Social Games and Genic Selection Drive Mammalian Mating System Evolution and Speciation

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abstract: Mating system theory based on economics of resource defense has been applied to describe social system diversity across taxa. Such models are generally successful but fail to account for stable mating systems across different environments or shifts in mating system without a change in ecological conditions. We propose an alternative approach to resource defense theory based on frequency-dependent competition among genetically determined alternative behavioral strategies characterizing many social systems (polygyny, monogamy, sneak). We modeled payoffs for competition, neighborhood choice, and paternal care to determine evolutionary transitions among mating systems. Our model predicts four stable outcomes driven by the balance between cooperative and agonistic behaviors: promiscuity (two or three strategies), polygyny, and monogamy. Phylogenetic analysis of 288 rodent species supports assumptions of our model and is consistent with patterns of evolutionarily stable states and mating system transitions. Support for model assumptions include that monogamy and polygyny evolve from promiscuity and that paternal care and monogamy are coadapted in rodents. As predicted by our model, monogamy and polygyny occur in sister taxa among rodents more often than by chance. Transitions to monogamy also favor higher speciation rates in subsequent lineages, relative to polygynous sister lineages. Taken together, our results suggest that genetically based neighborhood choice behavior and paternal care can drive transitions in mating system evolution. While our genic mating system theory could complement resource-based theory, it can explain mating system transitions regardless of resource distribution and provides alternative explanations, such as evolutionary inertia, when resource ecology and mating systems do not match.

Keywords: ESS, social games, mammals, mating systems, genic behavior.

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Introduction

Mating systems play a critical role in genetic, demographic, and social dynamics of populations. Prevailing models explaining mating system diversity emphasize links between resource and mate monopolization. If resources are defensible, polygynous males on high-quality territories will have access to more females than monogamous males on low-quality territories (Verner and Willson 1966; Orians 1969), and temporal variation in mate availability or sex ratio further accentuates this dichotomy between polygyny and monogamy (Emlen and Oring 1977; Houston et al. 2013; Gomes et al. 2018). However, paternal care can shift the advantage to a monogamous system (Maynard Smith 1977; Wakano and Ihara 2005; Jungwirth and Johnstone 2018). Indeed, the diversity of factors thought to influence variation in mating systems has led to calls for more integrative models to better predict mating system evolution, including the above considerations (Komers and Brotherton 1997; Houston et al. 2013; Klug 2018; Kvarnemo 2018) as well as social interactions (Alonzo 2010; Dillard and Westneat 2016). However, most past models, with some exceptions, favored extrinsic factors (e.g., resources, operational sex ratio, mate defensibility) in explaining the evolution of mating systems (e.g., Sandell and Liberg 1992; Ptak and Lachmann 2003; Gomes et al. 2018; reviewed in Vehrencamp and Bradbury 1984; Davies 1991; Shuster and Wade 2003). Few models include social competition and intrinsic genetic factors in driving mating system evolution or the likelihood of transitions between mating system states (Wakano and Ihara 2005; Alonzo 2007; Jungwirth and Johnstone 2018; see also Alonzo 2010; Dillard and Westneat 2016). Likewise, most empirical approaches to understanding such transitions have focused on extrinsic factors (Komers and Brotherton 1997; Lukas and Clutton-Brock 2013; Kvarnemo 2018). This is problematic because while the environment and the distribution of resources may change and shift the economic

advantages of a particular mating system, an existing mating system may remain static, given evolutionary inertia (i.e., lack of phenotypic change across species due to intrinsic factors) and the existence of genetically based mating system strategies. Likewise, intrinsic genetic factors could shift a mating system with no ostensible change in resource distribution in the environment (see also Alonzo 2010; Dillard and Westneat 2016). The limited theoretical attention to intrinsic factors means that we have an incomplete understanding of how genetically based alternative mating strategies affect the evolution of mating systems relative to extrinsic mechanisms. We propose that by influencing social interactions, genetic mechanisms underlying mating system strategies complement resource-based ecological approaches and could also shape mating system evolution independent of the defensibility of resources.

Frequency-dependent competition among genetically determined behavioral types could provide a general explanation for mating system evolution among species. Indeed, such competition drives mating systems within species (e.g., lizards [Sinervo 2001], birds [Küpper et al. 2016; Lamichhaney et al. 2016], isopods [Shuster and Sassaman 1996], and damselflies [Cordero et al. 1998; Svensson et al. 2005]) and can generate divergence between populations (Corl et al. 2010). Furthermore, genetic models of frequency-dependent competition may apply to diverse taxa. Recent molecular studies have revealed a genetic basis of male behavior in a number of species (Bester-Meredith et al. 1999; Young 1999; Lim and Young 2004; Young and Wang 2004; Ophir et al. 2008; Walum et al. 2008), including alternative male strategies and their underlying behaviors (Bishop et al. 2004; Knafo et al. 2008; Oliveira et al. 2008; Küpper et al. 2016; Lamichhaney et al. 2016). Here, we modeled such genetic strategies to test whether purely intrinsic factors associated with mating systems (i.e., genetically based fixed behaviors) predict evolutionary transitions among mating systems while ignoring the effects of resource availability and defensibility.

Game theoretic approaches have been used to model the evolution of mating systems since Maynard Smith (1977). His model explored the evolution of parental care and had implications for mating systems, since a defecting parent (i.e., one that provides no care) was assumed to seek additional mating opportunities. Indeed, this seminal article cemented the idea that monogamy and biparental care were linked (Houston et al. 2013; but see Komers and Brotherton 1997). The majority of such models focused on the conditions favoring monogamy or polygyny (e.g., Ranta and Kaitala 1999; Ptak and Lachmann 2003) or when multiple mating strategies coexist (e.g., Sinervo and Lively 1996). No doubt inspired by Emlen and Oring's (1977) verbal model, these game theoretic models investigated the influence of diverse factors on mating system evolution, such as the importance of parental care (Wakano and Ihara 2005; Jungwirth and Johnstone 2018), habitat quality (Ranta and Kaitala 1999), space use and the defensibility of resources (Sandell and Liberg 1992), and sex ratio (Kokko and Jennions 2008; Gomes et al. 2018). These models focused on the influence of extrinsic factors on mating system evolution. In contrast to these phenotypic models, a handful of studies examined how genetic systems might influence mating system evolution; these models yield surprising results (Ptak and Lachmann 2003; Sinervo et al. 2007; Moulherat et al. 2017). For example, Ptak and Lachmann (2003) showed that specific attention to allelic inheritance leads to a much broader state space where polygyny is stable based on a polygyny threshold scenario (i.e., resource defense polygyny). Likewise, Moulherat et al. (2017) showed that differences in gene expression (dominance vs. plasticity) alters the likelihood that a set of alternative male strategies is maintained within a population. Moreover, recent game theoretic models have suggested that social interactions can have important effects on model outcomes (Alonzo 2010; Dillard and Westneat 2016). For example, male-female conflict (Alonzo 2007), male-male cooperative interactions (Sinervo et al. 2007), and female-female interactions (Jungwirth and Johnstone 2018) can all alter the conditions favoring the expression of different mating patterns. Taken together, inclusion of explicit inheritance rules and social behaviors driven by these genes can generate shifts in the patterns of mating system due to factors other than classical extrinsic drivers, such as resource distribution and operational sex ratio. Our goal here is to build on these past efforts to examine the evolution of mating systems due solely to the impact of genes on specific behaviors controlling social interactions. We focus on intrinsic factors and ignore resource distribution, sex ratio, and other extrinsic factors. Specifically, we add two new elements to past models. First, we model three alternative strategies as in past studies on the maintenance of alternative mating strategies (e.g., Sinervo et al. 2007; Moulherat et al. 2017), but with a focus on mating system state when alternative strategies are not maintained as well as cases when multiple strategies are maintained. Second, we model two social behaviors (neighborhood choice and paternal care) driven by genic recognition of others, as suggested in recent empirical work (Bester-Meredith et al. 1999; Mateo 2004; Sinervo et al. 2006; Holmes and Mateo 2007; Widdig 2007; Ophir et al. 2008).

We extend previous game theoretic models based on competition among three fixed genetic strategies (Sinervo et al. 2007; Friedman and Sinervo 2016) by including paternal care and social neighborhood choice to explore mating system evolution. Variation in the level of aggression and cooperation or care among genotypes should influence both the monopolization of space and thus mates as well

as the degree of parental care provided by each strategy (Vehrencamp and Bradbury 1984; Davies 1991; Sinervo and Lively 1996; Shuster and Wade 2003; Schradin and Pillay 2005*a*). The strategies in our model can be described as (1) investment in aggression and therefore maintenance of a large territory overlapping with multiple females but without paternal care (polygyny); (2) lower aggression and smaller territory size but cooperation at territory boundaries (i.e., dear enemy effect [Temeles 1994]) coupled with investment in paternal care (monogamy); and (3) a nonterritorial strategy with no paternal care, which is often referred to as a sneaker strategy in otherwise territorial systems (sneak). Here, sneaker males employ deception to attain copulations through mimicking female behavior and avoiding male territorial interactions (Sinervo and Lively 1996; Alonzo et al. 2000; Jukema and Piersma 2006). We vary the fitness benefits of male care and neighborhood choice in our model to explore patterns of evolutionary transitions among mating system states. Our approach integrates the genetic contribution to competition within and among social strategies to show that specific behaviors facilitate evolutionary transitions in mating system regardless of resource distribution.

We test for qualitative consistency of assumptions and predictions of our model through phylogenetic comparative analyses using data on rodent mating systems and a well-supported phylogeny to identify social strategies associated with mating system transitions. The phylogenetic comparative analysis confirms key assumptions and predictions of our genetic model. While resource-based and genetic explanations are likely complementary and could interact in interesting ways, our effort here demonstrates the important role that genetic strategies can play in mating system evolution irrespective of resource distribution considerations.

Genetic Mating System Model

We modeled frequency-dependent social competition among three genetically determined strategies using a game theoretic approach (Maynard Smith 1982). We assumed that fitness is determined by additive effects of alleles at a single locus in a diploid sexual organism (table S1; tables S1–S7 are available online; Alonzo and Sinervo 2001; Sinervo et al. 2007; Friedman and Sinervo 2016; Barreto et al. 2017; Moulherat et al. 2017). The single gene we model has effects on a number of behaviors and is similar to empirical findings in systems with a supergene (e.g., ruffs [Küpper et al. 2016; Lamichhaney et al. 2016]), pleiotropic effects on multiple behaviors (e.g., slime molds [Queller et al. 2003; Foster et al. 2004]), or both (e.g., lizards [Sinervo et al. 2006]). We include three alleles that correspond to common alternative mating strategies (polygyny, monog-

amy, sneak) and have pleiotropic effects on behaviors (competition, settlement, care, and recognition). Allelic effects are represented by three genotypic payoff matrices described below (table S1) that determine offspring frequencies at recruitment for each diploid genotype (table S2). We explore how changing values of neighborhood choice (random settlement to four times higher probability of settlement by neighbors with specific strategy combinations) and paternal care (no care to threefold higher recruitment advantage of offspring) affect the evolutionarily stable strategy (ESS) mating system (Maynard Smith 1982) and transitions among mating systems.

Following population genetic theory (Wright 1968; Maynard Smith 1982; Sinervo and Lively 1996; Sinervo et al. 2007; Friedman and Sinervo 2016), we calculated the relative change in frequency of each of the six genotypes in adult cohorts described by the genotype vector g (with elements g_i and diploid subscripts $i = \rho\rho, \rho\kappa, \rho\sigma, \kappa\kappa, \kappa\sigma, \sigma\sigma$, where alleles ρ = polygyny, κ = monogamy, and σ = sneak):

$$g(t + 1) = s \times g(t) + (1 - s) \times g', \quad (1)$$

which includes adults at time t surviving (s) to the next year ($t + 1$) and recruitment of each genotype by juveniles (g'), as described below (eq. [3]), who replace adults that do not survive ($1 - s$). Variation in adult survival (s) had the sole effect of lengthening the periodicity of stable cycles when all three strategies were preserved, but no effect on the ESS.

We calculated genotype frequencies of juveniles by modifying the diploid genetic model proposed by Friedman and Sinervo (2016, eq. [5.11] in sec. 5.3) and Friedman et al. (2017, eq. 14 in supplemental material on inheritance from two parents). Note that here we modify variable names of the original to reflect the characters and behaviors in our extended model. In that model, frequencies of juveniles at recruitment are given by the vector g' (called s in the original, with elements g_i and diploid subscripts $i = \rho\rho, \rho\kappa, \rho\sigma, \kappa\kappa, \kappa\sigma, \sigma\sigma$, where haploid alleles ρ = polygyny, κ = monogamy, and σ = sneak), which is calculated by

$$g' = cg^{F}\mathbf{F} \circ \mathbf{A} \circ [H^1, \dots, H^6] \circ \mathbf{B} \circ \mathbf{M}g^{M}, \quad (2)$$

where g is a vector of genotype frequencies (variable s in the original) and the superscripts refer to the diploid genotype of adult males (g^M), females (g^F), and juveniles (g'); $[H^1, \dots, H^6]$ describes allele inheritance rules (see below), and matrices $\mathbf{F}$, $\mathbf{M}$, $\mathbf{A}$, and $\mathbf{B}$ reflect the outcome of survival of females (F) and males (M) and mate preferences of females (A) and males (B). We modified that model by first replacing survival matrices ($\mathbf{F}$, $\mathbf{M}$)—which we account for in equation (1) but which does not include genotype-specific survival rates—with fitness payoff matrices ($\boldsymbol{\Phi}$).

Second, we replaced mate choice behavioral matrices (**A**, **B**) with ones describing discrimination (**D**) and parental care behavior (**P**) in males. Values for these new matrices in our model are given in table S1, and we describe the behavior associated with each in separate sections below. Our modified model becomes

$$g' = cg^F\Phi^F \circ [H^1, \dots, H^6] \circ \mathbf{P} \circ \mathbf{D} \circ \Phi^M g^M. \quad (3)$$

This matrix formulation presents the order of events of reproduction, with female parental genotypes to the left (g^F), males to the right (g^M), and Mendelian ratios forming progeny in the middle [$H^1, \dots, H^6$] that are modified by selection on females (Φ^F) and males ($\mathbf{D} \circ \mathbf{P} \circ \Phi^M$). Genotype frequencies in the next generation (g') are a product of parental genotypes (female g^F, male g^M) combined to produce Mendelian ratios with a hex matrix consisting of 6×6 elements (table S2). Each of the 6×6 elements of the hex matrix contain six-element vectors, [$H^1, \dots, H^6$], that are Markov transition probabilities (i.e., Mendelian ratios) for progeny genotypes from random mating of a female genotype (i; rows) and a male genotype (j; columns). Given an equal sex ratio and no sex-specific selection, the frequencies of male and female genotypes of juveniles are symmetrical. Mendelian ratios are then modified by selection in matrices that describe competition (Φ) and male behaviors (**D** and **P**).

Payoffs from frequency-dependent competition among adult genotypes are described by the 6×6 matrix Φ as the outcome of competition between each strategy interacting with each of the other strategies as a result of social competition over mates (Φ is a 6×6 payoff matrix $= ((\varphi_{i,j}))$; Sinervo and Lively 1996; Friedman et al. 2017). Payoffs are modified by matrices **D** and **P**, which describe nonrandom association behaviors between individuals (see below; table S1). Matrix **D** describes choice of social neighborhood based on the genotypes that favor a focal individual's fitness (**D** is discrimination or targeting; see also Sinervo et al. 2007; Friedman and Sinervo 2016). Matrix **P** describes the association of male care behaviors from paternal care (**P** is paternal behavior). This matrix formulation is described in detail by Friedman and Sinervo (2016), and we use the Hadamard product notation (denoted by ∘), which describes element-by-element multiplication between the behavioral matrices, **P** and **D** (for a full description of this approach, see chap. 5 in Friedman and Sinervo 2016; for a model with additive genetic effects, see supplementary information in Friedman et al. 2017), whereas the products between other matrices (Φ) and vectors (g) are given by normal matrix multiplication among vectors or matrices. The scalar c is the normalization product required to obtain $\Sigma g'_i = 1$, following selection acting on the parental generation.

The competition matrices (Φ) provide estimates of fitness due to social competition within each sex. In the current model, we ignore frequency-dependent competition among female strategies (Φ^F) by setting all matrix elements to 1. The male competition payoff matrix (Φ^M; table S1A) describes the success of each male strategy in competition to acquire territory and mating opportunities either directly with females whose territories overlap or extrapair from females on neighboring territories (especially sneak). Competition occurs between each genotype pair in proportion to the frequency of those genotypes in the population (i.e., randomized encounters between males, modified by **D** and **P** below). The competition matrix (Φ^M) then describes the biases in the representation of alleles in the next generation (i.e., biases in fitness, either direct or extrapair) dependent on which strategies compete. We assume fitness intransitivity for competition (Φ^M matrix) among the three alternative alleles (polygyny > monogamy > sneak > polygyny; table S1A), which holds when expanded to all genotype pairs (table S1D). Such intransitivity is critical for a stable trimorphism (Bomze 1983; Sinervo and Lively 1996; Sinervo et al. 2007; Friedman and Sinervo 2016; Moulherat et al. 2017) and has been described in a number of species with very broad taxonomic coverage ranging from bacteria to plants to vertebrates (Sinervo and Calsbeek 2006; chap. 7 in Friedman and Sinervo 2016). In such systems, polygynous males are aggressive and outcompete monogamous males, but defense of larger harems by polygynous males makes them more susceptible to a sneak strategy. In contrast, monogamous males defend their single partner closely and therefore are not easily usurped by sneak. Furthermore, both polygyny and sneak adults have limited fitness when common as a result of density-dependent competition (i.e., competing with males of the same strategy; payoff$_{\rho,\rho} = c < 1$, payoff$_{\sigma,\sigma} = k < 1$; table S1A), whereas monogamous males do not (payoff$_{\kappa,\kappa} = 1$) since they maintain stable territorial boundaries with neighbors of the same genotype (dear enemy effect; Temeles 1994).

The neighborhood choice matrix (**D**; table S1B) describes the ability of juvenile males to recognize and settle in specific neighborhoods of adult male genotypes that will maximize their fitness. Discrimination behavior (d), which we have previously argued is a consequence of intransitive strategies (Sinervo et al. 2007; chap. 7 in Friedman and Sinervo 2016), allows individuals to seek out neighborhoods where they are competitively superior (Frean and Abraham 2001; Sinervo et al. 2007; table S1B). The level of discrimination, $\mathbf{D}_{i',i}$, produces the additive allelic fitness effect of this behavior ($\mathbf{D}_{\kappa,\sigma}$, $\mathbf{D}_{\rho,\kappa}$, and $\mathbf{D}_{\sigma,\rho}$; $d > 1$, otherwise $d = 1$; table S1B, S1D). Filiative (f) behavior is a parameter in the neighborhood choice payoff matrix that enhances self-genotype clustering among monogamous genotypes ($\mathbf{D}_{\kappa,\kappa}$; $f > 1$) to benefit from nonaggressive genetically similar neighbors (Sinervo

et al. 2006, 2007). The benefit of filiative behavior is calculated by the overlap in monogamy alleles between neighbors as an additive effect of alleles (table S1D). Both neighborhood choice and care behavior could occur either through direct genic recognition (as assumed in this model) or through other mechanisms, such as kin philopatry, strategy recognition, biased dispersal, or specific social habitat choice.

The paternal care payoff matrix (**P**; table S1C) describes effects of care by adult males on offspring recruitment (table S1C–S1E). We assume that paternal care is restricted to individuals with monogamy alleles who invest in offspring quality ($\mathbf{P}_{\kappa,\kappa}$; $p > 1$, otherwise $p = 1$; table S1C) rather than additional mates through social competition with other males (e.g., the competition payoff matrix, $\mathbf{\Phi}^{\mathrm{M}}$). This assumption is consistent with recent analyses in rodents showing that the same genes have effects on monogamy, affiliative behavior, and parental care (Bester-Meredith et al. 1999; Ferguson et al. 2001; Lim and Young 2004; Young and Wang 2004; Ophir et al. 2008; Schradin 2008; Okhovat et al. 2015). Care is given in direct proportion to the genetic similarity between sire and offspring as an additive allelic effect (probability of sharing κ alleles; table S1D, S1E) and thus depends on both paternal (M) and maternal (F) genotypes. We have modeled male care through genic recognition rather than care allocated equally to all young by monogamous males for two reasons. First, paternal care via allelic recognition of sire-offspring pairs is internally consistent with neighborhood choice behavior (matrix **D**), which also requires some sort of genic recognition. Second, such forms of recognition tied to social relationships, including paternal care, are observed in nature (Wang et al. 1994, 1998; Bester-Meredith et al. 1999; Marler et al. 2003; Mateo 2003; Neff 2003; Holmes and Mateo 2007; Widdig 2007; Nam et al. 2010). Care provided equally to all offspring regardless of allelic overlap would likely weaken selection and could form an interesting extension to our current model. Male care need not be elaborate but supplements maternal care through behaviors such as nest defense or thermoregulation to enhance progeny survival (see also Lukas and Clutton-Brock 2013). In contrast, polygyny and sneak genotypes provide no care and abandon progeny to seek out other mates.

Simulation Results

We used equations (1) and (3) to calculate gene frequencies across time and examine ESS mating systems for a given set of parameter values by searching for the central tendency after 1,000 generations (Sinervo et al. 2007; ESS usually fixed within 200 generations). To explore how behavior affects transitions between ESS mating systems, we varied parameters with particular emphasis placed on exploration of discrimination ($1 < d < 5$), filiative ($1 < f < 4$), and paternal care behaviors ($1 < p < 4$). The model assumed equal initial frequencies of all three alleles, but we also explored simulations with random start frequencies (1,000 starts for each parameter combination, fig. S1; figs. S1–S6 are available online).

Evolutionarily stable social systems are determined by conflict between competitive (discrimination) and cooperative behaviors (filiative, paternal; Hochberg et al. 2003), which clearly drive ESS outcomes of our model. Mating system simulations after 1,000 generations predicted one of four cases: (1) a noncycling stable equilibrium between polygyny and sneak alleles, (2) a stable interior attractor of all three alleles (length of cycles was verified for >500 generations; Sinervo et al. 2007), or (3) a pure ESS (single allele) of either polygyny (a) or monogamy (b; figs. 1, S2). The mixed ESS (sneak and monogamy) was never stable, and sneak alone was never an ESS.

Case 1. Stable coexistence between sneak and polygyny or a mixed ESS mating system, occurred for only a narrow parameter range when discrimination was absent ($d = 1$; random settlement) and both filiative and paternal care were low ($f < 1.3$, $p < 1.8$; values represent recruitment advantages of young over baseline levels; see bottom left of fig. 1, where $d = 1$).

Case 2. All strategies are retained in a rock-paper-scissors (RPS) cycle, which is either a Nash equilibrium (Sinervo and Lively 1996) or a mixed ESS akin to a multiple paternity mating system in circumstances where territory boundaries of alternative strategies within sex overlap somewhat and between-sex territories are unrelated (Sinervo and Lively 1996). Friedman and Sinervo (2016) discuss differences in Lotka-Volterra dynamics of an RPS that is an ESS versus a Nash equilibrium, but both game states retain three strategies because of RPS intransitivity with a stable interior attractor (Bomze 1983). The length of RPS cycles varied as a function of model parameters (discussed below). Such systems generate promiscuity as a result of multiple paternity patterns, but empirical spacing patterns (e.g., high variance in space use among individuals) suggest that they may contain alternative mating strategies described in our model. We therefore use the common term "promiscuity" to describe this mating system outcome with the coexistence of three alternative male strategies. Stronger density-dependent competition within the two male strategies of polygyny and sneak (low c, k) generally increased the stability of RPS cycles and coexistence as in past models (Sinervo et al. 2007). Similarly, better discrimination behavior (higher d) enhanced coexistence and cycle stability (see also Sinervo et al. 2007).
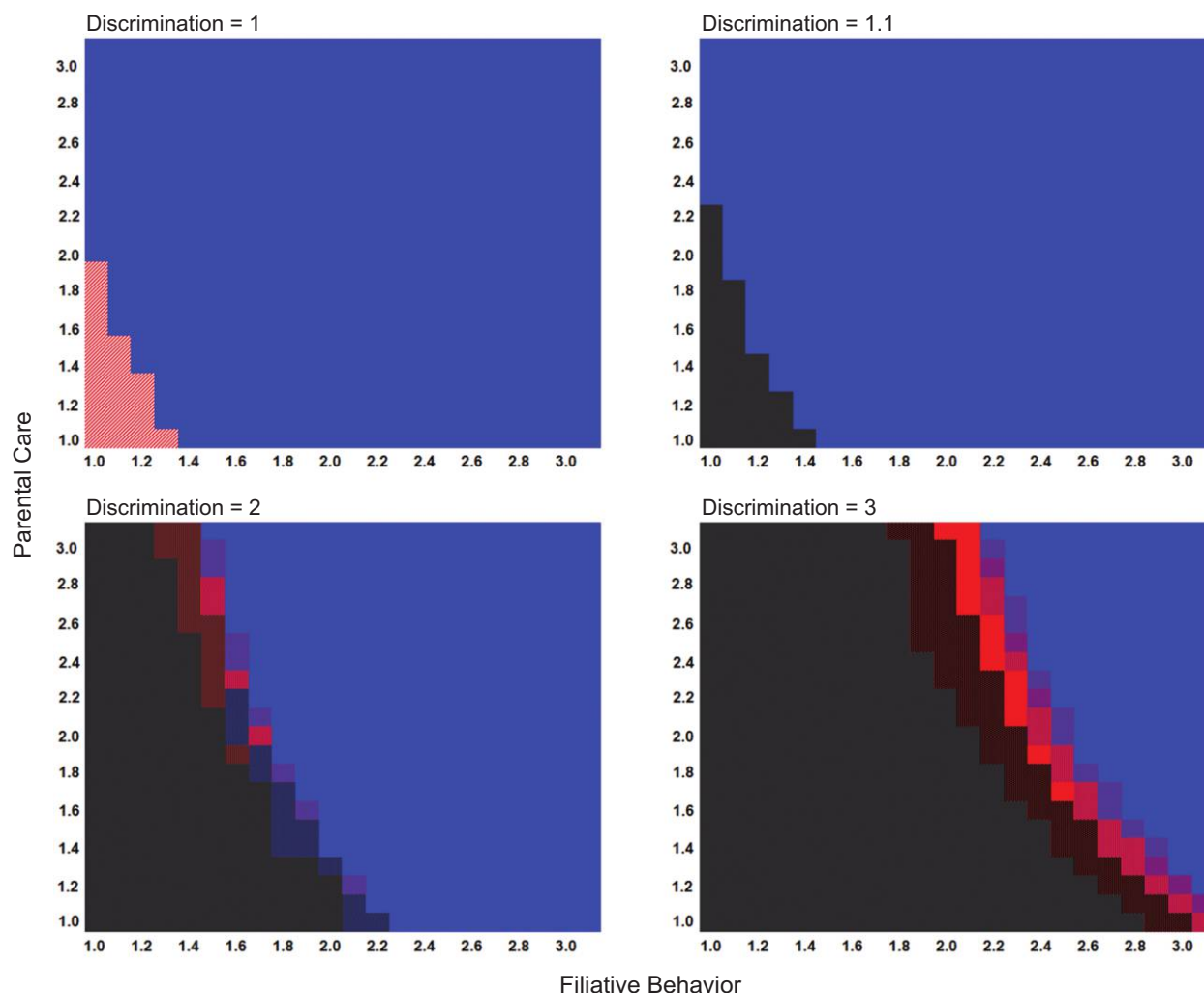
Figure 1: Shifts in evolutionarily stable strategy (ESS) mating system with increasing discrimination along a filiative and paternal care gradient. Mating system ESS as a function of filiative (self-attraction) and paternal care behaviors in monogamy for specific values of discrimination showing how polygyny only (red) resides in the parameter space between monogamy only (blue) and rock-paper-scissors promiscuity (black). Stippled areas for higher levels of discrimination represent domains where initial allele frequencies influence the ESS (in >10% of cases), with the dominant color being most commonly fixed (see fig. S1, available online). Notice that hatched red-gray zones (*bottom left*) for $d = 1$ reflect the only stable equilibrium between polygyny and sneak.

Case 3. Sneak is always lost, but either polygyny (case 3a) or monogamy (case 3b) is the pure ESS (fig. 1). As monogamy genotypes become prevalent (i.e., p, f increase), fitness of sneak is depressed through more frequent encounters with this superior competitor.

The ESS in case 3 (polygyny vs. monogamy) depends on levels of paternal care and filiative behaviors (red vs. blue areas in figs. 1, S2). Counterintuitively, polygyny fixes when monogamy has moderate levels of filiative and paternal behaviors (high levels of one or moderate levels of both; figs. 1, S2). This is because as the fitness of monogamy increases, sneak is rapidly eliminated, thereby removing polygyny's dominant competitor. However, moderate

monogamous behaviors are insufficient to outcompete polygyny, which is superior in male-male competition (Φ^M). As combinations of paternal and filiative behaviors increase (above ~1.5-fold higher fitness), polygyny is outcompeted, leaving monogamy as a pure ESS (see also Ranta and Kaitala 1999). As discrimination behavior increases, the ESS domain for polygyny expands because its fitness is enhanced by settling near clusters of monogamous males (increasing d across panels in fig. 1). Between the two pure ESS domains, a band of parameter values can fix for polygyny or monogamy or stay entrained in an RPS (promiscuity) depending on initial allele frequencies (figs. 1, S1). Thus, a mixed polygyny-monogamy state

should be rare and exist as only an unstable or quasi-stable equilibrium, which rapidly bifurcates to monogamy or polygyny depending on initial allele frequencies (fig. 1 when $d > 1$; fig. S1).

Empirical Test of the Model

We tested qualitative predictions about evolutionary transitions and ESS mating systems made by our model by comparing them with data (table S3) on the phylogenetic distribution of mating systems in rodents. We chose to test our model in rodents because considerable data on mating systems exist in the literature and because evidence for a genetic basis of the behaviors we model has been described (discussed in detail below). Extant rodent mating systems are often diagnosed by territorial spacing patterns among males and females or paternity, and categorization is congruent in taxa where both data are available (table S3; see methods for search strategy and categorization in the supplemental material). For taxa with sufficient data ($N = 288$), mating system was categorized as promiscuous (two to three strategies within a population; $N = 161$), monogamous ($N = 74$), polygynous ($N = 44$), and mixed polygyny-monogamy ($N = 9$).

   We surveyed peer-reviewed articles, reviews, books, and unpublished theses with sufficient information to infer mating system states in the order Rodentia (table S3). We categorized mating systems using (in order of priority) (1) genetic paternity and (2) degree of overlap of home ranges within and between each sex. Because extrapair paternity occurs at a low level even in monogamous species, we designated some taxa as monogamous if home range and social patterns suggested monogamy, despite evidence of extrapair offspring (<20% extrapair young). Molecular and home range data generally suggested the same mating system when both were available for the same species. In general, our approach for assessing species mating system agreed with past reviews (e.g., Waterman 2007), but in a few instances, our method yielded a different mating system (see footnotes in table S3) or we did not deem the primary data sufficient to categorize mating system in a species included elsewhere (indeterminate in table S3; figs. 2, S3). Our criteria for categorizing a species as showing paternal care behavior required clear evidence of male behavior (care/no care) in natural or seminatural systems (table S3; see also Lukas and Clutton-Brock 2013).

   We used the well-supported, time-calibrated phylogeny of rodents from Fabre et al. (2012) for our analyses on evolutionary transitions and speciation rates in rodent mating systems. We also included paternal care in our analyses to ascertain its association with mating system, which was an assumption of our model. Analyses were conducted in the R 3.5 environment (R Development Core Team

2018). We first tested whether among-species variation in mating system exhibited phylogenetic signal using the fitDiscrete function in the GEIGER package (Harmon et al. 2008). We applied the lamba transformation to obtain an estimate of phylogenetic signal. Next, we examined evolutionary transitions in mating system across the phylogeny by reconstructing ancestral character states using maximum likelihood. We used the ace function in the APE package (ver. 5.1; Paradis et al. 2004) and an asymmetric Mk model of evolution to reconstruct ancestral states. Within this model, we compared different models of evolutionary change, including equal rates, symmetric rates, and all rates different using the fitDiscrete function in the GEIGER package (Harmon et al. 2008). The all rates different model had a significantly lower log likelihood and Akaike information criterion (AIC) score (table S4). We determined unambiguous transitions to monogamy using the criterion of Mooers and Schluter (1999), where a difference of 2 between the log likelihood of any of the states is considered a clear transition. We used this maximum likelihood reconstruction to compare dates of origin of each mating system (monogamous, polygynous, and promiscuous) with a nested ANOVA since our model predicted that polygyny should arise as a consequence of (i.e., after) increased monogamous behaviors (increases in polygyny [red areas] in fig. 1 when $d \geq 2$ and fig. S1 when care behavior p increases). We estimated the proportion of transitions and time spent in different mating system states with a Bayesian stochastic character mapping analysis (Bollback 2006) to account for uncertainty in ancestral mating system states. The stochastic character mapping involved using the make.simmap function in the phytools package (Revell 2012). This function first estimates the conditional likelihood of each character state at all nodes of the tree. Next, it samples the posterior distribution of the transition rate matrix $\mathbf{Q}$ 1,000 times (100,000 generations sampled every 100 generations) using a Bayesian Markov chain Monte Carlo (MCMC). We estimated *pi*, the prior distribution of the root, from the results of the MCMC simulations. The output of stochastic character mapping includes the transition rate matrix $\mathbf{Q}$, the proportion of time spent in each character state, and the final transition probabilities.

   Sparse or unbalanced data sampling across a phylogeny could bias results of ancestral reconstruction of mating systems states (Salisbury and Kim 2001), which could be a concern given that we have sampled 276 of 2,277 species in Rodentia (ignoring subspecies). Our sample includes species from all six major clades identified by Fabre et al. (2012): Sciuroidea, Castorimorph, Ctenohystrica, Anomaluromorpha, Myomorpha, and Muroidea (table S5). In addition, we have species from 74% (31 of 42) of the recognized families/subfamilies and 26% of the genera (124 of 474) in the order Rodentia. Mating system was also not
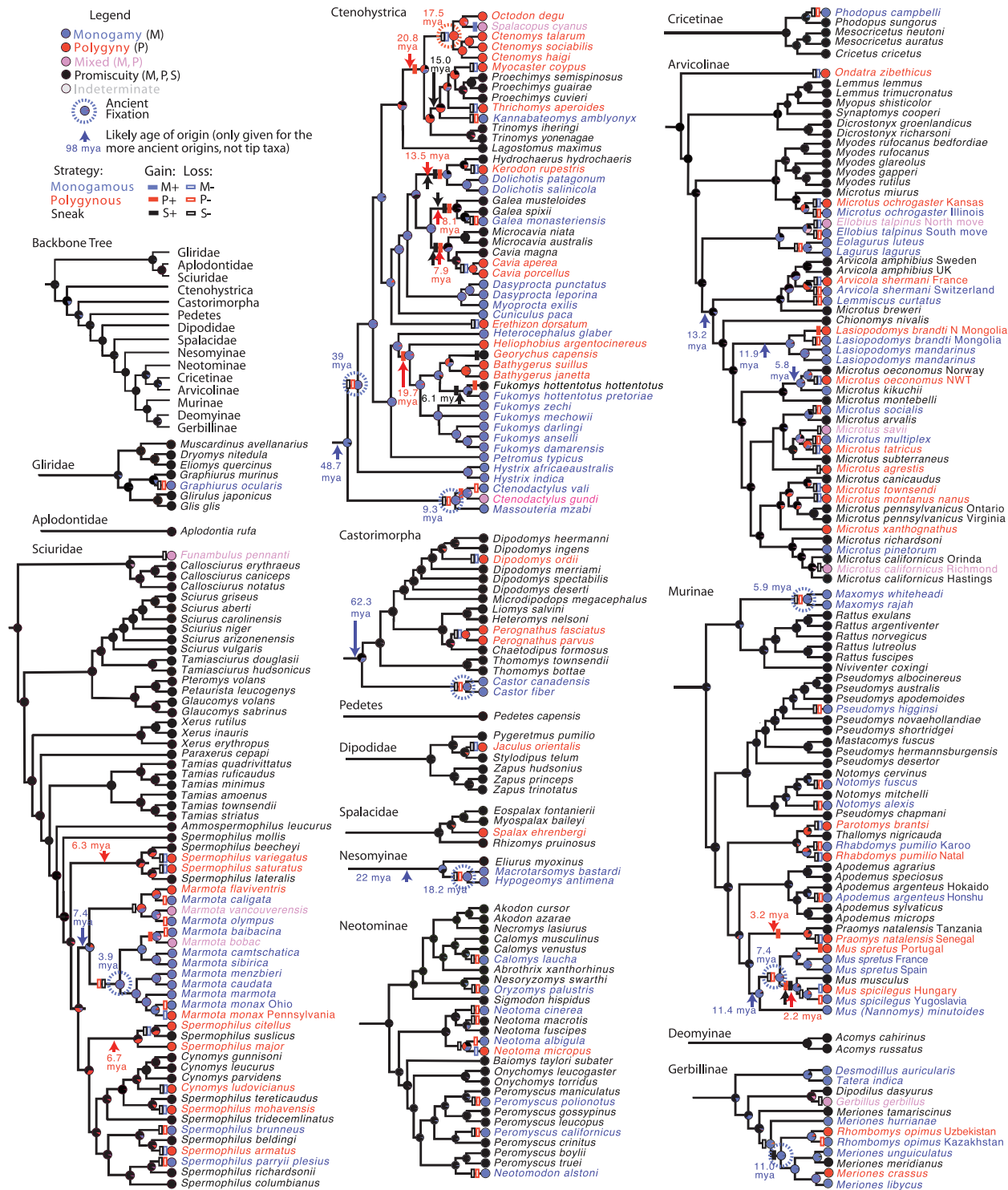
Figure 2: Ancestor reconstruction and distribution of mating systems mapped onto the rodent phylogeny using maximum likelihood. Mating systems are classified as monogamous (blue), polygynous (red), mixed monogamy-polygyny (pink), promiscuous (black), and undefined or indeterminate (gray). Bars along the branch lengths represent gains or losses of each pure strategy. Nodes show maximum likelihood reconstruction estimate of ancestral mating systems as a proportion of each type. Arrows and associated dates indicate the most likely node of origin (circled nodes), defined as the node where the frequency of the strategy first rises above a likelihood of 0.33 and subsequently fixes with likelihood >0.95.

heavily biased across the phylogeny: monogamous taxa occurred within 18 out of 31 families/subfamilies (58%) for which we had data on mating system, and polygyny occurred in 17 of 31 families/subfamilies (55%). Overall, our sampling is balanced in coverage despite being sparse in regard to total number of species.

We evaluated the hypothesis generated by our model that transitions to monogamy result in an increased diversification rate using a hidden state speciation and extinction (HiSSE) model. We compared the rate of speciation for monogamous species (λ_{mono}) with the remaining mating systems ($\lambda_{prom\ or\ polyg}$) to generate state-specific speciation rates for a binary character. In contrast to a standard binary state speciation and extinction (BiSSE) model, the hidden state speciation and extinction model includes hidden states to account for unmeasured traits that may influence the diversification rates for given states of an observed trait (Beaulieu and O'Meara 2016). As a consequence, a HiSSE approach estimates heterogeneity in diversification rates unrelated to the focal trait yet simultaneously accounts for the effects of the measured trait on diversification. A key advantage of HiSSE is that transition rates among states are estimated independently for the hidden and observed traits. In our analysis, we fit two BiSSE-like models and five HiSSE models. We fit two BiSSE-like models, which included a null analysis to estimate diversification rates independent of the mating system and a model including the influence of mating system on diversification rates. Our HiSSE models included (1) a null model where character states evolve independently, (2) a full model allowing the estimation of diversification rates for mating system and a hidden trait, (3) a model to estimate the effects of monogamy and a hidden trait on diversification rates, and (4) two character-independent diversification models (CID-2 and CID-4). These models have the advantage of assuming that the evolution of a trait is independent of the diversification rate without requiring diversification rates to be constant (Beaulieu and O'Meara 2016). The CID-2 model has the same number of parameters as the BiSSE-like model, whereas the CID-4 model has the equivalent number of parameters for a generalized HiSSE model. We used the diversitree (FitzJohn 2012) and hisse (Beaulieu and O'Meara 2016) packages in R to estimate the models of trait-dependent diversification.

The correlation between mating system and parental care was accomplished using a threshold model (Felsenstein 2012) and implemented using the threshBayes function in the phytools package (Revell 2012). We sampled 200,000 generations with a burn-in of 40,000 generations. We sampled every 500 trees to generate an estimate of the correlation between mating system and parental care. We used the HPDinterval function in the coda package (Plummer et al. 2006) to obtain the highest posterior distribution interval for the correlation coefficient from the MCMC sampling.

Support for Model Assumptions

Our review of rodent mating systems supported the major assumptions of our model. The first set of assumptions concerns the existence and ancestral state of three genetically determined alternative strategies. First, mating behavior in at least some rodent species—and, indeed, other taxonomically distant species—can in part be traced to alternative alleles at key loci (Bester-Meredith et al. 1999; Young et al. 1999; Lim and Young 2004; Lim et al. 2004; Young and Wang 2004; Fink et al. 2006; Walum et al. 2008), as assumed by our behavioral genetics model of mating system evolution. Furthermore, we found that mating systems exhibited significant phylogenetic signal ($\lambda = 0.754$, $P < .01$), suggesting that the notion of an underlying genetic cause is likely.

Three lines of evidence suggest that alternative mating strategies exist in rodents. Territorial spacing within some promiscuous rodent species is consistent with territorial expectations of three mating strategies assumed in our model (monogamy, polygyny, sneak; table S3). Indeed, studies with detailed territory maps of promiscuous species show that some males control large territories with several females, other males control smaller nonoverlapping territories and single females, whereas others are wide-ranging without control of a territory (Maza et al. 1973; Scantlebury et al. 2008), corresponding to the three strategies modeled. Detailed behavioral data in a few species support the existence of within-population alternative strategies similar to those in our model (Bishop et al. 2004; Scantlebury et al. 2008; Mills et al. 2009), although data on fitness asymmetries among strategies (i.e., intransitivity) are still unknown for any rodent system. Intraspecific color polymorphism versus monomorphism identifies mating systems in reptiles (Sinervo and Lively 1996; Corl et al. 2010), birds (Lank et al. 1995), and damselflies (Svensson et al. 2005), so we searched for similar patterns in our rodent data set. In rodents, we found instances of segregating coat color polymorphism (including some trimorphic species) in mixed or promiscuous species ($N = 18$; table S6), suggestive of alternative strategy markers, but we failed to document color polymorphism in any monogamous or polygynous taxa, which should be fixed for one strategy. Coat color patterns likely underestimate the prevalence of alternative strategy markers—which are more likely olfactory in rodents, given their heavy reliance on scent—but nonetheless suggest that alternative strategies are present in some rodent taxa.

Finally, estimates of ancestral character state transitions using maximum likelihood enabled us to quantify the

probability of ancestral mating system states at each node and the number and age of independent mating system transitions in rodents (figs. 2, S3). A promiscuous mating system (i.e., multiple strategies) is ancestral (figs. 2, S3), as assumed in our model. Taken together, these lines of evidence suggest that our model assumption of genetically based alternative strategies is valid for the available rodent data.

The second set of assumptions involves the prevalence of recognition and paternal care behaviors. Both discrimination and filiative behavior, which rely on genic recognition to produce spatial clustering, are observed in vertebrates (Emlen and Wrege 1988; Russell and Hatchwell 2001; Krakauer 2005), including rodents (Bester-Meredith et al. 1999; Mateo 2003, 2004; Widdig 2007; Green et al. 2015), and can drive social interactions (Mateo 2004; Krakauer 2005; Hain and Neff 2006; Sinervo et al. 2006; Holmes and Mateo 2007; Widdig 2007). Kin recognition is tied to specific genes (e.g., arginine vasopressin) that also affect mating system, social relationships, and paternal care in some rodents (Bester-Meredith et al. 1999; Young et al. 1999; Marler et al. 2003; Lim et al. 2004; Young and Wang 2004; Nam et al. 2010; Ophir et al. 2012). The key assumption linking evolution of monogamy to paternal care was also confirmed in the phylogenetic data set for the subset of species with clear evidence of parental care patterns. The threshold test implemented using the thresh-Bayes function in the phytools package (Revell 2012) found a strong association between monogamy and paternal care ($r = 0.90$ (highest posterior density interval $= 0.79$–0.97), $P < .05$; fig. S4). In our sample, all monogamous taxa exhibit paternal care. Some polygynous and mixed mating systems exhibit paternal care (50%), and all ($N = 7$) of those that do are recently derived within ancient monogamous clades where genes for care in polygynous males could represent a vestige of ancestral monogamy. Some promiscuous mating systems exhibit care (21%), as expected since they contain monogamy. Thus, model assumptions of genic recognition, biased settlement, and paternal care coupled with monogamy are valid for rodents.

The Congruence of Model Outcomes and Empirical Patterns

Patterns of evolutionary transitions in rodent mating systems are consistent with our model results that consider genetic mating strategies in the absence of variation in resource ecology. Most taxa are promiscuous (56%, 161 taxa), as expected given the large parameter domain for competitive behaviors (c, k, d) that maintain RPS cycles of three strategies when cooperative behaviors (f, p) are weak (black areas in fig. S2) or mixed polygyny-sneak when discrimination behavior (d) is absent (black areas

in fig. 1). The next most common mating systems in rodents are monogamy and polygyny, two ESSs found in our model for higher levels of cooperative behaviors (f, p; case 3 of simulation results). More taxa are monogamous than polygynous (72 vs. 45 species; sign test assuming 50:50; $P < .005$), as observed in our model output, since polygyny as a pure ESS exists only in a thin parameter space where cooperative behaviors (f, p) are high enough to eliminate sneak but not high enough to displace polygyny (red vs. blue areas in figs. 1, S1). Other potential mating systems (e.g., pure sneak, mixed sneak-monogamy) did not occur in our survey and were also not stable outcomes in our ESS model.

Evolutionary Transitions between Mating Systems

Our model showed that increases in the benefits of monogamous behaviors (filiative, paternal care) are largely responsible for transitions between mating system states (figs. 1, S1, S2). In our sample, many more rodent taxa are monogamous (26%) relative to mammals in general (3% [Kleiman 1977], 9% [Lukas and Clutton-Brock 2013]) but similar to some other orders (29% of primates and 16% of carnivores [Lukas and Clutton-Brock 2013]), and monogamy is present in most major rodent lineages (14 of 21; figs. 2, S3). Monogamy is also the most common unambiguous evolutionary transition from a promiscuous ancestor (we define unambiguous transition when a single strategy increases above 33% in likelihood analysis [Mooers and Schluter 1999], although probabilities are generally >50% in such cases; $N = 21$; figs. 2, S3) and more common than unambiguous evolutionary transitions to polygyny ($N = 12$). Our estimates of transitions among mating systems using a stochastic character mapping analysis suggest that evolutionary shifts from promiscuity to monogamy (20%) were much more common than those from promiscuity to polygyny (8%; figs. 3, S5), as expected from our model, which shows a larger parameter space associated with monogamy than polygyny (red vs. blue areas in figs. 1, S1). If increases in monogamous behaviors facilitate the evolution of polygyny, as predicted by our model (increase in f, p in figs. 1, S1), we would expect polygynous clades to be younger than monogamous ones. Transitions to monogamy are somewhat older than those to polygyny, although the difference is not significant (monogamy: mean age of origin $= 14.1$–3.1 million years ago, $N = 14$; polygyny: mean age of origin $= 9.7$–2.1 million years ago, $N = 5$; nested ANOVA, $P = .11$; fig. S3). Furthermore, we predict that polygyny should exist in clades where monogamy becomes more common since polygyny relies on monogamy to eliminate sneak for establishment as a pure ESS in our model (red areas as f, p increase in figs. 1, S1). If we restrict analysis of mating system origins to clades
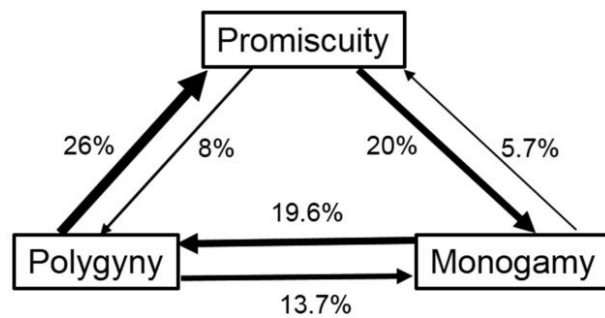
Figure 3: Frequency of transitions between mating system states estimated by stochastic character mapping reconstruction. The frequency of transitions from promiscuity to monogamy is greater than to polygyny, as predicted by our mating system model. Likewise, transitions from monogamy to polygyny are higher than the reverse, as predicted. Transitions back to promiscuity were not possible in our simple model but show up surprisingly frequently in the data. The stochastic character map phylogeny is shown in figure S5, available online.

with well-supported ancestral fixations of monogamy (e.g., nodes where likelihood of all other strategies are <0.05), then we can identify clades where polygyny is derived (fig. 2). By this criterion, there are eight independent fixations of monogamy, which outnumber the single independent fixation of polygyny, which is nested within a monogamous clade (fig. 2). Furthermore, transitions from monogamy to polygyny (19.6%) are more common than from polygyny to monogamy (13.7%; figs. 3; S5), as expected if increases in monogamous behaviors promote polygyny (red areas as f, p increase in figs. 1, S1).

Mating system transitions should also involve rare or unstable coexistence of two mating systems according to our model. Some species showed mixed mating systems comprised of monogamy and polygyny (i.e., sneak lost, nine taxa), which was never an ESS in our simulations but does exist as a transitory state when monogamy eliminates sneak. Thus, mixed monogamy-polygyny could be a transient state before fixation to monogamy or polygyny. Alternatively, mixed mating species may reflect a contact zone between neighboring populations fixed for polygyny and monogamy. In either case, rarity of mixed mating systems in rodents is consistent with our model.

We also found mating system transitions in rodents not seen in the model results. Unambiguous transitions from pure monogamy (likelihood probability >0.95) back to promiscuity (one case) or to polygyny or mixed systems (seven cases) suggest that mating system reversals occur. For example, ancestral Bathyergidae are monogamous, yet *Fukomys hottentotus hottentotus* is promiscuous (fig. 2; Bishop et al. 2004), reflecting a reinvasion of polygyny and sneak. Behavioral and genetic paternity patterns in

F. h. hottentotus include wide-ranging polygynous males, monogamous mate-guarding males, and diminutive sneaker males (Bishop et al. 2004), resembling other RPS systems (Sinervo and Calsbeek 2006; Sinervo et al. 2006, 2007). Such patterns in mating system transitions could reflect either uncertainty in the loss of mating systems (ancestral probability <0.05) or the appearance of new mating systems lost in the ancestor (novel mutation). The stochastic character mapping analysis likewise identified transitions that were not possible in our model formulation, including those from monogamy to promiscuity (5.6%) or from polygyny to promiscuity (26%), which was surprisingly common (figs. 3; S5). Future models that would allow for the reintroduction of lost strategies would be particularly informative on this issue. These patterns of mating system transitions back to multistrategy states evoke an evolutionary cycle of RPS intransitivity (Sinervo and Lively 1996), but at a phylogenetic level if it reflects reinvasion of new genetic strategies that were lost on previous evolutionary transitions.

Effects on Speciation Rates

Genetic mating system games can enhance speciation rates if diversification in one mating system exceeds those in others. Indeed, our model results suggest that increased monogamous behaviors (f, p) can lead to bifurcation of promiscuous taxa into monogamous or polygynous taxa. Such bifurcations can occur through rapid divergence between populations as monogamous behaviors increase (fig. 1; thin red band of polygyny vs. blue band of monogamy with little change in f and p when $d > 2$) or when different populations with the same degree of monogamous behaviors have different initial allele frequencies (fig. S1; boxes with both blue and red for the same values of p, d). We tested for the effects of mating system on diversification rates using HiSSE. The BiSSE-like model revealed that monogamous lineages had higher speciation rates ($\lambda_{mono} = 14.95$) than lineages with promiscuous or other mating systems ($\lambda_{prom} = 3.101$), suggesting that monogamous lineages diversified ~4.8 times faster than lineages with promiscuous mating systems. We contrasted results of the BiSSE model with those of a hidden states model using a model selection approach based on AIC and AIC model weights (table 1). The full model HiSSE (includes hidden states and independent transition rates) outperformed the remaining six models (two BiSSE and four other HiSSE). Lineages that evolved monogamous mating systems had higher diversification rates than those with promiscuity or polygyny as a result of higher speciation rates and lower overall turnover (λ and τ in table 2; fig. S6). Moreover, promiscuous mating systems had higher observed extinction rates than monogamous mating systems

Table 1: Results from binary state speciation and extinction (BiSSE)-like and hidden state speciation and extinction (HiSSE) analyses of trait-dependent diversification

Model	AIC	ΔAIC	AIC weight
HiSSE:			
Full	**−205.22**	**.00**	**.976**
Monogamy	−196.55	8.67	.011
CID4	−168.76	36.46	.000000012
Null	−139.01	66.21	4.08E−15
CID2	−139.00	66.21	4.08E−15
BiSSE:			
Full	−168.30	36.91	.0000000094
Null	−139.91	65.31	6.41E−15

Note: Values presented are Akaike information criterion (AIC) scores, differences (ΔAIC), and AIC weights for each model comparing diversification rates of monogamous versus promiscuous mating systems. Boldface indicates the best fit model.

(μ in table 2). Notably, the full model also showed the influence of a hidden state on diversification of rodents. Interestingly, the influence of the hidden state appears to affect promiscuous clades to a greater extent than monogamous clades. Furthermore, net turnover appeared to be higher in promiscuous lineages than monogamous lineages (τ in table 2; fig. S6). A higher speciation rate in monogamous clades from our HiSSE analysis should lead to more taxa from monogamous versus promiscuous clades. Indeed, a sister taxon comparison shows that transitions to monogamy in rodent clades yields a 4.74-fold greater number of species than sister clades retaining a promiscuous mating system (Wilcoxon signed rank test on log(species in sister clades): $S_{10} = 27.5$, $P = .002$; fig. 2; table S7).

Our model simulations show that a rise in monogamous behaviors (increasing f, p) in a more monogamous ancestor could lead to both monogamous and polygynous descendent species with little change in monogamous behaviors (rapid transitions to red and blue with increased f and p in figs. 1, S1) more often than from a promiscuous ancestor (i.e., low monogamous behaviors f, p), which should lead to a higher speciation rate in monogamous lineages. We tested this prediction by randomizing character states across the tree topology (including nodal values based on ancestral reconstructions), preserving the frequency of each mating system and observed an average of 8.1 pairs of descendent taxa where monogamy was sister to either polygyny or a polygyny-monogamy mixed mating system. Less than 1/200 randomizations ($P = .005$) had as many bifurcating pairs containing monogamy and polygyny as we observed in our data set ($N = 17$; figs. 2, S3), suggesting that monogamy and polygyny arise as sister taxa twice as often as expected by chance alone. Two mechanisms might lead to this pattern. First, monogamy enhances invasion of polygyny because weak monogamous

behaviors (slight increases in p and f shift from promiscuity in black to polygyny in red in figs. 1, S1) facilitate fixation of polygyny as a pure ESS, as predicted by our model. Likewise, if monogamous behaviors become less developed (p and f decrease; start frequencies with high monogamy but low p, f in fig. S1), polygyny can invade monogamy. Second, monogamy and polygyny could result from socially mediated speciation (Hochberg et al. 2003). Social traits in monogamous lineages when hybridized with polygynous lineages may yield hybrids with depressed fitness (Gill 1984), reinforcing speciation and fixation of different mating systems in adjacent populations. This process could be accelerated if genes for filiative behavior in males have pleiotropic effects on female mate choice (Sinervo et al. 2006), thereby leading to rapid reproductive isolation between individuals with or without monogamy genes.

Genetic Mechanisms of Mating System Transitions

Rapid shifts between genetically based mating systems rely on simple mutations that impact cooperative behaviors (f, p), regardless of the surrounding resource distribution. Evolutionary transitions between monogamy and polygyny in rodents have been linked to a point mutation in a vasopressin receptor gene (V1aR; Lim and Young 2004; Lim et al. 2004; Fink et al. 2006), and this gene is also linked to increased paternal behavior and reduced aggression (i.e., filiative behavior) in monogamous species (Bester-Meredith et al. 1999). Such mutations would provide a mechanism for the simultaneous rapid evolution of increased care and filiative behaviors needed for bifurcation into monogamy or polygyny and potentially lead to speciation. Moreover, pleiotropic effects of V1aR could lead to rapid evolution of more advanced forms of sociality through enhanced genic clustering, fidelity, care, and cooperation, which might explain why highly social species in rodents (e.g., mole rats and marmots) originate from monogamous lineages.

The cooperate-care strategy we equate with monogamy is a form of genic recognition that acts through filiative and paternal care behaviors and conflicts with polygynous

Table 2: Estimated rates of speciation (λ), extinction (μ), and net turnover (τ) derived from the full hidden state speciation and extinction model

	λ	μ	t
Promiscuity:			
Observed	3.35	.04	3.26
Hidden	9.70	1.99E−08	13.41
Monogamy:			
Observed	30.33	6.33E−08	2.23
Hidden	2.04	1.40	13.49

strategies. Work on genic recognition in mammals has shown patterns of genomic imprinting present in polygynous/promiscuous species but absent in monogamous sister taxa (e.g., *Peromyscus polionotus* vs. *Peromyseus maniculatus*, *Mus spretus* vs. *Mus spicelegus*; Haig 1996; Burt and Trivers 2006). Experimental crosses between sister taxa yield hybrid unfitness as a result of mismatches in imprinted loci of sires and counterstrategy imprinted loci of dams (Burt and Trivers 2006). Genomic imprinting may enhance speciation of monogamous and polygynous/promiscuous taxa (Gill 1984) due to alternative alleles for genic male care and contribute to accelerated bifurcation into monogamous and polygynous sister taxa. We predict that newly evolved genomic imprints should exist in the 23 independent transitions from ancient monogamy to promiscuity/polygyny.

We modeled complex behaviors driven by a single gene, and such a formulation could have important consequences for speciation. While a single gene with multiple effects facilitates theoretical analysis, there is also building evidence for such systems in the empirical literature. For example, genetic analysis of ruffs that show alternative male strategies shows that a large inversion has created a supergene that drives male color, mating behavior, and aggression (Küpper et al. 2016). Alternatively, a single gene can have pleiotropic effects on multiple behaviors, as has been found in cooperative behavior of slime molds (Queller et al. 2003; Foster et al. 2004), and is a likely mechanism underlying the association between hormone receptor genes in rodents (V1aR) and multiple mating and prosocial behaviors (Wang et al. 1994; Bester-Meredith et al. 1999; Lim et al. 2004; Young and Wang 2004; Albers 2012). Finally, such effects could be due to multiple genes that are tightly coupled through linkage disequilibrium despite being scattered across the genome, as described in lizards (Sinervo et al. 2006). If the behaviors and their underlying genes segregate in both males and females, then mate choice for specific behavioral types could generate correlational selection and build up such linkage (Alonzo and Sinervo 2001; Sinervo et al. 2008). Interestingly, such multiple effects that we describe here resemble magic traits explored in the speciation literature as a critical component generating rapid speciation in adjacent or sympatric populations (reviewed in Servedio et al. 2011). While magic traits describe traits that couple phenotypic traits for mate choice with fitness traits related to ecology, the genes we describe couple social behavior with reproductive success as a consequence of social selection (West-Eberhard 1983; Lyon and Montgomerie 2012), also referred to as socially mediated speciation (Hochberg et al. 2003). Indeed, expanding the definition of magic traits to include such socially selected cases could greatly increase the contexts under which speciation with gene flow is expected to arise.

Contrasting Genetic and Resource Ecological Mating System Models

The genetic mating system model we propose here both contrasts and complements classic resource ecological mating system models (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977; Davies 1991; Shuster and Wade 2003; Lukas and Clutton-Brock 2013). In contrast to resource ecological models, our genetic model is able to make predictions about evolutionary transitions between mating system states and the likely impact of such mating system transitions on speciation rates. In both cases, our model predictions are consistent with empirical data from rodents. Furthermore, the genetic model could provide an explanation for cases where mating system transitions do not match resource ecology transitions because of phylogenetic inertia when mating system is conserved despite resource distribution change or when mating system shifts despite resource ecology remaining static. Our survey of rodent mating systems contains examples of different populations of a single species with either different ($N = 14$) or the same ($N = 4$) mating system, and comparisons of the resource distributions of these populations could help identify cases where the genetic model provides added insight relative to the resource distribution ecological model.

While there is increasing evidence for a genetic basis of mating behavior (Wang et al. 1998; Lim et al. 2004; Young and Wang 2004; Walum et al. 2008; Corl et al. 2010; Küpper et al. 2016; Lamichhaney et al. 2016), there are cases where resource ecology likely has a direct influence on a mating system (Emlen and Oring 1977; Shuster and Wade 2003), suggesting that both mechanisms could interact. From this perspective, resource distribution shifts could explain reversals in mating system states (e.g., monogamous or polygynous back to promiscuous) not predicted by our genetic model through shifts in the costs and benefits of space use or cooperative behaviors. Indeed, phenotypic plasticity is common for behavioral strategies, and the real question might be how resource ecology and genetics interact to shape mating system state. Addition of fine-scale resource and environmental ecological data to our rodent mating system data set would allow an evaluation of the explanatory power of each mechanism in predicting mating system evolution and phylogenetic signal and would be a fruitful first step in this direction. Likewise, models for different genetic mechanisms underlying behavioral strategies (e.g., plasticity, dominance, heterozygote advantage; Moulherat et al. 2017) could broaden our understanding of behavioral genetic influences on mating system evolution, now that we have demonstrated the ability of a simple codominant genetic model to predict empirical patterns of mating system evolution in rodents.

Broader Implications

Genetically based social strategies in our model and identified in rodents (Young and Wang 2004) have broad implications for population ecology since territorial strategies (polygyny, monogamy, sneak) use space differently and have varying intensities of density regulation against their own strategy (table S1A; see also Sinervo et al. 2007). Density cycles in rodent species could be due to social competition among alternative strategies (Chitty 1996) in promiscuous taxa. Indeed, female density cycles have been identified in lizards with alternative mating strategies (Sinervo et al. 2000) because the strategies that evolve in females involve progeny size and progeny quantity. Likewise, density-dependent alternative reproductive strategies identified in the promiscuous bank vole (Mappes et al. 2008) could drive population density cycles. We also found three examples of coat color morphs in promiscuous rodent species that similarly show population density cycles, which might be expected when coat color genes have pleiotropic effects on social behavior (Broadhurst et al. 1974) and life history (table S6).

The strength of our hypothesis is the integration of multiple factors (e.g., territory spacing patterns, mating systems transitions, social speciation, genomic imprinting, color polymorphism, and density cycles) that jointly support a genic model of frequency-dependent competition to drive mating system evolution. Indeed, alternative strategies generate mating system variation and predicts evolutionary transitions among mating system states irrespective of resource ecology. While resource distribution and environmental ecology have some influence on the benefits of social behaviors, genetically based mating strategies themselves are sufficient to drive mating system evolution. Our model should generalize to other vertebrates. For example, many fish species exhibit alternative strategies that include parental and sneaker males or three strategies (Oliveira et al. 2008). In trimorphic bluegill sunfish, male care (nest guarding) is associated with genic recognition of progeny (Neff 2003) by polygynous rather than monogamous males, with evidence of RPS dynamics (Friedman and Sinervo 2016). Care-giving males form colonies where mutual defense (cooperation) enhances successful fry development (Côté and Gross 1993) by repulsion of sneakers and predators. Trimorphic alternative mating strategies consistent with an RPS game are also documented in a broad array of other taxa, including bacteria, flowers, crustaceans, insects, lizards, and birds (Shuster and Wade 2003; Sinervo and Calsbeek 2006; Sinervo et al. 2007; Oliveira et al. 2008; Friedman and Sinervo 2016). As such, frequency-dependent competition among alternative strategies could facilitate mating system evolution and speciation in many taxa through intrinsic effects of behavioral genetics.

Data and Code Availability

All data used in analyses come from the literature; both data and references are provided in table format in the supplemental material (table S2).

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Thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*) photographed at the Pawnee National Grassland in northeastern Colorado. Photo credit: Alexis S. Chaine.