

Modeling Mate Choice in Monogamous Mating Systems with Courtship

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We present a conceptual framework for the study of mate choice in monogamous mating systems with non-negligible courtship time. Within this framework, we develop a mate choice model for the common case where individuals have a changing social network of potential partners. The performance and robustness of different agent strategies is evaluated, emphasizing the important role that courtship plays in mate choice. Specifically, the courtship period can be used by individuals to swap to better partners when they become available. We found that using courtship as a mechanism for holding partners before full commitment to mating provides strategic advantages relative to sequential search using aspiration levels. Moreover, simple heuristics that require little computation provide a degree of robustness to environmental (parameter) changes that is unattainable by strategies based on more extensive information processing. Our model produces realistic patterns of assortative mating (high within-couple mate value correlations) and rates of mating that match empirical data on human sexual/romantic relationships much more closely than previous accounts from biology and the social sciences.

Keywords mate choice · mate search · courtship · human mating · heuristics · agent-based modeling · evolutionary functional analysis

1 Introduction

Perhaps the most important set of adaptations that humans and other animals are endowed with are those related to mating and reproduction (Bateson, 1983; Symons, 1979; Barkow, Cosmides, & Tooby, 1992; Buss, 1994). Although individuals can promote their genes indirectly by helping kin (as in social insects), a more direct strategy is to mate with a member of the opposite sex and produce offspring (Alcock, 1997). Therefore, it is expected that evolution would provide individuals in sexual species with specially designed

psychological mechanisms that allow them to perform these reproductive tasks efficiently. Discerning the structure of such mechanisms is crucial if we hope to understand the behavior and minds of humans and other animals.

Within the set of such mechanisms associated with mating and reproduction, the ones related to mate choice are central. Because individuals of the opposite sex tend to vary in their quality as suitable mates (e.g., due to genetic makeup, social status, or parental skills), and because mate quality strongly influences offspring quality, mate choice decisions are crucial to

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the fitness of offspring (Bateson, 1983). This is especially true when these decisions are performed in highly competitive settings, as is the case in monogamous mating systems where partner sharing is not beneficial and therefore not easily tolerated by (at least) one of the sexes. In such cases, both sexes tend to be highly choosy, leading to a process of mutual mate choice where each individual strives to get the best possible mate for itself.

It is thus not surprising that many computational and mathematical models have been proposed in the biological and social science literature that address the issue of mate choice behavior (Kalick & Hamilton, 1986; Todd & Miller, 1999; Parker, 1983; McNamara & Collins, 1990; Johnstone, 1997; Bergstrom & Real, 2000). These models allow important conclusions to be drawn about mating behavior of animals and humans, but very often they rely on assumptions that fail to hold in realistic mating environments, particularly for humans. Typical assumptions of models of mutual mate choice are that individuals search and encounter mates sequentially (usually without the ability to go back to, or “recall,” earlier mates), and that individuals make their mating choices as a single, *irreversible* decision whether to mate with an individual or not (Kalick & Hamilton, 1986; Todd & Miller, 1999; Parker, 1983; McNamara & Collins, 1990; Johnstone, 1997). This conflicts with the fact that humans use extensive courtship periods to establish long-term sexual/romantic relationships, and that this allows individuals to engage in relationships in tentative ways—possibly switching to better alternatives if they become available in the future (Buss, 1994; McKnight & Phillips, 1988; Weisfeld, 1999). As we show in this article, the existence of a non-negligible courtship time and access to potential alternative partners has, indeed, significant consequences for the strategic behavior of individuals when choosing mates.

Taking the opposite extreme from sequential choice, some earlier models make the unrealistic assumption that the complete set of potential mates in known instantaneously and is common to all members of the same sex (Bergstrom & Real, 2000). More generally, these models often assume that individuals seeking mates have complete and accurate information about the distribution of qualities of potential partners, about their own quality, and sometimes even about the preferences of other individuals (Parker, 1983; McNamara & Collins, 1990; Johnstone, 1997;

Bergstrom & Real, 2000). Given that such information is typically not available in the real world, it is not surprising that most of these models are of limited empirical validity.

In this article, we present a conceptual framework for modeling mate choice in the context of long-term relationships with extended courtship periods, with particular emphasis on the human case. (The results can also be generalized to other animals where similar assumptions hold.) Based on an evolutionary functional analysis, we develop an agent-based model that captures key aspects of this adaptive problem. Our model differs from previous computational and mathematical models of mutual mate choice in that it relies on more realistic assumptions about the specifics of the human social environment and the nature of human psychological constraints. In particular, we assume that individuals have dynamic, growing social networks of potential partners, instead of meeting these partners sequentially or having complete information about all of them instantaneously. Furthermore, our model postulates choice mechanisms (decision rules or heuristics and strategies that combine them) that are more psychologically plausible than those in previous models. We argue that individuals can make simple, efficient, and robust mating decisions by using heuristics that exploit the specifics of the adaptive problem domain rather than attempting to perform complex optimizations, thus constituting an example of *ecological rationality* (Todd, Krauss, & Fiddick, 2000). In addition to arguing for this new conceptual framework for understanding mating decisions, we demonstrate the empirical power of our model by showing that its predictions about overall relationship patterns observable at the population level fit data from the social sciences much better than competing models.

This article is organized as follows. In Section 2, we review work in the area of computational and mathematical modeling of mutual mate choice behavior in humans and animals. We focus only on models of two-sided matching (rather than one-sided search) because these are more relevant to the study of human behavior. In Section 3, we establish a conceptual framework for the study and computational modeling of human mate choice. Capitalizing on this framework, in Section 4 we present a model of (human) mate choice based on non-negligible courtship periods. Section 5 describes the different decision rules

used by agents, and Section 6 compares their performance. Section 7 presents the model predictions and makes an analysis of these predictions in the face of known empirical evidence. In Section 8, we compare our model results with those of previous models and discuss future research directions. Finally, Section 9 summarizes our conclusions.

2 Previous Work on Models of Mate Choice

Seminal studies of human mate choice using computer simulations were conducted by Kalick and Hamilton in the 1980s (Kalick & Hamilton, 1986). They started with the fact that observations of many human populations show that individuals in couples are highly correlated in attractiveness (correlations between 0.4 and 0.6 in different studies). This finding led social scientists in the 1960s to propose the “matching hypothesis” that people actively seek a mate matched to them in attractiveness. But this seemed to contradict experimental data indicating that people in general tend to prefer more physically attractive individuals as prospective partners (i.e., not taking their own attractiveness into account). To explain this apparent contradiction, Kalick and Hamilton set up individual-based simulations to study the relationship between individual-level preferences and population-level patterns. In their simulations, randomly selected individuals with particular attractiveness values are paired up sequentially in “dates.” Both individuals in a date then use a probabilistic acceptance criterion to decide whether or not they accept each other, and, if both agree, they mate and leave the population. A discounting factor was introduced to make individuals less choosy with time.

Kalick and Hamilton’s results demonstrated that universal preferences for high attractiveness, as opposed to preferences for similarity in attractiveness (matching), can produce realistic degrees of intracouple correlation of attractiveness (.55). This is because higher-attractiveness individuals tend to pair (and leave the mating pool) earlier than lower-quality individuals, leaving the lower-quality individuals with no option other than mating among themselves (Burley, 1983). One critique of Kalick and Hamilton’s support for preferences for high attractiveness was that an unrealistically high number of dates (evaluations of

members of the opposite sex) was required in the model for a realistic intracouple attractiveness correlation to be obtained and a significant percentage of the population to mate (e.g., it took 40 “dates” for the correlation to reach .43 and 86% of the individuals to mate, Aron, 1988).

More recently, Todd and Miller used a similar type of simulation to explore the efficacy of different individual rules for searching through a sequence of encountered potential mates (Todd & Miller, 1999). They were particularly interested in whether individuals could make reasonably good (satisficing) mate choices without having to check many potential partners. In their model, an “adolescence” (learning) period is used by individuals to adjust an *aspiration level* based on the feedback provided by the mating offers and rejections of potential mates they encounter. After the adolescence period, individuals make mating offers to everyone they meet who exceeds their aspiration level, and whenever both individuals in a pair make mutual offers to each other, they mate and are removed from the population. Todd and Miller’s results showed that simple learning rules can adjust individual aspiration levels quickly (e.g., after an adolescence comprising 12 dates or partner assessments) to yield mated pairs of highly matched mate value. However, these learning rules typically left an unrealistically large proportion of the population unmated (e.g., over 50%).

The animal behavior literature is rich in studies of mate choice, with the book *Mate Choice* (Bateson, 1983) setting the stage for the work done later in the area. In particular, the chapter by Parker (Parker, 1983) made a provisional formal analysis of (optimal) mating decisions when an infinite-horizon rate-maximization of matings is expected, with individuals alternating between searching and “processing” time. His work was further refined by McNamara and Collins with a full game-theoretical analysis of the problem (McNamara & Collins, 1990). They described a single stable strategy (a *Nash equilibrium*) where each sex is partitioned into a finite (or countable) sequence of categories with decreasing-quality intervals such that members of each category end up mated with members of the corresponding category in the opposite sex. In some cases, low-quality members of one of the sexes could end up never mating.

The problem of learning the distribution of qualities of available mates during sequential search was

tackled by Mazalov and colleagues (Mazalov, Perrin, & Dombrovsky, 1996). Their model of single-sex discrimination showed how individuals could learn the mean and variance of the mate quality distribution by incremental updating with each new potential mate seen, and how this information could be used at the same time to set a varying threshold for mate acceptance. They found that such learning could be advantageous compared to using a fixed strategy if there is enough variation in the distributions that can be encountered, and if the learning time is long enough. We also assume that such conditions hold in the mating situations we consider, and hence we include learning in our strategies; however, we avoid the full-optimization approach and the assumptions of fixed search horizons, fixed population distribution, and no search costs that Mazalov et al. adopted.

Considering more realistic constraints than the models just described, Johnstone presented a model of mutual choice where individuals have a limited time to mate (i.e., the duration of a breeding season, Johnstone, 1997). In his model, individuals encounter each other in random pairs and must decide whether or not to mate with this one partner for the duration of the breeding season. There is also a cost associated with delaying the mating decision, and the distribution of available mates changes over time. Using a numeric method (*iterative best response*), Johnstone computed optimal aspiration levels as a function of both an individual's quality and the time left in the breeding season. His results showed that as the breeding season progresses, high-quality individuals tend to become less choosy, whereas lower-quality individuals initially tend to increase their level of choosiness, but after a certain period also become less choosy with time. This initial increase in choosiness of lower-quality individuals arises as a way of exploiting the decrease in choosiness of high-quality individuals.

The above models, while representing theoretical advances, are limited by their reliance on unrealistic assumptions such as full information or constant search costs that are unlikely in environments where the rate of encounters is not deterministic. Similar kinds of assumptions are also found in other mate choice models presented in the animal behavior literature, when either one or both sexes discriminate between partners (Real, 1990; Dombrovsky & Perrin, 1994; Johnstone, Reynolds, & Deutsch, 1996). This often has the effect of removing most of the relevant

problem structure and therefore hampering the empirical validity of the models (Pepper & Smuts, 2000; Hammerstein & Riechert, 1988; Hammerstein, 1999; Simão & Todd, 2001). As Todd and Miller's work argues, these kinds of assumptions are neither psychologically or ecologically plausible nor necessary for building useful models (Todd & Miller, 1999; Todd, 1996). More generally, it is likely that animals, including humans, use simple decision mechanisms that exploit the rich information structure present in their task environments, rather than adhering to the normative, optimizing approach typically used in behavioral research (Reed, 1996; Gigerenzer, Todd, & ABC Research Group, 1999).

Similar criticisms can be aimed at models of two-sided matching presented in the economics literature. In a recent article, Bergstrom and Real review some of this work and suggest how it can provide insights for the study of animal behavior (Bergstrom & Real, 2000). Yet, they focus only on models where the set of all potential partners is defined and known beforehand. This has the effect of making researchers concentrate mainly on issues of global pairing stability. Because real-world scenarios are more likely to involve dynamic social networks, global stability is only temporarily (or never) obtained (Epstein & Axtell, 1996). Therefore, emphasizing full knowledge and stability only diverts attention from other issues of greater empirical relevance.

3 A Framework for Modeling Human Mate Choice

In this section, we summarize some of the key aspects that should be considered when modeling human mate choice from an adaptive perspective. This is used as the rationale for design decisions in the model presented in the next section. (As mentioned earlier, these considerations also apply to other species, particularly those that have a tendency to mate in monogamous pairs and that aggregate in groups or clusters, such as some species of birds.)

3.1 The Nature of Preferences

A central question to be asked when studying human mating is the nature of interpersonal attraction. From an evolutionary perspective, it is expected that humans

(like other animals) have traits that influence their ability to survive, reproduce, and successfully raise their offspring. They will also present some degree of variation in those features. Thus, it is reasonable to assume that evolution would endow individuals with the capability to discriminate among potential partners, preferring the ones with better traits. We can conceptualize preferences as being based on some combination of the different relevant features into an overall *mate value* or *mate quality*, as suggested by Donald Symons (Symons, 1979). Thus, as a first approximation, we can build useful models by relying only on a one-dimensional quality feature (see Section 8 for discussion of multi-dimensional qualities).

3.2 Courtship Processes

Much evidence exists for a universal tendency in humans to establish long-term sexual/romantic relationships. Although there is also evidence that humans like sexual variety and when possible will engage in short-term sexual relationships (Buss & Schmitt, 1993; Buss, 1994), several researchers argue that this is only a complementary strategy and not an alternative to the first pattern (Miller & Fishkin, 1997; Zeifman & Hazan, 1997). Once long-term relationships are established, both men and women substantially invest in the offspring that result from them (Symons, 1979). However, following the general pattern among mammals, human females have a much higher *minimal parental investment* than do males (Trivers, 1972). Thus, women are under selective pressure to be particularly careful to avoid choosing as mates men who would desert them after mating (Dawkins, 1976/1990). One way to be careful is to impose a costly courtship process on men, during which women can evaluate a man's commitment and willingness to invest in the relationship (and offspring). During the courtship process, men are expected to provide women with resources and, even more importantly, spend "quality" time with them (Buss, 1994; McKnight & Phillips, 1988). Time is an especially good predictor of commitment, because although a resourceful man can give gifts to several women, he can only be physically in one place at a time.

The issue of tactical assessment of partner willingness to commit to a relationship has been widely

studied in game-theoretical models presented in the literature within the category *battle of the sexes*—where fast or coy females (i.e., quick or slow to mate) and helpful or nonhelpful males compete against each other (Dawkins, 1976/1990; Schuster & Sigmund, 1981; Mylius, 1999; Wachtmeister & Enquist, 1999). Of particular importance to mate choice research, is the result that female *coyness* can evolve and invade a population, provided that two conditions are met: first, a combination of helpful and nonhelpful males must be present in the population; and second, females must obtain increasing information about the likelihood that a male will desert her after mating as courtship progresses—so that she is trading breeding season or reproductive lifetime for information (Wachtmeister & Enquist, 1999; Wachtmeister, 2000). Both of these conditions are typically valid for humans (Weisfeld, 1999; Buss, 1994). Therefore, in this article we make the assumption that individuals delay mating until a courtship period is completed (See Simão & Todd, 2002, for a detailed discussion of this issue.)

An important side effect of the courtship period in mating processes is that it can be used strategically as an opportunity to switch to a better partner if one becomes available. This is true not only for women, but also for men, because they are also choosy in selecting partners for long-term relationships. The decision to switch can be influenced by several factors, including time and investment already made in the current relationship, how much better the alternative partner is than the current one, and how likely it is that the alternative partner will not switch later to a better partner. From all of these considerations, it follows that human mate choice is better modeled as a process that takes time to complete, rather than as a single atomic event. Contrary to all previously proposed models of mate choice that we are aware of, the model that we present in Section 4 is the only one that incorporates this aspect of courtship within a background of a realistic social ecology.

3.3 Time Pressure to Mate

Everything else being equal, the earlier individuals mate, the better off they will be from an evolutionary point of view. This is because an individual's (reproductive) lifetime is limited, so that the earlier they mate, the more offspring they can potentially produce.

Moreover, in an uncertain and risky environment, the possibility of premature death is always present. Although these arguments may hold less in modern societies, human mate search strategies were designed by evolution with these factors firmly in place (Barkow et al., 1992). All sexual animals, not just humans, have limited time to find a mate and reproduce, but many arrange their reproduction periods in a noncontinuous way—usually in the form of breeding seasons, when the conditions for mating and reproduction are most suitable (Johnstone, 1997; Krebs & Davies, 1993). The model of human mate choice that we present in Section 4 can be adapted to animals with a breeding season by equating that time period with the limited reproductive lifetime in humans.¹

3.4 Interaction Possibilities

Despite the possibility of switching partners during a courtship process (as discussed in Section 3.2), there are several reasons why an individual might consider delaying entering into a relationship. When engaged in an ongoing relationship, the possibilities of meeting and interacting with individuals of the opposite sex might become significantly reduced (e.g., due to mate guarding, and the requirement to invest “quality” time and other resources in the current relationship). Moreover, changing partners might have inherent costs (e.g., retaliation by the current partner). This means that individuals should be sensitive to the quality of those that they accept as tentative mates, even when they can easily switch to another mate later. This choosiness can be accomplished either by setting an aspiration level for the minimal quality acceptable for tentative mates (the typical assumption made by the models discussed in Section 2), or by starting relationships with a low level of commitment and increasing it progressively, or a combination of both. In Section 4 we will compare the performance of all three kinds of strategies.

3.5 Estimating One’s Own Quality

In addition to needing to evaluate the mate quality of others, it may also be useful for individuals to perform a (rough) estimation of their own mate value. This information can be used in deciding whether or not to initiate a courtship process (e.g., to aim at others with a similar mate value), and how much to invest in that

courtship. This estimation can be based on at least two sources of information: the outcomes of past interactions with members of the same sex, and the outcomes of interactions with members of the opposite sex. The latter may provide more accurate information because it represents a direct window on the preferences of the opposite sex (Todd & Miller, 1999). In species like humans, where full maturity and maximum reproductive potential is reached after considerable time, namely, at the middle or end of adolescence in the case of females (Low, 1997), the opportunity is created for individuals to assess their mate quality (as perceived by others). In humans this takes the form of “flirting” games where individuals probe others for interest via short-term, low intimacy, contacts without engaging in a formal or socially recognized relationship (Montemayor, Adams, & Gullotta, 1994; Weisfeld, 1999). Barnacle geese, *Branta leucopsis*, have also been reported to engage in trial partnerships while they are young, although the adaptive reasons might not be the same as in humans (Jeugd & Blaakmeer, 2001). This trial testing can be done with little cost in terms of lost reproductive lifetime, exactly because maturity has not yet been reached during this period. In the model presented in the next section, we incorporate this aspect of human mating by introducing discrete time frames corresponding to juvenile and flirting periods where individuals assess their mate quality before engaging in a costly courtship process.

4 A Model of Mate Choice with Courtship

To take into account all of the important aspects of the adaptive problem outlined above, we have developed a new model of human mate choice. By incorporating a broader range of factors than previous models, we lay the foundations for a better understanding of sexual partnership formation in humans. We have also been able to account for a wider spread of empirical results, as we show in the next section. Our model is intended to capture scenarios where individuals have only partial knowledge of mating opportunities and are not aware of competitors. This will be the typical case in medium to large communities where the network of acquaintances is sparse.

We assume a population of constant size $2 \times P$ with a fixed sex ratio of 50% (so P is the number of

males or females). Individuals of both sexes have a one-dimensional quality parameter q_i , randomly generated from a normal distribution with mean μ and standard deviation σ , truncated such that $0 < Q_{\min} \leq q_i \leq Q_{\max}$. Individuals are always in one of two states: *single*, when they do not have a partner, and *courting*, when they are engaged in a courtship process. Time is modeled as a sequence of discrete steps. Pairs of males and females meet at a certain stochastic rate: In each time step each individual has a probability Y of meeting a new individual of the opposite sex.² Each individual maintains a list of the potential mates already met—the *alternatives list*. Single individuals are encountered before those already courting—only when no individual in a single state is available will already-courting ones be met and inserted in others' alternatives lists. This is intended to model in a simple way the fact that in the real world (everything else being equal), attempts to interact with single individuals will be more frequent than attempts to interact with individuals already courting. This is so because single individuals are more likely to be actively searching for partners, and because courting individuals are riskier bets given that they might be potentially too committed to break their current relationship.³

Within the alternatives list, one member can have the “special status” of being the individual's current *date*. This happens when both individuals previously agreed to court and have not changed partners in the mean time (see below). It is also possible for an individual not to be courting anybody (e.g., in the beginning of its “life,” or when it gets “dumped”). The length of time that two individuals are courting is regarded as the courtship time c_t . If a pair of individuals remain courting for a period of K (≥ 0) time steps (i.e., when $c_t > K$), they are deemed to mate and are removed from the population and replaced with two new individuals of random quality (one of each sex).

The alternatives list has a maximum size of N . This corresponds to the maximum number of opposite-sex individuals an agent can maintain in its social network to make courting proposals. If the social network becomes saturated, that is, if the alternatives list is filled, new meetings happen at the expense of forgetting one randomly selected individual already in the list (other than the current date). Once again, single individuals take precedence over courting ones and, therefore, will be removed only if there is no courting individual in the list.

Every individual has a maximum *reproductive* lifetime of L ($> K$) time steps. If individuals are unable to mate during this period they are removed from the population (they “die”). This not only creates a pressure for individuals to mate, but also solves the technical problem of keeping individuals with very low quality from clogging the population due to inability to mate. To replace the dead individual, a new one is created with the same sex.

In each time step, every individual has a certain probability of interacting with every member of its alternatives list. This probability is computed by considering a measure that we designate as the individual *interaction capability* (c_i), which correlates negatively with the degree of involvement in the current courtship process (and therefore c_t). This is intended to model increasing levels of intimacy and exclusivity as a courtship progresses (as discussed in Section 3.2). Specifically, we define $c_i = 1 - (c_t/K)^I$, where I is a constant that defines the shape of the “intimacy curve.” If an individual is single, its interaction capability is 1 (maximum value). The interaction probability between two individuals in a given time step is then computed as the minimum of the interaction capabilities of the two individuals. In particular, this means that if both individuals are single they are always able to interact. We call the set of all members of the alternatives list that an individual is probabilistically determined (by random roll of the die) to interact with in a particular time step the *interaction list*.

After the interaction lists are computed for all individuals, each one decides what action to perform based on his or her state. If an individual is single, he/she has to decide whether to try to start a relationship (with some member of the interaction list), or postpone that decision to see if a better alternative becomes available. If an individual is courting, he/she has to decide whether to continue to court the same partner or try to court another individual. To make these choices, binary decision functions are used. These functions output 1 if and only if the respective action is to be taken—that is, try to start a relationship or try to switch partners. They take as input variables several pieces of information such as the qualities of the individuals involved, their ages, and the current courtship time c_t (only in partner switching decisions). Specific decision functions are described in the next section.

Although an individual can make requests to court several others in each time step, he/she can only

```

for (i: all agents) {
    i proposes to best alternative in its proposals list
}
boolean nomatch = false;
int nloops = 0;
do {
    nomatch = false;
    for (i: all agents) {
        for (j: all members in proposals list of i (sorted by quality)) {
            if (j is proposing to i) {
                break;           // current value of j is preserved
            }
        }
        if (i isn't proposing to j) {
            nomatch = true;
        }
        i proposes to j;
    }
    nloops++;
} while (nomatch && nloops < MAX_LOOP);

```

Figure 1 Pseudocode for matching / proposal making algorithm.

court one individual at a particular point in time. Moreover, if an individual decides to switch to another partner, the c_i of the current pair is reset to 0, meaning that if this pair ever ends up courting again in the future, they will have to restart the courtship process from scratch.

If individual i requests to court individual j and individual j simultaneously requests to court individual i , they will start courting (i.e., the decision must be mutual). If an individual is accepted by several others as a date in a particular time step, then he/she will court the one with the highest quality. Any abandoned (“dumped”) individual will be left with no partner (unless he/she also successfully tried to court somebody else). If no individual that i requests to court accepts him/her, and if the partner of i did not start courting someone else, then the pair remains courting and their courtship time c_i is incremented by 1. Date requests of individuals are processed sequentially so

that if an individual was about to court an alternative and that alternative starts to court someone else, the first individual considers the next best alternative.

In Figure 1, we present more formally the matching (proposal making) algorithm used in each time step in pseudocode. For each agent we define a *proposals list*, which is the subset of individuals of the interaction list he/she decides to propose to (according to the decision function in use). This proposal list is sorted by decreasing quality of its members to allow a simple instantiation of preferences for higher quality individuals. Once all proposals lists are created (not shown in Figure 1), the algorithm starts by marking that all agents (of both sexes) will first propose to the best alternative in the proposals list (i.e., the highest-quality individual). Next, for each agent i the algorithm finds the best individual j in i 's proposal list that is proposing to him/her. If j does not correspond to i 's current proposal, i now proposes to j (thus reducing

his/her ambition level). Since j might also change proposals when this procedure is applied to him/her, the algorithm is repeated until no agent changes proposals. In particular, since a proposal first made by i might have been rejected (not matched) by some j only because j was aspiring too high, this allows agents to go back to better alternatives and retry proposals. This looping is also terminated if necessary after a maximum (large) number of iterations, to avoid possible endless loops when there is no global ordering of preferences. Because in our model we are assuming that preferences are universal and perceptions are error-free, this is not strictly necessary here. In this case, the algorithm has the property that, when terminated, each agent will be paired with the highest quality agent that has reciprocated the courting proposal.

To accommodate an *adolescence* or *flirting period* in which individuals try to gather information about and assess their quality (as discussed in Section 3.5), all individuals go through an initial phase of A time steps when they are introduced into the population. In this phase, they can make proposals and accept them or reject them, as described above, but they will not start a courtship process—in other words, they still remain single. The outcomes of these interactions are used solely for the purpose of allowing individuals to estimate their own quality. In the next section, we will describe a simple rule to perform that estimation in an effective way. Individuals in the adolescent flirting phase will preferentially meet other individuals in the same phase because they are the only ones receptive to courting proposals that do not involve exclusivity and increased levels of intimacy (the reverse applies to individuals who have already completed the flirting phase).

We also want to explore strategic scenarios where the adolescent flirting period of individuals does not completely coincide with the initial lifestage of low current reproductive value (see Section 3.5). To allow such possibilities in our model, we define a *juvenile period* of J time steps at the beginning of an individual's lifetime where his/her current reproductive value is considered negligible. Figure 2 depicts graphically the possible life-histories of agents as structured by the model, and the possible relationships between time periods. In the simplest case, A is equal to J (top timeline), which means that the only kind of behavior performed in the juvenile period is flirting, with real courtship (pair-formation) attempts starting immedi-

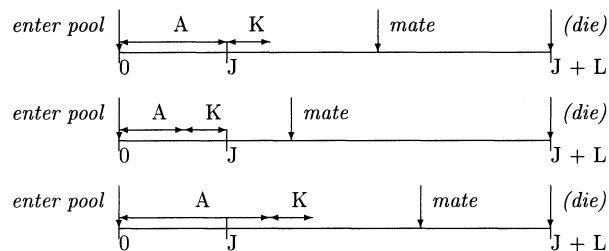


Figure 2 Possible agent life-histories: (top) juvenile period used only for flirting behavior ($A = J$); (middle) juvenile period used both for flirting and courting ($A < J \leq A + K$); (bottom) flirting behavior extends beyond the juvenile period ($A > J$).

ately after. When A is smaller than J (middle timeline), individuals are allowed to start courting before the juvenile period ends to save time and try to reap the advantages of mating earlier (i.e., sooner after the juvenile period ends). The only constraint to be maintained is that mating does not occur until the juvenile period is completed. This is implemented by simply enforcing the inequality $A + K \geq J$. Finally, when A is greater than J (bottom timeline), individuals extend flirting behavior beyond the juvenile period to try to assess more accurately their own quality. In Section 6.2, we will explore the strategic implications of using these alternative life-histories, to see whether less or more information-gathering is useful when balanced against more or less time left to reproduce once mated. As follows from the above, individuals that are unable to mate will die (and be removed from the population) when they reach age $J + L$.

5 Possible Strategies for Choosing and Switching Partners

To evaluate the success of decision rules and strategies, we assign mated individuals a fitness value $F(q_d, t) = q_d \times [(J + L) - t]/L$, where q_d is the quality of the individual's partner (date) and t is the individual's age at mating time. Thus we instantiate a payoff for high quality (rather than quality-matching), along with time pressure to mate early (in addition to the limited lifetime). The juvenile period constant J is added to the reproductive lifetime constant L , because we assume that postponing mating during J is costless. A more realistic version of the fitness function should also incorporate a dependency on the age of the partner, in

such a way that the oldest individual of the couple dictates the time available for the production of offspring (Kenrick & Keefe, 1992). To simplify matters, and because we will not address here the issue of age difference within couples, we deliberately ignore this. This has the important advantage of keeping preferences unidimensional (as discussed in Section 3.1).

Each mate choice strategy consists of two decision rules, one used when the agent is in the single state and the other in the courting or dating state. As a notational convention, all decision rules defined below for the single state will be prefixed by **S**, and for the courting (dating) state by **D**. Strategies will be prefixed by **Γ**. Thus, a strategy Γ_a is fully specified by a pair (S_b, D_c) , where b and c are identifiers (names) for the two specific decision rules in use, and a is the identifier for the strategy as a whole.

In the following sections, we introduce several decision rules that are combined in different ways to create strategies. We start by introducing a naive decision rule for the single state S_{naive} and a partner switching dating rule D_{swap} , which are combined to create a strategy named Γ_{swap} . The key feature of Γ_{swap} is that it does not require agents to estimate their own quality to make mating decisions. Next, we present a heuristic by which individuals can estimate their own quality. This heuristic is combined with two different decision rules, $S_{rational}$ and S_{frugal} , that dynamically set aspiration levels specifying the minimal quality accepted in a partner. S_{frugal} differs in character from $S_{rational}$, due to its greater simplicity and indirect estimation of environmental parameters. A dummy decision rule that never swaps partners, D_{null} , is then combined with these two decision rules to create two strategies— $\Gamma_{rational}$ and Γ_{frugal} , based purely on aspiration levels. Finally, a mixed strategy Γ_{mix} , which both uses aspiration levels and performs partner switching, is introduced. After the presentation of the strategies, we will perform a thorough evaluation of their relative performance.

5.1 Switching Partners

A naive decision rule to initiate relationships when single can be defined as follows:

$$S_{naive}(t_a) = \begin{cases} 0 & \text{if } t_a + K > J + L \\ 1 & \text{otherwise} \end{cases} \quad (1)$$

In the above, t_a is age of the prospective alternative date. The decision rule specifies that a single individual will propose to any agent encountered as long as that agent is not too old to complete courtship.

Next, given the previously defined fitness function F , we can establish the following decision rule for individuals to (try to) switch partners whenever they are already involved in a courtship process:

$$D_{swap}(q_a, q_d, c_t, t, t_a, t_d) = \begin{cases} 0 & \text{if } t + K > J + L \\ 0 & \text{if } t_a + K > J + L \\ 1 & \text{if } F(q_a, t + K) > F(q_d, t + K - c_t) \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

In the above equation, q_a is quality of the alternative partner considered, q_d is the quality of the current date, c_t the current courtship time, and t, t_d, t_a the ages of the focal individual, its date, and the alternative, respectively. The individual conditions are evaluated sequentially from top to bottom, and only when a condition does not hold will the next one be evaluated. The first and second conditions of the decision rule declare that if there is not enough time left to carry out a full courtship period (within one's own lifetime or that of the alternative), then the switch should not be attempted. The third condition declares that if the expected fitness of mating with the alternative (calculated using the total required courtship time K) is greater than the expected fitness of mating with the current date (calculated using the remaining courtship time $K - c_t$), then switching should be attempted. Finally, if none of the above conditions hold the current courtship process should continue undisturbed.

The more complete form of the third condition above would take into account the risk of the current date or the alternative abandoning the individual, but here we assume all individuals are insensitive to this risk. Specifically, fitness outcomes could be multiplied by the probability that a courtship process would be successfully completed and could also take into account the expected residual fitness (i.e., the fitness if the courtship is aborted). Making the swap decision without trying to compute all these terms goes in line with a view of agents with bounded rationality that do not bother to attempt to predict many aspects of an uncertain world and instead exploit the specifics of the

problem domain (Todd et al., 2000; Pfeifer & Scheier, 1999; Gigerenzer & Selten, 2001). In this case, we are reducing a game-theoretic problem to an individual-decision problem. This reduction might not be too problematic because an initial courting acceptance already implies some degree of certainty that the courtship will succeed. We do not make the claim that computing the likelihood of future rejection cannot be done, or that humans do not compute it, but rather that reasonably good mating decisions can be made without this extensive computation.⁴

Finally, a first strategy can be defined as: $\mathbf{\Gamma}_{\text{swap}} = (\mathbf{S}_{\text{naive}}, \mathbf{D}_{\text{swap}})$. As mentioned above, the distinguishing feature of this strategy is that it does not require individuals to estimate their own quality. Consequently, agents using $\mathbf{\Gamma}_{\text{swap}}$ remain idle during the juvenile period.

5.2 Flirting to Set Initial Aspiration Levels

We now turn to a second, slightly more sophisticated class of strategies. As we discussed in Section 3.4, when there are costs involved in entering and staying in a relationship, a natural type of strategy is for individuals to set acceptance or aspiration levels to decide whether or not to begin courting some partner. Potential partners falling below the aspiration level in quality are not sought (proposed to) as dates. Typically, this aspiration level will reflect to some extent the individual's own quality, with high quality individuals avoiding lower quality ones, and lower quality individuals having realistic aspiration levels tuned to their unfortunate lower rank. Rationally bounded agents should not be assumed to have information about their own relative quality automatically, because their rank is relative to all other individuals in the population. Instead, we model agents who must estimate their quality dynamically and use it to perform mating decisions as they go along. As mentioned earlier, the flirting period allows agents to make a first estimation of their quality and set their aspiration levels to a corresponding (here equal) level (Todd & Miller, 1999).

Specifically, an individual i starts out being totally nondiscriminating by setting their self-quality estimate q_i^* to 0. In each time step of the flirting period, i proposes to all individuals j in its interaction list that have a quality q_j greater than or equal to q_i^* (independent of whether or not it has proposed to j before, and what the outcome of such a proposal was). If a

proposal is accepted by j (i.e., matched by a corresponding proposal), and q_j is strictly greater than the current value of q_i^* , then the following update rule is used:

$$q_{i_{\text{new}}}^* = q_{i_{\text{old}}}^* \cdot (1 - \alpha) + q_j \cdot \alpha \quad (3)$$

In the above, α corresponds to the learning rate (we use the value .2 in our simulations). This updating procedure can be interpreted, metaphorically, as individuals trying to climb a ladder of qualities. At the end of the flirting period, (on average) the higher the quality of individuals the higher they have climbed in terms of their q_i^* self-estimate. Thus, due to the requirement of mutual acceptance, the final value for q_i^* will tend to approximate the actual individual quality q_i , as long as a reasonable number of individuals are met during the adolescent flirting period. This final q_i^* value is then used as an initial aspiration level after the flirting period.⁵ Because of this, we will borrow the symbol q_i^* and use it also to designate the aspiration level of an agent i after the flirting period.

Because the expectations of an individual should reflect not only its own quality but also the availability of partners, aspiration levels should be reduced whenever waiting for a higher quality partner does not pay off in terms of lost reproductive lifetime. Moreover, since the initial aspiration level might not have been properly calibrated, individuals should not be too confident about it. This means it might be advisable to attribute failure to mate after the flirting period to an inflated or inadequate value of the aspiration level—which, in turn, should prompt a drop in the value of q^* . Below, we describe two ways to perform this (downward) update of q^* . The first is based on a probabilistic estimate, which to some extent endorses the typical computation- and information-intense approach used in normative theories of decision making (Plous, 1993). The second employs a simple heuristic that dispenses altogether with such computations (Gigerenzer et al., 1999). It is worth noting that this kind of aspiration-dropping mechanism has been identified in animals other than humans. For example, female cockroaches of the species *Nauphoeta cinerea* have been found to have an internal biological clock that makes them less choosy as they get older (Moore & Moore, 2001).

5.2.1 Setting Aspiration Levels the Rational Way

A reasonable way to regulate the drop in the value of q^* over time is to try to predict the time t_w it will take for a partner of the desired quality to be obtained, and check if it pays off to wait that period instead of proposing to court a lower quality alternative already available. This computation of t_w can be done by keeping track of the (social) environment and continuously estimating relevant pieces of information, such as the rate at which individuals are met (\dot{y}), the fraction of individuals met that are single (s), and the mean and standard deviation of their quality distribution (μ, σ). To compute \dot{y} we simply divide the number of individuals met during an individual's life so far by its age (thus assuming lifetime uniformity in the meeting rate). To compute s we check the state of individuals when they are met. To compute μ and σ , we assume that the set of all individuals ever met (currently in the alternatives list or not) constitutes a representative population sample. We further postulate a range of qualities that the agent considers desirable, but still attainable, as $[q^*, \hat{q}]$, where $\hat{q} = \min[(q^* + \sigma) Q_{\max}]$ and Q_{\max} is the quality of the best individual ever observed. As a result agents still prefer others with quality of at least q^* , but do not take into account whether or not individuals are likely to reciprocate their proposals.

If agents make the assumption that qualities are normally distributed, the proportion f of individuals met whose quality falls within such an interval range can be approximated as: $f = N(\hat{q}, \mu, \sigma) - N(q^*, \mu, \sigma)$, where the function N stands for the cumulative normal distribution (with the specified mean and standard deviation). Given the definition of f , the mean meeting rate \dot{y} , and the proportion of singles s , we can thus approximate the average value for t_w as follows:

$$\bar{t}_w = \frac{1}{\rho \cdot f \cdot \dot{y} \cdot s} \quad (4)$$

where ρ corresponds to a residual uncertainty factor that measures the likelihood that the found partner will accept the courtship proposal (because its aspiration level is not higher than the agent's quality). As a simplification, we will assign ρ a constant value independent of the agent's quality (see discussion below). We can now define an update rule for q^* as follows:

$$q_{\text{new}}^* = \begin{cases} q_b & \text{if } F(q^*, t + K + \bar{t}_w) \leq F(q_b, t + K) \\ q_{\text{old}}^* & \text{otherwise} \end{cases} \quad (5)$$

In the above, q_b represents the quality of the best individual in the alternatives list whose quality is lower than q^* . This update rule essentially states that an individual will drop his/her aspirations to the level of the best known individual whenever waiting for a better alternative does not provide any fitness benefits. To be more rigorous, and compliant with expected utility maximization approaches, different values of \bar{t}_w and fitness gains could be averaged in the above equation for the different qualities within the interval range $[q^*, \hat{q}]$. Still, if we assume that \hat{q} and q^* differ only by a small amount (in the present case no more than σ), the approximation of \bar{t}_w is reasonable, because there will be little variation between the relative frequencies f of individual quality values within this small interval range.

With this update rule, and the update rule used in the flirting period, we can now define an aspiration-level-based decision rule for agents as follows:

$$\mathbf{S}_{\text{rational}}(q_a, q^*, t, t_a) = \begin{cases} 0 & \text{if } t_a + K > J + L \\ 1 & \text{if } q_a \geq q^* \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

The rule essentially states that agents will propose to any individual above the sought minimal quality, provided that they are not too old. All variables have the same meaning as before. We further define a strategy \mathbf{D}_{null} that never changes partners once courtship starts. This allows us to define a strategy based purely on dynamically computed aspiration levels, $\mathbf{r}_{\text{rational}} = (\mathbf{S}_{\text{rational}}, \mathbf{D}_{\text{null}})$.

We could further refine the update rule for q^* by introducing additional factors in the computation of the residual uncertainty ρ (e.g., the quality of the agent making the decision, an estimation of the distribution of aspiration levels of other individuals as a function of their quality and age, the accuracy of the rule used in the flirting period to estimate q^* , and others). But instead we will next pursue a different route: finding a simple but efficient update heuristic for q^* (Gigerenzer et al., 1999).

5.2.2 Setting Aspiration Levels the Simple Way An alternative approach to regulate the drop in the value of the aspiration level q^* is to keep track of the time an individual has been waiting for a partner and to lower his/her aspiration when a waiting time threshold t_{\max} is reached. This approach is more parsimonious than the one presented in the previous section, because estimating an appropriate value for t_{\max} does not require knowing environmental factors such as the meeting rate or distribution of qualities. Specifically, we will define this threshold t_{\max} as a fixed fraction κ of the maximum waiting time t'_{\max} for which there are fitness gains by mating with an individual with quality q^* rather than q_b (as defined above). Intuitively, the constant κ can be interpreted as a risk factor that specifies how much the individual is willing to bet in the attempt to court an individual with the current minimal sought quality—rather than the best (attainable) alternative that is likely to be already available to him/her. The value t'_{\max} can be computed straightforwardly by solving the algebraic equation: $F(q^*, t + K + t'_{\max}) = F(q_b, t + K)$, where t is the current age of the agent. This yields:

$$\begin{aligned} t_{\max} &= \kappa \times t'_{\max} \\ &= \kappa \times [(J + L) - (t + K)] \times \left(1 - \frac{q_b}{q^*}\right) \end{aligned} \quad (7)$$

The constant κ can be interpreted, once again metaphorically, as a risk factor that specifies how much the individual is willing to bet on its current aspiration level—the minimal quality partner sought, rather than the best (attainable) alternative that is likely to be already available to him/her. Although the above expression appears complex and therefore as difficult to implement in an agent as $\mathbf{S}_{\text{rational}}$, if we assume that evolution would endow agents with “innate” knowledge of the approximate value of the parameters J and L , then the information gathering demands on the agent are minimal. Specifically, an agent only needs to keep track of the highest quality individual seen so far.

We can now define a decision rule $\mathbf{S}_{\text{frugal}}$ as equivalent to $\mathbf{S}_{\text{rational}}$ but with the following update rule for q^* :

$$q_{\text{new}}^* = \begin{cases} q_b & \text{if } t_w > t_{\max} \\ q_{\text{old}}^* & \text{otherwise} \end{cases} \quad (8)$$

In the above, t_w represents the number of time steps an individual is waiting for a date of the minimal sought quality. Whenever the value of q^* is changed, t_w is reset to 0. A key feature of this strategy is that although statistically speaking the time an individual will have to wait for a partner of the sought minimal quality is independent of the time he/she is already waiting, this value reflects (albeit in a highly aggregate way) many relevant aspects of the social environment. Namely, it provides a summary of the effects of the quality of the agent, the accuracy of the quality estimate, the meeting rate, the availability of partners, and the lost fitness due to wasted reproductive time—all without making explicit observations or computations of these values.

Finally, a new strategy $\mathbf{\Gamma}_{\text{frugal}}$ can be defined as $\mathbf{\Gamma}_{\text{frugal}} = (\mathbf{S}_{\text{frugal}}, \mathbf{D}_{\text{null}})$. This is again a strategy based purely on aspiration levels, which never makes agents change partners after they start courtship.

5.3 Combining Aspiration Levels with Partner Switching

To investigate the advantages of combining partner switching strategies with aspiration level strategies, we define a new strategy $\mathbf{\Gamma}_{\text{mix}} = (\mathbf{S}'_{\text{frugal}}, \mathbf{D}_{\text{swap}})$. This strategy combines \mathbf{D}_{swap} with a slight variation of $\mathbf{S}_{\text{frugal}}$ in which the update rule is modified such that outcomes of broken relationships are also used in setting the values for q^* : Specifically, if an agent was previously courting and the partner took the initiative of breaking the relationship, q^* is updated to $\omega * q_d$, where q_d is the quality of the agent’s departing partner and $\omega \in [0, 1]$ is a correction factor to decrease the agent’s expectations to slightly below the quality of that partner (we will use the value .8). This procedure is likely (although not certain) to assign q^* an appropriate value, because the agent’s partner will break the relationship only to start courting a higher quality individual—and this gives a rough indication that the agent is aiming too high and is unable to retain partners of quality q_d . This will be the case whether the value of q^* goes down or goes up—as might happen when the agent was lucky getting a high-quality mate originally. Additionally, because the partner switching decision rule \mathbf{D}_{swap} gives partnerships a tentative character, it makes sense to have q^* drop in value faster by decreasing the risk factor κ in Equation 7.

6 Results—Comparing the Strategies

In this section, we investigate how the strategies just specified perform over a wide range of parameter settings, and what qualitative and quantitative aspects of those strategies explain the differences in performance. More specifically, we explore the strategic role that courtship plays in mate choice behavior, looking at the advantages of switching partners during courtship. We also ask how the simplicity of decision rules for setting aspiration levels impacts their efficiency and robustness, and what the consequences are of using combined strategies that rely both on aspiration levels and partner switching.

In Table 1, we present a summary of the model parameters with the (default) values used in the simulations and an indication of the rationale for those choices. For those model parameters where the actual value is likely to be highly contingent on the specifics of particular environmental ecologies, we present the interval ranges for which we performed sensitivity analysis. We set 10 time steps to correspond to one year. The parameters for the (quasi) normal quality

distribution were set by equating agent quality with the total number of offspring produced during a complete (female) lifetime using a data set from a particular human population, the Ache (Hill & Hurtado, 1996)—although similar values apply to other societies without significant contraceptive use. The intimacy constant I was set to 2.0 to model a quadratic reduction of interaction capabilities, which corresponds to a super-linear increase in couples' intimacy as courtship develops. Note that for the results shown in the next section, all of the strategies use a courtship period of $K = 10$, even when no swapping is allowed (in Γ_{rational} and Γ_{frugal}); this is to reflect the cost of courtship for assessing the likelihood of desertion, as discussed in Section 3.2, even though we do not explicitly model desertion here. Furthermore, we start by assuming that the flirting period A coincides with the juvenile period J , thus instantiating the first agent life-history depicted in Figure 2 (we consider other life-histories later). Each simulation was run until 20,000 agents were created, and the results shown correspond to averages across 10 runs (except when mentioned otherwise).

Table 1 Parameter settings: base values and interval ranges used in sensitivity analysis.

Parameter	Description	Value(s)	Range	Note
P	Population size/2	100	–	Small community
L	Reproductive lifetime	200	–	20 years (typical for women)
J	Juvenile period	30	–	3 years (early adolescence)
μ, σ	Quality distribution	8,2	–	No. offspring for
Q_{\min}, Q_{\max}	Lower, upper bound	4,12	–	Ache women
A	Adolescence period	30	[20, 40]	3 years (same as J)
K	Courtship time	10	[0, 40]	1 year
I	Intimacy constant	2	–	(see text)
Y	Meeting rate	.5	[.1, 1]	5 people met / year ($\times 2$, for M&F)
N	Max. size of alt. list	5	[2, 12]	No. simultaneous options

6.1 Strategy Comparison Across Parameter Settings

To compare the efficiency of the strategies, we use as a heuristic measure the average fitness ($F(q_d, t) = q_d \times$

$[(J + L) - t]/L$) of individuals with quality equal to or above average ($q_i \geq \mu$). Figure 3a shows these measures for the four strategies defined in Section 5: Γ_{swap} , Γ_{rational} (with uncertainty factor $\rho = .5$), Γ_{frugal} (with risk factor $\kappa = .3$), and Γ_{mix} (with a lower risk factor

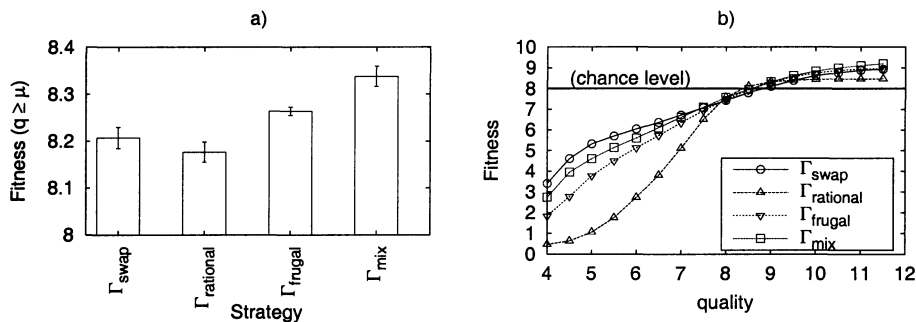


Figure 3 Fitness comparisons between the mate choice strategies. (a) Average fitness of individuals with quality above average using each strategy. (b) Average fitness of individuals using each strategy, as a function of their mate quality.

$\kappa = .1$ to take into consideration the possibility of switching partners as discussed in Section 5.3), with the parameter settings otherwise as specified in the previous section. The rationale for this measure is that more efficient strategies should move the fitness of individuals of high quality further above chance level (i.e., the level obtained by mating with the first individual encountered) than less efficient ones that select lower quality individuals. With our current parameter settings random mating would give all individuals a fitness value of about 8. In fact, as can be seen from Figure 3b, the small gains in the fitness of high quality individuals above the chance level is achieved in all strategies at the expense of a much greater reduction in the fitness of low quality individuals. Furthermore, since higher quality individuals have higher fitness they will deliver more replicas (offspring) to the next generation. Thus, the strategies that perform better for these individuals are the ones most likely to invade a population over evolutionary time. While a complete analysis of strategy performance and evolutionary stability would require a full-fledged game-theoretic analysis, because the fitness of individuals is contingent on the relative frequency of the different strategies existing in the population (Smith, 1982; Dugatkin & Reeve, 1998); here we focus on the above heuristic measurement as a considerable simplification, but still useful first step.

Figure 3a shows several important results. First, Γ_{swap} performs slightly better than Γ_{rational} . This is interesting because with Γ_{swap} , individuals do not try to estimate their own quality, but instead only try to retain partners and switch to better ones. Furthermore, Γ_{swap} performs efficiently in spite of a relatively small courtship time, along with a realistic reduction in interaction possibilities as courtship progresses.

To analyze the extent to which this result holds across parameter values, we present in Figures 4a and 4b how the performance of Γ_{swap} varies as a function of meeting rate Y and size of alternatives list N (keeping the courtship period K constant and equal to 10). As can be seen when $N = 5$ (Figure 4a), Γ_{swap} performs almost at the same level as Γ_{frugal} (and better than Γ_{rational}), for all values of Y presented—and with slightly increasing performance as Y increases. On the other hand, with $Y = .5$ (Figure 4b), Γ_{swap} requires a minimal value of $N = 5$ to reach a performance close to Γ_{frugal} —with no important changes in performance after N reaches the value 6. Thus, Γ_{swap} can work as an effective mating strategy, but at the expense of keeping track of (at least) a small number of alternatives. If agents could strategically choose which individuals to keep track of (e.g., only the ones with higher quality than the current partner), then this memory requirement could be reduced. Elsewhere we have shown that Γ_{swap} also performs rather well, in terms of producing mated pairs with high interpair quality correlation (see beginning of Section 2), for most values of Y , with very little gain from increasing courtship time beyond a small value (Simão & Todd, 2001). This indicates that Γ_{swap} allows individual individuals to make good mating decisions with reasonably few encounters. Intuitively, the power of Γ_{swap} arises from the fact that holding partners shields individuals against the uncertainty of whether or not they will be able to find better (and attainable) alternatives soon enough in the future.

Moving away, temporarily, from our focus on humans, we can see the relevance of these results on the effectiveness of Γ_{swap} for other animal species. First, the life-history of many species is such that their

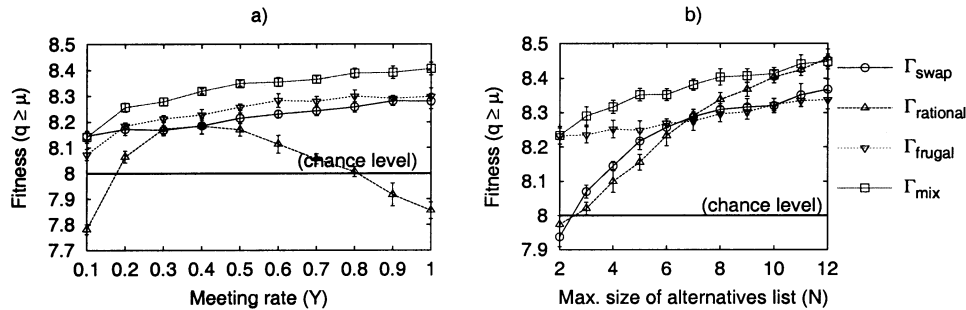


Figure 4 Average fitness for individuals with above-average quality ($q > \mu$) using the four strategies. (a) Comparing performance across changes in meeting rate Y (with $N = 5$). (b) Comparing performance across changes in maximum number of simultaneous alternatives N (with $Y = .5$).

juvenile period cannot be easily used by individuals to evaluate their own quality accurately without losing important reproductive time. This will be the case especially if an individual's absolute and relative quality varies between breeding periods—as can occur for seasonal birds (Johnstone, 1997; Alcock, 1997; Krebs & Davies, 1993). Second, the social and ecological constraints might be such that the relevant intersex interactions are too rare to allow a good estimation of one's own quality (although some animals may also rely on internal “gauges” such as health condition). Thus, aspiration-level-based strategies may not make sense for many species, but Γ_{swap} is a good alternative.

Wittenberger (Wittenberger, 1983) proposed a related mating tactic available to many animals, called the *sequential-comparison tactic*: Search for mates only until there is a drop in the quality of the next individual found, and then attempt to go back to the previous individual. If we think of previously visited individuals as tentative dates, then this strategy has some parallels with Γ_{swap} (when $N = 2$). The main difference is that the trigger for mating in the sequential-comparison tactic is finding a lower quality individual, while in Γ_{swap} a fixed courtship time is used. Because both strategies present drawbacks that the other can address—namely, Γ_{swap} requires several individuals to be met or be available during the courtship period to perform well, and the sequential-comparison strategy is prone to prolonged search times if the meeting rate is very low and might lead to bad decisions due to precocious mating—combinations of the two kinds of strategies can be envisioned (e.g., use a threshold time to find the next alternative, and use the quality of the alternatives found as a trigger for

mating). Empirical studies have indicated that some species use even more elaborate strategies, involving the sampling of increasingly restricted subsets of individuals before a choice is made (Patricelli & Borgia, 2001).

Another interesting aspect to be observed from Figures 3 and 4 is that Γ_{frugal} performs better than Γ_{rational} for many parameter values. In Figure 4b we can see that, when $Y = .5$, this holds when $N < 8$. Above $N = 8$ Γ_{rational} gains an advantage because the update rule it uses potentially changes the aspiration level q^* in every time step, and so can profit by seeing a larger and more representative pool of alternatives. In contrast to this, Γ_{frugal} only updates q^* after a certain waiting time has elapsed, and so is virtually unaffected by changes in N .

In a similar vein, Figure 4a that shows that Γ_{frugal} is very robust to changes in the value of Y , while Γ_{rational} exhibits a steep decrease in performance for values of Y greater than .5. This is somewhat surprising given the fact that the strategy directly estimates this meeting rate itself (see Section 5.2.1). But because the increased meeting rate makes all individuals more picky, waiting longer before lowering their aspiration levels (see Equation 4), this reduces the likelihood that the alternatives an agent meets that match or surpass its aspiration level will accept the agent in turn. It turns out that assigning a constant value to the uncertainty parameter ρ in Equation 4 is insufficient to implement a good strategy across the range of values for Y . The value $\rho = .5$ chosen at the beginning of this section provides the best performance for $Y = .5$, but for higher values of Y we found that smaller values of ρ deliver better performance. On the other hand, for small values of Y , higher values of ρ perform bet-

ter. This shows that Γ_{rational} is very sensitive to proper settings of ρ .

A tentative conclusion to derive from these results is that Γ_{rational} , by trying to guess what the future might bring in terms of partnerships, becomes very sensitive to variations or errors in the estimation of the wide range of factors involved in this calculation. As mentioned, this could be remedied by taking into account more factors in the computation of the parameter ρ in Equation 4, in a sense creating a more complex (implicit) model of the world. This would require, though, that agents collect even more information (unless a fixed value of ρ is adequate for all parameter values, or environmental settings, the agent might be exposed to). Not only would this be temporally and computationally expensive, it would also be highly prone to overfitting (Gigerenzer et al., 1999). Γ_{frugal} , on the other hand, by exploiting the information available in a single good piece of evidence—the time the agent is waiting for a partner—becomes robust to possible environmental fluctuations.

A further key aspect to draw from Figure 3a is that Γ_{mix} , by combining the advantages of $\mathbf{S}_{\text{frugal}}$ in setting minimal aspiration levels with the ability to swap partners during courtship as directed by \mathbf{D}_{swap} , is able to outperform the individual use of these rules in the two strategies Γ_{frugal} and Γ_{swap} . From Figures 4a and 4b, we can see that this result is robust across changes in Y and N . Intuitively, Γ_{mix} performs better because setting aspiration levels allows low-quality individuals to be avoided, while swapping allows the agent not to be too picky about the quality of the first accepted partner because of the possibility of later switching to a better partner. This result suggests that delaying mating with courtship—often interpreted in formal models of mating behavior solely as a signal of male commitment (Dawkins, 1976/1990; Schuster & Sigmund, 1981; Mylius, 1999; Wachtmeister & Enquist, 1999)—can also be used effectively (by both sexes) for mate selection. Moreover, given the dual composition of Γ_{mix} and its good performance, it might be argued that (at least for complex social species like humans) mate choice behavior and its underlying psychological mechanisms could be composed of not just one strategic component, but several elements which are activated in different periods or contexts in the individual's life. Together, the combination of these elements is orchestrated to produce

effective lifespan mating behavior. Although in this article we explore only strategic behavior that lasts until the time of first mating, we are currently working on further models of mate choice that extend the time frame under consideration (e.g., including rules to decide if a partner should be deserted once offspring have been produced). (See Simão & Todd, 2002, for further analysis of robustness of model results.)

6.2 Testing the Utility of Courtship with Alternative Life-histories

In the previous section, we found that being able to switch partners during a courtship period is superior to courtship without partner switching (that is, Γ_{mix} outperformed Γ_{frugal} and Γ_{rational}). This was not so surprising, as being able to swap upward in mate quality should clearly be beneficial. But that result did indicate another adaptive role for courtship—holding on to good potential mates, at least until a better one is found—beyond the usual proposal of courtship for testing male fidelity (see Section 3.2). Here we want to test this role for courtship more thoroughly, asking whether the ability to hold and switch partners can actually make using a courtship period better than not using any courtship period. That is, we will compare the mixed strategy Γ_{mix} with a courtship period including partner switching, against a variation of the Γ_{frugal} strategy that needs no courtship at all and just allows individuals to mate immediately after the juvenile period. Can delaying mating via courtship possibly outperform immediate mating, given the time cost paid by the former? If so, then we can infer that courtship can have an important strategic role in mate choice through the possibility to hold good partners and switch to better ones, in addition to its usefulness in assessing mate “honesty” (intention of not deserting after mating).

To test this question, we introduce two strategy variants that draw upon the different life-histories presented in Figure 2. First, we define the strategy Γ_{frugal}^- to be equivalent to Γ_{frugal} ($\kappa = .3$), but with the courtship period removed by setting $K = 0$ (thus corresponding to a degenerate case of the first life-history presented in Figure 2). Second, Γ_{mix}^- is defined as equivalent to Γ_{mix} ($\kappa = .1$), with the exception that it makes use of a reduced flirting period $A = J - K (= 20)$ so that courtship can begin while individuals are not

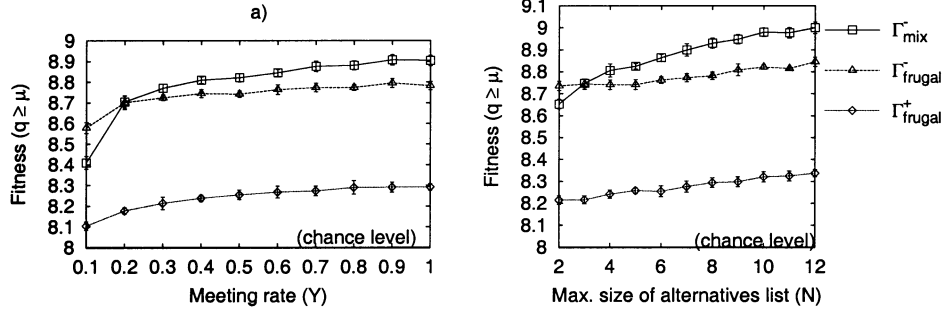


Figure 5 Average fitness for individuals with above-average quality ($q > \mu$) using four variant strategies. (a) Comparing performance across changes in meeting rate Y (with $N = 5$). (b) Comparing performance across changes in maximum number of simultaneous alternatives N (with $Y = .5$).

yet fully mature (thus corresponding to the second life-history presented in Figure 2). This means that Γ_{mix}^- does not pay as big a cost in terms of mating delay as would Γ_{mix} (otherwise there are no benefits of delaying mating and using the courtship period to switch partners—compare the plots for Γ_{mix} in Figure 4 where the fitness values are for most parameter setting below 8.4 with those in Figure 5 for Γ_{frugal}^- where the values are higher than this). With these two strategies, we can compare mate choice without courtship (i.e., beginning immediately following the juvenile period) using Γ_{frugal}^- with mate choice including courtship and partner switching using Γ_{mix}^- .

Figures 5a and b depict the performance of the strategy variants Γ_{mix}^- and Γ_{frugal}^- (along with Γ_{frugal}^+ , which is described below), as a function of Y (with $N = 5$) and N (with $Y = .5$) as in Figure 4. As can be seen, for all values of $Y \geq .2$ and $N \geq 3$, Γ_{mix}^- always performs better than Γ_{frugal}^- . Only for very low meeting rates does the Γ_{mix}^- strategy of courting and partner switching not prove beneficial. This is an important result, because it indicates that even in the ideal case where no courtship is required to evaluate the commitment of potential mates (i.e., here with $K = 0$), the costs of courtship in terms of delayed mating can still be outweighed by its benefits in finding and switching to better partners. In other words, courtship can serve not only the function of selecting for honest mates, but also selecting for good mates. Thus, models of the *battle of the sexes* (see Section 3.2) and models of sequential mate choice can profit from integration into more complex and realistic theories of reproductive behavior.

Finally, we can ask whether simply extending the adolescent flirting period (A) of Γ_{frugal}^- could make

this courtship-less strategy outperform the Γ_{mix}^- strategy with courtship. Will the opportunity to learn longer and set a better informed aspiration level be as effective as the opportunity to hold onto and switch partners during courtship? To find out, we created the strategy Γ_{frugal}^+ , defined to be equivalent to Γ_{frugal}^- but with an extended flirting period $A = 40$ (and still with $K = 0$). This strategy corresponds to a degenerate case of the third life-history in Figure 2. By comparing the performance curves of Γ_{frugal}^+ and Γ_{frugal}^- in Figure 5 with those of Γ_{frugal}^- in Figure 4, we see that extending the flirting period beyond the juvenile period (using time otherwise used for courtship) is not particularly advantageous. This is because only a small number of encounters are required for reasonable set-up of the aspiration level, and therefore Γ_{frugal}^+ delays mating unnecessarily. Note that this is in contrast to the findings of Mazalov et al. that longer learning leads to better mate choice (Mazalov et al., 1996). This result indicates that partner switching during courtship plays a qualitatively different role from just obtaining better estimates of one's own quality during an equivalent time period.

7 Testing Model Predictions

Now that we have compared the performance of plausible mating strategies, the next step is to use our model to generate predictions about human relationship patterns and evaluate those (whenever possible) against known empirical evidence. It is also of interest to inspect the concordance (or not) between the model predictions and those of more informal theories presented in the social sciences literature. Due to its high

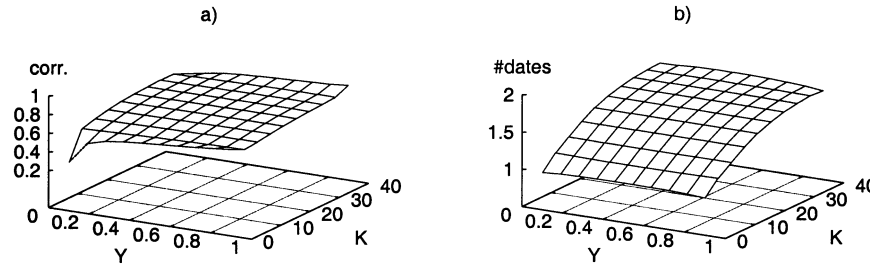


Figure 6 Predictions of the model across a range of settings for parameters Y (meeting rate) and K (courtship time). (a) Correlation of qualities in mated pairs. (b) Mean number of courtships before mating.

performance, robustness, and plausible psychological assumptions, we will take the strategy Γ_{mix}^- as a reasonable candidate to model human behavior (at the level of abstraction of interest to us). In the rest of this section, we use Γ_{mix}^- with the same base parameter settings as specified at the beginning of Section 6.

Figure 6a depicts the linear correlation between the qualities of individuals in mated pairs as a function of rate-of-meeting Y and courtship time K . The results show, as intuitively expected, that the more alternatives individuals are meeting (as $Y \times K$ gets bigger), the more likely they will mate with an individual close to them in quality. In fact, only very small meeting rates and courtship times are required to produce the reasonably high correlation coefficients empirically observed (mostly between .6 and .7) in sampled human populations (Kalick & Hamilton, 1986). This suggests that individuals are making good use of their mating potential even though they have no initial, direct knowledge of their own mate value.

Figure 6b shows the mean number of dates individuals engage in—including the very last one—until they settle down and mate (again as a function of Y and K). Our results show that for a wide range of parameter values most individuals mate with rather little search. For example, with $K = 8$ and $Y = .2$, we found that 98% of the individuals in the population were able to mate (and reach a correlation of qualities of .54), even though they only went through a small number of dates—1.26 on average. These findings are in accord with demographic data—it is estimated that in most human populations from 85 to 95% of the individuals are able to mate at least once in their lives (typically under the official seal of the marriage institution) (Coale, 1971; Fisher, 1989; Buss & Schmitt, 1993; Kalick & Hamilton, 1988). While the mean number of individuals courted may seem low, the

actual distribution should be compared with data from societies without contraceptive use, something we are still looking for. In any case, it should be stressed that the model’s realistic combination of statistics—reasonably high correlation of qualities in mated pairs, most of the population being able to mate, and low number of courtships—was never obtained with previous models of human mate choice (Kalick & Hamilton, 1986; Todd & Miller, 1999).

Our simulations also gave some indication that the average duration of terminated relationships is negatively correlated with the difference in quality between courting partners, as one might expect. To more clearly highlight this trend, we run a simulation with a much higher number of runs—50. In Figure 7a, we show the results for a particular setting of $Y (= .5)$ and $K (= 10)$. We can see that the higher the difference is in the qualities within a couple, the more unstable (less durable) the relationship is. Moreover, if individuals differ too much in quality they will never court. (The absolute quality of individuals taken alone is a less important predictor of the duration of relationships.) Similar findings were obtained in a number of empirical studies (see Kalick & Hamilton, 1986, for a short review).

On a more theoretical level, this result matches insights from well-established (but nonformal) social psychology theories about factors underlying satisfaction and stability in relationships, such as the theory of interdependence in close relationships and its extension, the *investment model* (Berscheid & Reis, 1998; Rusbult, Martz, & Agnew, 1998; Rusbult & Buunk, 1993). In this theory, three factors are identified as associated with commitment to a relationship, and consequently its stability: *satisfaction*, *quality of alternatives*, and *investment*. Subjective satisfaction and investment are known to be positively correlated

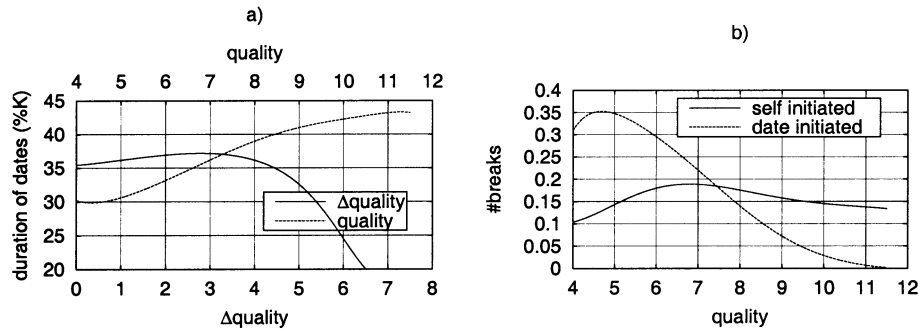


Figure 7 Relationship stability. (a) Average duration of relationships; (b) Average number of breaks ($K = 10$; $Y = .5$).

with relationship stability, while quality of alternatives is negatively correlated. Although in Rusbult's investment model these three factors have a broad holistic interpretation and they have not been interpreted as aspects of individual adaptive strategies for finding good mates, our model suggests that such an interpretation is reasonable. As depicted in Figure 7a, the relative quality of alternatives (compared to the current partner) is the most important variable in controlling partner switching behavior—and therefore the termination of relationships. Furthermore, if we equate courtship time in our model with investment, then we can also functionally explain the positive correlation between an individual's investment in a relationship and their commitment to maintain that relationship. Regarding the degree of satisfaction in relationships, it is empirically known that intensity of romantic feelings is higher when an individual perceives his/her partner as more attractive (Bunk, 1996; McKnight & Phillips, 1988). This is consistent with an evolutionary functional interpretation, such as the one we endorse here, where individuals seek and have a preference for high quality partners.

We also found that in our model, as expected, lower quality individuals are more likely to be “dumped” by their partners, with higher quality individuals taking the initiative of breaking relationships (Figure 7b). Furthermore, lower quality individuals on average need more courtships and more time to find a mate. This is because these individuals are more likely to be courting somebody with a higher quality, who will often take the initiative of breaking off the relationship.

8 Discussion and Future Work

In the previous sections, we presented a detailed performance analysis of alternative mating strategies and selected the most efficient one as a tentative candidate to explain (part of) human mating behavior. Methodologically speaking, we embraced an iterative processes of designing and evaluating plausible psychological mechanisms as an attempt to reverse-engineer the functional structure of the mechanisms making up the human mind. This approach goes very much in the programmatic direction of *evolutionary psychology*, in the strict sense defined by Tooby and Cosmides more than one decade ago but still little explored (Tooby & Cosmides, 1989).

Our results show that our model better fits empirical data concerning patterns of human mating than do previous models. Our model demonstrates that individuals can make successful mating pairs after a relatively few encounters with potential mates. In contrast, Kalick and Hamilton's attractiveness-preference model requires a high number of courtships (or at least individuals met) to achieve a realistic intracouple quality correlation and a realistic proportion of mated individuals (Kalick & Hamilton, 1986). This is because individuals in their model do not try to estimate their mate quality and use it in tuning their (probabilistic) aspiration level. Still, our model confirms Kalick and Hamilton's intuitions that a great deal of assortative mating in human populations can be explained by a common preference for the most attractive or “best” mates (also called “type” preferences). This does not exclude the possibility that for some quality dimensions there may be “homotypic” or “like prefers like” preferences instead (e.g., height, Ellis, 1992).

In our model, most individuals are able to find mates. Todd and Miller's model only produced unrealistically low proportions of individuals mated (Todd & Miller, 1999), because the aspiration-guided individuals miss too many opportunities, rather than taking an initial mate and possibly swapping later to a better one. Individuals in our simulations used simple heuristics to learn about the qualities of available partners during mutual search with unknown costs and no fixed time horizon. The learning model of Mazalov and colleagues concerned optimized single-sex searching with no search costs, fixed environmental distribution of mates, and known search time (Mazalov et al., 1996). Finally, while Johnstone's model produces statistics similar to ours, this is only accomplished by giving individuals initial knowledge of the distribution of qualities in the population and their own exact quality, and by assuming that the cost of waiting or searching for a potential partner is constant (Johnstone, 1997).

Beginning with such unrealistic assumptions does not allow us to learn much about the actual design of the psychological mechanisms regulating mating decisions. Our model and the strategies described here, on the other hand, rely on plausible socio-ecological assumptions and feasible psychological designs. In particular, we found that the use of ecologically valid information such as "waiting time" allows individuals to make efficient and robust decisions without requiring substantial information gathering or computation. Moreover, the possibility of switching (tentative) partners during courtship periods adds to the mating success of individuals. Overall, our methodological commitment to psychologically and environmentally plausible mate choice mechanisms allowed us to make a set of substantial predictions that matched empirical data, and thereby better understand the nature of the adaptive problem.

We are currently working to develop further our conceptual framework of human mate choice and to extend our model in several directions. First, we are interested in studying the nature of preferences and the effect of including extra preference dimensions in the models (e.g., age of partners). Multi-dimensional preferences are likely to make it harder to set up appropriate aspiration levels, because different rules will apply to different dimensions and trade-offs will often be involved. Therefore, we expect to find that the complementary ability to switch partners during

courtship is even more advantageous in this case. This is, because the trade-offs in different dimensions can be made based on comparisons between specific pairs of values (the values of the current partner and the alternative), instead of trying to estimate appropriate aspiration levels for all dimensions by taking into account what the future might bring. Second, because partnerships frequently do not last for the complete reproductive period of individuals—for example, people get divorced—we are currently working on a model that includes strategic behavior beyond the first mating and is conditional on the number and paternity of existing offspring (and can also be affected by contraceptive use). We also aim to explore the conditions in which different mating systems characteristic of human populations emerge, and the extent to which cultural distinctions and similarities can be captured in a broader model.

9 Conclusions

In this article, we have shown how an evolutionary (functional) analysis of mate choice can be combined with an agent-based modeling approach to gain insights into the processes underlying human sexual/romantic relationships. In particular, by building extended courtship processes, the ability to switch partners, and other key aspects of the mating game into our model, we have accounted for existing data and generated predictions in ways unattainable by earlier models or verbal theories. We hope that our work will motivate further research on more realistic and informative models of the psychological mechanisms underlying social behavior in humans (and other species). This should in turn help social psychology to escape the dangers of theory-blind empiricism and turn more to theory-guided experiments. Finally, we hope that the design and engineering insights that come from building computational models will help push forward a new view of ecologically rational social cognition: social beings as effective decision makers using simple mechanisms tuned to specific environmental contexts, rather than as general-purpose utility-maximizing calculators pounding at all social problems with the same big stick.

Notes

- 1 This would also require the additional modification of not replacing mated individuals, so that the breeding pool shrinks over time (see Section 4).
- 2 Since the rule is applied to both sexes, the average number of individuals met in each time step by each agent is in fact $2 \times Y$.
- 3 An alternative and more realistic way of modeling this differential meeting probability is to do it explicitly by having two different meeting rates. We will use only one to keep the set of model parameters to manageable size.
- 4 It is possible for instance to imagine a decision mechanism that will tend to accept dates of higher quality (despite the higher risk of later abandonment), unless reliable information about future rejection becomes available.
- 5 Similar kinds of heuristics are presented in (Todd & Miller, 1999), but these also use information from encounters that are unlikely to happen in the real world (namely, those where neither of the parties is interested in flirting or courting). Moreover, these heuristics are not combined with other update rules that regulate the drop in value of q^* to compensate for wasted reproductive lifetime if partners are not found (as we do below).

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