

Models of Density-Dependent Genic Selection and a New Rock-Paper-Scissors Social System

Barry Sinervo,^{1,*} Benoit Heulin,^{2,†} Yann Surget-Groba,^{3,‡} Jean Clobert,^{4,§} Donald B. Miles,^{5,||} Ammon Corl,^{1,#} Alexis Chaine,^{1,4,**} and Alison Davis^{1,††}

1. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064;
2. Centre National de la Recherche Scientifique (CNRS)–Unité Mixte de Recherche 6553, Station Biologique, 35380 Paimpont, France;
3. School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2DG, United Kingdom;
4. Station d'Ecologie Expérimentale du CNRS (Unité de Service et de Recherche 2936), Laboratoire Evolution et Diversité Biologique, Moulis, 09200 Saint-Girons, France;
5. Department of Biology, Ohio University, Athens, Ohio 45701

Submitted March 7, 2007; Accepted May 23, 2007;
Electronically published September 21, 2007

Online enhancement: table.

ABSTRACT: We describe new ESS models of density regulation driven by genic selection to explain the cyclical dynamics of a social system that exhibits a rock-paper-scissors (RPS) set of three alternative strategies. We tracked changes in morph frequency and fitness of *Lacerta vivipara* and found conspicuous RPS cycles. Morphs of *Uta* and *Lacerta* exhibited parallel survival-performance trade-offs. Frequency cycles in both species of lizards are driven by genic selection. In *Lacerta*, frequency of each allele in adult cohorts had significant impacts on juvenile recruitment, similar to mutualistic, altruistic, and antagonistic relations of RPS alleles in *Uta*. We constructed evolutionarily stable strategy (ESS) models in which adults impact juvenile recruitment as a function of self versus nonself color rec-

ognition. ESS models suggest that the rapid 4-year RPS cycles exhibited by *Lacerta* are not possible unless three factors are present: behaviors evolve that discriminate self versus nonself morphs at higher rates than random, self- versus non-self-recognition contributes to density regulation, and context-dependent mate choice evolves in females, which choose sire genotypes to enhance progeny survival. We suggest genic selection coupled to density regulation is widespread and thus fundamental to theories of social system evolution as well as theories of population regulation in diverse animal taxa.

Keywords: alternative mating strategy, rock-paper-scissor dynamic, evolutionarily stable strategy (ESS), genic selection, evolution of social systems.

The rock-paper-scissors (RPS) game has been modeled extensively (Wright 1968; Maynard Smith 1982; Sinervo and Lively 1996; Frean and Abraham 2001; Sinervo 2001a; Kerr et al. 2002; Semmann et al. 2004). Theory demonstrates that intraspecific polymorphism can be maintained indefinitely by negative frequency-dependent selection (FDS) in a cyclical dynamic. In RPS, each strategy beats one strategy but is also beaten by the third strategy. No strategy is an evolutionarily stable strategy (ESS; Maynard Smith 1982; Sinervo and Lively 1996; Sinervo 2001a), and the RPS cycle reflects an evolutionarily stable social system (ESSS). We refer to the RPS cycle with the new term “ESSS” because previous terms coined to describe two or more strategies that are maintained in one population (e.g., “ESState”) seem to connote that a stable state is reached. The term ESSS, which applies to both stable equilibria and cyclical systems, seems more general.

Despite long-standing theoretical interest in the RPS cycle (Maynard Smith 1982; Sinervo and Lively 1996; Frean and Abraham 2001; Kerr et al. 2002; Semmann et al. 2004; note that S. Wright [1968] derived frequency-dependent equations for the RPS cycle, but he did not coin the term “RPS” to describe his system of equations), the first biological RPS cycle was described only a decade ago in a lizard mating system (Sinervo and Lively 1996) and was described most recently in the bacterium *Esche-*

* Corresponding author; e-mail: sinervo@biology.ucsc.edu.

† E-mail: benoit.heulin@univ-rennes1.fr.

‡ E-mail: y.surget-groba@bangor.ac.uk.

§ E-mail: jean.clobert@ism.cnrs.fr.

|| E-mail: dmiles2@ohio.edu.

E-mail: corl@darwin.ucsc.edu.

** E-mail: alexis.chaine@ism.cnrs.fr.

†† E-mail: adavis@biology.ucsc.edu.

richia coli (Kerr et al. 2002; Kirkup and Riley 2004). Few other studies have documented RPS cycles even though they potentially affect many dimensions of social groups (Sinervo et al. 2006a) and other biological systems (Sinervo and Calsbeek 2006).

In side-blotched lizards, three alternative male strategies exhibit an RPS cycle of genotype frequency (Sinervo 2001a; Sinervo et al. 2001). Genetic crosses (Sinervo et al. 2001), linkage mapping studies (Sinervo et al. 2006a), and theory (Sinervo 2001a) confirm that transmission of color in *Uta* behaves like a single-locus factor with three alleles (*o*, *b*, *y*), yielding six color phenotypes that reflect six genotypes (*oo*, *bo*, *yo*, *bb*, *by*, *yy*) of the OBY locus. Alleles at the OBY locus have codominant effects on color expression. For example, the homozygote *oo*, which expresses only orange, is distinct from *bo*, which expresses blue and orange stripes, while *bb* expresses only blue color in the center of the throat. However, color alleles have dominant effects on male strategy: a single orange allele confers the aggressive O phenotypic strategy ($O = oo, bo, yo$), the presence of *y* in the absence of *o* confers the sneaky Y phenotypic strategy ($Y = by, yy$), and a homozygote *bb* confers the cooperative blue strategy ($B = bb$). Thus, *o* is genetically dominant to *y*, which is dominant to *b* (Sinervo 2001a; Sinervo and Clobert 2003). Color morphs exhibit physiologies correlated with mating behavior and territoriality (Sinervo et al. 2000b; Sinervo 2001a). The O males have high endurance and low survival, and they patrol large territories with large female harems that are usurped from neighboring males (Sinervo et al. 2000b; Zamudio and Sinervo 2000). The O male can be invaded by the sneaker strategy of Y males, which have low endurance, lack territoriality, mimic female behavior, and cuckold females in O harems at high rates (Zamudio and Sinervo 2000). The Y male in turn is beaten by a mate-guarding strategy involving pairs of cooperating B males (Sinervo and Clobert 2003; Sinervo et al. 2006a). Finally, the cooperative partnership of B can be invaded by O, which has higher resource-holding potential (RHP) than B, thereby completing the three-strategy RPS dynamic.

A recent study (Sinervo et al. 2006a) indicates that greenbeard self-recognition loci drive the B cooperation during RPS cycles of *Uta*. "Greenbeard" is a term coined by Dawkins (1976) to explain a mechanistic model of genic selection proposed by Hamilton (1964). In the theory of genic selection, greenbeard loci should exhibit three behaviors: a signal, self- or non-self-recognition of the signal, and signal recognition that elicits social acts, which benefit others that share self signals or detriment others with non-self signals. During phases of the RPS when Y males are common, B males engaged in cooperative partnerships receive high fitness that yields mutualistic benefits to both B male partners (Sinervo et al. 2006a). However, when O

is common, O males prefer to settle next to B males. The B male next to an O male receives low fitness, but these B males buffer their territorial B partners, which pass on an intact gene complex for cooperation to future generations. At these times when O is common, the B altruists in a cooperative partnership sire few if any progeny that survive, and their own patriline is thus extinguished. These altruists do, however, protect their B partners from the aggressive O male neighbors, and the protected B recipients sire many progeny that survive to breed. Thus, true greenbeard altruism (really bluebeard altruism) when O is common alternates with cyclical phases of greenbeard mutualism when Y is common. However, unlike the single social supergene envisaged by Hamilton (1964), several unlinked loci are required for self-recognition of genetic similarity and blue color in *Uta*. Gene mapping studies of self-recognition behavior in the deep 20-generation pedigree of *Uta* (Sinervo et al. 2006a) indicate that the OBY color locus and three physically unlinked recognition factors are coupled by correlational selection into a social supergene spanning much of the *Uta* genome. These loci are also shared between the sexes; female *Uta* mate as a function of self-recognition alleles shared with males (Sinervo et al. 2006a). In essence, such genic signal-recognition systems appear to be fundamental to the stability of RPS dynamics through complex social interactions among individuals.

Despite inferences on social system theory afforded by study of the OBY locus and RPS of *Uta*, hardly any studies have looked for such dynamics. In a recent review of FDS, Sinervo and Calsbeek (2006) used published data on FDS (Shuster and Wade 1991; Agren and Ericson 1995; Svensson et al. 2005) to compute payoff matrices and found that the RPS was common in mating system interactions. In previous mating system reviews (Sinervo 2001b; Zamudio and Sinervo 2003), we predicted that RPS dynamics should occur when (1) males control access to harems (high mating skew, coarse-grained social environment); (2) females lay many clutches, enhancing mating skew and contributing to density regulation; and (3) males are short-lived (e.g., coarse-grained temporal environment). European common lizards exhibit many, but not all, of these attributes. We were interested in whether *Lacerta vivipara* exhibited an RPS cycle and which attributes were necessary for RPS cycles. In 2002, we detected three color morphs of *L. vivipara* in the French Pyrenees. We initiated genetic and demographic studies to detect RPS cycles (2002–2006) and physiological studies (2004) to estimate endurance, which measures RHP (Maynard Smith 1982; Sinervo et al. 2000b; Zamudio and Sinervo 2003). Game theory (Maynard Smith 1982), along with observed RHP among players, can be used to assess whether strategies reflect an ESS through the construction of payoff matrices. We used

allele frequency change between cohorts of *L. vivipara* to provide direct evolutionary evidence of the forces of FDS, which stabilize the social system in an RPS dynamic.

Here we synthesize population genetic, population dynamic, and game theoretic approaches in our analysis of the forces that drive rapid RPS cycles of *Lacerta*. We address several empirical issues of RPS dynamics for *L. vivipara* that have already been characterized for *Uta*. Is color of *L. vivipara* associated with endurance and body size? Does survivorship vary among the morphs of *L. vivipara* in the wild? Do putative color alleles cycle in a rapid RPS cycle? Do fitness payoffs and FDS on the morphs of *L. vivipara* resemble those of *Uta*?

Drawing from these results, we used ESS models to investigate the role of self- versus non-self-recognition in producing RPS dynamics. We reconcile theory, which predicts slow RPS cycles, with the rapid *Lacerta* cycles observed in nature. Our ESS models include (1) frequency regulation due to self- versus non-self-recognition between adult and juvenile cohorts, (2) behaviors that allow discrimination of self versus nonself genotypes at rates higher than random (Sinervo et al. 2006a), and (3) context-dependent female choice (Alonzo and Sinervo 2001), which should evolve to enhance progeny survival as a function of RPS cycles. Comparing the social factors that promote RPS cycles in *Uta* and *Lacerta* affords an unprecedented opportunity to develop general models of social system dynamics for other taxa. Our theory predicts that genic selection, which is coupled to density regulation, should be common in the animal kingdom.

Material and Methods

Study Sites and Cohort Dynamics

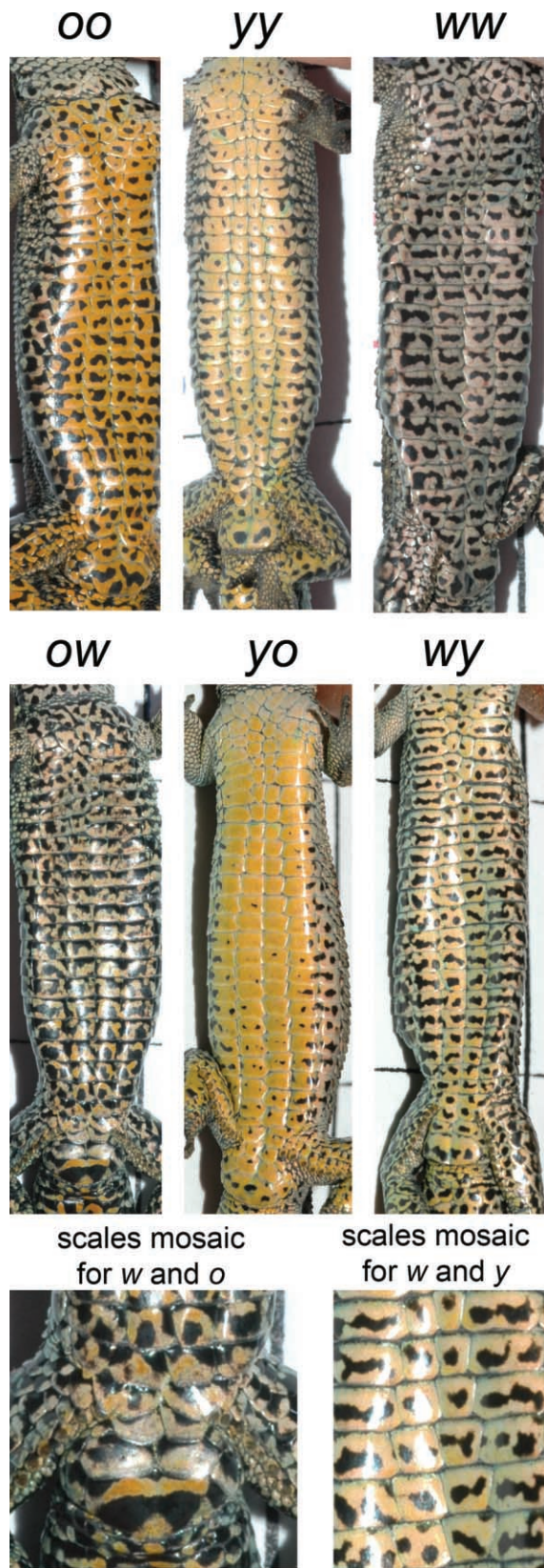
We studied color frequency of male *Lacerta vivipara* at five sites of the Ossau valley of the French Pyrenees (Heulin et al. 1997): three populations were sampled in peat bogs east of Louvie Jouzon (300 m a.s.l.), one population was sampled in a bog east of Gabas (1,500 m a.s.l.), and one population was studied in a wet alpine biotope near Col d'Aubisque, 0.25 km east of Crête Blanche (1,700 m a.s.l.). At Louvie, we sampled one site in 2002 and from 2004 to 2006 (LT02: $N = 17$, LT04: $N = 51$, LT05: $N = 51$, LT06: $N = 76$) and two adjacent sites from 2004 to 2006 (LS04–LS06: $N = 27, 35,$ and 34 ; LC04–LC06: $N = 20, 37,$ and 46). We sampled from 2002 to 2006 at Gabas (G02–G06, $N = 13, 20, 60, 60,$ and 52) and in 2002 and from 2004 to 2006 at Aubisque (A02: $N = 12$, A04–A06: $N = 47, 72, 49$). We marked the males individually, measured mass (g) and snout-vent length (SVL; mm), took a macrophotograph of color, and then released them.

Maturation and color change are tightly coupled to the

appearance of black spots on the ventrum (fig. 1). The size threshold of maturation was estimated to be 45 mm based on an analysis of when black spotting was 100% defined ($N = 71$ subadults scored for LT04). At low-elevation sites (Louvie), we were able to discriminate two distinct age cohorts based on a size discontinuity: 2+-year-old males (>50 mm snout-vent length) and 1-year-old males ($50 \text{ mm} \geq \text{SVL} > 45 \text{ mm}$). Thus, we could compute change in frequency of males across cohorts as well as across years, given robust cohort structure at all sites. Maturing cohorts at low elevation that were 1 year old (e.g., <50 mm, >45 mm) were designated by a quotation mark (i.e., "): LT04", LT05", LT06", LS04", LS05", LS06", LC04", and LC06". Maturing cohorts at high elevation that were 2 years old were designated A04", A05", A05", A06", G04", G05", and G06". We confirmed male recruitment at Louvie into mature age classes by releasing 100 neonates in 2004. All males matured in 1 year ($N = 7$ males). We also studied recruitment of marked neonates in 2004 at high elevation (Gabas $N = 100$; Aubisque $N = 100$). All males at both high-elevation sites matured in 2 years (<53 mm; $N = 15$). These cohort studies crucially allowed us to estimate the putative allele frequency in the previous generation and its impact on the allele frequency in the maturing cohort. The ratio of these allele frequencies gives relative fitness across generations.

Color Morphs

Male *L. vivipara* express six distinct color phenotypes parallel to color morphs of *Uta*. Analysis of *L. vivipara* with spectrophotometry (Vercken et al. 2006; B. Sinervo, unpublished data) indicates that color can be decomposed into three robust categories. Male *L. vivipara* with solid orange (*oo*), yellow (*yy*), or white (*ww*) bellies are putative homozygotes (fig. 1). Putative heterozygotes in *L. vivipara* exhibit two colors in distinct patches, even at the level of single scales, as described for *Uta* (Sinervo et al. 2001; Sinervo and Clobert 2003). Putative *wo* heterozygotes of *L. vivipara* exhibit white bellies with orange cloacal scales and a medial orange-white stripe that extends anteriorly from the vent. Similarly, *wy* males have white bellies, yellow cloacal scales, and a medial white-yellow stripe. Finally, *yo* males have yellow bellies, orange cloacal scales, and a medial orange-yellow stripe. In addition, males carrying *w* alleles in *L. vivipara* exhibit a conspicuous peak in UV wavelengths as observed in the blue color morph of *Uta* (B. Sinervo, unpublished data). As in *Uta* (Sinervo et al. 2001; Sinervo and Clobert 2003), we scored male *L. vivipara* as having zero, one, or two orange (*o*) color alleles or zero, one, or two white (*w*) color alleles. We used the two color scales (O, W) as covariates in analyses. For a given dependent trait, independent variables of color scales



test for additive genetic effects of putative color alleles, relative to a baseline color (Sinervo et al. 2001; Sinervo and Clobert 2003). In this case, Y is a baseline for O and W color scales. Thus, interaction terms ($O \times W$) and quadratic terms (O^2 or W^2) test for effects of genetic dominance of *o* and *w* alleles in a *y* background, on a given trait. We also used the six color phenotypes (*oo*, *yy*, *ww*, *wo*, *yo*, *yy*) as a factor in performance analyses.

Stability and Repeatability of Color and Interobserver Correlations

Interobserver correlations of O and W scales were $r^2 = 0.73$ and 0.63 , respectively (O: $F = 87.99$, $df = 1, 33$, $P < .0001$; W: $F = 54.48$, $df = 1, 33$, $P < .0001$; $N = 34$). Heulin scored male colors by eye on the first recapture (April–May). Sinervo scored males by eye on a second recapture in June–July and verified scores using photographs taken with a macro lens. Discrepancies in scoring between observers were always associated with the obscuring effects of the molt on one recapture but not the other. Inspection of photographs taken between years (see sample sizes noted above) indicates that color is extremely stable in males, even at the level of individual scales that exhibit a mosaic of two colors in putative heterozygotes. No males were observed to change color.

Physiological and Morphological Traits

To study RHP in *L. vivipara*, we captured a sample of males from Louvie (June 12–14, 2004, $N = 12, 3, 7, 5, 4, 10$, respectively, for *oo*, *ww*, *yy*, *wy*, *wo*, and *yo*), measured body mass, and tested their endurance on a motorized treadmill. We put males in an incubator at 30°C , the activity body temperature of *L. vivipara* (Van Damme et al. 1990). After warming up for 30 min, males were induced to run on a treadmill (0.5 km/h) by gently tapping their flanks until they were unable to maintain position on the belt (three lapses) or they lost their righting response (Lorenzon et al. 2000; Sinervo et al. 2000b; Sinervo and Calsbeek 2006). A lamp suspended above the belt was used to

Figure 1: Representative orange, yellow, and white male color morphs of putative homozygote (top row: *oo*, *yy*, *ww*) and heterozygote (center row: *wo*, *yo*, *wy*) classes of *Lacerta vivipara* from the Pyrenees. Heterozygote types most commonly have scales of one color on the lateral portions of the ventrum, while scales of the other color are concentrated at the cloaca and ventral midline. Scales of *wo* and *wy* individuals are enlarged in the bottom row to illustrate the gynandromorphic expression of color. In the case of the heterozygote *yo* (center), a smooth color gradient from cloaca to snout is present and the color is yellow orange compared to the orange red of *oo*.

maintain body temperatures of lizards at 30°C. Endurance was given by the elapsed time (s) for the trial.

Adult Survival Differences among Morphs

We tested for survival differences among male color morphs from Gabas with maximum likelihood inference afforded by the software program MARK (White 2005; <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>). We estimated survival of males at Gabas ($N = 80$; 2002–2005) from a first mark-recapture session in April–May and a second session in June–July followed by third and fourth sessions the following year. There were no significant differences among cohorts (e.g., 2002, 2003, 2004) in survival ($P > .92$), and we pooled cohorts to test for effects of O and W scales (covariates) on apparent survival (Φ) and catchability (p) with likelihood ratio and the Akaike Information Criterion (White 2005). Lack of catchability effects on morphs indicates that frequency was not distorted by capture biases.

In addition to the survival data at Gabas, we had data on males at Aubisque ($N = 53$) and Louvie ($N = 73$) that were marked in June 2004 and followed by recapture efforts in June 2005 and 2006. At Louvie and Aubisque, we also estimated capture efficiency for males that were marked in 2005 and recaptured with a first intensive recapture session in early June 2006 followed by a second recapture session 2 weeks later. The second session estimated directly the fraction of males missed on the first session. Given the very high catchability (0.87 at Louvie, 0.97 at Aubisque), we used logistic regression of O and W color scales on yearly male survival to confirm the more detailed patterns on survival and capture efficiency at Gabas.

Empirical Results

Endurance, Size, and Color in *Lacerta vivipara*

Male *L. vivipara* express six distinct color phenotypes (*oo*, *wo*, *yo*, *ww*, *wy*, *yy*) parallel to morphs of *Uta* (fig. 1). One important comparison between the morphs of *Uta* and *L. vivipara* relates to the impact of color alleles on performance traits such as endurance. If color is to be considered a badge, then traits such as RHP should be correlated with endurance and body size in *L. vivipara*, as has been shown in *Uta* (Sinervo et al. 2000b). In the sample of *L. vivipara* males from Louvie, male body mass was enhanced by *o* and *w* color alleles, relative to *y* color alleles, in a model that controlled for age class ($\text{slope}_{O \text{ color}} = 0.066 \pm 0.026$ [SE], $F = 6.22$, $df = 1, 37$, $P < .0001$; $\text{slope}_{W \text{ color}} = 0.093 \pm 0.038$, $F = 5.98$, $df = 1, 37$, $P < .02$; age class: $F = 6.99$, $df = 1, 37$, $P < .0001$; fig. 2).

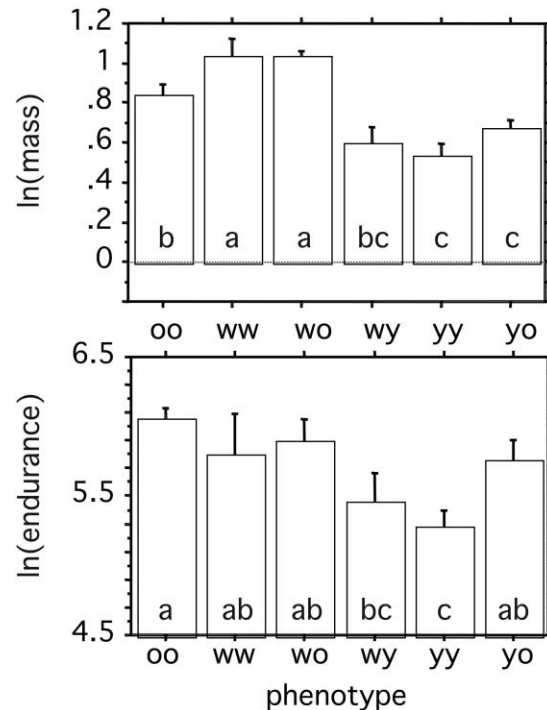


Figure 2: The \ln [mass (g)] and \ln (endurance) [\ln (s)] for putative color genotypes (*oo*, *ww*, *wo*, *wy*, *yy*, *yo*) of male color morphs of *Lacerta vivipara*. ANOVA reveals significant effects of a factor for color on both \ln (mass) ($F = 10.93$, $df = 5, 34$, $P < .001$) and \ln (endurance) ($F = 5.71$, $df = 5, 34$, $P < .006$). The color factor remained significant in a model with age class (1 year vs. 2+ years, \ln (mass): $F = 2.70$, $df = 5, 33$, $P < .04$); \ln (endurance): $F = 3.61$, $df = 5, 33$, $P < .01$). Homogeneous groups are indicated by letters.

ANCOVA of \ln (endurance) of *L. vivipara* revealed significant additive effects of *W* ($F = 7.17$, $df = 1, 35$, $P < .01$) and *O* color scales ($F = 27.37$, $df = 1, 35$, $P < .0001$), relative to *Y* color, and significant interaction terms for $O \times W$ ($F = 4.85$, $df = 1, 35$, $P < .03$) and W^2 terms ($F = 4.39$, $df = 1, 35$, $P < .04$). These terms indicate that *w* alleles have a dominant effect in an *o* background but a recessive effect in a *y* background (see fig. 2). The *O* color scale had only additive effects relative to *Y* color, as evinced by a nonsignificant O^2 term ($F = 0.02$, $df = 1, 35$, $P > .87$; fig. 2).

A simple ANCOVA indicated that *O* and *W* colors both had significant effects on \ln (endurance) relative to *Y*, however, the effect of *O* was stronger than the effect of *W* ($\text{slope}_O = 0.38 \pm 0.07$, $F = 5.27$, $df = 1, 37$, $P < .0001$; $\text{slope}_W = 0.23 \pm 0.097$, $F = 2.33$, $df = 1, 37$, $P < .03$; fig. 2). Including size effects in ANCOVA models allowed us to compute the contribution of size versus color on endurance. The \ln (endurance) of males scaled with near isometry with \ln (mass) (fig. 3A). A model of the joint

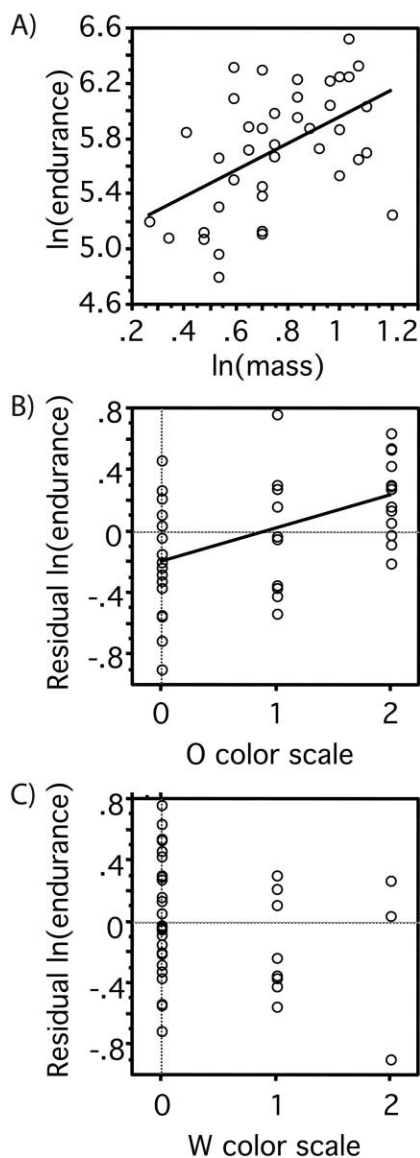


Figure 3: Allometry of $\ln[\text{mass (g)}]$ and $\ln(\text{endurance})$ [$\ln(\text{s})$] for putative color genotypes (*oo*, *ww*, *wo*, *wy*, *yy*, *yo*) of male color morphs of *Lacerta vivipara*. Analysis of residuals from the allometric relationship (A: allometric slope = 0.96 ± 0.27 [SE], $F = 12.96$, $df = 1, 39$, $P < .0009$) reveals that whereas the O color scale had significant effects on endurance that are independent of size (B: $F = 7.41$, $df = 1, 36$, $P < .01$), the effect of the W color scale was not significant (C: $F = 0.002$, $df = 1, 36$, $P > .96$), and thus, significant effects of W color on endurance when size is ignored (fig. 2; text) are due to the larger size of males with white color (fig. 2). Note the model of size-independent residuals of $\ln(\text{endurance})$ did not have a significant effect of age class (subadult male vs. adult male, $F = 0.11$, $df = 1, 36$, $P > .77$). Age had no effects on endurance other than size, given nonsignificant interaction terms for age class with O ($P > .63$) and W color scales ($P > .48$).

effects of O color, W color, and $\ln(\text{mass})$ on $\ln(\text{endurance})$ revealed effects of O (slope_O = 0.29 ± 0.08 , $F = 5.27$, $df = 1, 37$, $P < .003$) but not W (slope_W = 0.10 ± 0.12 , $F = 0.67$, $df = 1, 37$, $P > .42$). We complemented these tests with models of $\ln(\text{endurance})$ residuals with effects of $\ln(\text{mass})$ removed (fig. 3). The effect of O on residual $\ln(\text{endurance})$ was significant (fig. 3B), but the effect of W was not (fig. 3C). Analyses collectively indicate that O confers high size-independent (fig. 3) endurance when compared with W and Y, but W confers high endurance relative to Y through allometry.

Survival of Lacerta vivipara Morphs in the Wild

Life-history differences between male strategies can result from a trade-off between performance (RHP) and survival (Sinervo et al. 2000b). In *Uta*, orange color alleles contribute to lower survival, compared with blue or yellow (Sinervo and Lively 1996; Sinervo et al. 2000b). Do alleles in *L. vivipara* have similar effects on adult survival? Morph differences in survival would also provide a parsimonious explanation for the large size of males with *w* alleles (fig. 2). We measured *L. vivipara* survival rates at the three sites, two at high elevation and one at low elevation.

We analyzed the four sessions of mark-recapture data of male *L. vivipara* in the high-elevation Gabas population. A time-invariant model of catchability and survival had significantly worse fit compared with models that assumed catchability and survival varied over time (see table A1 in the online edition of the *American Naturalist*). All best-fit models included covariates for O and W. Comparison of these models indicated that interaction terms for survival ($\Phi[t] \times W$ or $\Phi[t] \times O$) should be retained, while interaction terms for catchability $p[t] \times W$ or $p[t] \times O$ should be dropped (table A1). Plots of survival between reproductive seasons indicated that *o* alleles reduced male survival, while *w* alleles enhanced male survival relative to *y* alleles (fig. 4). Capture efficiency at Gabas was estimated to be 0.91 for adult males marked in a previous year and recaptured on a first (April–May) and a second census (June) the next year. The second census estimates directly the proportion missed on the first census. Estimated male survival at Gabas between years was 0.34 (after correcting for a capture efficiency of 0.91). Thus, at Gabas, *w* alleles enhanced male survival compared with *o* or *y* alleles, while the high-RHP strategy of *o* alleles exacts survival costs. At Aubisque, we found the same negative effect of O ($\chi^2 = 3.72$, $P = .05$) and positive effect of W ($\chi^2 = 6.13$, $P = .01$) on survival from 2004 to 2005, but only the effect of W was significant in a logistic regression model with both terms (W: $\chi^2 = 4.46$, $P < .04$; O: $\chi^2 = 1.45$, $P > .22$). Survival was estimated at 0.33, correcting for a

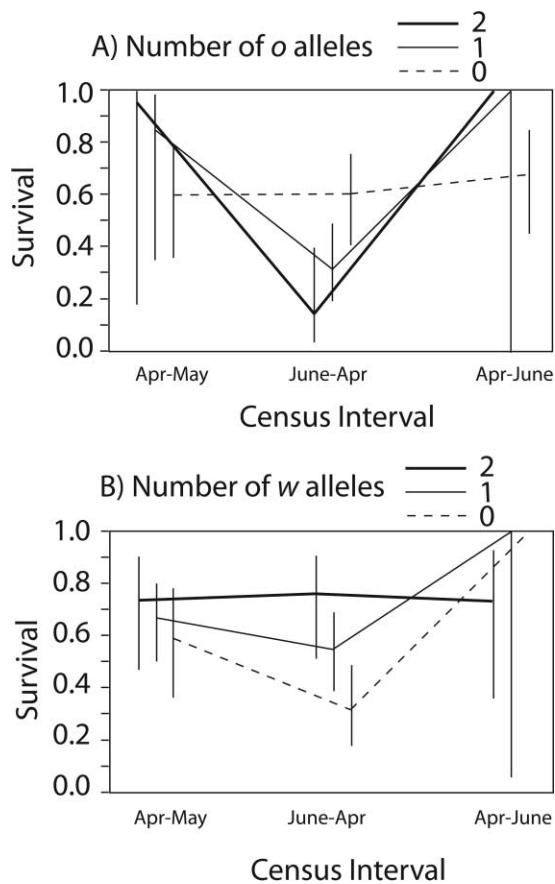


Figure 4: Additive effect of color alleles on apparent survival probability (SE) for cohorts of adult males at Gabas (2002–2005). Males with more *o* alleles had lower survival across years (June–April census), while males with more *w* alleles had higher survival relative to males with *y* alleles (0 on both scales). Survival across years is estimated from the census labeled June–April (center of the plot). Only three survival episodes can be computed from four recapture periods, and survival in the final (third), fairly short episode (labeled April–June) is confounded with catchability (White 2005), which is very high (0.91) in the Gabas population.

capture efficiency of 0.97. At Louvie, we did not find an additive effect of *O* or *W* color scales on adult survival (*W*: $\chi^2 = 0.06$, $P > .81$; *O*: $\chi^2 = 0.39$, $P > .45$). However, we found that one heterozygous genotype, *wo*, had higher survival than the other genotypes ($\chi^2 = 3.58$, $P = .06$). Survival of adult males at Louvie was estimated to be 0.18, correcting for a capture efficiency of 0.87.

Evolutionary Change in Male Color Frequency in *Lacerta vivipara*

Another feature of the *Uta* RPS cycle is the rapid allele frequency cycle (fig. 5D). Do *L. vivipara* exhibit a similar cycle of color allele frequency? Analysis of morph fre-

quency change between years for *L. vivipara* revealed that all between-year changes in allele frequency were significant as measured by χ^2 ($N = 14$ between-year changes; $N = 13$ years comparing the new mature cohort with the previous year's cohort). Closed RPS orbits were observed all sites (fig. 5A–5C).

The strength of selection driving RPS cycles can be summarized in terms of the average length of the vector for allele frequency change per year or per generation. In *L. vivipara*, at low elevation (Louvie), mean Euclidean change for frequency per year (\pm SE) was 0.28 ± 0.04 , but at high elevation (Aubisque and Gabas), it was 0.16 ± 0.03 , which reflected a significant difference in the rate of change ($F = 5.62$, $df = 1, 26$, $P = .02$). Thus, RPS periodicity was c , twofold faster at low (3–4 years) compared with high elevation (6–8 years). One versus 2 years to maturity at low versus high elevation is likely responsible for differences in cycle speed among sites. The frequency change per generation in *L. vivipara* was indeed similar at low and high elevation (0.28 ± 0.04 vs. 0.32 ± 0.06). The RPS dynamics are thus similar, after correcting for time to maturity. RPS cycle length in *Uta*, an annual species, is 4 years, similar to 4-year cycles in low-elevation *L. vivipara*, but allele change per generation is significantly ($F = 6.52$, $df = 1, 26$, $P = .02$) smaller in *Uta* (0.13 ± 0.03 ; fig. 5).

Payoffs of *Lacerta vivipara* Morphs and Frequency Regulation between Cohorts

The final striking feature of the RPS cycle of *Uta* relates to the payoffs that generate RPS dynamics (see the introduction to this article). Do fitness payoffs of *L. vivipara* resemble the *Uta* RPS, and is there evidence of similar greenbeard dynamics (i.e., mutualism vs. competition)? The pronounced age structure of *L. vivipara* cohorts (“Material and Methods”) afforded us the opportunity to partition allele frequency change across generations and compute relative fitness as a function of gene frequency of adult cohorts. Relative fitness (ω) when each putative allele is common was computed (Sinervo et al. 2001) from allele frequency change (fig. 5) from parental generation to newly mature cohort of recruits. Allele payoffs in *L. vivipara* conformed to an RPS game (fig. 6).

Individual regression coefficients were significant for allele fitness (ω) in recruits as a function of adult allele frequency (fig. 6); however, we also used MANOVA to compare genotype fitness of juvenile recruits as a function of a given allele frequency in adults of the previous generation (juvenile $\omega[o, w, y] \times$ adult *o*: $F = 9.66$, $df = 2, 8$, $P < .001$; juvenile $\omega[o, w, y] \times$ adult *w*: $F = 4.02$, $df = 2, 8$, $P = .06$; juvenile $\omega[o, w, y] \times$ adult *y*: $F = 8.04$, $df = 2, 8$, $P < .02$). MANOVA indicates that regres-

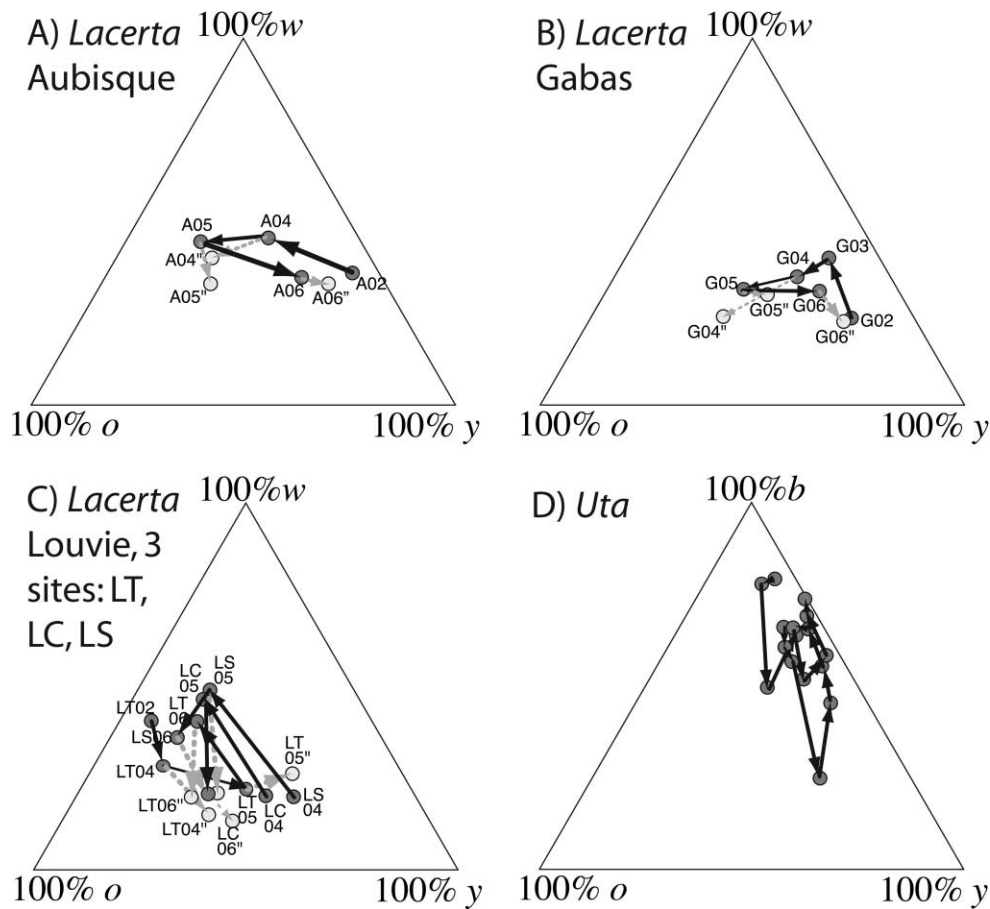


Figure 5: Changes in color allele frequency in *Lacerta* and *Uta* lizard species. Frequency change in *Lacerta vivipara* at high elevation (A, Aubisque; B, Gabas) and low elevation (C, Louvie, with sites LT, LC, LS). Allele frequency change in male *Uta* (D, 1991–2005) is provided for comparison. The solid arrows reflect between-year change, while the dashed arrows reflect frequency change between cohorts (e.g., old vs. maturing males, e.g., A04 vs. A04'') caught in the same year. All changes are significant based on χ^2 analysis of allele frequency. Line width indicates level of significance ($P < .05, < .01, < .001, < .0001$).

sion effects of each adult allele on fitness of juvenile genotypes differed significantly.

Payoffs of allele strategies in *L. vivipara* conformed to an RPS game and were parallel to those observed in *Uta* (Sinervo et al. 2006a). While *o* and *y* alleles in adult males had significant negative effects on recruitment of self genotypes, *w* alleles in adult males had no significant effect on recruitment of self genotypes in progeny (compare graphs on the diagonal, fig. 6A). The significant positive frequency-dependent effect of *w* alleles in juveniles on survival of self genotypes of juveniles was even more striking (fig. 6B). These patterns suggest that *L. vivipara* exhibits a form of genic selection in which *w* alleles confer protection on self genotypes, which is parallel to the cooperation observed among blue male *Uta*. A final comparison of the two species is noteworthy. *Uta* is an annual, and greenbeard cycles arise from territorial interactions

among adults (Sinervo et al. 2006a). *Lacerta vivipara* are wide ranging, and stable territoriality is not a possible source of genic selection. Adult *L. vivipara* do have relatively high interannual survival; thus, greenbeard effects between cohorts could contribute to genic density regulation (fig. 6). This regulatory effect of the adult generation on density recruitment of progeny could generate much more rapid cycles in a long-lived species. This is especially true in an intransitive dynamic, where adults of each type have an advantage over a single common juvenile type.

Theoretical Models of Genic Density Regulation

ESS Models of Self versus Nonself Density Regulation, Discrimination, and Mate Choice

Inspired by these salient natural history observations, we constructed a general class of ESS models to examine the

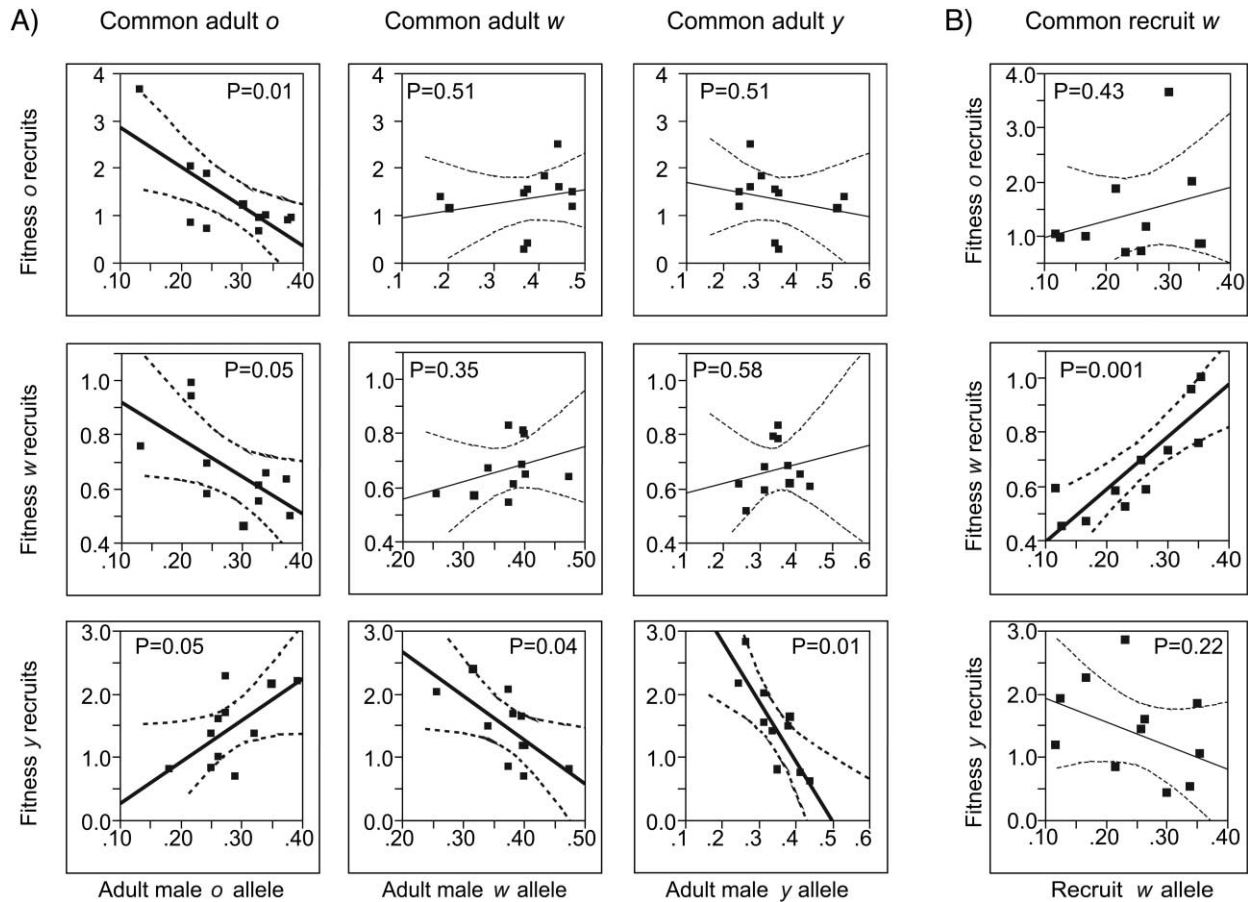


Figure 6: Genic selection between (adult-juvenile) and within cohorts (juvenile) of *Lacerta vivipara*. A, Payoff matrix for genotypes of juvenile recruits (rows) as a function of common adult allele frequency in the year of maturation (columns). The form of relationships (positive, negative, and neutral) in the payoffs among alleles is identical to theoretical payoffs in table 1A, which are predicted based on the resource-holding potential (i.e., endurance) of the morphs. B, Payoffs for rare juvenile recruits as a function of recruit frequency of the *w* allele. Only one column of the payoff matrix for within-cohort regulation is shown, the only column with a significant effect (only *w* had significant within-cohort effects; all other columns had nonsignificant effects). A high frequency of *w* in juvenile cohorts greatly enhanced the recruitment of other *w* juveniles.

role of self- versus non-self-recognition in RPS dynamics. We ignored effects of density cycles per se but modeled frequency cycles in a density-regulated population. We were especially interested in capturing rapid RPS cycles, in the face of age structure. Age structure should greatly lengthen the period of RPS cycles (Sinervo and Lively 1996). However, this need not be the case, given the effects of adult males on recruitment and survival of juvenile genotypes (fig. 6A). We assumed (table 1A) that between-cohort competition was governed by resource-holding potential of morphs, as determined in our endurance trials. These RHP differences should affect survival of progeny recruits as a function of adult morph frequency.

We augmented the basic payoff matrix of self- versus non-self-recognition (table 1A) with targeted discrimination behavior. To model discrimination behavior, we

assumed that each type finds and discriminates against other types that they exploit, at higher rates (d) than by chance alone (e.g., random encounter or panmixia; table 1B). Studies on *Uta* suggest that d is about fourfold higher (range for $d = 2-6$) than random encounter, where $d = 1$ (Alonzo and Sinervo 2001; Sinervo and Clobert 2003; Sinervo et al. 2006a). We also included a form of self- versus nonself mate choice. The observed genic selection by adult males on juvenile cohorts (fig. 6) favors a counterstrategy to evolve in females, which enhances progeny survival. We assumed that dams adopt a context-dependent decision rule (Alonzo and Sinervo 2001) and mate at a higher rate m with rare sire genotypes that afford the highest survival of a dam's progeny (table 1). Context-dependent mate choice is a form of mate discrimination that is analogous to discrimination behavior adopted by

Table 1: A model of self versus nonself density regulation

	Common adult male allele		
	<i>o</i>	<i>w</i>	<i>y</i>
A. Juvenile survival payoffs:			
<i>o</i>	$c < 1$	1	1
<i>w</i>	0	1	1
<i>y</i>	1	0	$k < 1$
B. Targeting behavior toward juveniles:			
<i>o</i>	1	1	$d > 1$
<i>w</i>	$d > 1$	1	1
<i>y</i>	1	$d > 1$	1

Note: A, Payoff matrix for density regulation exerted by adult male genotypes (top row) on survival of juvenile genotypes (left column). Diagonal elements of the payoff matrix (c or 1 or k) describe self-limitation or pure density-dependent regulation. For both common o adults and common y adults (c and k), juveniles of the same morph die owing to self-similarity, which is not the case for w (a value of 1 implies no effect on survival). Owing to aggression and resource-holding potential (RHP), males with o alleles eliminate juveniles with w (0) but also negatively impact survival of juveniles with o alleles ($0 \leq c < 1$). Juveniles with y are cryptic and do not engage in RHP encounters, and they are thus immune to the RHP of adult o (1). Adults with w alleles eliminate juveniles with y (0), but not juveniles with o (1), which have slightly higher RHP when they mature, despite their small size. Because y adult males have low RHP, they cannot eliminate juveniles that carry w or those that carry o (1), but y adults can inflict lower survival on juveniles with y alleles ($0 < k < 1, k > c$). The payoff matrix exhibits RPS intransitivity for each rare type: $\omega_{w,rare\ juvenile} > \omega_{o,common\ adult} > \omega_{w,rare\ juvenile} > \omega_{y,common\ adult}$ and $\omega_{o,rare\ juvenile} > \omega_{w,common\ adult}$. B, In more complex models, we assumed that adult males target and discriminate against juvenile genotypes at a higher rate, $d > 1$, than by chance alone. The matrix for mate choice has a form similar to that of targeting behavior, except m replaces d , and a high value for m is contingent on high fitness of progeny in the next generation (e.g., a context-dependent choice); otherwise $m = 1$.

adult males (table 1B), but mate discrimination should vary with RPS cycles. Thus, a simple genetic model of female and male behaviors is that both sexes use the same loci; however, to enhance fitness, females co-opt the self-versus non-self-recognition loci, which evolve in males under the force of genic selection. Equations for gene frequency change under frequency-dependent selection (Sinervo and Lively 1996; Alonzo and Sinervo 2001; Sinervo 2001a) are in a form that is standard for population genetic theory (eqq. [1]–[5]).

Following population genetic theory (Wright 1968; Maynard Smith 1982; Sinervo and Lively 1996; Alonzo and Sinervo 2001; Sinervo 2001a), relative change of genotype frequency, \mathbf{A}_p , of each maturing genotype of juvenile recruits (\mathbf{fp}_i , $i' = oo, bo, yo, bb, by, yy$), which is under survival selection by the adult male frequency (\mathbf{fs}_p , $i = oo, bo, yo, bb, by, yy$), is given by

$$\mathbf{A}_{i'} = \frac{\sum_i \mathbf{fs}_i \mathbf{P}_{i,i'}}{\sum_{i'} \sum_i \mathbf{fs}_i \mathbf{P}_{i,i'} \mathbf{fp}_{i'}} \quad (1)$$

The payoff matrix $\mathbf{P}_{i,i'}$ is the survival payoff of i' th progeny due to encounter with the i th adult male genotype and is derived from the additive payoffs of alleles (table 1A) that are converted to genotype payoffs (e.g., see table 2, for $c = 0.25, k = 0.5$). Various models of additive or dom-

inance genetic effects (one-locus) and epistatic effects (two-locus) can be used to convert additive allele payoffs to genotype payoffs (Sinervo 2001a). Here we consider only the additive genetic and dominance effects of color alleles on frequency-dependent recruitment.

Self-regulation is reflected in the diagonal elements of the density regulation payoff matrix ($\mathbf{P}_{i,i'}$). The parameter c , in the matrix of allelic effects (e.g., table 1A), reflects density regulation by o alleles in adult males on maturing o alleles in juveniles. Similarly, the parameter k reflects density regulation by y adults on y progeny. The model assumes less density regulation by w adults on w progeny, and the diagonal element for the w strategy is given to be

Table 2: Payoffs (rows) of rare juvenile genotypes against a given common adult genotype (columns)

	Common adult genotype					
	<i>oo</i>	<i>yo</i>	<i>wo</i>	<i>ww</i>	<i>wy</i>	<i>yy</i>
<i>oo</i>	.250	.625	.625	1.00	1.000	1.00
<i>yo</i>	.625	.688	.563	.50	.625	.75
<i>wo</i>	.0125	.563	.563	1.00	1.000	1.00
<i>ww</i>	.000	.500	.500	1.00	1.000	1.00
<i>wy</i>	.500	.625	.531	.50	.625	.75
<i>yy</i>	1.000	.750	.500	.50	.250	.50

Note: Diploid genotype payoffs for survival, assuming additive genetic effects in both rare and common strategies: $c = 0.25$ and $k = 0.5$.

1, relative to o and y strategies, which are more strongly self-density regulated than w (e.g., $1 > k > c$). This parameterization precisely captures the observed frequency dependence of alleles (fig. 6).

Discrimination behavior, $\mathbf{d}_{i',i}$, distorts the frequencies of encounters between adult males, \mathbf{fs}_p , with each of the i 'th juvenile genotypes and, thus, genotype frequency change in the next generation, $\mathbf{A}_{i'}$. While discrimination behaviors are given as additive allelic effects (table 1B), genotype behavior can be computed in an analogous fashion, as for the genotype payoff matrix (table 2) from the allele payoff matrix (table 1A). This yields a matrix of discrimination behaviors, $\mathbf{d}_{i',i}$, by adult male genotypes (i) against juvenile genotypes (i') that distorts genotype change:

$$\mathbf{A}_{i'} = \frac{\sum_i \mathbf{fs}_i \mathbf{P}_{i',i} \mathbf{d}_{i',i}}{\sum_{i'} \sum_i \mathbf{fs}_i \mathbf{P}_{i',i} \mathbf{d}_{i',i} \mathbf{fp}_{i'}}. \quad (2)$$

Relaxing the assumption of additivity in models (Sinervo 2001a) and assuming two forms of genetic dominance (e.g., a circular form of intransitive genetic dominance: $O = oo, yo$; $W = ww, wo$; $Y = wy, yy$ or the dominance observed in *Uta*: $O = oo, wo, yo$; $W = ww$; $Y = wy, yy$) had little impact on RPS dynamics (not shown). We also assumed an adult survival rate of $l = 0.18$ (e.g., Louvie), but predictions regarding RPS cycles in ESS models were very robust to varying adult survival across a very wide range ($0 \leq l < 0.5$). Thus, after progeny recruit to the adult population, we assume that frequency regulation per se among genotypes of adult cohorts is negligible relative to initial phases of juvenile recruitment to the adult class (e.g., when juveniles mature). Relaxing this assumption had little impact on the dynamics exhibited by the ESS model.

Production of juvenile genotypes follows standard Mendelian genetics, given allele frequencies in females, which are tracked separately from males. In models of context-dependent mate choice, rates of encounter of sire and female genotypes under panmixia, $\mathbf{fs}_i \times \mathbf{ff}_j$, are distorted by $\mathbf{m}_{i,j}$, which is context dependent (see below). The matrix form assumed for female mating discrimination $\mathbf{m}_{i,j}$ parallels the matrix of behaviors for male discrimination $\mathbf{d}_{i',i}$ during density regulation. Mate discrimination $\mathbf{m}_{i,j}$ is a function of female mating control (Alonzo and Sinervo 2001). For example, if females do not prefer morphs or they have no control over mating, then $\mathbf{m}_{i,j} = 1$. As female control over mating (m) increases, discrimination for preferred male genotypes increases (table 1). Genotype frequency change $\mathbf{A}_{i'}$ is a function of regulation of progeny frequency by the adult male cohort $\mathbf{P}_{i',i}$, adult morph frequency ($\mathbf{fs}_p, \mathbf{ff}_j$), targeted discrimination by males, $\mathbf{d}_{i',i}$ and

female mating discrimination matrix, $\mathbf{m}_{i,j}$. Female mate discrimination distorts the frequency of sires' genotypes at gametic union according to

$$\mathbf{fs}_{i'} = \frac{\sum_j \mathbf{m}_{i,j} \mathbf{ff}_j}{\sum_i \sum_j \mathbf{fs}_i \mathbf{m}_{i,j} \mathbf{ff}_j}. \quad (3)$$

Let $\mathbf{g}_{i,j,k}$ represent the probability of the i 'th male genotype mating with the j 'th female genotype and producing the k 'th genotype of offspring, which is derived from Mendelian inheritance for an autosomal locus with three alleles. For simplicity, we assumed no difference in the behavior of adult males toward male and female progeny during density regulation (although relaxation of this assumption yielded similar frequency dynamics as a model with male-only regulation of male recruits). Expected reproductive success of the j 'th female genotype mating with the i 'th male genotype is given by a summation over k 'th progeny genotype ($k = oo, wo, yo, ww, wy, yy$):

$$\mathbf{V}_{j,i} = \sum_k \mathbf{g}_{i,j,k} \mathbf{A}_{i'}. \quad (4)$$

Maximum expected reproductive success by the j 'th female (\mathbf{Z}_j), and preferred male morph i^* is given by the genotype of the male mate that maximizes success (Alonzo and Sinervo 2001):

$$\mathbf{Z}_j = \max\{\mathbf{V}_{j,oo}, \mathbf{V}_{j,wo}, \mathbf{V}_{j,yo}, \mathbf{V}_{j,ww}, \mathbf{V}_{j,wy}, \mathbf{V}_{j,yy}\}. \quad (5)$$

We assumed that female preference was additive with respect to sire alleles. We used a simple decision rule, that is, females should mate with rare sire genotypes, given long-term frequencies generated by RPS cycles (e.g., central tendency after 1,000 generations). This rule (Alonzo and Sinervo 2001) yields progeny of high fitness in the next generation, in the case of a cyclical RPS. The formula for the attractor (Sinervo and Lively 1996) of the payoff matrix was used as a starting condition to solve for female decision rules. Central tendencies were computed after 1,000 generations, and female decision rules were updated based on rarity of sire genotypes relative to the central tendency, until central tendencies stabilized (< 0.001 change). Central tendencies stabilized rapidly because the attractor computed from nonself versus self payoff matrices was a reasonable approximation of the attractor in more complex models. This is because we assumed symmetry of behaviors across rare genotypes for both $\mathbf{m}_{i,j}$ and $\mathbf{d}_{i',i}$ and additive genetic effects.

To determine the presence of cyclical dynamics and whether all alleles were maintained, we first varied c and k in the payoff matrix $\mathbf{P}_{i',i}$ (table 1A) from $0 \leq c, k \leq 1$ (0.1 increments) to estimate domains of RPS dynamics.

We then varied values of d ($1 \leq d \leq 4$, 0.1 increments), the level of self-discrimination, for the same range of values for c and k . Finally, we varied m , context-dependent mate discrimination, across the same range as d , but we show only simulations for $c = 0.25$ and $k = 0.5$ (fig. 7). To illustrate dynamics, we show cycles for $m = 1$ or 4 and $d = 1$ or 4.

Results from ESS Models of Self- versus Non-Self-Regulation

ESS models (fig. 7) indicate that rapid RPS cycles, as observed in *Lacerta vivipara*, are possible only if all three factors are acting: (1) self versus nonself density regulation, (2) discrimination behavior that targets nonself, and (3) context-dependent mate choice as a function of sire alleles. In the absence of discrimination behavior d , the w allele can be lost, depending on costs of self-limitation that act on o (c) relative to y (k) alleles. Increasing the cost of o relative to y (e.g., $c < k$) allowed w to invade, thereby entraining RPS cycles. Thus, RPS cycles will be entrained if $c < k$. However, high levels of discrimination (d) preserved all three alleles, yielding the RPS Nash equilibrium, regardless of whether $c < k$ or $k < c$. Rapid cycles also required context-dependent mate choice. Assuming values of m and d that are of a magnitude observed in *Uta* (Sinervo et al. 2001, 2006a), models accurately reproduced the period and amplitude of cycles in *Lacerta* across a large parameter domain ($0 \leq c < k < 1$, $d > 1.3$, $m > 1.3$; fig. 7).

Discussion

We describe a new rock-paper-scissors social system in the European common lizard *Lacerta vivipara* based on male survival and performance trade-offs (figs. 3, 4), frequency cycles (fig. 5), and the payoff matrix of alleles in nature (fig. 6). We show that Pyrenean *L. vivipara* have three color morphs, which are akin to the three color morphs of *Uta*. The orange males of *L. vivipara* have higher endurance than white or yellow males, while white males have higher endurance than yellow due to allometry. The finding that physiologically vigorous orange males of *L. vivipara* have low survival parallels findings for *Uta*, in which orange males have higher endurance but lower survival between years, compared with blue or yellow males (Sinervo and Lively 1996; Sinervo et al. 2006a). Finally, the observed payoff matrix of alleles (FDS in fig. 6), based on effects of adult allele frequency on juvenile recruits, indicates that the *Lacerta* RPS is generated by self versus nonself genic selection that conforms to the genic selection of the *Uta* RPS (Sinervo et al. 2006a).

The sign of fitness relations within versus among morph alleles can be used to diagnose whether frequency-depen-

dent selection is due to antagonism versus mutualism (Sinervo and Calsbeek 2006). Negative interactions between morphs of *L. vivipara*, notably for o adults on w recruits and w adults on y recruits, were indicative of antagonism. A negative interaction within morphs, notably for both o and y alleles versus self, was indicative of self-limitation. A positive interaction between morphs, notably for o adults on y recruits, was indicative of facilitation or immunity. A lack of self-limitation on w implies that w alleles exerted neutral effects on w juveniles (self), but at the same time that o and y alleles were self-limited. This reflects a form of greenbeard cooperation: w adult males had neutral effects on self, but w adults expressed strong negative fitness effects on nonself (i.e., y). Moreover, interactions within the juvenile cohort of w genotypes enhanced survival of self (fig. 6B), which is diagnostic of a mutualistic benefit of w among maturing juveniles (Sinervo and Calsbeek 2006). Finally, greenbeard antagonism, in which adults discriminated against nonself progeny genotypes, was pervasive across all morphs.

Physiological traits associated with RPS strategies are also parallel in *Uta* and *Lacerta*. In reptiles, endurance and size affect fitness (Sinervo and Huey 1990; Sinervo et al. 1992, 2000b; Clobert et al. 2000; Lorenzon et al. 2000; Le Gaillard et al. 2004; Sinervo and Calsbeek 2006); however, a simple relationship between fitness, size, and endurance is not consistent across studies or species. Our results confirm that links among these traits are complex and that these links contribute to RPS social systems. Links are best understood in a game theoretic framework (table 1). Alternative strategies involve trade-offs with survival (Sinervo and Svensson 2002), given effects on performance and RHP (Sinervo et al. 2000b). For example, high endurance of orange male *L. vivipara* beats the endurance strategy of white that involves only size (fig. 1; table 1). However, the orange strategy involves survival costs (fig. 4) and self-limitation (fig. 6). This allows yellow to invade, perhaps owing to sneaky and/or cryptic behavior and morphology. Yellow males are invaded in turn by the strategy of white males, in which endurance is due to allometry and not to costly alleles for high endurance, as in orange males. Large size due to high survival of white males explains why relations among endurance, size, and fitness can be uncoupled in some morphs but not in others, resulting in a complex physiological RPS game. When tied to self and nonself density regulation among cohorts (fig. 6), RHP interactions among types (table 1) generate RPS cycles.

Lacerta morphs are consistent with genetic determination of morph type. Color has comparably high heritability in free-ranging *Lacerta* and *Uta* ($h^2 = 0.48$ in female *Lacerta* [Vercken et al. 2006], cf. $h^2 = 0.48$ in female *Uta* [Sinervo et al. 2000a] and $h^2 = 1.0$ in male *Uta* [Sinervo

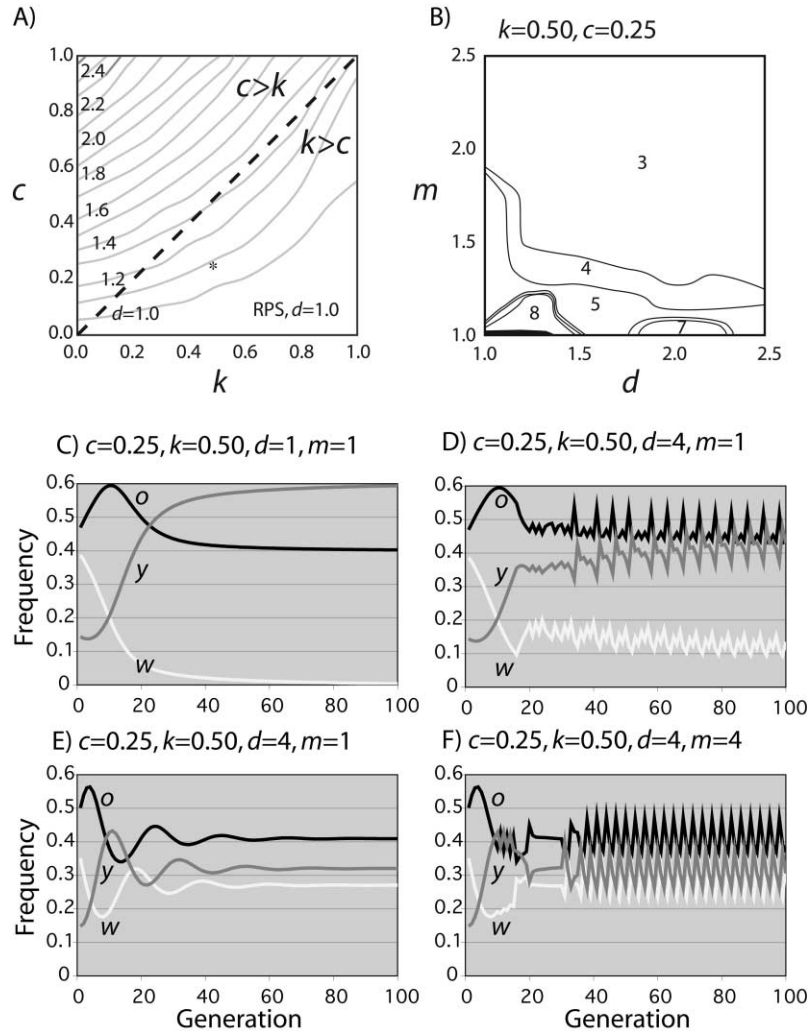


Figure 7: Evolutionarily stable strategy models of frequency regulation and self- versus non-self-discrimination. *A*, Three strategies are maintained for some values of k and c , self-limitation on y , and o , even in the absence of discrimination d (i.e., region labeled “RPS” [rock-paper-scissors], $d = 1.0$, which reflects panmixia). If no targeted discrimination is assumed, the w allele is lost for values of k and c that lie above the contour labeled $d = 1.0$. However, increasing levels of discrimination d expands the RPS domain where all three morphs are preserved. Contours describe RPS domains for consecutively increasing values of d . The evolutionarily stable strategy model (table 1) does not strictly assume that survival is more self-limiting for the hyperaggressive o compared to the cryptic y strategy ($0 \leq c < k < 1$). This domain corresponds to the area under the dashed diagonal ($c < k$). Thus, if $d > 1.5$, all values of $c < k$ generate an RPS cycle. If $d > 2.5$, all values of $k < c$ (i.e., y more self-limiting than o) generate an RPS cycle. *B*, Lengths of RPS cycles depend on the strength of both context-dependent mate choice m and discrimination behavior d . Results of simulations with $k = 0.5$ and $c = 0.25$ are shown (located at asterisk in *A*). RPS dynamics were observed for all values of m and d except in a small black region (e.g., when $d = 1.0$; area around asterisk in *A*). Domains that exhibited the same cycle length are delimited by contour lines. Rapid RPS cycles (≤ 4 generations long) are produced by values of $m > 1.3$ and $d > 1.3$. In *C–F*, we illustrate the effect on the form of RPS cycles of adding discrimination behavior and/or mate preference. Values of $m = 4$ and $d = 4$ were used because these values are comparable to observed strength of discrimination behavior in *Uta* (see text). *C*, The w allele can be lost when there is no discrimination or mate choice (e.g., $c = 0.25$, $k = 0.5$, $d = 1$, $m = 1$). *D*, A high level of discrimination behavior (e.g., $d > 2.5$; see above) will preserve the w allele and thereby entrain RPS cycles. However, cycles always dampen asymptotically toward the RPS attractor. *E*, Context-dependent mate choice by itself generates sustained RPS cycles, but cycles are often of longer period (> 5 generations). *F*, Discrimination behavior coupled with context-dependent mate choice generates rapid, perpetually sustaining RPS cycles, as observed in *Uta* and *Lacerta*.

et al. 2001]). Color in *L. vivipara* is very stable across years (see “Stability and Repeatability of Color and Interobserver Correlations”). The alternative to genetic control is a form of plastic morph determination. However, if *Lacerta* morphs were due to plasticity, we would not see RPS cycles; cycles and frequency overshoot of the RPS attractor should only be a feature of developmental systems that are genetic (Sinervo 2001a). Theory suggests that while limited plasticity is compatible with RPS cycles, plasticity can eliminate morphs and extinguish RPS cycles (Sinervo 2001a). Thus, while covariation of color, size, endurance, and survival may arise from plasticity and alternative developmental pathways, morphs of male *L. vivipara* are most likely governed by genes, as has been shown for female morphs of *L. vivipara* (Vercken et al. 2006).

In mating system reviews (Sinervo 2001b; Zamudio and Sinervo 2003), we postulated that an RPS cycle might evolve if (1) males control access to female harems (coarse-grained environment, high mating skew; see also Tompkins and Brown 2004), (2) females lay many clutches, thereby enhancing mating skew and density regulation, and (3) life span is short (coarse-grained temporal environment). Environmental grain is a requirement for genetic polymorphism (Levin 1962a, 1962b; Shuster and Wade 2003; Zamudio and Sinervo 2003). Conditions 1–3 are required for the complex dynamics that are displayed by alternative female morphs of *Uta*, which exhibit density and frequency cycles (Sinervo et al. 2000a). At low elevation, *L. vivipara* has rapid maturation (1 year) and high reproductive potential (up to three clutches). At high elevation, maturation takes 2 years, females lay one clutch (Heulin et al. 1997), and survival is high (0.33). Thus, attributes 2 and 3 are not always present, yet extremely rapid RPS cycles persist in *L. vivipara*.

Existence of rapid RPS cycles can thus be decoupled from a short life span, implying that species with a long life span might exhibit RPS cycles. Differences in maturation at high versus low elevation (2 years vs. 1 year) in Pyrenean *L. vivipara* only reduced allele frequency change by half, doubling the periodicity of the RPS. Nevertheless, the rate of change per generation at high and low elevation (0.32 vs. 0.28; fig. 6) is similar. Moreover, the magnitude of frequency change per generation is two- to threefold greater than that observed in *Uta* (0.13). *Uta* experiences the strongest chronic selection reported to date (Sinervo and Clobert 2003; Sinervo et al. 2000a, 2006a), yet the strength of selection driving RPS cycles in *Lacerta* must be about two- to threefold greater than *Uta*, given two- to threefold larger frequency excursions per generation. How can we reconcile such rapid cycles in *Lacerta* and strong frequency dependent selection in the face of cohort structure?

Invasion Conditions for Genic Self versus Nonsel Self Recognition Behavior

Theoretical models of the RPS cycle indicate that rapid cycles are not possible if selection arises purely from siring success (Sinervo 2001a, Laloï et al. 2004), especially in the face of age structure (Sinervo and Lively 1996). Cycles in such ESS models are >16 generations for a large parameter range. If RPS payoffs were due only to paternity success, age structure would increase RPS periodicity by introducing lags into the evolutionary response to selection (Sinervo and Lively 1996). If cohorts compete only during the adult phase, allele frequencies of older and younger cohorts would mix, thereby slowing cycles (Sinervo and Lively 1996). We suggest that rapid RPS cycles of *Lacerta* are governed by self versus nonself color recognition that impacts density-dependent recruitment, thereby accelerating the RPS dynamic. Self-recognition is known to drive RPS cycles in *Uta* (Sinervo and Clobert 2003; Sinervo et al. 2006a), and similar mechanisms are potentially present in *Lacerta* (Léna and de Fraipont 1998; Ronce et al. 1998; Aragon et al. 2006). Lizards of both species also show very strong size-dependent sensitivity to density, either as hatchlings or with increased competitive ability with age (Massot et al. 1992; Clobert et al. 1994; Sinervo et al. 2000a). Moreover, the observed density regulation in *Uta*, which drives rapid density cycles, is also consistent with our models of genic density regulation. Finally, the observed pattern of FDS among cohorts of *L. vivipara* (fig. 6) is entirely consistent with our model of genic density regulation.

To obtain rapid cycles and RPS intransitivity in the face of age structure, we developed explicit ESS models of genic selection in which older cohorts selectively remove younger cohorts (table 1). This novel ESS model links genic selection directly to population density regulation. While we apply genic regulation to male *Lacerta*, genic regulation could be generalized to female strategies (Sinervo et al. 2000a), making for a broad class of models that drive density cycles (Chitty 1996). Our model of genic selection is inspired by self versus nonself recognition loci that drive RPS cycles of *Uta*, RHP relations among morphs of *L. vivipara* (figs. 2, 3), predicted outcome of RHP interactions based on game theory (table 1), and observed frequency-dependent genic selection that drives density regulation in *Lacerta* (fig. 6).

Aggressive strategies can invade at low density of self, given that high RHP enhances their ability to exploit resources. A high-RHP strategy is however, strongly self-limiting ($0 \leq c < 1$) owing to self-aggression. The RHP strategy is invadable by less self-limiting (e.g., $c < k$ and off-diagonal payoffs for o and y) cryptic strategies. Cryptic strategies are invadable by a strategy that discriminates

and cooperates with self in density competition (w alleles in *Lacerta* or b alleles in *Uta*). Cooperation necessarily requires suppression of aggression toward self genotypes (Sinervo et al. 2006a). This social constraint makes cooperation susceptible to invasion by an aggressive RHP strategy, completing a density-dependent RPS cycle.

Self versus nonself frequency regulation favors the buildup of genic behaviors in males that seek out the morph that they can exploit (Sinervo and Clobert 2003; Sinervo et al. 2006a). Such discrimination behavior stabilizes the coexistence of three RPS strategies because morphs can target and exploit age classes more effectively than by chance encounters (Frean and Abraham 2001; Sinervo and Clobert 2003; Sinervo et al. 2006a). The behaviors we chose to model, discrimination and mate choice as a function of self versus nonself genotypes, are observed in *Uta* (Sinervo et al. 2006a; Bleay and Sinervo 2007). Discrimination, in which morphs direct social acts to other morphs from which they extract fitness, is under strong correlational selection (Sinervo and Clobert 2003). In *Uta*, morph alleles at the OBY locus are coupled to behaviors at unlinked self-recognition loci that enhance male dispersal (Sinervo et al. 2006b) and settlement (Sinervo et al. 2000a; Sinervo and Clobert 2003). These loci used in self versus nonself discrimination by males are shared between the sexes (Sinervo et al. 2000a). Thus, color recognition loci could be co-opted by females as an evolved counterstrategy to enhance progeny recruitment as a function of the phase of the RPS cycle (Alonzo and Sinervo 2001). A simple female counterstrategy, which we modeled, is to mate with the highest-payoff sire genotype, given her own genotype. Females should mate with the most rare nonself type when self types are common. Context-dependent mate choice is widespread (Alonzo and Sinervo 2001; Qvarnström 2001; Bleay and Sinervo 2007). Our results suggest that a novel origin of such behavior arises when genic selection impacts intrinsic density regulation. The origins of rare-male effects in female choice are likewise pervasive but poorly understood (Partridge 1988), and we suggest that such preference may be driven by cryptic RPS dynamics.

Theories of Intrinsic Density Regulation and the Generality of RPS Dynamics

Thus, results are of general importance for theories of density regulation, which have treated only impacts of kin selection on density regulation (Chitty 1996), not impacts of genic selection (Hamilton 1964; Dawkins 1976). RPS dynamics of self and nonself genic selection should invade any social system exhibiting intrinsic density regulation and RHP relations noted in table 1. ESS analysis shows that alleles, which discriminate self versus nonself, should

invade social systems under the force of genic selection even if they impose high genetic load or negatively impact individual fitness. The genetic load in *Uta* is large, and RPS cycles generate high standing levels of linkage disequilibrium due to correlational selection on traits that enhance morph fitness (Sinervo et al. 2000a, 2006a; Sinervo and Clobert 2003). Genic selection in *Uta* also promotes the evolution of true altruism (Hamilton 1964; Dawkins 1976), in which individual fitness is sacrificed to enhance gene propagation (Sinervo et al. 2006a).

Lacerta vivipara is phylogenetically divergent from *Uta*; the species last shared a common ancestor more than 175 million years ago (Estes 1983; Etheridge and de Queiroz 1988; Townsend et al. 2004), and lacertids are more closely related to snakes. Presence of an RPS cycle in *Lacerta* suggests that either the RPS cycle is very ancient or RPS mating systems are independently derived. Regardless of which scenario is the case, the existence of parallel color morphs and trait covariation is an important finding for social systems theory. RPS dynamics are likely to occur in other lizards. In Eurasian lacertids, we predict that species of *Podarcis* lizards, which occur in habitat similar to that of *Uta*, should exhibit morphs and RPS dynamics. Recent discovery (R. Calsbeek, J. Clobert, and B. Sinervo, unpublished data) of three color morphs in *Podarcis muralis* supports this prediction. Moreover, *Podarcis milisenensis* possesses three color morphs (orange, green, yellow; Arnold and Ovenden 2002). Among North American lizards, *Urosaurus*, *Uta*'s sister genus, should also exhibit RPS cycles, given that it exhibits three morphs (Carpenter 1995; D. B. Miles and B. Sinervo, unpublished data). The RPS social system may be common in agamid lizards, which also have vibrant colors.

An RPS cycle may be common in any species with three morphs, not just *Uta* and *Lacerta*. ESS analyses of payoffs in an isopod and a damselfly mating system, both of which exhibit three morphs, indicate that both species are governed by an RPS cycle (Sinervo and Calsbeek 2006). The role of RHP and physiology in a bacterial RPS cycle of *E. coli* is strikingly analogous to that of lizards, suggesting a general role for RHP traits in generating RPS dynamics (Sinervo and Calsbeek 2006). Colicins (col) plasmids are carried by strains of *E. coli* (Kerr et al. 2002; Kirkup and Riley 2004). Col plasmids code for a toxic col protein and immunity factors against that toxin. Col plasmids are costly, reducing growth of col strains relative to those lacking the plasmid. However, col bacteria can invade most noncol strains; cells of col strains that contact other strains lyse and release colicin. This reflects a strain altruistic act, analogous to genic selection in lizards, which clears the way for self. Col strains are invaded by strains with immunity to colicin, but immunity is costly for growth. Un-defended strains do not affect self or nonself strains and

are completely vulnerable to col strains, but the undefended strains pay no cost of immunity and have more rapid population growth rate than strains with immunity. Our ESS model, developed to explain RPS cycles of *Lacerta* (table 1), also captures the essence of the bacterial RPS dynamic. In this case, c is the cost of self-autolysis, and k is the cost of carrying col immunity on colony growth.

Given the empirical and theoretical import of the RPS cycle in elucidating genetical evolution in social systems, potential occurrence of the RPS cycle in other taxa can be predicted from our discovery of a new RPS cycle. Taxa having the following trait combinations—high density, high reproductive potential, and between-cohort density regulation—exhibit conditions for the evolution of RPS strategies of self versus nonself density regulation. An RPS cycle may occur in fishes such as African reef cichlids, which also possess intraspecific morphs (Seehausen and Schluter 2004). RPS dynamics might exist in birds such as the Gouldian finch, which possess three morphs (Pryke and Griffith 2006), or the ruff *Philomachus pugnax*, with a recently described third morph that is a female mimic (Jukema and Piersma 2006). The case of the ruff is salient because the existence of a near-perfect female mimic was suspected for years (van Rhijn 1991), but only recently was it confirmed (Jukema and Piersma 2006). Female-mimicking male morphs may be common, but given extreme crypticity, many cases may remain undiscovered. The trimorphic isopod, which exhibits RPS intransitivity (Sinervo and Calsbeek 2006), is another case with near-perfect female mimics (Shuster 1989), while damselflies exhibit RPS intransitivity (Sinervo and Calsbeek 2006) with near-perfect male mimics (Svensson et al. 2005). An RPS cycle may also exist in other sensory modalities that are cryptic to humans, such as olfaction in mammals (Sinervo and Zamudio 2002). In this regard, alleles at loci of the major histocompatibility complex of vertebrates may provide analogous self versus nonself recognition that generates genic selection and RPS cycles (Sinervo and Calsbeek 2006). In olfactory morphs that are cryptic to humans, RPS cycles might be more readily detected by studying buildup of linkage disequilibrium, which is associated with correlational selection and RPS cycles (Sinervo et al. 2006a). Cycles of nuclear alleles have been reported in snowshoe hares (Lidicker et al. 2000). Thus, intrinsic density cycles of rodents and hares (Chitty 1996) might be driven by genic selection that arises from self versus nonself density regulation, perhaps due to female genotypes and strategies.

We suggest that the RPS strategies, termed “deception,” “cooperation,” and “usurpation,” are the core strategies in many social species. However, cycles may be too long or their amplitude too weak to detect unless discrimination behaviors evolve that target social acts to self versus nonself

(Léna and de Fraipont 1998; Ronce et al. 1998; Aragon et al. 2006; Sinervo et al. 2006a). Once these loci evolve, or become coupled by correlational selection (Sinervo et al. 2006a), RPS cycles strengthen and the same loci could be co-opted for context-dependent mate choice as an adaptive female counterstrategy to the genic selection imposed by male strategies (Alonzo and Sinervo 2001; Qvarnström 2001; Calsbeek and Sinervo 2002; Richard et al. 2005; Sinervo et al. 2006a). In our model, loci for discrimination behavior, which enhance density regulation, could have a pleiotropic effect on female preference or, alternatively, build by correlational selection (Sinervo and Clobert 2003). This final step also occurs under runaway sexual selection because it involves loci for mate choice. However, this runaway sexual selection occurs in a cyclical dynamic (Sinervo and Svensson 2002), not simply an open-ended dynamic as in Fisherian runaway (Sinervo and Calsbeek 2006). As genetic correlations build between loci for mate choice and genic density regulation, rounds of selection in subsequent generations intensify, thereby accelerating RPS periodicity and increasing the ensuing genetic load imposed by genic density regulation.

A final point about the RPS cycle is salient. The RPS cycle is likely to govern culturally transmitted traits (Sinervo and Calsbeek 2006), given that cultural transmission of behavior via memes are analogous to genes (Dawkins 1976). Cultural conventions in which cooperation arises as a stable strategy to thwart the action of deception may be vulnerable to invasion by strategies that employ usurpation. Any usurpation strategy, which by its nature is noncooperative, might be invaded by deception. Many economic games (Semmann et al. 2004) are also governed by RPS rules of the general form found in our ESS models, including cultural conventions that govern human ecology and economy. With a little imagination, it is easy to analogize processes of targeted discrimination with hostile takeovers in economic transactions (and disassembly of a company) and processes of cooperation and context-dependent mate choice with mergers and acquisitions that depend on market conditions. Deceptive strategies in human economic ecology abound. New forms of economic cooperation thus evolve to thwart new mutant strategies of deception. Cooperation need not arise merely as a best response to deception in the case of mutual benefit. For example, cartels of self-recognizing members, interested in self-gain, can exert powerful collaborative effects that negatively affect nonself systems. There are even analogies of economic risk (Black and Scholes 1973) in the RPS cycle: demographic stochasticity makes usurpation vulnerable to loss and cooperation less risky (Calsbeek et al. 2002). Context-dependent mate choice by females evolves to limit losses in the context of risky RPS strategies. We suggest that RPS models might be fruitfully applied to economic

cycles, given that most human endeavors, regardless of scale (individual, group, corporation), are subject to density regulation. Finally, pervasive ethnocentric behavior of humans seems to be an inescapable aspect of our biological past, given that it impacts nonself density regulation even today. RPS dynamics driven by self versus nonself recognition of culturally transmitted signals may govern human altruism, mutualism, and antagonism, given that cycles of mutualism and altruism are conspicuous in RPS systems (Kerr et al. 2002; Sinervo and Calsbeek 2006; Sinervo et al. 2006a).

Moreover, the generality of RPS rules (table 1) governing density-dependent RHP competition in bacteria and lizards, an incredibly broad taxonomic swath, suggests that any biological system subject to self-limitation on growth might exhibit RPS dynamics (Sinervo and Calsbeek 2006). For example, ecosystem-level interactions that involve competitors, parasitism, and mutualism are likely to be governed by RPS intransitivity (Sinervo and Calsbeek 2006) if species interactions exhibit RHP relations of the form outlined in table 1.

Acknowledgments

Research was supported by a National Geographic grant to J.C., A. Corl, B.H., D.B.M., and B.S. and grants from the France-Berkeley Fund to M. Hochberg and B.S. B.S. was supported by the National Science Foundation, visiting research fellowships from the Centre National de la Recherche Scientifique (CNRS; 2001), and visiting professorships from the Pierre and Marie Curie Université in Paris (2003) and the Natural History Museum in Paris (2004). J.C. and B.H. were supported by funds from CNRS.

Literature Cited

- Agren, J., and L. Ericson. 1996. Population structure and morph-specific fitness differences in tristylous *Lythrum salicaria*. *Evolution* 50:126–139.
- Alonzo, S. H., and B. Sinervo. 2001. Mate choice games good genes and genetic cycles. *Behavioral Ecology and Sociobiology* 49:176–186.
- Aragon, P., M. Massot, and J. Clobert. 2006. Socially acquired information through olfactory cues. *Animal Behaviour* 72:965–974.
- Arnold, E. N., and D. W. Oviden. 2002. *Reptiles and amphibians of Europe*. Princeton University Press, Princeton, NJ.
- Black, F., and M. S. Scholes. 1973. The pricing of options and corporate liabilities. *Journal of Political Economics* 81:637–654.
- Bleay, C., and B. Sinervo. 2007. Discrete genetic variation in mate choice and a condition-dependent preference function in the side-blotched lizard: implications for the formation and maintenance of co-adapted gene complexes. *Behavioral Ecology* 18:304–310.
- Calsbeek, R., and B. Sinervo. 2002. The ontogeny of territoriality during maturation. *Oecologia (Berlin)* 132:468–477.
- Calsbeek, R., S. H. Alonzo, K. R. Zamudio, and B. Sinervo. 2002. Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations. *Proceedings of the Royal Society B: Biological Sciences* 269:157–164.
- Carpenter, G. C. 1995. The ontogeny of a variable social badge: throat color development in tree lizards (*Urosaurus ornatus*). *Journal of Herpetology* 29:7–13.
- Chitty, D. 1996. *Do lemmings commit suicide? beautiful hypotheses and ugly facts*. Oxford University Press, New York.
- Clobert, J., M. Massot, J. Lecomte, G. Sorci, M. de Fraipont, and R. Barbault. 1994. Determinants of dispersal behavior: the common lizard as a case study. Pages 183–206 in L. J. Vitt and E. R. Pianka, eds. *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, NJ.
- Clobert, J., J. A. Oppliger, G. Sorci, B. Ernande, J. Swallow, and T. Garland Jr. 2000. Endurance at birth, activity rate and parasitism in the common lizard. *Functional Ecology* 14:675–684.
- Dawkins, R. 1976. *The selfish gene*. Oxford University Press, Oxford.
- Estes, R. 1983. The fossil record and early distribution of lizards. Pages 365–398 in A. Rhodin and K. Miyata, eds. *Advances in herpetology and evolutionary biology: essay in honor of Ernest E. Williams*. Harvard Museum of Comparative Zoology, Cambridge, MA.
- Etheridge, R., and K. de Queiroz. 1988. A phylogeny of Iguanidae. Pages 283–367 in R. Estes and G. Pregill, eds. *Phylogenetic relationships of the lizard families*. Stanford University Press, Stanford, CA.
- Frean, M., and E. R. Abraham. 2001. Rock-paper-scissors and the survival of the weakest. *Proceedings of the Royal Society B: Biological Sciences* 268:1323–1327.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. 1, 2. *Journal of Theoretical Biology* 7:1–52.
- Heulin, B., K. Osenegg, J. Leconte, and D. Michel. 1997. Demography of a bimodal reproductive species of lizard (*Lacerta vivipara*): survival and density characteristics of oviparous populations. *Herpetologica* 53:432–444.
- Jukema, J., and T. Piersma. 2006. Permanent female mimics in a lekking shorebird. *Biology Letters* 2:161–164.
- Kerr, B., M. A. Riley, M. W. Feldman, and B. J. M. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418:171–174.
- Kirkup, C., and M. A. Riley. 2004. Antibiotic-mediated antagonism leads to a bacterial game of rock-paper-scissors *in vivo*. *Nature* 428:412–414.
- Laloi, D., M. Richard, J. Lecomte, M. Massot, and J. Clobert. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellites. *Molecular Ecology* 13:719–723.
- Le Gaillard, J.-F., J. Clobert, and R. Ferriere. 2004. Physical performance and Darwinian fitness. *Nature* 432:502–505.
- Léna, J. P., and M. de Fraipont. 1998. Kin recognition in the common lizard. *Behavioral Ecology and Sociobiology* 42:341–347.
- Levins, R. 1962a. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *American Naturalist* 96:361–373.
- . 1962b. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. *American Naturalist* 97:74–90.
- Lidicker, W. Z., J. O. Wolff, and R. A. Mowrey. 2000. Genetic change in a cyclic population of snowshoe hares. *Ecoscience* 7:247–255.
- Lorenzon, P., J. Clobert, and M. Massot. 2000. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution* 55:392–404.

- Massot, M., J. Clobert, T. Pilorge, J. Lecomte, and R. Barbault. 1992. Density dependence in the common lizard (*Lacerta vivipara*): demographical consequences of a density manipulation. *Ecology* 73:1742–1756.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Partridge, L. 1988. The rare-male effect: what is its evolutionary significance? *Philosophical Transactions of the Royal Society B: Biological Sciences* 319:525–539.
- Pryke, S. R., and S. C. Griffith. 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proceedings of the Royal Society B: Biological Sciences* 273:949–957.
- Qvarnström, A. 2001. Context-dependent benefits from mate choice. *Trends in Ecology & Evolution* 16:5–7.
- Richard, M., J. Lecomte, M. de Fraipont, and J. Clobert. 2005. Age-specific mating strategies and reproductive senescence. *Molecular Ecology* 14:3147–3155.
- Ronce, O., J. Clobert, and M. Massot. 1998. The evolution of offspring dispersal with mother age, some theory and one example. *Proceedings of the National Academy of Sciences of the USA* 95:600–605.
- Seehausen, O., and D. Schluter. 2004. Male-male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proceedings of the Royal Society B: Biological Sciences* 271:1345–1353.
- Semmann, D. H., J. Krambeck, and M. Milinski. 2004. Volunteering leads to rock-paper-scissors dynamics in a public goods game. *Nature* 425:390–393.
- Shuster, S. M. 1989. Male alternative reproductive behaviors in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in male fertilization success among α -, β - and γ -males. *Evolution* 34:1683–1698.
- Shuster, S. M., and M. J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350:606–661.
- . 2003. *Mating systems and strategies*. Princeton University Press, Princeton, NJ.
- Sinervo, B. 2001a. Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica* 112–113:417–434.
- . 2001b. Selection in local neighborhoods, graininess of social environments, and the ecology of alternative strategies. Pages 191–226 *In* L. Dugatkin, ed. *Model systems in behavioral ecology*. Princeton University Press, Princeton, NJ.
- . 2006. The developmental, physiological, neural, and genetic causes and consequences of frequency-dependent selection in the wild. *Annual Review of Ecology and Systematics* 37:581–610.
- Sinervo, B., and J. Clobert. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science* 300:1949–1951.
- Sinervo, B., and R. B. Huey. 1990. Allometric engineering: testing the causes of interpopulation differences in performance. *Science* 248:1106–1109.
- Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. *Nature* 380:240–243.
- Sinervo, B., and E. I. Svensson. 2002. Correlational selection and the evolution of genomic architecture. *Heredity* 89:329–338.
- Sinervo, B., and K. R. Zamudio. 2002. The evolution of alternative reproductive strategies: fitness differential heritability and genetic correlations between the sexes. *Journal of Heredity* 92:198–205.
- Sinervo, B., P. Doughty, R. B. Huey, and K. Zamudio. 1992. Allo-metric engineering: a causal analysis of natural selection on egg size. *Science* 258:1927–1930.
- Sinervo, B., E. I. Svensson, and T. Comendant. 2000a. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406:985–988.
- Sinervo, B., D. B. Miles, W. A. Frankino, M. Klukowski, and D. F. DeNardo. 2000b. Testosterone endurance and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior* 38:222–233.
- Sinervo, B., C. Bleay, and C. Adamopoulou. 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution* 55:2040–2052.
- Sinervo, B., A. Chaine, J. Clobert, R. Calsbeek, L. Hazard, L. Lancaster, A. G. McAdam, S. Alonzo, G. Corrigan, and M. E. Hochberg. 2006a. Color morphs and genetic cycles of greenbeard mutualism and transient altruism. *Proceedings of the National Academy of Sciences of the USA* 103:7372–7377.
- Sinervo, B., R. Calsbeek, T. Comendant, C. Adamopoulou, C. Both, and J. Clobert. 2006b. Genetic and maternal determinants of dispersal: the effect of sire genotype and size at birth on effective dispersal. *American Naturalist* 168:88–99.
- Svensson, E. I., J. Abbot, and R. Hardling. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *American Naturalist* 165:567–576.
- Tompkins, J. L., and G. S. Brown. 2004. Population density drives the local evolution of a threshold dimorphism. *Nature* 431:1099–1102.
- Townsend, T., A. Larson, E. Louis, and J. R. Macey. 2004. A new hypothesis of squamate evolutionary relationships from nuclear and mitochondrial DNA sequence data. *Systematic Biology* 53:735–757.
- Van Damme, R., D. Bauwens, and R. F. Verheyen. 1990. Evolutionary rigidity of thermal physiology: the case of the cool temperature lizard *Lacerta vivipara*. *Oikos* 57:61–67.
- van Rhijn, J. G. 1991. *The ruff*. Poyser, London.
- Vercken, E., M. Massot, B. Sinervo, and J. Clobert. 2006. Color polymorphism and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* 20:221–232.
- White, G. 2005. Correcting wildlife counts using detection probabilities. *Wildlife Research* 32:211–216.
- Wright, S. 1968. *Evolution and the genetics of populations*. University of Chicago Press, Chicago.
- Zamudio, K. R., and B. Sinervo. 2000. Polygyny, mate-guarding, and posthumous fertilizations as alternative male strategies. *Proceedings of the National Academy of Sciences of the USA* 97:14427–14432.
- . 2003. Ecological and social contexts for the evolution of alternative mating strategies. Pages 83–106 *in* S. F. Fox, T. A. Baird, and J. K. McCoy, eds. *Lizard social behavior*. Johns Hopkins University Press, Baltimore.