

The effect of sexually antagonistic selection on adaptive sex ratio allocation

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ABSTRACT

Question: How is sexually antagonistic selection predicted to affect sex ratio allocation and female mate choice?

Background: While extensive theory has examined adaptive sex allocation, no theory exists to address the effect of sexually antagonistic selection on adaptive sex-ratio bias. We examine this issue in the side-blotched lizard, *Uta stansburiana*, where females experience a trade-off between producing high-fitness sons and high-fitness daughters.

Mathematical method: We find the evolutionarily stable female choice and sex ratio pattern for individual females as a function of their own genotype, the genotype of their mate, and their social environment. Data collected on the side-blotched lizard over the last decade were used to structure and parameterize the model.

Assumptions: Females produce the sex allocation pattern that is the best response to their current social environment depending on their own genotype and the genotype of their mate.

Predictions: Our model predicts that sexually antagonistic selection can favour individual and population-level sex-ratio biases when sex allocation is allowed to be facultative. Individual females are predicted to differ in the direction of their bias based on the genotype of their mate and their own genotype. This context-dependent sex allocation can lead to some females specializing on producing sons while other females produce mainly daughters.

Keywords: alternative reproductive patterns, female mate choice, game theory, sex allocation, sex ratio, sexual selection, sexually antagonistic selection.

INTRODUCTION

Sex ratio theory predicts that allocation to each sex will depend on the expected reproductive gain obtained through producing male and female offspring (Fisher, 1930; Shaw, 1953; Hamilton, 1967; Trivers and Willard, 1973; Taylor, 1981; Charnov, 1982; Bull and Charnov, 1988; Charnov and Bull, 1989a, 1989b; Basolo, 1994; Taylor and Crespi, 1994; Hewison and Gaillard, 1999; Albrecht and Johnson, 2002; Wade *et al.*, 2003; Fawcett *et al.*, 2006). Fisher (1930) recognized that the fitness of male and female offspring is negatively frequency-dependent, with males generally obtaining high fitness when females

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are common and females obtaining high fitness when males are common. In the absence of any inherent differences in the costs and benefits of producing sons and daughters, this negative frequency dependence leads to the prediction that only an equal primary sex ratio will be evolutionarily stable (Fisher, 1930; Trivers and Willard, 1973; Charnov, 1982). However, deviations from an equal primary sex ratio may be adaptive if sons and daughters differ in their associated costs and benefits (Fisher, 1930; Trivers and Willard, 1973; Charnov, 1982; Wade *et al.*, 2003; Fawcett *et al.*, 2006) and unequal sex ratios are observed empirically at the population and individual level (Hamilton, 1967; Trivers and Willard, 1973; Charnov, 1982; Godfray and Waage, 1990; Shuster and Wade, 1991; Hardy, 1994; Godfray and Werren, 1996; Komdeur, 1996; Komdeur *et al.*, 1997; Hardy and Mayhew, 1998; Kojola, 1998; Kruuk *et al.*, 1999; Sheldon, 1999; Sheldon *et al.*, 1999; Campbell, 2000; West *et al.*, 2002; Sheldon and West, 2004). We suggest that sexually antagonistic selection may also favour adaptive sex ratio allocation as a function of both maternal and paternal trait values.

Recent research has demonstrated sexually antagonistic selection on male and female traits (Merila *et al.*, 1997; Chippindale *et al.*, 2001; Rice and Chippindale, 2001; Lindensfors, 2002; Sinervo and Calsbeek, 2003). For example, selection on male and female traits in the side-blotched lizard (*Uta stansburiana*) can differ in both magnitude and direction (Alonzo and Sinervo, 2001; Sinervo and Calsbeek, 2003; Calsbeek and Sinervo, 2004). Despite extensive interest in the evolutionary implications of sexually antagonistic selection, there is no existing theory or empirical data examining adaptive sex ratio allocation under antagonistic selection on genetically determined traits. Here, we ask how sexually antagonistic selection is predicted to affect adaptive patterns of sex allocation in the side-blotched lizard. While the model is species-specific, this focus allows us to fully parameterize the model and generate testable predictions for this species. Yet, the model presented here also addresses the basic and unanswered question of whether sexually antagonistic selection can select for deviations from an equal sex ratio.

In the side-blotched lizard, there is both empirical and theoretical evidence that females experience a trade-off between producing high-fitness sons and high-fitness daughters (Sinervo *et al.*, 2000b; Zamudio and Sinervo, 2000; Alonzo and Sinervo, 2001). Male side-blotched lizards exhibit genetically determined and sexually selected alternative reproductive phenotypes (orange, blue or yellow throats) that exhibit negatively frequency-dependent fitness (Sinervo and Lively, 1996; Sinervo, 1997; Sinervo and Svensson, 1998; Sinervo *et al.*, 2000b; Svensson and Sinervo, 2000; Zamudio and Sinervo, 2000). In this species, females also exhibit two alternative phenotypes that are genetically determined and cycle in frequency (Sinervo *et al.*, 2000b; Svensson and Sinervo, 2000; Zamudio and Sinervo, 2000). Asynchronous female and male morph cycles lead to sexually antagonistic selection (Sinervo and Calsbeek, 2003), and female mate choice and clutch sex ratio should depend on the relative advantage of producing high-quality male or female offspring. As a result, females of this species might be expected to bias the sex ratio of their clutch. Sex-ratio bias might also depend on the genotype of the female's mate and thus also on female control over mate choice.

We use a game-theoretical model to predict adaptive female mate choice and sex ratio allocation patterns for side-blotched lizards. An extensive decade-long data set on individual fitness, heritability of the morphs, population and genetic cycles, and offspring survival, is used to structure and parameterize the model. We extend a previous model of female mate choice in this species (Alonzo and Sinervo, 2001) to predict female choice and sex ratio allocation simultaneously as a function of her own genotype, her mate, and the social and environmental conditions she experiences. We first describe the study species and data used to parameterize and structure the model. We then examine a sex ratio and mate choice

model for the side-blotched lizard. We focus on the general question of how sexually antagonistic selection is predicted to affect adaptive sex ratio allocation and make both general and species predictions using our model.

THE STUDY SPECIES

As described above, three male throat colour morphs and two female alternative morphs are observed in the side-blotched lizard. DNA paternity data indicate that each male morph has a mating advantage when rare (Sinervo and Lively, 1996; Zamudio and Sinervo, 2000) (Fig. 1A). Orange-throated males defend large territories with many females but lose paternity to yellow-throated males that do not defend territories (Calsbeek *et al.*, 2002). Blue males guard fewer females but tend to have higher paternity (Calsbeek *et al.*, 2002). The expected frequency and relative paternity of male morphs cycle in the wild (Fig. 2A). [For further details on the male morphs in this species, see Sinervo and Lively (1996), Zamudio and Sinervo (2000), Sinervo and Zamudio (2001), Calsbeek and Sinervo (2002), Sinervo and Clobert (2003).]

Data on female cycles suggest that orange-throated females are favoured at low population densities because they produce large clutches of small eggs (Sinervo, 2000; Sinervo *et al.*, 2000a, 2000b; Svensson and Sinervo, 2000). Yellow-throated females gain an advantage at high population density through the production of fewer but larger hatchlings that experience higher survival than the small progeny from orange females (Alonzo and Sinervo, 2001) (Fig. 1B). Orange and yellow female morphs cycle in relative expected reproductive success and frequency every 2 years such that orange females are common in high-density years and yellow females occur at higher frequencies in low-density years (Fig. 2B). [For further details on female strategies in this species, see Sinervo (2000), Sinervo *et al.* (2000a, 2000b), Svensson and Sinervo (2000), Alonzo and Sinervo (2001).]

Controlled crosses indicate that a single Mendelian factor with three alleles can explain throat colour in males and females (Sinervo *et al.*, 2001), which has been confirmed with gene mapping (Sinervo *et al.*, 2006). We use capital letters to indicate phenotype (O, B, Y for males and O, Y for females) and lower-case italics to indicate alleles (*o*, *b*, *y*) and genotypes (*oo*, *bb*, *yy*, *by*, *oy*, *ob*). In both sexes, individuals with *o*-alleles express the orange throat colour morph (e.g. O males and females have a genotype *oo*, *ob* or *oy*). Blue (B) males are *bb* and yellow (Y) males are *yy* or *by*, while all yellow females lack the *o*-allele (e.g. *by*, *bb*, *yy*).

The model also incorporates estimates of progeny survival to maturity based on data spanning high- and low-density years of the female cycle and the three basic frequency conditions of the male cycle (i.e. blue males rare, orange males rare, and yellow males rare). Survival effects were calculated in terms of the additive contribution of each allele to the survival of progeny to maturity broken down by low versus high population density years (B. Sinervo and S.H. Alonzo, unpublished). These estimates indicate that male and female morphs differ not only in expected reproductive success (Fig. 1), but also in expected survival to maturity (Fig. 3).

In addition to strong intra-sexual competition (Sinervo and Lively, 1996; Zamudio and Sinervo, 2000) (Fig. 1A), evidence also exists for female mate choice and biased sex allocation in this species. Calsbeek and Sinervo (2002) observed that, when they experimentally decoupled male body size and territory quality in the wild, females prefer to reside with the smaller males on high-quality territories but preferentially sire offspring with large males on nearby territories. In addition, females exhibit both genetic (morph-specific) and context-dependent patterns of mate choice (Bleay and Sinervo, 2007). When females were given a choice between the

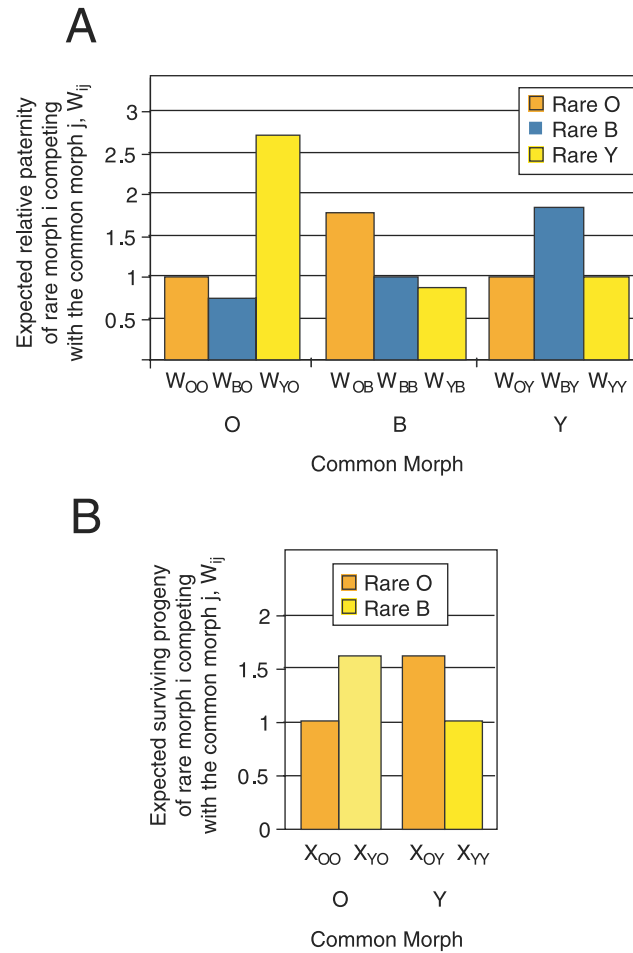


Fig. 1. (a) Male morphs have a competitive advantage when rare. DNA-determined paternity was used to estimate the fitness of male morphs in nature (Zamudio and Sinervo, 2000). Relative paternity of the morph i , W_i , is predicted using: $W_i = \sum f_j(t) W_{i,j}$, summed across $j = O, B, Y$ and where $W_{i,j}$ represents the expected relative paternity of a rare male of morph i competing with the common male of morph j . (b) Each female morph has a reproductive advantage when rare (measured as the number of progeny surviving to maturity). The frequency-dependence of female reproductive success was computed from data collected in the field during 1993 to 1998 (Sinervo *et al.*, 2000b). Expected surviving progeny of the morph i , X_i , can be predicted from female frequency (d_j): $X_i = \sum d_j(t) X_{i,j}$, where $j = O, Y$ and $X_{i,j}$ represents the expected number of surviving progeny of a female of the rare morph i when competing with the common female morph j .

three male colour morphs in the laboratory, yellow females always preferred yellow males while orange females preferred orange males for their first clutch and yellow males for their second clutch (Bleay and Sinervo, 2007). Females of the side-blotched lizard also exhibit striking within-clutch differential sex allocation consistent with cryptic female choice among males (Calsbeek and Sinervo, 2004). Under natural conditions, when females mated with two males of differing sizes, females produced more sons sired by larger males and more daughters sired

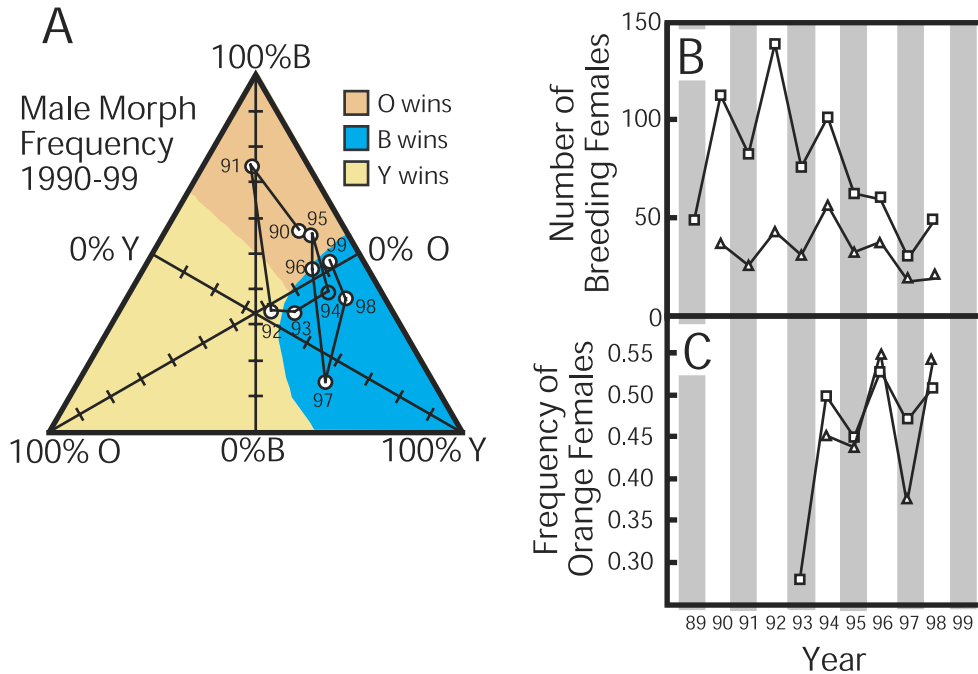


Fig. 2. (a) The proportion of each male strategy (O, B, Y) cycles in frequency. Observed frequencies are shown for 1990–1999. De Finetti diagram plots frequency of male morphs at time t [$f_j(t)$] as follows: 0–100% blue from base to apex, 0–100% orange from right side to left vertex, and 0–100% yellow from left side to right vertex. Shading indicates the morph with highest fitness. (b) Two-year cycles in female density and morph frequency are observed in the field. Orange females are at high frequency in high-density years (B shown in grey). Yellow females are at high frequency in low-density years (C shown in white).

by the smaller male. This biased sire-specific sex allocation can be explained by the existence of sexually antagonistic selection on body size in this species (Sinervo and Calsbeek, 2003), with small females and large males exhibiting higher survival. Bleay *et al.* (2007) also report evidence of a female-biased adult sex ratio but an equal sex ratio in hatchlings. Available evidence on mate choice suggests that heritable genetic factors influence female preference among male genotypes (Sinervo *et al.*, 2006); however, these factors are not linked to the throat colour locus. In addition, the results of mate choice studies in the laboratory suggest that while females express genotype-specific preferences, females also express context-dependent mate preferences (Bleay and Sinervo, 2007). Thus, it is possible to model mate choice and sex ratio allocation as traits that can evolve independent of throat colour.

OVERVIEW OF THE SEX RATIO ALLOCATION MODEL

As described above, sexually antagonistic selection induces a trade-off between making high-fitness male and female offspring (Alonzo and Sinervo, 2001). Here, we use a model that combines both game-theoretical methods and population genetic calculations to incorporate the available genetic and fitness information on this species to determine the sex ratio that will maximize female reproductive success if no genetic constraints on sex ratio expression exist.

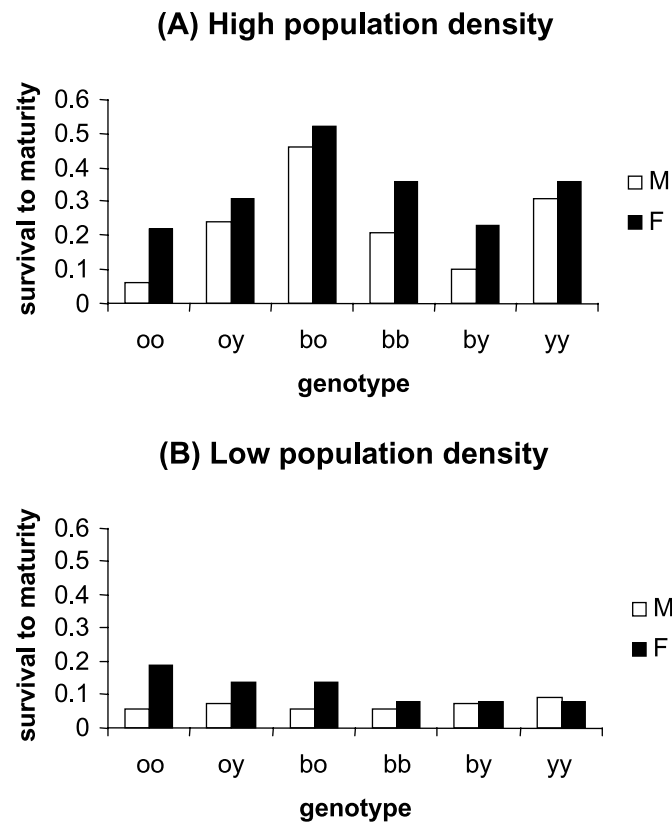


Fig. 3. Offspring survival to maturity is sex-, genotype-, and population density-specific. (A) Female survival is much higher than male survival in high-density years especially for individuals with blue (*b*) alleles. (B) Offspring survival also differs between the sexes and genotypes in low-density years (B. Sinervo and S.H. Alonzo, unpublished). High or low population density refers to the density experienced by the mother, which is the opposite of the density experienced by the offspring, since population density cycles between high and low in consecutive years.

In this model, female fitness depends not only on the social environment but also on the sex ratio allocation pattern of other females in the population. Our approach differs from a classic population genetics model that might examine how selection is predicted to drive changes in the frequency of alleles for specific sex allocation patterns. Instead, we use a phenotypic game-theoretical approach to find the evolutionarily stable sex ratio pattern. This novel approach of using genetic information to calculate fitness in a phenotypic model allowed us to explore an extremely complex strategy space in which female sex ratio allocation is facultative depending on a variety of factors, including female genotype, the genotype of the female's mate, the current social environment, and population density. For example, the underlying trait governing mate choice and sex ratio may be a genotype $\times$ environment interaction that all females share in common, but which results in a different allocation decision depending on the contexts noted above.

Our model first calculates the expected fitness associated with producing each type of offspring (three male morphs and two female morphs). We then calculate the expected

fitness from male and female offspring associated from a female mating with each male morph. The sex-ratio bias is then calculated for each mating based on the difference in success expected from male and female offspring. Thus, a sex ratio allocation pattern is predicted for each female morph dependent on their mate. Finally, the female mate preference and sex allocation pattern is found that maximizes maternal expected fitness. Female fitness is affected by population sex ratio and the frequency of each morph in the next generation and thus also depends on the behaviour of other females in the population. The model searches for the stable sex-ratio bias and mate choice behaviour of each female morph that maximizes female fitness.

As is the case in many phenotypic models (e.g. Charnov, 1982), we use the expected number of grand-offspring a female will produce as our measure of fitness. We then find the evolutionarily stable female choice and sex ratio allocation pattern that maximizes female fitness. Using the empirically derived estimates of fitness described above, we first calculate the expected number of offspring produced by each genotype, which is the same measure of fitness used in most population genetic models (Wolf and Wade, 2001). However, using a phenotypic model makes it necessary to calculate fitness across generations. Since a reproducing female will usually produce multiple genotypes and not all offspring have the same fitness (either by sex or by morph), we measure a mother's fitness as the weighted sum of the offspring she could produce based on her phenotype as well as the phenotype of the sire. Thus we incorporate the fact that not all sons and daughters will contribute equally to the next generation.

The effect of sex ratio on expected fitness

First, we derive the effect of sex ratio on the relative reproductive success of sons and daughters independent of their morph. Let R represent the sex ratio (proportion male). Let Ω_m represent the average number of offspring sired per son, Ω_f the average number of offspring produced per daughter, and w_m and w_f relative male and female expected fitness as a function of sex ratio. First, imagine that males compete for females and female fecundity E is unaffected by the sex ratio. Then individual female fitness is $\Omega_f = E$ and male fitness (assuming males compete 'ideally' for females) is $\Omega_m = ((1 - R)/R)E$. Mean individual fitness in the population w is given by

$$w = (1 - R)E + R \frac{(1 - R)}{R} E = 2(1 - R)E \quad (1)$$

and relative male and female fitness are

$$w_m = \frac{\Omega_m}{w} = \frac{1}{2R} \quad \text{and} \quad w_f = \frac{\Omega_f}{w} = \frac{1}{2(1 - R)} \quad (2)$$

Imagine instead that female fecundity depends on access to males (if, for example, males provide resources that limit reproduction). Then female reproductive success $\Omega_f = (R/(1 - R))m$, where m represents the average number of offspring produced per male and male reproductive success is $\Omega_m = m$. Following the same logic as before, mean population fitness is

$$w = (1 - R) \frac{R}{(1 - R)} m + Rm = 2Rm \quad (3)$$

and relative male and female fitness are $w_m = \Omega_m/w = 1/(2R)$ and $w_m = \Omega_m/w = 1/(2(1-R))$ respectively. In both cases, the effect of sex ratio on relative fitness is given by equation (2) above.

Calculating offspring fitness

Expected reproductive success of male and female offspring will depend on the population's sex ratio, the current frequencies of male and female morphs, and the population density. As described above, recent data also indicate that offspring survival is sex-, genotype-, and density-dependent. Reproductive success of male offspring of morph i (M_i) is a function of the population sex ratio R as derived above (equation 2), expected survival $S_{m,i}$, male morph frequency in the next generation (f'_j , where $j = O, B, Y$), and the frequency-dependent relative paternity of each morph W_i (Maynard Smith, 1982; Sinervo and Lively, 1996) ($W_i = \sum W_{i,j} f'_j$ from Fig. 1A):

$$M_i = \left(\frac{1}{2R} \right) S_{m,i} \sum f'_j W_{i,j} \quad (4)$$

where the sum is over $j = O, B, Y$ (e.g. f'_O, f'_B , and f'_Y).

All of the equations and parameters are based on relative fitness. Expected reproductive success of female offspring is determined by female throat-colour morph, expected survival, and the population sex ratio. Population density cycles between years (Sinervo *et al.*, 2000b; Svensson and Sinervo, 2000). In low-density years, the social environment of female parents consists of a low density and frequency of orange neighbours, but female progeny will predictably experience a high density and frequency of orange neighbours in the ensuing year. Therefore, we allow female choice and sex allocation to depend on population density (i.e. high or low). Expected reproductive success of female morph i ($i = O, Y$) in the next generation (F_i) is a function of the population sex ratio R (as derived above in equation 2), female offspring survival $S_{f,i}$, frequency (or density) in the next generation (d'_j), and the frequency-dependence of female reproductive success X_i (where $X_i = \sum X_{ij} d'_j$ from Fig. 1B):

$$F_i = \left(\frac{1}{2(1-R)} \right) S_{f,i} \sum d'_j X_{i,j} \quad (5)$$

where the sum is over $j = O, Y$ (e.g. d'_O and d'_Y).

For any mating between morphs, we can calculate the expected fitness associated with either male or female offspring. The phenotypes produced will depend on the phenotype of the female (O or B) and that of her mate (O, B or Y). If we assume that male behaviour and female strategy are determined as described above by a single locus with three alleles (o, b or y), from known allele frequencies we can derive the probability that each female morph (O or Y) will produce orange, blue or yellow male offspring (O, B, Y) and orange or yellow female offspring (O, Y) from Mendelian laws of inheritance (see also Sinervo, 2001). For example, let $p_{O,B,Y}$ represent the probability that orange females mating with blue males produce yellow male offspring and $q_{O,B,Y}$ represent the probability that orange females mating with blue males produce yellow female offspring. We let $V_{f,i,j}$ represent the expected fitness from female offspring for female morph i mating with male morph j , and let $V_{m,i,j}$

represent the expected fitness from male offspring of the same pair. Expected reproductive success from male offspring of female morph i ($i = O, Y$) mating with male morph j ($j = O, B, Y$) is given by:

$$V_{m,i,j} = p_{i,j,O}M_O + p_{i,j,B}M_B + p_{i,j,Y}M_Y \quad (6)$$

and for the same mating the expected fitness from female offspring is

$$V_{f,i,j} = q_{i,j,O}F_O + q_{i,j,Y}F_Y \quad (7)$$

where the fitness associated with the mating will depend on the sex ratio produced by the female.

Calculating female sex-ratio bias

We calculate the sex-ratio bias that is predicted for each female morph as a function of the fitness of their male and female offspring given her mate and the population's sex ratio. The predicted sex-ratio bias depends on the difference between fitness expected per female and per male offspring. The function assumes that for large differences in fitness females produce strongly biased clutches, whereas for small differences in fitness females only produce weakly biased clutches. This function allows the model to search for the sex-ratio bias per mating that is stable given what other females in the population are doing. The parameter ε represents the strength of the response to differences in fitness expected from male and female offspring. This method is used in game-theoretical models of this kind to allow the model to search for a stable solution (McNamara *et al.*, 1997; Clark and Mangel, 2000). This method finds the sex-ratio bias at which fitness cannot be increased by allocating more to either sons or daughters. The value of ε does not affect the direction or relative strength of the sex-ratio bias predicted. The sex ratio predicted for a female of morph i mating with a male of morph j is given by the function

$$R_{i,j} = \frac{e^{\varepsilon(V_{m,i,j} - V_{f,i,j})}}{e^{\varepsilon(V_{m,i,j} - V_{f,i,j})} + e^{-\varepsilon(V_{m,i,j} - V_{f,i,j})}} \quad (8)$$

The algorithm then searches for the stable sex ratio allocation and mate choice patterns (i.e. they are the best response to themselves). [For more information on this general method, see McNamara *et al.* (1997), Alonzo and Warner (2000), Clark and Mangel (2000), Alonzo (2002).]

Calculating female preference

Females should show a preference based on expected reproductive success of their progeny. Expected reproductive success of female morph i ($i = O, Y$) mating with male morph j ($j = O, B, Y$) is given by:

$$V_{i,j} = R_{i,j}V_{m,i,j} + (1 - R_{i,j})V_{f,i,j} \quad (9)$$

The maximum expected reproductive success of female morph i (Z_i), and thus that of the preferred male morph, is given by the male mate that maximizes success:

$$Z_i = \max \{V_{i,O}, V_{i,B}, V_{i,Y}\} \quad (10)$$

Generating frequencies in the next generation

Offspring fitness is affected by the population sex ratio and morph frequency (male and female) in the next generation. Morph frequency in the next generation is a function of the following parameters in the current generation: (1) male morph frequency (f_j) and mating success (e.g. $W_i = \sum f_j W_{i,j}$ for $j = O, B, Y$), (2) female morph frequency (N_i), (3) female preferences, (4) female control over mating (b_c), and (5) offspring survival ($S_{m,i}$ and $S_{f,i}$). Let $P_{i,j}$ represent the probability that female morph i mates with male morph j and let $b_{i,j}$ represent the female's bias towards mating with each male morph. A female's preference is predicted by the solution of equation (10). If females do not prefer a morph, their bias towards that morph is $b_{i,j} = 1$. If females prefer a morph, their bias is determined by female control over mating $b_{i,j} = b_c$, which ranges from low control ($b_c = 1$) to high control ($b_c = 100$). Bias is simply a parameter that weights the probability a female will mate with each morph. If control is low, male morph frequency and interactions between males will drive the mating probability. As female control b_c over mating increases, $b_{i,j}$ for the preferred morph increases as does the probability ($P_{i,j}$) that the female mates with her preferred morph. The probability that female morph i will mate with male morph j is given by:

$$P_{ij} = \frac{W_i f_j b_{ij}}{\sum_j W_j f_j b_{ij}} \quad (11)$$

The frequency of each morph is calculated from the probability of mating and the probabilities of producing each morph from a given mating. The solution of f'_o , and analogous equations for f'_b and f'_y , generates the frequency in the next generation, and f'_o is given by:

$$f'_o = \frac{\sum_{j=o,b,y} [S_{m,o} P_{o,j}(p_{o,j,o}) N_o + S_{f,o} P_{y,j}(p_{y,j,o}) N_y]}{\sum_{i=o,b,y} \sum_{j=o,b,y} [S_{m,i} P_{i,j}(p_{o,j,i}) N_o + S_{f,i} P_{y,j}(p_{y,j,i}) N_y]} \quad (12)$$

The population sex ratio in the next generation is affected by female mate choice, female control, and the survival of male and female offspring of each phenotype. The proportion of males in the next generation will be determined by the proportion of males that are produced by each female morph given the probability she mates with each male morph multiplied by the probability of a son's survival given his phenotype. The proportion of daughters is also determined by female sex ratio allocation (determined by the solution of equation 8), female morph frequency, offspring survival, and the probability each female will mate. Thus the proportion of males in the next generation that survive to reproductive maturity is given by

$$R = \frac{\sum_{i=o,b,y} \sum_{j=o,b,y} \sum_{k=o,y} R_{k,j} S_{m,i} P_{k,j}(p_{k,j,i}) N_k}{\sum_{i=o,b,y} \sum_{j=o,b,y} \sum_{k=o,y} R_{k,j} S_{m,i} P_{k,j}(p_{k,j,i}) N_k + \sum_{i=o,y} \sum_{j=o,b,y} \sum_{k=o,y} (1 - R_{k,j}) S_{f,i} P_{k,j}(q_{k,j,i}) N_k} \quad (13)$$

Solving the model

We use a best response method to find the stable female choice and sex-ratio bias strategy to a population-level pattern (Houston and McNamara, 1988, 1999; Mangel and Clark, 1988; McNamara *et al.*, 1997; Clark and Mangel, 2000). The algorithm searches until a stable female preference and sex-ratio bias is found given morph frequencies and densities in the present generation. The only model parameters that have not been estimated from the extensive decade-long data set (Sinervo and Lively, 1996; Sinervo, 1997; Sinervo *et al.*, 2000b; Svensson and Sinervo, 2000; Zamudio and Sinervo, 2000; Sinervo and Zamudio, 2001) (Figs. 1–3) are female control b_c and the sex-ratio bias parameter ε . Sensitivity analyses, ranging from no to complete control, indicate qualitative predictions are robust to female control. The sex ratio parameter does not affect the outcome of the model but only the model's ability to find a stable solution by allowing the best response method to search through all possible values of sex-ratio bias for the stable pattern. In a few cases, the method was still unable to find a stable solution. However, this result was uncommon and occurred evenly across the parameter space. When cycling is found, cycles occur around the quantitative sex-ratio bias predicted but not the direction of the bias. Therefore, the cycling behaviour of the model does not affect the results we present below.

RESULTS

In most cases, individual females are predicted to express biased sex ratios, while the population sex ratio does not deviate significantly from an equal primary sex ratio. Of course, this result relies on the assumption that facultative sex ratio allocation is unconstrained in its expression. In the side-blotched lizard, sex ratio allocation is predicted to depend on the genotype of the female and her sire as well as the social environment and population density. In general, the existence of sexually antagonistic selection is predicted to lead to individual females specializing in producing either more sons or daughters dependent on their own genotype and the genotype of their mate. However, in the side-blotched lizard the direction of the specialization is not determined simply by female or male sire genotype but instead also depends on the density and social environment. For example, orange females are not always predicted to produce male-biased sex ratios. Instead, a gene $\times$ environment interaction determines the direction of the expected sex-ratio bias. Another general pattern is that females are predicted to produce different sex ratios depending on their sire. Females may be able to increase their fitness through sex ratio allocation even if they are unable to have complete control over mating and fertilization. In general, the model predicts that sexually antagonistic selection can favour primary sex ratios at the individual and even population level that deviate from unity. However, the expected pattern of sex allocation is highly context-dependent, varying with the genotype of the dam, the genotype of the sire, and the social environment.

Female choice to maximize fitness through sons and daughters

Female choice patterns differ between female morphs and for individual morphs between high- and low-density years. Orange females are predicted to prefer blue males in high-density years (Fig. 4A, left). This maximizes fitness through sons and daughters by producing high-surviving *bo* sons and daughters (Fig. 3). In contrast, yellow females are

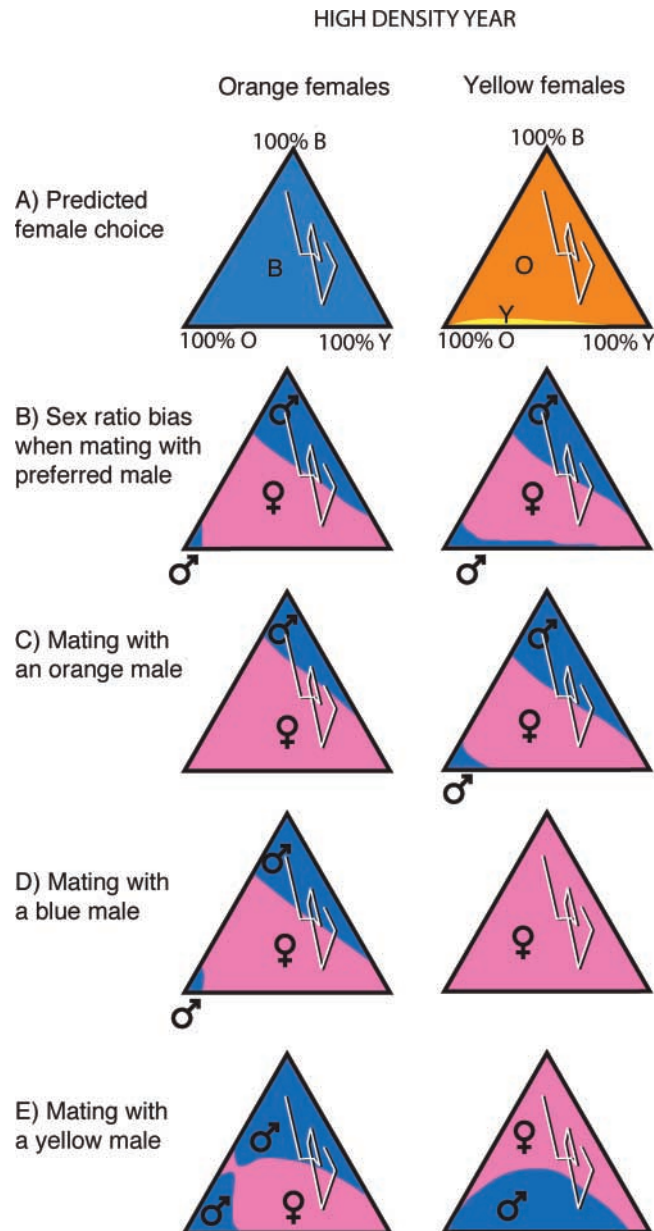


Fig. 4. Predicted female choice and sex-ratio bias in a high to low orange (and density) year when offspring survival is genotype- and sex-specific (low female control). The triangles are De Finetti diagrams where each point in the triangle represents one possible combination of the frequency of the three male morphs. The axes are as follows: the frequency of blue increases 0–100% from base to apex, the frequency of orange increases 0–100% from right side to left vertex, and the frequency of yellow increases 0–100% from left side to right vertex. The shading and labels represents the preferred male colour morph (O = orange, Y = yellow, and B = blue) or the direction of the sex-ratio bias (female symbol = female-biased, male symbol = male-biased). White lines show the cycle of male morph frequencies observed in the wild over the last decade.

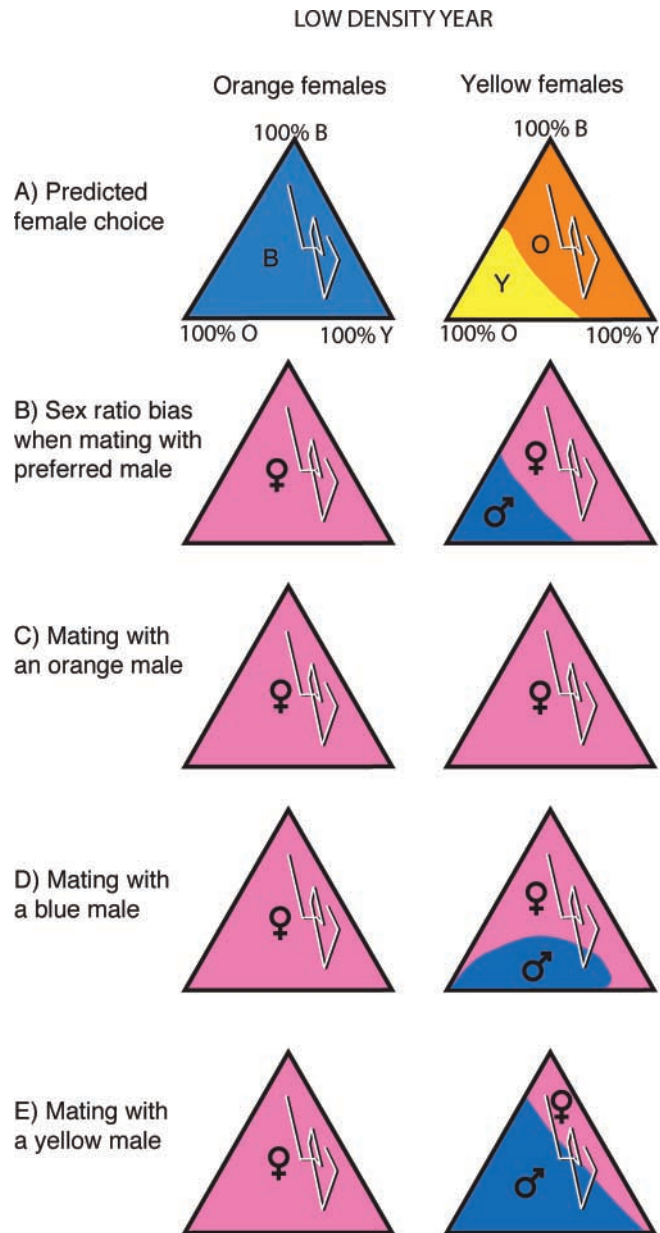


Fig. 5. Predicted female choice and sex-ratio bias in a low to high orange (and density) year when offspring survival is genotype- and sex-specific (low female control). The triangles are De Finetti diagrams where each point in the triangle represents one possible combination of the frequency of the three male morphs. The axes are as follows: the frequency of blue increases 0–100% from base to apex, the frequency of orange increases 0–100% from right side to left vertex, and the frequency of yellow increases 0–100% from left side to right vertex. The shading and labels represents the preferred male colour morph (O = orange, Y = yellow, and B = blue) or the direction of the sex-ratio bias (female symbol = female-biased, male symbol = male-biased). White lines show the cycle of male morph frequencies observed in the wild over the last decade.

predicted to prefer mainly orange males to produce high-fitness *bo* sons and daughters (Fig. 4A, right). Thus choice depends not only on quality of the offspring but also on the genes carried by the female herself. In low-density years, orange and yellow females are predicted to mainly prefer orange males (Fig. 5A), which allows them to produce high-surviving daughters (*oo*, *bo*, and *yo*) and high reproductive success sons (Figs. 1 and 3). However, when orange males are common, yellow females are predicted to mate with yellow males because they can produce high-surviving and high reproductive success sons (Fig. 5, right). When we allow for plasticity in sex ratio production, sex-ratio biases are predicted and depend in part on female morph, mate phenotype, morph frequencies, and population density (Figs. 4C–E and 5C–E).

Sex ratio patterns at the population level

The predicted primary population-level sex ratio varies from unity to female-biased at the population level even though some females are predicted to produce male-biased sex ratios (Fig. 6). Predicted sex-ratio bias is lowest when blue alleles are rare and both yellow and orange alleles are common (Fig. 6). In contrast, the population is expected to be female-biased when blue alleles are common (Fig. 6). Even if the population sex ratio is near unity, the occurrence of female alternative reproductive morphs can allow for each morph to produce either mainly male or female offspring. However, whether the two female morphs differ in their production depends on their mate and social conditions as well as on their own genetics. The model predicts that orange females will often bias towards daughters because of the overwhelming advantage orange females have in producing high surviving orange daughters at low density. Thus orange females may exhibit a specialization in the production of high reproductive success daughters (Fig. 5B–E, left).

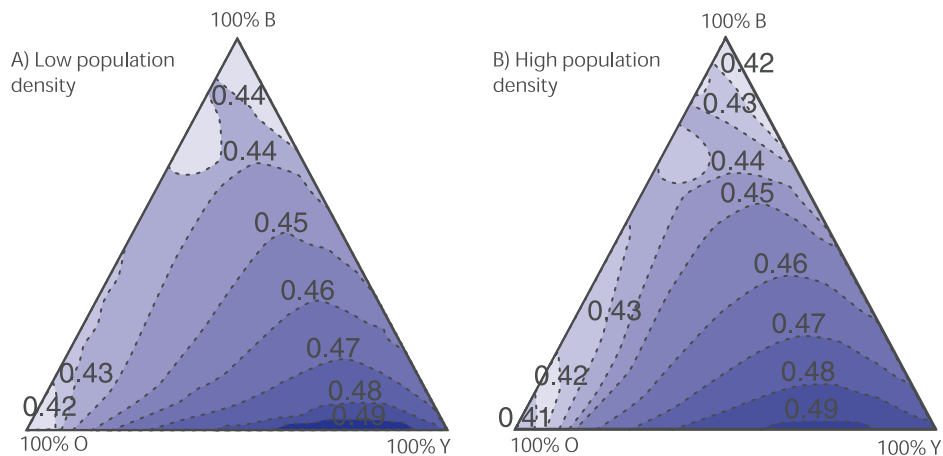


Fig. 6. The primary sex ratio (proportion male) at the population level is predicted to vary from unity to female-biased in the presence of sexually antagonistic selection. Results are shown for low female control, although qualitative patterns are similar for other values of female control. Axes as in Fig. 4.

Individual sex allocation when females mate with their preferred male

First we consider predicted sex-ratio bias when females obtain their preferred mate. In high-density years, both orange and yellow females are predicted to bias their sex ratio towards males when blue males are common and towards females as orange and yellow males become more common (Fig. 4B). As female control increases, the frequency of cases in which female biases are predicted increases and the bias towards male offspring is predicted to decrease.

In low-density years, orange females are predicted to produce female-biased sex ratios independent of male morph frequency and female control (Fig. 5B). Yellow females are predicted to produce mainly female-biased sex ratios, and only produce male-biased ratios when orange males are very common (Fig. 5). The frequency with which male-biased sex ratios are predicted for yellow females increases as female control increases. However, mainly female-biased sex ratios are predicted for the male morph frequencies observed in the field.

Sex-ratio bias in the absence of female choice

The above sub-section describes female sex-ratio bias assuming females have mated with their preferred males. However, it is also interesting to ask what sex ratio would be produced if females mate with a specific (and potentially non-preferred) male morph (Figs. 4 and 5C–E). This is a common occurrence in the side-blotched lizard because some of the male strategies (O, Y) adopt coercive copulatory behaviours (Zamudio and Sinervo, 2000). Females can increase their fitness even if they cannot control mating by biasing their sex ratio towards the sex that will have higher fitness (given their mate). In essence, sex-ratio bias may give females a form of cryptic control even when female choice is thwarted. For example, in high-density years orange females are predicted to prefer blue males and to produce male-biased sex ratios when blue males are common and female-biased sex ratios when orange male morphs are more common. However, when mating with orange males, orange females would be predicted to produce mainly female-biased sex ratios, whereas mating with yellow males would lead to mainly male-biased sex ratios (Fig. 4C–E, left). Yellow females are predicted to prefer orange males in high-density years and bias their sex ratio towards males when blue males are common and towards females when yellow and blue males are more common if they mate with their preferred orange male. However, if they mate with a blue male, they are predicted to always produce female-biased sex ratios (Fig. 4D, right) and produce mainly female-biased sex ratios when they mate with yellow males (Fig. 4E, right). Thus, variation in sex-ratio bias is predicted not only between years or between female genotypes, but also dependent on the individual mate (or mates) the female may experience.

Effects of female control on sex bias and female choice

Female control directly affects the probability that a female will mate with her preferred male. However, it has indirect effects through mating frequencies and context-dependent sex-ratio bias on both the change in morph frequencies between generations and the sex-ratio bias in the next generation. However, female control did not have a strong effect on predicted patterns of female choice in this model. This is probably due to the importance of

survival differences among the morphs. Differences in offspring survival to maturity are not affected by the behaviour of other females in the population, whereas reproductive success is strongly affected by the behaviour of other females. Therefore, in cases where survival selection outweighs fecundity selection, control will have little effect (such as in high-density years). However, as female control increases for yellow females, they are predicted to have an increased preference for yellow males when orange males are common and yellow males are rare. This effect is due to sexual selection on rare-male morphs. Generally, female control does not have strong qualitative effects on female choice or sex-ratio bias patterns.

DISCUSSION

Our results clearly indicate that sexually antagonistic selection on sons and daughters can favour individual sex allocation patterns that deviate from unity and that female fitness is predicted to be higher in the presence of facultative sex ratio allocation. Females are not predicted to consistently specialize on producing one sex. Instead, when we allow sex ratio allocation to be context-dependent, individual experience (such as the genotype of the sire) and environmental factors (such as population density and the frequency of male morphs) are predicted to affect the magnitude and direction of the sex-ratio bias. Although individual females are predicted to produce biased sex ratios, the population is not generally predicted to exhibit large sex-ratio biases. This prediction is consistent with observed patterns in the side-blotched lizard where females exhibit sire-specific sex allocation (Calsbeek and Sinervo, 2004), yet strong deviations from an equal primary sex ratio are not found at the population level (Bleay *et al.*, 2007). As a result, understanding patterns of sex allocation in this and potentially many other species will require very fine-scale information on the fitness of sons and daughters in various contexts as well as whether the sex ratio of an individual female has the potential to be facultative.

Predictions for *U. stansburiana*

In the side-blotched lizard, females are predicted to bias their individual sex ratios even though population-level patterns may not be sex-biased. This prediction is consistent with the observation that hatchling sex ratios are not strongly sex-biased (Bleay *et al.*, 2007) but that females may bias sex allocation within a clutch depending on sire phenotype (Calsbeek and Sinervo, 2004). The direction of the bias is predicted to depend on the current social environment, population density, the genotype of the female's mate, female control over mating, and the female's genotype (Figs. 4 and 5). In general, the population-level prediction is that a female-biased sex-ratio will be observed (Fig. 6), which is in line with other theory considering the effect of sexual selection on sex allocation (Wade *et al.*, 2003) and the observed adult sex ratio in the wild (Bleay *et al.*, 2007). Female choice and sex-ratio bias are predicted to be context-dependent and respond to local conditions and individual experience. Evidence already exists that females exhibit morph-specific and context-dependent mate choice in the laboratory (Bleay and Sinervo, 2007). Future studies should examine morph-specific female preferences dependent on the local frequency of male morphs and population density. The predicted sex ratio is the result of a trade-off between the expected reproductive success of sons and daughters. Yet, both selection on survival and expected reproductive success of progeny affect the reproductive gain of producing sons or daughters. The stable sex ratio is predicted to occur where the difference in intrinsic reproductive gain is balanced by the

advantage of being the rarer sex. In high-density years, survival selection affects offspring fitness more strongly than sexual selection at maturity and survival differences determine sex-ratio bias and female choice. In contrast, in low-density years, the frequency-dependent reproductive success of males and females determines female behaviour. Preliminary results indicate that sex-ratio biases are observed and are both context- and genotype-dependent (B. Sinervo *et al.*, unpublished data).

In the side-blotched lizard, females appear to have some control over mating (Calsbeek and Sinervo, 2002) but also experience forced copulations (Zamudio and Sinervo, 2000). Sex ratio allocation may allow females to increase their expected fitness by producing the offspring type that maximizes fitness given an unpreferred mate (Calsbeek and Sinervo, 2004). Similarly, females' ability to produce biased sex ratios at the individual level may decrease conflict over mating between males and females. The largest difference between the predicted sex-ratio bias when mating with preferred versus forced-copulated partners exists when females prefer either orange or blue males and they mate with a yellow male. The strategy of yellow males is to seek out copulations with females on other males' territories, and yellow males are not usually predicted to be preferred by females. Consequently, the side-blotched lizard female is likely to be under selection for sex-ratio control. The available mate choice studies indicate that O and Y female morphs exhibit context-dependent and genotype-specific preferences in the laboratory (Bleay and Sinervo, 2007). The predicted changes in population sex ratio require knowledge of the neighbourhoods experienced by individual females, as these neighbourhoods provide the necessary cues for context-dependent sex allocation. Recent evidence supports this basic assumption (Calsbeek and Sinervo, 2004). Empirical tests of the predictions are currently underway in the side-blotched lizard.

General predictions

Sexually antagonistic selection generates a trade-off between sons and daughters that favours sex allocation patterns that depend on the genotype of the female, the genotype of her mate, and the current social environment. For example, individual females are predicted in some cases to produce female-biased sex ratios if they obtain their preferred mate but male-biased sex ratios if they do not. This complicates the comparison of theoretical predictions and empirical results for two reasons. First, individual variation in bias will mean that sex ratio data that are already difficult to obtain will require an even larger sample size to allow for enough power to detect sex-ratio biases in the wild. Second, multiple interacting factors will influence predicted sex ratio patterns and extremely general models may not be able to explain observed variation. Instead, a thorough understanding of individual fitness as a function of individual state, social and environmental conditions, dam and sire genotype, and the behaviour of other individuals in the population will be required to make predictions and understand observed variation or even the absence of sex-ratio bias patterns. Furthermore, if sex-ratio bias is plastic, a more favourable approach to testing the models is to vary the cues hypothesized to induce changes in sex ratio in laboratory experiments and test for predicted sex ratio changes. For example, experiments on both wasps and Atlantic silversides have successfully tested theories of sex ratio evolution in the laboratory by studying plasticity in sex ratio allocation (Werren, 1980, 1983; Conover and Fleisher, 1986; Conover *et al.*, 1992). Furthermore, the indirect genetic effect of sire genotype on female fitness should also be considered when interpreting patterns of sex ratio variation (e.g. Ellegren *et al.*, 1996; Griffith *et al.*, 2003; Wade *et al.*, 2003; Fawcett *et al.*, 2006).

Although extensive theory and empirical data on sex ratio allocation exist, the ability of theory to predict and explain observed sex ratio patterns has been mixed (e.g. Sheldon, 1998; West *et al.*, 2002). In many cases, researchers have failed to find significant sex-ratio biases where they are predicted. Although this may be in part a problem of statistical power, existing theory certainly does not explain all of the patterns that emerge. Generally, our results demonstrate that it is important to consider the possibility that female sex-ratio bias may be plastic. If females were required to produce only one sex ratio independent of individual genotype and experience, a sex-ratio bias would not have been predicted by our model. Instead, we predict that individual-level patterns of sex-ratio bias will be favoured whenever variation among females exists that affects the form and direction of sexually antagonistic selection or the strength of sexual selection on their sons. Furthermore, sex-ratio bias may depend on the condition, genotype, and experience of individual females.

Although the predictions presented here are specific to the side-blotched lizard, the importance of considering the complex biology of any individual species when trying to understand sex ratio patterns is apparent. It is striking that the vertebrate systems in which sex ratio allocation are best understood (e.g. Seychelles warblers and red deer) are systems in which extensive data on natural and sexual selection have been collected over multiple years and complete censuses of the population are possible (Komdeur, 1996; Komdeur *et al.*, 1997; Kruuk *et al.*, 1999). Furthermore, knowledge of individual experience, condition, and even genotype plays an important role in explaining patterns of sex-ratio bias. In all of these systems, population and individual deviations from a sex ratio of unity are observed under some conditions but not under others. This level of variation in sex ratio allocation patterns within a population complicates our efforts to measure general patterns. We argue that if our intent is to explain and predict patterns of sex ratio allocation, we must allow for plasticity in sex-ratio bias as well as consider both individual situation and population state when trying to predict patterns of sex allocation. While the quantitative predictions of our model apply mainly to the side-blotched lizard, our results clearly indicate more generally that sexually antagonistic selection can favour individual- and population-level primary sex ratios that deviate from unity, especially since sex allocation may depend on individual genotype, indirect genetic effects, and the current social environment.

ACKNOWLEDGEMENTS

We thank Chloe Adamopoulou, Ryan Calsbeek, and Tosha Commendant for helpful discussions. We also thank Peter Taylor for his patient and thorough editorial comments. S.H.A. was supported by National Science Foundation Grants DBI-9974233, IOB-0110506, and IOB-0450807, and Yale University. B.S. was supported by National Science Foundation grants IBN-9631757, DEB-0108577, and LTREB DEB-051597.

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