Mating games: the evolution of human mating transactions

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We propose a new, evolutionary, game-theoretic model of conditional human mating strategies that integrates currently disconnected bodies of data into a single mathematically-explicit theory of human mating transactions. The model focuses on the problem of how much resource a male must provide to a female to secure and retain her as a mate. By using bidding-game models, we show how the male's minimally required resource incentive varies as a function of his own mate value, the value of the female, and the distribution of the mate values of their available alternative mates. The resulting theory parsimoniously accounts for strategic pluralism within the sexes, mate choice differences between the sexes, and assortative mating, while generating a rich set of testable new predictions about human mating behavior. *Key words:* assortative mating, evolution, game theory, human mating, mate choice, mating strategies. *[Behav Ecol 15:748–756 (2004)]*

Sexual selection theory (Darwin, 1871) has recently been used by a number of evolutionary thinkers to explain men's and women's particular, and often conflicting, mating strategies (see Buss, 1994; Buss and Schmitt, 1993; Gangestad and Simpson, 2000). In this article, we extend such work by developing a set of mathematically explicit game-theoretic models of mate choice between potential mates. Our quantitative models incorporate evolutionarily-relevant contextual cues (phenotypic quality, resources, and outside options), into game theoretic models designed to generate the evolutionarily stable strategy (ESS) for mating transactions at specific moments in time. Using the concept of the ESS and game theory allows us to predict the evolved solution (specific mating behaviors of men and women based on their contextual particulars) to the adaptive problem of constrained mate choice in humans (Dugatkin and Reeve, 1998; Maynard Smith, 1982; Parker and Maynard Smith, 1990).

Indeed, we are not the first theorists to explore human mate choice in terms of transactions involving specific exchanges and tradeoffs between men and women. Many psychologists have used verbal models based on evolutionary theory and marketplace analogies to derive predictions about human mating behavior (see, for instance, Baize and Schroeder, 1995; Buss and Schmitt, 1993; Frank, 1988; Gangestad and Simpson, 2000; Green et al., 1984; Harrison and Saeed, 1977; Li et al., 2002; Murstein, 1972; Noë et al., 2001; Pawlowski and Dunbar, 1999; Regan 1998a; Thornhill and Thornhill, 1992). However, men's and women's mating strategies are highly variable, responding to a number of important interacting contextual cues. Verbal models can be an unreliable guide to understanding such phenomena as such models are not well equipped to solve the outcome of complex interactions rigorously. Furthermore, because the predictions generated from a verbal model are not quantitative, they can contain a number of hidden assumptions that are exposed in explicitly quantitative models, putting weak constraints on what predictions a verbal model generates. In

the following, we present quantitative models that both formalize the conclusions that these investigators have reached on more intuitive grounds, in addition to generating new predictions about human mating behavior.

In our integrated models, an individual's optimal mating strategy at a given moment is derived via game theoretic models that incorporate the following variables: (1) the total value of the focal male (the sum of his resource holdings and phenotypic quality), (2) total value of the focal female (the sum of her resource holdings and phenotypic quality), (3) the distribution of values of each sex's competition, (4) the distribution of values in the pool of alternative mates, and on (5) any environmental inputs such as the ease with which new mates are found, the ease with which males can generate resources to provide to females, or the relative importance of phenotypic quality and resources for offspring success in a given environment. In each of our models, males exert control over their desirability to females by regulating the amount of resources offered to potential mates both as a function of their own attractiveness and the overall mate value of the female. Because male resource offerings to females clearly affect female mating decisions and are necessarily under the control of those males, both male and female fitness are necessarily intertwined in mating transactions. In other words, the best strategy for one depends on the action simultaneously taken by, hence the best option for, the other, and a formal game-theoretic analysis is required to reveal the ESSs (here equivalent to the Nash equilibria) for both sexes.

The following theory is, to our knowledge, the first set of mathematical models developed for a comprehensive understanding of the evolution of human mating strategies. Moreover, although in its first stage of development, the models parsimoniously unify our understanding of previously disconnected empirical data on human mating and generate a rich set of testable predictions. Indeed, the models also may be tested in any species in which males transfer resources to females so as to secure fertilizations with those females.

GENERAL FEATURES OF THE MODELS

The models that follow yield specific predictions about human mating behaviors based on the assumption that natural selection has equipped humans' cognitive architecture

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with algorithms designed to facilitate behaviors that maximize net fitness benefits in light of everyone else's behavior. The variables incorporated into these models are heritable phenotypic mate quality, q, and resources, R, both of which may vary over an individual's lifetime and are of great import to offspring success (Buss, 1998; Møeller et al., Thornhill and Møeller, 1997; Trivers, 1972). Indeed, these qualities reflect characteristics by which men and women assess mate quality (Borgerhof Mulder, 1988; Buss, 1989; Kenrick and Keefe, 1992; Voland and Engel, 1990; Waynforth and Dunbar, 1995).

In our mating transaction models, the focal male is assumed to have a heritable phenotypic quality, q_m and the focal female is assumed to have a heritable phenotypic quality, q_f. If reproduction were to ensue between these individuals, these qualities would combine additively in determining offspring success. Although these qualities are defined as those that sum up to determine potential offspring success and thus are actually equal to one-half the parental qualities as defined in conventional quantitative genetics theory (Falconer, 1981), we will suppress the coefficient of ½ for notational convenience. In addition to these heritable qualities, the male can generate and invest a given amount of resources, R_m, in the female and any potential offspring at a cost, zR_m, to himself, where z is a coefficient inversely related to the male's resource generating efficiency. When a male chooses to invest amount R_m of his resources in a particular female, that investment has the potential to increase their offspring success by an amount vR_m. Here, v is a coefficient that converts the amount of resource investment to the expected increase in offspring success; thus vR_m, similar to q, is in units of offspring success.

The cost of resource investment by the male is generated by his loss of additional mating opportunities resulting from the reduction in amount of resources to invest in other mates, loss of time to invest in seeking additional mates, as well as by survival costs involved in resource acquisition. Resources, consequently, can be best thought of as anything that imposes a fitness cost on the investing male and benefits the male's mate and her offspring, such as time, work directed at acquiring resources, money, food, and demonstrations of parental care (Trivers, 1972). The female also possesses an amount of resources, R_f, all of which she is assumed to invest in the offspring of her chosen mate. In this article, we make the simplifying assumption from basic sexual selection theory that, although a male may be favored to reserve resources to use for acquiring other mates (because male reproductive success increases with an increasing number of sex partners), a female will invest all of her resources directly or indirectly in her offspring (because female reproductive success increases weakly or not at all with an increasing number of mates; Bateman, 1948; Trivers, 1972). In a later article, we will examine the results associated with relaxing this assumption, although it doesn't change any of the major predictions of this simplified model (Hill SE and Reeve HK, in preparation).

Investment decisions

Once a male or a female piques the interest of a potential mate, a decision must be made by each party whether or not the other is a potentially suitable mate. The male must assess the female's mate value and determine whether it is worth his while to offer a resource incentive sufficient to prevent her from mating with an alternative male with whom he is, or could potentially be, in competition. The female, conversely, must assess this bid relative to bids potentially available elsewhere to determine whether she should accept or reject this male's offer. A male's resource bid for a female is assumed

to come at the expense of opportunities to mate with additional females, and a female's decision to accept the bid is assumed to prevent her from capitalizing on outside mating opportunities.

The models developed below generate predictions about human mating behavior at particular moments in time based on assessments of cumulative future fitness. Thus, the values of all of the variables are potentially time-dependent, that is, conditioned upon the time period t. For example, a female's heritable phenotypic quality, q_f, acts as a function of her age, which is dependent on time, t, yielding $q_f(t)$ as her time-indexed phenotypic quality. Here, the amount of resource that the male is favored to invest will be influenced by the fact that female quality rapidly declines with age owing to decreasing probability of successful pregnancy. Thus, the values of each of the parameters, such as quality, should be viewed as time-dependent integrals over all future reproductive episodes, for example,

$$q_f(t) = \int_t^T Q_f(x)dx.$$

Here, $Q(x)$ is the age-specific quality of offspring that the couple could potentially have at time x, and T is the female's lifespan. This is appropriate because selection should act to maximize the present and future fitness consequences of any behavioral decision. Similarly, the duration of resource flow from the male to the female is expected to be conditioned by t, as the evolutionarily stable amount of resource investment is expected to change over time. This dynamic structure of our models allows them to serve either as models of pair formation or as pair maintenance, because the latter are distinguished only by the time period t. Henceforth, we suppress t in our notation but stipulate that the values of all variables refer only to specific moments in the ontogeny of a pair bond. In a separate article, we shall use this dynamic formulation of our models to construct a comprehensive theory of the evolutionarily stable duration of pair-bonds.

Model 1: two males bidding for one female (2 × 1 model)

In our first model, we will look at a case in which there are three interacting potential mates, two males and one female. The 2 × 1 model is solved by examining the outcome of the female assessing the bids of the two highest value males available to her. The bidding males have genetic qualities q_m and q_m', and the female has genetic quality q_f. We assume for simplicity that the female will pair with one of the two bidding males. By convention, we specify that the "primed" variables refer to the "losing" male. Each male can generate and invest a given amount, R_m (or R_m'), of resources in the female at a cost, zR_m (or $z'R_m'$), to himself. A male offering a resource investment of the amount R_m to a female has the potential to increase offspring success by vR_m. The female possesses an amount of resource R_f, all of which is available to invest in increasing her offspring success.

In the 2 × 1 model, the resource incentive offered to the female will be determined by a bidding contest between the males. The winning male will always be the male who can still profitably bid higher than can the male whose bid is so high that he breaks even. It is thus that the female will always end up with some amount of resources from the winning male in the 2 × 1 (see Expression 8, below). It is not necessary for the males to know each other in order for a bidding game to take place, although each is necessarily aware of the presence of the other. This information is available to the male either by monitoring the behavior of the female or by actually empirically observing the female with the counter-bidder.

The fitness change of the first (winning) male if he mates with the female is equal to

$$q_m + q_f + vR_m + vR_f - zR_m \qquad (1)$$

and that of the losing male if he were to mate with the female is equal to

$$q'_m + q_f + vR'_m + vR_f - z'R'_m. \qquad (2)$$

To predict who the winning male will be, we must first determine the amount of resources, R'_m, that would cause the second male to break even by equating expression 2 to zero and solving for R'_m. In doing so, we obtain

$$(q_f = q'_m + vR_f)/(z' - v). \qquad (3)$$

Next, we substitute the latter maximum bid of the second male into the expression for the female's fitness if she chooses to mate with him, that is,

$$q'_m + q_f + vR'_m + vR_f \qquad (4)$$

to obtain

$$z'(q_f = q'_m + vR_f)/(z' - v). \qquad (5)$$

The first male must be willing to provide enough resources to make the female's fitness for mating with him just slightly above her fitness, as given by Expression 5. The female's fitness for mating with the first male is

$$q_m + q_f + vR_m + vR_f. \qquad (6)$$

Thus, we find the resource incentive given by the winning male by equating Expressions 5 and 6 and solving for R_m. This resource incentive is equal to

$$\frac{\frac{z'(q_f + q'_m + vR_f)}{z' - v} - q_f - q_m - vR_f}{v}. \qquad (7)$$

The resource incentive will increase as (1) the winning male's quality (q_m) decreases, (2) the female's quality (q_f) increases, (3) the losing male's quality (q'_m) increases, (4) the female's own resource (R_f) increases, and (5) the losing male's resource generating efficiency increases (i.e., z' decreases) (Table 1).

The intuitive reasons for the above effects are as follows. Decreasing quality of the focal male (q_m) means that the female will require more resources (R_m) from the focal male if she is to be favored to choose him. Similarly, the higher the quality of the second male (q'_m), the more resources (R_m) our female must receive from the focal male if she is to be favored to choose him. Females of higher quality are expected to receive a larger resource incentive because both males will be willing to bid more for a higher-quality female, and the males must be able to out-bid one another to reap the benefits therein.

Similarly, a female with more of her own resources will command a higher winning resource bid. This effect occurs because of the lesser fitness impact the male's resources will have on such a female, making her more difficult to impress. Lastly, when the second male is more efficient at generating resources (has a low $z'R'_m$), we expect that he will increase the maximum possible resource bid and thus the magnitude of the matching bid by the winning male. The male able to provide the female with a larger sum of total quality while still increasing his fitness will be the winner, whereas the male who breaks even first will have to seek a less costly mate.

We can calculate each male's maximum profitable bid (as we did for the second male in Expression 3), and compute the fitness difference to the female that would result from mating with the first versus second male, given that the males are making their maximum profitable bids. From the resulting

Table 1

Effect of model parameters on magnitude of the female's resource incentive in the 2 × 1 model

Variable	Derivative of resource incentive on variable	Sign	Effect of increase on resource incentive magnitude
q_m	$-1/v$	−	Decrease
q_f	$1/(z' - v)$	+	Increase
q'_m	$1/v + 1/(z' - v)$	+	Increase
R_f	$v/(z' - v)$	+	Increase
Z	0	0	No Effect
Z'	$-(q_f + q'_m + vR_f)/(z' - v)^2$	−	Decrease

difference, it can be inferred that the winning male will always be the one with the higher total value, which equals of the following quantity:

$$q_m + \frac{v(q_m + q_f + zR_f)}{z - v}. \qquad (8)$$

As is intuitive, Expression 8 predicts that the higher-quality male (higher q_m) and the male with greater resource potential (low z) will tend to be the winner. When these two criteria are in conflict (i.e., one male has a higher quality, q_m, but the other male has the lower resource holding potential, higher z), it also follows from Expression 8 that the female will give greater relative weight to the male's genetic quality in her choice when resources less strongly affect offspring success (e.g., in areas where there is a high pathogen load) than does her mate's genetic quality (i.e., v low) and vice versa.

The mate constancy theorem

The 2 × 1 model predicts that the total value of the female's mate will be constant, depending only on her own value, the cost associated with leaving, and the value of the losing male. Let V_m ($=q_m + vR_m$) be the total value of the female's mate and V_f ($=q_f + vR_f$) be the total value of the female herself. Substituting expression 7 into V_m and rearranging yields

$$V_m = (vV_f + z'q'_m)/(z' - v) \qquad (9)$$

This mate constancy theorem (MCT 1) arises because males adjust the amount of resources they invest depending on the value of the female and their own genetic quality. The opposing effects of a male's quality and the amount of resources he must yield exactly cancel to yield a fixed total value for each female as a function of her total value, V_f.

Positive assortative mating with respect to total mate value
The MCT for the 2 × 1 model predicts that the total value of a female's mate will positively covary with her own value (as V_f increases, V_m increases). Thus, the 2 × 1 model predicts positive assortment of mates with respect to total value.

Conditions for yielding a resource incentive (male strategies)
As mentioned in the previous model, males, similar to females, are not expected to be interested in pursuing every potentially available mate. Thus, we must again determine the conditions under which the male should feel inclined to yield a positive resource incentive. We know from Expression 7 that a male who wants to win a 2 × 1 bidding war must provide some amount of resource incentive to the female.

Thus, we must next ask what the conditions are under which a given male should attempt to win the favor of a female by making this required bid. Predicting when a male is expected to bid a resource incentive is equivalent to knowing when his fitness change is positive (given that the male provides the resource incentive in Expression 7). The resulting expression is cumbersome, but its analysis yields the following predictions. The male should be increasingly likely to yield a resource incentive when (1) his own quality increases (q_m), (2) the female's quality (q_f) increases if $z < z'$ and as her quality decreases if $z > z'$, (3) the quality of the losing male (q'_m) decreases, (4) the resource generating potential of the losing male decreases (z' increases), and (5) the resource generating potential of the winning male increases (z increases).

Model 2: two females bidding for one male (1×2 model)

In our second model, there are again three interacting potential mates; however, this time our players are two females and one male. As will be further discussed below, this model is rarely expected to occur in typical human mating systems, except in cases in which there is a female-biased sex ratio or marked social inequality leading to hypergyny. The 1×2 model is solved by examining the outcome of an opportune male assessing the bids of the two highest valued females available to him. The bidding females have genetic qualities q_f and q'_f, and the male has genetic quality q_m. We again will specify that the "primed" variables refer to the losing female. As in all previous models, the male can generate and invest a given amount of resources, R_m, in either female at a cost, zR_m, to himself. As before, a male choosing to invest amount R_m of his resources in a female has the potential to increase offspring success by amount vR_m. In addition to this, the females possess amounts of resource R_f and R'_f, respectively, all of which are also available to invest in the male's offspring.

In the 1×2 model, the resources offered to the winning female will be determined by a bidding contest between the two females. Here, each female will reduce the magnitude of the resources demanded until the losing female can no longer afford to accept a lower resource incentive from the male. As was the case with our 2×1 model, it is not necessary for the females to know each other in order for such a bidding game to take place, although each is necessarily aware of the presence of the other. This information is available to the females either by monitoring the behavior of the male or by actually empirically observing the male with the counter-bidder.

The fitness of the first (winning) female if she mates with the male is equal to

$$q_m + q_f + vR_m + vR_f \qquad (10)$$

and that of the second (losing) female if she were to mate with the male is equal to

$$q_m + q'_f + vR_m + vR'_f. \qquad (11)$$

If the second female instead leaves the male, her expected fitness is

$$y[q'_m + q'_f + vR'_m + vR'_f]. \qquad (12)$$

The parameter y describes the female's probability of finding another mate should she leave.

Thus, to predict who the winning female will be, we must first determine the minimum amount of resources, R_m, that the male can provide that will cause the second female to break even. We can obtain this amount by equating Expressions 11 and 12 and solving for R_m. In doing so, we obtain

$$\frac{y[q'_f + q'_m + v(R'_f + R'_m)] - q'_f - q_m - vR'_f}{v}. \qquad (13)$$

Next, we substitute the latter minimum resource incentive of the second female into the expression for the male's fitness if he chooses to mate with her, that is,

$$q_m + q'_f + vR_m + vR'_f - zR_m, \qquad (14)$$

to obtain

$$y[q'_f + q'_m + v(R'_f + R'_m)] \\ + \frac{z\{q'_f + q_m + vR_f' - y[q'_f + q'_m + v(R'_f + R'_m)]\}}{v}. \qquad (15)$$

The first female must be willing to reduce her resource demand enough to make the male's fitness for mating with her equal to his fitness as given by Expression 15. The male's fitness for mating with the first female is

$$q_m + q_f + vR_m + vR_f - zR_m. \qquad (16)$$

Thus, we find the resource incentive given by the winning male by equating Expressions 15 and 16 and solving for R_m. This resource incentive is equal to

$$\frac{q_f - q'_f + v(R_f - R'_f)}{z - v} \\ - \frac{q'_f + q_m + vR'_f - y[q'_f + q'_m + v(R'_f + R'_m)]}{v}. \qquad (17)$$

The amount of resources provided by the male to the winning female will increase as (1) the male's quality decreases, (2) the quality of the winning female increases, (3) the losing female's quality decreases, (4) the amount of resource possessed by the winning female increases, (5) the resource possessed by the losing female decreases, (6) the resource generating potential of the male increases, (7) the fitness cost associated with leaving to look for mates elsewhere, $(1 - y)$, decreases, (8) the quality of the losing female's future mate increases, and (9) the resource amount yielded by losing female's future mate increases (Table 2).

The novel prediction in this model is that the male will pay the winning female less when the value of the losing female goes up. Intuitively, this occurs because a higher-valued losing female will be more effective in driving down the winning female's demand for resources from the male. Should the focal female fail to drop her demand in the presence of a high-valued competitor, the male would be too tempted to choose the other female instead. Thus, the quality of the losing female is directly related to the male's "leverage" over the winning female.

The winning female will be the female that, when she makes her minimum profitable bid, would potentially yield higher offspring success for the male. Again, we are assuming that this female's minimum profitable bid will still yield her a fitness benefit greater than that available to her if she were to find a mate elsewhere. We then calculate each female's minimum profitable bid and take the difference in the male's theoretical offspring success from mating with each, given that they are making their minimum bids. From the resulting difference, it can be inferred that the winning female will always be the one with the higher value:

$$q_f + vR_f. \qquad (18)$$

As is intuitive, Expression 18 predicts that the higher-quality female (higher q_f) and the female with more resources (high R_f) will tend to be the winner. When these two criteria are in conflict, it also follows from Expression 18 that the male will

Table 2
Effect of model parameters on magnitude of the female's resource incentive in the 1 × 2 model

Variable	Derivative of resource incentive on variable	Sign	Effect of increase on resource incentive magnitude
q_m	$-1/v$	−	Decrease
q_f	$1/(z - v)$	+	Increase
q'_f	$(y - 1)/v + 1/(v - z)$	−	Decrease
R_f	$v/(z - v)$	+	Increase
R'_f	$y - z \, (z - v)$	−	Decrease
z	$[q'_f - q_f + v(R'_f - R_f)]/(z - v)^2$	−	Decrease
y	$R'_f + R'_m + (q'_f + q'_m)/v$	+	Increase
q'_m	Y/v	+	Increase
R'_m	Y	+	Increase

give greater relative weight to the female's genetic quality in his choice when her resources less strongly affect offspring success (v low) or when females don't vary much in R_f. This is more often the case than not, as in most societies there tends to be relatively low variance between the amounts of resources that females have available to themselves, and female phenotypic quality (health and youth) is more closely tied to offspring success than is the male's.

The MCT2

Similar to the model that came before it, the 1 × 2 model also predicts that the total value of females' mates will be constant. In this model, this constant value depends only on the values of both the winning and losing female, the fitness cost associated with leaving, and the average value of future potential mates available to the losing female. This is solved by using the equations $V_m = (q_m + vR_m)$ (the total value of the female's mate), $V'_f = (q'_f + vR'_f)$ (the total value of the losing female), and $V_f = (q_f + vR_f)$ (the total value of the winning female). Substituting Expression 17 into V_m and rearranging yields

$$V_m = y(q'_m + vR_m) - (1 - y)V'_f + v(V_f - V'_f)/(z - v) \quad (19)$$

This MCT (MCT2) arises because the winning female must demand fewer resources as the value of the male increases, and these two opposing effects exactly cancel to yield a fixed total value for the female's mate.

Positive assortative mating with respect to total mate value
The MCT for the 1 × 2 model predicts that the total value of a female's mate will be positively associated with her own value and will be negatively associated with the losing female's value.

Comparisons of the models

We now briefly compare the major predictions of the models and the implications of these predictions.
1. Per the MCT for all models, the overall value of a female's mates should remain relatively constant, providing the female's value and the value of the alternative mates available to her don't change. This occurs as a result of males adjusting their resource incentives according to their own quality and the mate value of the female. We believe that this is a novel prediction, as we are not aware

of any prior model from which this prediction was derived.
2. Individuals pursuing short-term mates will be less concerned with future gains from such mates and will pursue individuals able to provide them with immediate fitness benefits. Individuals looking for long-term mates, on the other hand, will be more likely to pursue individuals who express cues associated with present and future benefits. For example, females seeking short-term mates would be expected to emphasize male genetic quality over male future resource-generating potential.
3. In both models, the resource incentive decreases as the winning male's genetic quality increases, and increases as the alternative male's genetic quality increases. Higher genetic quality of the focal male and lower genetic quality of the alternative male increase the "leverage" that the focal male has in negotiating resource transactions with the prospective female mate. We believe that the latter half of this prediction is novel, as we are unaware of any other models that have derived this prediction. This prediction should be tested quantitatively by comparing the resources offered by males as both a function of their own characteristics as well as those of their competitors.
4. Similarly, whenever the alternative male's ability to acquire resources affects the resource incentive given by the winning male, the effect will be positive, again because it reduces the focal male's leverage in the resource transaction. This should be tested quantitatively by comparing the resources offered by males as a function of the relevant traits of competing males.
5. Increasing the genetic quality or resource holdings of the female increases the resource incentive in both the 2 × 1 and 1 × 2 models. In either kind of bidding war, a female's value can be used as leverage in forcing a more favorable outcome for her. This should be tested quantitatively by comparing the resources offered by males as a function of the female's characteristics.
6. Both the 2 × 1 and 1 × 2 bidding game models predict that mates will positively assort with respect to total mate value.
7. In both models, it is predicted that each potential mate bases its optimal mating decision at least in part on the comparison between its own mate value and that of its opponents and prospective mates; therefore, individuals should constantly be assessing their own mate value relative to those of other players of both sexes. This is because the amount of resources yielded by the male depends on the values of all competing males, in addition to the values of all of the females for whom a male is willing to bid. This prediction should be tested by doing longitudinal tests of how individuals' mating behaviors change as the result of changes in their perceived same-sex competition and potentially available mates.
8. In both models, if one member of a pair-bond has a substantial rise in total value, the other member must either increase the resource incentive (the male) or decrease the amount of resources demanded (female) or else the other individual will be favored to leave. This should be tested empirically by doing a longitudinal study of romantic couples that measures the relationship between mate value fluctuations and conflicts over resources (e.g., conflicts about money or the amount of time spent caring for children).

9. Whenever the female's access to future mates affects the resource incentive, this effect will be positive because it reduces the focal male's leverage in the resource transaction. Also, when the female is being bid for by a larger group of males, her resource incentive should increase because the value of second-ranked male will tend to increase as the number of males increases.

10. In conjunction with prediction 9, females attempting to get a male to yield more resources are likely to mimic behaviors associated with being pursued by other males to reduce the bidding male's leverage and increase his resource bid.

11. In a 1×2 bidding game between females, increased value of the losing female reduces the resource incentive yielded by a male, because a higher-value losing female can more effectively undercut her opponent's reduction in demands for resources. Thus, a higher-quality losing female in effect increases the male's leverage in the resource transaction with the winning female.

12. In conjunction with prediction 11, males attempting to invest a lesser amount of resources in a given female are likely to mimic behaviors that signal to a bidding female that he is being pursued by other high-quality females.

Data bearing on the models

We briefly examine the empirical evidence bearing on the above predictions in the order in which they are presented. A major result of our models is the MCT (prediction 1), that is, that the total value of a female's mate should be roughly constant, with a negative relationship between the quality and resource investment of different male mates. Combining this prediction with prediction 2, we would expect that short-term mates of females, which thereby invest less cumulative resources in those females, should exhibit relatively high phenotypic quality when compared with their long-term mates. Indeed, researchers have repeatedly demonstrated that, when looking for short-term mates, women place a greater value on physical attractiveness than they do when looking for long-term mates (Buss and Schmitt, 1993; Gangestad and Simpson, 1990; Kenrick et al., 1990, Regan, 1998a,b) and are altogether more concerned with physical attractiveness than with resource acquisition (Li et al., 2002). When looking for long-term mates, however, females value cues of long-term provisioning, such as a promising career and financial prospects, whereas they are less concerned with phenotypic quality (Buss, 1998, 1999; Buss and Schmitt, 1993; Li et al., 2002). This result falls out naturally from our resource transaction models and is just one manifestation of the prediction that there should be a negative correlation between the male quality and male resource holdings for a given female's set of mates. This prediction should be highly amenable to further quantitative test.

In addition, the MCT (1 and 2) predicts that the value of all of a female's mates should increase as a function of her own value. This relationship is not predicted to occur between a male and all of his mates, however. The reasoning for this is as follows: because males adjust the resource incentive offered based on the value of a given mate, the value of a male's short-term mates is expected to covary with the sum of his quality and the (amount of his offered resource incentive (which depends on the overall value of the female), but not necessarily his overall value. Thus, the value of the females that he mates with will increase as a function of the resource amount offered; only a male's long-term mate is predicted to positively covary with his overall value. Indeed, the literature lends initial support for this predicted difference between the sexes (although it has been previously unexplained as the predicted result of a rigorous model). Men's self-perceived mate value was found to be only weakly correlated with their mate selection standards, whereas women's mate value correlated positively with their minimum criteria for both long-term and short-term mates (Regan, 1998a). Furthermore, as predicted by the MCT, the sex difference between the strength of these correlations was greater in the short-term than in the long-term mating context. The correlation between self-perceived mate value and mate selection standards strengthened for males as they moved from short-term to long-term mates, whereas positive correlation remained strong for females in both contexts. Men and women are equally as choosy when choosing a long-term mate (Buss, 1998; Regan, 1998a).

As a corollary of this, the existing data are also consistent with the prediction that the resource incentive yielded to the female acts as a decreasing function of a given male's quality (prediction 3). There appear to be tradeoffs between a male's phenotypic quality and willingness to invest, as male's attractiveness is associated with a much greater likelihood of pursuing a short-term mating strategy and greater sexual success with females (Burley, 1986; Gangestad and Simpson, 2000; Landolt et al., 1995; Little et al., 2000; Rowe et al., 1997). Thus, as the quality of the male increases, he is less likely to have to invest the time and resources involved in a long-term relationship in order to gain sexual access.

In addition, the existing data lend initial support for the predictions that individuals base their optimal mating decisions at least in part by a comparison of their own mate value and that of their opponents and prospective mates, and that these relative values guide mating transactions (predictions 4, 5, 6, and 7). For example, researchers have found that individuals' self-perceived mate value shifts depending on the quality of same-sexed individuals to whom they are exposed. In one such study, the self-assessed mate value of females was found to be adversely affected by exposure to highly physically attractive women, whereas men's self-assessed mate value went down when they were exposed to highly socially dominant men (Cash et al., 1983; Gutierres et al., 1999). As predicted by the models, although individuals' opinions on their own absolute attractiveness (females) and dominance (males) did not change, their self-perceived mate value did.

Furthermore, as predicted by our models, psychologists have shown that similar contrast effects occur when individuals are judging the attractiveness of members of the opposite sex. Kenrick and Gutierres (1980) have shown that men exposed to a television program depicting highly attractive females rated photographs of average women as being significantly less attractive than did a comparable control group. More work in this area needs to be done to determine whether this effect occurs in female subjects as well.

It has been suggested that these comparisons between self and others play an active role in courtship strategies and decisions, as self evaluations of mate value are highly predictive of the qualities desired in a long-term mate (Kenrick et al., 1993). Individuals with higher mate value expect more from potential mates, as such individuals are able to command higher value mates in the mating market. As predicted by both the 1×2 and 2×1 models, humans tend to positively assort with respect to overall value (Blau, 1964; Frank, 1988; Harrison and Saeed, 1977; Hirschman, 1987; Keller et al., 1996; Kenrick et al., 1993; Miller, 2000; Pawlowski and Dunbar, 1999; Regan, 1998b; Thiessen and Gregg, 1980; Thornhill and Thornhill, 1992).

In a similar vein, researchers have shown that males also tend to change their level of commitment to their partners relative to the quality of members of the opposite sex to which they are exposed. In one such study, after groups of men looked at photographs of either highly attractive women or women of average attractiveness, they were asked to evaluate their commitment to their current romantic partners (Kenrick et al., 1994). The men who had viewed the pictures of attractive women thereafter judged their actual partners to be less attractive than did the men who had viewed pictures of women who were average in attractiveness. In addition, the men who had viewed the attractive women also rated themselves as less committed to, less satisfied with, and less serious about their actual partners. This is exactly what is expected to occur based on prediction 7. Individuals are expected to be constantly be assessing their own value relative to other players of both sexes, and the amount of resources that a male is willing to invest will decrease as the assessed value of alternative mates goes up.

DISCUSSION

Indeed, most of the existing data in the human mating literature supports the predictions generated by the 2×1 model (the most frequently expected outcome of an arbitrary number of individuals in a given mating game). It is further interesting to note that the quantitative theory underlying these models is, to our knowledge, the first of its kind to unify these separate bodies of data. Although more precise research bearing on predictions yielded from the models is necessary, the existing data are, thus far, a remarkable fit to the theory.

Assuming the Bateman principle (Bateman, 1948) and parental investment theory (Trivers, 1972), the 1×2 model is expected to be applicable to human mating systems far less frequently than is the 2×1 model. The inherent sex difference in the benefits accrued from multiple matings means that the 1×2 model is only likely to emerge in human mating systems in which the sex ratio is strongly female-biased or there is marked social inequality leading to hypergyny. Hypergyny occurs in societies in which, owing to striking wealth inequalities, the number of high-value females greatly exceeds the number of comparably valued males. Indeed, in areas meeting this criterion, the novel prediction that females will have less leverage in mating transactions and will receive a lesser resource incentive, appears to be supported. For instance, the Ache of eastern Paraguay have a male-to-female sex ratio of roughly 1:2, and men are documented as being highly promiscuous, with individuals averaging 11 sex partners during their lifetimes (Hill and Hurtado, 1996). In addition, females in hypergynous societies receive smaller resource incentives than would a comparably valued female in a nonhypergynous society. Females in such societies typically have to share their mate's resources with cowives in addition to having to provide a sum of resources (dowry) to acquire a high-quality mate. Indeed, this practice often times leads to dowry competition among females' families to ensure that she gets mated to a suitable male (Dickemann, 1979). Further work is required to determine whether low resource investment by males is associated with female-skewed sex ratios and hypergyny as predicted by the 1×2 model; however, it looks promising.

Our models of resource transactions between mates have much in common with transactional models of reproductive skew and paternity skew (Shellman-Reeve and Reeve, 2000) in which reproduction is traded for cooperative benefits. Other theoretical approaches might be usefully applied to the analysis of games between potential mates (e.g., tug-of-war theory: Reeve et al., 1998), but the advantage of the transactional approach is that it makes more quantitatively precise predictions about the magnitudes of resource transactions and relates them more explicitly to the social and ecological context. If the transactional predictions ultimately fail, then these alternative approaches may need to be pursued.

Implications of the models

More data are undoubtedly needed to test the specific predictions generated by our models. In addition, there are many corollaries to the model predictions that deserve testing. For instance, one could test the prediction that males looking for a mate may attempt to facilitate such a search by favoring attendance at social functions that are primarily attended by females. By doing so, the male would (1) increase the male's odds of being the center of a 1×2 bidding war, (2) probabilistically increase the value of the highest-valued female, (3) probabilistically increase the value of the second-highest valued female (who works to undercut the resource demand of the highest-ranked female), and (4) increase his odds of being the highest valued male. All of the above have the potential to increase the chances both that the male will meet a high-valued female, and that he will be able to "afford" such a female. A similar prediction can made about females attempting to meet a mate. Females looking for a mate may facilitate such a search by attending functions primarily attended my males. By doing so, the female would (1) increase the chance of being the focus of a 2×1 bidding war, (2) probabilistically increase the value of the highest-ranked male willing to make a bid, (3) probabilistically increase the value of the second-highest ranked male willing to make a bid (who works to out-bid of the higher-valued male), (4) increase her chances of being the highest-value female. Thus, the existence of bidding wars generates a positive force for grouping in humans, but the favored group composition differs between males and females. A further corollary is that paired mates may often disagree on which kinds of social functions to attend; that is, females can increase their resource incentives by surrounding themselves with many high-quality males, and males can reduce their required resource incentives to their mates by surrounding themselves with many high-quality females. These are but two examples of the types of predictions generated both directly and indirectly by our models that could potentially provide new insight into the human mating psyche.

Limitations of the current models

This model is the first step in modeling human mating transactions, and as such, it is certainly not yet exhaustive in the variables included or in the situations modeled. For instance, our current model assumes that individuals infer statistically expected mate value accurately and are not vulnerable to systematic deception about mate value, assumptions that may not always be met in human mating systems. Mate value signaling, false signaling, and signal receiving are certainly salient issues in human mating, and will be examined incorporating modern evolutionary theories of communication in a subsequent paper (Hill SE and Reeve HK, in preparation). Furthermore, we recognize the need to incorporate the multitude of costs and benefits associated with leaving a potential mate. Costs accumulated from social stigmatization and loss of resource investment that accompany mate loss, and the potential fitness benefits acquired from bet-hedging via genetic diversification are but a few examples of these unmentioned factors. Additional factors not yet incorporated in these initial stages of the model's

development are diminishing fitness returns for increasing resource investment in offspring and the influence of kin on mate choice, both easily incorporated in extensions of the model. Furthermore, mate choice may be affected by time constraints and the costs associated with mate choice, as demonstrated by Johnstone (1997). Despite the theoretical economy of our model, it appears able to integrate and successfully account for many of the major features of human mating decisions (see above discussion of empirical evidence).

Conclusion

Human mating strategies are the predictable outputs of cognitive algorithms shaped by natural selection to incorporate evolutionarily-relevant contextual cues and generate evolutionarily stable behaviors appropriate to each context. By simultaneously incorporating quality, resources, and outside options, our models of such strategies appear able to account for differences between the sexes, strategic pluralism within each sex, and large-scale properties of mating systems such as positive assortment with respect to mate value. Our quantitative models confirm the reasoning of existing verbal models (Buss and Schmitt, 1993; Gangestad and Simpson, 2000) and generate novel and detailed predictions, in addition to paving the way for a comprehensive theory of within-pair conflict, expected duration of pair-bonds, communication between mates, and a new and deeper theory of mating systems in different human societies.

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