The Evolution of Alternative Reproductive Strategies: Fitness Differential, Heritability, and Genetic Correlation Between the Sexes

B. Sinervo and K. R. Zamudio

Paternity analyses using molecular markers have become standard in studies of mating systems, parentage, and kinship. In systems where individuals exhibit alternative mating strategies, molecular analyses have been productively used to estimate the reproductive success of each behavioral type and hence the fitness consequences to each individual. Here we review the fitness results in a system of five alternative mating strategies present in one population of side-blotched lizards (Uta stansburiana). Males in this population adopt one of three behavioral strategies that differ in their degree of territoriality and mate guarding. In contrast, females adopt one of two strategies that differ in offspring quantity and quality. We use paternity analyses to estimate the fitness of each morph, the heritability of reproductive strategy, and the correlation in strategy between the sexes and discuss the implications of our findings for the evolution and maintenance of reproductive polymorphism in this and other systems.

Alternative mating behaviors are common in the animal kingdom, and often such strategies are accompanied by correlated morphological traits such as plumage variation in birds (Lank et al. 1995), throat color polymorphisms in lizards (Thompson et al. 1993), and color or size polymorphisms in fish (Gross 1985, 1991). DNA paternity studies have become the standard for analyzing fitness differences among individuals in experimental crosses in the laboratory and in nature (e.g., DeWoody et al. 1998; Jones et al. 1998). Most commonly genetic studies seek to identify progeny and reproductive success of various behavioral phenotypes to ascertain the fitness differential among them, and consequently the selective advantage of adopting specific strategies. On the other hand, paternity analyses are not commonly used to address the genetic basis of these alternative strategies (but see Lank et al. 1995). Evolution by natural selection is defined as the differential reproduction or survival arising from heritable variation in phenotypes (Endler 1986). Understanding the heritability of morphological and behavioral traits is thus an important step toward understanding their evolutionary dynamics and predicting evolutionary outcomes in specific contexts (Endler and Arnold 1983). Thus heritability studies complement detailed analyses of selective benefits afforded by analysis of fitness (Mousseau and Roff 1987).

Alternative mating strategies are generally thought to confer a context-dependent fitness advantage to a given mating type (Alonzo and Sinervo 2000; Alonzo and Warner 2000; Sinervo and Lively 1996). Behavioral ecologists studying alternative mating systems use game theory to determine the fitness payoff of a given mating strategy when in competition with other strategies. The solution of the payoff matrix is focused on finding the evolutionarily stable strategy (ESS; Austad 1984; Maynard Smith 1982). The ESS receives the highest fitness payoff when rare and common, and thus this strategy is able to eliminate other strategies from the population. If a single ESS does not exist, stability of the system must be in an evolutionarily stable state in which all strategies coexist indefinitely. While these game theory predictions are often used in the analysis of behaviors, phenotypic models are often constructed in the absence of information on the genetic basis of these traits, or their heritability. The outcome of natural selection critically depends on whether behavioral phenotypes have a genetic basis, or whether they arise from behavioral plasticity (Gross 1985; Maynard Smith 1982). If reproductive strategies have a genetic basis, then each should have equal fitness in the long term.
If they are to coexist (Shuster and Wade 1991, 1992). Of course, the fitness differentials among morphs can also depend on the genetics of the traits under consideration. Consider a system of three alternative male strategies that is determined by a single locus, in which two homozygotes each produce an alternative strategy, while heterozygotes produce a third strategy. If fitness of the heterozygote is higher than the two homozygotes, then the system exhibits overdominance in fitness. Overdominance in fitness will maintain genetic variation as a protected polymorphism. Equal male fitness is guaranteed to be absent in such a system.

A second mechanism for the maintenance of alternative mating strategies is that each behavioral phenotype has a frequency-dependent advantage (Maynard Smith 1982). The most common form of selection that acts to preserve polymorphism within populations is negative frequency-dependent selection (Alonzo and Warner 2000), in which a strategy has low fitness when common, but high fitness when rare. Such a system will often yield two strategies: as the frequency of a rare strategy increases, its fitness declines. The converse is true for the other morph, thereby promoting the stable equilibrium. However, with more than two strategies, the system may also result in oscillations if the three morphs satisfy conditions for a rock-paper-scissors game (Maynard Smith 1982; Sinervo and Lively 1996).

It is clear that evolutionary stability and evolutionary dynamics in any system of mating strategies critically depends on the heritability underlying these traits. In addition, if females also exhibit similar reproductive strategies, genetic correlation of strategies between the sexes can also have a profound effect on evolutionary dynamics. Here we review the results of fitness studies that address the reproductive success in a system of three alternative male strategies in the side-blotched lizard (Uta stansburiana) that are maintained by cyclic frequency-dependent selection (Sinervo and Lively 1996; Zamudio and Sinervo 2000) and two alternative strategies in female side-blotched lizards (Sinervo et al. 2000b) that are maintained by cyclic density- and frequency-dependent selection. Using paternity analyses, we estimate the heritable variation in throat color phenotypes of free-ranging side-blotched lizards and the genetic correlation of alternative strategies between the sexes (Falconer and MacKay 1996). Both parameters have profound implications for the evolutionary dynamics of throat color in this population and for the evolution of context-dependent mate choice (Alonzo and Sinervo 2001). To illustrate the generality of these ideas, we review two additional mating systems in which paternity markers have been used to study the heritability or fitness consequences of alternative morphs. We discuss other systems in which genetic markers might be useful in identifying cryptic morphs.

Materials and Methods

Overview of Breeding Study

This analysis is part of a long-term population biology study of side-blotched lizards at one site near Los Baños Grandes, California (see Sinervo and DeNardo 1996) for details on the field site). Every adult in the population was assigned to a unique toe clip and the throat colors of parents were scored at the time of first capture (Sinervo and Lively 1996; Sinervo et al. 2000b). Gravid females were brought into the laboratory and maintained until they oviposited their eggs. Eggs were incubated in the laboratory under standard conditions and upon hatching, offspring were released at the site of original capture (see Sinervo and Doughty [1996] for details of animal husbandry).

Toe clips from adults and hatchlings were used for genetic assessment of paternity. DNA paternity analyses based on nine microsatellite loci (Zamudio and Sinervo 2000) were used to determine the sire from the putative pool of sires in our closed population. Microsatellite loci were amplified from genomic template via polymerase chain reaction (PCR) and length polymorphism was assessed with fluorescently labeled primers on an automated sequencer, ABI 377 (Applied Biosystems).

We used territory maps in conjunction with data on male and female movement and maximal within-season dispersal over the outcrop to determine “lizard neighborhoods” (DeNardo and Sinervo 1994) and restrict the paternity search to smaller groups of putative fathers. Few males (less than 5% of sightings) move between plots and no male has been seen moving beyond adjacent plots (based on N = 2328 map locations). We used two computer programs, Kinship version 1.1.2 (Goodnight et al. 1996) and Cervus (Marshall et al. 1998), to assign paternity for hatchlings born during the 1992 and 1996 breeding seasons. In Kinship we accepted a male as sire of a hatching if the likelihood of paternity was significantly different (P < .05) from that expected for unrelated males. Thus this method is based on exclusion, yet uses likelihood ratio tests to estimate the most probable sire among the nonexcluded males. However, depending on overall levels of relatedness within neighborhoods, this method could erroneously assign as sires males with only slightly higher likelihoods. This would be most likely in systems where potential fathers are often brothers or father-son pairs. We compared these results to paternity analyses performed with the program Cervus (Marshall et al. 1998) using confidence intervals of 80 and 95%. Sire assignments were very similar, although the total numbers of sires assigned were lower in the second analysis (Zamudio and Sinervo 2000). Given the similarity of the results, we report here on the paternity results from the Kinship analysis, and use these to estimate heritability and genetic correlations (Falconer and MacKay 1996; Li 1975). From the 1992 and 1996 datasets, we recovered a total of 20 sire-son pairs and 43 sire-daughter pairs for which paternity was determined with confidence and for which we obtained throat scores of the progeny at maturity.

Throat Color Scores and the Development of Adult Coloration

We scored throat color of all parents during the breeding season and of their progeny that were recaptured at maturity the following year. An initial analysis based on only 1 year of data indicated that the presence of orange, blue, and yellow on male side-blotched lizard throats is discrete and heritable in nature (Zamudio and Sinervo 2000). However, at that time we had only 1 year of paternity results and 11 sire-offspring pairs. Further examination of throat coloration and variation in the population suggests a discrete character and we can discern six color phenotypes that are correlated with the behavioral strategies. Putative homozygous males have solid throat colors—orange (oo), dark blue (bb), or yellow (yy)—and represent the three discrete color morphs we analyzed previously (Zamudio and Sinervo 2000). Three discrete heterozygous phenotypes have intermediate phenotypes. Putative blue-yellow heterozygotes (by) have alternating yellow and pale blue stripes that are markedly paler than the dark blue of homozygotes. Blue-orange heterozygotes (bo) have alternating blue and orange stripes on the throat and light orange flanks, much lighter than the vibrant or-
ange flanks of orange homozygotes. Yellow-orange heterozygotes (yo) have yellow throats with pale blue stripes and pale orange flank markings. Presence of any orange (oo, bo, yo) results in males that adopt the highly aggressive usurper male strategy (Calsbeek R and Sinervo B, unpublished data). The presence of blue results in males that adopt the mate-guarding strategy (bb). The presence of yellow in the absence of orange (by, yy) results in males that adopt the sneaker strategy.

Females in this population also have colored throats. However, side-blotched lizards are sexually dimorphic, and in general the coloration of females is more muted than in males. This is particularly true of the blue coloration. However, the orange coloration in females can be as vibrant as in males, and is discrete from the yellow alternative color phenotype (Sinervo et al. 2000b). We can score only four phenotypes from oo, or bb phenotypes from by, suggesting o and b alleles may be dominant to y in females, and we cannot resolve clear intermediates in females, largely because females do not express the flank coloration seen in males. Presence of any orange in females (e.g., oo and bo) results in an r-strategy phenotype, while absence of orange (e.g., by and yy) results in a K-strategy phenotype (Sinervo et al. 2000b). While blue is present in some females, it appears to have no detectable effect on female life history (Sinervo et al. 2000b).

To estimate heritability and take into account the intermediate phenotypes in the population, we constructed a three-class score for orange. Putative orange homozygotes (oo) received a score of 1, putative orange-blue and yellow-orange heterozygotes (yo, bo) received a score of 0.5, and those with orange absent (blue or yellow only, bb, by, yy) received a score of 0. Such a scoring system takes into account the additive effects of underlying genetic factors on throat color (Li 1975), which is also related directly to heritability and additive genetic variation (Falconer and MacKay 1996). Fisher’s (1918) contribution to the neo-Darwinian revolution was the insight that the same methods and inferences can be applied to heritable variation regardless of whether one or many loci give rise to a trait (Li 1975; Provine 1971). In particular the heritability of a single locus trait based on the additive effect of an allele to the phenotypic score for parents and progeny can be estimated by parent-offspring regression. The heritability derived by regression analysis is not biased by the underlying single-locus trait, which has a nonnormal distribution. However, if the trait is due to a single locus then the statistical inference of the significance of a slope (i.e., heritability) and the standard error about the slope may be biased because normality assumptions of the y variable are violated (Mitchell-Olds and Shaw 1987). To avoid this problem we tested for the significance of slopes by randomizing sire and color associations (1000 times) and compared our observed patterns to the simulated null hypothesis. We were particularly interested in the heritability of orange color from sire to son and from sire to daughter. Thus we scored sons according to the system described above for sires. However, daughters only express a marked difference in yellow versus orange, so we lumped any female with orange into the orange category (score 1). Females lacking orange were placed into the yellow category (score 0). Yellow is baseline on all throat scales, which is consistent with ontogeny of color. All juveniles have yellow throats, and if color changes, it does so at maturity.

Results

Heredity and Genetic Correlations of Throat Coloration Between the Sexes

Based on sire-son regression (Figure 1), we found significant heritability for orange \( h^2 = 1.24 \pm 0.41 \) (±SE), \( F_{1,15} = 9.06, P < 0.02, N = 20, \) based on 1000 randomizations). Similarly the heritability for throat color from sire-daughter regression was significant \( h^2 = 0.88 \pm 0.32, F_{1,41} = 7.15, P < .01, N = 43, \) based on 1000 randomizations).

We also specifically tested for a significant difference between sire-son and sire-daughter regression slopes with analysis of covariance (ANCOVA). The slopes of the regression line for sire-daughter pairs was significantly lower than the slope of the regression line for sire-son pairs (ANCOVA difference in slope, sire x progeny sex effect, \( F_{1,59} = 4.69, P < .03, \) effect of sire \( F_{1,59} = 4.82, P < .03, \) effect of progeny sex). 

Fitness Differentials Among Male and Female Morphs

Male side-blotched lizards in this population exhibit three throat color morphs that are associated with alternative mating strategies (Sinervo and Lively 1996; Zamudio and Sinervo 2000). Orange-throated males are polygynous and defend large territories that overlap with the territories of many females. Orange-throated males tend to be larger than the other two morphs. Yellow-throated sneaker males are female mimics and cuckold orange males at a high rate (Zamudio and Sinervo 2000). Yellow males do not defend a territory and their small size is an advantage in obtaining access to orange male territory through female mimicry. Blue-throated males avoid cuckoldry by mate guarding; however, blue-throated males are less successful in defending their territory against ultradominant orange-throated males that can usurp space and thereby gain access to females (Calsbeek R and Sinervo B, unpublished data). The incidence of male throat color morphs cycles among years from a high frequency of orange, to yellow, then blue, in a fashion analogous to a rock-paper-scissors game (Figure 2). The genetic cycle in males has a 4- to 5-year period and is driven by frequency dependent selection that favors rare morphs in any given year (Sinervo, in press; Sinervo and Lively 1996; Zamudio and Sinervo 2000).

The overt differences in behavior seen among male morphs are not as obvious in females, but orange females seem more aggressive (qualitatively) than yellow-throated females. Female color morphs exhibit striking differences in reproductive strategy (Sinervo et al. 2000b). The frequency of female throat color morphs cycles in a more rapid 2-year period and is coupled to a rapid 2-year cycle in popu-
genetic variation associated with daughter (Figure 2). The significantly lower additive sense heritability $1.24$ is evidenced by the heritability of throat color in free-ranging females ($h^2 = 0.48$, Sinervo et al. 2000a). This lower estimate is possibly due to maternal effects and associated natural selection.

Throat color variation is genetically correlated between the sexes (Figure 1), as evidenced by the heritability of throat color between females and their male sires. Thus the rock-paper-scissors game of male morphs is necessarily coupled to the offspring quantity and quality game of female morphs. The simple observation that genetic variation between male and female throat color morphs is correlated has profound implications for the evolution of alternative strategies. We discuss the general implications of our findings by reviewing the genetic mechanisms controlling alternative strategies in lizards and other systems with alternative strategies. Furthermore, we discuss the selective consequences of the genetic correlation for the evolution of female choice and the evolution of correlated life-history variation.

The expression of genetically determined throat coloration in male and female lizards appears to be mediated by the endocrine system (Moore 1991; Moore and Thompson 1990). Orange coloration can be induced in adult females by injecting them with progesterone (Cooper and Greenberg 1992). Blue coloration appears to be under the control of testosterone in the tree lizard (Urosaurus ornatus; Hews et al. 1994; Hews and Moore 1995). Moreover, the higher levels of aggression evident in orange-throated males (Sinervo and Lively 1996; Calsbeek R and Sinervo B, unpublished data) is correlated with high levels of testosterone (Sinervo et al. 2000a), which is the general activator of aggression in lizards (Moore 1988). One metabolic pathway by which testosterone is produced is through steroid metabolism of progesterone (Crews et al. 1983; Moore et al. 1985). Thus a pleiotropic explanation for the correlation of coloration and behavior between the sexes is that they are controlled by the action of an alternative allele for a regulatory gene that determines the rate at which progesterone is converted into testosterone. A highly active regulatory gene would increase testosterone and reduce progesterone. The converse would be true for a less active allele. It is also noteworthy that progesterone is also produced by corpora lutea of females (Crews et al. 1983; Moore et al. 1985). Thus the positive genetic correlation between large clutches and orange throat color (Sinervo et al. 2000b) may arise from yet another common endocrine mechanism. In this case, follicle stimulating hormone (FSH; Sinervo and Licht 1991), which is the primary gonadotropin of squamate reptiles (Licht et al. 1977). Alternatively, morphs may arise from genetic variation in the regulator of FSH, gonadotropin releasing hormone (GnRH; Phillips et al. 1987; Phillips and Lasley 1987), and GnRH has been implicated in the development of alternative morphs in teleost fish (Grober et al. 1994).

**Genetic Cycles, Male and Female Alternative Strategies, and Mate Choice**

In the side-blotched lizard mating system, a total of five alternative morphs are present, three in males and two in females. If the male and female strategies are coupled and determined by a single locus, as is suggested by our heritability estimates, then genetic models predict the observed pattern of a 4- to 5-year cycle in males and a 2-year cycle in females (Alonzo and Sinervo 2001); we would not predict this pattern if alternative strategies in males and females arise from multiple loci that are unlinked. Frequency-dependent fitness

---

**Discussion**

**Heritability of Throat Color and the Mechanistic Basis for Genetic Correlations**

Our DNA-based paternity study demonstrates very high levels of additive genetic variation in throat color in free-ranging side-blotched lizards (Figure 1; narrow-sense heritability $1.24 \pm 0.41$ based on sire-son and $0.88 \pm 0.32$ based on sire-daughter). The significantly lower additive genetic variation associated with daughters is indicative of an interaction between sex and expression of throat color (Falcoconer and MacKay 1996). We previously reported a lower heritability for orange/yellow color found in a large study of free-ranging females ($h^2 = 0.48$, Sinervo et al. 2000a). This lower estimate is possibly due to maternal effects and associated natural selection.

Throat color variation is genetically correlated between the sexes (Figure 1), as evidenced by the heritability of throat color between females and their male sires. Thus the rock-paper-scissors game of male morphs is necessarily coupled to the offspring quantity and quality game of female morphs. The simple observation that genetic variation between male and female throat color morphs is correlated has profound implications for the evolution of alternative strategies. We discuss the general implications of our findings by reviewing the genetic mechanisms controlling alternative strategies in lizards and other systems with alternative strategies. Furthermore, we discuss the selective consequences of the genetic correlation for the evolution of female choice and the evolution of correlated life-history variation.

The expression of genetically determined throat coloration in male and female lizards appears to be mediated by the endocrine system (Moore 1991; Moore and Thompson 1990). Orange coloration can be induced in adult females by injecting them with progesterone (Cooper and Greenberg 1992). Blue coloration appears to be under the control of testosterone in the tree lizard (Urosaurus ornatus; Hews et al. 1994; Hews and Moore 1995). Moreover, the higher levels of aggression evident in orange-throated males (Sinervo and Lively 1996; Calsbeek R and Sinervo B, unpublished data) is correlated with high levels of testosterone (Sinervo et al. 2000a), which is the general activator of aggression in lizards (Moore 1988). One metabolic pathway by which testosterone is produced is through steroid metabolism of progesterone (Crews et al. 1983; Moore et al. 1985). Thus a pleiotropic explanation for the correlation of coloration and behavior between the sexes is that they are controlled by the action of an alternative allele for a regulatory gene that determines the rate at which progesterone is converted into testosterone. A highly active regulatory gene would increase testosterone and reduce progesterone. The converse would be true for a less active allele. It is also noteworthy that progesterone is also produced by corpora lutea of females (Crews et al. 1983; Moore et al. 1985). Thus the positive genetic correlation between large clutches and orange throat color (Sinervo et al. 2000b) may arise from yet another common endocrine mechanism. In this case, follicle stimulating hormone (FSH; Sinervo and Licht 1991), which is the primary gonadotropin of squamate reptiles (Licht et al. 1977). Alternatively, morphs may arise from genetic variation in the regulator of FSH, gonadotropin releasing hormone (GnRH; Phillips et al. 1987; Phillips and Lasley 1987), and GnRH has been implicated in the development of alternative morphs in teleost fish (Grober et al. 1994).

**Genetic Cycles, Male and Female Alternative Strategies, and Mate Choice**

In the side-blotched lizard mating system, a total of five alternative morphs are present, three in males and two in females. If the male and female strategies are coupled and determined by a single locus, as is suggested by our heritability estimates, then genetic models predict the observed pattern of a 4- to 5-year cycle in males and a 2-year cycle in females (Alonzo and Sinervo 2001); we would not predict this pattern if alternative strategies in males and females arise from multiple loci that are unlinked. Frequency-dependent fitness
Male mating strategies in the ruff (*Philomachus pugnax*) provide another example of how alternative male phenotypes can be maintained in a latent genetic form in females by the action of sex steroids. Ruffs breed and nest in northern Europe, and are named for the distinct neck plumage exhibited by males. Independent male

in both sexes results in different morphs having high fitness each year of the cycle. Thus the fitness of hatchlings of each sex will depend on the stage of the male and female cycles at that particular time. In this situation, theory predicts the evolution of context-dependent mate choice. Females should prefer rare male morphs to maximize the fitness of sons (a rare male morph has high fitness), but prefer orange sires to maximize the fitness of daughters depending on the phase of the female cycle (Alonzo and Sinervo 2001) (Figure 4).

**Evolution of Male and Female Strategies and Self-Reinforcing Genetic Correlations**

Expression of alternative male morphs in many species may have genetically correlated effects on life-history traits of females through a genetic correlation between the sexes. The genetic and demographic link in side-blotched lizards has been made explicit by our demonstration of a genetic correlation between male and female throat color (Figure 1). The degree to which expression of alternative male strategies “spills over” into the female phenotype depends on whether male traits carry an advantage for females in a game theoretic context. If male physiological traits have a negative impact on all female traits, it should be possible to turn off their expression via endocrine mechanisms (Moore 1991). However, if the advantages and disadvantages of male-specific behavior depend on context, their phenotypic expression in females can potentially be refined by the action of frequency-dependent selection. For example, the aggressive phenotype of orange-throated males is also reflected in higher levels of aggression in orange females, which attempt to exclude other females from their territories (Comendant T and Sinervo B, unpublished data). This aggressive strategy is effective at low density and these females monopolize the highest quality territories. However, at high density aggressive behavior appears to be a fitness liability. Orange females suffer from immunosuppression and reduced fitness at high density (Svensson E, et al., unpublished data). This situation is analogous to that in males; orange males also suffer higher adult mortality rates than either blue or yellow males (Sinervo and Lively 1996). In contrast, yellow females are more resilient and do not suffer from density-dependent reductions in fitness (Sinervo et al. 2000b). Thus while the *r* strategy phenotype of orange females may be advantageous when orange females are at low frequency, the *K* strategy phenotype of yellow females fares far better at high orange density and frequency.

A context-dependent form of aggression would be advantageous in orange females according to the following rule: express aggression at low density but suppress aggression at high density. Life-history trade-offs may preclude such plasticity from evolving. Once a female morph has adopted a given strategy, covariation formed as that strategy increases in frequency becomes its downfall under the opposite social conditions. Sinervo et al. (2000b) demonstrated that correlational selection associated with density and frequency cycles is sufficient to form genetic correlations among unlinked loci for throat color, clutch size, and egg mass. Correlational selection is disruptive (Brodie 1992) in that it shapes genetic covariation to either side of the clutch and egg-size trade-off (Sinervo 2000). As each strategy becomes better adapted to a different phase of the density cycle, oscillations are reinforced, owing to adaptation by each strategy.

Adaptation of morphs due to correlational selection will equilibrate when segregation and recombination erode favorable linkage disequilibrium as fast as it is formed by selection. This results in a chronic selective load (Wallace 1970) on morphs that can only be reduced if life-history loci become physically linked to throat-color loci. Thus selection pressure favoring genomic rearrangements of loci related to morph fitness may be very strong (Sinervo et al. 2000b). This genetic correlation, reinforced in a game-theoretic context, provides a selective mechanism by which supergenes involving multiple unlinked loci (e.g., life-history traits and color loci) might become linked in systems of alternative strategies.

**Alternative Male Behaviors and Morphology in the Ruff**

Male mating strategies in the ruff (*Philomachus pugnax*) provide another example of how alternative male phenotypes can be maintained in a latent genetic form in females by the action of sex steroids. Ruffs breed and nest in northern Europe, and are named for the distinct neck plumage exhibited by males. Independent male
ruffs defend a territory (and females) against other independents (Lank et al. 1995). Males defend territories in leks, where many males aggregate and display to attract visiting females (Höglund and Alatalo 1995). Nonterritorial satellite males move among territories and attempt to copulate with females on territories of the dominant males.

In this case, obvious alternative strategies are suppressed in females by the action of sex-determining mechanisms. Lank et al. (1995) used minisatellites to determine which males sired the chicks on ruff breeding grounds in Finland. They also scored the morphology of the female parent’s brother and father to determine the likely phenotype that the female would have expressed had she been male. Such genetic sleuthing is particularly important with sexually dimorphic traits, which have a sex-limited expression; females might carry genes for morphology that they pass on to their male offspring. The field-caught chicks in this experiment were reared to maturity and the breeding morphology of the male progeny scored. Because only two phenotypes are seen in the ruff, it is likely that a single genetic locus with a dominant and a recessive allele control the mating phenotypes. Genetic crosses rule out the possibility that the gene is sex linked, therefore the sex-limited expression of plumage must arise from the suppression mechanisms involving sex steroids. Lank et al. (1999) further tested this idea by implanting female ruffs with testosterone and inducing the male phenotype.

Behavioral observations suggest that male fitness arises from the female preference for larger leks (Lank and Smith 1992; Höglund and Alatalo 1995) and that each morph has an advantage that varies with lek density. Visiting smaller leks increases satellite fitness, while being in the largest leks optimizes resident fitness. Thus residents would benefit by allowing satellites to remain on the lek, even if they must allow satellites to have copulations, because the largest leks attract the most females. Satellites, however, should leave once the lek gets too large and their success begins to fall. Thus in this system, female choice also plays an important role in the dynamics of male strategies (Hugie and Lank 1997).

Epistatic Genes for Alternative Male Strategy and Sex Ratios in Marine Isopods
A second example of genes that control alternative male behaviors is found in the marine isopod, *Paracerceis sculptra*. The genes for alternative male behavior are epistatically linked to genes that control alternative female strategies of sex ratio. Shuster and his colleagues have characterized three alternative male morphs (Shuster and Sassaman 1997; Shuster and Wade 1991): large alpha males that defend harems of females, medium-sized beta males that mimic female behavior and morphology, and small-sized secretive gamma “sneaking” males. Shuster (1989) used cuticular markers to assess male fitness in laboratory-reared isopods (Shuster and Wade 1991, 1992) and used the results on siring success to determine that fitnesses of the three morphs were approximately equal. However, the rules used to construct the fitness inferences were frequency-dependent in form. Whether or not such frequency dependence contributes to the stability of the morphs has yet to be resolved.

Shuster and Sassaman (1997) further investigated the heritability of these behaviors and developed a genetic model that explains patterns of inheritance of the three morphs. Three alleles, α, β, and γ at the Alternative male strategy (Ams) locus provide a reasonable explanation of the general pattern of inheritance of male morphs. The three alleles have the following dominance relations: β is dominant to both γ and α, γ is dominant to α, and α is recessive to both β and γ. The α allele occurs at a high frequency in the population (93%) compared to either β (1%) or γ (6%). Thus the vast majority of β and γ individuals in the population are likely to be heterozygotes. They also found that genetic crosses between females and the predominant male genotypes resulted in significant departures from a 50:50 sex ratio of the progeny. The existence of a second locus termed transformer (Thr, 1 or 2) is required to adequately explain the aberrant sex ratio found in certain genetic crosses. The Thr locus causes males to transform into females, or females to transform into males. However, the direction of sex change depends on the genotype at the Ams locus. Thus the epistatic interaction between two loci governs the expression of male and female behaviors in this marine isopod. The Ams gene interacts in a nonadditive fashion with the Thr gene. The researcher’s ability to resolve the additional locus only came about because of linkage information of the genetic cuticular markers and other electrophoretic markers, highlighting the importance of such markers in the genetic analysis of morphotypes.

The involvement of a sex-distorting factor in the sex transformer locus may be analogous to a context-dependent control of sex ratio found in side-blotched lizards (Adamoupolou C and Sinervo B, unpublished data). Sex ratio games arise when local mate competition leads to a sexually selected advantage in one sex over another (Trivers and Willard 1973). In the case of alternative male strategies, only a few of the despotic male mating types are required to hold harems (e.g., orange males in lizards and alpha males in isopods). Thus selection will favor sex ratio adjustment (or perhaps a frequency-driven sex ratio distorter) in those females that are likely to give rise to sons with a despotic morphotype. Rather than flood the market with an excess of despots, only a few well-provisioned despotic sons should be produced, and thus an excess of daughters. In lizards, sex ratio adjustment should be context dependent, because the production of many orange daughters is a fitness liability only in alternate years of the female cycle (Alonzo and Sinervo 2001; Adamoupolou C and Sinervo B, unpublished data). The offspring quantity and quality game predicts that orange females should produce orange sons when surrounded by other orange females. In laboratory experiments where we manipulated the number of orange neighbors in terraria (Adamoupolou C and Sinervo B, unpublished data), we found that orange females altered sex ratio in response to the number of orange neighbors in the predicted fashion. Orange females produced more daughters when there were no orange neighbors, but more sons when orange neighbors were common.

The Evolution of Coadapted Morph Gene Complexes Versus Plastic Strategies
The degree to which the ruff and isopod mating systems are in equilibrium remains to be determined. However, sex ratio appears to undergo dramatic oscillations in the isopod system (Shuster 1990; Shuster and Sassaman 1997). If these oscillations are driven by a sex ratio game that is selectively related to the alternative male strategy locus, then these dynamics may be similar to those reported for the side-blotched lizard. Both the isopod and the lizard are short-lived species; side-blotched lizards are nearly annuals, and isopod females are semelparous (Shuster 1990). The short generation times of both
species allows for the resolution of rapid genetic cycles. However, even moderate interannual survival found in more long-lived species, such as the ruff, would not preclude oscillations (Sinervo and Lively 1996). In long-lived species with overlapping generations, oscillatory dynamics may also be present, although not on a time scale observable by humans. An effective approach to discerning whether oscillations occur is to elucidate the frequency-dependent selection that drives alternative mating systems. Most evolutionary dynamics can be predicted from the frequency dependent selection, and from knowledge of the genetic factors underlying trait evolution.

It is noteworthy that all of the alternative strategies uncovered to date involve visual signals. The color signals of side-blotched lizards are quite conspicuous to organisms with fine visual acuity in the visible range. However, alternative mating strategies may be more common than published examples indicate. A recent review by Zamudio and Sinervo (in press) suggests that many more species of lizards, some less conspicuously colored than others, may exhibit alternative mating systems that have not yet been studied in detail. Likewise, in other systems, alternative male morphs most certainly remain cryptic to human observers. We uncovered the more subtle alternative female phenotypes in side-blotched lizards only after consideration of the more obvious male strategies that are correlated with overt behaviors (Sinervo et al. 2000b). The female game in lizards involves density cycles and the model for the evolution of these cycles is remarkably similar to a hypothesis proposed for population cycles in rodents (Chitty 1958, 1960). If rodent cycles do indeed turn out to be driven by alternative female strategies, then correlated alternative male strategies are also likely to be found in rodents. Many species may use alternative strategies, but some sensory modalities are difficult to study in nature and this may obscure obvious morphs. The dominant sensory modality of mammals is olfaction (Drickamer 1992; Mikiesic and Drickamer 1992), which is notoriously difficult to measure. In these cases, paternity markers (especially if linked to the “alternative morph” locus) may be most useful to measure fitness and identify cryptic morphs.

Context-Dependent Good Genes, Mate Choice, and Alternative Strategies

Given the genetic correlation for throat color between the sexes, theory predicts that male and female games in side-blotched lizards promote the evolution of a context-dependent mate choice game. At any point in the cycle, progeny in the next generation will benefit from a specific set of alternative strategies. The high heritability of traits, and the fact that even heterozygous individuals benefit from a given allele depending on the phase of the cycle, select for mate choice as a function of throat-color alleles. For example, even a homozygous yellow female can produce orange daughters if she mates with an orange male (especially a homozygous orange male). Yellow females will be favored if they mate with orange males in crash years because her daughters will experience a boom when orange allelles in female progeny have high fitness (Sinervo et al. 2000b).

Previous theories of mate choice invariably assume that choice evolves at a genetic locus (Kirkpatrick 1982; Lande 1981; Pomiankowski 1988) or is related to a genetically determined preexisting bias (Ryan 1997). Most current models assume that mate choice arises from a genetic change in preference alleles for traits (see Andersson 1994). Our model of context-dependent mate choice assumes that mechanisms of mate choice must be flexible with respect to social cues. Thus a rigid genetic choice is not assumed. In context-dependent male choice, behavioral mechanisms evolve that allow flexible mate choice based on the current social environment. Frequency-dependent selection favors evolution of such context-dependent male choice whenever the impact of choice on progeny fitness varies in time or space, and this change can be predicted from environmental or social cues.

In Uta stansburiana, evolutionary games cause morph fitness to cycle, and morph frequency provides a reliable cue for mate choice. Temporal or spatially varying frequency-dependent selection is common in many species with alternative morphs (Zamudio and Sinervo 2000). Thus our hypothesis should be applicable to many species with alternative strategies (fish: Gross 1985, Hoffman et al. 1985; birds: Lank et al. 1995; lizards: Moore and Thompson 1990; isopods: Shuster and Wade 1991). The theory will also apply to groups with population cycles, such as mammals (Boonstra et al. 1998; Chitty 1960; Moorcroft et al. 1996), where cycle phase is predictable from density-induced stress (Johnson et al. 1992). Females should choose mates that supply progeny with good genes, but the specific preferred traits will depend on the phase of the cycle. Alleles that enhance fecundity are preferred during the $r$ phase of population growth. However, alleles that enhance disease resistance may be preferred during a crash and a crash is imminent.

The Future of Molecular Techniques and Genetic Analysis of Mating Systems

We used paternity analysis of the side-blotched lizard system to discern fitness differential among morphs and estimate heritability in nature. From these, we predict the genetic effects of sire on both sons and daughters. Thus paternity analysis has not only allowed for an estimation of the relevant fitness effects, but also the genetic origin of the traits of interest. Genetic correlations between the sexes have profound implications for the evolutionary dynamics of mating strategies and the evolution of mate choice. Molecular markers will continue to play a major role in future analysis of mating strategies, reproductive success, and the importance of mate choice in maintaining polymorphism in mating systems. The next step in the application of such technology is to develop genetic markers that might be used in selection analyses on how mating systems promote the evolution of genetic correlations, and thereby lead to changes in the genomic architecture of the species. Tracking the linkage disequilibrium between throat color and unlinked genetic markers that arises from selection (Rieseberg et al. 1996) would elucidate the genetic signature of correlational selection in the wild and the nonlinear fitness epistasis that is likely to affect alternative morphs. This may be particularly useful in species in which signals are not visible to the eye, but genetic markers might reveal oscillatory behavior of linked loci (e.g., rodent cycles). Thus application of molecular markers in parentage and kinship studies may also uncover cryptic morphs (Lidicker et al. 2000).

References


Austad SN, 1984. A classification of alternative repro-


Corresponding Editor: John C. Avise