Self-recognition, color signals, and cycles of greenbeard mutualism and altruism


*Department of Ecology and Evolutionary Biology, University of California, Earth and Marine Sciences Building, Santa Cruz, CA 95064; **Laboratoire D’Ecologie, Centre National de la Recherche Scientifique, Unité Mixte de Recherche 7625, Bâtiment A, Eme Etage, Case 237, 7 Quai Saint Bernard, F-75252 Paris Cedex 05, France; †Laboratoire Evolution et Diversité Biologique, Station Biologique du Centre National de la Recherche Scientifique Moulis, 09200 Saint-Girons, France; ‡Center for Tropical Research, Institute of the Environment, University of California, 1609 Hersh Hall, Los Angeles, CA 90095; ††Department of Biology and Molecular Biology, Montclair State University, 1 Normal Avenue, Upper Montclair, NJ 07043; **Department of Fisheries and Wildlife and Department of Zoology, Michigan State University, 13 Natural Resources Building, East Lansing, MI 48824; †‡Department of Ecology and Evolutionary Biology, Yale University, 427 Osborn Memorial Laboratory, New Haven, CT 06520-8106; †§Institut des Sciences de l’Evolution, Centre National de la Recherche Scientifique, Unité Mixte de Recherche 5554, Université Montpellier II, 34095 Montpellier, France; and †Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501

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Altruism presents a challenge to evolutionary theory because selection should favor selfish over caring strategies. Greenbeard altruism resolves this paradox by allowing cooperators to identify individuals carrying similar alleles producing a form of genic selection. In side-blotched lizards, genically similar but unrelated blue male morphs settle on adjacent territories and cooperate. Here we show that payoffs of cooperation depend on asymmetric costs of orange neighbors. One blue male experiences low fitness and buffers his unrelated partner against aggressive orange males despite the potential benefits of defection. We show that recognition behavior is highly inheritable in nature, and we map genetic factors underlying color and self-recognition behavior of genic similarity in both sexes. Recognition and cooperation arise from genome-wide factors based on our mapping study of the location of genes responsible for self-recognition behavior, recognition of blue color, and the color locus. Our results provide an example of greenbeard interactions in a vertebrate that are typified by cycles of greenbeard mutualism interspersed with phases of transient true altruism. Such cycles provide a mechanism encouraging the origin and stability of true altruism.

Results and Discussion

Dyad Formation and Kin Philopatry. A key component of non-kin greenbeards is the ability of unrelated individuals to find a partner. We used microsatellite loci to determine which neighbors share enough alleles (e.g., genically similar) such that they could be sire–progeny pairs or sibs (13–18). A sire–progeny criterion of relatedness (r = 0.5) is more stringent than that of natural half sibs (r = 0.25) given the polyandrous mating system (18). Precise maternal pedigrees provided definitive evidence that cooperating males are unrelated. Although a greenbeard is not incompatible with kin selection, its action potentially confounds genic selection with kin nepotism. We tested for kin philopatry in associations of genetically similar males.

Genetically similar bb neighbors occur at ~3.4 times the expected rate (15 pairs observed, 4.4 expected; χ² = 20.8, 1 d.f., P < 0.0001) on sib-randomized plots. Dyadic males are unrelated based on the maternal pedigree (15). Blue males do not preferentially settle close to other B males, relative to O and Y males (F₁,575 = 3.14, P < 0.05; number of B neighbors: B = 1.58 ± 0.15, Y = 1.47 ± 0.14, O = 2.10 ± 0.22; B = Y < *O, P < 0.05, in post hoc tests). Thus, self-recognition and settlement of genetically similar bb males are determined by more than just blue color. Experimental randomization of sibs in this sample may have precluded kin groups from forming, biasing settlement in favor of unrelated bb male dyads. Thus, if males use phenotype matching to find and cooperate with kin, observed settlement of unrelated yet genetically similar males may be an artifact of kin randomization.

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Abbreviations: RPS, rock–paper–scissors; LD, linkage disequilibrium.

To whom correspondence should be addressed. E-mail: sinervo@biology.ucsc.edu.

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A large-scale experiment in which progeny were released on sibship-intact plots tested specifically for kin philopatry in forming associations of genetically similar males. On sibship-intact plots, five genetically similar \(bb\)-\(bb\) dyads formed, two \(bb\)-\(by\) dyads formed, and one \(by\)-\(yo\) dyad formed. No dyads were kin based on the pedigree. Thus, 10 \(bb\) males (five pairs) formed dyads of 35 \(bb\) males reflecting 29% of all \(bb\) males, comparable to that observed on sib-randomized plots (33%). This finding reflects a nonrandom pattern largely restricted to \(bb\) males (dyadic \(bb\); 5 pairs observed, 0.5 expected; dyadic \(non-bb\); 3 pairs observed, 6.9 expected; \(x^2 = 43.3, 1\) d.f., \(P < 0.0001\)). Thus, presence of kin has no effect on formation of \(bb\) dyads among genetically similar males at maturity.

To determine why kin philopatry does not contribute to \(bb\) dyad formation, we compared survival and dispersal on sibship-intact and randomized plots. On sibship-randomized plots we recovered 58 males at maturity of 424 neonates including seven sib pairs. On sibship-intact plots we recovered 58 males at maturity of 910 neonates and only three sib pairs (only 1 male was \(bb\)). On sibship-intact plots, none of the three sib pairs formed dyads because they settled at an average distance [25.5 ± 6.5 m (SE)] greater than between dyadic \(bb\) cooperators (<10 m). Survival of sib pairs was higher on sib-randomized than sib-intact plots (14/424 vs. 6/910; \(x^2 = 13.7, 1\) d.f., \(P < 0.001\)). Higher mortality on sibship-intact plots suggests that hatching kin competition favors dispersal, not philopatry, posing a constraint on kin cooperation. Dyads are thus more likely to form between unrelated but genetically similar males.

Associations of \(bb\) dyads could arise from mutual attraction to environmental features (e.g., rocks or \(bb\) females) rather than from greenbeard recognition. Four lines of evidence indicate that this is not the case. First, dyads lack consistency in location among years (\(n = 15, 8, 7\) and 7 dyads in 1992, 1998, and 1999). Minimum distance between nearest dyads across years averaged 18.8 ± 2.7 m. Second, manipulating a likely point of attraction, large rock piles (20, 21), does not affect \(bb\) dyad formation. Half of the \(bb\) dyads formed >10 m away from piles (\(n = 7\) of 14), and 21 of 38 \(bb\) males settled >10 m from piles. Third, dams with \(b\) alleles were less likely to overlap territories with \(bb\) dyads than loners [1.16 ± 0.38 vs. 1.98 ± 0.25 (SE); \(F_{1,2.5} = 3.34, P = 0.07\)]. Dyads are not attracted to overall female density; dyadic \(bb\) males had fewer females per territory than loner \(bb\) males (1.77 ± 0.38 vs. 2.64 ± 0.21 females; \(F_{1,117} = 3.93, P = 0.05\)). Fourth, \(bb\) dyads are genetically similar across nine microsatellite loci, not just \(OBY\), implying a genetic cause.

**Genetic Architecture of Self-Recognition Behavior and the \(OBY\) Color Locus.** Cosettlement of dyadic \(bb\) males implies that \(b\) color-recognition and self-recognition (e.g., genetic similarity) should have a simple genetic basis. We found that \(bb\) dyadic recognition was heritable (1998–1999, \(h^2 = 0.97 ± 0.30\); mid-parent regression: \(F_{1,29} = 12.26, P < 0.002\) and similar for sons (\(h^2 = 0.89\) and daughters (\(h^2 = 1.05\) [analysis of covariance: \(F_{1,26} = 0.70, P = 0.51\)]. Thus, females and males share self-recognition alleles, which can promote assortative mating in females for dyadic \(bb\) males (B.S., unpublished data). High heritability implies alternative alleles besides self-attraction, which could include “self-repulsion” or “neutral” settlement behaviors with respect to genetically similar neighbors. Such alleles could explain previously documented patterns of \(O\) hyperdispersion and \(Y\) settlement (15).

High heritability also implies that genetic factors underlying color and self-recognition can be mapped to microsatellite markers with decay of linkage disequilibrium (LD) in progeny, given high LD among microsatellite loci and dyadic behavior (Fig. 1A and B). We constructed a primary linkage map and then mapped (Fig. 1C) genetic variation for \(OBY\) color alleles and self-recognition of \(bb\) dyads. The three alleles of the \(OBY\) locus (14) mapped to a single genetic factor between \(Plkn\) and \(SpHill\). In contrast, self-recognition behavior of genetically similar males with \(b\) alleles mapped to three linkage groups (\(10000M, NGff\), and \(SmnC\)), implying that high heritability for self-recognition and cosettlement of dyadic \(bb\) males and nonrandom mating of dams with dyadic \(bb\) sires is due to at least three unlinked genetic factors. Our results therefore indicate that the “greenbeard” corresponds to self-recognition of multiple loci including, but not limited to, \(b\) alleles of the \(OBY\) locus: highly successful \(bb\) cooperators must share alleles at all four loci.

**Fitness Costs and Benefits of \(bb\) Dyads and the RPS Cycle.** For altruism to occur, participating individuals must find a suitable partner, and
in the RPS game (17–19).

4.83

males (Fig. 2). However, reduced fitness of dyadic males is

neighbors has low fitness compared with the male with few O

from O neighbors, their strategy still loses to O genotypes that have

3.43; post hoc test: loner

0.03) of dyadic

S,loner

1.76; GMrecruits: S,recipient = 0.80, W,donor = 0.22, W,loner = 0.19). If genetically similar bb males are available it pays to cooperate: GM fitness of dyads is higher than loner males (GMrecruits[W,donor + W,recipient]/2) = 2.86, GMrecruits = 0.64). Thus, the dyadic strategy is mutualistic in the long run (15), but high average fitness of greenbeard b alleles balances transient altruistic costs paid by donors when O is common. Both males should accept these risks of cooperation even though one will receive approximately zero payoff.

In ensuing phases of the RPS, O frequency falls because when common O is susceptible to the Y male strategy, which mimics females and cuckold O males (16–18). In these years, bb males gain fitness from Y neighbors, but only if they form cooperative dyads of genetically similar bb males. Although frequency of Y neighbors

a cost must result from their otherwise mutualistic interactions. Costs of altruism can be measured relative to a loner strategy that does not participate in this group behavior. Settlement of O males beside bb males reduces average fitness of dyadic bb relative to loner bb males (Fig. 2). However, reduced fitness of dyadic males is primarily borne by one male (Fig. 3). The male with many O neighbors has low fitness compared with the male with few O neighbors (ΔWΔN>O; Fig. 3). Even though loner bb males gain fitness from O neighbors, their strategy still loses to O genotypes that have higher siring success overall (W,loner bb = 1.80 ± 0.27, W,bb = 4.83 ± 1.91, W,bb = 1.90 ± 0.76, W,bb = 3.53 ± 0.98; analysis of covariance: F,1,114 = 3.43; post hoc test: loner bb and oo significantly lower than bo and yo). This finding reflects the fact that O beats B in the RPS game (17–19).

In the notation of fitness costs and benefits, dyadic bb males with more O neighbors are donors and those with fewer O neighbors are beneficiaries or recipients of social acts. Fitness asymmetries in dyads may be larger when the number of O males (N,O[t]) cycles to high frequency because of RPS dynamics (16–19), which leads to the interesting possibility that among-year changes of O frequency may alter social interactions among generations of bb males from altruism (W,recipient > W,loner > W,donor) to mutualism (W,recipient > W,donor > W,loner).

To determine whether bb dyads fit criteria for altruism or mutualism, frequency-dependent payoffs for recipients and donors were compared with loners using fitness relations (β parameters supplied in Figs. 2 and 3). Fitness of a strategy at time (W, t) where j = recipient, donor, or loner) is a function of N,O[t] and fitness asymmetry, ΔWΔN,O[t] (slope, Fig. 3), of dyads:

\[ W_{\text{recipient}}[t] = \beta_1 + \beta_2 \times N,O[t] + \Delta W_{\Delta N,O}[t]/2, \]

\[ W_{\text{donor}}[t] = \beta_1 + \beta_2 \times N,O[t] - \Delta W_{\Delta N,O}[t]/2, \]

\[ W_{\text{loner}}[t] = \beta_3 + \beta_4 \times N,O[t]. \]

Costs and benefits of cooperation for dyads, ΔWΔN,O[t], depend on ΔN,O[t], which arises from random asymmetries in O settlement next to dyadic males (Fig. 3 A and B):

\[ \Delta W_{\Delta N,O}[t] = \beta_5 \times \Delta N,O[t]. \]

ΔWΔN,O[t] can be expressed in terms of N,O[t] by noting that ΔN,O[t] depends on N,O[t] (Fig. 3C), a relation that arises from small neighborhood effects on variance in number of O neighbors (19):

\[ \Delta W_{\Delta N,O}[t] = \beta_3 \times (\beta_6 \times N,O[t]). \]

Eqs. 1–5, parameterized by field estimates of fitness (Figs. 2 and 3), allow us to calculate fitness of strategies over time (Fig. 4B), given N,O[t] for bb dyads over 14 generations (t = 1990–2003; Fig. 4A). In the long run, geometric mean (GM) (22) fitness of donor and loner males are similar, even though short-term fitness of donor males dips close to zero (Fig. 4; GMrecruits: S,recipient = 3.53, W,donor = 2.11, W,loner = 1.76; GMrecruits: S,recipient = 0.80, W,donor = 0.22, W,loner = 0.19). If genetically similar bb males are available it pays to cooperate: GM fitness of dyads is higher than loner males (GMrecruits[W,donor + W,recipient]/2) = 2.86, GMrecruits = 0.64). Thus, the dyadic strategy is mutualistic in the long run (15), but high average fitness of greenbeard b alleles balances transient altruistic costs paid by donors when O is common. Both males should accept these risks of cooperation even though one will receive approximately zero payoff.

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Fig. 2. Fitness effects of crowding by O males on dyadic and loner bb males. Siring success is significantly related to number of O neighbors (N,O) for dyadic and loner bb males (P < 0.05 all regressions; analysis of covariance: differences in slope significant; W,C,F1,19 = 13.38, P = 0.0004; W,C,F1,31 = 12.60, P = 0.0006). Data give parameter estimates for dyads (A, β1 and β2; B, β1 and β2) and loners (C, β1 and β2; D, β1 and β2) used in evolutionarily stable strategy (ESS) analysis.

Fig. 3. Fitness effects of asymmetries in O male crowding on dyadic males and relationship of the asymmetry in O male crowding to average number of O males next to dyadic bb males. Difference in number of O male neighbors (ΔN,O) is related to difference in siring success (A) (ΔW,S:F1,28 = 4.82, P = 0.03) and recruits (B) (ΔW,R:F1,28 = 4.82, P = 0.03) of dyadic bb males. (C) ΔN,O depends on average number of O neighbors (N,O) for dyadic bb males (F1,31 = 7.15, P = 0.01). A and B give estimates for β5 for W,S and W,R, respectively, and C is used to convert N,O[t] to ΔN,O[t] (β5).
RPS cycles drive cycles of mutualism and altruism in recipient and donor males of a dyadic pair relative to loner males. (A) Mean number of O neighbors (±SE) for bb males (N0) as a function of RPS cycles (11, 12). (B) Progeny recruits for recipients, donors, and loners computed using Eqs. 1–5. RPS cycles drive N0(t), generating alternating phases of altruism (A) and mutualism (M).

(fY) does not affect fitness of loner bb males who only have genetically dissimilar neighbors (siring: Ws = 2.22 − 0.97 × fY, F1,64 = 0.73, P = 0.39; recipients: WR = 0.42 − 0.35 × fY, F1,64 = 0.73, P = 0.39). fY enhances fitness of bb dyads (Ws = 0.77 + 3.53 × fY, F1,22 = 3.76, P = 0.06, WR = 0.00 + 0.85 × fY, F1,22 = 5.05, P = 0.03). A significant difference between effects of fY on loner vs. dyadic bb males (Ws; F1,82 = 6.06, P = 0.01; WR; F1,82 = 4.32, P = 0.04) indicates that fY affects the strategies differently. During the Y phase of the RPS, the bb greenbeard is mutualistic. As bb males invade during this mutualistic phase, conditions are reestablished for invasion of O males, thereby fueling a return to bb altruism. Evolutionarily stable strategy (ESS) analyses (Eqs. 1–5) are supported by comparisons of average fitness of bb recipients, donors, and loners during mutualistic versus altruistic phases of the RPS cycle (Table 1). Therefore, dyad formation among genetically similar males is favored on average by mutualistic benefits to each bb. However, not all years are mutualistic: at high N0, donor males have lower fitness relative to recipients and loner males.

**Stability of Altruism in the Face of Egoists.** Mutuality is stable from the perspective of an egoist; because both partners benefit there is little risk of defection. Altruism is not stable for donors who get low fitness. Donors should defect and opt for a higher payoff strategy if one exists. The low fitness of donor males when O is common indicates that donor males should use the presence of O neighbors as a cue to defect. However, defection requires that donor males have a viable recourse.

A viable defection strategy would be for donors to displace recipients, provided recipients become donors. If so, fitness asymmetry of dyadic males should be correlated with an asymmetry in resource holding potential. However, we found no effect of resource holding potential traits (21) on fitness asymmetry of donors and recipients (mass: F1,26 = 1.02, P > 0.32; condition: F1,26 = 1.35, P > 0.26).

Another viable recourse for donors includes partner abandonment for a higher-payoff territory (i.e., adopt loner strategy) when O males settle beside donors at the beginning of the breeding season (21–23). Such a relocation strategy is possible. Loner bb males can obtain a territory 2–3 weeks after most males (20, 22) and do not lose fitness relative to loners that remain stationary [n = 8 loners that moved (Wb = 2.33 ± 0.91, Ws = 0.35 ± 0.32) vs. n = 54 that were stationary (Ws = 2.09 ± 0.40, Wb = 0.20 ± 0.14); Ws: F1,57 = 0.22, P > 0.64, not significant; no year effect: F1,57 = 0.43, P > 0.72; Wb: F1,57 = 0.06, P > 0.80, not significant; no year effect: F1,57 = 1.56, P > 0.20]. Potential payoffs of defection would be more appropriately measured for bb males that abandon dyads; however, no bb males that have formed a dyad with a genetically similar male have ever been observed to move (0/40) despite obvious fitness benefits that donors could obtain via defection. By contrast, loners can avoid fitness costs of inappropriate social neighborhoods by abandoning territories at a significantly higher rate (8/82; likelihood ratio = 6.63, P < 0.01, 1 d.f.) and finding new sites. Therefore, the donor is truly altruistic by foregoing potential benefits of defection in years with high N0.

**Evolution of Greenbeard Dynamics: A Synthesis.** Donor males of bb dyads of side-blotched lizards are true altruists when O males are common in that they forgo potential benefits of defection.

![Fig. 4. RPS cycles drive cycles of mutualism and altruism in recipient and donor males of a dyadic pair relative to loner males. (A) Mean number of O neighbors (±SE) for bb males (N0) as a function of RPS cycles (11, 12). (B) Progeny recruits for recipients, donors, and loners computed using Eqs. 1–5. RPS cycles drive N0(t), generating alternating phases of altruism (A) and mutualism (M).](image)
Because few males survive more than one breeding season, future $bb$ dyads form from progeny in altruistic phases of the RPS; few come from donors. Dyads are stabilized by high fitness of $bb$ alleles or genetic selection but not destabilized by defection of egoists. Nonrandom settlement and cooperation of genetically similar $bb$ males is, therefore, an evolutionary greenbeard that stabilizes dyads across generations. Because $bb$ dyads have higher fitness than loner males, the greenbeard is best viewed as mutualistic in the long run. Periods of true altruism, restricted to generations in $O$ phases of the RPS, are best viewed as “transient” altruism.

We have mapped key genetic factors for self-recognition of genetic similarity and a key signal locus, OBY. These loci express the three traits necessary for greenbeard behavior: signal, recognition, and donation (6). OBY color is a component of both greenbeard donation and signal, given relations with territoriality, stamina, testosterone, and aggression (23, 24). Thus, blue color is a signal for identifying other potential cooperators with similar territorial restraint, symmetry in stamina, and lower aggression relative to $O$ males. Greenbeard recognition may also arise from self-referent phenotype matching (25). For example, self-referent signals like head-bob rate (26) or odor (27), used in individual recognition, could be the traits that are governed by color- and self-recognition loci (Fig. 1C) that stabilize $bb$ cooperation. However, recombination of alternative alleles from $O$ and $O$ genotypes among unlinked loci for the signal, self-recognition, and donation of $bb$ cooperation will invariably generate many loner $bb$ males that lack an intact greenbeard complex. Loner $bb$ males may thus be deficient in one or more cooperative greenbeard traits, yielding low fitness relative to dyadic $bb$ males. Our inferences on genomic architecture of OBY and self-recognition loci, based on the field pedigree, were greatly aided by the genetics of $Uta$, which harbors high levels of LD (Fig. 1) owing to chronic correlational selection that favors an intact signal-recognition complex in $bb$ males, and alternative alleles that are favored in $O$ and $Y$ male strategies.

If Dawkins (6) had chosen another color in his hypothetical example of altruism, he might have presaged the bluebeard of cooperation in $Uta$. A salient difference between bluebeard recognition in $Uta$ and Hamiltonian (5) supergenes envisioned by Dawkins (6) is the genome-wide nature of the $Uta$ bluebeard. The $b$ allele segregates at a key signal locus, but at least three other self-recognition and color-recognition factors (Fig. 1C) are linked to OBY signals by correlational selection on the benefits afforded by self-recognition and cooperation (15). Correlational selection exists because all signal-recognition donation components are required for $bb$ cooperation, but such alleles are harmful for other morphs like $O$, which have aggressive behaviors that destabilize cooperation (15). Hamilton (5) did not consider the power of correlational selection in coupling suites of traits and driving coordinated evolution of the many loci required for complex behaviors like cooperation. Correlational selection that couples traits in one morph intensifies selection on other morphs in the next generation (15). Thus, social systems like the RPS cause adaptation to be self-reinforcing in a Red Queen cycle (13, 14, 28). The correlational selection that bundles components for signal, self-recognition, and self-attraction plays a profound role in building the genome-wide bluebeard of $Uta$. Correlational selection on recognition systems should be general for all forms of evolutionary cooperation (28).

Evolution in $kin$ altruism, sharing a fraction of genes is not sufficient for donation; specific genes that allow recognition of $kin$, exclude cheaters, and coordinate donations are required. A proximate explanation for $kin$ altruism is not that $kin$ share a fractional number of genes; rather, $kin$ altruists share key genes for signal, self-recognition, and donation behavior. Our view is that cooperators need to share alleles at three key loci for signal, recognition, and donation. Given that all three loci are required to secure the benefits of cooperation, correlational selection will build genetic correlations among these loci. Overall genetic similarity of $kin$ is thus a by-product of correlational selection on these loci rather than a cause of cooperation. Once key loci for cooperation exist, they cause genome-wide similarity to build by coopting more loci into this gene complex. Adding more loci allows for the complex to protect against erosion of linkages due to intragenomic conflict (10) and invasion by cheaters, as well as an added by-product of spreading benefits of cooperation across the genome.

One reason we may not find many examples of greenbeards is that we typically look for simple ones with few genes (7–12). Other examples with many shared genes are described as kin selection (29–31), even without a pedigree (32, 33). These cases may arise from greenbeard correlational selection acting on either kin or unrelated pairs. This process-based view of greenbeard correlational selection, which acts on many signal-recognition donation loci, provides a promising avenue for mapping genes that govern behavior in nature, as we have done in $Uta$. Our experiments on $Uta$ also show that juvenile kin competition poses a severe constraint on evolution of $kin$ cooperation in adults because dispersal is favored. Thus, juvenile kin competition enhances conditions for evolution of adult greenbeard cooperation. Conversely, novel social behaviors that ameliorate juvenile kin competition would enhance evolution of adult kin cooperation. For example, elaborate chambers constructed by social insects for juvenile development may have reduced sib competition, favoring evolution of adult kin altruism.

Do other species harbor cooperation arising from unlinked loci assembled in a coadapted complex of greenbeard signals, recognition, and donation? A fruitful place to look is in examples of $kin$ altruism (29–31), which may harbor loci for signal, recognition, and donation behavior that are under correlational selection. In addition, the scarcity of examples of non-kin altruism may be because transient altruism is masked by long-term mutualism in studies that ignore temporal dynamics, or because mutualism would be expected to replace altruism over the evolutionary long run by means of a build-up of genes that stabilize cooperation. Cycles of altruism and mutualism may also be encouraged by RPS dynamics (28). The link between RPS cycles and altruism is highlighted by a bacterial RPS (34) played out among toxin-producing, toxin-resistant, and undefended clones. When crowded, some cells of toxic clones release toxins by autolysis. This self-sacrificial act reflects $kin$ altruism that benefits the growing clone by destroying neighboring clones lacking resistance. In this sense, Eqs. 1–5 for greenbeard cycles, along with equations for other players of the RPS social system (16, 17), define a more general dynamic of alternative social strategies. We suggest that RPS strategies reflect more fundamental social strategies (35) of usurpation ($O$: badge of resource holding potential), cooperation ($B$: badge of cooperation), and deception ($Y$: sneaker) and that such social system dynamics are common in nature (reviewed in ref. 28). Perhaps altruism in other species can be maintained by similar frequency-dependent cycles of mutualism and altruism driven by these basic social strategies. In turn, such cycles of mutualism and altruism may provide the boost needed for successful spread of altruistic genes in early evolutionary stages of altruism.

Materials and Methods

Population Census. Maternal pedigrees are known with certainty: dams taken from nature lay eggs in the laboratory on first-to-third clutches (15–18). Dams are returned to territories between clutches. Marked progeny are randomly released with respect to parental territories (2–3 days hatching) on sib-randomized plots monitored since 1989. Progeny survival is censused at maturity. Adult $Uta$ are restricted to patchy rock outcrops. The focal site is 400 m in radius. We search populations around this focal site (2-km radius). Emigration does not confound fitness (15, 18). Surviving progeny are unlikely to be missed; capture probability on a 3-week census is 0.97 (36). We census every 2–3 weeks to record color during the breeding season.
Territory Maps. Multiple passes are made over the site to map all male and female territories. For example, a total of $N = 1049$, 801, 478, and 597 male locations were mapped in 1992, 1996, 1998, and 1999, respectively, yielding an average of 8.4, 13.6, 7.2, and 11.0 sightings per male (15). The minimum convex polygon that circumscribes locations defines a lizard’s territory. Males with adjacent territorial edges are neighbors. Territory data (1990–2003) provide frequency of neighboring morphs ($N_B, N_C$, and $N_Y$).

DNA Paternity. To build paternal links, we genotyped (on an ABI 377 from Applied Biosystems) nine microsatellites from extracted DNA by means of PCR (18). We genotyped 124, 56, 44, 40, 43, and 147 sires, 68, 96, 40, 35, 48, and 100 dams, and 458, 160, 212, 78, 103, and 284 progeny from 1992, 1996, 1998, 1999, 2001, and 2002, respectively. Paternity was assigned in KINSHIP (maximum likelihood and exclusionary criteria) (37). The delete-one jackknife method (38) was used to test for significance of regression ($B$) relating fitness to frequency of neighboring morphs.

Sibship-Intact Plots. We constructed four sibship-intact plots: three founded (14) in 1999 and one in 2000. Using the same methods described above, we released 910 male and 893 female progeny or sib pairs; relatedness coefficient $= 0.5$. We searched all pairwise cases of sires in a neighborhood. Maximum likelihood (18, 37) was used to establish which males met this “kin” criteria ($P \leq 0.01$) relative to all other males rejected as kin ($P > 0.01$). Neighboring males could be sibling or sire–progeny pairs, reflecting high genetic similarity; however, none were kin (e.g., sibs, half-sibs, cousins, and sires) based on the maternal pedigree (18).

Male Association Tests. Across all possible pairwise comparisons of $bb$ males (279 pairs) residing in the same population, we found that 15 pairs met the maximum likelihood criterion of genetic similarity (see Genetic Similarity), or 5.4% of $bb$ pairs. Eighty-two $bb$ pairs were actual neighbors; thus, we expect 4.4 genetically similar $bb$ pairs by chance alone to be neighbors. A similar test was used on sibship-intact plots, but we also pooled males into a non-$bb$ class (see Dyad Formation and Kin Philopatry).

Linkage Mapping. We built a primary linkage map of nine microsatellites (1992 pedigree: 48 families; $n = 368$) using CRMAP 2.4 (39). We mapped genetic variation and coded for color alleles (14) and self-recognition (1998–1999 pedigree: 25 families, 105 individuals). Significant transmission LD (CRMAP 2.4, logarithm of odds $\geq 3.0$) (40) between genetic variation in OBY color alleles and microsatellite marker loci indicated cosegregation on the same linkage. Markers with logarithm of odds $< 3.0$ recombinated at 0.5 (e.g., 100 cM). We mapped self-recognition behavior, coded as 0 for males not forming dyads with genetically similar males, 1 for dyadic males with genetically similar neighbors with one $bb$ allele, and 2 for dyadic males with genetically similar neighbors with at least two $bb$ alleles. Dyadic behavior is not restricted to $bb$ dyads, but also drives female settlement. The pedigree indicates that few males mated with female kin (15), so “female–male dyadic” behavior may also be due to shared genes for recognition. Females were scored as above, 0, 1, and 2+, based on number of genetically similar mates that also had $bb$ alleles.

Rock Pool Experiment. We manipulated the thermal environment by building 75 rock piles ($0.5–1.0$ m), which are attractive to both sexes (20, 22). Rock piles were 0.5–1.0 m in height, composed of 10–40 boulders, and spaced at 35.5 ± 3.1 m (SE). Adults ($n = 244$ males) recruited naturally to rock piles ($\approx 80\%$), and we also seeded hatchlings from laboratory crosses (20%) (20, 22).

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