

SOCIALLY MEDIATED SPECIATION

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Abstract.—We employ a simple model to show that social selection can lead to prezygotic reproductive isolation. The evolution of social discrimination causes the congealing of phenotypically similar individuals into different, spatially distinct tribes. However, tribal formation is only obtained for certain types of social behavior: altruistic and selfish acts can produce tribes, whereas spiteful and mutualistic behaviors never do. Moreover, reduced hybrid fitness at tribal borders leads to the selection of mating preferences, which then spread to the core areas of the respective tribes. Unlike models of resource competition, our model generates reproductive isolation in an ecologically homogeneous environment. We elaborate on how altruistic acts can lead to reproductive isolation, but also predict that certain types of competition can lead to the speciation effect. Our theory provides a framework for how individual-level interactions mold lineage diversification, with parapatric speciation as a possible end product.

Key words.—Altruism, competition, diversification, reproductive isolation, selfishness, social behavior, speciation.

Received October 3, 2002. Accepted November 13, 2002.

Assortative mating can be a powerful force in the generation of phenotypic variation since it potentially inflates homozygote frequencies from the predicted Hardy-Weinberg equilibrium. Generating such variation usually means greater selection differentials and the establishment of linkage disequilibria with other key genetic loci (Lande 1984). One of the most interesting consequences of assortative mating is that preferences may evolve to reinforce prezygotic reproductive isolation (Kirkpatrick 2000), giving rise to protospesies.

Numerous studies have considered how ecological selection can drive reproductive isolation (RI) through assortative mating and reduced hybrid fitness (Kirkpatrick and Ravigné 2002). In these models, an individual's fitness is determined by interactions between its phenotype and the environment. However, many species are social (Krebs and Davies 1993) and individual fitness in these systems is influenced by direct interactions between phenotypes (West-Eberhard 1983; Wolf et al. 1999). To our knowledge no theoretical investigation has examined the effects of social behaviors on speciation, even though the idea has a rich history in evolutionary biology (West-Eberhard 1983).

HYPOTHESIS AND MODEL

Under certain conditions, spatially restricted or “viscous” interactions between individuals are conducive to the evolutionary maintenance of altruistic behaviors in which a player donates to a recipient at a cost to itself (Wilson et al. 1992; Queller 1992). Phenotypic variants such as defectors and cheats are potential hazards to honest altruistic donations and theory predicts that discriminatory behavior based on phenotypic differences will be selected to avoid costly nonreciprocal donations (Komdeur and Hatchwell 1999). We hypothesized that the viscosity of the very systems that favor

altruistic behaviors should, in turn, promote assortative mating between like phenotypes, with prezygotic RI as a possible end product (Lande 1981; Kirkpatrick 2000). Altruism is just one of many possible social acts and we also investigated how spiteful, selfish, and mutualistic behaviors (Hamilton 1964, 1970) could influence patterns.

We simulate an explicitly spatial model of individual interactions over a $N_i \times N_j$ grid wrapped over a torus. Each cell is either occupied or not by a “player.” Each player has a spatial location and three independent evolving haploid characters: a phenotypic marker M (with alleles $M1$ and $M2$), its tolerance T for socially interacting with any of its eight closest neighbors, and P the expression of mating preferences.

During a generation the following sequential events occur. Each player has a constant probability of mortality p . Social acts then determine the reproductive potential of each player. Each player is involved in two social interactions with each of the up to eight adjacent players: once as potential donor and once as a potential recipient. The social fitness of a player is the sum of donations d received from each of its neighbors, less the sum of costs c of the donations made to each of these same adjacent players. For altruistic acts, both donations and costs are positive ($d, c > 0$), whereas these quantities are $d < 0, c > 0$ for spiteful acts, $d < 0, c < 0$ for selfishness, and $d > 0, c < 0$ for mutualism.

The rule for performing an act is simple: if a player has the *Tall* allele (Tolerate all), then it always performs its social act to each of its neighbors, whereas if it has the *Tself* (Tolerate self), *Tnonsel* (Tolerate nonself), or *Tnone* (Tolerate none) allele, then it acts to players with the same marker (hereafter called a “tag”) only, the alternative tag only, or to no players at all, respectively. We assume that the player with the highest social fitness in the eight nearest cells to a vacated one then chooses a mate at random from the re-

maintaining nearest cells based on the formers mating preference. If the player with the highest social fitness has the *Pall* allele, then it always mates with the randomly chosen individual, whereas if it has the *Pself*, or *Pnonself* allele, then it only mates if a randomly chosen player has the same marker or the alternative tag, respectively. If no mates corresponding to the preference are present, then no offspring is produced. Therefore, sexual selection occurs in our model, and is based on social fitness. We assume free recombination for all loci and no explicit memory in past encounters (Axelrod and Hamilton 1981; Nowak and Sigmund 1998; Riolo et al. 2001).

SIMULATION METHODS

Each simulation begins with every occupied cell carrying the tag allele *M1*, the no mating preference allele *Pall*, and one of the four *T* alleles randomly allocated with equal probability. All players in the system have the same donation (d) and cost (c) constants. Mutation is assumed to occur with equal probability 0.001 between alleles, per generation mortality is $P = 0.2$, and the system grid is 900 ($n = 30$) cells. The RI criterion is that the frequency of the *Pself* allele exceeds 90% and both tags are at least 10% frequency in the population.

RESULTS

Although our model has several random variables (and consequently no two numerical simulations are identical), results are highly reproducible. We find that a novel tag is able to invade the resident population for a range of conditions. However, depending on the social act employed by honest players, the invading tag either subsequently goes extinct, eliminates the resident tag, or coexists with the resident tag.

Tribal formation and satisfaction of the RI criterion occurs for a subset of altruistic and of selfish acts (Fig. 1). Specifically, we observe that d and c must be sufficiently different from one another for the RI criterion to be met. The mechanism leading to tribal formation and RI can be understood as follows. Take the case of a rule for an altruistic act. To invade the resident, invading tag mutants and their immediate descendants must acquire the *Tself* allele via mutation or inheritance. The invading patch of like-tagged individuals (hereafter called a ‘‘tribe’’) grows because it receives donations from the naive resident phenotypes (*Tall*, *Tnonself*), but tends not to reciprocate. The invasion is only slowed and finally halted as the *Tself* allele establishes itself in the resident population: intolerant resident-tagged players counter the spreading wave of intolerant invaders, creating fixed borders of mutual intolerance. The formation of tribes thus requires the evolution of facultative behaviors at the *T* locus. A similar scenario holds for selfish acts, except here selfish individuals are selected to accomplish their acts by evolving to interact only with oppositely tagged players (*Tnonself*).

Under an altruistic act rule, net cooperation (+ +) reigns within tribal centers and interactions are avoided at the borders, whereas with selfishness, net antagonistic behaviors (– –) are suppressed in homogeneously tagged regions yet expressed in border zones. However, we find that the evolu-

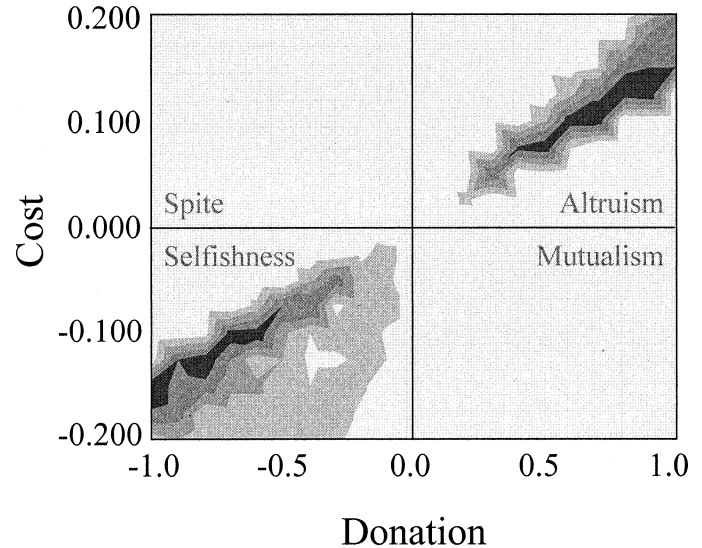


FIG. 1. Reproductive isolation as a function of donations (d) and costs (c) of social acts. This figure is composed of a 21 by 21 grid of observations, each observation being the mean frequency (of 20 replicates) for which the RI criterion is satisfied between time step 2501 to 3000. Increasingly darker shading indicates 20–40%, 40–60%, 60–80%, and 80–100% of simulations met the RI criterion, respectively. For methods and parameters see Simulation Methods.

tionary path to these net interactions is only attained under altruistic and selfish act rules; this is despite the fact that summing mutualistic (+ +) and spiteful (– –) acts between any two adjacent individuals also produce net cooperation (+ +) and spiteful (– –) associations, respectively. Given mutualistic acts, indiscriminate use of the behavior is favored, as any interaction brings the actor a net gain. In contrast for spiteful acts, total suppression of the behavior is favored as any interaction results in a net loss to the actor. In either case, the evolution of discriminating responses is suppressed, barring the establishment of coherent tribes. Below we focus on altruistic act rules, but analogous interpretations apply to selfish acts.

Theoretical study shows that altruistic behaviors are vulnerable to the invasion of defector strategies (Axelrod and Hamilton 1981; Queller 1992; Nowak and Sigmund 1998; Koella 2000). To see why altruistic acts in our model prevail in the face of defectors (*Tnone*), take the simplified case of an asexual model and a straight border between two alternative alleles at the *T* locus. Once a defector genotype (*Tnone*) begins to invade a system of honest donors (*Tall*), the former’s social fitness when competing with the latter rapidly declines, approaching $3d$ when the local frequencies of both types are equal. This is because a border defector has three honest and five defecting neighbors. The social fitness of honest donors is $5d - 8c$, because it will have five honest neighbors and donate to these plus three defector neighbors. In a contest between the two alleles for a vacated cell at the border, the honest player’s progeny will win if its social fitness exceeds that of its neighboring defector, and the condition for this, $5d - 8c > 3d$, or $d > 4c$ is very close to the observation in numerical simulations of the sexual model (Fig. 2A). These considerations also hold for the *Tself* genotype: although its fitness is identical to *Tnone* in the special case of perfect

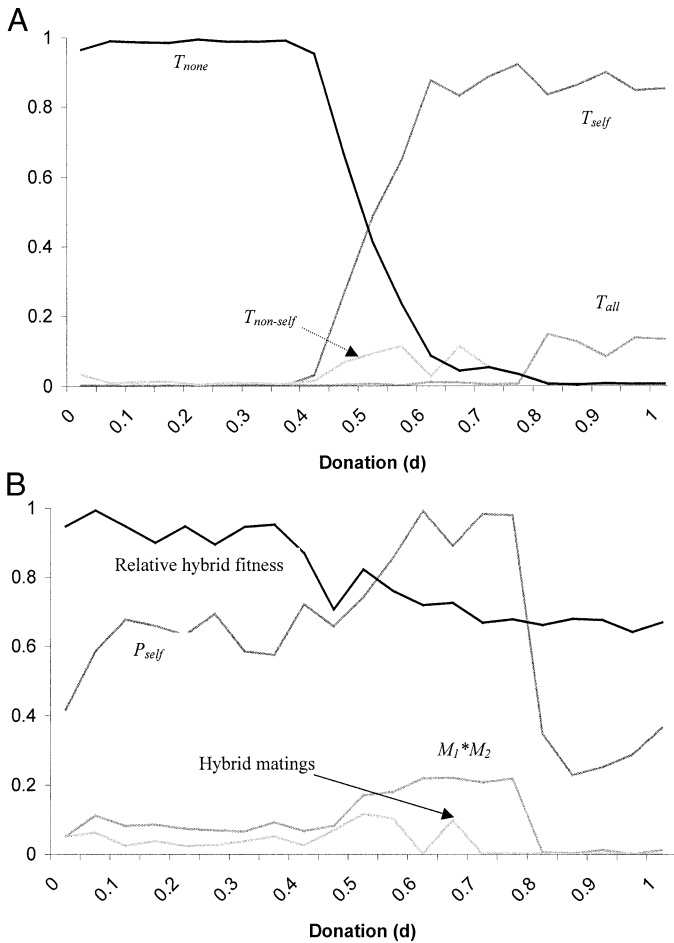


FIG. 2. Effect of donations (d) on key variables in altruistic systems. (A) Tolerance allele frequencies. (B) Selection for mating preferences. $M_1 * M_2$ measures the evenness in the frequencies of the two tags and reflects the long-term stability of tag coexistence. Methods and parameters as in Simulation Methods except $c = 0.1$.

linkage disequilibrium (that is, where T_{self} is embodied on one tag and T_{none} in the alternative tag), via recombination or mutation, T_{none} always eventually invades the tribe harboring T_{self} and eliminates it for $d < 4c$. The aforementioned formulation with a neighborhood size of $n = 8$ should generalize for any spatially constrained social topology, yielding the general approximate condition preventing the invasion of a border defector, $d/cn > 1/L$, where L describes the difference in the number of donations received for opposing honest and defector players. This condition suggests that the geometry of individual interactions (parameters n and L) has important implications for the persistence of altruism.

We have shown that complete defectors reign when honest donation levels are insufficient, and this impedes the spatial segregation of the tags into tribes. How does the facultative discrimination ($T = self$) needed to generate and maintain tribes prevail? When $d > 4c$ the contest turns to all-out donors (T_{all}) versus discriminating donors (T_{self}). In an environment where only one tag is present, both of these alleles have the same social fitness. However, if both tags are present, then T_{self} functions as a facultative defector, not donating to individuals carrying the alternate tag. Analogous to competition

between the all-out defector (T_{none}) and donors (T_{all} , T_{self}) described above, the facultative defector defeats the all-out donor as long as donations are not too high. Specifically, T_{self} tends to dominate for $4c < d < 8c$ and create the conditions for tribal formation. For donations beyond $8c$, T_{all} coexists with T_{self} (Fig. 2A), with the former compromising the integrity of the standoff between different tags and preventing the formation of tribes.

We find that tribal formation also promotes assortative mating and leads to the selection of discriminatory mating preferences (Fig. 2B). This occurs as follows. At low donation levels ($d < 4c$), defectors (T_{none}) dominate and there is little or no difference between progeny arising from matings between differently tagged parents and like-tagged matings. The two tags coexist but do not form tribes. For intermediate donations ($4c < d < 8c$), the T_{self} discriminating allele invades and the fitness of offspring resulting from matings between differently tagged parents (hereafter called ‘hybrid-matings’) decreases. At tribal borders this, in turn, selects for the P_{self} allele, which is able to invade the interior of both tag populations due to assortative mating at the M locus. Numerical simulations show that two tribes coexist and the P_{self} allele goes to fixation over part of the interval $4c < d < 8c$ (Fig. 2B). At still higher donation levels ($d > 8c$), despite the fact that hybrid fitness is reduced, the T_{all} allele is selected, compromising the integrity of tribal borders, thereby lowering the frequency of assortative mating and lessening selection of the P_{self} allele. Only a single tag persists. The aforementioned formulation with a neighborhood size of $n = 8$, should generalize for any spatially constrained social topology, yielding the general approximate conditions for establishing assortative mating: $1/L < d/cn < 1$. These conditions on the spread of assortative mating and the general condition for the invasion of border defectors ($1/L > d/cn$) explain why RI occurs in a wedge of the parameter space for d and c (i.e., bounded between the upper limit of assortative mating and lower limit of a boundary defector). Note that given d and c , the propensity for RI increases as the difference in the number of donations received for opposing (border) honest and defector players (L) increases, and for intermediate social neighborhood size (n). Large L could occur, for instance, if honest border donors were to learn to discriminate border defectors based on the latter’s behavior only.

Figure 3 shows a typical example of the evolution of RI over the first 1500 generations of a simulation. As tribes begin to form, alternatively tagged players (M_1 and M_2) are strongly favored on opposite sides of the tribe boundaries. Once this spatial pattern of the T_{self} and M alleles begins to crystallize, hybrid unfitness at tribal borders selects for the P_{self} allele at the mating preference locus, and this mating preference allele rapidly spreads to tribal centers due to assortative mating. In the typical example in Figure 3, hybrid fitness first rapidly decreases following the invasion of the novel tag. The ensuing social selection becomes strong enough in generation 300 to favor the T_{self} allele, and tribes gradually form. However, this social discrimination involving oppositely tagged individuals does not affect hybrid fitness, nor the frequency of hybrid matings. Rather, low hybrid fitness selects for the P_{self} allele, thereby lowering the fre-

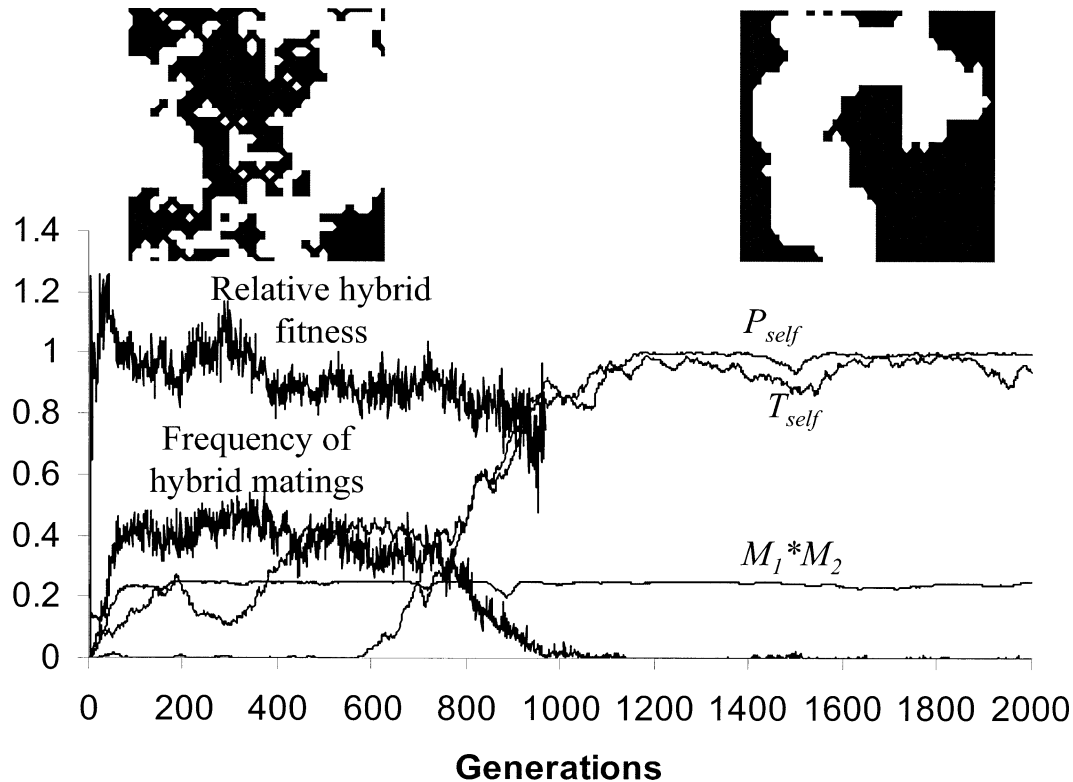


FIG. 3. Dynamics of tribal formation and reproductive isolation. Left and right graphical inserts show the spatial distributions of the two tags (dark shaded) at generations 150 and 1500, respectively. Because of very small sample sizes, relative hybrid fitness is not accounted beyond generation 1000. Other parameters as in Simulation Methods except $c = 0.1$ and $d = 0.6$.

quency of hybrid matings to near zero. In the example shown in Figure 3, this occurs 300 generations after selection for the T_{self} allele begins, with mating preference reaching fixation about 500 generations thereafter.

CONCLUSIONS

The theory developed here forges links between two active areas in evolutionary biology. The first is the identification of key features in how species may be formed in sympatry and parapatry. It has been shown theoretically that neutral markers affecting mating preferences can lead to assortative mating and reproductive isolation in nonspatial (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999) and spatial (Payne and Krakauer 1997) settings. Our results extend these observations to show how social selection in the absence of divergent natural selection can establish the conditions for reproductive isolation—a possibility recently emphasized by Schluter (2000, pg. 212) as “. . . a substantial departure from classical ecological views on the causes of speciation in adaptive radiation.”

The second is the endeavor to understand the evolution of seemingly counter-productive social acts such as altruism (e.g., Hamilton 1964; Trivers 1971; Axelrod and Hamilton 1981; Dugatkin 1997; Nowak and Sigmund 1998; Koella 2000). Theory suggests that as long as honest donations are sufficiently high, altruists can persist in the face of cheats (Sherratt and Roberts 1998). Our results generalize this finding to facultative behaviors, suggesting that intermediate al-

truistic donations not only protect altruists from cheats, but also set up the conditions for the evolution of discrimination of nonself.

If indeed discrimination of phenotypic differences leading to relative cooperation between like phenotypes is widespread, then we would expect the underlying social acts to be an important mediating force in genetic and phenotypic patterning and diversity in systems with repeated acts between individuals. Examples include sessile (Shoemaker and Ross 1996; Macnair and Gardner 1998; Grosberg and Hart 2000), territorial (Temeles 1994), and long-lived (Barbujani and Sokal 1990) species. For instance, territoriality is thought to be evolutionarily stable owing to an iterated prisoner's dilemma form of cooperation (Axelrod and Hamilton 1981) in which neighbors are better off cooperating than cheating and crossing established boundaries (Dugatkin 1997). Even unrelated neighbors can mutually defend against strangers in a “dear enemy” alliance (West-Eberhard 1983; Temeles 1994). For example, avian song is used in tag-based identification between territorial males (Baker et al. 1981; Godard 1993) and song is also employed by females during mate choice to identify local males (Baker et al. 1981). Tag divergence may also occur in organisms with chemically based recognition, such as social insects (Keller and Ross 1998) and microorganisms (Crespi 2001). For instance, many ant species use chemical cues for recognition and colony similarity may promote cooperation between colonies with similar tags but divergence between those with alternative tags

(Shoemaker and Ross 1996). More speculatively, social interactions may have also contributed to the enormous species radiation of Lake Malawi haplochromine cichlids, which are territorial habitat specialists with limited dispersal (Danley and Kocher 2001). Finally, our model need not require a genetic basis, as for some culturally transmitted tags (Boyd and Richerson 1985), but nevertheless maintain stable tribal boundaries with (Barbujani and Sokal 1990) or without (Wright and Wilkinson 2001) genetic structure.

Although most of our results focused on altruistic behaviors, we found that selfish acts could also generate the speciation effect. Intriguingly, the positive/negative (+ -) effect of selfish behavior is reminiscent of interspecific competition, and we suspect that this type of act could be at the heart of certain speciation events attributed to generic competition (Schluter 2000). If this is true, then a strong prediction of our theory is that behavioral interference yielding unprofitable (- -) acts *cannot* lead to spatial assortative mating and speciation via the mechanism identified in our study.

In closing, our model, based on simple but realistic assumptions about signals, social acts and mate choice, is able to explain assortative mating, hybrid unfitness, and the evolution of mating preferences—major steps in the process of speciation (Dobzhansky 1940; Schluter 2000). It should enable theoreticians and experimentalists to evaluate the driving forces behind genetic and cultural diversification in as yet neglected ways.

ACKNOWLEDGMENTS

We thank J. van Alphen, G. Barbujani, P. Crowley, R. Crozier, K. Foster, D. Friedman, V. Janssen, L. Keller, M. Kirkpatrick, L. Lehmann, N. Perrin, and D. Waller for valuable discussions. Special thanks to S. Billiard and V. Ravné for comments on the manuscript. MEH was funded by the French Ministry of Research and Education and the Centre National de la Recherche Scientifique (CNRS), BS by the National Science Foundation and the CNRS, and SPB by the CNRS (Poste Rouge) and the European Union (Marie Curie Fellowship).

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Corresponding Editor: D. Waller