POSTCOPULATORY FERTILIZATION BIAS AS A FORM OF CRYPTIC SEXUAL SELECTION

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Males and females share most of their genetic material yet often experience very different selection pressures. Some traits that are adaptive when expressed in males may therefore be maladaptive when expressed in females. Recent studies demonstrating negative correlations in fitness between parents and their opposite-sex progeny suggest that natural selection may favor a reduction in trait correlations between the sexes to partially mitigate intralocus sexual conflict. We studied sex-specific forms of selection acting in *Anolis* lizards in the Greater Antilles, a group for which the importance of natural selection has been well documented in species-level diversification, but for which less is known about sexual selection. Using the brown anole (*Anolis sagrei*), we measured fitness-related variation in morphology (body size), and variation in two traits reflecting whole animal physiological condition: running endurance and immune function. Correlations between body size and physiological traits were opposite between males and females and the form of natural selection acting on physiological traits significantly differed between the sexes. Moreover, physiological traits in progeny were correlated with the body-size of their sires, but correlations were null or even negative between parents and their opposite-sex progeny. Although results based on phenotypic and genetic correlations, as well as the action of natural selection, suggest the potential for intralocus sexual conflict, females used sire body size as a cue to sort sperm for the production of either sons or daughters. Our results suggest that intralocus sexual conflict may be at least partly resolved through post-copulatory sperm choice in *A. sagrei*.

KEY WORDS: Island, lizard, physiology, selection, sexual conflict, sperm.

Divergence in the reproductive interests of males and females may lead to sexual antagonism in mating systems (Losos et al. 1997; Chippindale et al. 2001; Leal and Fleishman 2002; Ogden and Thorpe 2002; Ebehard 2005). Interlocus sexual conflict, characterized by sex-specific expression of antagonistic traits, may generate an evolutionary chase in which the evolution of a trait in one sex is detrimental to the other sex and is countered by the evolution of another trait (Parker 1979). For example, in *Drosophila melanogaster*, seminal fluid proteins reducing female remating rates to increase paternity assurance are countered by the evolution of female resistance to sperm toxicity (Rice 1996; Rice and Holland 1997). In contrast to interlocus conflict, intralocus sexual conflict arises when traits expressed in both males and females differ in fitness optima between the sexes, thereby constraining the evolution of the traits and preventing males and females from reaching their fitness optima (Chippindale et al. 2001; Rice and Chippindale 2001; Parker 2006). Strong empirical evidence for intralocus conflict comes again from studies on *Drosophila*, where elimination of female-driven selection pressures generated populations in which males enjoyed enhanced fitness, whereas females suffered diminished fitness (Pischedda and Chippindale 2006).

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Fisher (1930) was the first to propose that because traits expressed in both males and females usually have a common genetic basis, alternative fitness optima for those traits should lead to antagonistic selection between the sexes. Lande (1980) formalized this theory, and a recent extension by Day and Bondurianski (2004) suggested that sexual selection should favor reduced expression of the between-sex component of trait heritability (e.g., father–daughter or mother–son) to minimize possible intralocus conflict. Several recent studies have built on this hypothesis, and demonstrated sexual conflict by showing that the heritability of fitness was negatively correlated between parents and their opposite sex progeny (Fedorka and Mousseau 2004; Pischedda and Chippindale 2006; Foerster et al. 2007). These studies showed that high fitness sires produced high fitness sons, and at the same time produced low fitness daughters. Similarly, dams with high fitness tended to produce high fitness daughters and low fitness sons. As suggested by Chippindale et al. (2001), one could therefore expect females to at least partly mitigate the intralocus conflict by selecting different sires for the production of sons and daughters.

Although these studies elegantly demonstrate correlations in total fitness between parents and progeny, we still lack clear illustrations of sex differences in the action of selection on phenotypic traits in the wild (Preziosi and Fairbairn 2000; Fairbairn 2007), and how they influence the nature of sexual conflict in mating systems. Here we build on a growing number of studies aimed at examining the importance of sex differences in natural populations, using the brown anole (*Anolis sagrei*) as a study system. Previous studies of *Anolis* lizards have indicated an important role for natural selection acting on morphology [e.g., limb length: (Losos et al. 1997) body size: (Calsbeek and Smith 2007)] and physiology [e.g., immune function: (Calsbeek et al., 2008) locomotor performance: (Calsbeek and Irschick 2007)], although less is known about how these traits influence reproductive decisions. Body size, an important trait in the ecomorphological diversification of anoles, shows extensive variation between the sexes in *A. sagrei* (Butler and Losos 2002; Butler et al. 2007). In addition, natural selection has previously been found to act on both male and female body size in this species (Calsbeek et al. 2007b), although explicit sex-based comparisons were not made in that study. Because differences in body size are thought to reflect differences in habitat use (Butler and Losos 2002; Butler et al. 2007), we might expect variation in this trait to be associated with differing life-history strategies, and hence possibly correlated with sexually antagonistic traits. For example, sex-specific differences in selection on physiological traits are predicted by "the susceptible male hypothesis" (Rolff 2002) which suggests that compared to males, females should invest more in longevity, and hence immune function.

We used experiments in the laboratory in combination with surveys of natural populations to provide insight into the role of natural selection in generating and/or maintaining intralocus sexual conflict. We also investigated the potential resolution of conflict through female reproductive choice. First, we tested whether expression of traits reflecting whole animal physiological condition (Arnold 1983; Stoehr and Kokko 2006), namely stamina and immune function, differed between male and females, and whether the action of selection on these traits also differed between the sexes. Given that an organism's limited resources can generate trade-offs between life-history traits (Bonneaud et al. 2003; Stoehr and Kokko 2006) and since the optimal combination of life-history traits over the life of an individual may differ between the sexes (Bateman 1948), we also tested whether the correlations between stamina and immune function were sex-specific. Second, we tested whether between-sex heritability estimates of size-related traits appeared to be reduced in anoles using the intersexual correlation coefficient r_{MF} (Fisher 1930). Finally, we captured males and gravid females from the wild and reared their offspring to assess natural variation in male siring success, and whether females would engage in adaptive mate-choice to reduce intralocus sexual conflict (Chippindale et al. 2001).

Methods

Anolis sagrei is a small (40–70 mm snout-vent-length; SVL) semi-arboreal lizard with a broad tropical and sub-tropical distribution. It is the most common anole in the Bahamas and a member of the "trunk-ground" ecomorph in the Greater Antilles adaptive radiation. We studied wild populations of *A. sagrei* in the Bahamas from 2004 to 2005. Initial lizard captures took place in spring during May and June on Kidd cay, an offshore island connected to the mainland by a >80 m cement causeway supporting no lizard habitat. The island is small ($\sim$0.084 km^2) and near Great Exuma, Bahamas (23°31'N, 75°49.5'W). It contains both broad diameter vegetation including palm trees (*Pseudophoenix* spp.) and Australian pine trees (*Casuarina equisetifolia)* (mean perch diameter = 230 mm), and narrow diameter vegetation such as sea-grape (*Coccoloba uvifera)*, sea hibiscus (*Hibiscus tiliaceus*), and buttonwood (*Conocarpus erectus*) (mean perch diameter = 25 mm). All lizards were sexed, weighed with a Pesola spring scale (nearest g), and measured for snout-vent-length (SVL; nearest mm). Hind and forelimb lengths were measured with dial calipers from the point of insertion into the abdomen to the femoral-tibial and humero-radio-ulnar joints. Lizards were marked with unique combinations of nontoxic colored elastomer dye, injected in the ventral side of the hind and forelimbs (Nauwelaerts et al. 2000). Tags are not visible to predators and serve as permanent identification in the wild, allowing us to track the fate of every individual over the course of the study (Calsbeek and Irschick 2007; Calsbeek and Smith 2007).

BREEDING EXPERIMENTS AND GENOTYPING

We raised field-caught lizards and their progeny in the laboratory to measure the heritability of morphology, and to assess female mate choice as a function of male morphology. During June 2004, we collected male and female *A. sagrei* from one of our study populations near Georgetown Exuma, Bahamas. We captured lizards during the middle of the breeding season, ensuring that females had mated prior to capture. To determine paternity, we captured and sampled tissue (tail tips) from all neighboring males that might have mated with the females (Calsbeek et al. 2007a). All lizards were weighed and measured as above, and morphological measures were used to assess cryptic female choice (below). Each female was housed in a separate 10-gallon terrarium and was provided with full spectrum lighting, and ad libitum food (*Achaeta* crickets) and water. A potted plant was also provided in which the female was allowed to lay her eggs.

Eggs were left undisturbed to incubate in the potted plants until hatching. We raised F1 progeny from known dams in the laboratory and assigned paternity using a library of eight microsatellite loci (Bardelbeden et al. 2004). We genotyped all progeny, dams, and candidate sires, and assigned paternity with the software package CERVUS. Males were assigned as sire if the confidence of paternity exceeded 95%. Because females were housed individually, maternity of all offspring was known with certainty. Progeny were sexed at hatching (males have enlarged postanal scales). Siblings were randomized into separate terraria until maturity in an attempt to minimize the potentially confounding influence of family origin on development.

Given the outcome of paternity results from 2004 (see Results section below) we began breeding F1 lizards in the laboratory during 2005, but experimentally controlled the females' access to sires of differing body size. During 2005, 17 virgin females were each housed in separate tanks with one large and one small male [Mean (SE) $SVL_{LARGE} = 58.53$ mm (± 2.69); $SVL_{SMALL} = 48.63$ mm (± 3.49)], and allowed to mate over the course of two weeks. Twenty-five additional virgin females were allowed to mate with a single male that was assigned at random. All pairings of F1 males with virgin females were made to prevent any inbreeding effects (i.e., no pairings of full or half-siblings and no first cousins). Paternity analyses were conducted on F2 progeny as in 2004 except in the case of monogamous females for whose progeny paternity was already known.

PHYSIOLOGICAL TRAITS

We measured variation in two physiological traits: stamina (Arnold 1983) and immune function (Blount et al. 2003) on lizards in the field during spring 2005. Running time to exhaustion (i.e., stamina) is the cumulative result of many underlying physiological processes, and likely indicates overall vigor (Arnold 1983). We estimated stamina for all lizards by running them to exhaustion on an electrical treadmill (0.4 km/hr). Because anoles do not run well on level surfaces (Perry et al. 2004), the treadmill was set at a 20° incline. Lizards were motivated to run by manually tapping the hind limb (Le Galliard et al. 2004). Fatigue was considered complete following three consecutive failed attempts to induce running, and/or the loss of the righting response.

We estimated immune function (>2 weeks poststamina) for all lizards in the field and laboratory (F1 and F2) by using a PHA assay (Goto et al. 1978) (phytohemaglutinin-PHA-P; Sigma). Response to PHA is a standard estimate of immune function in wild individuals (Martin et al. 2006), but we do not attempt to discuss here whether a higher response to PHA is more or less adaptive (Kennedy and Nager 2006). We challenged males with 0.20 mg PHA in 0.02 mL phosphate buffered saline (PBS) and females with 0.10 mg PHA in 0.01 mL PBS, injected in the left hind-foot pad. We injected the same volume of PBS in the right hind-foot pad as a control. We measured the thickness of each foot pad with dial calipers (± 0.01 mm) at the injection site, prior to and 24 h post-injection, and assessed the intensity of the response as the difference in swelling between the PHA-injected and the control foot pad. Lizards were held overnight in separate containers during the PHA test. Because animals that were measured in the wild had to be recaptured two weeks after stamina trials, not all animals were tested and sample sizes differ for statistical tests.

VIABILITY STUDIES

To measure natural selection on physiological traits, we estimated sex-specific differences in viability as a function of stamina and immune function. During spring 2005, we captured all of the 112 male and 128 female sub-adult *A. sagrei* that were naturally present on Kidd cay. To supplement sample size for our studies of natural selection (below), we also captured an additional 300 lizards from an adjacent site (250 m away) and released them to two additional offshore cays (92 females and 110 males to Flamingo bay cay; 98 males to Nightmare cay). We have been studying natural selection on these cays for several years; details are available elsewhere (Calsbeek and Irschick 2007; Calsbeek and Smith 2007). All lizards were uniquely marked, measured, and released at their original point of capture. We measured viability selection on 540 lizards over the four-month period from first capture in spring to our population censuses conducted in autumn. This time frame encompasses survival to sexual maturity and the end of the first breeding season and is an estimate of one component of fitness (survival). Each day we walked multiple transects over the entire study site and captured surviving lizards. Lizards were marked with a small spot of white paint to prevent recapture. Censuses can be considered exhaustive because although the majority of surviving lizards were captured within the first two days, censuses continued for two to three weeks, or until three consecutive days of searching turned up no new marked

lizards. Lizards that were not recovered during our censuses were considered dead; a reasonable assumption given that emigration from islands is rare, except during hurricanes (Calsbeek and Smith 2003), none of which affected our study islands during this study. Recapture efficiencies were ~97% based on regression of the number of lizards captured each day (log transformed) against the cumulative days of capture effort.

We measured the strength of linear (i.e., directional, β) and nonlinear (i.e., stabilizing/disruptive $\gamma_{1,1}$ or correlational $\gamma_{1,2}$) selection using separate regressions of morphological and physiological traits against survival to the fall census. We calculated relative fitness (standardized by the population mean) separately for each sex. All trait distributions were standardized to mean zero and unit standard deviation. Because the dependent variable "survival" was binomially distributed (live/die), we report significance values of each selection gradient from a logistic regression that accounts for binomial error variance (Janzen and Stern 1998).

Selection surfaces were computed using nonparametric cubic-spline regression (Schluter 1988; Schluter and Nychka 1994). This method makes no a priori assumptions about data distributions. To find the best-fit cubic spline, we searched a range of possible smoothing parameters (λ) to find the value of λ that minimized the generalized cross validation (GCV) score. We then used this λ to plot the best-fit cubic spline to survival data. Figures show datapoints intermediate between zero and one. These values are the estimated (y-hats) values of survival that were calculated from jackknife analyses (Schluter 1988; Schluter and Nychka 1994).

HERITABILITY AND PATERNITY ANALYSES

We estimated r_{MF} of body size and limb-length using all four parent–offspring regressions (i.e., father–daughter, mother–son, mother–daughter, father–son). We used mean values for progeny morphology (standardized by year) and performed weighted least squares regression against standardized parent morphology (by year) with family sizes as weights. Although the use of restricted maximum likelihood methods (REML) for estimating variance components has increased in recent years, its application is limited here (Lynch and Walsh 1998) by several characteristics of our data. First, females lay one egg per clutch and this limits the replication of sires that is needed for nested analyses of variance (ANOVA). Second, the relationship between sires and their daughters was negative (see Results) and negative variance components cannot be measured using REML (Lynch and Walsh 1998). Generally, sire-offspring regressions provide reliable estimates of trait heritability, as these are free from maternal effects. To provide additional support for our estimates of heritability, we verified the significance of these regressions with 1000 randomizations of the sire-offspring regressions. Significance values were computed as the fraction of iterations in which the randomized correlation was

at least as strong as that observed in our data. r_{MF} was calculated following (Bonduriansky and Rowe 2005) as:

$$r_{MF} = \sqrt{\frac{h_{FD}^2 \cdot h_{MS}^2}{h_{MD}^2 \cdot h_{FS}^2}},$$

where subscripts represent heritability estimates from Father–Daughter (FD), Mother–Son (MS), Mother–Daughter (MD) and Father–Son (FS) respectively. Because this quantity is derived from the ratio of inter- to intrasexual heritability, it is predicted to decrease as selection acts to reduce the costs of intralocus sexual conflict (Fisher 1930; Lande 1980; Bonduriansky and Rowe 2005). We predicted significant correlations only between parents and their same-sex progeny.

We tested whether the sex of F1 progeny produced by field-caught females depended on sire body size using multivariate ANOVA, with sire size nested within females and the dependent variables "numbers of sons and daughters." In 2005, we used controlled mating in the laboratory and tested the same hypothesis as above. We performed an additional test using a generalized linear model with a logit link function to account for binomial error variance in the dependent variable "progeny sex." We note that this is not an analysis of sex ratio biasing, but rather a test of how females allocate progeny gender based on sire size.

Results

CORRELATIONS BETWEEN PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS

Raw values of stamina, and of swelling in response to PHA (immune response), were both significantly dependent on body size (SVL) (ANOVA; immune swelling: $r^2 = 0.293$, $F_{1,78} = 32.31$, $P < 0.0001$; stamina: $r^2 = 0.29$, $F_{1,125} = 51.07$, $P < 0.0001$).

Males and females significantly differed in body size in the field (ANOVA, $F_{1,131} = 322.97$, $P < 0.0001$; $\bar{X}_{males} = 55.16$ mm ± 4.88 and $\bar{X}_{females} = 42.76$ mm ± 2.89). Immune response varied with body size in the field (males $r^2 = 0.13$, $F_{1,226} = 5.88$, $P < 0.0001$; quadratic effect $F = 0.02$, $P = 0.88$, Fig. 1A, females: $r^2 = 0.04$, $F_{1,108} = 4.74$, $P = 0.03$, quadratic effect $F_{1,107} = 2.57$, $P = 0.01$, Fig. 1B) and these relationships were significantly different (sex $\times$ SVL^2 $F = 2.19$, $P = 0.03$). Similarly, stamina varied with body size, but only in males (males: $r^2 = 0.002$, $F_{1,205} = 0.41$, $P = 0.52$, quadratic effect $F_{1,204} = -2.76$, $P = 0.006$, Fig. 1C, females: $r^2 = 0.003$, $F_{1,193} = 0.59$, $P = 0.44$, Fig. 1D). The difference in the relationship between the sexes was not significant (sex $\times$ SVL ANCOVA $F = -1.78$, $P = 0.09$).

We detected similar, although not identical, relationships between traits correlated with body size in the laboratory. Both immune function and stamina varied with body size in the laboratory, and these relationships also differed between the
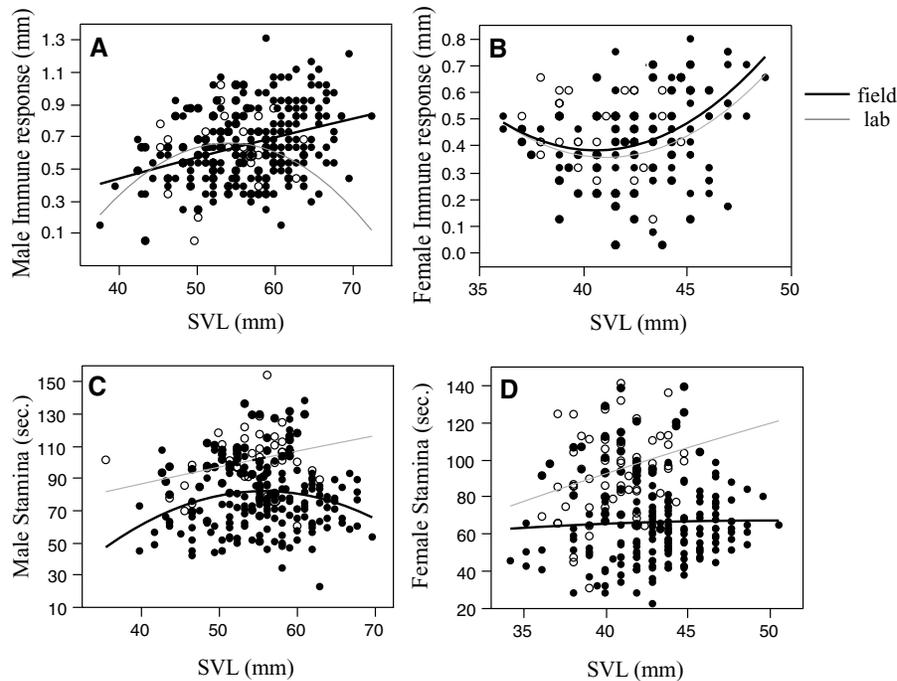
Figure 1. Negative intersexual correlations in three components of fitness are consistent with the interpretation that conflict genes have antagonistic fitness effects in males and females. Males of intermediate and large size had the highest response to PHA (immune function) (A) but females of intermediate size had the lowest response (B). Body size and stamina were positively correlated in both males and females (C and D) but the slope of this relationship was significantly greater for females than males resulting in a significant sex × body size interaction ($P < 0.0035$; note the difference in scale on the x-axes to accommodate sexual size dimorphism). Physiological measures are based on 76 male and 84 female progeny in the laboratory (light line, open symbols). Field measures (heavy line, filled symbols) of immune function were based on 113 females and 231 males, and measures of stamina were based on 200 females and 211 males. Model fits were compared by checking all possible model subsets and choosing parameters that minimized the Akaike information criterion score (AIC).

sexes. For example, males of intermediate size had the highest immune function (quadratic effect of SVL $F_{1,83} = 4.8$, $P = 0.03$ Fig. 1A), whereas females of intermediate size had the lowest immune function (quadratic effect of SVL $F_{1,92} = 4.8$, $P = 0.006$) and the difference between the sexes was significant (analysis of covariance [ANCOVA] sex × SVL, $F_{1,154} = 1.91$, $P < 0.05$; Fig. 1B). Stamina was positively related to body size in both sexes (e.g., males $r^2 = 0.08$, $P = 0.004$; females $r^2 = 0.08$, $P = 0.007$), and the slope of this relationship was significantly different between males and females (ANCOVA sex × SVL, $F_{1,183} = 8.81$, $P < 0.004$; 1C, D). All interaction effects remained significant following Bonferroni corrections for multiple comparisons.

Because stamina and immune swelling were both significantly correlated with body size, we corrected these measures for body size in all subsequent analyses by calculating the residuals from the regressions of stamina and immune swelling on SVL. All relevant analyses provided qualitatively similar results using raw and residual trait values.

SEX DIFFERENCES IN PHYSIOLOGICAL TRAITS AND IN SELECTION ON THOSE TRAITS IN THE FIELD

Stamina did not differ significantly between the sexes (ANOVA, $r^2 = 0.004$, $F_{1,125} = 0.55$, $P = 0.46$, $\bar{X}_{males} = 71.13$ sec. ± 17.14 and $\bar{X}_{females} = 53.20$ sec. ± 13.95). Immune function did not differ between the sexes either ($\bar{X}_{males} = 5.97$ mm. ± 2.26 and $\bar{X}_{females} = 3.72$ mm. ± 1.66), but was differently related to stamina between the sexes (ANOVA, $r^2 = 0.1355$; sex: $F_{1,70} = 0.04$, $P = 0.847$; stamina: $F_{1,70} = 0.21$, $P = 0.648$; sex × stamina: $F_{1,70} = 10.73$, $P = 0.0016$; Fig. 2). The traits were significantly related in both sexes but in opposite directions: the relationship between stamina and immune function was positive in females (ANOVA, $r^2 = 0.13$; $F_{1,35} = 5.27$, $P = 0.028$) but negative in males (ANOVA, $r^2 = 0.14$; $F_{1,35} = 5.61$, $P = 0.024$), suggesting a trade-off in males only (Stoehr and Kokko 2006) (Fig. 2).

We recaptured 50 of 220 females (23% survival) and 108 of 320 males (34% survival) during our fall censuses. Selection on body size was directional in females, favoring larger body size ($\beta = 0.33 \pm 0.13$; $\chi^2 = 7.03$, $P = 0.008$; Fig. 3), but was nearly
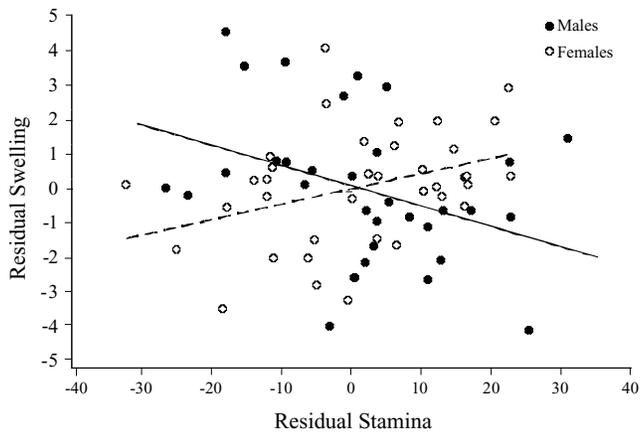
Figure 2. Mean values of stamina and immune swelling did not differ significantly between the sexes in the wild. However, we found a significant correlation between immune swelling and stamina that differed in males and females, such that immune swelling traded off with stamina in males, but the traits were positively correlated in females.

flat and nonsignificant in males ($\beta = 0.13 \pm 0.08$; $\chi^2 = 2.81, P = 0.09$; Fig. 3). The difference in selection on male and female body size was significant (Sex $\times$ SVL; $\chi^2 = 3.95, P = 0.04$). Selection on immune function was directional in females ($\beta = 0.45 \pm 0.15$ Wald $\chi^2 = 8.59, P = 0.003$ Fig. 3), as was selection on female stamina, although this result was not significant ($\beta = 0.260 \pm 0.15$ Wald $\chi^2 = 2.78, P = 0.09$). By contrast, although we did

not detect any significant linear component to selection on stamina ($\beta = 0.06 \pm 0.05$) or immune function ($\beta = 0.08 \pm 0.05$) in males, we measured significant quadratic selection on both traits. Natural selection was significant and stabilizing on immune function in males ($\gamma_{1,1} = -0.17 \pm 0.13$; Wald $\chi^2 = 4.13, P = 0.04$; Fig. 3) and was disruptive (although nonsignificantly) on stamina ($\gamma_{1,1} = 0.21 \pm 0.13$ Wald $\chi^2 = 2.33, P = 0.12$; Fig. 3), a result consistent with the observed trade-off in the two traits in males (Fig. 2). Differences in the form of natural selection were significant for both traits (sex $\times$ immune function $\chi^2 = 7.02, P = 0.008$; sex $\times$ stamina $\chi^2 = 3.62, P = 0.05$). Finally, we observed correlational selection acting on both traits together in males ($\gamma_{1,2} = -0.35 \pm 0.17$; Wald $\chi^2 = 3.76, P = 0.05$; Fig. 4A) but not females ($\gamma_{1,2} = 0.21 \pm 0.21$ Wald $\chi^2 = 0.77, P = 0.38$; Fig. 4B), a difference in the form of selection, which was itself significant (sex $\times$ immune function $\times$ stamina; $F_{1,90} = 4.34, P = 0.04$).

SEX-SPECIFIC CORRELATIONS BETWEEN PARENT AND OFFSPRING

In line with our predictions based on recent theory (Day and Bonduriasky 2004), measures of the heritability of body size (SVL) were only significant between parents and their same-sex progeny. We measured significant heritability of body size between sires and their sons ($h^2 = 1.02 \pm 0.29$; $F_{1,13} = 4.39, P = 0.05$; Fig. 5A), but we detected a nonsignificant negative genetic-correlation between sires and daughters (rG $= -0.62 \pm 0.20$; $F_{1,16} = 2.65$,
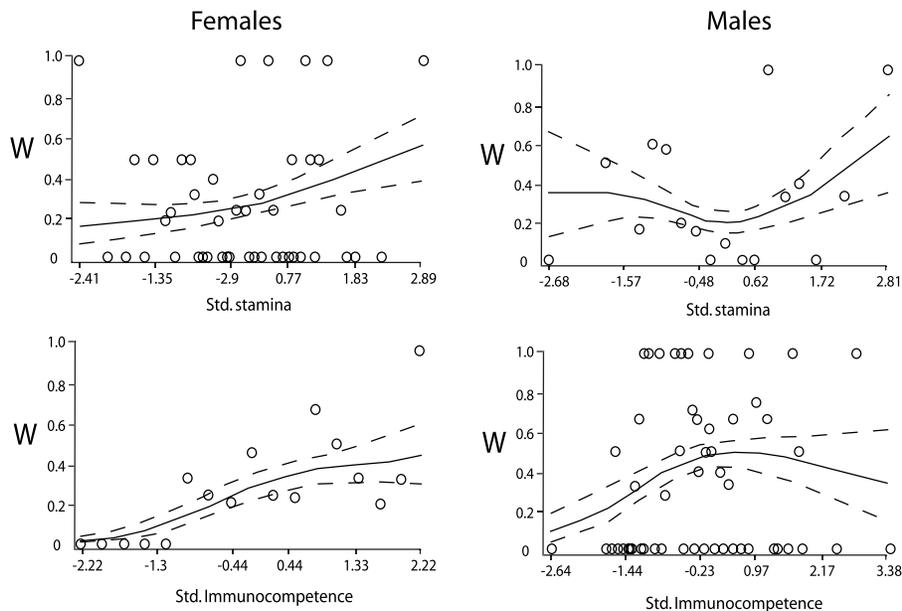

Figure 3. Sexually antagonistic selection on physiological performance traits showing relative fitness (W, probability of survival) as a function of stamina (top) and immunocompetence (bottom) in *A. sagrei* males and females. Traits were standardized to mean zero and unit variance within each sex. Fitness surfaces (solid lines) and 95% confidence intervals (dashed lines) are derived from nonparametric cubic-splines with 500 bootstrap replicates. Sex differences in the form of natural selection were significant for both stamina and immunocompetence.
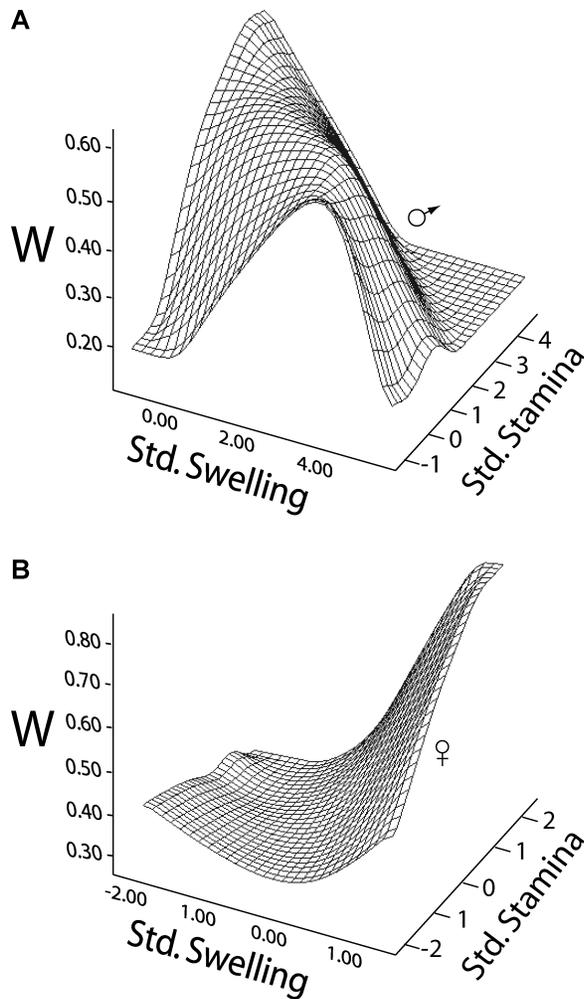
Figure 4. Fitness surfaces for males (A) and females (B) captured from our study population and censused four months later during 2005. Surfaces indicate a fitness trade-off between traits in males but not females. Fitness surfaces were estimated using nonparametric regression (Schluter and Nychka 1994), and are graphical representations of the correlational selection gradients reported in the text. W represents fitness (probability of survival to maturity) and datapoints were estimated by resampling using the cubic spline approach. Trait values were standardized (mean zero, unit standard deviation) prior to analysis.

$-0.73 \pm 0.13; F_{1,16} = 7.68, P < 0.01$). Limb heritability between dams and daughters showed a positive trend that was nearly significant ($F_{1,38} = 3.24; h^2 = 0.41 \pm 0.17 P = 0.08$) whereas the genetic correlation between dams and sons was nearly flat and not significant ($F_{1,32} = 2.24; rG = 0.62 \pm 0.32, P = 0.14$). All significant tests remained significant in randomization analyses (see methods, P-values ranging from 0.019–0.03). Because the sire-daughter estimate was negative (in both limb length and body size analyses), the quantity r_{MF} in our study would be an imaginary number with no biological relevance. For ease of interpretation, we set the negative relationship to zero and this in turn resulted in a value of zero for the quantity r_{MF}.

CRYPTIC FEMALE CHOICE

We also found support for the predictions of Chippindale et al. (2001) according to which females should use different sires to make sons and daughters. During 2004, promiscuous females were significantly more likely to produce sons with the sperm from larger sires and daughters with the sperm from smaller sires (ANOVA [pilai trace]: progeny sex × sire body-size, $F_{2,49} = 6.57$, $P < 0.003$; Fig. 6A). Our controlled breeding study during 2005 further supported these results, although the difference was only pronounced for daughters (ANOVA progeny sex × sire size, $F_{1,30} = 4.35, P = 0.045$; Fig. 6B). An alternative interpretation for this result is that gender allocation arises through a sire effect. If motility or abundance of X or Y sperm was body-size dependent, then large and small sire body size would influence progeny gender. Two predictions that would follow from this alternative, are that sex ratios produced by monogamous females should vary as a function of sire body size and that sex ratios produced by individual males should be biased. However, neither of these predictions was supported by our data. Large and small sires did not produce biased sex ratios (ANOVA $F_{1,29} = 0.35, P = 0.55$), nor did monogamous females bias progeny gender as a function of sire size (linear regression sex ratio vs. sire SVL; $r^2 = 0.0002, P = 0.98$ based on $N = 175$ progeny from 25 monogamous dams). Thus, progeny gender allocation appears to be under maternal control and further, may depend on having some means of comparing relative sire size (see below).

We tested whether females mated to males of disparate size were more likely to make nonrandom choices concerning progeny gender assignment than females mated to multiple males more similar in size. We scored the female's choice as "1" or "0" depending on whether her sons were sired by large and small males respectively and whether her daughters were sired by small and large males respectively (i.e., whether the female's choice was congruent with our predictions based on the observed sexual conflict). We tested the binomial dependent variable against male size using multiple logistic regression. Females were more likely to make the predicted decision of progeny gender assignment with
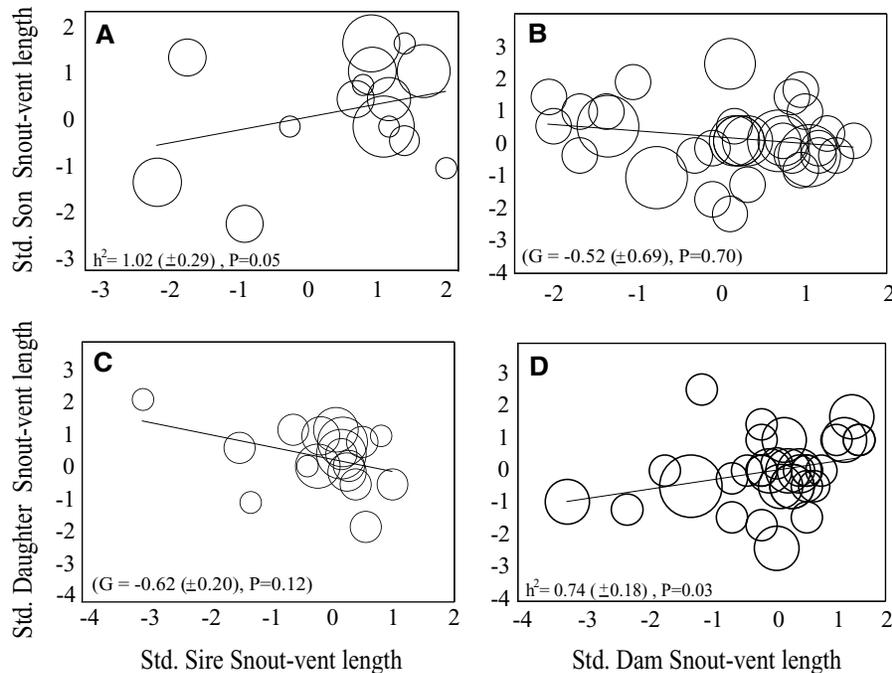
$P < 0.12$; Fig. 5B). Similarly, heritability of body size between dams and daughters showed a significant positive relationship ($h^2 = 0.74 \pm 0.18; F_{1,38} = 4.63, P = 0.04$; Fig. 5C) whereas the genetic correlation between dams and sons was negative and not significant (rG $= -0.52 \pm 0.69; F_{1,32} = 0.36, P = 0.37$; Fig. 5D).

We found similar patterns using limb length, a trait that has repeatedly proven seminal in studies of performance in anoles (Irschick et al. 2005; Losos et al. 1997). We measured significant heritability of limb length (data not shown) between sires and their sons ($h^2 = 0.78 \pm 0.13; F_{1,13} = 9.25, P < 0.01$), but again found a negative genetic correlation between sires and daughters (rG $=$

Figure 5. Consistent with predictions from sexual conflict theory, we found evidence for (A) Positive heritability (sire-son); (B) negative genetic correlation (sire-daughter); (C) zero heritability (dam-son); and (D) Positive heritability (mother–daughter) in body size in the laboratory. Trait values were standardized to mean zero with unit variance prior to analysis. Changing sign in the relationship between opposite sex parents and offspring resulted in a value of 0 for r_{MF}. Points represent mean values for 104 progeny from 17 sires and 39 dams in the weighted least squares regression, and point sizes are proportional to the number of progeny in each family.

increasing difference in the size of males with which the female mated (Δsire snout-vent-length $\chi^2 = 4.56$, $P = 0.03$ based on $N = 101$ progeny from 19 promiscuous dams and to which we could assign sires).

Discussion

We have demonstrated several important elements of sexual antagonism in *A. sagrei* from the Bahamas. First, we have shown correlations between stamina, immune function, and body size, and that these correlations differ in sign between the sexes in both the field and the laboratory. Second, we have shown that these traits are subject to sex-specific forms of natural selection in the wild. Third, we have demonstrated the sex-specific heritability of body size in the laboratory, a trait which, as noted above, was correlated with both stamina and immune function. Given that all of the traits we measured showed negative intersexual correlations, females face potential intralocus sexual conflict. In this situation, we would theoretically expect randomly mating females to produce a higher frequency of progeny with low-fitness trait combinations relative to progeny produced by choosey females. Consistent with this hypothesis, we found that females that mated with both large and small males sorted sperm and produced sons more often with the sperm from large sires and daughters more

often with the sperm from smaller sires, potentially circumventing the conflict. Finally, results show that a female's ability to make this differential progeny gender allocation increased with increasing disparity in sire size.

Recent theoretical findings (Day and Bonduriansky 2004; Bonduriansky and Rowe 2005) propose that sexual dimorphism is the result of alternative fitness optima between the sexes. In a result consistent with this hypothesis regarding intralocus sexual conflict (Day and Bonduriansky 2004; Bonduriansky and Rowe 2005), we found that two physiological traits, stamina and immune function, were differently correlated between the sexes. Stamina is likely to be especially important for fitness in males as it may play a seminal role in territory defense (Sinervo et al. 2000). In addition, selection on locomotor performance is stronger on males than females (Calsbeek and Irschick 2007) because the sexes use different regions of the habitat (Butler and Losos 2002; Butler et al. 2007), with males perching higher and in more complex vegetation than females (Calsbeek and Irschick 2007). Although the nature of the immune response elicited by PHA is complex and hence difficult to interpret here (Kennedy and Nager 2006; Martin et al. 2006), it nevertheless remains useful for investigating differences between groups, independently of whether it is better to exhibit a larger or smaller immune swelling. Immune function is likely to also be a fitness-related trait in lizards in
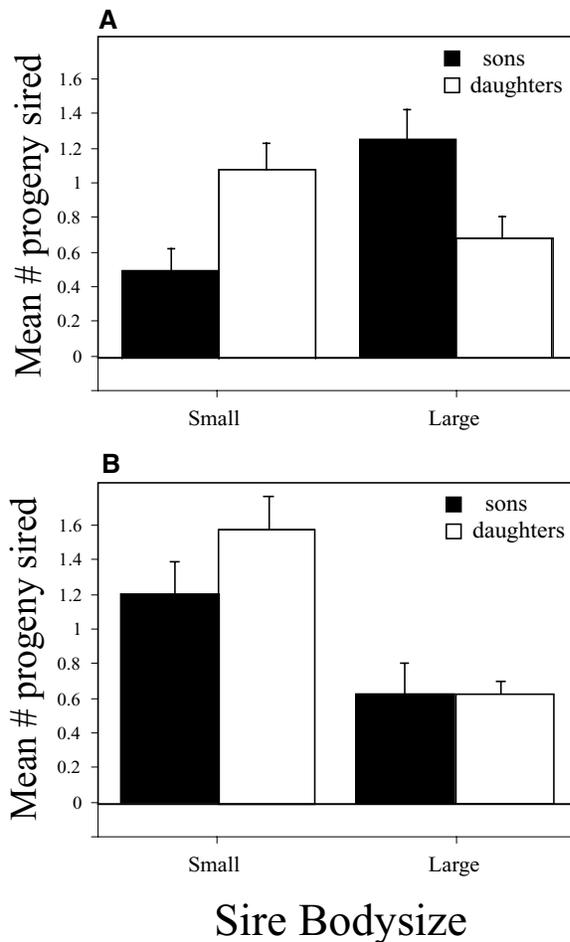
Figure 6. Results from multivariate ANOVA with the numbers of sons and daughters as dependent variables and sire body size nested within females as the independent variable. (A) Wild-caught female *Anolis sagrei* made significantly more sons with the sperm form larger sires, and more daughters with the sperm from smaller sires. (B) Results were similar in controlled laboratory matings in which females mated with one large and one small male, although the pattern was stronger in daughters than sons. Histogram bars show mean values ($\pm$ SE).

the Bahamas because they are challenged with ectoparasites (e.g., ticks) and blood-borne pathogens including malaria (Bonneaud et al., unpubl. data). The sex differences in investment in immunity displayed in our system corroborate the hypothesis that females should invest more in immune function than males (Rolff 2002), given that female fitness is more likely linked to longevity than is male fitness (Stoehr and Kokko 2006).

Negative intersexual correlations in fitness-related traits provide strong evidence for sexual conflict (Merila et al. 1997; Chippindale et al. 2001; Pai and Yan 2002; Gehring et al. 2004; Fedorka and Zuk 2005; Parker 2006) and indeed, results based on our viability studies suggest that these traits can have different selective optima between the sexes. Several recent studies have shown that

traits expressed in both sexes and having a common genetic basis may generate alternative fitness optima for those traits, leading to antagonistic selection between the sexes (Chippindale et al. 2001; Rice and Chippindale 2001; Parker 2006). Theoretical work (Day and Bondurianksy 2004) has suggested that selection should therefore favor reduced expression of the between-sex component of trait heritability (e.g., father–daughter or mother–son) to mitigate this intralocus sexual conflict. Our results largely support these ideas by providing empirical support from the wild.

One caveat to consider here is that our study of selection was conducted in a single year. Some nonsignificant patterns in our data may therefore be partially explained by our power to resolve selection. Interannual variation in the strength and forms of selection could also alter the importance of different traits to fitness, and would thereby change the nature of sexual conflict working in the system. We do not yet know the impact of such changes in either the short or long term. However, lack of predictability in the action of selection has been well documented in other systems (Grant and Grant 2002, 2006), and underscores the importance of ecological variation among years in maintaining phenotypic variation within populations. This has at least two important implications for our study. First, if changing ecological conditions alter adaptive landscapes, then females might allocate sperm differently in different years. Second, interannual variation in selection should provide at least a partial explanation for the maintenance of a broad range of phenotypes within our study populations. Nevertheless, as has been shown in previous studies (e.g., Darwin's finches above), interannual variation in selection pressure does not preclude adaptive trait evolution.

Trunk ground anoles are sexually dimorphic in body size both in general (Butler et al. 2000) as well as specifically in our study populations, where male body size is both larger and more variable compared with females (Calsbeek and Irschick 2007; Calsbeek and Smith 2007). In this study, we found significant heritability of male body size and limb length, but null or even negative correlations between sires and daughters, indicating that large sires produced large sons but not large daughters, whereas small sires produce small sons but not small daughters. What could cause the unusual pattern of changing sign of the genetic correlations between opposite sex parents? One explanation at the proximate level is genomic imprinting (Reik et al. 2001; Reik and Walter 2001; Wilkins and Haig 2003), a process by which alleles retain a "memory" of the parent from which they were inherited. For example, when inherited from the father, alleles in mice can increase nutrient uptake at the mother's expense, but these same alleles are silenced when inherited through the mother (Ferguson-Smith and Surani 2001). The evolution of genomic imprinting is thought to have been favored when multiple males sire the offspring of one female (Haig 1997, 1999). Although the precise mechanisms leading to the expression of a single parental allele are not fully

understood, it probably involves epigenetic modifications such as DNA methylation (Mochizuki et al. 1996; Klose and Bird 2006) and is one possible mechanism for the patterns reported here. Ultimately, the reduced intersexual correlations in traits subject to strong sexual selection are consistent with the theory proposed by Day and Bonduriansky (2004). Reduced heritability through the opposite sex parent is the adaptive outcome of selection for alternative fitness optima between males and females.

Chippindale et al. (2001) suggested that to mitigate the influence of sexual conflict in *Drosophila*, females should select different sires for the production of sons and daughters. We found that, in both the field and the laboratory, female *A. sagrei* mated with large and small males, but produced mostly sons with the sperm from large sires and mostly daughters with the sperm from smaller sires. Given the curious nature of parent/offspring size relationships, females that differentially allocate sperm from large and small sires would often produce large sons with high stamina but low immune function and daughters with higher stamina and higher immune function. Our data on natural selection suggest that these character combinations are indeed likely to be adaptive. For example, stamina may reflect whole-animal physiological vigor (Arnold 1983) and is likely to be important for males in that it aids in prolonged territory defense (Sinervo et al. 2000; Miles et al. 2001; Perry et al. 2004). Trade-offs with other traits could also explain selection on immune function or stamina (Svensson et al. 2001) and the phenotypic correlations and selection results both suggest that such trade-offs may favor stamina over immune function in males but not in females, a result that may be general across taxa (Rolff 2002; Stoehr and Kokko 2006).

Although we do not yet understand the proximate mechanism by which females sort sperm from alternative sires into sons and daughters, it appears that females require multiple mates to make decisions regarding progeny gender allocation (recall the result that monogamous females do not bias sex ratios but that progeny sex allocation becomes more pronounced with larger differences in relative male body size). Just as body size is a continuous trait, variation in the expression of intralocus sexual conflict should also be continuous. Under these circumstances, females would only be capable of making decisions based on the relative difference in sire size (Calsbeek and Sinervo 2004) and the greater the disparity in relative male body size, the greater the female's ability to sort sperm adaptively. Although further work is needed, this idea is supported by our data showing that the accuracy of female gender manipulation increases with the difference in sire size. Irrespective of the mechanism, the evolution of fertilization biasing could provide females a means of partially reducing the costs of sexual conflict (Parker 2006). This is because females that sort sperm enhance fitness by using male-benefit genes to produce sons and female-benefit genes to produce daughters.

An alternative interpretation of the pattern of sperm sorting is that gender biasing arises from a sire effect in which large and small males produce more viable and/or motile Y and X sperm respectively (Wilkinson et al. 1998). However, results from controlled monogamous mating in the laboratory do not support this alternative; sex ratios of 175 progeny from 25 dams were not related to sire body size when females mated with a single sire. Sex determination has not been well characterized in this group, although some cytogenetic evidence suggests an XY mode of inheritance (i.e., male heterogamety). In addition, unpublished pilot studies in our laboratory do not indicate any effect of environment, such as temperature, on sex determination (although the subtly different pattern of gender assignment from the laboratory suggests that environmental cues could play a role in choices made by the female). Thus, the more parsimonious interpretation of these patterns is that progeny gender biasing arises by cryptic female choice.

Traditional definitions of sexual conflict propose that sexually antagonistic traits increase the fitness of one sex at the expense of the other (Trivers and Willard 1973; Chippindale et al. 2001; Rice and Chippindale 2001; Parker 2006). In *A. sagrei*, male body size is a naturally and sexually selected cue that can be exploited by females to partially mitigate intralocus sexual conflict, and promiscuous females that capitalize on this signal reduce the reproductive success of males by distributing paternity of several sires across her eggs. This process is subtly different from other forms of conflict, in that male body size per se may not result in large costs for females. Rather, by signaling to the female whether they carry alleles for high-quality sons or daughters, large and small males become victims of their own sexually selected traits. The question remains however, whether direct fitness costs of lost paternity may be partially compensated by indirect fitness gains through the production of high-quality sons or daughters, or by the subsequent viability benefits arising from divergent morphologies in alternative habitats (Calsbeek and Irschick 2007). The net fitness consequences of fertilization biasing to males may be a novel example of "winning by losing" (Eberhard 2005), if for example, sons have more than twice the fitness when sired by larger compared with smaller sires.

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