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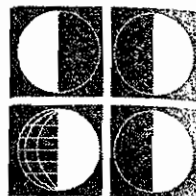
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# Required Parental Investment and Mating Patterns: A Quantitative Analysis in the Context of Evolutionarily Stable Strategies

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**ABSTRACT:** Much social psychological research has been dedicated to understanding mating strategies from the standpoint of genetic-fitness payout (e.g., Simpson and Gangestad, 2000). The current work is designed to provide a coherent, quantitative model for predicting different classes of mating strategies in both males and females. Specifically, the framework developed in this paper is an elaboration of Dawkins' (1989) quantitative assessment of different male and female mating strategies. Dawkins suggests that the prevalence of different strategies employed should be predictable in terms of evolutionary stable strategies. In the current work, a quantitative analysis predicting the prevalence of different mating strategies within each sex was conducted. The mathematical functions derived suggest that variability in the costs associated with raising offspring affects the expected prevalence of mating strategies differently for males and females. According to the present model, variability in female strategies should be less affected by changes in parental investment (PI) than variability in male strategies. Important predictions regarding male and female mating strategies across cultures are discussed.

## INTRODUCTION

A current trend in social psychological work on human mating has focused on evolutionary factors underlying patterns of human mating behaviors (Buss, 2003). From this perspective, human mating behaviors are conceptualized as manifestations of unconscious strategies honed by natural selection in ways to optimize gene proliferation. Research along these lines (in both humans and non-humans) has been most fruitful and has provided insights into several disparate phenomena such as factors desired in potential mates (Buss et al., 1990), facial features found attractive in potential mates (Cunningham, 1986), the impact of morphological

asymmetry on attractiveness judgments (Thornhill and Gangestad, 1994), and factors associated with satisfaction in long-term relationships (Shackelford and Buss, 1997).

One important theme underlying this body of literature concerns sex differences in mating strategies. In the simplest terms, from this perspective, males and females are predicted to differ in terms of general mating strategies in ways that are ultimately determined by anatomical differences. This line of reasoning is derived from Trivers' (1972) parental investment (PI) model, which suggests that mating and parenting-relevant behaviors should be predicted by the minimum amount of parental investment an adult of a species needs to contribute to successfully reproduce. Applied to adult humans, this model suggests that males should be more likely to seek short-term mates due

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to their relatively small required parental contribution (one sexual act) and that females should be more likely to seek long-term mates due to their relatively greater required parental contribution (e.g., one sexual act, pregnancy, labor, birth, etc).

While this conceptualization of broad sex differences in mating strategies as a function of parental investment considerations has been fruitful in describing general empirical outcomes in the domain of human mating (Buss, 2003), it is clear that framing mating strategies in exclusively sex-linked terms represents an oversimplification (Gangestad and Simpson, 2000). For instance, females will often engage in extra-pair copulation (Gangestad and Thornhill, 1997) under certain circumstances; as such, females display both long-term and short-term mating strategies as a function of environmental factors. Further, female infidelity (indicative of short-term strategism) has been documented consistently by researchers on infidelity. For instance, female infidelity in humans has been found to be reliably associated with an optimal strategy in that females who engage in extra-pair copulations tend to do so with males who score lower on indices of fluctuating asymmetry (and are judged as more physically attractive), thereby increasing the likelihood that any offspring from such copulations would have relatively fit genes (Gangestad and Thornhill, 1997). In other words, instead of one single female strategy existing (regarding monogamy), multiple strategies exist.

As such, consistent with an evolutionary framework, multiple strategies may typify a species and may, thus, co-exist in a population. Essentially, this idea, which corresponds to *strategic pluralism*, suggests that more than one strategy regarding some behavior may be adaptive and

may concurrently typify a species. For instance, male blue gills come in two varieties: large males who are effective at defending territories and smaller (and faster) males who employ a *sneaker* strategy by trying to fertilize eggs released by females who are drawn to larger males (Gross, 1982). Regarding sexual strategies in humans, this notion of strategic pluralism suggests that multiple male and female strategies may exist.

#### DAWKINS' TREATMENT OF EVOLUTIONARY STABILITY AND MATING

In his classic treatise on evolutionary principles, *The Selfish Gene*, Dawkins (1989) addresses strategic pluralism within the sexes using a quantitative framework steeped in game theory. The current work was primarily designed to examine the ramifications of variability in PI on outcomes related to strategic pluralism within the sexes in the context of Dawkins' model. Dawkins' model provides a clear and simple framework for understanding factors underlying different male and female mating strategies. One of the main factors addressed by Dawkins is the cost of raising offspring, conceptually synonymous with PI.

In his model, Dawkins discusses two simple behavioral strategies for each sex in a generic manner. For each sex, he discusses both a long and a short-term general mating strategy. Further, to explicate fundamental ideas that underlie mating strategies from an evolutionary perspective, Dawkins provides some basic rules for each 'player.' For males, he addresses the *philanderer* and the *faithful* individual. By definition, a philanderer will not spend time/resources courting a female and will not stay with a female after copulation. A faithful male will spend time

on courtship and can always be counted on to stay around to help raise a child. The two female strategies are framed as *coy* and *fast*. The rules governing coy females suggest that such females will not copulate with males until after having undergone extensive courtship. Fast females, on the other hand, will copulate with males regardless of time spent on courtship.

Some might argue that this four-strategy solution is too simplistic. Clearly, males and females have more mating-relevant behavioral patterns to choose from than these aforementioned patterns. However, these four strategies provide a useful framework for understanding basic potential patterns of behavior. Dawkins introduces these strategies partly to explicate the concept of evolutionarily stable strategies (ESS) in the context of mating strategies. The ESS idea, rooted in game theory, suggests that an optimal behavior from an evolutionary standpoint depends on the behaviors or unconscious strategies employed by conspecifics (Maynard Smith, 1988). Ultimately, from this quantitative perspective, stable ratios between different phenotypes, or behavioral outcomes, will be achieved within a population.

With regard to mating strategies Dawkins discusses three important mating-relevant variables, including the benefit of raising offspring successfully, the cost of raising offspring, and the cost of energy and time spent on courtship. To mathematically demonstrate the concept of ESS, Dawkins assigns arbitrary values for each of these variables. Of importance, while these variables are arbitrary, they are weighted in a relative manner that matches the empirical world when considering mating outcomes in a variety

of mammalian species, including humans. Also, while these values relate conceptually to reproductive success with regard to genetic fitness in general, in the immediate, they correspond to arbitrary units. Dawkins assigns 15 points to raising offspring successfully, -20 points to the cost of raising offspring (this number may be incurred to either one parent or may be divided equally between two parents), and -3 points to the cost of engaging in an extended courtship.

The exact values assigned to these variables are not as important as the relative weighting among them, namely the relationship between the costs and benefits of raising offspring, and the relatively lower costs of courtship. These points can be considered to represent time invested, opportunity cost, resources invested or a combination of the above. Each player, when given a choice between strategies, will attempt to maximize his or her utility by choosing the strategy or combination of strategies that will result in the highest expected number of points for that player. Utility is not necessarily a linear function (e.g., a score of 10 is not necessarily twice as good as a score of 5) but is necessarily an increasing function (e.g., a score of 6 is always better than a score of 5).

As can be seen, for one individual to (a) successfully raise an offspring, (b) raise that offspring alone, and (c) engage in an extended courtship, he or she would ultimately lose points and score -8. As this outcome corresponds to a lower utility than zero reproduction, it is clearly quite undesirable; a population of such individuals would not produce much offspring and would die out. Given such parameters, however, individuals can score positively if the burden of child-rearing is split among two individuals.

For instance, if an individual engages in an extended courtship and raises a child successfully with the cooperation of a competent partner, that individual would score in the black (+2 points), which is clearly superior to zero reproduction from a fitness standpoint.

According to the notion of the ESS, the prevalence of different phenotypes will converge at a ratio in which the payout for one phenotype will equal the payout for any alternative phenotype; there would be no incentive to change strategy as improvement would be impossible. In other words, the expected returns for multiple strategies are equal to one another and there is no incentive for a participant to change his or her strategic behavior. If one strategy provided a higher expected return, then a given participant would tend to implement that strategy over any alternatives; this in turn would affect the expected return of a second participant's strategy, causing a change in the second player's optimal strategy. Such a change would, in turn, have an effect on the first player's optimal strategy, and so on.

In an iterative game, an equilibrium is reached whereby neither player can improve his or her payout; the point where such an equilibrium exists corresponds to stability. Thus, if two strategies that are both designed to solve a particular adaptive problem exist, ultimately, they should exist in ratios in the population such that the expected payouts for the different strategies are equal to each other. In the case of Dawkins' mating strategy analysis, an ESS exists when  $5/6$  females are coy, with  $1/6$  being fast, and  $5/8$  of males are faithful, with  $3/8$  being philanderers. Note that this may be interpreted as either  $5/6$  of the female population is coy, or

that any particular individual female is coy  $5/6$  of the time; in a repeated game with a large population, these two interpretations are equivalent.

This solution has several implications. First, one interesting point not addressed by Dawkins is that the average expected payout for males is higher than it is for females. Given this ESS solution, the expected payout for either kind of female would be 1.25 while the expected payout for either kind of male would be 2.5 (these payouts correspond to the points at which the mean expected payout for the two female strategies are equal and the point at which the mean expected payout for the two male strategies are equal, respectively). In fact, this asymmetry across the sexes in absolute size of payout necessarily exists given that only females can be taxed, in this scheme, by the situation of having to raise an offspring alone.

Additionally, this ESS solution has interesting implications for a simplistic understanding pertaining to sex differences in mating strategies. While much current social psychological work is often summarized in a way suggesting, simply, that males tend to employ short-term strategies while females tend to utilize long-term strategies, Dawkins' ESS solution suggests that the predominant strategy of both males and females would be long-term in nature (at least given the arbitrary payout amounts included therein). We are aware that several additional variables could be included in this model and, similarly, that multiple ways of operationalizing the variables included could be addressed. Note that the Discussion includes a section titled "Limitations of the Model" that is designed to address such points.

### ASYMMETRICAL VARIABILITY IN MATING STRATEGIES ACROSS THE SEXES

The primary purpose of the current work concerns another implication of Dawkins' quantitative model in regard to mating strategies. Specifically, this work is designed to elaborate on an implicit point of Dawkins' model; the issue of whether, according to this model, the variability of change in the ratios of these different phenotypes is greater for males than for females as a function of changes in the cost of raising offspring. Recall that Dawkins considers three variables: benefit of raising offspring successfully, cost of raising offspring, and cost of extended courtship. Of these three variables, only cost of raising offspring potentially differs across the sexes (at least as conceptualized in Dawkins (1989) model). For males and females, the potential benefits of successfully raising an offspring and the potential costs of courtship are always the same in this model. However, with regard to cost of raising offspring, due to consequences dictated by internal fertilization, the possibility exists that females may end up raising an offspring alone, whereas the possibility of a male raising an offspring alone need not exist conceptually.

This asymmetry regarding cost of raising offspring suggests that as the costs of raising offspring change, ratios associated with the different male strategies should be more likely to vary compared with the ratios associated with the different female strategies. Thus, while both males and females will likely alter their mating strategies as a function of absolute costs of raising an offspring, the utilization of female strategies should vary less compared with the utilization of male strategies. This prediction rests largely on the

premise that females have less flexibility in their strategies as they need to guard against the possibility of raising an offspring alone, regardless of other factors. Due to an anatomy that does not require as much parental investment, males are not bound by this constraint and, as such, their mating patterns should be unfettered by this constraint and should vary more markedly as a function of changes in cost of raising offspring.

### METHOD AND ANALYSIS

To address whether the frequency of male and female phenotypes vary asymmetrically as a function of variability in the cost of raising offspring, an equation speaking to Dawkins' ESS solution was developed. Next, functions pertaining to differential ratios of the prevalence of each of the four strategies were plotted against the cost of raising offspring. Finally, functions speaking to variability in payout for each phenotype were computed and plotted against the cost of raising offspring.

### CALCULATING EQUILIBRIUM FUNCTIONS

First, Dawkins' model was decomposed into four basic equations corresponding to the relevant payouts to each sex in the context of all possible strategies being potentially employed within and across the sexes. A coy female matched with a Faithful male corresponds to a payout to each participant of  $C - \frac{1}{2}(R) - W$ , where  $C$  refers to the benefits of raising a child,  $R$  corresponds to the cost of raising offspring, and  $W$  represents the opportunity-related cost of courtship time. Payouts for the (Fast, Faithful) pairing are identical for members of each sex at  $C - \frac{1}{2}(R)$ . The (Coy, Philandering) match-up results in no payout for a mem-

ber of either sex, since no mating occurs. Payouts by sex do not diverge until we examine the (Fast, Philandering) strategy pair, in which the male receives a payout of C, while the female bears the full cost of PI and receives a lesser payout of  $C - R$ .

As can be seen from these equations, PI is the variable that differentiates between the utilization of male and female strategies; each other variable affects both the male and female equally for any given strategy pair. To examine strategy equilibrium functions for any given level of the variable R, leaving the values of C and W as given, we undertook a two-part process. First, we determined whether either sex had a dominant strategy for a given value of R; here, "dominant strategy" is defined as one in which an individual of a particular sex would be better off choosing one strategy over another *regardless of the strategy choice employed by members of the opposite sex*. In other words, if a given strategy for a player would provide a higher payout than any alternative strategy for that player, across the game matrix of potential outcomes, then it is in the best interests of that player to always choose that strategy. If a dominant strategy exists, then natural selection would tend to favor individuals who always pursue that strategy because they would receive a higher payout than individuals who do not. In addition, in a repeated-game environment, a member of the opposite sex would recognize if his or her opponent had a dominant strategy and in turn would choose the strategy which would maximize his or her own payout. If either party has a dominant strategy, then the equilibrium function will represent the case in which a given party will choose that dominant strategy all of the time (probability = 1.0).

The second part of calculating the strategy equilibrium occurred only when neither party possessed a dominant strategy. Here a process similar to the one employed by Dawkins was utilized; by solving the set of simultaneous payout equations, the strategy equilibrium for any given value of R can be calculated. This equilibrium would produce the optimal probability distribution of strategies for each sex, i.e., Probability(Coy) =  $x$ , Probability(Fast) =  $1-x$ , Probability(Faithful) =  $y$ , Probability(Philander) =  $1-y$ . At a strategy equilibrium for a given value at R, there will be distinct probabilities  $x$  and  $y$  that will result in optimal payouts for each sex, and there would be no incentive for either sex to diverge from this probability-weighted set of strategy choices. It is immaterial whether this equilibrium results from a pure evolutionarily stable strategy, or one that oscillates around an equilibrium point (see Schuster and Sigmund, 1981), as the current work conceptualizes a repeated series of games within a population.

#### DETERMINING DOMINANT STRATEGIES

First, dominant strategies were computed for instances in which rearing costs (R) were either relatively low or relatively high. Given the arbitrary point values, low rearing costs were considered as costs that generally led to the outcome in which benefit of successful child bearing (C) largely outweighed penalties associated with rearing costs (R). In the current scenario, that point was calculated as  $(R \leq 15)$ ; at this point, a dominant strategy exists. For such low rearing costs, the dominant strategy for the female is to pursue the fast strategy all of the time, since then her expected payout would be higher than her expected payout from choosing the coy strategy, regardless of

what the male chooses to do. Strategy equilibrium for relatively low costs of child rearing then is Probability(Fast) = 1.0, Probability(Philandering) = 1.0.

The other dominant strategy exists in the scenario in which costs of child rearing are relatively high ( $R \geq 24$  in this model). At these high costs, the male will always choose to philander. Regardless of whether the female chooses to be coy or fast, the male would receive a higher payout by philandering than he would receive by remaining faithful. At these high levels of cost of child rearing, even a partial share of parental responsibility held by the male would overwhelm the benefits to him of having offspring. Given the male's incentive to philander, the female will always choose to be coy, since she will receive a higher payout than if she were fast. Strategy equilibrium for relatively high costs of child rearing is Probability(Coy) = 1.0, Probability(Philandering) = 1.0. Note that this strategy implies that no reproduction will occur (as coy females would, by definition, never mate with philandering males).

The study becomes more interesting at intermediate values of  $R$ , when there is no dominant strategy for either sex. In this range, a male would pursue a combination of faithful and philandering strategies such that he would attempt to optimize his expected return; similarly a female would pursue a combination of coy and fast strategies that would provide her with the greatest expected utility. Again, please note that these probabilities represent the actions of the population over time, as in any single interaction a male or a female can only choose a single strategy; over time, the populations of all males and all females will adopt the optimal sex-appropriate strategies. In order to determine the equilibrium level for any

given value of  $R$ , sets of simultaneous equations are solved for each sex in order to provide the expected breakdown of strategies that would result in an equilibrium level. At such an equilibrium level, members of neither sex would be expected to deviate from their distribution of strategies insofar as any deviation would result in a lower expected payout.

Figure 1 shows the expected prevalence of male and female strategies, given the varying cost of rearing a child. In other words, the strategy distribution was determined for a member of a given sex such that, given the strategy distribution of the member of the opposite sex, the member of the given sex would be unable to achieve a higher payout by varying from that strategy distribution. Mechanically, this function is calculated by setting the probability-weighted payout for members of each sex equal for each strategy, then solving for that probability. To cite the example from Dawkins (1989), given an ( $R = 20$ ), that strategy distribution for females is 5/6 Coy and 1/6 Fast and for males is 5/8 Faithful and 3/8 Philandering. Given that males are 5/8 Faithful and 3/8 Philandering, a female cannot do any better than by pursuing a strategy that is 5/6 Coy and 1/6 Fast; similarly, given that females are 5/6 Coy and 1/6 Fast, a male cannot do any better than by pursuing a 5/8 Faithful, 3/8 Philandering strategy. Similarly, in our model, for each value of  $R$  between 15 and 24, unique optimal equilibrium strategies exist for both males and females.

For the sake of clarity in Figure 1, we have chosen to exhibit only one strategy for each sex since the two strategies for each sex are mutually exclusive. Since Fast is the dominant female strategy for relatively low levels of  $R$  and the Philandering strategy is the dominant male



strategy for relatively high levels of  $R$ , only these two strategies are represented; the percentage of Coy females and Faithful males can be represented as 1 minus the probability of Fast females and Philandering males, respectively. For example, at  $R = 10$ , all females will choose to be Fast and all males will choose to Philander, while at  $R = 24$ , no females will choose to be fast (all females will choose to be coy) and 0.25 of males will choose to philander (0.75 of males will choose to be faithful).

For relatively low levels of  $R$ , Fast female behavior dominates leading to philanderer male behavior. At the inflection point of ( $R = 15$ ), the probability of fast behavior drops to 0.375, then decreases linearly as a function of increasing  $R$ . For

relatively high levels of  $R$ , Philandering male behavior dominates (leading to coy female behavior), then drops dramatically to 0.25 at the inflection point of ( $R = 24$ ). As  $R$  decreases, Philandering behavior increases in a curvilinear fashion until the probability equals 1.0.

In addition to the prevalence of specific strategies for both males and females as a function of  $PI$ , the expected payout function for a given member of either sex was also calculated as a function of  $PI$ . The payout is easily determined given the previously calculated prevalence of strategies and is represented graphically in Figure 2. The payout for males is constant for relatively low levels of  $PI$  ( $R < 15$ ), while female payout gradually decreases toward zero as  $R$

approaches 15, since the female is supporting all costs of raising offspring. Similarly, for relatively high levels of PI ( $R \geq 24$ ) the payout to a given member of each sex is zero, since the combination of a Coy female and a Philandering male will not result in offspring. For intermediate values of PI, the payout for a male decreases linearly towards zero as  $R$  increases; however, the payout for the female at first increases from zero, peaks, then decreases toward zero in a non-linear manner.

The relative values of PI can be separated into three groups: relatively low PI, intermediate PI, and relatively high PI. In the case of Dawkins' model, these ranges are characterized by  $R < 15$ ,  $15 \leq R \leq 24$ ,  $R > 24$ . With both low PI and high PI, a dominant strategy exists for one sex, and therefore, there is no variation in

strategies, both below and above a certain level of PI. Of most interest to the observer is the shifting of strategy patterns within the intermediate range of PI, at the inflection points between low and intermediate PI, and between intermediate and high PI.

Within the intermediate PI range, male behavior is, overall, much more sensitive to changes in  $R$  than is female behavior. Returning to Figure 1, observe that within the intermediate range, male philandering varies between 1.0 and 0.25, while female fastness only varies between 0.375 and 0, which is exactly half the applicable male range. Not only is male behavior more variable throughout the entire intermediate range, but it is also much more sensitive to PI variability at lower levels of  $R$  than at higher levels of  $R$ . For example, as  $R$  increases from 15 to 16, male

philandering drops from 1.0 to .075, and as  $R$  increases from 23 to 24, male philandering decreases from 0.273 to 0.25. In fact, at higher levels of  $PI$  in the intermediate range, female behavior is more sensitive to changes in  $PI$  than is male behavior; as  $R$  increases from 23 to 24, female fastness drops from 0.043 to 0.

## DISCUSSION

This work was designed to elaborate on work in the behavioral sciences regarding strategic pluralism in mating strategies across and within the sexes. The notion of strategic pluralism, suggesting that there are different kinds of potentially successful mating strategies employed by males and females, has been the focus of considerable recent work by evolutionary psychologists (Gangestad & Simpson, 2000). Such work is based on the idea that a variety of mating strategies employed by members of both sexes may well have adaptive qualities. Whether a particular strategy is adaptive depends importantly on context.

In conceptualizing mating strategies from a game-theory perspective, Dawkins (1989) provided the elements of a mathematical model that have potentially important implications for predicting the likelihood of the use of different strategies across and within the sexes. Dawkins' model is simple by design. This simplicity allows for a presentation of expected outcomes associated with the conceptual variables that are central to our modern understanding of mating strategies across species. In particular, Dawkins focuses on costs associated with courtship, costs associated with rearing offspring, and genetically relevant benefits associated with successfully rearing offspring. Based on important theoretical

treatises regarding evolutionary factors underlying mating (e.g., Trivers, 1972) and current work by evolutionary psychologists designed to assess factors underlying mating outcomes (e.g., Buss, 2003), these variables incorporated by Dawkins clearly represent important ultimate factors in determining human mating outcomes.

In formalizing the mathematical functions underlying Dawkins' reasoning, the first interesting finding concerned what Dawkins meant by his *equilibrium function*. He states that "it turns out that a population in which 5/6 of the females are coy and, and 5/8 of the males are faithful, is evolutionarily stable" (Dawkins, 1989, p. 153). Interestingly, at this point, the expected payout for either female strategy is 1.25 units while the expected payout for either male strategy is 2.5 units. This mathematical model always, in this sense, provides greater utility to males than to females. This inherent inequality across the sexes is derived from the fact that the potential burden of raising offspring alone and incurring full parental investment costs is an exclusively female burden. Under no conditions in this model (and under nearly no natural conditions in internally fertilizing species) will a male incur such costs.

Figures 1 and 2 represent the theoretical equilibrium and payout functions associated with Dawkins' model. Several interesting hypothetical points are explicated by these functions. For one, these functions specify the points at which males and females would not mate because costs would invariably outweigh benefits. As the costs associated with  $PI$  increase to a particular point (given the arbitrary values, the point at which ( $R = 24$ )), all females would be coy and all males would be philanderers; no mating

would occur given the definitions of these constructs.

An additional point that is of considerable interest regarding the current analysis pertains to the differences in the nature of the functions between males and females. As can be seen in Figure 1, male and female functions, representing the differential prevalence of the different male and female strategies as a function of PI, both change as a function of PI. However, the shape and slope of these functions are different between the sexes. Most notably, the male function demonstrates more variability across levels of PI compared with the female function. An implication of this point is that changes in PI have asymmetrical effects regarding the prevalence of male versus female strategies. Changes in PI, according to this analysis, are associated with more variability in male behavior compared with female behavior. As PI increases, males and females are both more inclined to pursue long-term strategies; however, such increases in PI make males *especially* inclined to pursue such strategies (except in the instance where female payout is more sensitive to PI than males in the upper limit of the PI range). Similarly, as PI decreases, males are *especially*, compared with females, inclined to pursue short-term strategies.

This notion, regarding PI as having a greater effect on changes in male strategies compared with female strategies, captures the essence of several ideas and findings pertinent to mating outcomes across species. For instance, consider Bateman's principle (1948). This principle suggests that male reproductive success should vary more than female reproductive success. Bateman found evidence for this notion in his seminal work on fruit flies (which has been extended to

sexually reproducing species in general): Almost all female fruit flies mate with one or two partners in a lifetime. However, for males, the numbers of mating partners are roughly equally distributed among 0, 1, 2, and 3. For a male, attracting several mates is relatively adaptive and is likely to increase reproductive success. This same point is not true for females; for females, mating with several partners does not have the effect of increasing reproductive success in the form of more young. Thus, for females, there are relatively clear constraints on mating strategies and females tend to generally utilize a strategy based on choosiness (choosing males based on fitness considerations). The outcomes for males end up varying more compared with the outcomes for females. As is typical of females across species, female fruitflies necessarily incur higher PI costs than males (due primarily to larger, more costly gametes). This higher PI seems to be associated with less variability in reproductive success.

Bateman's principle speaks to differences in reproductive success across the sexes as a function of differences in PI, while the analysis presented in the current work speaks to differences in prevalence of mating strategies across the sexes as a function of PI. While these notions are not identical, they both suggest that changes in PI are associated with more variability for males than for females, largely due to the fact that PI is inherently higher for females.

An example from a recent cross-cultural study of sex differences in reactions to infidelity explicates the utility of the mathematical model presented here more explicitly. Buunk, Angleitner, Oubaid, and Buss (1996) studied sex differences in reactions to infidelity. This re-

search followed past research which found that males tend to be more distressed by sexual, rather than emotional, infidelity, while females tend to show the opposite pattern (Buss, Larsen, and Semmelroth, 1992).

Buunk et al. (1996) examined this phenomenon cross culturally by examining sex differences in separate samples of participants from the United States, The Netherlands, and Germany. The Netherlands and Germany were examined in particular as these cultures are marked by relatively relaxed attitudes toward sexuality. Additionally, pertinent to the current work, costs associated with raising offspring are different in these countries than in the United States. Women are given considerably more financial help with raising children in these (and other) European countries compared with the United States. For instance, in Germany the national childcare statute states that "Childcare leave can be claimed starting from the end of the period of maternity protection, i.e., from 8 or 12 weeks after the birth (maternity protection), up to the end of the month in which the child becomes 18 months old" (European Foundation for the Improvement of Living and Working Conditions Homepage, 2002). Such a statute, which is considerably more sympathetic to new mothers than comparable rules in the United States, in effect lowers PI for female citizens of that country.

Thus, in effect, Buunk et al. (1996) examined an important index of mating-relevant strategies (reactions to potential infidelity) as a function of cultural variability in PI. This study provides a clear test of the points raised by the analysis presented in the current work. The researchers predicted that the standard sex differences in reactions to infidelity

would be moderated by culture. This notion was supported by their findings. While males across the different cultures were generally more distressed by sexual infidelity than females, this trend was less pronounced in the German and Dutch samples. These findings conceptually and empirically demonstrate an instance of PI differentials across cultures varying as a function of sex.

Pertinent to the current work, Buunk et al.'s (1996) findings also speak to differential variability in male and female responding as a function of PI. The outcome variable addressed in this research was the percentage of individuals in a sample who reported more distress to sexual than emotional infidelity; generally, males tended to show such a different pattern (more distress to sexual than to emotional infidelity) from females. Interestingly, the sex difference was greatest in the United States sample, followed by The Netherlands and German samples, respectively. Relevant to the current reasoning, the variability across the cultures was clearly more the result of variability in male responses across cultures (co-varying with conceptual changes in PI) than variability in female responses. In the U.S., The Netherlands, and Germany, the percentages of females choosing the sexual infidelity option were 17 percent, 30 percent, and 15 percent, respectively. The standard deviation for female responses was 6.65. On the other hand, the percentages for males in these same countries choosing the sexual infidelity option were 60 percent (U.S.), 50 percent (The Netherlands), and 27 percent (Germany). The standard deviation for males (13.82) was more than twice the standard deviation for females.

These cross-cultural findings are provocative when considered in light of

the mathematical model presented in this paper. Relatively low PI at a cultural level (represented here by both the Dutch and German cultures) is associated with manifestations of sexual strategies across the sexes in a way that is as would be predicted by the current presentation of Dawkins' model.

While Buunk et al.'s (1996) findings speak clearly to the utility of the principles pertaining to asymmetrical effects of mating across the sexes as a function of PI, their research was not designed with this particular aspect of sex differences in mind. Buunk et al. (1996) were interested in sex differences in reactions to infidelity as a function of culture. They indicate that their findings demonstrate "that the magnitude of this sex difference (in reactions to emotional versus sexual infidelity) differs across cultures" (Buunk et al., 1996, p. 362). The fact that this finding is derived, empirically, from the fact that males' responses varied considerably across cultures (as a function of variability in PI) is not addressed by these researchers. The mathematical delineation of Dawkins' (1989) model (presented here) and the articulation of implications pertaining to differential effects in male versus female variability in strategies as a function of changes in PI allows for an analysis of existing findings, such as those presented by Buunk et al. (1996), in a new light.

Other research on sexual strategies from a cross-cultural perspective is consistent with this analysis. For instance, in a recent paper by David Schmitt (Director of the International Sexuality Description Project) and his colleagues (2003), variability in the percentage of males who desire multiple partners (average  $SD = 6.38$ ) was considerably larger than the variability in the comparable percentage

for their female counterparts (average  $SD = 1.51$ ). Note that this pattern of heterogeneity of variance was not addressed explicitly in Schmitt's (2003) paper; it was, rather, derived from our analysis of their Table 5 (p. 93). These findings are clearly consistent with the prediction from the current model suggesting that male strategies should vary more across cultures than females. The ideas explicated herein suggest that an examination of variability between the sexes in cross-cultural research on sexual strategies may be as informative as an examination of indices of central tendency. Future work re-examining prior cross-cultural research on mating patterns in terms of sex differences in variability of mating-relevant variables (particularly as a function of variability in variables that reflect costs in raising offspring) would likely be extremely informative in this light.

Accordingly, the mathematical model presented here may be of heuristic value. Specifically, the functions presented here allow for an empirical test of the basic assumptions. Largely, to be sure, these assumptions are synonymous with the assumptions of Trivers' (1972) Parental Investment Theory and its scholarly offspring (e.g., Simpson and Gangestad, 2000). However, this model also spells out a potentially new wrinkle in Parental Investment Theory: this notion of asymmetrical male and female strategic variability as a function of PI. This particular point may be the subject of future empirical work in several ways.

For instance, this sex-differences-variability postulate may be addressed in work that conceptualizes the relationship between PI and sexual strategies in an intrapsychic mode. Specifically, it is proposed that future work on this question operationally defines long versus short-

term sexual strategies using Simpson and Gangestad's (1991) measure of sociosexuality (the Sociosexuality Inventory or SOI). This measure taps individual differences in willingness to engage in unrestricted sex. Sociosexuality has been found to predict several mating-relevant outcomes consistent with the fundamental ideas of parental investment theory. For instance, in one study, males who scored high in sociosexuality were more likely to use direct competition tactics in trying to obtain a date, manifesting behaviors expected to correspond to the use of short-term tactics (Simpson, Gangestad, Christensen, and Leck, 1999). In a sense, the SOI may be thought of as an index of individual differences in the proclivity toward long- versus short-term mating tactics. Thus, this measure may be useful in operationally defining the prevalence of different uses of long- versus short-term tactics in tests of the sex-differences-variability postulate outlined here.

For instance, to test the empirical validity of this model some cultural index of PI may be computed based on variables pertaining to nations' financial laws regarding raising children. Nations vary in terms of how supportive they are in providing for new mothers in general and single mothers in particular. In the nations being studied, patterns of long- versus short-term mating strategies across both sexes could be measured. The SOI would likely be one useful such index, as it represents a valid measure of the proclivity toward long- versus short-term mating tactics and can be used for both males and females. Collecting large samples of SOI and other sexual strategy-relevant data across cultures that empirically vary in PI would allow for a clear test of the utility of the mathematical model presented in the current work.

#### LIMITATIONS OF THE MODEL

The three-variable model included in this analysis is necessarily simplistic. One issue that needs to be considered in examining the utility of this analysis and in considering empirical work that could test predictions of this model pertains to additional variables that may be relevant. For instance, number of other viable offspring that an individual already has may affect mating strategies. Along these lines, Weekes-Shackelford, Easton, and Stone (in press) argue that the number of offspring from a prior relationship affects one's mating strategy. An analysis of the current evolutionary psychology literature may provide insights into several variables that could be included in this model.

Another issue that could be addressed in future work on this model pertains to sex differences in costs and benefits associated with the different variables. In this current model, only cost of raising offspring varied across the sexes. In actuality, other variables may vary across the sexes as well. Costs of courtship are conceptualized as identical across the sexes in the current model—in actuality, these costs may vary across the sexes (and such variability may be moderated by cultural effects). Similarly, benefits of successful childrearing may in fact differ on average across the sexes. As females are more likely to be certain of their parental status than are males, successful raising of an offspring likely benefits females (on average) more than males (who may potentially invest time in raising non-genetically related offspring).

Also, the current model assumes that the cost of raising offspring is to be equally split for members of couple who stay together. This assumption may not match the empirical world. Similarly, the

current model assumes that a philandering male who sires an offspring benefits as much as does a faithful male who both sires and raises *his* offspring. As the child of the philanderer does not benefit from bi-parental care, this assumption may not be particularly valid. Thus, future work on this model would benefit from taking a more nuanced approach to operationally defining these variables.

#### CONSIDERATIONS IN LIGHT OF RECENT WORK ADDRESSING THE ESS MODEL

Recently, a variety of theorists have raised several concerns regarding the general ESS model used to understand mating strategies (e.g., Wade and Shuster, 2002). Such concerns revolve around a variety of issues. For instance, in their mathematical formulation, Webb, Houston, McNamara, and Szekely (1999) describe the ESS model as consistent with the current work in that their findings suggest that bi-parental care leads to equal payouts across the sexes while female parental care leads to males being overbenefitted.

Such an outcome is consistent with our current conceptualization of human mating, as humans typically oscillate between monogamy and polygyny (Buss, 2003), thus leading to a scenario in which males would be slightly overbenefitted, on average, compared with females. This point, which is clearly consistent with the Parental Investment Theory, however, does not, according to Webb et al. (1999), take into account important other considerations such as decisions regarding whether to accept a mate after mating or to re-mate. According to these authors, the decisions associated with re-mating versus staying with a mate are crucial and should be included in mathematical models of mating strategies. Specifically, they

assert that "discussion of parental care behaviour should incorporate both the behavior of unmated animals and the feedback loop between parental care behavior and remating probabilities" (p. 989). In particular, these authors suggest that mathematical models of mating strategies would likely increase their validity if they more explicitly addressed the idea of mixed-strategies within the sexes.

Queller (1997) suggests that ESS models need to incorporate sex ratios as a relevant variable. In particular, Queller (1997) suggests that ratios of *reproducing* males and females play into animals' decisions to employ long- versus short-term strategies. He asserts that males will, on average, benefit more than females only under the conditions in which there are fewer reproducing males than females. Given Bateman's (1948) principle, this scenario may accurately pertain to a variety of species, including humans. Specifically, if males vary more in their mating/reproducing than females, and more females reproduce *at all* than males, then, based on Queller's (1997) model, when these reproductively relevant asymmetries exist across the sexes, males would in fact benefit on average more so than females. This pattern is consistent with Figure 2 of the current work pertaining to different male and female payouts based on the model used in the current work.

Wade and Shuster (2002) argue that past ESS models are limited in that they do not address outcome-related differences between direct and indirect effects on offspring viability. Separately, these authors point out that past ESS models do not take into account the fact that successful males preclude other males from having mating opportunities. Wade and Shuster (2002) suggest that past ESS



models erroneously indicate that males benefit more than females on average precisely because such models fail to take this point regarding the effects of successful males on the opportunity costs of other males into account.

While limitations regarding the current model certainly exist, the models' implications regarding differential effects of

parental investment variability on the relative prevalence of short- versus long-term mating strategies across the sexes is intriguing and has important implications. Future work addressing the asymmetrical sex difference described herein using more comprehensive models may be fruitful in helping predict actual mating patterns.

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