching, but males have a higher growth rate early in life and sexual size dimorphism becomes pronounced after the onset of sexual maturity (Cox et al. 2009a). The size at sexual maturity has been documented at 34-38 mm snout-vent length (SVL) for females and 30-39 mm for males (Lee et al. 1989b; Cox and Calsbeek 2011; Norval et al. 2012). The largest young-of-the year individuals in our study population reach the upper estimates of these minimum body-sizes for sexual maturity within 60 days. Following the overwinter period, all surviving individuals of the young-of-the-year cohort will attain sexual maturity.

We conducted our study on a closed population of anoles living on a man-made spoil island in the Matanzas River within the Guana Tolomato Matanzas National Estuarine Research Reserve (Palm Coast, Florida, 29°63′N, 81°21′W). The island has a total area of approximately 4,800 m^2. The interior habitat of the island is comprised of red cedar and palm trees, while the outer area of the island, which is often below the high tide line, is sparsely vegetated with short grasses and ringed with mangroves. Lizards inhabit all parts of the island but reach their highest density ($> 2/m^2$) in the island's interior.

Mark-recapture

We captured, marked, and tracked the survival of 4,609 unique young-of-the-year individuals in our study population, over three annual breeding seasons from July 2015 through October 2017. Each year, we captured each lizard by hand or handheld noose during complete population censuses done first during the late summer approximately 60 days after the emergence of the first hatchlings of the season (July 24 - August 7), repeated in the fall (October 1 - 14), and again the following spring (March 26 - April 5). We held each captured lizard for 24 hours, during which time we phenotyped individuals and assigned newly captured individuals a unique and permanent toe-clip identification number. We searched the island exhaustively for 7-14 days during each census and consider recapture success in this closed population to be a robust estimate of survival for both males and females in our study. We sexed individuals by using the post-anal scale dimorphism (males have enlarged post-anal scales) and measured each for a snout-to-vent length (SVL) measurement of body size (Lovern and Wade 2003). We measured growth rate (mm/d) as the difference in SVL between capture events divided by the number of days between captures. We marked each lizard with a spot of acrylic paint on the dorsum to prevent recapture during the same census and returned all lizards to their recorded location of capture on the island within 24 hours.

Statistical Analyses

Selection on body size over ontogeny

Age-related variation in body size is likely to account for a large portion of the phenotypic variance in body size at the juvenile life stage, because anoles hatch from eggs laid continuously throughout the breeding season. To characterize any changes in selection across ontogeny at a fine scale, we conducted an analysis for the late summer episode of selection (July-October) that first pooled data for all three years (2015-2017), and then partitioned the dataset into overlapping size classes. These size classes were created by partitioning young-of-the-year into overlapping 1-cm increments of SVL (15-24 mm, 20-29 mm, 25-34 mm, 30-39 mm, 35-45 mm, 45-55 mm). Due to the overlapping size-classes, most individuals were included in analyses for two different size classes. Conducting separate analyses for each of these size classes allowed us to characterize selection for each sex at different points in ontogeny ranging from newly hatched (15-24 mm) to transitioning into sexual maturity (35-45 mm).

We estimated selection on body size within each size class using SVL standardized to a mean of zero in units of standard deviation within each sex and size class at the start of the episode of selection (Lande and Arnold 1983; Arnold and Wade 1984). We calculated relative fitness of individuals as survival (1 or 0) divided by the mean survival for all individuals of the same sex and size class during each episode of selection. We estimated linear (directional) selection (S ± 1SE) as the slope of the standard least squares regression of relative fitness on standardized SVL. We report P values for S from logistic regressions with a binomially distributed response variable (survival = 1 or 0) and a logit link (Janzen and Stern 1998).

To test for sexually antagonistic natural selection on body size within each size class, we pooled males and females of the same size class and used logistic models with relative fitness (standardized within each sex and size class) as the dependent variable and effects of sex, SVL, and year, as well as all two-way interactions and the three-way interaction of sex × SVL × year. We explicitly tested for a sex difference in linear (directional) selection on body size with the sex × SVL interaction for each size class.

Sex-specific fitness surfaces

To visualize and compare the sex-specific forms of selection acting on the entire young-of-the-year cohort, we created univariate selection surfaces for survival as a function of body size for each episode of selection (late summer and overwinter) using pooled data from all years. Selection surfaces were fitted as cubic splines produced using a generalized additive model with REML smoothness estimation in the R package MGCV (Schluter 1988; Wood 2001, 2004).

Overall patterns of selection on body size

To test for sex-specific patterns of selection across the entire young-of-the-year cohort, we estimated linear and quadratic selection on body size within each sex for each episode of selection (late summer and overwinter) for each year (2015, 2016, 2017). Thus, we estimated selection for five episodes of selection in total (3 late summer and 2 overwinter). Work to estimate overwinter selection for 2017-2018 is ongoing. As above, we estimated linear (directional) selection (S ± SE) as the slope of the standard least squares regression of relative survival on standardized SVL with both relative survival and standardized SVL calculated within each sex. We estimated quadratic (i.e. stabilizing or disruptive) selection (c ± SE) as the slope of the regression of relative survival on standardized SVL^2. We also included a linear SVL term in each quadratic model. The parameter estimates and standard errors for the quadratic terms were doubled to estimate stabilizing or disruptive selection (c ± 1SE) (Stinchcombe et al. 2008). As above, all *P*-values for S or c were from logistic regressions with a binomially distributed response variable (survival = 1 or 0) and a logit link (Janzen and Stern 1998). We explicitly tested for sex differences in linear selection with the sex × SVL interaction, and also included effects of sex and SVL. We tested for sex differences in quadratic selection with the sex × SVL^2 interaction in standard least squares models with relative fitness as the response variable, and also included effects of sex, SVL and SVL^2.

Finally, in order to characterizes overall patterns of selection across years, for each episode of selection (late summer and overwinter) we pooled data for all three years (2015-2017) and again estimated linear and quadratic selection on body size within each sex for each episode of selection (late summer and overwinter) across all years of the study.

Selection on growth rate

To test for a tradeoff between any benefits of large size and rapid maturation and costs of rapid growth, we estimated selection on growth rate. We did this with models that tested whether summer growth rate predicted overwinter survival (October to April). Because size is asymptotic in this species and initial SVL is correlated with growth rate, we first regressed $\log_{10}$ growth rate from July to October on $\log_{10}$ SVL as measured in July and then used the residuals from this regression as our size-corrected measure of growth rate. Then, to estimate selection gradients for each sex, we used multivariate models that regressed relative survival on late summer growth rate and SVL (as measured in October) as well as the growth rate × SVL interaction. This analysis was limited to individuals that were captured in July and again in October. P-values for these tests were taken from logistic models fitted with survival (1 or 0) as binomial response variable and a logit link.

Results

Selection on body size over ontogeny

Sex-specific estimates of selection on body size within each 10-mm size class shifted from positive to negative directional selection when moving from the smallest class (15-24 mm) to the largest class occupied by both sexes (35-44 mm) (Fig. 1), and body size was significantly correlated with survival in 4 out of 5 size classes (SVL effects in Table 1). We did not detect significant sex differences in selection on body size for any but the largest (35-44 mm) size class, where selection on female size was strongly negative and selection on male size was absent (Fig. 1; sex × SVL, Table 1). There were no sex differences in selection within the other size classes (Table 1). However, females had significantly greater survival rates than males within 3 of the 5 size classes compared (sex effect; Table 1). Survival rates also differed by year in 4 of the 5 size classes (year effect; Table 1).

Sex-specific fitness surfaces

The univariate fitness surfaces for body size reveal a sex difference in the form of selection during the summer episode of selection (July to October) when looking across all years (2015-2017). For young-of-the-year individuals of both sexes, fitness increases sharply with body size up until intermediate sizes near the point at which they are expected to mature. Then fitness begins to decline with body size in females, such that the overall fitness surface is concave in females and indicative of stabilizing selection (Fig. 2a). In contrast, the male fitness surface shows no such decline for individuals approaching the size of sexual maturity, but instead levels off at intermediate sizes such that the probability of survival remains constant and high for the largest male size classes (Fig. 2b).

During the overwinter episodes of selection, the fitness surfaces for both females and males were characteristic of directional selection favoring large body size in both sexes (Fig. S1). However, for females there is a negative curvature to the fitness surface as the prediction for survival began to decrease for individuals 39 to 45 mm in snout-vent length. For the males there is no decline in the probability of survival at the largest body sizes and the positive relationship between body size and survival becomes increasingly steep at body sizes larger than 40 mm snout-vent length (Fig. S1).

Overall patterns of selection on body size

Within each episode of selection, directional selection was generally positive and strong for both sexes at with values of S ranging from 0.12 to 0.65 across all five episodes of selection. Each of the corresponding ten sex-specific estimates of directional selection were statistically different from zero (Table 2). Sex differences in linear selection (sex × SVL) on body size were significant for two out of five episodes of selection (Table 2). In both of these cases, directional selection was stronger in males.

Within the same episodes of selection, estimates of quadratic selection were negative (stabilizing selection) for nine out of ten sex-specific estimates of selection (Table 2). For females, all estimates of quadratic selection were negative and four out of five of these were statistically significant. For males, only two out of five estimates differed from zero and both of these were from late summer episodes of selection (Table 2). Sex differences in quadratic selection (sex $\times$ SVL^2) were detected for two out of five episodes of selection. In both of these cases, sex differences in quadratic selection occurred during a late summer episode and were characterized by stronger stabilizing selection on females.

When these data were pooled to assess overall patterns of selection across years, there were no sex differences in the linear relationship between body size and survival (sex × SVL; Table 3) for either the late summer or overwinter episodes of selection. The correlation between body size and survival was significant for both episodes of selection

(SVL; Table 3) as was the variation in survival between years (year; Table 3). Females had higher survival than males for both the late summer and overwinter episodes (sex; Table 3).

While we did not detect a sex difference in the linear relationship between body size and survival, we did find a sex difference in quadratic selection (sex × SVL^2) across all years for the late summer episode of selection (Table 4). This sex difference in quadratic selection was not seen for the overwinter episode of selection. The overall relationship between SVL^2 and survival was significant for both episodes of selection (SVL^2; Table 4), as was the year-to-year variation in survival (year; Table 4). This effect of year differed by sex for the late summer episode of selection, but not for the overwinter episode (sex × year; Table 4).

Selection on growth rate

For both females and males at the juvenile life stage, selection during the overwinter episodes (2015, 2016) acted against a high growth rate in the preceding summer episode (Fig. 3). In this multivariate analysis, selection independently favored large body size over the same overwinter episodes of selection (Fig. 3). There was no correlational selection on growth rate and body size in either year for either females (growth rate × SVL: 2015: $\gamma_{1,2} = -0.05 \pm 0.15$, $P = 0.75$; 2016: $\gamma_{1,2} = -0.61 \pm 0.36$, $P = 0.08$) or males (growth rate × SVL: 2015: $\gamma_{1,2} = -0.03 \pm 0.23$, $P = 0.86$; 2016: $\gamma_{1,2} = 0.09 \pm 0.25$, $P = 0.76$).

Discussion

We found that natural selection on body size becomes sexually antagonistic at the point in ontogeny when young-of-the-year females and males approach sexual maturity. This sex difference in selection is apparent with a between-sex comparison of the fitness surfaces for the late summer episode of selection (Fig. 2). With this visualization, it is clear that, while large body size is favored in both sexes when individuals are < 30 mm in snout-vent length, for individuals > 30 mm, the relationship between body size and survival clearly differs by sex. Examining these fitness surfaces in the context of the biology of *Anolis sagrei* leads us to interpret this result as evidence for the development of sexually antagonistic selection over ontogeny because this sex difference in selection manifests at precisely the body size when individuals are making the transition to sexual maturity and when sexual size dimorphism becomes highly pronounced (Cox et al. 2017). This sex difference in fitness surfaces is corroborated by the significant sex difference in quadratic selection (sex × SVL^2) for this late summer episode when analyzing data pooled across all three years of study, as well as by the sex difference in linear selection observed within the 35-44 mm size class, which is presumably made up of the oldest animals within the young-of-the-year cohort (i.e., those reaching sexual maturity within the same summer season in which they hatched).

Overall selection on body size differs between females and males for the summer episode of selection primarily in the strength of negative quadratic (stabilizing) selection (Fig. 1). The female selection surface appears as an almost textbook example of strong stabilizing selection. However, because of the age structure within a typical *A. sagrei* population, we do not interpret this as stabilizing selection on body size per se. Rather, it presumably reflects a change in the relationship between size and fitness across ontogeny. Hatchlings emerge from eggs continuously throughout the breeding season (late May through October) because adult female anoles can produce a single egg clutch every 7-10 days. This complicates interpretations of selection on body size for the young-of-the-year cohort. Phenotypic variation in body size at the juvenile life stage within any sample reflects variation in age, growth rate, and we assume only a limited degree of variation in breeding value for size. Undoubtedly, much of the variation in body size is related to age, and selection favoring large body size among the smallest individuals reflects the high risk of mortality that steadily decreases in the first few weeks post hatching. After this initial period favoring larger body size, the fitness surface turns sharply negative for young-of-the-year females larger than 30 mm, while male survival probability continues to increase with size until 39 mm at which point the change in survival probability with increasing body size becomes negligible. Females and males in some populations can reach sexual maturity at sizes as small as 34 and 30 mm respectively (Lee et al. 1989b; Norval et al. 2012). Thus, individuals that have already reached a size of 30 mm at the outset of the late summer episode of selection (late-July) are expected to become sexually mature before the end of the episode (October).

The negative selection on body size observed for females approaching maturity may reflect a high survival cost of reproduction for females large enough to begin reproduction within the same season in which they hatched. Severe survival costs of reproduction in the wild have been experimentally demonstrated in this species (Cox and Calsbeek 2010a; Cox et al. 2010). The reduced survival associated with female reproduction is likely to be driven by reductions in immune function, energy storage, speed of locomotion and an increase in parasites that have all been associated with female reproduction in *A. sagrei* (Cox and Calsbeek 2010a; Cox et al. 2010; Reedy et al. 2016). It is important to note that the largest females in the largest juvenile size classes experiencing negative selection on body size begin to overlap in size with the smallest adult yearling females in the population (hatched in the prior season). However, these adult females (> 6 months old) of similar body size (42-44 mm SVL) to the largest young-of-the-year females (~ 2 months old) do not experience selection against large body size. The probability of survival over this late summer episode (July to October) for these smallest adult females is more than 200% greater than it is for the largest young-of-the-year females (Reedy unpublished data). It may be that becoming reproductive within the same summer season in which an individual was hatched renders the costs of reproduction more extreme for females. This is consistent with data from other species where females trade off lifespan against early maturity (Descamps et al. 2006; Massot et al. 2011; Lemaître et al. 2015). Interestingly, the overwinter fitness surfaces for both females and males may also be consistent with the interpretation that negative curvature to the fitness surface occurs when the largest individuals mature and begin to pay costs of reproduction (Fig. S1). Although for females, large body size is associated with a higher probability of survival in the overwinter period, there is again a negative curvature to the female fitness surface which occurs near the size where animals transition to sexual maturity, but the curvature is less pronounced and occurs at a slightly larger size than it does during the late summer episode. For males, the overwinter fitness surface differs from the late summer fitness surface in that there is no longer a leveling off of the gains in expected survival at the largest body sizes. These differences between the late summer and overwinter fitness surfaces for both sexes may be explained if individuals reaching the size of sexual maturity in the winter months are not likely to pay costs of reproduction until the mating season begins in the spring.

When estimating directional selection on the young-of-the-year cohort as a whole, large body size was similarly favored in both sexes. In light of the clear sex differences in selection that are observed when comparing fitness surfaces and detected with between sex-comparisons of quadratic selection, the lack of sex differences in linear selection for the young-of-year cohort as a whole serves as a caution against pooling individuals at different ontogenetic stages when characterizing natural selection (Arnold and Wade 1984). Estimates of directional selection on body size tended to be stronger in males than in females, but the fitness surfaces show that this was strongly driven by the negative curvature of the female fitness surface as large body size was selected against for the largest females in the cohort. Given the significant curvature of both the female and male fitness surfaces for the entire young-of-the-year cohort, any estimates of linear or quadratic selection for the entire cohort would be lacking as descriptors of overall selection. This highlights the utility of plotting the fitness surface with flexible non-linear visualizations and interpreting results in the context of natural history (Schluter 1988; Shaw and Geyer 2010).

Although linear selection differentials showed that the overall probability of survival in any episode of selection increased with body size, our estimates of selection on growth suggest that rapidly attaining a large body size comes with survival cost for both sexes. We found that rapid growth during the summer negatively affected the chances of overwinter survival even when accounting for selection that favored larger body size. The tradeoff between growth and survival is expected under life-history theory (Stearns 1989; Roff et al. 2006) and has been frequently observed in studies of plants (Wright et al. 2010; Adler et al. 2014) and inferred in animal populations (Ambrose Jr and Irlandi 1992; Biro et al. 2004). In wild animal populations, this tradeoff has been more difficult to test for directly given the challenge of collecting longitudinal data on growth and survival, but high growth rate in animals has frequently been associated with reductions in immunity and self-maintenance which are likely to lead to reduced survival (Soler et al. 2003; Uller et al. 2006; Korfel et al. 2015; Lozano-Durán and Zipfel 2015). *Anolis sagrei* males have much more rapid growth than do females. In our study population, we have observed significantly higher mortality rates for young-of-the-year males as compared to females. This sex difference in juvenile mortality may be explained by a combination of sex differences in growth rate and the survival cost of rapid growth.

Alternatively, the tradeoff between growth rate and survival can also be mediated through predation (Biro et al. 2004). Growth rate has been shown to have consistent repeatable differences between individuals in a variety of taxa including reptiles (Smith and Wettermark 1995; Stamps et al. 1998; Björklund et al. 2003). If rapid growth rate is associated with increased activity levels and increased foraging which speeds growth, but increases the risk of predation this tradeoff could be entirely predator mediated (Stamps 2007; Hussey et al. 2017). It is also possible that variation in growth rate is solely a reflection of variation in energetic state. However, if this were the case, it is difficult to explain why greater energetic resources would lead to a decreased probability of survival such as we observed with our selection analysis for juvenile growth rate. Although growth rate certainly is affected by energy intake, the selection against growth rate that we observed suggests that the variation is growth rates is determined by factors other than just energy intake. No matter the underlying cause, our results illustrate selection against rapid growth in young-of-the-year individuals of both sexes and this effect is independent of selection on body size. We interpret this result as evidence for a life history tradeoff between growth and survival.

We provide evidence for the development of sexually antagonistic selection over ontogeny. We observe sexually concordant selection for the earliest life stages and sexually antagonistic selection emerging simultaneously with the onset of sexual maturity for young-of-the-year individuals making the transition to sexual maturity within the same season in which they hatched. Additionally, we detected selection against rapid growth for both males and females. This selection against growth occurred despite strong linear selection for larger body size across young-of-the-year of both sexes. We interpret this as evidence of a life-history tradeoff between growth and survival.

Acknowledgements

We thank A. Castro-Gilliard, A. Chung, R. Costello, C. Cox, R. Bhave, D. Delaney, W. Evans, L. Ferrante, L. Finks, C. Giordano, A. Harrison, F. Hingst, N. Kiriazis, M. Kustra, T. Mitchell, B. Pope, M. Rimkus, A. Roche, C. Sams, A. Willey, and T. Wittman for assistance in the field. This study was conducted under a research permit from the Guana Tolomato Matanzas National Estuarine Research Reserve and approval of the University of Virginia Animal Care and Use Committee (protocol 3896). This project was funded by a National Science Foundation CAREER award (DEB-1453089 to RMC).

References

Adler, P. B., R. Salguero-Gómez, A. Compagnoni, J. S. Hsu, J. Ray-Mukherjee, C. Mbeau-Ache, and M. Franco. 2014. Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences 111:740-745.

Ambrose Jr, W. G. and E. A. Irlandi. 1992. Height of attachment on seagrass leads to trade-off between growth and survival in the bay scallop Argopecten irradians. Marine Ecology Progress Series:45-51.

Andrews, R. and A. S. Rand. 1974. Reproductive effort in anoline lizards. Ecology 55:1317-1327.

Arnold, S. J. and M. J. Wade. 1984. On the measurement of natural and sexual selection: applications. Evolution 38:720-734.

Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends in Ecology & Evolution 17:369-378.

Berger, D., K. Grieshop, M. I. Lind, J. Goenaga, A. A. Maklakov, and G. Arnqvist. 2014. Intralocus sexual conflict and environmental stress. Evolution 68:2184-2196.

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. The American Naturalist 188:E98-E112.

Biro, P. A., M. V. Abrahams, J. R. Post, and E. A. Parkinson. 2004. Predators select against high growth rates and risk–taking behaviour in domestic trout populations. Proceedings of the Royal Society of London B: Biological Sciences 271:2233-2237.

Björklund, M., H. Hirvonen, T. Seppä, N. Peuhkuri, and J. Piironen. 2003. Phenotypic variation in growth trajectories in the Arctic charr Salvelinus alpinus. Journal of evolutionary biology 16:543-550.

Bonduriansky, R. and S. F. Chenoweth. 2009. Intralocus sexual conflict. Trends in ecology & evolution 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. Functional ecology 22:443-453.

Brommer, J. E., M. Kirkpatrick, A. Qvarnström, and L. Gustafsson. 2007. The intersexual genetic correlation for lifetime fitness in the wild and its implications for sexual selection. PLoS one 2:e744.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends in Ecology & Evolution 18:41-47.

Chippindale, A. K., J. R. Gibson, and W. R. Rice. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in Drosophila. Proceedings of the National Academy of Sciences 98:1671-1675.

Clutton-Brock, T. and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562-573.

Connallon, T. and A. G. Clark. 2014. Evolutionary inevitability of sexual antagonism. Proceedings of the Royal Society of London B: Biological Sciences 281:20132123.

Cox, R. and R. Calsbeek. 2011. An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. Journal of Evolutionary Biology 24:343-353.

Cox, R., D. Stenquist, and R. Calsbeek. 2009. Testosterone, growth and the evolution of sexual size dimorphism. Journal of evolutionary biology 22:1586-1598.

Cox, R. M. and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. The American Naturalist 173:176-187.

Cox, R. M. and R. Calsbeek. 2010a. Severe costs of reproduction persist in Anolis lizards despite the evolution of a single-egg clutch. Evolution 64:1321-1330.

Cox, R. M. and R. Calsbeek. 2010b. Sex-specific selection and intraspecific variation in sexual size dimorphism Evolution 64:798-809.

Cox, R. M., C. L. Cox, J. W. McGlothlin, D. C. Card, A. L. Andrew, and T. A. Castoe. 2017. Hormonally mediated increases in sex-biased gene expression accompany the breakdown of between-sex genetic correlations in a sexually dimorphic lizard. The American Naturalist 189:315-332.

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. Functional Ecology 24:1262-1269.

Delcourt, M., M. W. Blows, and H. D. Rundle. 2009. Sexually antagonistic genetic variance for fitness in an ancestral and a novel environment. Proceedings of the Royal Society of London B: Biological Sciences 276.

Descamps, S., S. Boutin, D. Berteaux, and J.-M. Gaillard. 2006. Best squirrels trade a long life for an early reproduction. Proceedings of the Royal Society of London B: Biological Sciences 273:2369-2374.

Ercit, K. 2016. Temporal variation in selection on male and female traits in wild tree crickets. Ecology and evolution 6:5118-5128.

Foerster, K., T. Coulson, B. C. Sheldon, J. M. Pemberton, T. H. Clutton-Brock, and L. E. Kruuk. 2007. Sexually antagonistic genetic variation for fitness in red deer. Nature 447:1107.

Gotanda, K. M. and A. P. Hendry. 2014. Using adaptive traits to consider potential consequences of temporal variation in selection: male guppy colour through time and space. Biological journal of the Linnean Society 112:108-122.

Gotthard, K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, Pararge aegeria. Oecologia 99:281-289.

Hussey, N. E., J. D. DiBattista, J. W. Moore, E. J. Ward, A. T. Fisk, S. Kessel, T. L. Guttridge, K. A. Feldheim, B. R. Franks, and S. H. Gruber. 2017. Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. Pp. 20170166. Proc. R. Soc. B. The Royal Society.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology 74:673-684.

Innocenti, P. and E. H. Morrow. 2010. A joint index for the intensity of sex-specific selection Evolution 64:2775-2778.

Janzen, F. J. and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection. Evolution 52:1564-1571.

Korfel, C. A., J. D. Chamberlain, and M. E. Gifford. 2015. A test of energetic trade-offs between growth and immune function in watersnakes. Oecologia 179:343-351.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292-305.

Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210-1226.

Lee, J. C., D. Clayton, S. Eisenstein, and I. Perez. 1989. The reproductive cycle of Anolis sagrei in southern Florida. Copeia:930-937.

Lemaître, J.-F., V. Berger, C. Bonenfant, M. Douhard, M. Gamelon, F. Plard, and J.-M. Gaillard. 2015. Early-late life trade-offs and the evolution of ageing in the wild. Proc. R. Soc. B 282:20150209.

Long, T. A. and W. R. Rice. 2007. Adult locomotory activity mediates intralocus sexual conflict in a laboratory-adapted population of Drosophila melanogaster. Proceedings of the Royal Society of London B: Biological Sciences 274:3105-3112.

Lovern, M. B. and J. Wade. 2003. Yolk testosterone varies with sex in eggs of the lizard, Anolis carolinensis. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 295:206-210.

Lozano-Durán, R. and C. Zipfel. 2015. Trade-off between growth and immunity: role of brassinosteroids. Trends in plant science 20:12-19.

Maklakov, A. A., S. J. Simpson, F. Zajitschek, M. D. Hall, J. Dessmann, F. Clissold, D. Raubenheimer, R. Bonduriansky, and R. C. Brooks. 2008. Sex-specific fitness effects of nutrient intake on reproduction and lifespan. Current Biology 18:1062-1066.

Mank, J. E. 2008. Sex chromosomes and the evolution of sexual dimorphism: lessons from the genome. The American Naturalist 173:141-150.

Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An integrative study of ageing in a wild population of common lizards. Functional Ecology 25:848-858.

Metcalfe, N. B. and P. Monaghan. 2003. Growth versus lifespan: perspectives from evolutionary ecology. Experimental gerontology 38:935-940.

Norval, G., S. R. Goldberg, and J.-J. Mao. 2012. The reproductive cycle of the brown anole (Anolis sagrei), an introduced lizard species in Taiwan. Russ. J. Herpetol 19:75-81.

Parker, G. 1979. Sexual selection and sexual conflict. Sexual selection and reproductive competition in insects 123:166.

Pischedda, A. and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual selection. PLoS biology 4:e356.

Prasad, N., S. Bedhomme, T. Day, and A. Chippindale. 2006. An evolutionary cost of separate genders revealed by male-limited evolution. The American Naturalist 169:29-37.

Reedy, A. M., C. L. Cox, A. K. Chung, W. J. Evans, and R. M. Cox. 2016. Both sexes suffer increased parasitism and reduced energy storage as costs of reproduction in the brown anole, Anolis sagrei. Biological journal of the Linnean Society 117:516-527.

Rice, W. and A. Chippindale. 2001. Intersexual ontogenetic conflict. Journal of Evolutionary Biology 14:685-693.

Roff, D. A., E. Heibo, and L. Vøllestad. 2006. The importance of growth and mortality costs in the evolution of the optimal life history. Journal of Evolutionary Biology 19:1920-1930.

Schärer, L., L. Rowe, and G. Arnqvist. 2012. Anisogamy, chance and the evolution of sex roles. Trends in Ecology & Evolution 27:260-264.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution:849-861.

Schoener, T. W. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. science 331:426-429.

Shaw, R. G. and C. J. Geyer. 2010. Inferring fitness landscapes. Evolution 64:2510-2520.

Siepielski, A. M., J. D. DiBattista, and S. M. Carlson. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. Ecology letters 12:1261-1276.

Smith, H. G. and K.-J. Wettermark. 1995. Heritability of nestling growth in cross-fostered European Starlings Sturnus vulgaris. Genetics 141:657-665.

Soler, J. J., L. de Neve, T. Pérez–Contreras, M. Soler, and G. Sorci. 2003. Trade-off between immunocompetence and growth in magpies: an experimental study. Proceedings of the Royal Society of London B: Biological Sciences 270:241-248.

Stamps, J., M. Mangel, and J. Phillips. 1998. A new look at relationships between size at maturity and asymptotic size. The American Naturalist 152:470-479.

Stamps, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. Ecology letters 10:355-363.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional ecology 3:259-268.

Stinchcombe, J. R., A. F. Agrawal, P. A. Hohenlohe, S. J. Arnold, and M. W. Blows. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? Evolution 62:2435-2440.

Tarka, M., M. Åkesson, D. Hasselquist, and B. Hansson. 2013. Intralocus sexual conflict over wing length in a wild migratory bird. The American Naturalist 183:62-73.

Uller, T., C. Isaksson, and M. Olsson. 2006. Immune challenge reduces reproductive output and growth in a lizard. Functional Ecology 20:873-879.

Wedell, N., C. Kvarnemo, and T. Tregenza. 2006. Sexual conflict and life histories. Animal Behaviour 71:999-1011.

Weimerskirch, H., C. Barbraud, and P. Lys. 2000. Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. Ecology 81:309-318.

Wood, S. N. 2001. mgcv: GAMs and generalized ridge regression for R. R news 1:20-25.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association 99:673-686.

Wright, S. J., K. Kitajima, N. J. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, and S. Diaz. 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664-3674.

Tables

Table 1.

Size Class (mm)	Model effect	*P*	X^2	df
15-24	Sex	0.07	3.27	11, 1412
	SVL	**< 0.001**	**38.55**	
	Year	**< 0.001**	**131.99**	
	Sex × SVL	0.63	0.23	
	Sex × Year	**0.001**	**13.66**	
	Year × SVL	0.06	5.47	
	Sex × Year × SVL	0.75	0.58	
20-29	**Sex**	**< 0.001**	**25.05**	11, 1775
	SVL	**< 0.001**	**64.15**	
	Year	**< 0.001**	**114.28**	
	Sex × SVL	0.10	2.76	
	Sex × Year	**0.05**	**5.86**	
	Year × SVL	**0.002**	**12.54**	
	Sex × Year × SVL	0.24	2.86	
25-34	**Sex**	**< 0.001**	**23.73**	11, 1128
	SVL	**0.001**	**10.23**	
	Year	**< 0.001**	**65.40**	
	Sex × SVL	0.17	1.88	
	Sex × Year	0.86	0.29	
	Year × SVL	0.25	2.76	
	Sex × Year × SVL	0.50	1.39	
30-39	Sex	0.64	0.21	11, 614
	SVL	0.49	0.48	
	Year	**< 0.001**	**24.14**	
	Sex × SVL	0.12	2.45	
	Sex × Year	0.90	0.22	
	Year × SVL	**0.003**	**11.54**	
	Sex × Year × SVL	0.41	1.77	
35-44	**Sex**	**0.01**	**6.73**	11, 324
	SVL	**0.008**	7.00	
	Year	**0.05**	**5.85**	
	Sex × SVL	**0.01**	**6.07**	
	Sex × Year	**0.04**	**6.27**	
	Year × SVL	**0.03**	**6.72**	
	Sex × Year × SVL	0.12	4.31	

Table 1. Results of generalized linear models testing for differences in survival related to sex, SVL, year and their two and three-way interactions for the young-of-the-year cohort during the late summer episode of selection. To examine selection within narrow windows across ontogeny, the dataset was partitioned into overlapping size class of 1 cm. Models were run with pooled data from 2015, 2016, and 2017.

Table 2

Year	Episode	Sex	N	Linear Selection S ± 1SE	P-value Sex × SVL	Quadratic Selection c ± 1SE	P-value Sex × SVL^2
2015	summer	F	436	0.12 ± 0.04 *	0.09	-0.20 ± 0.06 *	**0.04**
		M	362	0.24 ± 0.06 **		-0.06 ± 0.10	
	overwinter	F	817	0.40 ± 0.05 **	**< 0.01**	-0.01 ± 0.10	0.83
		M	577	0.65 ± 0.07 **		0.07 ± 0.14	
2016	summer	F	448	0.51 ± 0.05 **	0.13	-0.44 ± 0.12 **	0.38
		M	384	0.39 ± 0.06 **		-0.24 ± 0.12 †	
	overwinter	F	151	0.49 ± 0.12 **	0.90	-0.24 ± 0.14 †	0.62
		M	163	0.47 ± 0.14 **		-0.04 ± 0.22	
2017	summer	F	641	0.32 ± 0.06 **	**0.01**	-0.54 ± 0.12 **	**<0.01**
		M	651	0.53 ± 0.06 **		-0.16 ± 0.12 †	

Table 2. Standardized linear and quadratic selection differentials for natural selection on snout-vent length (SVL). Symbols indicate the level of significance for (†) $P < 0.05$, (*) $P < 0.01$, and (**) $P < 0.001$. Significant P-values for the Sex × SVL or Sex × SVL^2 interactions indicate a significant sex difference in linear or quadratic selection and come from a model which regressed relative fitness on sex, SVL and sex × SVL.

Table 3.

Episode	Model effect	*P*	X^2	df
late summer	**Sex**	**< 0.001**	12.54	11, 2921
	SVL	**< 0.001**	202.13	
	Year	**< 0.001**	134.87	
	Sex × SVL	0.80	0.07	
	Sex × Year	**< 0.01**	11.35	
	Year × SVL	**< 0.001**	14.62	
	Sex × Year × SVL	**0.04**	6.62	
overwinter	**Sex**	**< 0.001**	11.17	7, 1707
	SVL	**< 0.001**	93.49	
	Year	**< 0.001**	21.18	
	Sex × SVL	0.58	0.31	
	Sex × Year	0.53	0.40	
	Year × SVL	0.54	0.38	
	Sex × Year × SVL	0.25	1.34	

Table 3. Results of generalized linear models testing for differences in survival related to sex, SVL, year and their two and three-way interactions for the young-of-the-year cohort during two distinct episodes of selection. Models were run using pooled data from 2015, 2016, and 2017 for the late summer episode of selection and pooled data from 2015 and 2016 for the overwinter episode.

Table 4.

Episode	Model effect	*P*	X^2	df
late summer	**Sex**	**< 0.001**	13.16	12, 2921
	SVL	**< 0.001**	240.10	
	SVL²	**< 0.001**	50.12	
	Year	**< 0.001**	135.80	
	Sex × SVL²	**< 0.01**	10.28	
	Sex × Year	**< 0.01**	13.61	
	Year × SVL²	0.68	0.78	
	Sex × Year × SVL²	0.88	0.26	
overwinter	**Sex**	**< 0.01**	6.69	8, 1707
	SVL	**< 0.001**	157.44	
	SVL²	**0.01**	6.14	
	Year	**< 0.001**	12.37	
	Sex × SVL²	0.26	1.26	
	Sex × Year	0.57	0.32	
	Year × SVL²	0.14	2.17	
	Sex × Year × SVL²	0.33	0.95	

Table 4. Results of generalized linear models testing for differences in survival related to sex, SVL, SVL^{2,},year and the two and three-way interactions with SVL^{2,} for the young-of-the-year cohort during two distinct episodes of selection. Models were run using pooled data from 2015, 2016, and 2017 for the late summer episode of selection and pooled data from 2015 and 2016 for the overwinter episode.

Figures

Figure 1.

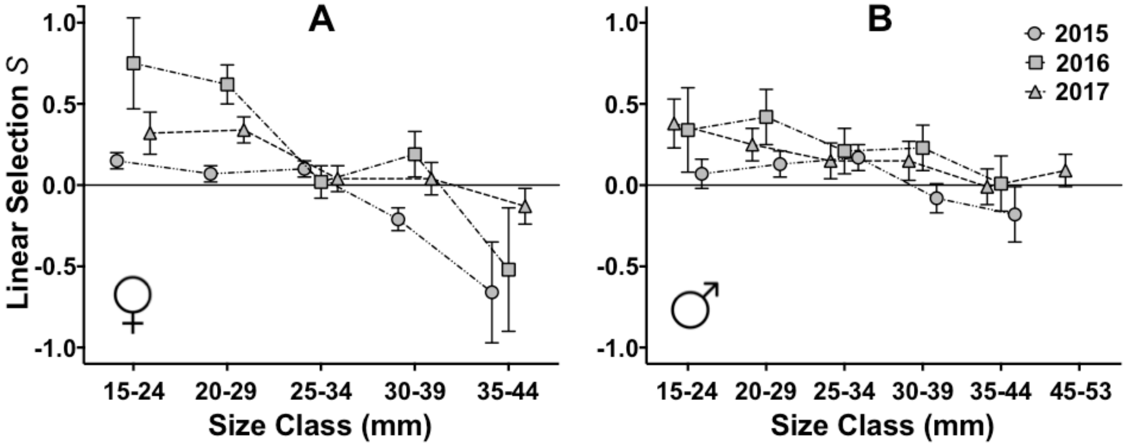


Figure 1. Linear selection differentials (± 1 SE) for natural selection on (A) female and (B) male body size (snout-vent length) calculated separately within each of five overlapping size classes for the late summer (July to October) episode of selection. Each line connects selection differentials from within the same year. Data are from 2015 (n = 436 females; 362 males), 2016 (n = 448 females; 384 males), and 2017 (n = 641 females; 651 males). Note that the ranges on the x-axes differ because only males grew to body sizes greater than 45 mm at the time of measurement (July) and only during the 2017 season.

Figure 2.

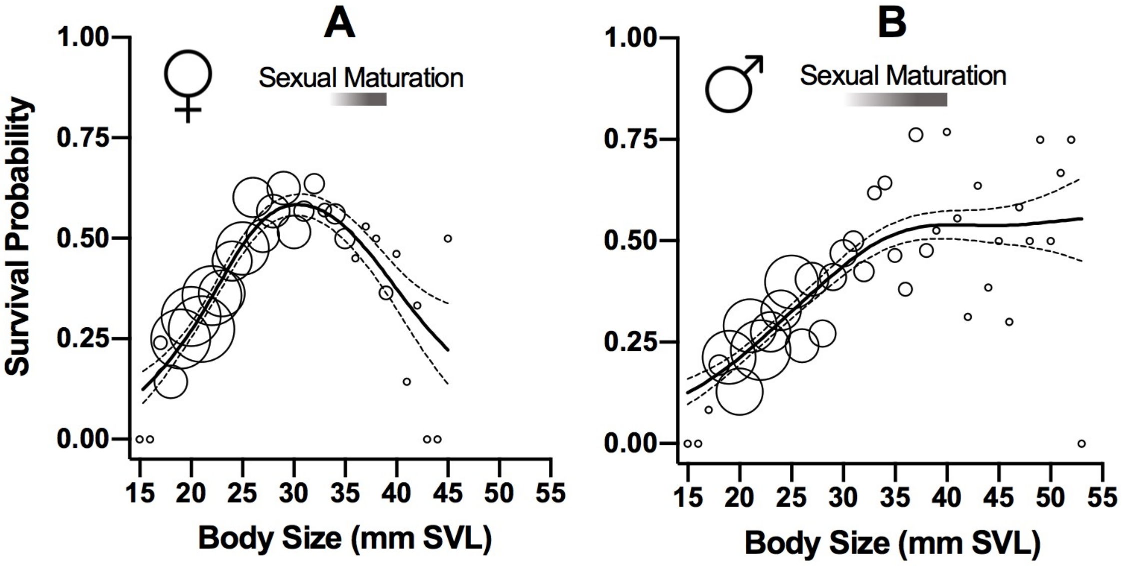


Figure 2. Fitness surfaces for survival as a function of body size (SVL) in (A) females (*n* = 1,525) and (B) males (*n* = 1,397) using data from all young-of-the-year pooled across three years (2015-2017) for the late summer (July to October) episode of selection. Survival probability increases with body size for both sexes at the smallest body sizes. (A) Once young-of-the-year females reach 30 mm in body size, their probability of survival peaks and then decreases sharply with increasing body size. (B) In contrast, once young-of-the-year males reach 39 mm in size, their probability of survival peaks and then remains consistently high with increasing body size. The size of each data point is scaled by sample size at a given body size. The body-size range of the expected transition to sexual maturity is shown with the bar at the top of each plot. The largest points are representative of 135 individuals while the smallest points indicate <14 individuals. Solid lines indicate predicted survival as fit with a generalized additive model and dashed lines denote ± 1 SE.

Figure 3.

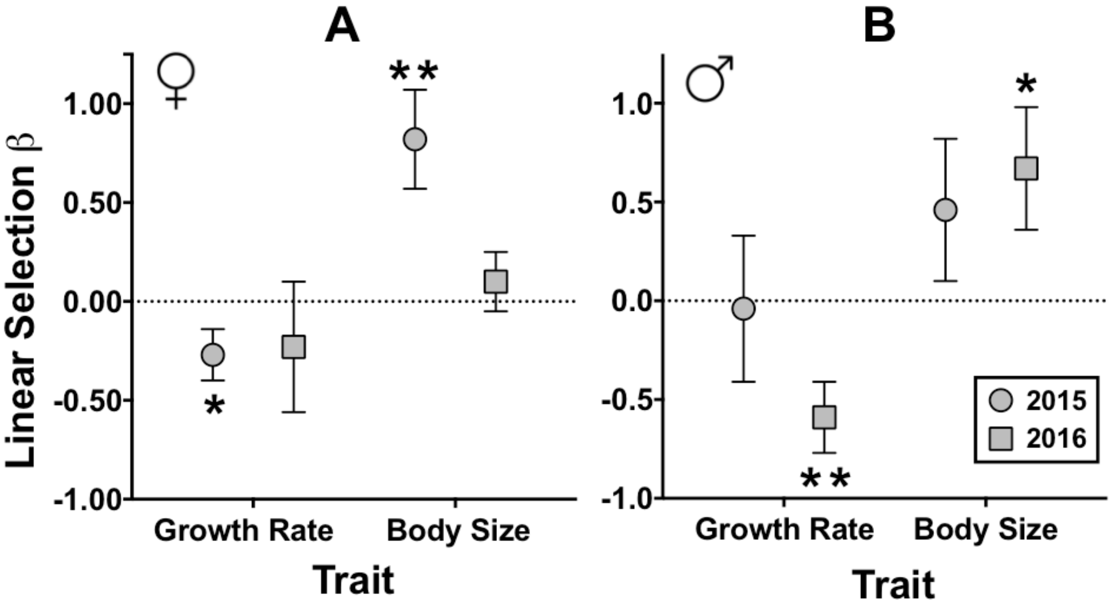


Figure 3. Multivariate selection gradients ($\beta \pm 1$ SE) at the juvenile life stage for overwinter selection on late summer growth rate and body size (SVL), shown separately for **(A)** females in 2015 ($n = 224$) and 2016 ($n = 65$), and (**B**) males in 2015 ($n = 135$) and 2016 ($n = 63$). For both sexes, selection tended to favor slow growth rates, but large body sizes. Statistical significance is denoted as * ($P < 0.05$) and ** ($P < 0.01$).

Supplemental Figures

Figure S1

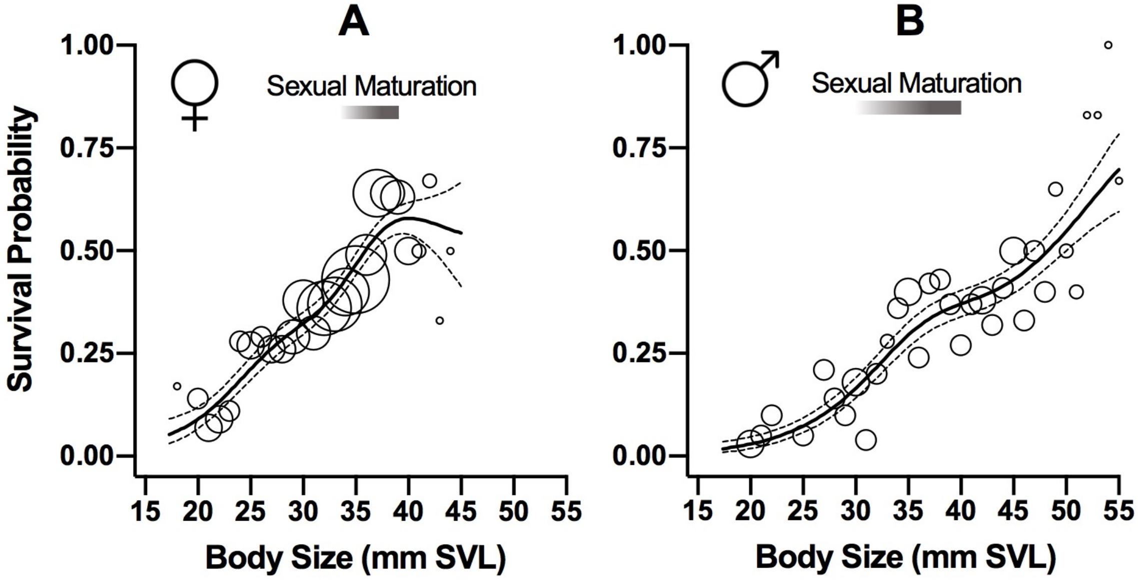


Figure S1. Fitness surfaces for survival as a function of body size (SVL) in (A) females (n = 968) and (B) males (n = 740) using data from all young-of-the-year pooled across two years (2015-2016) for the overwinter (October to April) episode of selection. Survival probability increases with body size for both sexes at the smallest body sizes. (A) Once young-of-the-year females reach 38 mm in body size, their probability of survival peaks and decreases slightly with increasing body size. (B) In contrast, once young-of-the-year males reach 41 mm in size, the positive relationship between body size and survival becomes increasingly steep. Overlap with the range of adult body-size is shown with the bar at the top of each plot and shading indicates the range of size at which the transition to sexual maturity occurs. The size of each data point is scaled by sample size at a given body size. The largest points are representative of 86 individuals while the smallest points indicate <9 individuals. Solid lines indicate predicted survival as fit with a generalized additive model and dashed lines denote ± 1 SE.

Chapter Four:

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

---

Formatted as a coauthored manuscript: Reedy, A.M., W.J. Evans, and R.M. Cox

Abstract

The tradeoff between reproduction and survival is a central principle of life-history theory and has been used to explain the diversity in life-history strategies across species. Although some species appear to have lower annual survival rates than would be predicted by reproductive effort alone, unexplained variation around this tradeoff has typically been thought of as error variance. Sexual-conflict theory provides a hypothesis that could explain residual variation in survival via sex differences in selection. If selection on males is producing a correlated evolutionary response in female life-history traits, then this may prevent females from evolving optimal levels of survival and reproduction. To test for a tradeoff between survival and reproduction and to test the hypothesis that sex differences in selection affect life-history tradeoffs in females, we compiled a comparative dataset of annual survival rates and reproductive effort for 82 lizard species representing 14 families. We found strong evidence for a tradeoff between annual survival and annual female reproductive effort at the species level, even when accounting for phylogenic relationships among species. To test whether residual variance around this observed tradeoff could be explained by sexual conflict, we used sexual size dimorphism (SSD) as a proxy for sex differences in selection and a history of intralocus sexual conflict. We predicted that greater SSD would be associated with lower survival than expected for a given level of reproductive effort. After accounting for phylogenetic relationships, we did not find support for this prediction. Unexpectedly, when testing this prediction with a directional index of SSD, we found that SSD was correlated with variation in residual survival, such that females of female-larger species tended to show lower survival than would be expected for their level of reproductive effort, while

females from male-larger species showed greater than expected annual survival rates for their level of reproductive effort, suggesting that life-history evolution in females may be affected more strongly by intralocus sexual conflict in species with female-larger SSD. We interpret these results as evidence that sex differences in selection may play a role in explaining variation in life-history traits that falls outside of classic life-history theory.

Introduction

Species with high per-season reproductive effort are generally short lived, while those with low per-season reproductive effort are typically long lived (Tinkle 1969; Promislow and Harvey 1990; Shine and Schwarzkopf 1992; Sæther and Bakke 2000). This pattern is interpreted as evidence for the tradeoff between survival and reproduction that is the foundation of modern life-history theory (Williams 1966; Stearns 1989; Roff 1993). Selection favors both high survival and high reproductive output, but the tradeoff between these two components of fitness prevents the evolution of high levels of both. In this context, the tradeoff has been a very successful paradigm for answering 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).

With an increase in empirical work on sexual conflict over the last decade, there has been a surge of recent interest in how the divergent reproductive strategies of males and females may hinder one or both sexes from achieving the optimal resolution of the tradeoff between reproduction and survival (Maklakov and Lummaa 2013). Intralocus sexual conflict occurs when females and males have sex-specific fitness optima for traits with a genetic basis that is shared by both sexes. If selection on life-history traits with a shared genetic basis differs between the sexes, intralocus sexual conflict may prevent one or both sexes from resolving the tradeoff between survival and reproduction in a way that optimizes sex-specific fitness (Holland and Rice 1999; Maklakov et al. 2007; Bonduriansky et al. 2008; Berger et al. 2016). Much of the study of life history has focused on females because the development of life-history theory was set in the context of demography and population growth, to which males do not directly contribute (Cox 2014b). Undoubtedly, the relative ease of measuring reproductive effort in females has also played a role in this life-history focus on females. Perhaps for these reasons, it remains largely an open question whether selection on males, and a resultant correlated evolutionary response in females, compromises how females resolve the tradeoff between survival and reproduction (Lessells 2012; Pennell and Morrow 2013).

Phylogenetic comparative studies have illustrated the tradeoff between species means for reproductive effort and survival across groups as diverse as insects, mammals, fish and reptiles (Read and Harvey 1989b; Gunderson 1997; Jervis et al. 2001; Jervis et al. 2007). Such exploration of the evolution of life-history traits through comparative methods have often been conducted with data from females only (Cox 2014b). However, recent empirical work on intralocus sexual conflict suggests that sexually antagonistic selection may explain variation in life-history traits that is not explained by the classic life-history tradeoffs (Harano et al. 2010; Lewis et al. 2011; Berg and Maklakov 2012).

Intralocus sexual conflict results when selection acts antagonistically on a trait shared by both sexes, and it provides a strong rationale for why selection on males may prevent females from resolving the central life-history tradeoff between survival and reproduction in a way that maximizes fitness (Wedell et al. 2006; Bonduriansky et al.

2008). The evolutionary interests of males and females are likely to be misaligned due to the inherent differences in the ways that they achieve fitness. Because males often have greater variance in mating success, males are hypothesized to play a life-history strategy that prioritizes high mating success at the expense of self-maintenance. This male reproductive strategy has been categorized as “live fast, die young” and favors reproductive investment in rapid growth, aggressive behavior, weapons, or ornaments at the expense of traits such as immunity and self-maintenance (Vinogradov 1998; Bonduriansky et al. 2008). This paradigm predicts that males are likely to sacrifice investment in their own survival to gain increased reproductive success (Vinogradov 1998). Although total lifetime reproductive investment should be equal between the sexes, because transmitting genes to the next generation is of equal evolutionary importance to both sexes, females are predicted to optimize their lifetime fitness with a slower life history favoring a greater degree of self-maintenance, and an associated longer lifespan (Bonduriansky et al. 2008). For this reason, it has been hypothesized that selection on male life-history, and the correlated evolutionary response in females, will prevent females from reaching their fitness optimum in the tradeoff between survival and reproduction (Lande 1980; Promislow 2003; Maklakov and Lummaa 2013; Adler and Bonduriansky 2014), but this idea has not been tested with species-level data.

In this study, we first characterized the interspecific tradeoff between annual survival rates and annual reproductive effort using phylogenetic comparative methods to account for the non-independence of species-level data. Then, to test the hypothesis that intralocus sexual conflict prevents females from reaching their sex-specific optima for life-history traits, we tested whether residual variance around the tradeoff was explained by intralocus sexual conflict. We predict that the relationship between survival and reproductive effort across species will be strongly negative, but that sexual conflict will explain residual variance around this tradeoff. We used sexual size dimorphism (SSD) as a proxy for intralocus sexual conflict with the assumption that high degrees of sexual dimorphism indicate that selection favors different phenotypes in males and females, and hence a history of stronger sexual antagonism (Parker 1992; Cox et al. 2003; Cox et al. 2007). Thus, our specific a priori prediction is that species with high SSD will have lower survival values than predicted for their level of reproductive effort. Alternatively, rather than indicating a history of sexual conflict, high values of SSD could signify that sexual conflict has been largely resolved (Bonduriansky and Rowe 2005; Cox and Calsbeek 2009). If this is the case, we would expect that sexual conflict over life-history has also been resolved, and these species would have higher survival than predicted for their level of reproductive effort. Finally, if sexual conflict over life history is absent we would predict no correlation between SSD and the residual survival around the tradeoff between survival and reproductive effort.

Methods

Comparative Dataset

We compiled a dataset with estimates of three parameters for each species included: Annual survival, annual reproductive effort (RE), and sexual size dimorphism (SSD) (Table S1). Our dataset includes 82 lizard species from 14 families. These data were obtained from several reviews of reptile life history (Shine and Charnov 1992;

Clobert et al. 1998; Charnov et al. 2007; Meiri et al. 2012) and sexual size dimorphism (Cox et al. 2003; Cox et al. 2007; Scharf and Meiri 2013), augmented with species-specific searches of the primary literature when one of the three parameters was not listed in the above sources for a given species.

We used a directional index of SSD calculated with snout-vent length (SVL):

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

We followed convention by expressing this value as positive in female-larger species and negative in male-larger species to indicate the direction of SSD (Lovich and Gibbons 1992).

We calculated annual reproductive effort as:

$$\mathrm{RE} = \frac{\text{mean clutch mass}}{\text{mean female mass}} \text{ x } \text{number of clutches per year}$$

Most estimates of annual survival rates that we obtained were reported as apparent survival equivalent to the percentage of marked animals recaptured, while only a few studies used Cormack-Jolly-Seber models or related statistical approaches to estimate actual survival probabilities in light of imperfect recapture success (Schaub and Royle 2014). However, we did not distinguish between these different methods of estimating of annual survival in our analyses. When all three parameters were not available from a single study within a single population, we created a composite data point combining parameters from different studies and populations of the same species. Field estimates of life-history parameters are expected to come with a limited degree of precision, but are not generally expected to suffer from low accuracy or bias (Krebs 1989; Charnov et al.

2007). In cases where multiple studies provided estimates for a parameter, we used the mean of all studies for that parameter.

Nonphylogenetic analyses

To test the prediction of a tradeoff between survival and reproduction, we regressed mean annual survival for each species on mean annual reproductive effort. 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 greater SSD reflects a greater history of sexual antagonism and will be associated with a lower survival rate than would be expected based on reproductive effort. However, if the resolution of sexual conflict differs between male-larger and female-larger species, using the absolute value of SSD may obscure a relationship between SSD and survival. Considering this, we then used our directional index of SSD that allowed us to test whether the degree to which dimorphism was male- or female-biased revealed a different association between SSD and residual survival. In addition, we also analyzed SSD as a discrete categorical variable with three states: male-larger (males >5% larger than females), female-larger (females >5% larger than males), and monomorphic (sex difference < 5% in either direction). We then tested for differences in residual survival between those states.

As a complimentary analysis to those described above, we also used a multivariate-approach that did not rely on the creation of a residual survival variable. To test the hypothesis that intralocus sexual conflict explains variation in survival while controlling for other variables, we used a multiple regression of annual survival on SSD, annual reproductive effort, and female body size (SVL). We included SVL in the model as a covariate because of the established connection between body size and annual survival as well as the tendency for SSD to scale with body size (Abouheif and Fairbairn 1997).

Phylogenetic analyses

We carried out phylogenetically based comparative analyses in R using a published phylogeny for lizards and snakes (Pyron et al. 2013; R Core Team 2013). We trimmed this large phylogeny to remove those species not included in our dataset using the packages APE (Analysis of Phylogenetics and Evolution) 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, Trachylepis buettneri*). 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, Trachylepis perrotetii*). We tested for phylogenetic signal in survival rate, reproductive effort, residual survival, and SSD using the packages Picante and Phytools by calculating Blomberg's K and Pagel's λ for each trait (Blomberg et al. 2003; Kembel et al. 2010; Revell 2012). Values of K are calculated using the variance/covariance matrix of the phylogenetic relationships and testing against the null assumption of trait values expected under Brownian motion. A significant value of $K > 0$ indicates phylogenetic signal within the phylogeny for a given trait, and a value of $K = 1$ corresponds to the amount of phylogentic signal expected under Brownian motion. $K < 1$

indicates greater variance within than among clades, whereas $K > 1$ indicates greater variance among than within clades, relative to that predicted under Brownian motion (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).

To test our hypotheses while accounting for the non-independence of species-level data, we first computed phylogenetically independent contrasts for annual survival, reproductive effort, 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 reproductive effort. 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). Additionally, we analyzed SSD as a discrete categorical variable with three states (male-larger, monomorphic, female-larger) and tested for differences in phylogenetically corrected coefficients of residual survival using a PGLS model run in the package CAPER (Orme 2013). Similar to our non-phylogenetic analyses, we also used PGLS multiple regression in CAPER with annual survival as a response variable and SSD, annual reproductive effort, and mean SVL of females as independent variables (Orme 2013).

Results

Non-phylogenetic analyses

We found a strong negative correlation between mean annual survival and mean reproductive effort of females ($R = 0.59$ $P < 0.001$; Fig. 1a). Residual survival from this regression was not correlated with the absolute magnitude of SSD ($R = 0.14$; $P = 0.19$). However, residual survival was correlated with the directional index of SSD, such that survival tended to be higher than expected based on reproductive effort for male-larger species and lower than expected for female-larger species ($R = 0.44$; $P < 0.001$; Fig. 2a). When SSD was analyzed as a discrete categorical variable, the same pattern was observed ($F_{2,80} = 5.69$; $P = 0.005$; Fig. 2b) and post hoc Tukey HSD analysis indicated that male-larger species have significantly higher values of residual survival than female-larger species, but neither differed from monomorphic species. Similarly, multiple regression showed that annual survival decreased with increasing annual reproductive effort ($F_{3,78} = 30.23$; $P < 0.001$) and decreased as SSD shifted from male- to female-larger ($F_{3,78} = 4.29$; $P = 0.04$) even when controlling for the overall increase in annual survival with body size ($F_{3,79} = 19.57$; $P < 0.001$).

Phylogenetic analyses

We detected significant phylogenetic signal in annual survival rate, annual reproductive effort of females, residual survival, SSD, and body size of females (SVL), with values of K ranging from 0.4 to 0.6 and values of λ ranging from 0.47 to 0.86 (Table 1). The negative correlation between annual survival and reproductive effort remained significant when accounting for phylogeny by using independent contrasts ($R = 0.48$; $P < 0.001$; Fig 1b). When accounting for phylogeny across species, we found that evolutionary shifts from male-larger to female-larger SSD were accompanied by evolutionary shifts toward lower values of survival than predicted for a given level of reproductive investment ($R = 0.26$; $P = 0.011$; Fig 2c). We found the same result when we analyzed SSD as a categorical variable; phylogenetically corrected coefficients of residual survival were greater for male-larger species than for monomorphic and female-larger species, which did not differ from each other ($F_{2,78} = 4.11$; $P = 0.02$; Fig 2d). PGLS multiple regression showed that annual survival decreases with reproductive effort ($t_{3,77} = -6.87$; $P < 0.001$), decreases with the degree of female bias in SSD ($t_{3,77} = -3.16$; $P = 0.002$) and increases with female body size ($t_{3,77} = 2.91$; $P = 0.005$). Therefore, phylogenetically based analyses supported all of the same patterns observed when treating species as independent data points.

Discussion

Annual reproductive effort is a strong predictor of the annual survival rate of adult females across the 82 lizard-species in our dataset, even when accounting for variance due to phylogeny and body size. Our results provide one the clearest interspecific demonstrations of this fundamental cornerstone of life-history theory in any taxonomic group (Williams 1966; Tinkle 1969; Linden and Møller 1989; Shine and Schwarzkopf 1992; De Paepe and Taddei 2006; Charnov et al. 2007). Additionally, our results are consistent with the hypothesis that error variance around this tradeoff, rather than being biologically unimportant, may be explained in part by intralocus sexual conflict. We interpret the correlation between sexual size dimorphism and residual survival as consistent with the hypothesis that sex differences in selection can prevent females from optimizing their level of reproductive effort and investment in survival at a level that would maximize fitness under the tradeoff. Moving from extreme male-larger SSD through monomorphism to extreme female-larger SSD, we found that species had increasingly lower survival than would be predicted for their level of reproductive effort. Although this result did not match our prediction that greater SSD, whether male-larger or female-larger, would lead to lower levels of residual survival, the effect of the directional index of SSD on residual survival leaves scope for the idea that sex differences in selection can prevent females from reaching their sex specific optima for major life-history traits (Bonduriansky et al. 2008; Maklakov and Lummaa 2013). We further interpret this result as suggesting that sexual conflict may be resolved to a greater degree in species with male-larger SSD as compared to species with female-larger SSD.

Estimating life-history parameters such as survival rate and reproductive effort from field data is inherently prone to measurement error. There are some cases for which estimates of either parameter found in the literature for a single species can vary considerably. For example, estimates of annual survival in *Urosaurus ornatus* ranged from 0.11 to 0.56 across five populations, while estimates of the number of clutches per year ranged from 1.5 to 3.5 (Charnov et al. 2007). Such variation likely reflects both real biological variation in parameters as well as the difficulty in measuring life-history parameters in wild populations. Perhaps because of the complexity involved in estimating these life-history parameters in nature, residual variation around the negative relationship between survival and reproductive effort is implicitly treated as measurement error not requiring explanation. We propose that this variance around tradeoff between survival and reproduction may reflect constraint preventing the optimization of life-history traits. In this paradigm, when comparative studies regress survival on reproduction, the tradeoff is not represented by the line of best fit with error distributed around it, but rather the tradeoff is the unseen fitness ceiling against which species with the highest values of residual survival are pushing and the line of best fit is the average resolution of the tradeoff in light of constraints such as sexual conflict (Fig. 3). In our study, the correlation of residual variation around the tradeoff with the directional index of SSD suggests that this residual variation is more than just the result of measurement error.

Although sexual selection and fecundity selection are thought to be evolutionary drivers of male- and female-larger SSD respectively, it is important to note that they are not necessarily measures of contemporary sex differences in selection (Badyaev 2002; Cox and John-Alder 2007). While phylogenetic comparative methods have offered some support that SSD in reptiles is driven by sexual selection in male larger species and fecundity selection in female larger species, they have also highlighted how much unexplained variation in SSD remains when considering the extent of variation in SSD across lizard species (Cox et al. 2003; Cox et al. 2007). However, all else being equal, SSD suggests historical or current sex differences in selection expected to shape both SSD and life-history traits in these species. Thus, we interpret the correlation between SSD and residual survival in our dataset as evidence that sex differences in selection play a role into how effectively a species can optimize the adult survival rate and level of female reproductive effort.

In our dataset, most species fall roughly along an axis that runs between low reproductive effort with high survival and high reproductive effort with low survival. This is congruent with the established life-history continuum between fast and slow life histories which has been used to explain life history variation in many taxa (Jones et al.

2008). Our data are also remarkably consistent with a model for the evolution of lifetime reproductive effort by Charnov et al. (2007) that predicts an approximate lifetime reproductive effort of 1.4 times the mass of an adult female. This model was shown to have general predictive power across taxa. When lifetime reproductive data from 54 lizard species and 40 mammal species were analyzed separately, mean lifetime reproductive effort in these groups was found to be 1.43 and 1.41 respectively (Charnov et al. 2007). Our dataset, which utilized annual rather than lifetime reproductive effort, corroborates this idea of a near-universal upper limit to reproductive effort that is imposed by the tradeoff between survival and reproduction. This corroboration of a general limit to lifetime reproductive effort by our dataset is perhaps somewhat unsurprising, given that 49 of the 82 species in our dataset are also found within the Charnov et al. (2007) dataset. Nonetheless, in our analysis, the line of best fit for the tradeoff between survival and reproduction gives a maximal predicted annual reproductive effort (where annual survival reaches 0) of 1.63, slightly above the theoretical predicted lifetime reproductive effort. The total parameter space above this tradeoff is largely devoid of species in our dataset and emphasizes the biological reality of the tradeoff (Fig 3). The absence of species in the parameter space far above the tradeoff is consistent with the idea that the highest fitness combinations of survival and reproduction at the species level are rendered unattainable by all but the "Darwinian demon" of thought exercises (Law 1979).

On the contrary, the parameter space characterized by low survival and low reproductive effort contained several species. We predicted that species with low residual survival would be those with the greatest degree of SSD regardless of whether the larger sex was male or female. Our finding that the absolute magnitude of SSD is uncorrelated with residual survival was contrary to this prediction and does not support the hypothesis that sexual conflict constrains the tradeoff between survival and reproduction for females. However, when we used a directional measure of SSD that ranges from highly male-larger to highly female-larger, we found higher residual survival in male-larger species and lower survival in female-larger species. This result does support the general hypothesis that sex differences in selection play a role in how fully a species can optimize levels of survival and reproduction. Although the idea that selection on one sex can constrain the evolution of a life-history trait in the opposite sex has rarely been tested with a comparative approach, a study by Promislow et al. (1992) found a negative correlation between female mortality and the brightness of male plumage. The authors interpreted this in the context of male-biased mortality associated with sexual selection on males. If female mortality rates represent the baseline mortality for the species, then bright plumage in males, which is expected to come with a sex-biased mortality cost for males, will evolve only when mortality rates are low for the species (Promislow et al. 1992). This same logic is a potential explanation for our result of greater residual survival for male-larger species. If male-larger sexual size dimorphism comes with a high mortality cost for males, then perhaps male-larger sexual size dimorphism evolves only in species where mortality rates are relatively high for a given level of reproductive effort. This explanation is consistent with the pattern observed in our data where the species with the highest levels of residual survival tended to be the species that have evolved the greatest degree of male-larger sexual size dimorphism. This explanation differs from our main hypothesis in that, in this scenario, it is the female mortality rate that is constraining the evolution of male-larger sexual size dimorphism rather than selection on males constraining the evolution of female life history. Despite that key difference of the sex facing the constraint, it is an explanation that is still consistent with the idea that intralocus sexual conflict will affect life history traits.

That residual survival is correlated with the directional index of SSD may also suggest a difference in the dynamics of intralocus sexual conflict that occurs when sexual selection on males rather than fecundity selection on females is driving the evolution of dimorphism. The degree of size dimorphism for male biased SSD is typically larger than it is for female biased SSD (Fairbairn 1997). It is possible that this greater degree of SSD reflects historically strong sexually antagonistic selection and conflict that is now resolved allowing for extreme dimorphism (Bonduriansky and Chenoweth 2009). Resolution of conflict through the breakdown of the between-sex genetic correlation for body size would free females from being hampered in their independent evolution by selection on males (Lande 1987; Fairbairn and Roff 2006; Cox et al. 2017). Although we cannot directly test this with our data, the greater residual survival for species with male biased SSD in our data is consistent with this explanation. Another possible explanation for the differences in residual survival between male larger and female larger species may be simply that the traits under fecundity selection in females are prone to intralocus sexual conflict (Pischedda and Chippindale 2006). Although SSD is measured as a continuous index and selection on body size is implicated in both, male biased and female biased SSD almost certainly reflect historical selection on completely different sets of traits.

Although natural selection should always act against the low fitness combination of low survival and low reproductive output, it may be that the existence of species far below the apparent optimum levels of survival and reproduction is explained by species-specific constraints imposed by environment, genetics, lifestyle or morphology (Shine 1992). In such cases, a specific constraint restricts reproduction below the optimal level and renders the tradeoff with survival irrelevant to imposing limits on a species' annual survival rate. For example, some gecko species produce large tails which store energy reserves in the form of fat, and are capable of autotomizing their tails to escape a predation attempt (Parker 1972). If predation risk is high for these species and tail autotomy is frequent, this imposes a high energetic cost and prevents investment in reproduction (Vitt and Congdon 1978; Dial and Fitzpatrick 1981). All five gecko species in our dataset had negative residual survival values, and the species with the lowest residual survival, *Coleonyx variegatus*, experiences a high intensity of predation as evidenced by a 74.1% rate of tail loss (Parker 1972). It should be noted that a potential caveat to interpreting low residual survival in our dataset is that the possibility exists that survival has been underestimated by mark-recapture. Although some estimates of survival in the dataset were derived by calculating encounter probabilities and adjusting survival rates accordingly following capture-mark-recapture analysis with Cormack-Jolly-Seber models (White and Burnham 1999), for many others, actual survival is likely greater than value estimated by simply using the percentage of individuals recaptured. Despite the potential for some estimates of survival to be artificially low, we interpret the wide range of points below the tradeoff, but the limited range of points above, as evidence for a hard upper-limit in reproductive effort imposed by the tradeoff between survival and reproduction.

In conclusion, our results illustrate a clear example of the tradeoff between survival and reproduction at the species level for lizards. Furthermore, they suggest that the tradeoff places an upper limit on the levels of annual survival and annual reproductive effort that can evolve together. Residual variation exists around this tradeoff and a directional index of sexual size dimorphism correlates with residual survival. Residual survival was not correlated with the absolute magnitude of SSD. However, as SSD becomes less male biased and more female biased, we find that species tend to have lower levels of survival than those that would be predicted by annual reproductive effort alone. We interpret this result as evidence that intralocus sexual conflict may hinder life-history evolution in females.

Acknowledgements

We thank E.D. Brodie III for feedback on an early version of this study. We thank E. Martins for the helpful conversation at the 2015 NimBios Evolutionary Quantitative Genetics tutorial. We thank the Jefferson Scholars Foundation for support to A. Reedy and W. Evans. We thank R. Bhave, L. Mitchem, H. Seears, and T. Wittman, for feedback on early data analysis. We thank C.L. Cox and A.F. Kahrl for help with phylogenetic comparative methods in R.

References

Abouheif, E. and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. The American Naturalist 149:540-562.

Adler, M. I. and R. Bonduriansky. 2014. Sexual conflict, life span, and aging. Cold Spring Harbor perspectives in biology 6:a017566.

Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends in Ecology & Evolution 17:369-378.

Berg, E. C. and A. A. Maklakov. 2012. Sexes suffer from suboptimal lifespan because of genetic conflict in a seed beetle. Proceedings of the Royal Society of London B: Biological Sciences 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. The American Naturalist 188:E98-E112.

Blanck, A., P. A. Tedesco, and N. Lamouroux. 2007. Relationships between life-history strategies of European freshwater fish species and their habitat preferences. Freshwater Biology 52:843-859.

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 in ecology & evolution 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. Functional ecology 22:443-453.

Bonduriansky, R. and L. Rowe. 2005. Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in Prochyliza xanthostoma (Diptera: Piophilidae). Evolution 59:1965-1975.

Charnov, E. L., R. Warne, and M. Moses. 2007. Lifetime reproductive effort. The American Naturalist 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.

Cox, R. M. 2014. Integrating costs of reproduction between the sexes. Integrative Organismal Biology:153-168.

Cox, R. M., M. A. Butler, and H. B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Sex, size and gender roles: evolutionary studies of sexual size dimorphism:38-49.

Cox, R. M. and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. The American Naturalist 173:176-187.

Cox, R. M., C. L. Cox, J. W. McGlothlin, D. C. Card, A. L. Andrew, and T. A. Castoe. 2017. Hormonally mediated increases in sex-biased gene expression accompany the breakdown of between-sex genetic correlations in a sexually dimorphic lizard. The American Naturalist 189:315-332.

Cox, R. M. and H. B. John-Alder. 2007. Growing apart together: the development of contrasting sexual size dimorphisms in sympatric Sceloporus lizards. Herpetologica 63:245-257.

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.

Crespi, B. J. and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56:1008-1020.

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 biology 4:e193.

Dial, B. E. and L. C. Fitzpatrick. 1981. The energetic costs of tail autotomy to reproduction in the lizard Coleonyx brevis (Sauria: Gekkonidae). Oecologia 51:310-317.

Fairbairn, D. and D. Roff. 2006. The quantitative genetics of sexual dimorphism: assessing the importance of sex-linkage. Heredity 97:319.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual review of ecology and systematics 28:659-687.

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist 125:1-15.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic biology 41:18-32.

Gunderson, D. R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Canadian Journal of Fisheries and Aquatic Sciences 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. Current Biology 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. Proceedings of the National Academy of Sciences 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. Biological Journal of the Linnean Society 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'. Journal of Animal Ecology 70:442-458.

Jones, O. R., J. M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, and M. Charpentier. 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. Ecology Letters 11:664-673.

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.

Krebs, C. J. 1989. Ecological methodology. Harper & Row New York.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292-305.

Lande, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. Sexual selection: testing the alternatives:83-94.

Law, R. 1979. Optimal life histories under age-specific predation. The American Naturalist 114:399-417.

Lessells, K. 2012. Sexual conflict. Wiley Online Library.

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 in Ecology & Evolution 4:367-371.

Lovich, J. E. and J. W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging 56:269-269.

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.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological monographs 65:101-127.

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.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289-290.

Parker, G. 1992. The evolution of sexual size dimorphism in fish. Journal of Fish Biology 41:1-20.

Parker, W. S. 1972. Aspects of the ecology of a Sonoran Desert population of the western banded gecko, Coleonyx variegatus (Sauria, Eublepharinae). American Midland Naturalist:209-224.

Pennell, T. M. and E. H. Morrow. 2013. Two sexes, one genome: the evolutionary dynamics of intralocus sexual conflict. Ecology and evolution 3:1819-1834.

Pischedda, A. and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual selection. PLoS biology 4:e356.

Promislow, D. 2003. Mate choice, sexual conflict, and evolution of senescence. Behavior genetics 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. Journal of Zoology 220:417-437.

Promislow, D. E., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society of London B: Biological Sciences 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 evolutionary biology 13:93.

Read, A. F. and P. H. Harvey. 1989. Life history differences among the eutherian radiations. Journal of Zoology 219:329-353.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217-223.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos:257-267.

Roff, D. 1993. Evolution of life histories: theory and analysis. Springer Science & Business Media.

Roff, D. and D. Fairbairn. 2007. The evolution of trade-offs: where are we? Journal of evolutionary biology 20:433-447.

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. The American Naturalist 108:783-790.

Scharf, I. and S. Meiri. 2013. Sexual dimorphism of heads and abdomens: different approaches to 'being large'in female and male lizards. Biological Journal of the Linnean Society 110:665-673.

Schaub, M. and J. A. Royle. 2014. Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. Methods in Ecology and Evolution 5:1316-1326.

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 E. L. Charnov. 1992. Patterns of survival, growth, and maturation in snakes and lizards. The American Naturalist 139:1257-1269.

Shine, R. and L. Schwarzkopf. 1992. The evolution of reproductive effort in lizards and snakes. Evolution 46:62-75.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional ecology 3:259-268.

Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annual review of ecology and systematics 16:339-361.

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. The American Naturalist 103:501-516.

Vinogradov, A. E. 1998. Male reproductive strategy and decreased longevity. Acta biotheoretica 46:157-160.

Vitt, L. J. and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. The American Naturalist 112:595-608.

Wedell, N., C. Kvarnemo, and T. Tregenza. 2006. Sexual conflict and life histories. Animal Behaviour 71:999-1011.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46:S120-S139.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist 100:687-690.

Table. 1

Trait	**Blomberg's K**	***P* value**	**Pagel's λ**	***P* value**
Annual Survival	0.47	< 0.01	0.86	< 0.01
Annual Reproductive Effort	0.46	< 0.01	0.73	< 0.01
Residual Survival	0.45	< 0.01	0.76	< 0.01
Sexual Size Dimorphism	0.40	< 0.01	0.47	< 0.01
Snout-Vent Length	0.60	< 0.01	0.84	< 0.01

Table 1. Measures of phylogenetic signal (Blomberg's *K* and Pagel's **λ**) were significantly greater than zero for all traits measured in this study.

Figures

Figure 1.

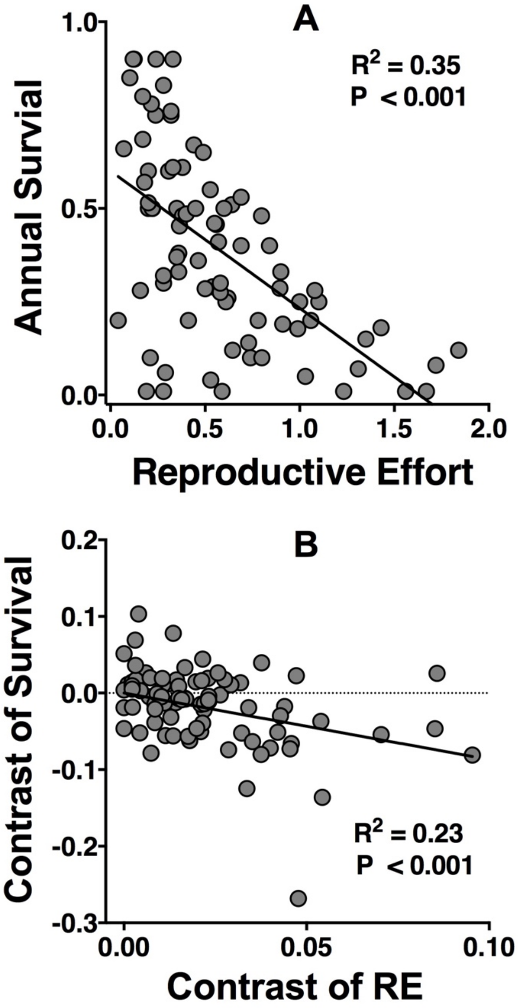


Figure 1. (A) Across 82 lizard species, mean annual survival rate of adult females decreases as mean annual reproductive effort increases. Annual reproductive effort is measured as the mean mass of eggs or offspring produced per year, divided by the mean body mass of adult females. (B) This tradeoff remains apparent when accounting for phylogenetic signal using independent contrasts of annual survival and reproductive effort, such that inferred evolutionary increases in reproductive effort are associated with evolutionary decreases in annual survival.

Figure 2.

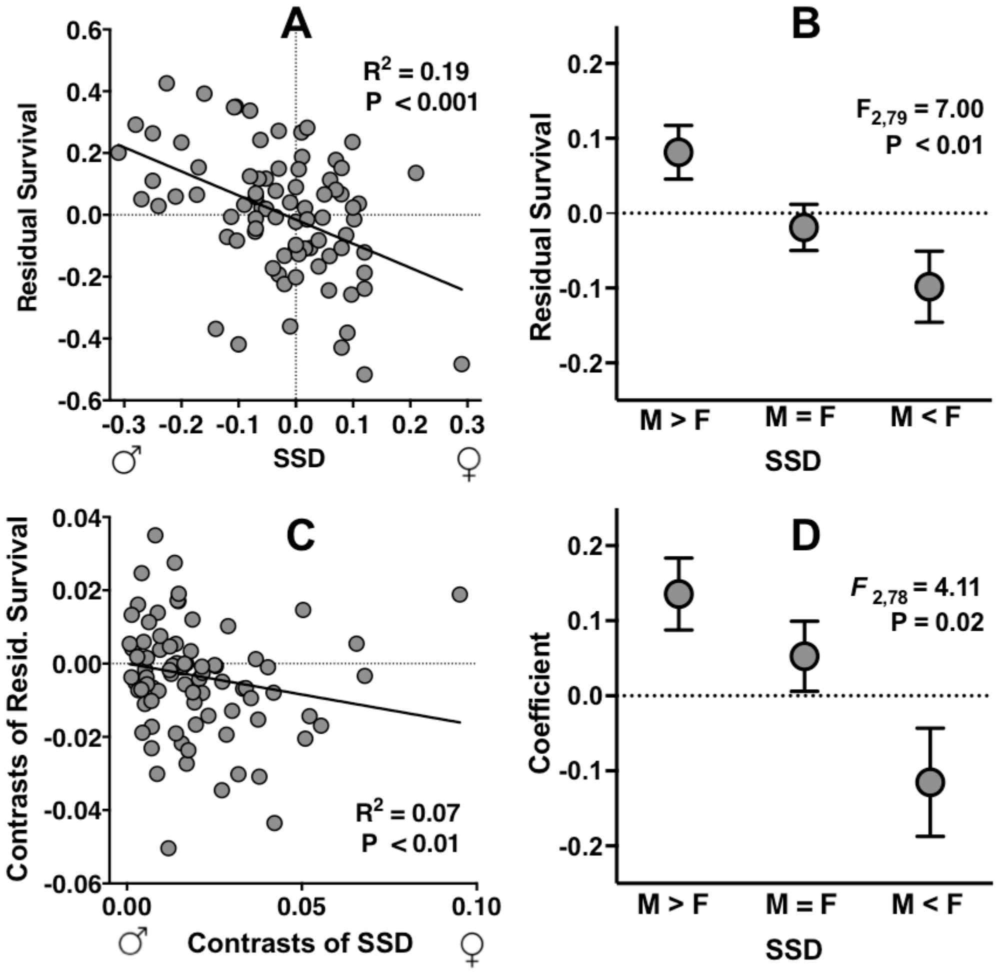


Figure 2. (A) Across the range of sexual size dimorphism (SSD), male-larger species tend to show higher residual survival than female-larger species. (B) Least-square mean residual survival (± SEM) when SSD is categorized as male-larger (males > 5% larger than females), monomorphic (< 5% sex difference in mean SVL), or female-larger (females > 5% larger than males). (C) When accounting for phylogeny with independent contrasts of residual survival and SSD, evolutionary decreases in residual survival tend be accompanied by evolutionary shifts toward female-larger SSD. (D) Coefficients of residual survival from a PGLS model with SSD as a categorical variable and assuming a Brownian motion model of trait evolution.

Figure 3.

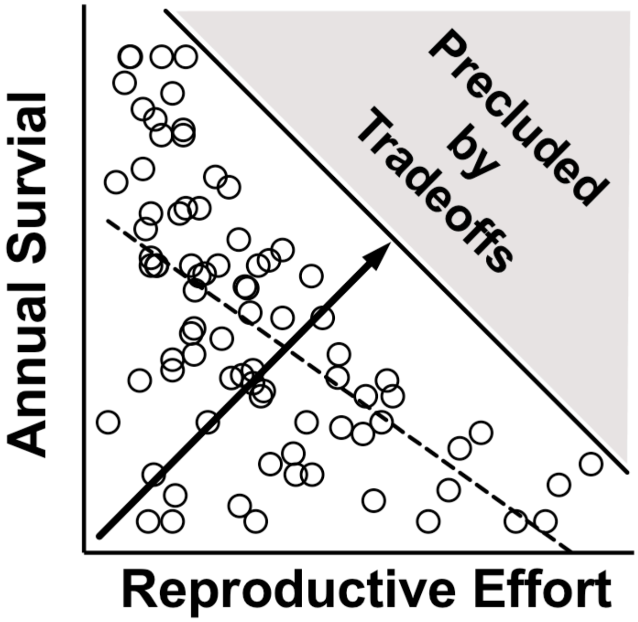
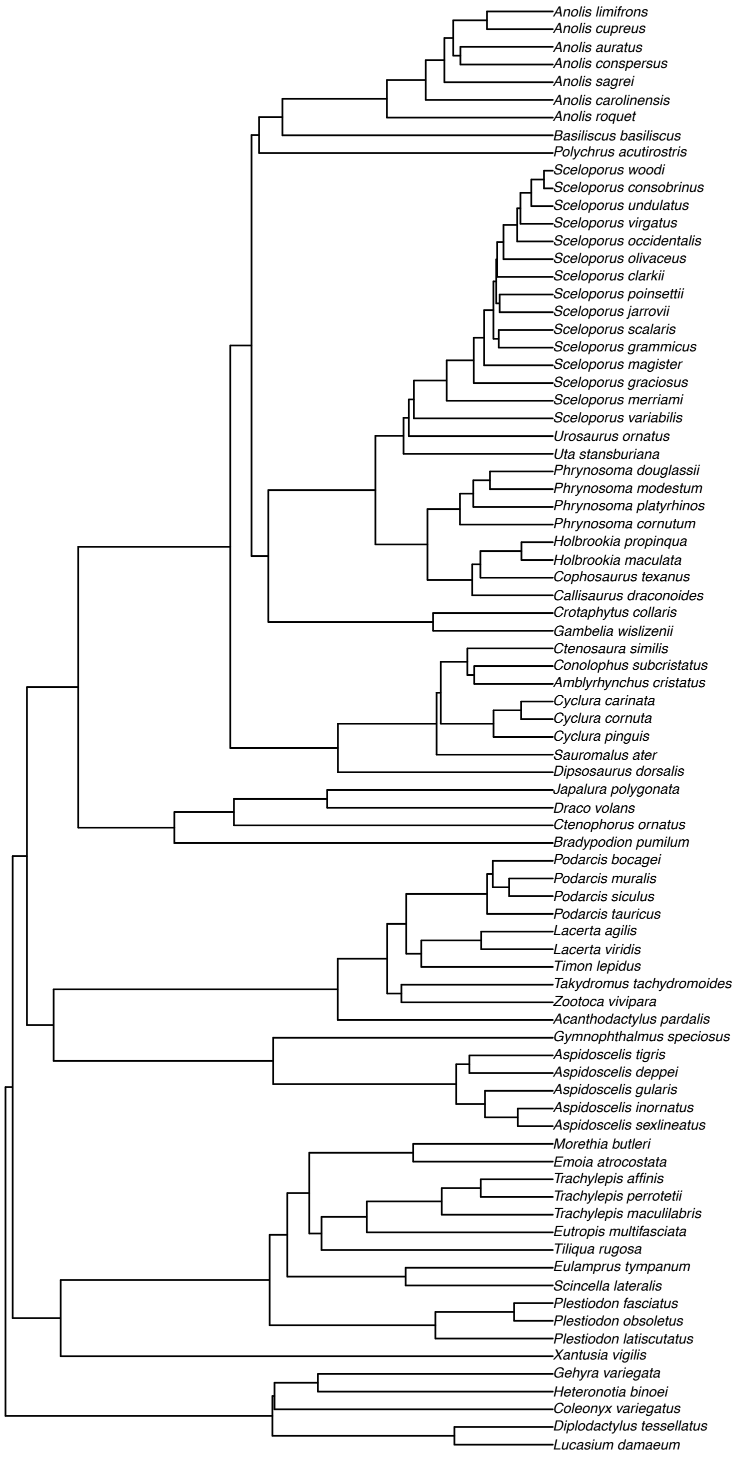


Figure 3. A conceptual diagram layered over our study data. The line of best fit (dashed line) illustrates the average resolution of the tradeoff between survival and reproduction in light of intralocus sexual conflict. The line running above and nearly parallel to the line of best fit (solid line) represents the hypothetical lower boundary for combinations of survival and reproduction which are precluded by tradeoffs. The shaded area above represents the life-history parameter space that is inaccessible due to these tradeoffs. The arrow represents the general vector of selection which is always pushing species towards greater fitness and towards the parameter space for combinations of survival and reproduction which cannot be reached due to tradeoffs.

Supplemental Figure S1.



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 Table S1.

Family	Species	Female SVL	SSD	Categorical SSD	Reproductive Effort	Annual Survival	Sources
Agamidae	*Ctenophorus ornatus*	69	-0.09	Male	0.35	0.50	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Agamidae	*Draco volans*	76.6	0.09	Female	0.04	0.20	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Agamidae	*Japalura swinhonis*	76.1	-0.1	Male	0.21	0.10	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Chamaeleonidae	*Bradypodion pumilum*	64.02	0.04	Mono	1.03	0.05	Cox et al. 2003, Katz et al. 2013, Meiri et al. 2012
Corytophanidae	*Basiliscus basiliscus*	168	-0.173	Male	0.9	0.33	Van Devender 1982, Charnov et al. 2007, Shine and Schwarzkopf 1992, Rand and Marx 1967
Crotaphytidae	*Gambelia wislizenii*	111.49	0.102	Female	0.222	0.50	Cox et al. 2003, Charnov et al. 2007, Tinkle and Hadley 1975, Meiri 2012
Crotaphytidae	*Crotaphytus collaris*	91.8	-0.06	Male	0.38	0.48	Cox et al. 2003, Sexton et al. 1992, Trauth 1978, Charnov et al. 2007, Shine and Schwarzkopf 1992, Vitt&Price 1982
Eublepharidae	*Coleonyx variegatus*	63.09	0.08	Female	0.29	0.06	Parker 1972, Meiri et al. 2012- hatchling mass, Vitt and Cogdon 1978
Gekkonidae	*Heteronotia binoei*	46.7	0.097	Female	0.158	0.28	Cox et al. 2003, Henle 1990a, Henle 1991
Gekkonidae	*Gehyra variegata*	51	0.0467	Mono	0.364	0.45	Cox et al. 2003, Henle 1990b, Werner and Seifan 2006

Gekkonidae	*Diplodactylus tessellatus*	50.2	0.0577	Female	0.412	0.20	Henle 1990a, Henle 1991, Meiri et al. 2012
Gekkonidae	*Lucasium damaeum*	50.7	0.0588	Female	0.36	0.33	Henle 1990a, Henle 1991, Meiri et al. 2012
Gymnophthalmidae	*Gymnophthalmus speciosus*	42	0.12	Female	0.19	0.01	Telford 1971, Cox et al. 2003, Meiri et al. 2012
Iguanidae	*Conolophus subcristatus*	349	-0.16	Male	0.24	0.90	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Iguanidae	*Sauromalus ater*	175.4	-0.062	Male	0.239	0.75	Charnov et al. 2007, Cox et al. 2003, Meiri et al. 2012
Iguanidae	*Cyclura cornuta*	475	-0.105	Male	0.125	0.90	Charnov et al. 2007, Clobert et al. 1998, Powell and Glor 2000, Weiwandt 1977
Iguanidae	*Amblyrhynchus cristatus*	279	-0.28	Male	0.102	0.85	Charnov et al. 2007, Meiri et al. 2012
Iguanidae	*Cyclura pinguis*	468	-0.108	Male	0.12	0.90	Charnov et al.2007, Clobert et al. 1998, Mitchell 1999
Iguanidae	*Dipsosaurus dorsalis*	117	-0.053	Male	0.307	0.60	Cox et al. 2003, Charnov et al. 2007, Krekorian 1984, Mayhew 1971, Krekorian 1976, Fitch 1981, Carothers 1984
Iguanidae	*Ctenosaura similis*	276	-0.25	Male	0.216	0.78	Cox et al. 2003, Meiri et al. 2012, Clobert et al. 1998, Fitch & Henderson 1977a, 1978
Iguanidae	*Cyclura carinata*	225.4	-0.226	Male	0.33	0.90	Cox et al. 2003, Shine and Schwarzkopf 1992
Lacertidae	*Podarcis siculus*	56	-0.12	Male	0.91	0.19	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Lacertidae	*Timon lepidus*	152.2	-0.08	Male	0.28	0.83	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Lacertidae	*Podarcis muralis*	57.1	0	Mono	0.62	0.26	Brana 1996, Cox et al. 2003, Meiri et al. 2012

Lacertidae	*Lacerta viridis*	106.47	-0.035	Mono	0.2	0.60	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Lacertidae	*Podarcis bocagei*	53.51	-0.03	Mono	0.32	0.75	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Lacertidae	*Podarcis tauricus*	61.3	-0.03	Mono	0.64	0.51	Altunýþýk et al. 2016-SURV, SSD, SVL, Meiri et al. 2012
Lacertidae	*Takydromus tachydromoides*	56	0.016	Mono	1	0.25	Charnov et al. 2007, Cox et al. 2003, Shine and Schwarzkopf 1992, Meiri et al. 2012
Lacertidae	*Zootoca vivipara*	53.59	0.088	Female	0.464	0.36	Charnov et al. 2007, Cox et al. 2003 Shine and Charnov 1992, Meiri et al. 2012
Lacertidae	*Acanthodactylus pardalis*	77	0.1	Female	0.57	0.41	Scharf and Meiri 2013, Clobert 1998
Lacertidae	*Lacerta agilis*	90	-0.01	Mono	0.18	0.57	Scharf and Meiri 2013, Clobert 1998
Phrynosomatidae	*Holbrookia propinqua*	50.25	-0.065	Male	1.72	0.08	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Sceloporus grammicus*	48.91	-0.03	Mono	0.28	0.30	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Sceloporus variabilis*	53.07	-0.24	Male	1.67	0.01	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Sceloporus jarrovii*	72.29	-0.103	Male	0.36	0.38	Charnov et al. 2007, Cox et al. 2003, Shine and Schwarzkopf 1992, Meiri et al. 2012
Phrynosomatidae	*Sceloporus graciosus*	54.5	0.011	Mono	0.69	0.53	Charnov et al. 2007, Cox et al. 2003, Shine and Schwarzkopf 1992
Phrynosomatidae	*Sceloporus magister*	94.75	-0.17	Male	0.38	0.61	Charnov et al. 2007, Cox et al. 2003, Vitt and Cogdon 1978, Shine 1992

Phrynosomatidae	*Holbrookia maculata*	52	0.025	Mono	0.54	0.29	Charnov et al. 1998, Jones and Ballinger 1987, Cox et al. 2003, Shine and Schwarzkopf 1992,
Phrynosomatidae	*Urosaurus ornatus*	47.95	-0.052	Male	0.895	0.29	Charnov et al. 2007, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Cophosaurus texanus*	64.2	-0.21	Male	1.101	0.25	Charnov et al. 2007, Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012, Vitt and Price 1982
Phrynosomatidae	*Phrynosoma modestum*	62.8	0.12	Female	0.73	0.14	Charnov et al. 2007, Cox et al 2003,
Phrynosomatidae	*Sceloporus woodi*	50.5	0.06	Female	0.84	0.40	Charnov et al. 2007, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Phrynosoma platyrhinos*	77.83	0.005	Mono	0.527	0.55	Charnov et al. 2007, Cox et al. 2003,
Phrynosomatidae	*Phrynosoma cornutum*	69.6	0.07	Female	0.798	0.48	Charnov et al. 2007, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Sceloporus olivaceus*	93	0.12	Female	0.61	0.25	Charnov et al. 2007, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Sceloporus clarkii*	94.89	-0.08	Male	0.6	0.50	Charnov et al. 2007, Cox et al. 2003, Vitt and Cogdon 1978, Dunham and Miles 1985
Phrynosomatidae	*Sceloporus consobrinus*	60.96	0.016	Mono	0.78	0.20	Charnov et al. 2007, Fitch 1978, Meiri et al. 2012
Phrynosomatidae	*Sceloporus merriami*	48.9	-0.07	Male	0.69	0.40	Cox et al. 2003, Charnov et al. 2007, Meiri et al. 2012

Phrynosomatidae	*Phrynosoma douglassii*	66.9	0.099	Female	0.44	0.67	Cox et al 2003, Shine and Schwarzkopf 1992
Phrynosomatidae	*Sceloporus undulatus*	70.33	0.0795	Female	0.559	0.46	Cox et al. 2003, Charnov et al. 2007, Vitt and Price 1982
Phrynosomatidae	*Callisaurus draconoides*	79.5	-0.113	Male	1.059	0.20	Cox et al. 2003, Charnov et al. 2007, Meiri et al. 2012
Phrynosomatidae	*Uta stansburiana*	47.57	-0.071	Male	0.99	0.18	Cox et al. 2003, Charnov et al. 2007, Shine and Charnov 1992, Shine and Schwarzkopf 1992
Phrynosomatidae	*Sceloporus virgatus*	54.4	0.11	Female	0.4	0.49	Cox et al. 2003, Charnov et al. 2007, Vinegar 1975, Shine and Charnov 1992, Shine and Schwarzkopf 1992
Phrynosomatidae	*Sceloporus scalaris*	51.25	0.08	Female	0.58	0.28	Cox et al. 2003, Charnove et al. 2007, Shine and Schwarzkopf 1992, Vitt and Cogdon 1978, Newlin 1976
Phrynosomatidae	*Sceloporus poinsettii*	96.95	-0.2	Male	0.49	0.65	Charnov et al. 2007, Cox et al. 2003, Meiri et al. 2012
Phrynosomatidae	*Sceloporus occidentalis*	70.38	0.07	Female	1.08	0.28	Cox et al. 2003, Eisen 2001-survival, Meiri et al. 2012
Polychrotidae	*Anolis roquet*	62	-0.31	Male	1.84	0.12	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Polychrotidae	*Polychrus acutirostris*	125	0.21	Female	0.33	0.61	Clobert et al. 1998 , Cox et al. 2003, Meiri et al. 2012
Polychrotidae	*Anolis cupreus*	40	-0.07	Male	1.56	0.01	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Polychrotidae	*Anolis nebulosus*	42.5	-0.07	Male	1.309	0.07	Clobert et al. 1998, Cox et al. 2003, Ramírez-Bautista and Vitt 1997

Polychrotidae	*Anolis tropidolepis*	50.1	-0.01	Mono	0.53	0.04	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Polychrotidae	*Anolis limifrons*	41.85	-0.02	Mono	1.233	0.01	Cox et al. 2003, Andrews and Nichols 1990, Andrews and Rand 1974, Andrews and Sexton 1981
Polychrotidae	*Anolis carolinensis*	47.3	-0.27	Male	1.35	0.15	Cox et al. 2003, Gordon 1956, Andrews 1985, Shine 1992, Schoener and Schoener 1982
Polychrotidae	*Anolis sagrei*	47.59	-0.25	Male	1.43	0.18	Meiri et al. 2012, Reedy et al. unpublished data
Scincidae	*Eutropis multifasciata*	95	-0.07	Male	0.45	0.50	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Scincidae	*Trachylepis maculilabris*	69.9	-0.02	Mono	0.74	0.10	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Scincidae	*Tiliqua rugosa*	299.7	0.01	Mono	0.17	0.80	Clobert et al. 1998, Meiri et al. 2012
Scincidae	*Morethia boulengeri*	39	0.12	Female	0.645	0.12	Charnov et al 2007, Clobert et al. 1998, Cox et al. 2003, Meiri et al 2012
Scincidae	*Trachylepis buettneri*	90	0.29	Female	0.28	0.01	Cox et al. 2003, Meiri et al. 2012
Scincidae	*Eulamprus tympanum*	83	0	Mono	0.07	0.66	Charnov et al 2007, Meiri et al 2012, **Daughtry et al. 2006**
Scincidae	*Plestiodon latiscutatus*	70	0.02	Mono	0.32	0.76	Cox et al. 2003, Hasegawa 1994, Meiri 2012
Scincidae	*Emoia atrocostata*	89.6	-0.04	Mono	0.28	0.32	Cox et al. 2003, Charnov et al. 2007, Meiri et al. 2012

Scincidae	*Plestiodon fasciatus*	68	0	Mono	0.2	0.50	Cox et al. 2003, Charnov et al. 2007, Meiri et al. 2012, Dunham and Miles 1985
Scincidae	*Plestiodon obsoletus*	113.9	0.02	Mono	0.22	0.50	Cox et al. 2003, Charnove et al. 2007, Meiri et al. 2012
Scincidae	*Scincella lateralis*	47.8	0.05	Mono	0.55	0.46	Cox et al. 2003, Meiri et al. 2012
Scincidae	*Trachylepis affinis*	80	0	Mono	0.8	0.10	Scharf and Meiri 2013-Mean SSD
Teiidae	*Aspidoscelis deppei*	63.8	-0.14	Male	0.59	0.01	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Teiidae	*Aspidoscelis tigris*	82.3	-0.035	Mono	0.2	0.52	Cox et al. 2003, Charnov et al. 2007, Shine and Charnov 1992
Teiidae	*Aspidoscelis sexlineatus*	73.3	0.005	Mono	0.5	0.29	Cox et al. 2003, Charnov et al. 2007, Shine and Charnov 1992, Shine and Schwarzkopf 1992
Teiidae	*Aspidoscelis inornatus*	58	0.04	Mono	0.58	0.30	Cox et al. 2003, Meiri et al. 2012
Teiidae	*Aspidoscelis gularis*	89	0	Mono	0.35	0.37	Clobert et al. 1998, Cox et al. 2003, Meiri et al. 2012
Xantusiidae	*Xantusia vigilis*	41	0.08	Female	0.17	0.69	Cox et al. 2003, Charnov et al. 2007, Shine and Charnov 1992

Supplemental Table S1. The above dataset used for all analysis. **Female SVL** is the grand mean SVL values reported for adult females across studies. **SSD** is the directional index of sexual size dimorphism. Values for female-larger species are reported as positive numbers and values for male-larger species are reported as negative numbers. **Categorical SSD** is SSD expressed as categorical variable with three states: male-larger (males >5% larger than females), female-larger (females >5% larger than males), and monomorphic (sex difference < 5% in either direction). **Reproductive Effort** is mean total annual clutch mass divided by the mean mass of adult females. **Annual Survival** is the grand mean of reported values for annual survival

References for Table S1.

Abouheif, E. and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. The American Naturalist 149:540-562.

Adkins, E. K. 1977. Effects of diverse androgens on the sexual behavior and morphology of castrated male quail. Horm. Behav. 8:201-207.

Adler, M. I. and R. Bonduriansky. 2014. Sexual conflict, life span, and aging. Cold Spring Harbor perspectives in biology 6:a017566.

Adler, P. B., R. Salguero-Gómez, A. Compagnoni, J. S. Hsu, J. Ray-Mukherjee, C. Mbeau-Ache, and M. Franco. 2014. Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences 111:740-745.

Albert, D., R. Jonik, and M. Walsh. 1992. Hormone-dependent aggression in male and female rats: experiential, hormonal, and neural foundations. Neuroscience & Biobehavioral Reviews 16:177-192.

Alexander, N. 2012. Review: analysis of parasite and other skewed counts. Tropical Medicine & International Health 17:684-693.

Allander, K. 1997. Reproductive investment and parasite susceptibility in the great tit. Functional Ecology 11:358-364.

Ambrose Jr, W. G. and E. A. Irlandi. 1992. Height of attachment on seagrass leads to trade-off between growth and survival in the bay scallop Argopecten irradians. Marine Ecology Progress Series:45-51.

Andrews, R. and A. S. Rand. 1974a. Reproductive effort in anoline lizards. Ecology 55:1317-1327.

Andrews, R. and A. S. Rand. 1974b. Reproductive effort in anoline lizards. Ecology 55:1317-1327.

Ardia, D. R., K. A. Schat, and D. W. Winkler. 2003. Reproductive effort reduces long-term immune function in breeding tree-swallows (*Tachycineta bicolor*). Proc. Roy. Soc. B 270:1679-1683.

Arnold, A. P. 1975. The effects of castration and androgen replacement on song, courtship, and aggression in zebra finches (*Poephila guttata*). J. Exp. Zool. 191:309-325.

Arnold, S. J. and M. J. Wade. 1984. On the measurement of natural and sexual selection: applications. Evolution 38:720-734.

Arnott, G. and R. W. Elwood. 2009. Gender differences in aggressive behaviour in convict cichlids. Animal behaviour 78:1221-1227.

Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends in Ecology & Evolution 17:369-378.

Barfield, R., D. Busch, and K. Wallen. 1972. Gonadal influence on agonistic behavior in the male domestic rat. Horm. Behav. 3:247-259.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2:349-368.

Berg, E. C. and A. A. Maklakov. 2012. Sexes suffer from suboptimal lifespan because of genetic conflict in a seed beetle. Proceedings of the Royal Society of London B: Biological Sciences 279:4296-4302.

Berger, D., K. Grieshop, M. I. Lind, J. Goenaga, A. A. Maklakov, and G. Arnqvist. 2014. Intralocus sexual conflict and environmental stress. Evolution 68:2184-2196.

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. The American Naturalist 188:E98-E112.

Biro, P. A., M. V. Abrahams, J. R. Post, and E. A. Parkinson. 2004. Predators select against high growth rates and risk–taking behaviour in domestic trout populations. Proceedings of the Royal Society of London B: Biological Sciences 271:2233-2237.

Björklund, M., H. Hirvonen, T. Seppä, N. Peuhkuri, and J. Piironen. 2003. Phenotypic variation in growth trajectories in the Arctic charr Salvelinus alpinus. Journal of evolutionary biology 16:543-550.

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 in ecology & evolution 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. Functional ecology 22:443-453.

Bonduriansky, R. and L. Rowe. 2005. Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in Prochyliza xanthostoma (Diptera: Piophilidae). Evolution 59:1965-1975.

Brommer, J. E., M. Kirkpatrick, A. Qvarnström, and L. Gustafsson. 2007. The intersexual genetic correlation for lifetime fitness in the wild and its implications for sexual selection. PLoS one 2:e744.

Brooks, R. 2000. Negative genetic correlation between male sexual attractiveness and survival. Nature 406:67.

Bulmer, M. and G. Parker. 2002. The evolution of anisogamy: a game-theoretic approach. Proceedings of the Royal Society of London B: Biological Sciences 269:2381-2388.

Cain, K. E. and E. D. Ketterson. 2013. Costs and benefits of competitive traits in females: aggression, maternal care and reproductive success. PLoS One 8:e77816.

Cain, K. E. and K. A. Rosvall. 2014. Next steps for understanding the selective relevance of female-female competition. Frontiers in Ecology and Evolution 2:32.

Calsbeek, R., C. Bonneaud, S. Prabhu, N. Manoukis, and T. B. Smith. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards. Evol. Ecol. Res. 9:495.

Calsbeek, R., C. Bonneaud, and T. B. Smith. 2008. Differential fitness effects of immunocompetence and neighbourhood density in alternative female lizard morphs. J. Anim. Ecol. 77:103-109.

Chapman, B. and R. Chapman. 1964. Observations on the biology of the lizard *Agama agama* in Ghana. Proceedings of the Zoological Society of London 143:121-132.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends in Ecology & Evolution 18:41-47.

Charnov, E. L., R. Warne, and M. Moses. 2007. Lifetime reproductive effort. The American Naturalist 170:E129-E142.

Chippindale, A. K., J. R. Gibson, and W. R. Rice. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in Drosophila. Proceedings of the National Academy of Sciences 98:1671-1675.

Christe, P., O. Glaizot, N. Strepparava, G. Devevey, and L. Fumagalli. 2011. Twofold cost of reproduction: an increase in parental effort leads to higher malarial parasitaemia and to a decrease in resistance to oxidative stress. Proceedings of the Royal Society of London B: Biological Sciences:rspb20111546.

Christe, P., O. Glaizot, N. Strepparava, G. Devevey, and L. Fumagalli. 2012. Twofold cost of reproduction: an increase in parental effort leads to higher malarial parasitaemia and to a decrease in resistance to oxidative stress. Proc. Roy. Soc. B 279:1142-1149.

Chu, C. Y. C. and R. D. Lee. 2012. Sexual dimorphism and sexual selection: a unified economic analysis. Theor. Popul. Biol. 82:335-363.

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.

Clutton-Brock, T. 1982. The functions of antlers. Behaviour 79:108-124.

Clutton-Brock, T. 2007. Sexual selection in males and females. Science 318:1882-1885.

Clutton-Brock, T. and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562-573.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press.

Clutton-Brock, T. H., S. Albon, R. Gibson, and F. E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus L.). Animal Behaviour 27:211-225.

Clutton-Brock, T. H. and G. A. Parker. 1992. Potential reproductive rates and the operation of sexual selection. Q. Rev. Biol. 67:437-456.

Cole, L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29:103-137.

Connallon, T. and A. G. Clark. 2014. Evolutionary inevitability of sexual antagonism. Proceedings of the Royal Society of London B: Biological Sciences 281:20132123.

Cooper Jr, W. E. 1999. Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, Eumeces laticeps. Behavioral Ecology and Sociobiology 47:54-59.

Cooper, W. E. 1977. Information analysis of agonistic behavioral sequences in male iguanid lizards, Anolis carolinensis. Copeia 1977:721-735.

Coustau, C. and C. Chevillon. 2000. Resistance to xenobiotics and parasites: can we count the cost? Trends Ecol. Evol. 15:378-383.

Cox, C. L., A. F. Hanninen, A. M. Reedy, and R. M. Cox. 2014a. Female anoles retain responsiveness to testosterone despite the evolution of androgen-mediated sexual dimorphism. Funct. Ecol. 29:758-769.

Cox, C. L., A. F. Hanninen, A. M. Reedy, and R. M. Cox. 2015. Female anoles retain responsiveness to testosterone despite the evolution of androgen-mediated sexual dimorphism. Functional Ecology 29:758-767.

Cox, R. and R. Calsbeek. 2011. An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. J. Evol. Biol. 24:343-353.

Cox, R., D. Stenquist, and R. Calsbeek. 2009a. Testosterone, growth and the evolution of sexual size dimorphism. Journal of evolutionary biology 22:1586-1598.

Cox, R. M. 2006. A test of the reproductive cost hypothesis for sexual size dimorphism in Yarrow's Spiny Lizard, *Sceloporus jarrovii*. J. Anim. Ecol. 75:1361-1369.

Cox, R. M. 2014a. Integrating costs of reproduction between the sexes *in* L. B. Martin, Woods L.B., Ghalambor C., ed. Integrative Organismal Biology. Wiley Scientific.

Cox, R. M. 2014b. Integrating costs of reproduction between the sexes. Pp. 153-168 *in* C. K. G. L. B. Martin, H. A. Woods, ed. Integrative Organismal Biology. Wiley Scientific.

Cox, R. M. 2014c. Integrating costs of reproduction between the sexes. Integrative Organismal Biology:153-168.

Cox, R. M., M. A. Butler, and H. B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Sex, size and gender roles: evolutionary studies of sexual size dimorphism:38-49.

Cox, R. M. and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. The American Naturalist 173:176-187.

Cox, R. M. and R. Calsbeek. 2010a. Severe costs of reproduction persist in Anolis lizards despite the evolution of a single-egg clutch. Evolution 64:1321-1330.

Cox, R. M. and R. Calsbeek. 2010b. Severe costs of reproduction persist in Anolis lizards despite the evolution of a single-egg clutch. Evolution 64:1321-1330.

Cox, R. M. and R. Calsbeek. 2010c. Sex-specific selection and intraspecific variation in sexual size dimorphism Evolution 64:798-809.

Cox, R. M., C. L. Cox, J. W. McGlothlin, D. C. Card, A. L. Andrew, and T. A. Castoe. 2017. Hormonally mediated increases in sex-biased gene expression accompany the breakdown of between-sex genetic correlations in a sexually dimorphic lizard. The American Naturalist 189:315-332.

Cox, R. M. and H. B. John-Alder. 2005. Testosterone has opposite effects on male growth in lizards (*Sceloporus spp*.) with opposite patterns of sexual size dimorphism. J. Exp. Biol. 208:4679-4687.

Cox, R. M. and H. B. John-Alder. 2007. Growing apart together: the development of contrasting sexual size dimorphisms in sympatric Sceloporus lizards. Herpetologica 63:245-257.

Cox, R. M. and H. B. John-Alder. 2007. Increased mite parasitism as a cost of testosterone in male striped plateau lizards *Sceloporus virgatus*. Funct. Ecol. 21:327-334.

Cox, R. M., M. B. Lovern, and R. Calsbeek. 2014b. 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. Functional Ecology 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.

Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2005. Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. Physiol. Biochem. Zool. 78:531-545.

Cox, R. M., D. S. Stenquist, J. P. Henningsen, and R. Calsbeek. 2009b. Manipulating testosterone to assess links between behavior, morphology, and performance in the brown anole *Anolis sagrei*. Physiol. Biochem. Zool. 82:686-698.

Dawkins, R. and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131.

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 biology 4:e193.

Deckel, A. W. 1995. Laterality of aggressive responses in Anolis. Journal of Experimental Zoology 272:194-200.

Delcourt, M., M. W. Blows, and H. D. Rundle. 2009. Sexually antagonistic genetic variance for fitness in an ancestral and a novel environment. Proceedings of the Royal Society of London B: Biological Sciences 276.

Derickson, W. K. 1976. Lipid storage and utilization in reptiles. Am. Zool. 16:711-723.

Descamps, S., S. Boutin, D. Berteaux, and J.-M. Gaillard. 2006. Best squirrels trade a long life for an early reproduction. Proceedings of the Royal Society of London B: Biological Sciences 273:2369-2374.

Dial, B. E. and L. C. Fitzpatrick. 1981. The energetic costs of tail autotomy to reproduction in the lizard Coleonyx brevis (Sauria: Gekkonidae). Oecologia 51:310-317.

Driessens, T., B. Vanhooydonck, and R. Van Damme. 2014. Deterring predators, daunting opponents or drawing partners? Signaling rates across diverse contexts in the lizard Anolis sagrei. Behavioral ecology and sociobiology 68:173-184.

Dugas, M. B., C. N. Wamelink, and C. L. Richards-Zawacki. 2015a. Both sexes pay a cost of reproduction in a frog with biparental care. Biological journal of the Linnean Society 115:211-218.

Dugas, M. B., C. N. Wamelink, and C. L. Richards-Zawacki. 2015b. Both sexes pay a cost of reproduction in a frog with biparental care. Biol. J. Linn. Soc.

Edwards, J. R. and S. P. Lailvaux. 2013. Do interspecific interactions between females drive shifts in habitat use? A test using the lizards Anolis carolinensis and A. sagrei. Biological Journal of the Linnean Society 110:843-851.

Emlen, D. J. 2008. The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics 39:387-413.

Ercit, K. 2016. Temporal variation in selection on male and female traits in wild tree crickets. Ecology and evolution 6:5118-5128.

Evans, L. T. 1938. Cuban field studies on territoriality of the lizard Anolis sagrei. Journal of Comparative Psychology 25:97.

Fairbairn, D. and D. Roff. 2006. The quantitative genetics of sexual dimorphism: assessing the importance of sex-linkage. Heredity 97:319.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual review of ecology and systematics 28:659-687.

Fedorka, K. M., M. Zuk, and T. A. Mousseau. 2004. Immune suppression and the cost of reproduction in the ground cricket, Allonemobius socius. Evolution 58:2478-2485.

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist 125:1-15.

Fisher, J. 1954. Evolution and bird sociality. Evolution as a Process 71:83.

Fisher, R. 1930a. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Fisher, R. A. 1930b. The genetical theory of natural selection: a complete variorum edition. Oxford University Press.

Foerster, K., T. Coulson, B. C. Sheldon, J. M. Pemberton, T. H. Clutton-Brock, and L. E. Kruuk. 2007. Sexually antagonistic genetic variation for fitness in red deer. Nature 447:1107.

Folstad, I. and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139:603-622.

Foote, C. J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. Behaviour 115:283-314.

Fox, S. F. and T. A. Baird. 1992. The dear enemy phenomenon in the collared lizard, Crotaphytus collaris, with a cautionary note on experimental methodology. Animal Behaviour 44:780-782.

French, S. S., D. F. DeNardo, and M. C. Moore. 2007. Trade-offs between the reproductive and immune systems: facultative responses to resources or obligate responses to reproduction? Am. Nat. 170:79-89.

Gadgil, M. and W. H. Bossert. 1970. Life historical consequences of natural selection. Am. Nat. 104:1-24.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic biology 41:18-32.

Gill, S. A., E. D. Alfson, and M. Hau. 2007. Context matters: female aggression and testosterone in a year-round territorial neotropical songbird (Thryothorus leucotis). Proceedings of the Royal Society of London B: Biological Sciences 274:2187-2194.

Goldberg, S. R. and C. R. Bursey. 1989. *Physaloptera retusa* (Nematoda, Physalopteridae) in naturally infected sagebrush lizards, *Sceloporus graciosus* (Iguanidae). J. Wildl. Dis. 25:425-429.

Gotanda, K. M. and A. P. Hendry. 2014. Using adaptive traits to consider potential consequences of temporal variation in selection: male guppy colour through time and space. Biological journal of the Linnean Society 112:108-122.

Goto, N., H. Kodama, K. Okada, and Y. Fujimoto. 1978. Suppression of phytohemagglutinin skin response in thymectomized chickens. Poult. Sci. 57:246-250.

Gotthard, K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, Pararge aegeria. Oecologia 99:281-289.

Grant, J. W. and P. E. Foam. 2002. Effect of operational sex ratio on female female versus male male competitive aggression. Canadian Journal of Zoology 80:2242-2246.

Greenberg, B. and G. K. Noble. 1944. Social behavior of the American chameleon (Anolis carolinensis Voigt). Physiological Zoology 17:392-439.

Greiner, E. C. 2003. Coccidiosis in reptiles. Pp. 49-56 *in* Elsevier, ed. Semin. Avian. Exot. Pet.

Grether, G. F. 1997. Survival cost of an intrasexually selected ornament in a damselfly. Proceedings of the Royal Society of London B: Biological Sciences 264:207-210.

Gunderson, D. R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Canadian Journal of Fisheries and Aquatic Sciences 54:990-998.

Gustafsson, L., D. Nordling, M. Andersson, B. Sheldon, and A. Qvarnström. 1997. Infectious diseases, reproductive effort and the cost of reproduction in birds. Pp. 53-61 *in* W. D. Hamilton, and J. C. Howard, eds. Infection, Polymorphism and Evolution. Springer, New York.

Gvozdík, L. and R. Damme. 2003. Evolutionary maintenance of sexual dimorphism in head size in the lizard Zootoca vivipara: a test of two hypotheses. Journal of Zoology 259:7-13.

Harano, T., K. Okada, S. Nakayama, T. Miyatake, and D. J. Hosken. 2010. Intralocus sexual conflict unresolved by sex-limited trait expression. Current Biology 20:2036-2039.

Harding, C. F., K. Sheridan, and M. J. Walters. 1983. Hormonal specificity and activation of sexual behavior in male zebra finches. Horm. Behav. 17:111-133.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2007. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129-131.

Harrison, A. and S. Poe. 2012. Evolution of an ornament, the dewlap, in females of the lizard genus Anolis. Biological Journal of the Linnean Society 106:191-201.

Harshman, L. G. and A. J. Zera. 2007. The cost of reproduction: the devil in the details. Trends Ecol. Evol. 22:80-86.

Hegemann, A., K. D. Matson, H. Flinks, and B. I. Tieleman. 2013. Offspring pay sooner, parents pay later: experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. Frontiers in zoology 10:77.

Herrel, A., R. Joachim, B. Vanhooydonck, and D. J. Irschick. 2006. Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard Anolis lineatopus. Biological Journal of the Linnean Society 89:443-454.

Herrel, A., L. D. McBrayer, and P. M. Larson. 2007. Functional basis for sexual differences in bite force in the lizard Anolis carolinensis. Biological Journal of the Linnean Society 91:111-119.

Hews, D. K., M. Castellano, and E. Hara. 2004. Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. Animal Behaviour 68:1201-1207.

Hews, D. K. and R. A. Worthington. 2002. Fighting from the right side of the brain: left visual field preference during aggression in free-ranging male tree lizards (Urosaurus ornatus). Brain, Behavior and Evolution 58:356-361.

Hoffman, C. L., A. V. Ruiz-Lambides, E. Davila, E. Maldonado, M. S. Gerald, and D. Maestripieri. 2008. Sex differences in survival costs of reproduction in a promiscuous primate. Behav. Ecol. Sociobiol. 62:1711-1718.

Holland, B. and W. R. Rice. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. Proceedings of the National Academy of Sciences 96:5083-5088.

Hurst, G. D., R. G. Sharpe, A. H. Broomfield, L. E. Walker, T. M. Majerus, I. A. Zakharov, and M. E. Majerus. 1995. Sexually transmitted disease in a promiscuous insect, *Adalia bipunctata*. Ecol. Entomol. 20:230-236.

Hussey, N. E., J. D. DiBattista, J. W. Moore, E. J. Ward, A. T. Fisk, S. Kessel, T. L. Guttridge, K. A. Feldheim, B. R. Franks, and S. H. Gruber. 2017. Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. Pp. 20170166. Proc. R. Soc. B. The Royal Society.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology 74:673-684.

Innocenti, P. and E. H. Morrow. 2010. A joint index for the intensity of sex-specific selection Evolution 64:2775-2778.

Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. American Naturalist 117:962-974.

Jakobsson, S., O. Brick, and C. Kullberg. 1995. Escalated fighting behaviour incurs increased predation risk. Animal Behaviour 49:235-239.

Janzen, F. J. and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection. Evolution 52:1564-1571.

Jenssen, T. A., N. Greenberg, and K. A. Hovde. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. Herpetol. Monogr. 9:41-62.

Jenssen, T. A. and S. C. Nunez. 1998. Spatial and breeding relationships of the lizard, Anolis carolinensis: evidence of intrasexual selection. Behaviour 1998:981-1003.

Jenssen, T. A., K. S. Orrell, M. B. Lovern, and S. Ross. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, Anolis carolinensis. Copeia 2000:140-149.

Jervis, M. A., C. L. Boggs, and P. N. Ferns. 2007. Egg maturation strategy and survival trade-offs in holometabolous insects: a comparative approach. Biological Journal of the Linnean Society 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’. Journal of Animal Ecology 70:442-458.

Jones, A. G., J. R. Arguello, and S. J. Arnold. 2002a. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough–skinned newt. Proceedings of the Royal Society of London B: Biological Sciences 269:2533-2539.

Jones, A. G., J. R. Arguello, and S. J. Arnold. 2002b. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough–skinned newt. Proc. Roy. Soc. B 269:2533-2539.

Jones, O. R., J. M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, and M. Charpentier. 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. Ecology Letters 11:664-673.

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.

Kennedy, M. W. and R. G. Nager. 2006. The perils and prospects of using phytohaemagglutinin in evolutionary ecology. Trends Ecol. Evol. 21:653-655.

Ketterson, E. D., V. Nolan Jr, L. Wolf, C. Ziegenfus, A. M. Dufty Jr, G. F. Ball, and T. S. Johnsen. 1991. Testosterone and avian life histories: the effect of experimentally elevated testosterone on corticosterone and body mass in dark-eyed juncos. Horm. Behav. 25:489-503.

Kodric-Brown, A. and J. H. Brown. 1987. Anisogamy, sexual selection, and the evolution and maintenance of sex. Evolutionary Ecology 1:95-105.

Koivula, M., E. Koskela, T. Mappes, and T. A. Oksanen. 2003. Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. Ecology 84:398-405.

Kokko, H. and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. J. Evol. Biol. 21:919-948.

Korfel, C. A., J. D. Chamberlain, and M. E. Gifford. 2015. A test of energetic trade-offs between growth and immune function in watersnakes. Oecologia 179:343-351.

Kotiaho, J. S. and L. W. Simmons. 2003a. Longevity cost of reproduction for males but no longevity cost of mating or courtship for females in the male-dimorphic dung beetle Onthophagus binodis. Journal of Insect Physiology 49:817-822.

Kotiaho, J. S. and L. W. Simmons. 2003b. Longevity cost of reproduction for males but no longevity cost of mating or courtship for females in the male-dimorphic dung beetle, *Onthophagus binodis*. J. Insect Physiol. 49:817-822.

Krebs, C. J. 1989. Ecological methodology. Harper & Row New York.

Lailvaux, S. P. and D. J. Irschick. 2007. The evolution of performance-based male fighting ability in Caribbean Anolis lizards. The American Naturalist 170:573-586.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292-305.

Lande, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. Sexual selection: testing the alternatives:83-94.

Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210-1226.

Landwer, A. 1994. Manipulation of egg production reveals costs of reproduction in the tree lizard (*Urosaurus ornatus*). Oecologia 100:243-249.

Langford, G. J., B. A. Willobee, and L. F. Isidoro. 2013. Transmission, Host Specificity, and Seasonal Occurrence of *Cyrtosomum penneri* (Nematoda: Atractidae) in Lizards from Florida. J. Parasitol. 99:241-246.

Law, R. 1979. Optimal life histories under age-specific predation. The American Naturalist 114:399-417.

Lee, J. C., D. Clayton, S. Eisenstein, and I. Perez. 1989a. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 4:930-937.

Lee, J. C., D. Clayton, S. Eisenstein, and I. Perez. 1989b. The reproductive cycle of Anolis sagrei in southern Florida. Copeia:930-937.

Lemaître, J.-F., V. Berger, C. Bonenfant, M. Douhard, M. Gamelon, F. Plard, and J.-M. Gaillard. 2015. Early-late life trade-offs and the evolution of ageing in the wild. Proc. R. Soc. B 282:20150209.

Lessells, K. 2012. Sexual conflict. Wiley Online Library.

Levine, N. D. 1968. Nematode parasites of domestic animals and of man. Burgess Pub. Co, Minneapolis.

Levitan, D. R. 1996. Effects of gamete traits on fertilization in the sea and the evolution of sexual dimorphism. Nature 382:153.

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.

Licht, P. and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. University of California Press.

Lin, E. J. 1979. Fatbody and liver cycles in two tropical lizards *Chamaeleo hohneli* and *Chamaeleo jacksoni* (Reptilia, Lacertilia, Chamaeleonidae). J. Herpetol. 13:113-117.

Lind, M. I., M. K. Zwoinska, S. Meurling, H. Carlsson, and A. A. Maklakov. 2015. Sex-specific tradeoffs with growth and fitness following life-span extension by rapamycin in an outcrossing nematode, Caenorhabditis remanei. Journals of Gerontology Series A: Biomedical Sciences and Medical Sciences 71:882-890.

Linden, M. and A. P. Møller. 1989. Cost of reproduction and covariation of life history traits in birds. Trends in Ecology & Evolution 4:367-371.

Lochmiller, R. L. and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? Oikos 88:87-98.

Lockhart, A. B., P. H. Thrall, and J. Antonovics. 1996. Sexually transmitted diseases in animals: ecological and evolutionary implications. Biol. Rev. 71:415-471.

Logue, D., I. Abiola, D. Rains, N. Bailey, M. Zuk, and W. Cade. 2010. Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song. Proceedings of the Royal Society of London B: Biological Sciences 277:2571-2575.

Long, T. A. and W. R. Rice. 2007. Adult locomotory activity mediates intralocus sexual conflict in a laboratory-adapted population of Drosophila melanogaster. Proceedings of the Royal Society of London B: Biological Sciences 274:3105-3112.

López, P. and J. Martín. 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards, Podarcis hispanica. Behavioral Ecology and Sociobiology 49:111-116.

Lovern, M. B. and J. Wade. 2003. Yolk testosterone varies with sex in eggs of the lizard, Anolis carolinensis. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 295:206-210.

Lovich, J. E. and J. W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging 56:269-269.

Lozano-Durán, R. and C. Zipfel. 2015. Trade-off between growth and immunity: role of brassinosteroids. Trends in plant science 20:12-19.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends in Ecology & Evolution 6:183-186.

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.

Maklakov, A. A., S. J. Simpson, F. Zajitschek, M. D. Hall, J. Dessmann, F. Clissold, D. Raubenheimer, R. Bonduriansky, and R. C. Brooks. 2008. Sex-specific fitness effects of nutrient intake on reproduction and lifespan. Current Biology 18:1062-1066.

Mank, J. E. 2008. Sex chromosomes and the evolution of sexual dimorphism: lessons from the genome. The American Naturalist 173:141-150.

Marler, C. A., G. Walsberg, M. L. White, M. Moore, and C. Marler. 1995. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. Behav. Ecol. Sociobiol. 37:225-231.

Martin, L. B., D. M. Hawley, and D. R. Ardia. 2011. An introduction to ecological immunology. Funct. Ecol. 25:1-4.

Martin, L. B., A. Scheuerlein, and M. Wikelski. 2003. Immune activity elevates energy expenditure of house sparrows: a link between direct and indirect costs? Proc. Roy. Soc. Lond. B 270:153-158.

Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An integrative study of ageing in a wild population of common lizards. Functional Ecology 25:848-858.

McCullough, E. L. and D. J. Emlen. 2013. Evaluating the costs of a sexually selected weapon: big horns at a small price. Animal Behaviour 86:977-985.

McCurdy, D. G., D. Shutler, A. Mullie, and M. R. Forbes. 1998. Sex-biased parasitism of avian hosts: relations to blood parasite taxon and mating system. Oikos 82:303-312.

McElligott, A. G., M. P. Gammell, H. C. Harty, D. R. Paini, D. T. Murphy, J. T. Walsh, and T. J. Hayden. 2001. Sexual size dimorphism in fallow deer (Dama dama): do larger, heavier males gain greater mating success? Behavioral Ecology and Sociobiology 49:266-272.

McElligott, A. G., V. Mattiangeli, S. Mattiello, M. Verga, C. A. Reynolds, and T. J. Hayden. 1998. Fighting tactics of fallow bucks (Dama dama, Cervidae): reducing the risks of serious conflict. Ethology 104:789-803.

McKean, K. A. and B. P. Lazzaro. 2011. The costs of immunity and the evolution of immunological defense mechanisms. Pp. 299-310 *in* T. Flatt, and A. Heyland, eds. Mechanisms of Life History Evolution. Oxford University Press, Oxford, UK.

McMann, S. 1993. Contextual signalling and the structure of dyadic encounters in Anolis carolinensis. Animal Behaviour 46:657-668.

Meiri, S., J. H. Brown, and R. M. Sibly. 2012. The ecology of lizard reproductive output. Global Ecology and Biogeography 21:592-602.

Metcalfe, N. B. and P. Monaghan. 2003. Growth versus lifespan: perspectives from evolutionary ecology. Experimental gerontology 38:935-940.

Michener, G. R. and L. Locklear. 1990. Differential costs of reproductive effort for male and female Richardson's ground squirrels. Ecology:855-868.

Moczek, A. P. and D. J. Emlen. 2000. Male horn dimorphism in the scarab beetle, Onthophagus taurus: do alternative reproductive tactics favour alternative phenotypes? Animal behaviour 59:459-466.

Moore, S. L. and K. Wilson. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. Science 297:2015-2018.

Neat, F. C., A. C. Taylor, and F. A. Huntingford. 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Animal Behaviour 55:875-882.

Nordling, D., M. Andersson, S. Zohari, and L. Gustafsson. 1998. Reproductive effort reduces specific immune response and parasite resistance. Proc. Roy. Soc. B 265:1291-1298.

Norris, K. and M. R. Evans. 2000. Ecological immunology: life history trade-offs and immune defense in birds. Behav. Ecol. 11:19-26.

Norval, G., C. R. Bursey, S. R. Goldberg, J.-J. Mao, and K. Slater. 2011. Origin of the helminth community of an exotic invasive lizard, the brown anole, *Anolis sagrei* (Squamata: Polychrotidae), in southwestern Taiwan. Pac. Sci. 65:383-390.

Norval, G., S. R. Goldberg, and J.-J. Mao. 2012. The reproductive cycle of the brown anole (Anolis sagrei), an introduced lizard species in Taiwan. Russ. J. Herpetol 19:75-81.

Nunn, C. L., P. Lindenfors, E. R. Pursall, and J. Rolff. 2009. On sexual dimorphism in immune function. Philos. T. Roy. Soc. B 364:61-69.

Nur, N. 1984. The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. The Journal of Animal Ecology:479-496.

Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R package version 5:1-36.

Orrell, K. S. and T. A. Jenssen. 2003. Heterosexual signalling by the lizard Anolis carolinensis, with intersexual comparisons across contexts. Behaviour 140:603-634.

Owen, J. P. and D. H. Clayton. 2007. Where are the parasites in the PHA response? Trends Ecol. Evol. 22:228-229.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289-290.

Parker, G. 1979. Sexual selection and sexual conflict. Sexual selection and reproductive competition in insects 123:166.

Parker, G. 1992. The evolution of sexual size dimorphism in fish. Journal of Fish Biology 41:1-20.

Parker, G. A. 1982. Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. Journal of Theoretical Biology 96:281-294.

Parker, W. S. 1972. Aspects of the ecology of a Sonoran Desert population of the western banded gecko, Coleonyx variegatus (Sauria, Eublepharinae). American Midland Naturalist:209-224.

Paterson, A. V. 2002. Effects of an individual's removal on space use and behavior in territorial neighborhoods of brown anoles (Anolis sagrei). Herpetologica 58:382-393.

Paterson, A. V. and S. McMann. 2004. Differential headbob displays toward neighbors and nonneighbors in the territorial lizard Anolis sagrei. Journal of Herpetology 38:288-291.

Paukku, S. and J. S. Kotiaho. 2005. Cost of reproduction in Callosobruchus maculatus: effects of mating on male longevity and the effect of male mating status on female longevity. J. Insect Physiol. 51:1220-1226.

Penn, D. J. and K. R. Smith. 2007. Differential fitness costs of reproduction between the sexes. Proceedings of the National Academy of Sciences 104:553-558.

Pennell, T. M. and E. H. Morrow. 2013. Two sexes, one genome: the evolutionary dynamics of intralocus sexual conflict. Ecology and evolution 3:1819-1834.

Pischedda, A. and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual selection. PLoS biology 4:e356.

Prasad, N., S. Bedhomme, T. Day, and A. Chippindale. 2006. An evolutionary cost of separate genders revealed by male-limited evolution. The American Naturalist 169:29-37.

Pratt, A. E., D. K. McLain, and G. R. Lathrop. 2003. The assessment game in sand fiddler crab contests for breeding burrows. Animal Behaviour 65:945-955.

Promislow, D. 2003. Mate choice, sexual conflict, and evolution of senescence. Behavior genetics 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. Journal of Zoology 220:417-437.

Promislow, D. E., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society of London B: Biological Sciences 250:143-150.

Pruetz, J. D. and L. A. Isbell. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (Chlorocebus aethiops) and patas monkeys (Erythrocebus patas) living in simple habitats. Behavioral Ecology and Sociobiology 49:38-47.

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 evolutionary biology 13:93.

Qualls, C. P. and R. G. Jaeger. 1991. Dear enemy recognition in Anolis carolinenis. Journal of Herpetology 25:361-363.

Queller, D. C. 1997a. Why do females care more than males? Proceedings of the Royal Society of London B: Biological Sciences 264:1555-1557.

Queller, D. C. 1997b. Why do females care more than males? Proc. Roy. Soc. B 264:1555-1557.

Read, A. and P. H. Harvey. 1989a. Life history differences among the eutherian radiations. Journal of Zoology 219:329-353.

Read, A. F. and P. H. Harvey. 1989b. Life history differences among the eutherian radiations. Journal of Zoology 219:329-353.

Reedy, A. M., C. L. Cox, A. K. Chung, W. J. Evans, and R. M. Cox. 2016. Both sexes suffer increased parasitism and reduced energy storage as costs of reproduction in the brown anole, Anolis sagrei. Biological journal of the Linnean Society 117:516-527.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217-223.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos:257-267.

Reznick, D. 1992. Measuring the costs of reproduction. Trends Ecol. Evol. 7:42-45.

Rice, W. and A. Chippindale. 2001. Intersexual ontogenetic conflict. Journal of Evolutionary Biology 14:685-693.

Rigby, M. C., R. F. Hechinger, and L. Stevens. 2002. Why should parasite resistance be costly? Trends Parasitol. 18:116-120.

Roberts, M. L., K. L. Buchanan, and M. R. Evans. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. Anim. Behav. 68:227-239.

Roff, D. 1993. Evolution of life histories: theory and analysis. Springer Science & Business Media.

Roff, D. and D. Fairbairn. 2007. The evolution of trade-offs: where are we? Journal of evolutionary biology 20:433-447.

Roff, D. A., E. Heibo, and L. Vøllestad. 2006. The importance of growth and mortality costs in the evolution of the optimal life history. Journal of Evolutionary Biology 19:1920-1930.

Rolff, J. 2002. Bateman's principle and immunity. Proc. Roy. Soc. B 269:867-872.

Rose, M. R. and B. Charlesworth. 1981. Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. Genetics 97:173-186.

Rosvall, K. A. 2011. Maintenance of variation in sexually selected traits in females: a case study using intrasexual aggression in tree swallows Tachycineta bicolor. Journal of Avian Biology 42:454-462.

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.

Sandell, M. I. and H. G. Smith. 1997. Female aggression in the European starling during the breeding season. Animal Behaviour 53:13-23.

Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. The American Naturalist 108:783-790.

Schärer, L., L. Rowe, and G. Arnqvist. 2012. Anisogamy, chance and the evolution of sex roles. Trends in Ecology & Evolution 27:260-264.

Scharf, I. and S. Meiri. 2013. Sexual dimorphism of heads and abdomens: different approaches to 'being large' in female and male lizards. Biological Journal of the Linnean Society 110:665-673.

Schaub, M. and J. A. Royle. 2014. Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. Methods in Ecology and Evolution 5:1316-1326.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution:849-861.

Schmid-Hempel, P. and D. Ebert. 2003. On the evolutionary ecology of specific immune defence. Trends Ecol. Evol. 18:27-32.

Schoener, T. W. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. science 331:426-429.

Schoener, T. W. and A. Schoener. 1980. Densities, sex ratios, and population structure in four species of Bahamian Anolis lizards. The Journal of Animal Ecology 1980:19-53.

Schoener, T. W. and A. Schoener. 1982. Intraspecific Variation in Home-Range Size in Some Anolis Lizards. Ecology 63:809-823.

Schuett, G. W. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. Animal Behaviour 54:213-224.

Sexton, O. J., E. P. Ortleb, L. M. Hathaway, R. E. Ballinger, and P. Licht. 1971. Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. Ecology 52:202-215.

Shaw, R. G. and C. J. Geyer. 2010. Inferring fitness landscapes. Evolution 64:2510-2520.

Sheldon, B. C. and S. Verlhust. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends Ecol. Evol. 11:317-321.

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 E. L. Charnov. 1992. Patterns of survival, growth, and maturation in snakes and lizards. The American Naturalist 139:1257-1269.

Shine, R. and L. Schwarzkopf. 1992. The evolution of reproductive effort in lizards and snakes. Evolution 46:62-75.

Siepielski, A. M., J. D. DiBattista, and S. M. Carlson. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. Ecology letters 12:1261-1276.

Simon, V. B. 2007. Not all signals are equal: male brown anole lizards (Anolis sagrei) selectively decrease pushup frequency following a simulated predatory attack. Ethology 113:793-801.

Slagsvold, T. and J. T. Lifjeld. 1994. Polygyny in birds: the role of competition between females for male parental care. American Naturalist 143:59-94.

Smith, H. G. and K.-J. Wettermark. 1995. Heritability of nestling growth in cross-fostered European Starlings Sturnus vulgaris. Genetics 141:657-665.

Smith, J. M. and G. A. Parker. 1976. The logic of asymmetric contests. Animal behaviour 24:159-175.

Smits, J., G. R. Bortolotti, and J. L. Tella. 1999. Simplifying the phytohaemagglutinin skin-testing technique in studies of avian immunocompetence. Funct. Ecol. 13:567-572.

Soler, J. J., L. de Neve, T. Pérez–Contreras, M. Soler, and G. Sorci. 2003. Trade-off between immunocompetence and growth in magpies: an experimental study. Proceedings of the Royal Society of London B: Biological Sciences 270:241-248.

Spence, R. and C. Smith. 2005. Male territoriality mediates density and sex ratio effects on oviposition in the zebrafish, Danio rerio. Animal Behaviour 69:1317-1323.

Stamps, J. 1977a. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Stamps, J. 1977b. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Stamps, J. and V. Krishnan. 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Animal Behaviour 55:461-472.

Stamps, J., M. Mangel, and J. Phillips. 1998. A new look at relationships between size at maturity and asymptotic size. The American Naturalist 152:470-479.

Stamps, J. A. 2007. Growth-mortality tradeoffs and ‘personality traits’ in animals. Ecology letters 10:355-363.

Stamps, J. A. and V. Krishnan. 1997. Functions of fights in territory establishment. The American Naturalist 150:393-405.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional ecology 3:259-268.

Stinchcombe, J. R., A. F. Agrawal, P. A. Hohenlohe, S. J. Arnold, and M. W. Blows. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? Evolution 62:2435-2440.

Tarka, M., M. Åkesson, D. Hasselquist, and B. Hansson. 2013. Intralocus sexual conflict over wing length in a wild migratory bird. The American Naturalist 183:62-73.

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. The American Naturalist 103:501-516.

Tokarz, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (Anolis sagrei). Animal Behaviour 33:746-753.

Tokarz, R. R. 1986. Hormonal regulation of male reproductive behavior in the lizard *Anolis sagrei*: A test of the aromatization hypothesis. Horm. Behav. 20:364-377.

Tokarz, R. R. 1995. Importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*: an experimental test. Anim. Behav. 49:661-669.

Tokarz, R. R. 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. Herpetologica 54:388-394.

Tokarz, R. R. and J. W. Beck. 1987. Behaviour of the suspected lizard competitors Anolis sagrei and Anolis carolinensis: an experimental test for behavioural interference. Animal Behaviour 35:722-734.

Tokarz, R. R., S. McMann, L. Seitz, and H. B. John-Alder. 1998. Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (*Anolis sagrei*). Physiol. Zool. 71:139-146.

Tokarz, R. R., S. McMann, L. C. Smith, and H. John-Alder. 2002. Effects of Testosterone Treatment and Season on the Frequency of Dewlap Extensions during Male–Male Interactions in the Lizard *Anolis sagrei*. Horm. Behav. 41:70-79.

Trivers, R. 1972a. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), Sexual selection and the descent of man. Chicago# Aldine.

Trivers, R. 1972b. Parental investment and sexual selection. Pp. 136-179. *in* B. Campbell, ed. Sexual Selection and the Descent of Man, 1871-1971. Aldine-Atherton, Chicago

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in Anolis garmani. Evolution 1976:253-269.

Uller, T., C. Isaksson, and M. Olsson. 2006. Immune challenge reduces reproductive output and growth in a lizard. Functional Ecology 20:873-879.

Van Doorn, G. S. 2009. Intralocus sexual conflict. Annals of the New York Academy of Sciences 1168:52-71.

Vanhooydonck, B., A. Herrel, R. Van Damme, and D. Irschick. 2005. Does dewlap size predict male bite performance in Jamaican Anolis lizards? Functional Ecology 19:38-42.

Vass, E., A. J. Nappi, and Y. Carton. 1993. Comparative study of immune competence and host susceptibility in *Drosophila melanogaster* parasitized by *Leptopilina boulardi* and *Asobara tabida*. J. Parasitol. 79:106-112.

Velando, A. and C. Alonso-Alvarez. 2003. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. J. Anim. Ecol. 72:846-856.

Vinegar, M. B. 1972. The function of breeding coloration in the lizard, Sceloporus virgatus. Copeia 1972:660-664.

Vinogradov, A. E. 1998. Male reproductive strategy and decreased longevity. Acta biotheoretica 46:157-160.

Vitt, L. J. and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. The American Naturalist 112:595-608.

Wade, M. J. 1979. Sexual selection and variance in reproductive success. The American Naturalist 114:742-747.

Watson, P. J. and S. A. Field. 2004. Costs increase as ritualized fighting progresses within and between phases in the sierra dome spider, Neriene litigiosa. Animal Behaviour 68:473-482.

Webberley, K. M., G. D. Hurst, R. W. Husband, J. Schulenburg, J. J. Sloggett, V. Isham, J. Buszko, and M. E. Majerus. 2004. Host reproduction and a sexually transmitted disease: causes and consequences of *Coccipolipus hippodamiae* distribution on coccinellid beetles. J. Anim. Ecol. 73:1-10.

Wedekind, C. and I. Folstad. 1994. Adaptive or nonadaptive immunosuppression by sex hormones? Am. Nat. 143:936-938.

Wedell, N., C. Kvarnemo, and T. Tregenza. 2006. Sexual conflict and life histories. Animal Behaviour 71:999-1011.

Weimerskirch, H., C. Barbraud, and P. Lys. 2000. Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. Ecology 81:309-318.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46:S120-S139.

Wigby, S. and T. Chapman. 2005. Sex peptide causes mating costs in female Drosophila melanogaster. Current Biology 15:316-321.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist 100:687-690.

Wolff, J. O. 1993. Why are female small mammals territorial? Oikos:364-370.

Wood, S. N. 2001. mgcv: GAMs and generalized ridge regression for R. R news 1:20-25.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association 99:673-686.

Wright, S. J., K. Kitajima, N. J. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, and S. Diaz. 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664-3674.

Zahavi, A. 1975. Mate selection - a selection for a handicap. J. Theor. Biol. 53:205-214.