The effect of near-continuous male attractiveness on mate guarding strategies under social monogamy

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Females of many socially monogamous species actively seek out other males to mate with. Males of these species should endeavor to keep their females from succeeding in finding other breeding partners, as socially monogamous males will likely be expected to provide parental care, and would be better off providing parental care to their own offspring. On the other hand, they can only guard their mates so much, and may actually gain more benefit by attempting to cuckold other males in the population by breeding with other females rather than guarding their own females. The optimality of all of these decisions depends upon what other individuals in the population are doing. Hanna Kokko and Lesley Morrell showed that the evolutionarily stable mate-guarding strategies are complicated and nonlinear in the case when only attractive and unattractive males were considered to be competing with one another (Kokko and Morrell 2005). However, it is likely that by adding more levels of male attractiveness, the evolutionarily stable guarding strategies will become even less predictable. Additionally, the assumption of multiple attractiveness levels, rather than just two, may give us a better understanding of the kinds of competitive effects that are actually occurring in genuine populations, as real populations undoubtedly have more variation in attractiveness than was captured in the earlier model.

THE MODEL

My model is built off of the model of Kokko and Morrell, with the addition of more levels of attractiveness. As in their model, I assume that mate-guarding becomes more efficient when it is practiced more often, and that there is a trade-off between mate guarding and gaining offspring outside of the monogamous pair.

Mate guarding is modeled as the time t ($0 \leq t \leq 1$) that the male spends in close proximity to his social mate, with the remaining 1-t spent elsewhere. When the male is elsewhere he is free to search for extrapair matings, but his mate is also more likely to gain extrapair matings when he is away. Additionally, I assume that males can vary in attractiveness, and that guarding time can vary with attractiveness.

As in the Kokko and Morrell paper, I define within-pair paternity using a function that varies between 0 and 1, increases as a function of t, the male's guarding effort, of t_{pop}, the population-wide guarding level, and of the attractiveness of the male. The function I used is:

$$p_w(t,k) = gt^{kc_{pop}} . \tag{1.1}$$

In this equation, k is a parameter that measures female infidelity, and varies with the attractiveness of the individual. Unattractive individuals will have higher k values than attractive males, meaning that females paired to unattractive males will be more likely to be unfaithful than those paired to attractive males if the males put the same amount of effort into guarding.

Parameter g measures the efficiency of mate guarding, with low values meaning that within-pair paternity increases slowly with increased guarding effort. In this model, males can never achieve full paternity, even if they guard full time, thus $g < 1$.

The parameter c_{pop} indicates the severity of competitive pressure from other males in the population. $c_{pop} = \sum_i x_i(1-t_i^*)a_i$ is the average competitiveness of a male population member, when x_i is the proportion of males that are of attractiveness i, a_i is their relative efficiency in competing for extrapair mates ($0 < a < 1$), and t_i^* is the optimal guarding strategy for the population.

Extrapair paternity over the population is calculated as

$$p_E(t) = \frac{(1-p_{w_{pop}})(1-t)a}{c_{pop}}, \tag{1.2}$$

where 1-p_{wpop} is the per brood paternity available for extrapair mates, and $\frac{(1-t)a}{c_{pop}}$ indicates each male's relative competitiveness for that paternity. Fitness is then equal to the sum of a males within-pair and extrapair paternity.

Unlike the paper by Kokko and Morrell, I allow an arbitrary number of male attractiveness levels. Given a number of attractiveness levels, I assign a proportion of the total population to each level based on a binomial distribution. Thus, the two-level problem is equivalent to the one presented in their paper, where half of the population is attractive, and half is unattractive. However, with more levels, only a small proportion of the population is of very high or very low attractiveness. For example, with five attractiveness levels, 1/16 of the population is attractive, 1/16 is unattractive, ¼ is of slightly above-average attractiveness, ¼ is slightly below-average, and 3/8 of the population is average.

In Kokko and Morrell's paper, evolutionarily stable guarding strategies were found numerically. Since t values are constrained, $0 \le t \le 1$, it is possible to quickly compute fitness values across all possible combinations of guarding times $\{t_1, t_2\}$ (they used a grid of values with an accuracy of 0.005). The optimal strategy was the one where no local change in t_1 increased the fitness of attractive males, and no local change in t_2 increased the fitness of unattractive males.

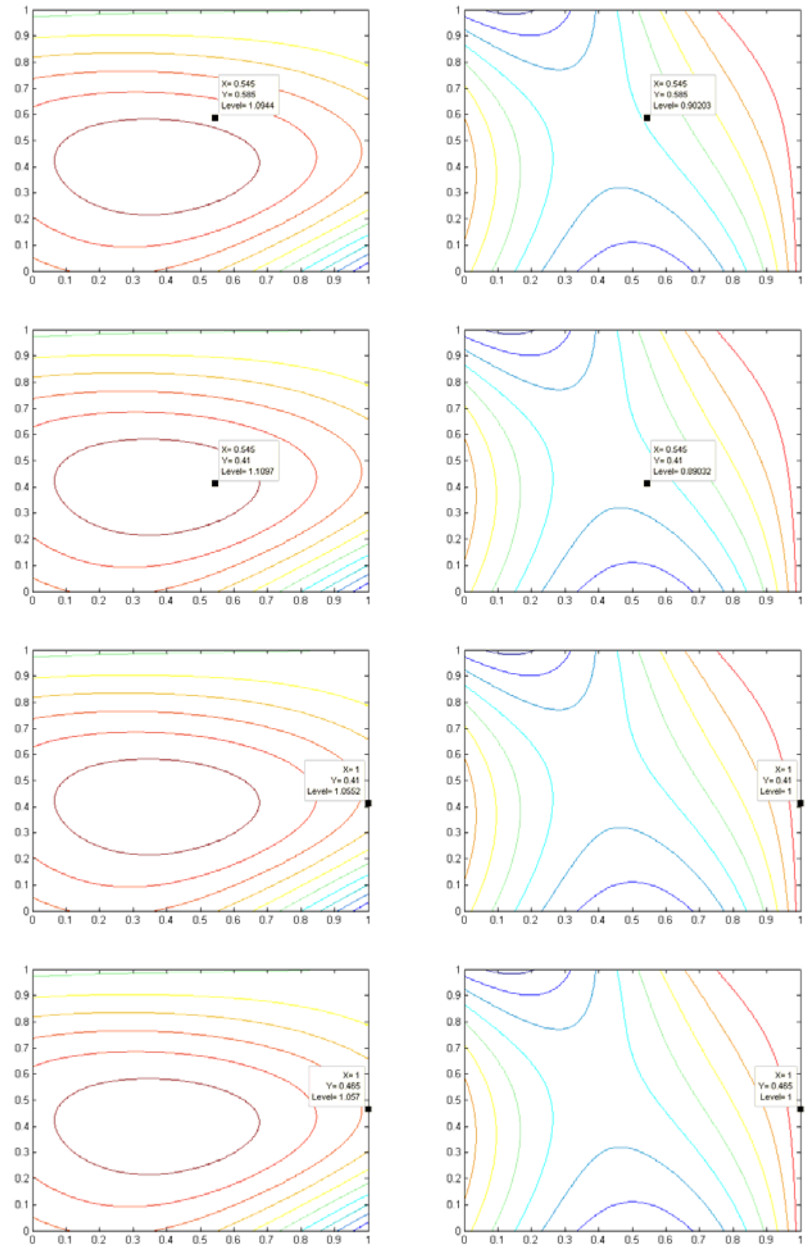

Figure 1. Paired contour plots of fitness in a two-level optimization. The contours on the left represent fitness levels for attractive males and those on the right represent the levels for unattractive males. An optimum solution is found by starting in a given area, moving up or down from that level to an optimum fitness level on the attractive males' curve. Then the unattractive male can move left or right to optimize his own fitness. This serial optimization is repeated until neither individual can increase his own fitness by guarding slightly more or less given the other individual's guarding strategy.

My solution procedure requires far less computation and thus allows me to compute solutions over more attractiveness levels more efficiently. The algorithm is as follows. Begin with an arbitrary set of guarding times $\{t_i\}$. Change guard time for one attractiveness level at a time, optimizing the fitness of that attractiveness level given the guarding strategies of all other levels. Repeat this strategy over all attractiveness levels, until no further adjustments can be made to optimize the fitness of a given attractiveness level. A schematic of this solution algorithm's effectiveness over a precomputed set of fitness curves is presented in figure 1. The solution strategy is identical with more attractiveness levels, but is more difficult to visualize.

RESULTS

The relationship between female infidelity and the evolutionarily stable guarding strategies is not straightforward. When only two attractiveness levels are considered, the within-pair paternity function that I used predicts an initial increase in guarding effort with increasing amounts of female infidelity, then a decrease once females become more unfaithful (figure 2).

Males behaving optimally trade off paternity at home with paternity elsewhere. Guarding effort increases and decreases more steeply for unattractive males, as they put a great deal of effort into guarding in order to ensure a similar level of within-pair paternity to make up for their inferior extrapair efforts. However, it seems that their guarding effort becomes ineffective at lower levels of female infidelity than for attractive males. In fact, at certain intermediate levels of female infidelity, the optimal strategy for unattractive males is to not guard at all, and compete for extrapair copulations with attractive males, who do better in those situations. Additionally, once infidelity reaches sufficiently high levels, neither level guards, instead getting more fitness from extra-pair copulations.

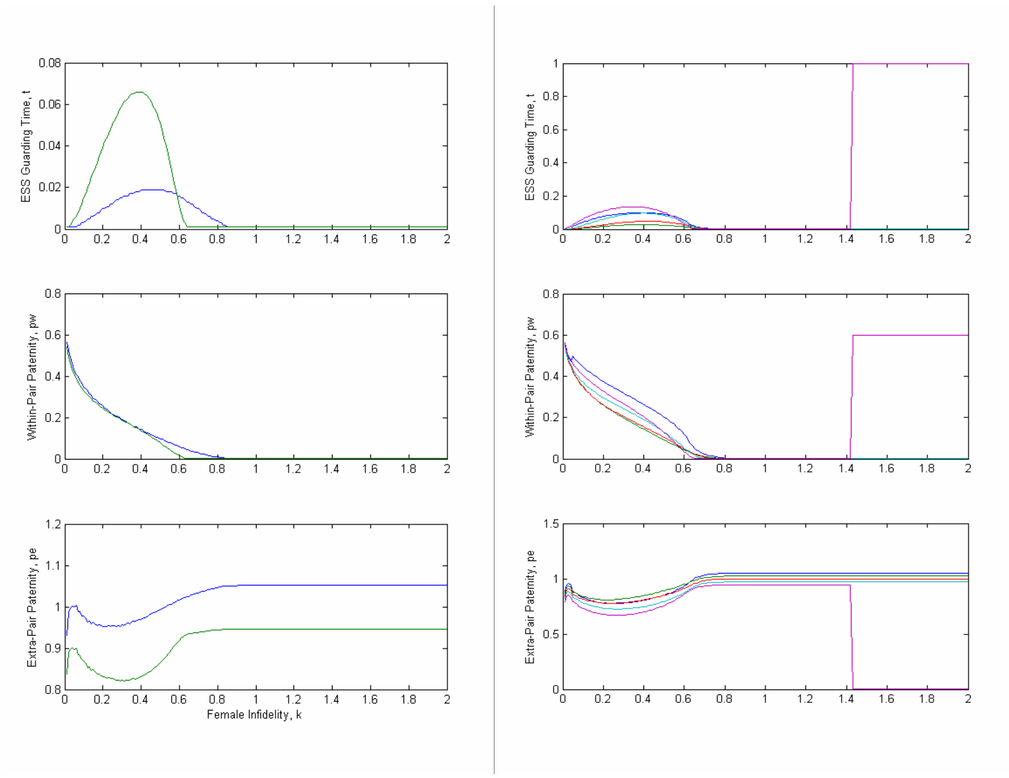

Figure 2. Evolutionarily stable guarding times, *t**, along with the within-pair and extra-pair paternity for males of differing levels of attractiveness, as a function of female infidelity, *k*. In the example on the left, there are two levels of attractiveness; attractive males (blue) and unattractive males (green). The example on the right has five levels of attractiveness, with attractive males (blue), unattractive males (pink), and three average levels in between (green, red, and aqua in descending order of attractiveness). Both examples used parameter values $k_{ratio} = 1.5$, $g = 0.6$, $a_{ratio} = 0.9$.

The extension of this model to five levels provided more nonintuitive results. The basic form of the guarding curves are the same, with an initial jump in guarding times with increasing infidelity accompanied by a decrease in the corresponding extra-pair paternity across the population. Unattractive males guard the most for infidelity values between about 0 and 0.5. Unexpectedly, the attractive males compete with the slightly substandard males for second most guarding time. This allows the attractive males to obtain much higher within-pair paternity than any other attractiveness group, with unattractive males getting the second most within-pair paternity. Also, while unattractive males get relatively little extra-pair paternity, attractive males still gain at least an average amount of paternity in extra-pair situations despite their extensive mate-guarding.

Average and slightly above-average males guard very little, and do better away from home than at home.

Once infidelity levels get sufficiently high, with *k* approximately 1.4, unattractive males go from not guarding at all, like the rest of the levels, to guarding all of the time. This is a clear trade-off in which, due to everyone else's strategies, unattractive males are better off putting all of their eggs in one basket.

With fifty levels of female attractiveness, the patterns are similar (Figure 3). Very attractive and very unattractive males still guard more than their slightly more average counterparts, and average to slightly above average males still guard least of all, and do best in the extra-pair arena. Additionally, guarding is more persistent despite increased infidelity in attractive males whose guarding is likely to be more effective.

As above, when female infidelity is raised to sufficiently high levels, a certain proportion of the unattractive population starts guarding full time. For the most unattractive males, this occurs at a *k* value around 1, but new unattractive male levels guard full time as infidelity is raised even further. By $k = 2$, nearly all males of below-average attractiveness guard full time, trading off their bad extra-pair paternity for slightly better within-pair paternity.

When unattractive males are very unattractive in comparison to the attractive males, they are more likely to guard a lot, with attractive males guarding very little (Figure 4). As relative attractiveness becomes more even, the relative guard times even out as well. The attractive males now have more to worry about, and so they guard more to compensate. Average to above-average males guard less than either attractive or unattractive males under all relative attractiveness ratios.

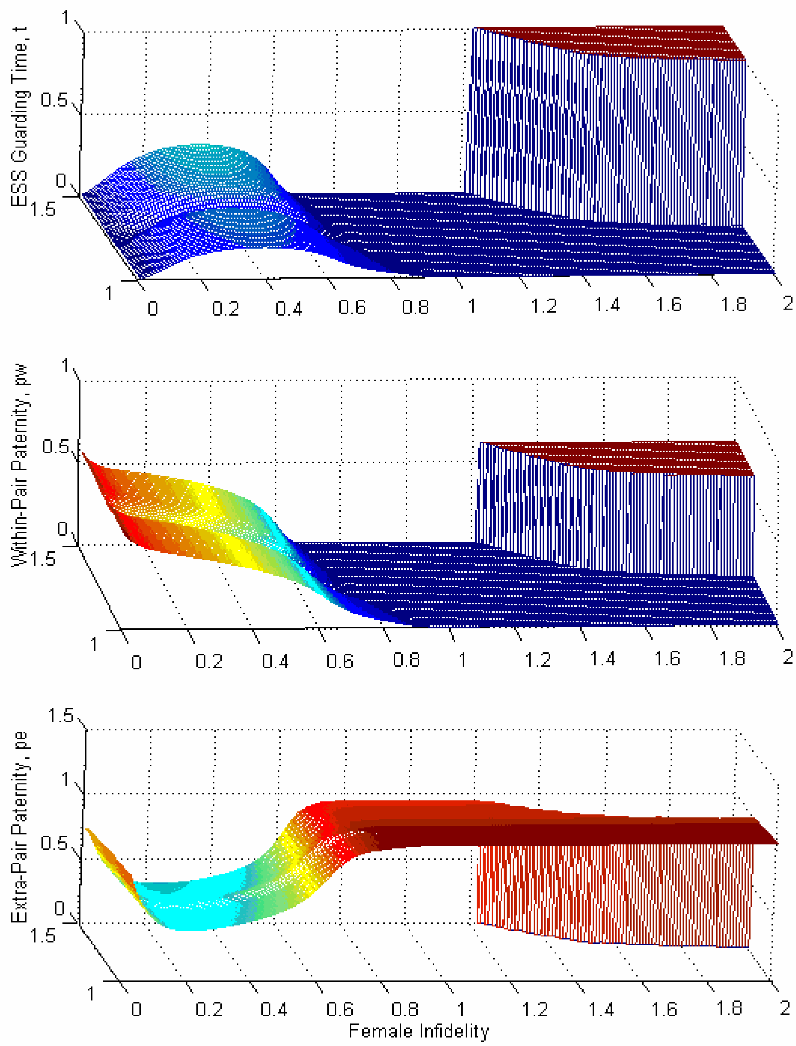

Figure 3. The impact of increasing female infidelity on the evolutionarily stable guarding times, within-pair paternity, and extra-pair paternity in a population with fifty levels of attractiveness. The depth axis represents how many times more likely females are to "cheat" on individuals of that level. Thus, attractive males are at the front of these graphs, and unattractive males are at the back. Parameter values used are g = 0.6, k_{ratio} = 1.5, and a_{ratio} = 0.9.

DISCUSSION

My modeling shows that patterns of mate guarding have an effect on the paternity of males of different levels of attractiveness, and that these relationships are not straightforward or linear. By adding more levels of attractiveness, I showed that optimal strategies really do depend on the population in question. The model of Kokko and

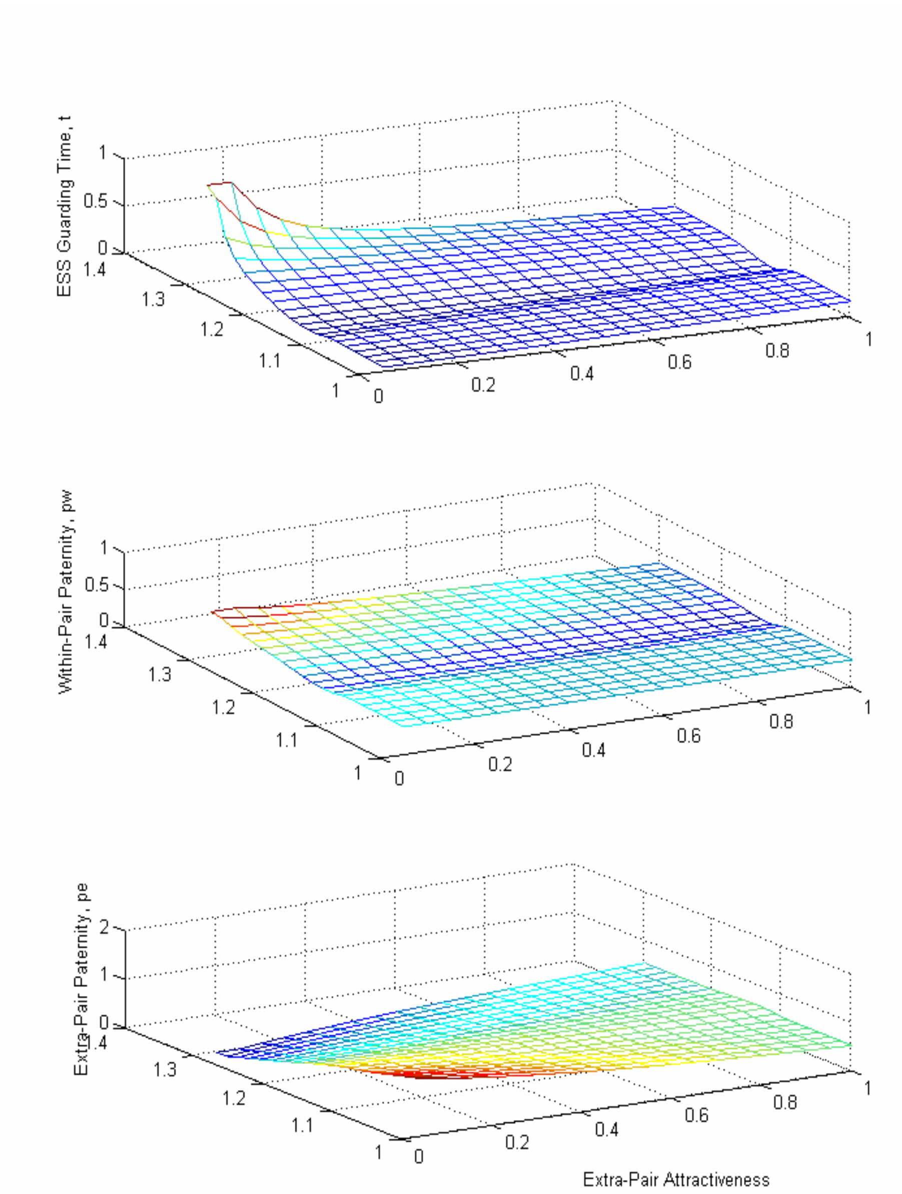

Figure 4. Evolutionarily stable guarding times, within-pair paternity, and extra-pair paternity as a function of extra-pair attractiveness ratio, with twenty attractiveness levels. Depth axis represents attractiveness as measured by how many times more likely females are to cheat. Attractive males are at front of graphs, unattractive males are at back. Parameter values used are g = 0.6, k_{ratio} = 1.3.

Morrell also showed these surprising nonlinear relationships between guarding time, relative attractiveness, and the rates of female infidelity, but made no comment about what these patterns may look like in actual populations.

Rather than stating simply that males of a higher attractiveness should guard more or less at given parameter values, I can say that males of average to slightly above-average attractiveness are better off guarding their mates very little under all regimes. This allows them to outcompete the unattractive males for their mates, giving them very high extra-pair paternity.

It is also interesting to note that when female infidelity levels got high enough, unattractive males decided to spend all of their time mate guarding, while the rest of the population didn't guard at all. This illustrates the trade-offs that are necessarily made by all of the animals in the optimal guarding regime. All of the attractiveness levels must balance their chances of "at home" paternity with their probability of paternity elsewhere.

My model predicts a pattern similar to the one seen in human society. Ugly guys and rich guys (unattractive and attractive, respectively), both spend more time guarding their females, by being jealous and following them around, or by giving them gifts to prevent them from straying, than their average to slightly above-average counterparts. Additionally, my model predicts that when the range between ugly and attractive in our society is very pronounced, the ugly or otherwise unattractive men should spend more of their time guarding their mates, in order to ensure that they get at least some paternity at home. My model doesn't take into account romantic love, or other human factors, but still does a relatively good job of predicting some human behaviors.

REFERENCES

Kokko, H. and L. J. Morrell. 2005. Mate, guarding, male attractiveness, and paternity under social monogamy. Behavioral Ecology 16: 724-731.