PATERNAL CONDITION DRIVES PROGENY SEX-RATIO BIAS IN A LIZARD THAT LACKS PARENTAL CARE

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Sex-allocation theory predicts that females in good condition should preferentially produce offspring of the sex that benefits the most from an increase in maternal investment. However, it is generally assumed that the condition of the sire has little effect on progeny sex ratio, particularly in species that lack parental care. We used a controlled breeding experiment and molecular paternity analyses to examine the effects of both maternal and paternal condition on progeny sex ratio and progeny fitness in the brown anole (*Anolis sagrei*), a polygynous lizard that lacks parental care. Contrary to the predictions of sex-allocation theory, we found no relationship between maternal condition and progeny sex ratio. By contrast, progeny sex ratio shifted dramatically from female-biased to male-biased as paternal condition increased. This pattern was driven entirely by an increase in the production of sons as paternal condition improved. Despite strong natural selection favoring large size and high condition in both sons and daughters, we found no evidence that progeny survival was related to paternal condition. Our results emphasize the importance of considering the paternal phenotype in studies of sex allocation and highlight the need for further research into the pathways that link paternal condition to progeny fitness.

In their landmark paper on adaptive sex allocation, Trivers and Willard (1973) hypothesized that mothers in a good physiological condition should bias the sex ratio of their progeny in favor of the sex that provides the greatest relative fitness return for a given increase in maternal investment. This influential idea has sparked numerous theoretical extensions and empirical tests in what has become one of the most active research areas in evolutionary biology (Burley 1982; Charnov 1982; Frank 1990; Godfray and Werren 1996; Leimar 1996; Hardy 2002; Komdeur and Pen 2002; Wapstra et al. 2007; West 2009). Indeed, Carranza (2002) speculated that "probably no other case exists in behavioral ecology where a couple of pages have sired so many studies." Despite this substantial body of subsequent research, the generality of the Trivers–Willard hypothesis remains largely uncertain outside of mammals (Brown 2001; Cameron 2004; Sheldon and West 2004), whose high levels of maternal investment provided the original template for the theory (Trivers and Willard 1973). However, the underlying assumption that progeny sex ratio can be altered in response to environmental stimuli has been verified in a variety of organisms, many of which lack extensive parental care (Charnov 1982; Hardy 2002; West and Sheldon 2002; Wapstra et al. 2007; West 2009).

The original Trivers–Willard (1973) hypothesis was tailored to the mating system and reproductive biology of caribou (i.e., polygyny, single offspring per reproductive episode, extensive post-partum maternal investment). Under these conditions, Trivers and Willard predicted that mothers in a good condition should preferentially produce sons. This specific prediction was

based on three assumptions: mothers in a good condition produce offspring in a good condition, offspring in a good condition become adults in a good condition, and differences in adult condition have a greater impact on the reproductive success of males than of females. This final assumption is derived from the observation that, for most polygynous species, reproductive success is more skewed among males than among females (Andersson 1994). Thus, differences in relative fitness are predicted to be greater between high- and low-condition males than between high- and low-condition females, and mothers in a good condition should therefore invest preferentially in sons. These assumptions are realistic for many polygynous mammals, and recent meta-analyses have found general support for the Trivers–Willard hypothesis in this group (Cameron 2004; Sheldon and West 2004).

Much of the significance of the Trivers–Willard hypothesis stems from the fact that its basic argument provides a very general theory for sex allocation that can be extended beyond its specific predictions for polygynous mammals (Charnov 1982; West 2009). For example, if daughters benefit more from increased maternal investment than do sons, then predictions about adaptive sex ratios are reversed. Likewise, if factors other than maternal condition differentially influence the fitness of sons and daughters, then females should bias the sex ratio in light of these additional factors. This generality is important when considering species that deviate from the original mammalian template envisioned by Trivers and Willard (1973). For example, in most lizards, maternal investment is restricted to the initial provisioning of the egg or embryo (Wapstra et al. 2007). Moreover, because many lizards produce multiple offspring per clutch or reproductive season, maternal investment strategies often involve trade-offs between offspring quality and offspring quantity (Sinervo et al. 2000). If mothers in good condition preferentially increase offspring quantity rather than offspring quality, then the original assumptions of the Trivers–Willard hypothesis may not apply. Perhaps consequently, those few studies that have tested the Trivers–Willard hypothesis in lizards have generated mixed results (Fox and McCoy 2000; Olsson and Shine 2001; Lovern and Passek 2002; Uller et al. 2006; Warner et al. 2007). It is therefore important to test not only the effect of maternal condition on progeny sex ratio, but also the underlying assumptions that maternal condition influences progeny phenotypes, and that maternal condition differentially influences the relative fitness of sons and daughters.

Although the original Trivers–Willard hypothesis focused on maternal condition, paternal condition can also influence sex allocation if fathers in good condition are better able to provision their offspring (e.g., Korpimaki et al. 2000). Paternal condition could also influence sex allocation by signaling other direct (e.g., high-quality territory) or indirect (i.e., "good genes") benefits of mating with high-condition males, provided these benefits differentially influence the fitness of sons and daughters. Indeed,

females of many species bias progeny sex allocation on the basis of phenotypic indicators of paternal quality, such as coloration, ornamentation, and body size (Ellegren et al. 1996; Svensson and Nilsson 1996; Kolliker et al. 1999; Sheldon et al. 1999; Calsbeek and Sinervo 2002; West and Sheldon 2002; Olsson et al. 2005; Roed et al. 2007). However, sex-allocation studies have generally neglected the possibility that females select for indirect genetic benefits on the basis of male condition per se (Roed et al. 2007).

In this study, we simultaneously examined the effects of both maternal and paternal condition on progeny sex ratio in the brown anole (*Anolis sagrei*), an oviparous lizard that lacks parental investment beyond the initial provisioning of the egg. Brown anoles are ideally suited for such a test because they are thought to posses a mechanism for biasing progeny sex ratio on the basis of sire phenotypes (Calsbeek and Bonneaud 2008; Cox and Calsbeek 2010). Moreover, the polygynous mating system, female-biased adult sex ratio, and extreme male-biased sexual size dimorphism of this species indicate that reproductive success is more highly skewed among males than among females, as assumed by the Trivers–Willard hypothesis. We therefore predicted that progeny sex ratio should become increasingly male-biased as both maternal and paternal condition increase. We also tested for maternal and paternal effects on sons and daughters by examining correlations between parental condition and progeny phenotypes. Finally, we tested the actual fitness consequences of progeny sex allocation by tracking the survival of sons and daughters and examining their fitness as a function of both maternal and paternal condition. We predicted that any conditional bias in sex ratio would be accompanied by an increase in the relative fitness of that sex that was preferentially produced by dams or sires in good condition.

Materials and Methods
BREEDING DESIGN

We raised sires and dams in a laboratory common-garden to minimize nongenetic variation in body size. Sires and dams were hatched from eggs laid in captivity by an initial stock of 69 females collected from Great Exuma, The Bahamas (23°30′N, 75°45′W). A subset of dams was captured from this population as adults and maintained in captivity for over three months until they depleted any stored sperm (Calsbeek et al. 2007; Calsbeek and Bonneaud 2008). Our results did not differ with respect to the inclusion or exclusion of these dams. We fed all animals an ad libitum diet of fruit flies (*Drosophila,* for hatchlings) and crickets (*Acheta,* for juveniles and adults). Food was dusted weekly with vitamin and mineral supplements (Repta-Vitamin, Fluker Farms, Port Allen, LA). Adults were housed individually in 10-gal glass terraria placed under a 40-W incandescent bulb in a reflective hood for heat (diurnal temperature range = 26–35°C) and two Repti Glo

5.0 full-spectrum fluorescent bulbs for ultraviolet radiation (5% UVB, Hagen, Montreal).

Brown anoles store sperm for several months and repeatedly lay single eggs at ca. 11-day intervals (Calsbeek et al. 2007; Calsbeek and Bonneaud 2008). In our colony, a single bout of mating can result in the production of up to 16 successive progeny over a three-month period (Fig. S1). We provided each captive dam with two potential mates that were matched for age but paired randomly with respect to body condition. This paired mating design was implemented as a part of a separate study investigating mate choice as a function of male body size (Cox and Calsbeek 2010). However, this design also allowed us to approximate the natural reproductive biology of the species, as most wild female anoles produce offspring by more than one sire (Calsbeek and Bonneaud 2008). We allowed dams to assess both males together for two days and then permitted each male to mate exclusively with the dam for one week to minimize the influence of direct male–male interactions on mating success. We also allowed each male to mate with two dams, once as the first and once as the second male, thus controlling for potential effects of mating precedence on fertilization success.

We allowed dams to oviposit in potted plants within their cages and left the eggs undisturbed until hatching. In previous studies, we found that this method resulted in higher hatching success than did the removal and relocation of eggs to standardized incubation conditions. All potted plants were connected to a central, automated watering system and placed directly beneath a 40-W incandescent bulb. Hence, incubation conditions were standardized across cages. We identified the sex of each hatchling on the basis of enlarged postanal scales (present only in males) and dorsal color pattern (females express a dorsal pattern polymorphism that is absent in males; Calsbeek et al. 2010). These sexing methods have proven completely accurate over six years of captive breeding involving thousands of individual hatchlings (Calsbeek and Bonneaud 2008; Cox et al. 2009).

PATERNITY ANALYSES

We collected tissue samples (2-mm, tail tip) from all progeny, dams, and candidate sires and then genotyped each individual at six microsatellite loci: AAGG-38, AAAG-70, AAAG-76, AAAG-91, AAAG-94, and AAAG-95 (Bardeleben et al. 2004). We performed PCR at a total volume of 10 μL with 1 μL template DNA, 1$\times$ GeneAmp PCR Buffer II (Applied Biosystems, Carlsbad, CA), 1.5 or 2.0 mM $MgCl_2$ (Table S1), 0.4 mM dNTPs, 0.25 μM of each primer (forward and reverse), and 0.3 U of *Taq* polymerase. PCR cycles consisted of an initial denaturation step at 94°C for 5 min followed by 29 or 35 cycles of 45 sec at 94°C (Table S1), 1 min at primer-specific annealing temperatures (T_a, Table S1), and 1 min at 72°C, followed by a final extension for 5 min at 72°C. All PCRs were performed on a DNAEngine Thermal

Cycler (Bio Rad Laboratories, Hercules, CA). Loci were pooled for genotyping (Table S1) on an ABI3100 Genetic Analyzer (Applied Biosystems) and all genotypes were scored by visual inspection using GeneMapper software against a GeneScan 500 LIZ size standard (Applied Biosystems).

We collected a total of 133 sons and 119 daughters. Because dams were housed individually, maternity was known with certainty for all of these offspring. We assigned paternity using the software package CERVUS (Marshall et al. 1998) following methods reported elsewhere (Calsbeek and Bonneaud 2008). A total of 24 tissue samples from hatchlings, four samples from dams, and 10 samples from potential sires were either lost or failed to amplify at most loci. Consequently, paternity could only be confidently assigned to 110 sons (83%) and 101 daughters (85%).

SEX RATIO AND PARENTAL CONDITION

Prior to mating trails, we measured snout-vent length (SVL, nearest millimeter) and body mass (nearest 0.01 g) for all dams and sires. We measured dams prior to the onset of reproduction to avoid confounding their reproductive state (i.e., gravid or not) with their estimated body condition. Although it would be ideal to have a separate measure of maternal condition at the time each subsequent egg was fertilized, we deemed it impractical and potentially stressful to continually palpate females to document their frequent transitions in reproductive condition. We calculated body condition using residuals from the regression of $\log_{10}$ body mass on $\log_{10}$ SVL for all dams and potential sires included in the study, with separate regressions for each sex. We confirmed that this measure of body condition is correlated with the wet mass of abdominal fat bodies (i.e., stored energy) in a separate study of dissected females ($r^2 = 0.35$; $n = 28$; $P < 0.001$). For analysis, we treated body condition as a continuous variable. However, for graphical convenience, we also categorized body condition as "poor" (<0.5 SD), "average" (±0.5 SD), or "good" (>0.5 SD) relative to the population mean for each sex. Similar statistical results were obtained regardless of whether condition was treated as continuous or categorical.

We analyzed patterns of progeny sex allocation by treating each sire ($n = 59$) or dam ($n = 67$) that produced progeny as an observation and summing his or her total progeny across both potential mates. We calculated sex ratio as the proportion of sons to total progeny and tested for effects of maternal or paternal condition on sex ratio using generalized linear models (GLMs) with logit links and binomial error distributions, following procedures advocated by Wilson and Hardy (2002). The ratio of Pearson's χ^2 to residual degrees of freedom never differed significantly from 1 ($P > 0.05$), so we did not scale for overdispersion (Wilson and Hardy 2002). We conducted these analyses in two different ways. First, because the precision of an estimate of sex ratio increases with the number of offspring contributing to that estimate, we

weighted sex ratios by the number of progeny contributing to each estimate. This is particularly useful in situations such as ours, where many sires and dams produced only a few progeny and were thus prone to extreme sex ratios (Fig. S1). Second, we conducted similar analyses using unweighted estimates of sex ratio. These two weighting schemes always yielded similar results (see Results).

To determine whether observed patterns of sex-ratio bias were driven by the differential production of sons versus daughters, we analyzed the total number of sons or daughters, rather than the proportion of sons, as a response variable for each dam or sire. We did this by regressing the number of sons or daughters against maternal or paternal condition using GLMs with log links and Poisson error distributions. We also tested for interactions between maternal and paternal condition by constructing similar GLMs using each sire–dam pair ($n = 81$) as an observation. Interactions between maternal and paternal condition were never significant ($P > 0.38$ for all analyses) and main effects of maternal and paternal condition were qualitatively identical to those observed when treating each sire or dam as an observation. Thus, we focus on results obtained using each individual sire or dam as an observation.

Our calculation of a single sex ratio based on all of the sequential progeny produced by a dam assumes that these individual fertilization decisions are all related to her condition at the time of mating. As an alternative, we also tested whether the sex of the first offspring that each dam produced was related to her condition at the beginning of the reproductive season. We did this using GLM with a logit link and binomial error distribution. This analysis is robust to any error due to changes in maternal condition that could influence subsequent allocation decisions.

PROGENY PHENOTYPES AND PARENTAL CONDITION
We tested for effects of parental condition on progeny phenotypes by regressing SVL, body mass, and body condition (residuals of $\log_{10}$ body mass on $\log_{10}$ SVL) against maternal or paternal condition. These measurements were collected for all progeny at hatching. To avoid statistical nonindependence of datapoints, we calculated a single mean value for all of the sons or daughters of a given sire or dam and weighted these means by the number of progeny contributing to the estimate.

NATURAL SELECTION ON PROGENY PHENOTYPES
We released 62 sons and 54 daughters from our breeding experiment onto a small island of natural habitat in The Bahamas (23°30′N, 75°45′W) in September of 2008. Prior to release, we permanently marked each hatchling with a unique toe clip. We recaptured surviving progeny eight months later (May 2009), at which point they were approaching sexual maturity. The use of an offshore island prevented dispersal, and the small size (431 m^2) of the island allowed us to search it thoroughly and capture nearly

every surviving lizard (Calsbeek and Smith 2007). We have previously reported analyses of natural selection on these progeny (Cox and Calsbeek 2010), but we now expand upon this original study by including new analyses in the context of parental condition, new multivariate selection gradients, new quadratic selection gradients, and new measures of selection on hatchling viability in captivity prior to release.

We quantified viability selection by regressing relative survival (0 or 1 divided by mean survival) on trait values standardized to the population mean in unit variance (Arnold and Wade 1984). We calculated relative survival and standardized trait values separately within each sex. We used SVL at release, mass at release, and condition at release as traits for these analyses. Because SVL and mass were highly correlated, we conducted separate selection analyses for each morphological trait to avoid problems of multicollinearity (Lande and Arnold 1983; Fairbairn and Reeve 2001). We included hatch date as a trait in each analysis so that we could estimate selection acting directly on morphological variation, rather than age. We calculated directional selection gradients from the partial regression coefficients of ordinary least squares regressions including a single morphological trait and hatch date (see Appendix S1). We estimated nonlinear selection gradients (i.e., stabilizing or disruptive selection) from separate regressions that included quadratic terms for the morphological trait and hatch date, as well as morphology × hatch date interactions. We calculated nonlinear selection gradients by doubling the regression coefficients and their standard errors for quadratic terms (Stinchcombe et al. 2008). We assessed statistical significance ($P < 0.05$) using logistic regression to account for the binomial distribution of survival (Janzen and Stern 1998). We inferred sex differences in selection from significant sex × trait interactions in these analyses. We used cubic splines (Schluter 1988) with binomial error distributions (live, die) to visualize fitness surfaces for each trait.

In addition to measuring natural selection in the wild, we also measured survival in captivity from hatching until release to the wild ($n = 90$ sons, 75 daughters). We estimated linear and quadratic selection gradients for SVL, body mass, and condition at hatching using methods identical to those described above, but substituting survival in captivity as the measure of fitness. The progeny that we released were maintained in captivity for a variable period (range: 7–90 days) prior to release and their probability of survival decreased with time spent in captivity ($\chi^2 = 9.87$; $P = 0.002$). Therefore, we tested for significant selection within each sex, and for differences in selection between sexes, using logistic regressions with hatch date as a covariate.

PROGENY FITNESS AND PARENTAL CONDITION
To assess progeny fitness as a function of maternal and paternal condition, we calculated a single mean probability of survival

for all of the sons or daughters produced by each individual sire or dam. We calculated these survival probabilities separately for hatchlings in captivity ($n = 165$ progeny, 48 dams, 32 sires) and for a subset of these progeny following their release to the wild ($n = 116$ progeny, 46 dams, 32 sires). Differences between these sample sizes and the larger samples reported for analyses of sex ratio ($n = 252$ progeny, 67 dams, 59 sires) occur because breeding trials were conducted in two rounds. Survival was not measured for progeny resulting from the second round of breeding trials.

We calculated relative fitness for each sire or dam by dividing the mean probabilities of survival for all their sons and all their daughters by the population mean measures of fitness for all sires or dams. We calculated relative fitness separately for sons and daughters so that we could directly compare the overall fitness payoffs of producing offspring of either sex. We then regressed the relative fitness of sons and daughters against parental condition, which was standardized in unit variance to the separate means for dams and sires. We tested for an adaptive function of sex-ratio bias by examining how relative fitness was influenced by the interaction between progeny sex and parental condition using GLMs with Poisson error distributions and log links. We weighted each sire or dam's estimate of relative fitness by the number of progeny contributing to that estimate and also conducted similar analyses using unweighted estimates. These two weighting schemes generally gave similar results (see Results).

We also assessed the adaptive significance of sex-ratio bias by measuring the growth of all surviving progeny from release (shortly after hatching) to recapture (near sexual maturity). We expressed growth as change in SVL and body mass and tested for effects of sex, maternal (or paternal) condition, and the interaction of sex × maternal (or paternal) condition using ordinary least squares regression.

Results
SEX RATIO AND PARENTAL CONDITION
At the population level, dams produced an approximately balanced sex ratio (133 sons, 119 daughters; $\chi^2 = 0.78$; $P = 0.38$). The total sex ratio produced by each dam was not related to her initial condition (weighted by total number of offspring: $\chi^2 = 0.27$; $P = 0.60$; unweighted: $\chi^2 = 0.01$; $P = 0.94$; Fig. 1), nor were dams in good condition more likely to produce a son as their first offspring ($\chi^2 = 0.20$; $P = 0.65$). By contrast, progeny sex ratio shifted markedly from female-biased to male-biased as paternal condition increased (weighted by total number of offspring: $\chi^2 = 8.82$; $P = 0.003$; unweighted: $\chi^2 = 6.04$; $P = 0.014$; Fig. 1). Analyzing the total number of sons sired by each male as the response variable revealed that this effect on progeny sex ratio was driven entirely by an increase in the production of sons as paternal
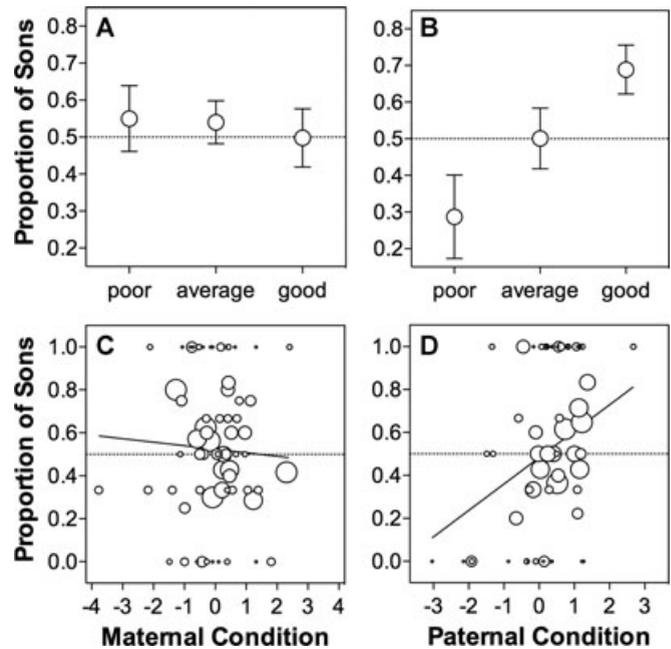

Figure 1. Progeny sex ratio did not vary as a function of maternal condition (left), but it increased sharply with paternal condition (right). Top panels report mean sex ratios (±1SE) as a function of condition, categorized as "poor" (<0.5 SD), "average" (±0.5 SD), or "good" (>0.5 SD) relative to the population means for each sex. Bottom panels report sex ratios for each individual dam or sire as a function of continuous variation in condition, expressed in units of SD relative to the means for each sex. Symbol size corresponds to the number of progeny produced by each dam or sire (range: 1–16). Ordinary least squares regressions are shown for illustrative purposes only. Significance tests were based on generalized linear models with logit links and binomial error distributions (see text).

condition improved ($\chi^2 = 8.19$; $P = 0.004$; Fig. 2). By contrast, the total number of daughters produced by each sire was unrelated to his condition ($\chi^2 = 0.02$; $P = 0.89$; Fig. 2). Maternal condition was unrelated to either the total number of sons ($\chi^2 = 0.22$; $P = 0.64$) or the total number of daughters ($\chi^2 = 0.80$; $P = 0.37$) produced by each dam (Fig. 2).

PARENTAL CONDITION AND PROGENY PHENOTYPES
We did not detect any associations between maternal condition and the SVL, mass, or condition of progeny at hatching (Table 1). Nor did we find any significant associations between paternal condition and most aspects of progeny phenotype (Table 1), with the exception of a very weak positive relationship between the body condition of sires and that of their daughters ($r^2 = 0.099$; $F_{1,30} = 3.28$; $P = 0.080$).

NATURAL SELECTION ON PROGENY PHENOTYPES
Hatchling survival in captivity was identical for sons and daughters (79%) and was positively correlated with mass and condition
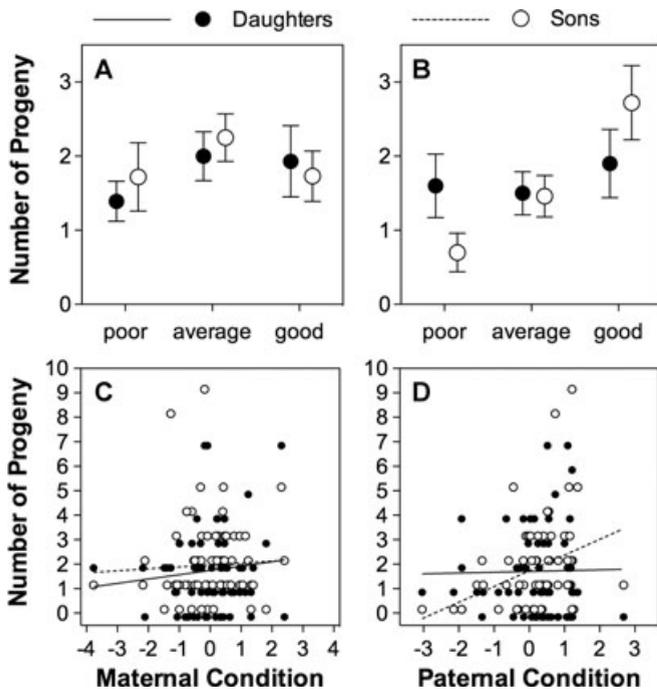
Figure 2. Production of sons and daughters was unrelated to maternal condition (left), but the production of sons increased with paternal condition (right). Top panels report mean numbers of progeny (±1SE) as a function of body condition, categorized as "poor" (<0.5 SD), "average" (±0.5 SD), or "good" (>0.5 SD) relative to the means for each sex. Bottom panels report the numbers of sons and daughters for each individual dam or sire as a function of continuous variation in condition, expressed in units of SD relative to the population means for each sex. For clarity, symbols for sons and daughters are vertically offset at each increment on the y-axis. Ordinary least-squares regressions are shown for illustrative purposes only. Significance tests were based on generalized linear models with log links and Poisson error distributions (see text).

at hatching (Table 2). We did not detect significant quadratic selection on any morphological traits (Table 2) and patterns of selection in captivity did not differ between sons and daughters ($\chi^2 < 0.78$; $P > 0.37$ for all interactions with progeny sex).

Juvenile survival in the wild did not differ significantly between sons (16%) and daughters (24%) ($\chi^2 = 1.14$; $P = 0.28$). Directional selection strongly favored large SVL at release, large body mass at release, and high body condition at release (Table 2, Fig. 3). However, selection was relatively stronger in sons than in daughters with respect to SVL (sex × SVL at release: $\chi^2 = 8.82$; $P = 0.003$) and body mass (sex × mass at release: $\chi^2 = 6.65$; $P = 0.009$) (Table 2). Selection on body condition did not differ between sexes (sex × condition at release: $\chi^2 = 0.58$; $P = 0.45$). In addition to these strong directional components, selection on SVL and mass was characterized by negative (i.e., stabilizing) quadratic gradients (Table 2), although this nonlinear component of selection was only significant in the case of body mass of daughters ($\chi^2 = 3.92$; $P = 0.048$) and only when hatch date was included in our multivariate analyses (Table 2).

PARENTAL CONDITION AND PROGENY FITNESS

Survival of hatchlings in captivity was unrelated to either maternal or paternal condition and relationships between parental condition and survival did not differ between sons and daughters (progeny sex x parental condition: all $P > 0.70$). However, maternal condition was positively correlated with the survival of daughters in the wild (weighted: $\chi^2 = 6.80$; $P = 0.009$; unweighted: $\chi^2 = 8.34$; $P = 0.004$; Fig. 4A), but weakly or even negatively related to the survival of sons in the wild, depending upon the weighting scheme (weighted: $\chi^2 = 5.63$; $P = 0.018$; unweighted: $\chi^2 = 0.10$; $P = 0.76$; Fig. 4C). Thus, mothers in good condition produced daughters with higher fitness relative to their sons (progeny

Table 1. Progeny phenotypes at hatching were not correlated with either maternal or paternal condition. Statistics are reported for regressions using the weighted means for all sons or daughters of a given sire or dam.

Progeny sex Phenotypic trait	Maternal condition			Paternal condition		
	df	r^2	P	df	r^2	P
Daughters						
Snout-vent length	47	−0.003	0.695	31	−0.021	0.425
Body mass	47	0.000	0.991	31	0.043	0.225
Condition	47	0.001	0.853	31	0.099	0.080
Sons						
Snout-vent length	57	0.007	0.537	37	0.013	0.493
Body mass	57	0.016	0.333	37	−0.007	0.621
Condition	57	0.012	0.406	37	−0.002	0.797

Table 2. Selection gradients for linear (β) and quadratic (γ) selection on hatchling females (F) and males (M). Gradients are partial regression coefficients from models including hatch date and a single morphological trait (see Appendix S1 for equations). Separate regressions were performed for each morphological trait to avoid problems of multicollinearity. Quadratic selection gradients were calculated by doubling regression coefficients and their standard errors. Selection on morphology at hatching was estimated from variation in survival over a two-month period in captivity. Selection on morphology at release was estimated from variation in survival over an eight-month period following release to the wild. Asterisks indicate statistical significance ($P<0.05$), as determined by logistic regression.

	Sex	N	Linear selection $\beta\pm1SE$	Quadratic selection $\gamma\pm1SE$
Hatchling viability				
SVL at	F	75	0.11±0.07	−0.15±0.10
hatching	M	90	0.05±0.05	0.04±0.06
	Both	165	0.07±0.04	−0.01±0.05
Mass at	F	75	0.17±0.07*	0.10±0.12
hatching	M	90	0.11±0.05*	0.06±0.07
	Both	165	0.12±0.05*	0.01±0.05
Condition at	F	75	0.13±0.07	0.09±0.15
hatching	M	90	0.12±0.05*	−0.13±0.14
	Both	165	0.12±0.04*	0.04±0.06
Juvenile viability				
SVL at	F	54	0.74±0.46	−0.94±1.76
release	M	62	2.08±0.48*	−0.62±1.06
	Both	116	1.41±0.33*	−0.45±0.84
Mass at	F	54	1.11±0.38*	−1.80±1.04*
release	M	62	2.05±0.32*	−0.62±0.66
	Both	116	1.60±0.26*	−1.20±0.68
Condition at	F	54	0.55±0.20*	0.38±0.31
release	M	62	0.22±0.18	0.03±0.19
	Both	116	0.36±0.14*	0.22±0.14

sex × maternal condition; weighted: $\chi^2 = 12.23$; $P < 0.001$; unweighted: $\chi^2 = 5.31$; $P = 0.021$). Paternal condition was not related to the survival of either daughters (weighted: $\chi^2 = 0.30$; $P = 0.58$; unweighted: $\chi^2 = 1.13$; $P = 0.29$; Fig. 4B) or sons (weighted: $\chi^2 = 0.01$; $P = 0.97$; unweighted: $\chi^2 = 0.03$; $P = 0.87$; Fig. 4D), nor did relationships between paternal condition and progeny survival in the wild differ between sons and daughters (weighted: $\chi^2 = 0.19$; $P = 0.65$; unweighted: $\chi^2 = 0.83$; $P = 0.36$).

Juvenile males grew significantly more than females with respect to both SVL ($F_{1,18} = 4.35$; $P = 0.05$) and body mass ($F_{1,18} = 11.22$; $P = 0.003$). Growth in SVL was weakly influenced by the interaction between progeny sex and paternal condition ($F_{1,18} = 2.48$; $P = 0.13$), and growth in body mass was weakly influenced by the interaction between progeny sex and maternal

condition ($F_{1,18} = 2.71$; $P = 0.12$). In each case, the growth of sons tended to increase with maternal or paternal condition, whereas the growth of daughters was unrelated to maternal or paternal condition.

Discussion

At the population level, brown anoles produce offspring in an approximately balanced sex ratio (Calsbeek and Bonneaud 2008; Cox et al. 2009; this study). At the individual level, however, we found that sex allocation was biased such that the production of sons increased sharply with the body condition of the sire. By contrast, the production of daughters was independent of the sire's body condition. Consequently, dams produced a female-biased sex ratio when mating with sires in poor condition and a male-biased sex ratio when mating with sires in good condition. Previous studies have shown that female lizards, including brown anoles, bias sex allocation as a function of paternal body size (Calsbeek and Sinervo 2004; Calsbeek and Bonneaud 2008; Cox and Calsbeek 2010), but ours is the first to demonstrate such a relationship for condition, a trait that is statistically uncorrelated with body size.

There are at least three mechanisms by which paternal condition can affect the fitness of progeny and thereby influence sex-allocation strategies. First, fathers in good condition may be better able to provision their offspring (e.g., Korpimaki et al. 2000). This explanation is not applicable to brown anoles, which lack parental care. Second, paternal body condition may signal direct benefits, such as high-quality territory, which could provide a favorable environment for progeny growth and survival. Brown anoles are territorial, and body size (although not condition per se) is known to confer an advantage in male–male competition (Tokarz 1985). Territory size or quality could also impact the fitness of sons more so than that of daughters because it is a primary determinant of male reproductive success in anoles and other lizards (Trivers 1976; Hews 1990; Tokarz 1998; Lebas 2001). The sires in our experiment were raised in captivity, so we could not assess the correlation between their condition and the size or quality of their territories, nor could we examine the fitness of progeny with respect to paternal territories. Thus, direct benefits correlated with paternal condition remain a plausible but untested explanation for the observed sex-ratio bias.

A third possibility is that body condition may signal genetic quality by reflecting the overall performance of a male's genotype in a given environment, such that females receive genetic benefits for their progeny by mating with males in good condition. Other vertebrates are known to bias progeny sex ratio with respect to various phenotypic indicators of paternal quality, such as nuptial coloration, ornamentation, and body size (Ellegren et al. 1996; Rowe and Houle 1996; Svensson and Nilsson 1996;
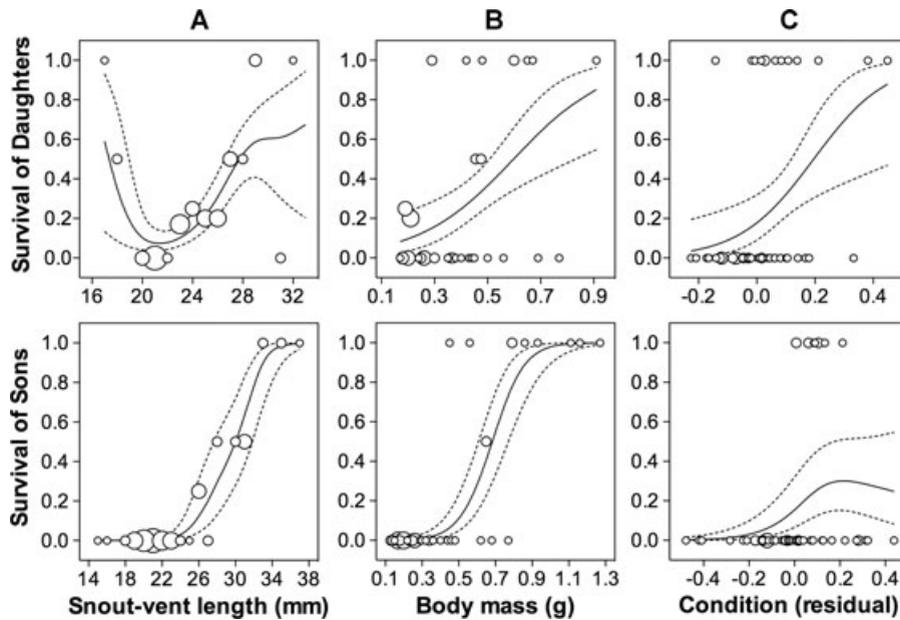
Figure 3. Natural selection favored (A) large snout-vent length, (B) large body mass, and (C) high body condition in juvenile females (top) and males (bottom). Survival was measured over an eight-month period in the wild. Datapoints are average survival probabilities for each phenotypic value. Symbol size corresponds to the number of individuals contributing to each estimate (range: 1–11). Fitness surfaces are best-fit cubic splines ±1SE from 500 bootstrap iterations. For illustrative clarity, splines were fit using bivariate analyses and therefore do not account for effects of hatch date. See Table 2 for linear and quadratic selection gradients that account for effects of hatch date.

Kolliker et al. 1999; Calsbeek and Sinervo 2004; Olsson et al. 2005; Roed et al. 2007; but see Leech et al. 2001). Although many of these studies have demonstrated correlations between sex-ratio bias and the fitness of the sire, most have not actually tested the predicted adaptive consequences by measuring the resultant fitness of progeny (Calsbeek and Sinervo 2004; Olsson et al. 2005; Cox and Calsbeek 2010).

We tested the adaptive significance of sex-ratio bias by tracking the survival of sons and daughters immediately after hatching in captivity, and as juveniles when released to their natural habitat. Despite strong selection for large size and high condition, the fitness of both sons and daughters was unrelated to paternal condition. This is perhaps not surprising, given that sires in good condition did not produce sons or daughters of significantly larger size or better condition at hatching. We did detect a nonsignificant trend for the growth of sons, but not daughters, to increase as a function of paternal condition. Given the importance of body size in territory acquisition and mating success of males (Tokarz 1985, 1998), this suggests a possible adaptive explanation for the observed sex-ratio bias. However, we consider this interpretation tentative due to the small number of offspring and correspondingly weak statistical support. Thus, despite a strong relationship between progeny sex ratio and paternal condition, we have no direct evidence for an adaptive function of this sex-ratio bias.

We propose two potential, nonexclusive explanations for this result. First, although condition may provide a reliable index of paternal quality among wild males, its relevance to heritable fitness variation in our simplified laboratory common-garden environment is debatable. Future studies would benefit from similar analyses of paternal condition and progeny fitness against a common environmental background, preferably in wild populations. Second, any genetic benefits conferred by sires in good condition may be manifest primarily with respect to adult mating success, whereas our selection analyses were based on juvenile viability. Indeed, the sex-specific benefits of maternal investment originally envisioned by Trivers and Willard (1973) are based upon the assumption that males have a higher reproductive value than daughters due to their greater variance in adult reproductive success. However, it is noteworthy that several studies of lizards have documented adaptive consequences of sex-ratio bias with respect to juvenile growth, juvenile survival, and the timing of maturation (Calsbeek and Sinervo 2004; Uller et al. 2004; Olsson et al. 2005; Cox and Calsbeek 2010), rather than adult reproductive success per se.

Contrary to the predictions of Trivers and Willard (1973), we found no evidence that females biased the sex ratio of their progeny on the basis of their own condition. One possibility is that our single measure of maternal condition at the onset of breeding failed to capture relevant fluctuations in condition as successive progeny were fertilized. However, even when considering only the first offspring produced by each dam, maternal condition was unrelated to progeny sex. Another concern is that
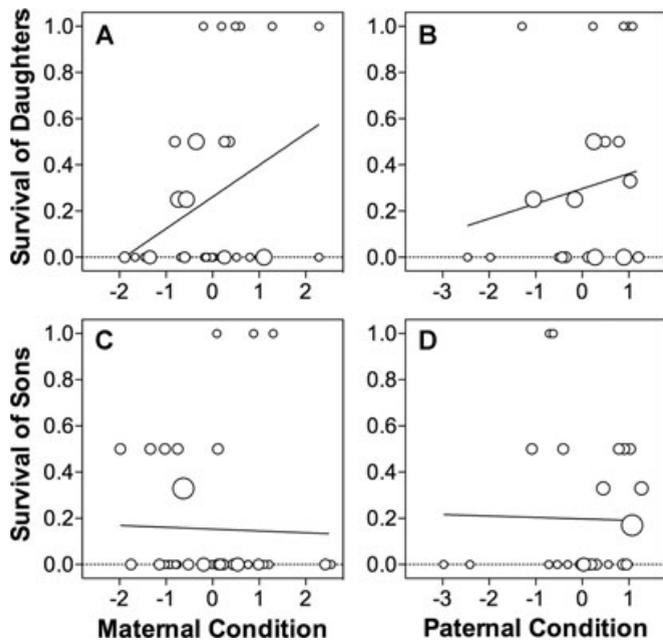
Figure 4. Survival of daughters (top) and sons (bottom) in the wild as a function of maternal (left) and paternal (right) condition, expressed in units of SD relative to the means for each sex. Individual symbols report the average survival of all sons or daughters produced by each dam or sire. Symbol size corresponds to the number of sons or daughters contributing to each estimate (range: 1–6). Ordinary least squares regression lines are shown for illustrative purposes only. Significance tests were based on generalized linear models with log links and Poisson error distributions using relative fitness and standardized measures of condition (see text). Only the relationship in panel A is statistically significant.

simple morphological estimates of body condition may be poor predictors of sex-ratio bias (Sheldon and West 2004). Nonetheless, we detected a strong sex-ratio bias using an identical measure of paternal condition. A third possibility is that females base their sex-allocation decisions on a comparative assessment of their own condition relative to other females in the population. Our breeding design isolated dams from other females, so further studies would be required to address this possibility.

Although support for the Trivers–Willard hypothesis has been reported for birds and mammals (Olsen and Cockburn 1991; Bradbury and Blakey 1998; Nager et al. 1999; Cameron 2004; Cockburn et al. 2004; Sheldon and West 2004), individual studies often give highly divergent results (Komdeur and Pen 2002; Sheldon and West 2004). Other studies of lizards report no correlation between maternal condition and progeny sex ratios (Lovern and Passek 2002; Uller et al. 2006), or contrasting patterns in different study seasons (Olsson and Shine 2001). In some lizards, energetically compromised females apparently invest more resources per egg than those in good condition (Fox and McCoy 2000; Warner et al. 2007), reversing the predictions that would

otherwise derive from the Trivers–Willard hypothesis. However, in only one case were these alternative predictions supported by a positive correlation between maternal investment and progeny sex ratio (Warner et al. 2007). Thus, despite considerable evidence that lizards can adaptively alter progeny sex ratios (Olsson and Shine 2001; Calsbeek and Sinervo 2004; Olsson et al. 2005; Uller et al. 2006; Warner et al. 2007; Calsbeek and Bonneaud 2008; Cox and Calsbeek 2010), this group currently provides only weak and inconsistent support for the original prediction of the Trivers–Willard hypothesis.

In part, this weak support for the Trivers–Willard hypothesis may reflect important differences between the reproductive biology of lizards and the original assumptions derived from large mammals. Foremost among these differences are the general absence of postpartum maternal investment and the prevalence of multiegg clutches or litters in many lizards, the latter of which could permit mothers in good condition to increase their fitness by investing in offspring quantity rather than offspring quality (Fox and McCoy 2000; Warner et al. 2007). Each of these features would generally act to weaken the link between maternal condition and progeny condition. Indeed, we found no evidence for such a link in our study. Moreover, we found no evidence that dams in good condition produced sons with high fitness. By contrast, we found a positive correlation between maternal condition and the survival of daughters. If these effects on juvenile viability were representative of the effects of maternal condition on the total lifetime fitness of sons and daughters, then general sex-allocation theory would predict that female anoles in good condition should produce a female-biased sex ratio, rather than the male-biased sex ratio predicted by the original Trivers–Willard hypothesis. This underscores the importance of establishing the actual relationships between maternal condition and progeny fitness prior to making predictions about adaptive progeny sex ratios. Unfortunately, data linking progeny fitness to maternal condition are lacking for most studies of sex allocation (West 2009).

Although our data show that brown anoles produce biased sex ratios as a function of paternal phenotype, we currently lack a detailed mechanistic understanding of how this bias occurs. Because we only measured "secondary" sex ratios at hatching, we cannot determine whether the observed bias was caused by differential fertilization (i.e., "primary" sex-ratio bias), differential embryonic viability, or a combination of these effects. Moreover, any differential fertilization could occur as a form of cryptic female choice, or because sires in good condition contribute more sperm with male sex-determining loci. In other lizards, male-biased sex ratios occur because sperm with male sex-determining loci exhibit increased viability during storage in the female reproductive tract (Olsson et al. 2007). Because offspring in our study were produced primarily with stored sperm, this is an intriguing possibility, especially if the viability of sperm is also related to

paternal condition. Although the mechanism of sex determinism is unknown for brown anoles, other *Anolis* species exhibit XY and XXY male heterogamety or genetic sex determination without heteromorphic sex chromosomes (Gorman and Atkins 1966; Janzen and Phillips 2006). If this pattern of genetic sex determination is conserved in brown anoles, then our results add to the growing body of evidence contradicting Williams' (1979) suggestion that chromosomal sex determination should constrain adaptive sex-ratio bias (Ellegren et al. 1996; Sheldon et al. 1999; Calsbeek and Sinervo 2004; Olsson et al. 2005). However, even in *Anolis* species with genetic sex determination, maternal effects (e.g., provisioning of the yolk with testosterone) are thought to influence offspring sex, possibly by the altering the fertilization success of male- and female-inducing sperm (Lovern and Wade 2003). Collectively, these unanswered questions suggest a number of promising avenues for future research into the mechanistic basis of sex-ratio bias and its relation to both maternal and paternal effects.

In summary, we have shown that brown anoles bias the production of sons as a function of paternal condition. This bias could reflect direct (e.g., high-quality territory) and/or indirect benefits (i.e., sex-specific good genes) associated with paternal condition, each of which would presumably increase the fitness of sons more so than that of daughters. We did not investigate direct benefits in this study, but our tests for indirect genetic benefits did not strongly support an adaptive interpretation for the observed sex-ratio bias. Further studies of wild populations are required to disentangle these possibilities and to provide a rigorous test for the presumed adaptive significance of sex-ratio bias. Although classic sex-allocation theory has focused on maternal effects on progeny sex ratio, our results emphasize the importance of also considering the paternal phenotype, even in species where parental care is absent.

LITERATURE CITED
Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

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

Bardeleben, C., V. Palchevskiy, R. Calsbeek, and R. K. Wayne. 2004. Isolation of polymorphic tetranucleotide microsatellite markers for the brown anole (*Anolis sagrei*). Mol. Ecol. Notes 4:176–178.

Bradbury, J. W., and J. K. Blakey. 1998. Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*. Proc. R. Soc. Lond. B 265:895–899.

Brown, G. R. 2001. Sex-biased investment in non-human primates: can Trivers and Willard's theory be tested? Anim. Behav. 61:683–694.

Burley, N. T. 1982. Facultative sex-ratio manipulation. Am. Nat. 120:81–107.

Calsbeek, R., and C. Bonneaud. 2008. Postcopulatory fertilization bias as a form of cryptic sexual selection. Evolution 62:1137–1148.

Calsbeek, R., L. A. Bonvini, and R. M. Cox. 2010. Geographic variation, frequency-dependent selection, and the maintenance of a female-limited polymorphism. Evolution 64:116–125.

Calsbeek, R., and B. Sinervo. 2002. Uncoupling direct and indirect components of female choice in the wild. Proc. Natl. Acad. Sci. USA 99:14897–14802.

———. 2004. Within-clutch variation in offspring sex determined by differences in sire body size: cryptic mate choice in the wild. J. Evol. Biol. 17:464–470.

Calsbeek, R., and T. B. Smith. 2007. Probing the adaptive landscape on experimental islands: density dependent selection on lizard body size. Evolution 61:1052–1061.

Calsbeek, R., C. Bonneaud, S. Prabhu, N. Manoukis, and T. B. Smith. 2007. Multiple paternity and sperm storage lead to increased genetic diversity in the Cuban anole, *Anolis sagrei*. Evol. Ecol. Res. 9:495–503.

Cameron, E. Z. 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism. Proc. R. Soc. Lond. B 271:1723–1728.

Carranza, J. 2002. What did Trivers and Willard really predict? Anim. Behav. 63:F1–F3.

Charnov, E. L. 1982. The theory of sex allocation. Princeton Univ. Press, Princeton, NJ.

Cockburn, A., S. Legge, and M. C. Double. 2004. Sex ratios in birds and mammals: can the hypotheses be disentangled? Pp. 266 *in* I. C. W. Hardy, ed. Sex ratios: concepts and research methods. Cambridge Univ. Press, Cambridge, UK.

Cox, R. M., and R. Calsbeek. 2010. Cryptic sex-ratio bias provides indirect genetic benefits despite sexual conflict. Science 328:92–94.

Cox, R. M., D. S. Stenquist, and R. Calsbeek. 2009. Testosterone, growth, and the evolution of sexual size dimorphism. J. Evol. Biol. 22:1586–1598.

Ellegren, H., L. Gustafsson, and B. C. Sheldon. 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. Proc. Natl. Acad. Sci. USA 93:11723–11728.

Fairbairn, D. J., and J. P. Reeve. 2001. Natural selection. Pp. 29–43 *in* C. W. Fox, D. A. Roff, and D. J. Fairbairn, eds. Evolutionary ecology: concepts and case studies. Oxford Univ. Press, New York, NY.

Fox, S. F., and J. K. McCoy. 2000. The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. Oecologia 122:327–334.

Frank, S. A. 1990. Sex allocation theory for birds and mammals. Annu. Rev. Ecol. Syst. 21:13–55.

Godfray, H. C. J., and J. H. Werren. 1996. Recent developments in sex ratio studies. Trends Ecol. Evol. 11:59–63.

Gorman, G. C., and L. Atkins. 1966. Chromosomal heteromorphism in some male lizards of the genus Anolis. Am. Nat. 100:579–583.

Hardy, I. C. W. 2002. Sex ratios: concepts and research methods. Cambridge Univ. Press, Cambridge, UK.

Hews, D. K. 1990. Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. Evolution 44:1956–1966.

Janzen, F. J., and P. C. Phillips. 2006. Exploring the evolution of environmental sex determination, especially in reptiles. J. Evol. Biol. 19:1775–1784.

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

Kolliker, M., P. Heeb, I. Werner, A. C. Mateman, C. M. Lessells, and H. Richner. 1999. Offspring sex ratio is related to male body size in the great tit (*Parus major*). Behav. Ecol. 10:68–72.

Komdeur, J., and I. Pen. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. Proc. R. Soc. Lond. B 357:373–380.

Korpimaki, E., C. A. May, D. T. Parkin, J. H. Wetton, and J. Wiehn. 2000. Environmental- and parental condition-related variation in sex ratio of kestrel broods. J. Avian Biol. 31:128–134.

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

Lebas, N. R. 2001. Microsatellite determination of male reproductive success in a natural population of the territorial ornate dragon lizard, *Ctenophorus ornatus*. Mol. Ecol. 10:193–203.

Leech, D. I., I. R. Hartley, I. R. K. Stewart, S. C. Griffith, and T. Burke. 2001. No effect of parental quality or extrapair paternity on brood sex ratio in the blue tit (*Parus caeruleus*). Behav. Ecol. 12:674–680.

Leimar, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. Behav. Ecol. 7:316–325.

Lovern, M. B., and K. M. Passek. 2002. Sequential alternation of offspring sex from successive eggs by female green anoles, *Anolis carolinensis*. Can. J. Zool. 80:78–82.

Lovern, M. B., and G. N. Wade. 2003. Yolk testosterone varies with sex in eggs of the lizard, *Anolis carolinensis*. J. Exp. Zool. 295A:206–210.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol. Ecol. 7:639–655.

Nager, R. G., P. Monaghan, R. Griffiths, D. C. Houston, and R. Dawson. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. Proc. Natl. Acad. Sci. USA 96:570–573.

Olsen, P. D., and A. Cockburn. 1991. Female-biased sex allocation in peregrine falcons and other raptors. Behav. Ecol. Sociobiol. 28:417–423.

Olsson, M., and R. Shine. 2001. Facultative sex allocation in snow skink lizards (*Niveoscincus microlepidotus*). J. Evol. Biol. 14:120–128.

Olsson, M., E. Wapstra, and T. Uller. 2005. Differential sex allocation in sand lizards: bright males induce daughter production in a species with heteromorphic sex chromosomes. Biol. Lett. 1:378–380.

Olsson, M., T. Schwartz, T. Uller, and M. Healey. 2007. Sons are made from old stores: sperm storage effects on sex ratio in a lizard. Biol. Lett. 3:491–493.

Roed, K. H., O. Holand, A. Mysterud, A. Tverdal, J. Kumpula, and M. Nieminen. 2007. Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. Proc. R. Soc. Lond. B 274:727–733.

Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. Proc. R. Soc. Lond. B 263:1415–1421.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.

Sheldon, B. C., and S. A. West. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. Am. Nat. 163:40–54.

Sheldon, B. C., S. Andersson, S. C. Griffith, J. Ornborg, and J. Sendecka. 1999. Ultraviolet colour variation influences blue tit sex ratios. Nature 402:874–877.

Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988.

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.

Svensson, E., and J.-A. Nilsson. 1996. Mate quality affects offspring sex ratio in blue tits. Proc. R. Soc. Lond. B 263:357–361.

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.

———. 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. Herpetologica 54:388–394.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–269.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Uller, T., M. Massot, M. Richard, J. Lecomte, and J. Clobert. 2004. Long-lasting fitness consequences of prenatal sex ratio in a viviparous lizards. Evolution 58:2511–2516.

Uller, T., B. Mott, G. Odierna, and M. Olsson. 2006. Consistent sex ratio bias of individual female dragon lizards. Biol. Lett. 2:569–572.

Wapstra, E., T. Uller, I. Pen, J. Komdeur, M. Olsson, and R. Shine. 2007. Disentangling the complexities of vertebrate sex allocation: a role for squamate reptiles? Oikos 116:1051–1057.

Warner, D. A., M. B. Lovern, and R. Shine. 2007. Maternal nutrition affects reproductive output and sex allocation in a lizard with environmental sex determination. Proc. R. Soc. Lond. B 274:883–890.

West, S. A. 2009. Sex allocation. Princeton Univ. Press, Princeton, NJ.

West, S. A., and B. C. Sheldon. 2002. Constraints in the evolution of sex ratio adjustment. Science 295:1685–1688.

Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc. R. Soc. Lond. B 205:567–580.

Wilson, K., and I. C. W. Hardy. 2002. Statistical analysis of sex ratios: an introduction. Pp. 48–92 *in* I. C. W. Hardy, ed. Sex ratios: concepts and research methods. Cambridge Univ. Press, Cambridge, UK.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Equations for multivariate selection analyses on progeny phenotypes.

Figure S1. Frequency distributions for the number of offspring produced by individual (A) dams, and (B) sires. Box-and-whisker plots show the median (line), quartiles (box), and 10–90% quantiles (whiskers).

Table S1. PCR amplification conditions modified from Bardeleben et al. (2004).

Supporting Information may be found in the online version of this article.

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