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Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana*

Abstract According to mate choice models, a female should prefer males with traits that are reliable indicators of genetic quality which the sire can pass on to their progeny. However, good genes may depend on the social environment, and female choice for good genes should be context dependent. The side-blotched lizard, *Uta stansburiana*, exhibits genetically based throat colors (orange, blue, or yellow) that could be used as a sexually selected signal since they reliably predict the genetic quality of mates. The frequencies of male and female morphs cycle between years, and both male and female morphs have an advantage when rare; thus genetic quality will depend on morph frequency. A female should choose a sire that maximizes the reproductive success of both male and female progeny. We examine a game theoretical model that predicts female mate choice as a function of morph frequency and population density. The model predicts the following flexible mate choice rule: both female morphs should prefer rare males in 'boom years' of the female cycle (e.g., 'rarest-of-N rule'), but prefer orange males in 'crash years' of the female cycle ('orange-male rule'). Cues from the current social environment should be used by females to choose a mate that maximizes the future reproductive success of progeny, given the social environment of the next generation. We predict that the cue is the density of aggressive orange females. In the side-blotched lizard, cycling mate choice games and context-dependent mate choice are predicted to maintain genetic variation in the presence of choice for good genes.

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Introduction

Theories of sexual selection are typically dichotomized into female choice and male-male competition (Darwin 1859, 1871). Yet the interplay between the two components of sexual selection is rarely treated (Andersson 1994). Female choice for good genes is usually described as conferring fitness benefits to the offspring in the form of increased growth, fecundity, or survival. However, females should also choose mates that confer good genes for success in intrasexual competition. As a result, intersexual selection will be inherently linked to intrasexual selection, and one must consider interactions within and between each sex to predict genetic quality, and thus patterns of female mate choice.

Females are often predicted to choose mates that will increase the fitness of their offspring, and there is an extensive literature describing patterns of intersexual selection and female mate choice. In the case of good-gene models, a female should prefer males with traits that are reliable indicators of genetic quality that can be passed on to their offspring (Pomiankowski 1988). However, causes have rarely been ascribed to a particular 'good gene' (stalk-eyed flies provide a notable exception; Wilkinson et al. 1998). Instead, progeny performance is typically studied to assess a male's overall genetic quality as a function of sexually selected ornaments (Kempenaers et al. 1992; Hasselquist et al. 1996).

Evidence is increasing that female choice rules can be both complex and highly plastic (e.g., Dugatkin and Godin 1992, 1993; Warner et al. 1995; Briggs et al. 1996; Dugatkin 1996; Godin and Briggs 1996). Therefore, female choice may not be expressed as a fixed preference for males of one type, but depend on social environment, ecological conditions, or individual experience. Clearly, some traits will be beneficial in all environments. However, the genetic quality of other traits, espe-

cially those that affect social interactions, may depend strongly on the social environment. In a stochastic environment, female choice may vary, and females should choose males that confer good genes to their offspring in the context of the environment. Females may use local cues to project future conditions their offspring will experience. As a result, the genes that are 'good' may vary, and female choice should be context dependent rather than fixed for a single trait.

Male side-blotched lizards (*Uta stansburiana*) exhibit a genetically based and sexually selected signal (orange, blue, or yellow throats) that predicts the genetic quality of a mate in the context of genetic cycles. DNA paternity data indicate that each male morph has an advantage when rare. Thus, we might predict that a female should mate with a male that produces sons with the rare male morph. However, a female should choose a sire that maximizes reproductive success of both male and female progeny. In this species, females also exhibit two throat color morphs that cycle in frequency. Orange females produce large clutches of small eggs and experience higher success in low-density years, while yellow females produce smaller clutches of large eggs and experience higher fitness in high-density years. As a result, the fitness of female offspring will be determined by density in the next year. Asynchronous female and male morph cycles can lead to a trade-off between male and female offspring, and female mate choice should depend on the relative advantage of producing high-quality male or female offspring.

Female choice for good genes will depend on the underlying genetics of the trait as well as the social environment. Using a best-response game theoretical approach, we model female mate choice for good genes in the side-blotched lizard as a function of female and male morph frequency, and population density in the parental generation. The model is used to predict the context-dependent pattern of female choice. Although our model is structured to examine the side-blotched lizard, the general predictions apply to other systems with alternative strategies (e.g., fish: Gross 1984; birds: Lank et al. 1995; lizards: Moore and Thompson 1990). The genetic quality of mates will often be context dependent, and our model examines the effect of such variation on intersexual selection. Moreover, our model addresses the frequency-dependent selection governing mate choice and male competition which is fundamental to the ecology of sexual selection. In the side-blotched lizard, female fitness will be affected by genetic cycles, and thus females are expected to choose good genes even as the fitness-conferring genes cycle. Using the side-blotched lizard as an illustrative example, we show that female choice for good genes may be context dependent and can influence the evolution of traits involved in both intra- and intersexual selection.

The genetic basis of alternative male and female morphs

In the side-blotched lizard, males exhibit three alternative reproductive behaviors and females exhibit two alternative life history strategies with throat color as the indicator trait. The presence of orange, blue, and yellow throat color is heritable in nature, and the six putative male genotypes can be lumped into three behavioral morphs: blue, orange, and yellow (Sinervo and Zamudio, in press). In contrast, although throat color is significantly heritable in females, only two female morphs are found: yellow and orange (Sinervo et al. 2000). Parent-offspring regression indicates that a single Mendelian factor with three alleles can explain throat color in males and females (Sinervo et al. 2000). For clarity, we use capital letters to indicate strategy (O, B, Y for males; O, Y for females) and lowercase italics to indicate alleles (*o*, *b*, *y*) and genotypes (*oo*, *bb*, *yy*, *by*, *oy*, *ob*). Empirical data and theoretical models (Sinervo and Zamudio, in press) strongly support a simple Mendelian model of inheritance of male behavioral strategy in which the *o* allele is dominant [i.e., orange (O) males have genotype *oo*, *ob*, or *oy*], and the *b* allele is recessive to the *y* allele [i.e., blue (B) males are *bb* and yellow (Y) males are *yy* or *by*]. The *o* allele is dominant in females [i.e., *oo*, *ob*, *oy* are orange (O)], and females lacking the *o* allele [i.e., *by*, *bb*, *yy*] are yellow. In fact, the *b* allele is recessive to the *o* and *y* alleles. In females, the presence of *o* or *y* is genetically correlated with clutch size, egg mass, and offspring survival, while the *b* allele does not appear to have any effect on female life history strategies (Sinervo and Zamudio, in press). For the model described below, we assume that male behavioral strategy (orange, blue, or yellow) and female strategy (orange, yellow) is determined by the three-allele, one-locus genetics described above. We further assume complete dominance for the expression of the behavior, and that male behavior and female strategy determine fitness. However, we also explore the effect on female choice of varying the underlying genetics.

Interactions between males

In *U. stansburiana*, there are three male territorial strategies, and each morph has a mating advantage when rare. As a result, the frequency of male alternative strategies cycle, and the male morph with a mating advantage changes during the genetic cycle. DNA paternity data (pay-off matrix; Fig. 1a) have confirmed predictions of a rock-paper-scissors model previously proposed for side-blotched lizards (detailed information in Sinervo and Lively 1996; B. Sinervo, K. Zamudio, G. Corrigan, D. Rollo, unpublished data; Zamudio and Sinervo, in press). In the male rock-paper-scissors game, rare yellow beats common orange ($W_{YO} > W_{OO}$), rare blue beats common yellow ($W_{BY} > W_{YY}$), and rare orange beats common blue
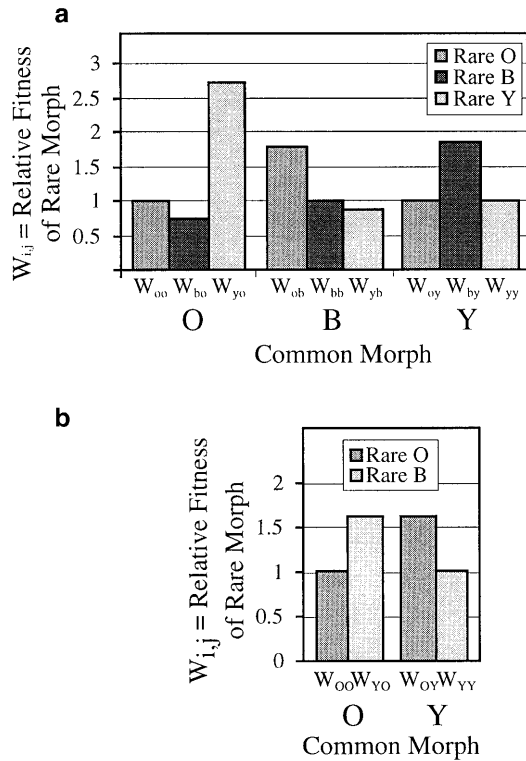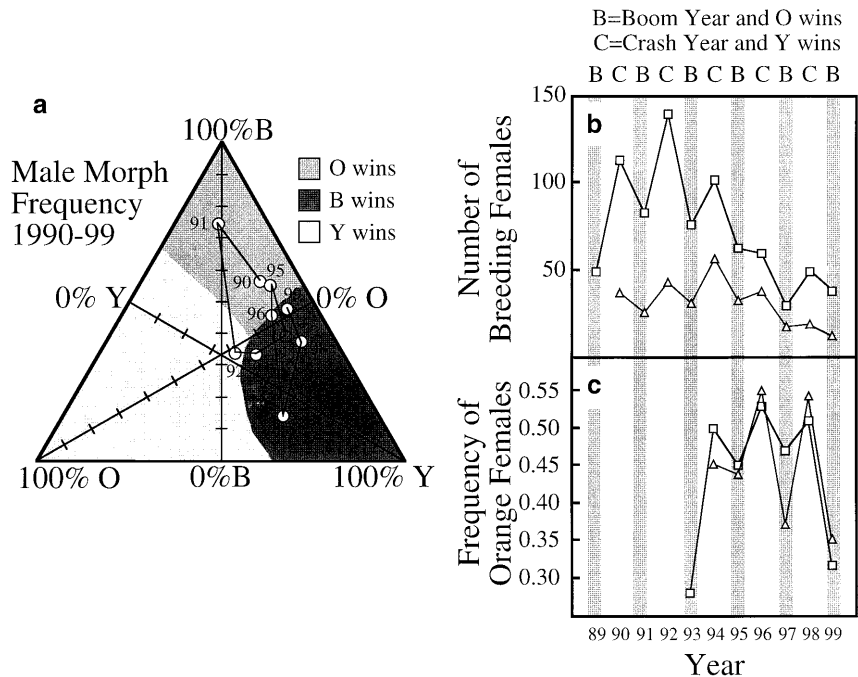
Fig. 1 a DNA-determined paternity was used to estimate fitness of morphs in nature (Zamudio and Sinervo, in press a, B. Sinervo, K. Zamudio, G. Corrigan, D. Rollo, unpublished data). Male morphs have high fitness when rare and when competing with one common morph as in a rock-paper-scissors game. Fitness of the ith morph, W_i, is predicted using $W_i = \sum f_j(t)W_{i,j}$, summed across the jth (O, B, Y) neighbor. **b** Each female morph has a fitness advantage when rare (fitness reflects number of progeny recruited to maturity). A pay-off matrix for female morphs was computed from data collected in the field during 1993–1998 (Sinervo et al. 2000). Fitness of the ith morph, W_i, can be predicted from female frequency (f_j): $W_i = \sum f_j(t)W_{i,j}$, where j=O, Y

($W_{OB} > W_{BB}$) (Fig. 2a). Fitness was estimated from nine nuclear microsatellites from paternity data collected in 1992 (Zamudio and Sinervo, in press a). The fitness of each rare strategy was estimated when competitors were common (analysis based on statistically independent neighborhoods). Ultradominant orange-throated males maintain large territories with many females, but are unable to thwart sneaky tactics of yellow-throated males that mimic females. Rare yellow males obtain 2.8 times the fitness of common orange neighbors (Fig. 1a) and rare yellow rises in frequency. Blue males mate guard fewer females than orange males and curb cuckoldry by yellow males. Rare blue males obtain 1.8 times the fitness of common yellow and rare blue rises in frequency. However, mate-guarding blue males lose to orange males (Fig. 1a). Rare orange males obtain 1.8 times the fitness of common blues and rare orange rises in frequency (Fig. 1a). The game drives a male morph cycle in nature. As male morphs cycle, so will the fitness of male offspring and the genetic quality associated with each male morph.

Interactions between females

Data on female cycles suggests that orange-throated females, 'r-strategists,' are favored at low population densities because they produce large clutches of small eggs. However, r-strategists saturate territories with their progeny within a single year and thereby depress territory quality on a population-wide basis. Yellow-throated females, 'K-strategists,' gain an advantage at high density through production of fewer but larger hatchlings that enjoy higher survival at the expense of small progeny from r-strategists, which crash in the ensuing year (Fig. 1b). Female morphs cycle in frequency every 2 years

Fig. 2 a The proportion of each male strategy (O, B, Y) cycles in frequency. Observed frequencies are shown for 1990–1999. The deFinetti diagram graphs 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. *Colors* indicate the morph with highest fitness. **b,c** Two-year cycles in female density and morph frequency are observed in the field. Orange females are at high frequency in high-density 'boom' years (*B* shown in *gray*). Yellow females are at higher frequency in low-density 'crash' years (*C* shown in *white*)

(Fig. 2b). Orange females producing many small offspring have a fitness advantage when yellow females are common and density is low ('boom' years). In contrast, yellow females producing few large offspring have higher fitness when orange females are common and density is high ('crash' years). Boom (low-density) or crash (high-density) years refer to the experience of the mother during reproduction and the survival of her offspring to the next year. At low densities, the population size will increase ('boom') while at high densities the population will decrease ('crash'). Past research estimated female fitness as a function of density and frequency of female neighbors (Sinervo et al. 2000). For detailed information on estimating female morph fitness from a decade of field-collected data see Sinervo et al. (2000). The rare advantage of yellow females always occurs at high density, which is when orange female neighbors are also at high frequency. Conversely, the rare advantage of orange females always occurs at low density, which is when yellow neighbors are at high frequency. Thus, the genetic quality of female offspring will differ between boom and crash years.

Overview of the mate choice model

Given that the fitness of male morphs cycles, female choice should depend on expected morph frequency in the next generation, and females should choose mates based on their current social environment. Offspring fitness will be affected by the social environment in the next year. As a result, the fitness of choosing a male will depend not only on the current social environment, but also on mate choice decisions of other females in the population. Frequency-dependent male mating success drives the rock-paper-scissors game between males. The female r- and K-strategy game influences female offspring fitness through density-dependent survival. Females could influence the fitness of their offspring through mate choice. We assume that females can bias their mating to the male morph that yields highest reproductive success. Female preference should also change as morph frequency cycles. Mate choice can drive morph frequency in the next generation. As a result, female preference is affected by the behavior of other females in the population and game models must be used to predict stable female preference (Maynard Smith 1982). First, we find the female preference for each male morph that maximizes expected reproductive success. Then we calculate resulting morph frequencies as a function of female behavior.

Calculating female preference

Females should show a preference based on the expected reproductive success of their progeny. The reproductive value for male offspring of the ith morph (M_i) is a function of male morph frequency in the next generation ($f2_j$,

where j=O, B, Y) and the pay-off matrix for the rock-paper-scissors game (Maynard Smith 1982; Sinervo and Lively 1996; e.g., same as $W_{i,j}$ from Fig. 1a), which is given by:

$$M_i = \Sigma(f2_j \, W_{i,j}), \quad \text{where sum is over j=O, B, Y}$$
$$(\text{e.g., } f2_O, f2_B, \text{ and } f2_Y) \tag{1}$$

The expected reproductive success of female offspring is determined by the r- and K-strategy game. Boom and crash years alternate (Sinervo et al. 2000). In boom years, the social environment of female parents consists of a low density and frequency of orange neighbors, but female progeny will predictably experience a high density and frequency of orange neighbors in the ensuing crash year. Therefore females can project from their present experience whether their offspring will experience a boom or crash year. The expected reproductive success of the ith female morph (i=O, Y) in the next generation (F_i) is a function of frequency (or density) in the next generation ($d2_j$) and the female pay-off matrix (e.g., $X_{i,j}$ from Fig. 1b), which is given by:

$$F_i = \Sigma(d2_j \, X_{i,j}), \quad \text{where sum is over j=O, Y}$$
$$(\text{e.g., } d2_O, \text{ and } d2_Y) \tag{2}$$

If we assume that male behavior and female strategy are determined as described above by a single locus with three alleles (o, b, or y), 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. For example, let $p_{O,B,Y}$ represent the probability of orange females mating with blue males producing yellow male offspring and $q_{O,B,Y}$ represent the probability orange females mating with blue males producing yellow female offspring. Preference of the ith morph is also affected by the proportion of male (R) and female offspring ($1-R$) and survival of male (λ_m) and female offspring (λ_f). For the analyses presented here, we assume male and female offspring have equal probabilities of survival. Expected reproductive success of the ith (i=O, Y) female morph mating with jth (j=O, B, Y) male morph is given by:

$$V_{i,j} = R\lambda_m \, [p_{i,j,O}M_O + p_{i,j,B}M_B + p_{i,j,Y}M_Y]$$
$$+ (1-R)\lambda_f(q_{i,j,O}F_O + q_{i,j,Y}F_Y). \tag{3}$$

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

$$Z_i = \max\{V_{i,O}, V_{i,B}, V_{i,Y}\} \tag{4}$$

Generating frequencies in the next generation

Offspring fitness will be a determined by the frequency of morphs in the next generation which is a function of the following parameters in the current generation: (1)

male morph frequency (f_j) and mating success (e.g., $W_i = \Sigma f_j W_{i,j}$ for j=O,B,Y, (2) female morph frequency (N_i), (3) female preferences, and (4) female control b_c. Let $P_{i,j}$ represent the probability that the ith female morph mates with the jth male morph and let $b_{i,j}$ represent the female's bias towards each male morph. A female's preference is predicted by the solution of Eq.4. 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 the ith female morph will mate with the jth male morph is given by:

$$P_{ij} = \frac{W_j f_j b_{ij}}{\sum_j W_j f_j b_{ij}} \tag{5}$$

The frequency of each morph is calculated from the probability of mating and the probabilities of producing each morph from a given mating. Solution of the equation for $f2_o$, and analogous equations for $f2_b$ and $f2_y$, generates morph frequency in the next generation, and $f2_o$ is given by:

$$f2_o = \sum_{j=o,b,y} [P_{o,j}(p_{o,j,o})N_o + P_{y,j}(p_{y,j,o})N_y] \tag{6}$$

Solving the model

The stable female preference cannot be found analytically. Instead, we use a best-response method to find the stable female choice strategy to a given population-level preference (Houston and McNamara 1987, 1988, 1999; Mangel and Clark 1988; McNamara et al. 1997; Clark and Mangel 2000). The algorithm searches until a stable female preference is found given morph frequencies and densities in the present generation. For more details on the method see Alonzo and Warner (2000). The only model parameter that has not been estimated from the extensive decade-long data set (Sinervo and Lively 1996; Sinervo et al. 2000; Zamudio and Sinervo in press a, unpublished data) is female control. Sensitivity analyses, ranging from no to complete control, indicate that qualitative predictions are robust to female control (see below). We have assumed that male offspring fitness is determined by the field-derived fitness function. Therefore, we do not allow female choice to alter the male pay-off matrix. As long as female control is low, intrasexual selection is strong compared to intersexual selection, or female choice enhances the rare-morph advantage, predictions should be robust to this assumption of the model. Male territoriality mainly determines the

distribution of mating success in this species, and thus female mating biases should not greatly alter the male fitness function. Similarly, the model makes the simplifying assumption that the fitness of male offspring is affected by the state of the female population only indirectly through the effect of female choice on male morph frequency in the next generation. Male fitness is affected primarily by female choice and male interactions in the field, and thus the state of the female population has little direct affect on male fitness.

Sensitivity analyses on dominance

For the above calculations, we assumed that male behavioral strategy (O, B, Y) and female life history strategy (O, Y) are controlled by three alleles (o, b, y) at one locus and determined from the genotype (oo, ob, bb, by, yy) as described above. Thus we assumed, for example, that a male adopting the blue strategy had the same fitness whether a heterozygote (oy or ob) or a homozygote (oo). We also examined the effect of varying these assumptions on model predictions. In each case, we examined the fitness of an orange or yellow female mating with each male behavioral morph. However, dominance determines the relationship between genotype and phenotype, and thus affects morph fitness and the probability of producing offspring of each morph. We examined all possible situations of complete dominance (heterozygote fitness equal to homozygote fitness) and codominance (heterozygote fitness intermediate to homozygote fitness). For simplicity, the possibility of overdominance was not explored. One can calculate the value of a male offspring of genotype ab (M_{ab})

$$M_{ab} = h_{ab}M_{aa} + (1-h_{ab})M_{bb} \tag{7}$$

where h_{ab} represents dominance of allele *a* over allele *b* ($0 < h_{ab} < 1$). For codominance, $h_{ab}=0.5$, and for complete dominance, $h_{ab}=0$ or 1. A similar calculation can be made for the female offspring value F_{ab}:

$$F_{ab} = h_{ab}F_{aa} + (1-h_{ab})F_{bb} \tag{8}$$

The probability that a female of a given phenotype will generate offspring of each phenotype $p_{i,j,k}$ and $q_{i,j,k}$ will depend on genetic dominance, but can be calculated as above from the allele and phenotype frequencies. We examined all possible combinations of complete dominance between each set of male and female alleles as well as codominance in females and codominance in males.

Model predictions

Male fitness depends on male morph frequency and female fitness depends on population density and female morph frequency. Since, throat color is heritable in males and females, and thus male morph is a predictable indi-

cator of genetic quality, females may choose males for their good genes. However, the genetic quality of male and female offspring will be context dependent. Imagine that a female is experiencing a high-density year and yellow males are rare. Which male morph should females prefer? Using the male and female field-derived fitness functions, we can predict the mate which will generate the highest fitness offspring for each female morph. We first consider female preference for producing high-quality male and female offspring separately. We then consider the more realistic case where females must choose mates that maximize male and female offspring fitness simultaneously.

Which male morph is preferred when females are only interested in maximizing fitness of male progeny?

Predictions of the model are intuitive if we first consider this simple heuristic example. In such situations, male progeny will have high fitness next year if they are themselves rare (see Fig. 2a). Thus, their mother should mate with the male morph that produces rare-morph progeny (Fig. 3). Females mating with rare males will likewise produce sons that are the rare morph. Comparing Fig. 2a and Fig. 3, one can see that there are slight differences between the rare-male phenotypic advantage and predicted female preference. This difference is driven by the underlying genetics and the expected change in morph frequency between generations. However, females are generally predicted to prefer the rare male morph when only maximizing the fitness of male offspring.

Which male morph is preferred when females are only interested in maximizing fitness of female progeny?

Female offspring fitness does not depend on male morph frequency. Instead, density in the next generation affects
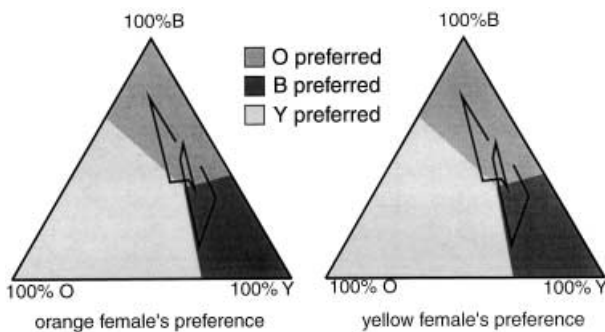

Fig. 3 Predicted female preference for male offspring only when females have low control b_c=1 (given the best-fit genetic model) as a function of male phenotype frequency and density. Axes as in Fig. 2a. *Black lines* represent the observed cycle of male morphs 1990–1999 as shown in Fig. 2a

whether orange or yellow females confer greater fitness to their mothers. Females experiencing a high-density year have daughters that experience a low-density year. If the dam experiences a high-density year, orange daughters will have higher fitness, and yellow and orange females are predicted to prefer orange males. If the dam experiences a low-density year, females are predicted to prefer blue or yellow males to produce yellow daughters. Based on phenotype alone, one would predict that females should simply prefer yellow males, and a female preference for blue males in low-density years would seem counter-intuitive. We must consider the underlying genetics to understand this prediction. Given our best genetic model, blue males are *bb*. Thus, blue males carry alleles that mainly produce yellow female offspring (yellow females can be *bb*, *by*, or *yy*). Yellow males will be *by* or *yy*, and thus also carry genes that will mainly produce yellow female offspring. As a result, females are predicted to prefer orange males in high-density years so that they can produce orange daughters with high fitness in the following low-density year. In contrast, females are predicted to avoid orange males during low-density years so they can produce yellow daughters with high fitness in ensuing high-density years. Clearly, female choice for good genes depends not only on the trait under selection, but also on the genetics determining those traits.

Which female preference maximizes fitness of male and female offspring?

A more realistic preference should be based on the value of both male and female progeny, which depends on whether it is a boom or crash year (e.g., female morph frequency) and male morph frequency (Fig. 4a). Rather than being straightforward, a female may face a trade-off. Females may prefer a given male morph to enhance reproductive success of male progeny at the expense of female progeny (or vice versa). The trade-off is stronger in crash versus boom years and thus preferences for both female morphs differ between crash and boom years. Females are predicted to gain significant increases in fitness when mating with their preferred male (Fig. 4b), and thus we would predict that female preference for male strategies should be observed in the field.

The trade-off is apparent in the following scenario (Fig. 4). When orange males are rare, orange females should choose an orange sire to enhance male progeny fitness. This choice also benefits female progeny if the next year is a boom year when orange daughters are favored but the choice is disastrous if the next year is a crash year when orange daughters do poorly. Thus, in crash years, orange females should prefer orange males because their largely orange daughters will experience a boom year when orange females do well. In boom years, orange females should no longer exclusively prefer orange, but rather they should prefer rare males because the highest fitness gains are obtained through sons.

Change in preference by yellow females between boom and crash years is also intuitively appealing. In crash years, yellow females that mate with orange sires (e.g., *oo*, *oy*, *ob*) produce mainly orange daughters that do well in the ensuing boom year. However, in boom years, yellow females should prefer rare males and maximize fitness through sons because orange sires would yield low-quality orange daughters in the ensuing crash year.

Given the observed frequencies of male morphs, a flexible decision rule for both female morphs would be to prefer rare males in boom years (e.g., 'rarest-of-N rule'), but prefer orange males in crash years ('orange-male rule'). Rare males are always superior in boom years. Orange males are superior mates in most crash years. Based on field data, orange males should be preferred by females in 8 out of 10 crash years (as compared to 3 out of 10 in boom years) of the natural male cycle. An obvious, but important, prediction of our model is also that this simple rule will generate interannual variation in mate choice. Similarly, if local populations differ in their morph frequencies and densities, context-dependent female choice will lead to variation within years in female mate choice.
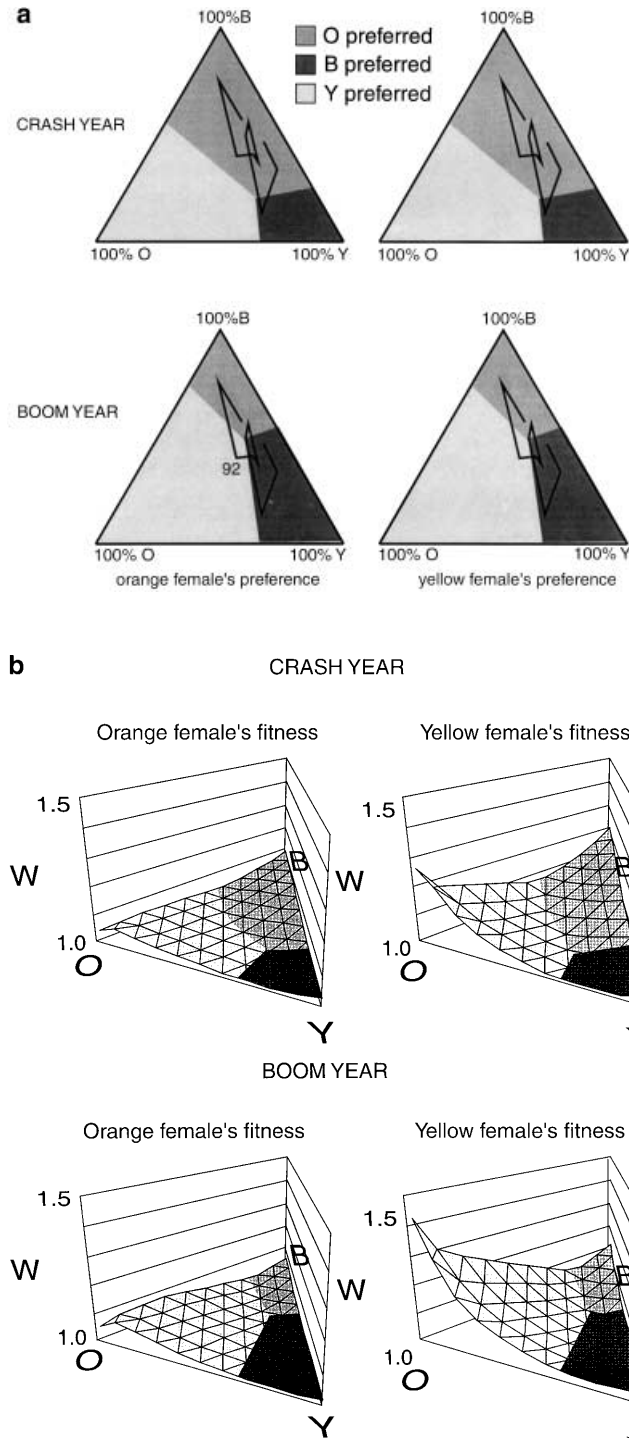
The effect of varying dominance

The results presented thus far have focused on the best-fit genetic model for the inheritance of male behavior (O, B, Y) and female strategy (O, Y). We also examined all possible combinations of complete dominance as well as codominance of male and female behavior. Genetic dominance may differentially affect the behavior adopted by individuals, the throat color observed, and the fitness gained by each genotype. For simplicity, we have focused solely on the genetic dominance driving individual strategy and assumed that behavior determines fitness. Dominance directly affects the fitness of male and female offspring as well as the probability of producing offspring of each phenotype. As a result, altering the dominance in the model clearly impacts the quantitative predictions of female mate choice. However, the general qualitative pattern of rare-male advantage in 'boom' years and a preference for orange males in 'crash' years remains the same. However, the underlying genetics do affect the resolution of the trade-off between male and female offspring, and thus the predicted preference.

To demonstrate both the importance of the underlying genetics as well as the robustness of the basic predictions, we contrast the predictions of the best-fit model (Figs. 3, 4) with an alternative dominance situation. In the best-fit genetic model, both orange males and orange females are *oo*, *ob*, or *oy*. Imagine instead that the *y* allele is dominant to *o* but recessive to *b* in males. As a result, orange males are *oo* or *ob*, blue males are *bb* or *by*, and yellow males are *yy* or *oy*. Although the basic pattern of female choice remains the same, the quantitative predictions do change (Figs. 5, 6), and the fitness associ-

Fig. 4 a Predicted female preference for male offspring and female offspring when females have low control (given the best-fit genetic model) as a function of male phenotype frequency and density. Axes as in Fig. 2a. Boom and crash years indicate the densities experienced by the mother. **b** Relative fitness gains by mating with the preferred male versus mating at random. *Color* indicates predicted female preference for each set of male morph frequencies. Male frequency axes as in Fig. 2a
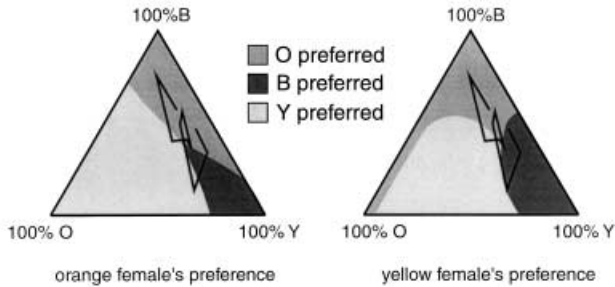
Fig. 5 Predicted female preference for male offspring only when females have low control (given the alternative genetic model) as a function of male phenotype frequency and density. Axes as in Fig. 2a

ated with choice changes as well (Fig. 6b). To understand the differences, first consider female choice for males when maximizing only female offspring. In the first situation, females are predicted to prefer orange males in crash years and mate with either yellow or blue males in boom years (see above). In contrast, when the *y* allele is dominant to the *o* allele, females should prefer blue males over yellow males in a boom year because blue males only carry genes to produce mainly yellow daughters (*bb* or *by*) while some yellow males carry genes that make orange daughters (e.g., *oy*). As a result, the trade-off between female and male offspring is altered (Fig. 6a). However, differences exist even when focusing solely on male offspring (Figs. 3, 5). The largest difference can be seen when we compare the preference of yellow females. In the best-fit genetic model, yellow and orange females are predicted to exhibit the same preference. However, in the alternative genetic model, yellow and orange females show differences in predicted mate choice (Figs. 5, 6). Yellow females have a stronger preference for orange males when the *o* allele is recessive to *y* in males. This change in preference is driven by differences in the probability of producing each morph when mating with an orange male.

Although the underlying genetics clearly affect female choice, in cases similar to the best genetic models, the qualitative pattern remains. For both situations, rare males have a mating advantage except in crash years when females largely prefer orange males. Crash years increase the preference for orange males, while boom years decrease the overall preference for orange males. However, in some situations, each female morph may exhibit a different preference. As a result, variation in female choice may be not only context dependent, but depend on female morph as well.

The effect of varying female control

Although forced copulations appear to occur in this species, recent evidence argues that females do have some control over mating (R. Calsbeek, S.H. Alonzo, B. Sinervo, K. Zamudio, unpublished data; B. Sinervo, personal observation). As female control increases in the
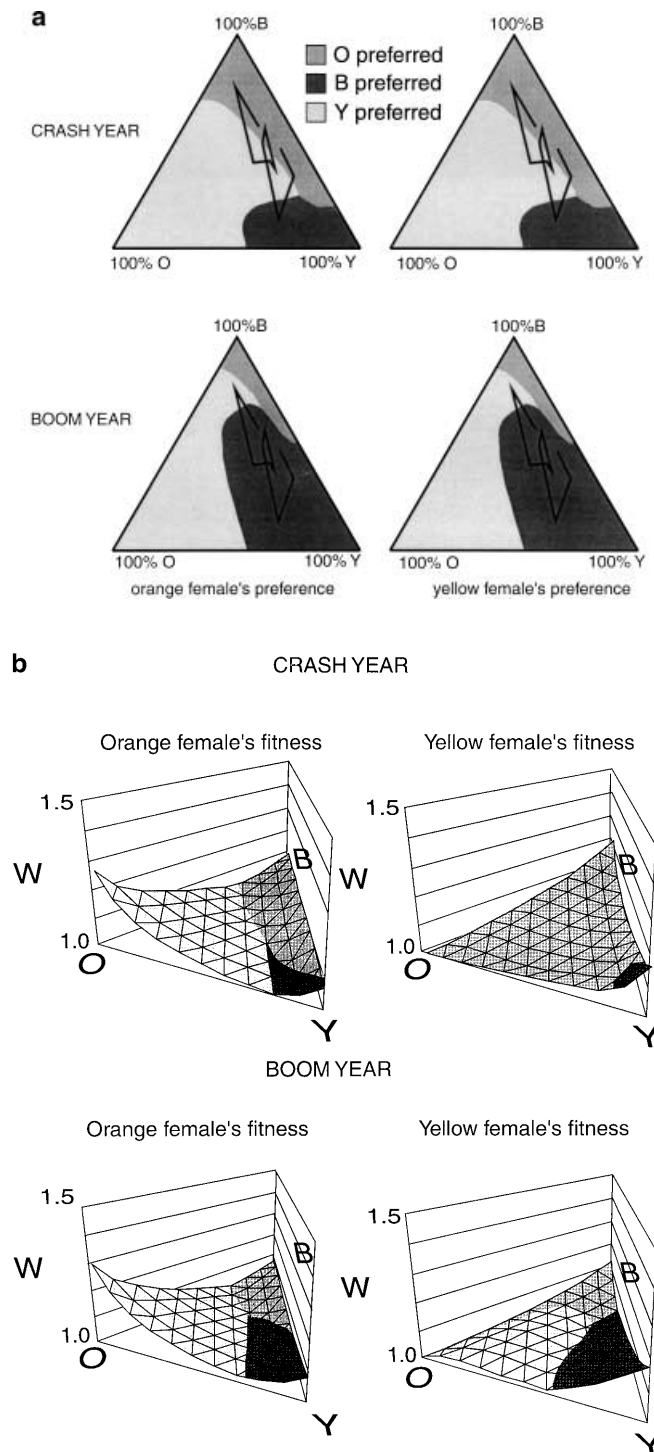

Fig. 6 a Predicted female preference for male offspring and female offspring when females have low control (given the alternative genetic model). Axes as in Fig. 2a. **b** Relative fitness gains by mating with the preferred male versus mating at random. Axes as in Fig. 3b

model, females mate more frequently with their preferred male. This can have the effect of increasing the interannual change in morph frequencies (Fig. 7). Incomplete female control (b_c small) gives changes in male
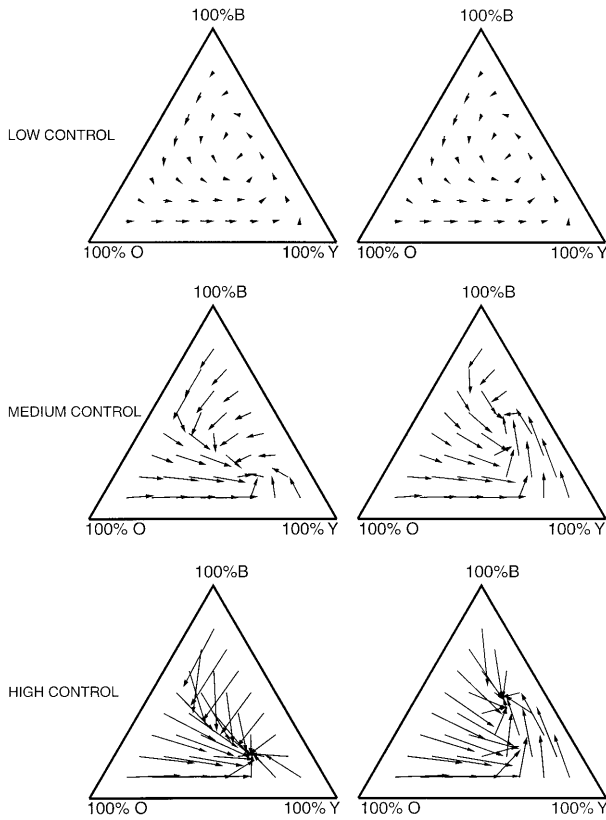
Fig. 7 Predicted change in male morph phenotype frequencies between generations when females have low (**b**$_c$=1), medium (**b**$_c$=10), and high (**b**$_c$=100) control over mating. Axes as in Fig. 2a
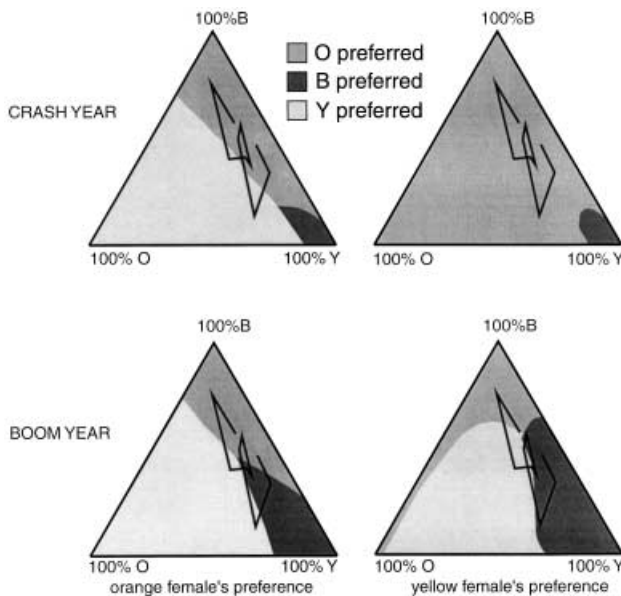

Fig. 8 Predicted female preference for male offspring and female offspring when females have high control (best-fit genetic model, **b**$_c$=100). Axes as in Fig. 2a

morph frequencies which are comparable to observed frequency change between years. Although female control alters the degree to which morph frequencies change between years (Fig. 7), it does not have a qualitative effect on female choice (Fig. 8). Although, the boundaries change, the general mate choice rule remains the same (Fig. 8). As a result, predictions of the model are robust to extreme changes (from low to complete control) in a female's ability to mate with her preferred male. However, female control and the pattern of female choice have a strong effect on the change in allele frequencies between generations. Thus female choice and female control over mating will have an important effect on the temporal dynamics of the male morph cycle.

Discussion

Female side-blotched lizards are predicted to adopt the following flexible mate choice rule: both female morphs should prefer rare males in 'boom years' of the female cycle (e.g., 'rarest-of-N rule'), but prefer orange males in 'crash years' of the female cycle ('orange-male rule'). Past models have predicted that female choice for good genes may deplete additive genetic variation (Andersson 1994). However, female choice for good genes in this species is predicted to generate variation in female choice among years and could help maintain the genetic male alternatives in the population. Although specific parameter values alter the quantitative predictions, female choice for the rare morph is a robust qualitative pattern. Females prefer rare males except when density-dependent selection on female offspring gives orange males an advantage over the rare male (Fig. 4). Similarly, female choice may differ between female morphs within a year and is predicted to vary between years as population density and morph frequency cycle. Variation within a year between sites in population density and morph frequency is common, and female choice is predicted to vary between sites. As a result, choice for good genes in this species may be observed empirically as either among-year variation in female choice within a population or between-site variation within a year.

Given the strength and predictability of genetic cycles in lizards, cues from the current social environment could be used by females to choose a mate based on genes that maximize future reproductive success of progeny, given the social environment of the next generation. In this system, females could use a single cue to predict future reproductive success of progeny – the local density of aggressive orange-throated female neighbors. Individuals, and especially females, of this species are basically philopatric (Doughty and Sinervo 1994; Doughty et al. 1994). Thus density of other individuals on their natal site will provide a reliable cue of population density and morph frequency in the next reproductive period. Female preference is predicted to respond to local morph frequency and population density. Experiments are current-

ly underway to test the ability of the model to predict female choice patterns in the field.

Genetic effects on choice

Genetic dominance affects the predictions of the model. Clearly, a female choosing good genes will be influenced by the genetics of the trait under selection and the expression of that trait in her offspring. Although the qualitative results are robust to small changes in the underlying genetics, understanding the genetics of a trait clearly increases the depth of our understanding of mate choice for good genes in any system.

Female control

Basic predictions are robust to changes in female control in the model. However, it is also important to realize that a female's control over mating will influence both optimal female choice rules and the pattern observed in the field. If female control is high, morphs will also cycle more rapidly than if control is low (Fig. 7). Although the basic predictions do not depend greatly on female control, the repercussion of female choice and empirical observations will be affected by female control. When females prefer the rare male morph, females will accelerate male morph cycles (Fig. 7). Thus female choice has a direct effect on the male game and on observed intersexual selection.

Good genes and sexy sons

In our model, choice for good genes generates variation in female choice, and good genes confer increased female survival and male success in intrasexual competition. Rules that generate variation in female choice either between individuals or across time can help maintain genetic variation in sexually selected traits. For example, although male/male competition generates the negative-frequency dependence of the male alternatives, female choice for the rare morph inherently allows the stable coexistence of male alternatives. Given recent evidence that female choice depends on social environment, experience, and condition (e.g., Dugatkin and Godin 1992, 1993; Warner et al. 1995; Briggs et al. 1996; Dugatkin 1996; Godin and Briggs 1996), the focus of many models of sexual selection on choice for specific traits rather than female choice rules represents an oversimplification of the process.

Previous theories of sexual selection have invariably assumed that choice evolves at a genetic locus, several genetic loci, or due to a preexisting genetic bias (e.g., Lande 1981; Kirkpatrick 1982; Endler and McLellan 1988; Pomiankowski 1988; Ryan 1990). Thus, current models assume that mate choice arises from a genetic change in preference alleles (see Andersson 1994). Our model assumes that mate choice must be flexible with respect to social cues. A rigid genetic choice is not assumed. Behavioral mechanisms evolve which allow flexible mate choice based on the current social environment. Thus, we allow for the existence of female choice rules that determine context-dependent choice for good genes. Simple female choice rules can generate variation in female choice that alters the dynamics of sexual selection compared to classic fixed preference models. In the side-blotched lizard, we are not dealing with a unidirectional runaway process that might deplete genetic variation. Instead, variation in the genetic quality of traits is predicted to lead to female choice rules that actually maintain genetic variation in traits.

Cognition required for the model

Our model may require cognitive ability (Janetos 1980; Real 1990, 1991), which has already been demonstrated for males of this species. Males distinguish neighbors from strangers, assess the physiological vigor of neighbors (e.g., stamina), and flee or confront neighbors that are either stronger or weaker (Y. Brandt and B. Sinervo, unpublished data). Pilot studies indicate that females are capable of similar cognitive feats (T. Comendant, unpublished data), but cognition may not be required. High orange frequency may trigger an endocrine stress response (Johnson et al. 1992), and could be used as a physiological mechanism for altering female mate choice. If so, female side-blotched lizards could readily exercise the 'rarest-of-N rule' in high-density years, and the 'orange-male rule' in low-density years.

Testing the model

A rigorous test of the model represents an enormous task since it requires multiple years of data with in-depth measures of female behavior and DNA-determined paternity. These tests are currently underway, and both naturally occurring and experimentally manipulated densities and morph frequencies are being examined. However, existing evidence is consistent with the predictions of our model. In 1992, yellow males were relatively rare, yellow females were at high frequencies, and the population was at high density. In this year, females were significantly closer to their yellow mates (17 ± 3 m) than their orange (28 ± 4) or blue (30 ± 5) mates (Zamudio and Sinervo, in press b). This pattern is consistent with female choice to maximize fitness through the production of sons.

General implications

These results have a few broad implications. First, in our model, interactions between individuals of a single sex (male/male competition and female/female games) di-

rectly influence female choice and thus intersexual selection. As a result, interactions between the sexes are inherently linked to interactions within a sex, and interactions within and between the sexes must be considered to truly understand observed patterns of female choice. Second, female choice for good genes can only be understood by considering the underlying genetics of the trait or traits under selection. For example, understanding female choice for blue males in crash years requires knowledge of the underlying genetics of male throat color. Third, female choice for good genes may result in a trade-off between high-quality female offspring and high-quality male offspring. As a result, observed preferences will depend on the resolution of this trade-off. Furthermore, choice for good genes may not be static, but instead vary as genetic quality is determined by social environment or ecological conditions. Thus female mate choice for good genes can maintain genetic alternatives in cycling genetic games. Finally, female choice can accelerate or slow change in morph frequencies through time. Thus female choice is directly affecting the rate of evolution of a trait involved in intrasexual competition.

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