

Mate guarding, male attractiveness, and paternity under social monogamy

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Socially monogamous species vary widely in the frequency of extrapair offspring, but this is usually discussed assuming that females are free to express mate choice. Using game-theory modeling, we investigate the evolution of male mate guarding, and the relationship between paternity and mate-guarding intensity. We show that the relationship between evolutionarily stable mate-guarding behavior and the risk of cuckoldry can be complicated and nonlinear. Because male fitness accumulates both through paternity at his own nest and through his paternity elsewhere, males evolve to guard little either if females are very faithful or if they are very unfaithful. Attractive males are usually expected to guard less than unattractive males, but within-pair paternity may correlate either positively or negatively with the number of extrapair offspring fertilized by a male. Negative correlations, whereby attractive males are cuckolded more, become more likely if the reason behind female extrapair behavior applies to most females (e.g., fertility insurance) rather than the subset mated to unattractive males (e.g., when females seek “good genes”) and if mate guarding is efficient in controlling female behavior. We discuss the current state of empirical knowledge with respect to these findings. *Key words:* extrapair paternity, mate guarding, self-consistent model, sexual conflict. [*Behav Ecol* 16:724–731 (2005)]

Females of numerous socially monogamous species, particularly birds, have been shown to actively seek extrapair fertilizations (Griffith et al., 2002; Petrie et al., 1998; Westneat and Stewart, 2003; Westneat et al., 1990). For a female, having offspring fathered by a male other than her social partner has a number of potential benefits (reviewed in Jennions and Petrie, 2000). These include improving the genetic quality of offspring (e.g., Hasselquist et al., 1996), genetic compatibility (Johnsen et al., 2000), security against infertility of her mate (Krokene et al., 1998; Sheldon, 1994; Whitekiller et al., 2000), and inbreeding avoidance (Blomqvist et al., 2002; Foerster et al., 2003). Species vary widely in the frequency of extrapair young: in birds, the observed frequencies range from 0% to 76% (Griffith et al., 2002; Westneat and Stewart, 2003). Such variation has been explained by factors such as population density (Møller and Birkhead, 1993; but see Westneat and Sherman, 1997; Wink and Dyrce, 1999), breeding synchrony (Stutchbury and Morton, 1995; but see Griffith et al., 2002), the magnitude of variation in fitness-related traits in the population (Møller, 1997; Petrie et al., 1998), and the relative importance of male parental care (Møller, 2000), amongst others (reviewed in Griffith et al., 2002).

The extensive review of extrapair paternity by Griffith et al. (2002) does not mention mate guarding as a factor influencing paternity. However, if females are mating outside the pair bond, a male should endeavor to protect his paternity and guard against cuckoldry. While female infidelity can obviously select for mate-guarding behavior (Fishman et al., 2003; Van Rhijn, 1991), it also implies that males can have fitness opportunities away from their own social mate, which could potentially select for males who maintain less physical

proximity to their social mate. Whenever mate guarding plays a role in the sexual conflict over paternity, one should investigate how it influences the evolution of within-pair versus extrapair paternity and to what extent it limits the expression of female preferences (Green et al., 2002; Valera et al., 2003). Using the terminology of Westneat and Stewart (2003), extrapair paternity is a population-level variable (a “metatrait”) that emerges from the interactions of at least three individuals: the female, her social mate, and the potential extrapair male(s).

The matter is further complicated by plastic male and female behaviors. Females or males may follow adaptive rules of differential allocation where their reproductive effort and mating effort depend on the attractiveness, or quality, of their mate and themselves (reviewed in Magrath and Komdeur, 2003; Sheldon, 2000). It is reasonable to expect that optimal levels of mate guarding can be similarly plastic (Komdeur, 2001). But should an attractive male guard more or less than an unattractive male, and should we consequently expect a positive or negative correlation between the paternity a male gains at home and elsewhere? Here we shall show, using game-theoretic modeling, that the answer is not straightforward.

Both theoretically and empirically, mate guarding has been studied much more extensively in crustaceans and in insects than in vertebrates (e.g., Carroll, 1993; Grafen and Ridley, 1983; Härdling et al., 2004; Jablonski and Vepsäläinen, 1995; Jivoff and Hines, 1998; Jormalainen, 1998; Mathews, 2002; Parker, 1974; Plaistow et al., 2003). In nonvertebrates, precopulatory or postcopulatory guarding is maintained by continuous physical contact. In mate-guarding vertebrates (e.g., birds, lizards, and primates), males cannot guard their social mates in this way. Instead, mate-guarding males maintain proximity to their females and are thus at least partially able to fend off intruders or to form a disincentive for the female to seek potential extrapair males. Male birds commonly accompany females almost continuously from before the onset of incubation. The guarding period thus

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coincides with female fertility. By guarding in such a way, males face a trade-off, as they cannot simultaneously maximize both within-pair and extrapair paternity (Hasselquist and Bensch, 1991). However, a compromise strategy, where males guard during the fertile period of their female and seek extrapair copulations outside this time, appears to be an evolutionary stable strategy (Fishman et al., 2003; see also Saino et al., 1999) when female fertility is asynchronous within a population.

However, there are many cases where males are unable to simultaneously achieve high success at home and elsewhere. In many species there is considerable overlap between the fertile periods of females due to more or less synchronous breeding (Birkhead and Biggins, 1987). Females may also store sperm to some extent (Birkhead, 1998), which further extends the overlap between “profitable” times to approach different females. In such cases, we may expect that males face a trade-off with respect to time. When a temporal separation of guarding and extrapair activities is not possible, males must decide how much time to allocate to the two mutually exclusive activities of mate guarding and spending mating effort outside the pair bond. Currently we lack theory on how this conflict should be resolved, with two notable exceptions. Van Rhijn (1991) provided a simple simulation that highlights the frequency-dependent nature of the problem but does not solve for evolutionary equilibria, and Alonzo and Warner (2000) studied a specific system where mate guarding trades off with sperm production in a fish. Here, our aim is to develop general predictions on mate guarding and patterns of parentage in socially monogamous species.

THE MODEL

In our model, we assume that mate guarding can only be 100% efficient when it occurs 100% of the time (Chuang-Dobbs et al., 2001, and references therein; see also Johnsen et al., 1998a) and that there is a trade-off between mate guarding and gaining extrapair offspring (Gil et al., 1999; Hasselquist and Bensch, 1991; but see Stutchbury, 1998).

We assume that females’ fertile periods are synchronous, or alternatively, that females may be fertile at different times, but males do not know when the optimal time to guard a particular female is. Either case results in a time trade-off between mate guarding and mate acquisition, which we model by assuming that the male can only be performing one of these activities at a time. Thus, mate guarding is modeled as the time t ($0 \leq t \leq 1$) that the male spends “at home” (i.e., in close proximity to his social mate). The remaining time $1 - t$ is spent “elsewhere” (away from the male’s social mate), and during this time the male is free to search for extrapair matings. The assumptions on the timing of female fertility mean that males cannot improve their fitness by tailoring their guarding time t depending on their social mate’s or other females’ fertility. Thus, each male is assumed to use a constant value of guarding time t throughout the mating season. We assume, however, that males can be either attractive or unattractive, and guarding time can vary according to attractiveness.

To predict male fitness, we must assume a function that relates mate guarding effort and his attractiveness to his paternity at home (within-pair paternity p_W) and elsewhere (extrapair paternity p_E). Biologically reasonable functions for p_W and p_E must satisfy the following conditions:

- (1) Within-pair paternity p_W should obtain values between 0 and 1. It should be an increasing function of t , the male’s own guarding effort, and of t_{pop} , the mean guarding time used by males in the population. The latter relationship arises because guarding males will

not be able to attempt cuckoldry as often as non-guarding males.

- (2) Extrapair paternity p_E should decrease with t and with t_{pop} , for similar reasons as above.
- (3) If males vary in attractiveness, more attractive males should achieve more within-pair paternity than less attractive males, for the same guarding effort. Likewise, they should achieve more extrapair paternity, if the time spent not guarding is the same. With diminishing differences in attractiveness and guarding time between males, the expected paternities achieved should approach each other as well.
- (4) The distribution of paternity in the whole population must satisfy self-consistency (Houston and McNamara, 2002; Kokko and Jennions, 2003; Queller, 1997; Webb et al., 1999). This means that the total paternity achieved by all males must sum up to 1 per brood; for example, it is impossible that all males achieve 100% within-pair paternity and also gain paternity in other broods.

A very large number of functions relating guarding time to p_W and p_E satisfy the above criteria, and it is not feasible to study every possibility. We chose to study two very different, and flexible, families of functions for p_W . We examined the following two possibilities:

$$p_W(t,k) = \frac{t}{t + k(1 - t)^g c_{pop}} \tag{1a}$$

and

$$p_W(t,k) = g t^{k c_{pop}}. \tag{1b}$$

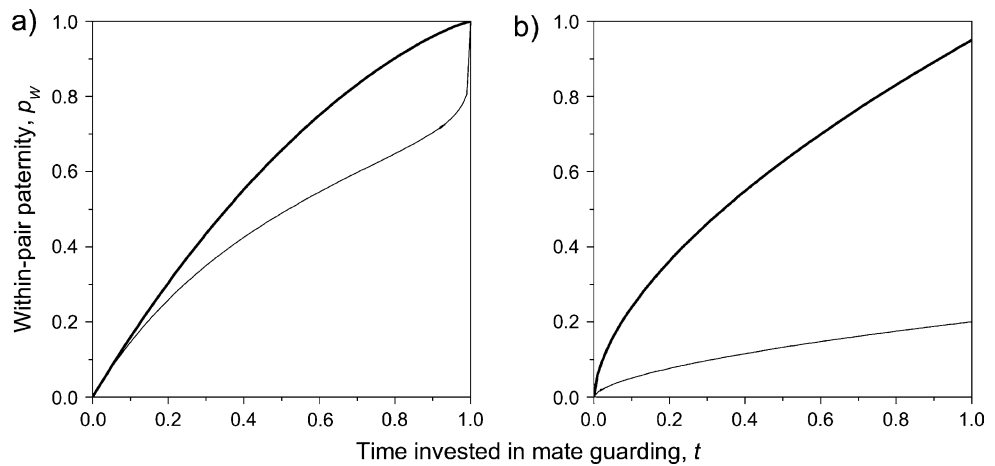
In these equations, the parameter k measures female infidelity. This is a measure of the eagerness with which females, paired to a male of specific attractiveness, seek extrapair copulations (and consequently how good they are at escaping male mate-guarding efforts). k will have different values for females paired to different males, if these differ in attractiveness. In our examples, we have either assumed no variation (same k for all males), or that a proportion x of males are highly attractive and experience female infidelity k_1 , and the remaining $1 - x$ are less attractive and experience infidelity $k_2 > k_1$. The infidelity parameter k alters the shape of the guarding curve: if females seek extrapair paternity very actively (high k), the guarding time t needs to be close to 100% ($t = 1$) before paternity approaches its maximum. When k is small, much smaller levels of guarding are sufficient to yield high paternity. We call k “female infidelity,” but it must be noted that it does not necessarily reflect observed levels of extrapair paternity: the latter results from an interaction between k (female behavior) and mate guarding (male behavior). Therefore, $k_2 > k_1$ does not mean that we assume a priori that less attractive males will achieve less within-pair paternity, rather, they will achieve less if they do not compensate for their unattractiveness by guarding more.

The parameter g in Equations 1a and 1b measures the efficiency of mate guarding. Small values of g imply that paternity improves slowly with increasing guarding effort. The difference between Models 1a and 1b lies in the shape of paternity increase. In Model 1a, males can achieve full paternity if they guard full time, but g determines how quickly this goal is reached (Figure 1a). In Model 1b, we assume that males cannot achieve full paternity even if they guard full time: $g < 1$ for this equation.

The parameter c_{pop} measures the competitive pressure from other male members of the population, which is a decreasing function of their mate-guarding effort t_{pop} . $c_{pop} = x(1 - t_{1,pop}) + (1 - x)(1 - t_{2,pop})$ describes the average

Figure 1

Model assumptions regarding within-pair paternity p_W . (a) Model 1a where 100% guarding time will lead to full paternity. The effect of the guarding efficiency is exemplified with two values of g (solid line, $g = 1.2$, dotted line, $g = 0.2$). Other parameters: $k = 1.2$, $t_{\text{pop}} = 0.5$. (b) The alternative Model 1b, where males do not achieve 100% paternity even if they guard full time. The effect of the guarding efficiency is exemplified with two values of g (solid line, $g = 0.95$, dotted line, $g = 0.2$). Other parameters: $k = 1.2$, $t_{\text{pop}} = 0.5$.



competitiveness of a population member, when the population strategy of guarding, $\{t_{1,\text{pop}}, t_{2,\text{pop}}\}$, is attractiveness dependent. The parameter a measures how efficiently the unattractive males compete for mates in extrapair situations, compared with attractive ones ($0 < a < 1$). In case of no quality variation, we set $a = 1$, which yields $c_{\text{pop}} = 1 - t_{\text{pop}}$.

The self-consistency argument (criterion (4) in the list above) requires that paternity sums up such that every offspring has one father (Houston and McNamara, 2002; Webb et al., 1999). This is achieved by first calculating the population-wide average paternity at home. This equals $p_{W\text{pop}} = x p_W(t_{\text{pop}}, k_1) + (1 - x) p_W(t_{\text{pop}}, k_2)$, where either Equation 1a or Equation 1b is used to calculate $p_W(t, k)$. Note that if males do not vary in quality, $x = 1$ and the equation simplifies accordingly.

Thereafter, we express extrapair paternity for the focal male as

$$p_E(t) = (1 - p_{W\text{pop}})c/c_{\text{pop}}. \quad (2)$$

Here, $1 - p_{W\text{pop}}$ is the paternity (per brood) available for extrapair males, and c/c_{pop} is the competitiveness of the focal male in getting a share of this paternity, relative to average members of the male population. If males do not vary in quality, the share simply depends on the time a male spends not guarding: $c/c_{\text{pop}} = (1 - t)/(1 - t_{\text{pop}})$. If they do, we have $c = 1 - t_1$ for attractive males whose guard time equals t_1 , $c = (1 - t_2)a$ for unattractive males who guard the amount t_2 , and c_{pop} as defined above. Fitness is equal to the sum of paternity at home and elsewhere and the evolutionarily stable guarding

time t^* is obtained by creating pairwise invasion plots (see, e.g., Dieckmann, 1997, for the exact procedure). In cases where males vary in attractiveness, the game is solved by numerically seeking the values $t_{1,\text{pop}}$ and $t_{2,\text{pop}}$ for which no other t_1 or t_2 can lead to increased fitness, $p_W(t_i) + p_E(t_i)$, for either type of male ($i = 1, 2$). The numerical procedure is simple, as the region of biologically feasible values for t is constrained, $0 \leq t \leq 1$, thus allowing to check all combinations of $\{t_1, t_2\}$ values (in practice, using a grid of values with a desired accuracy). We computed solutions with an accuracy of 0.005.

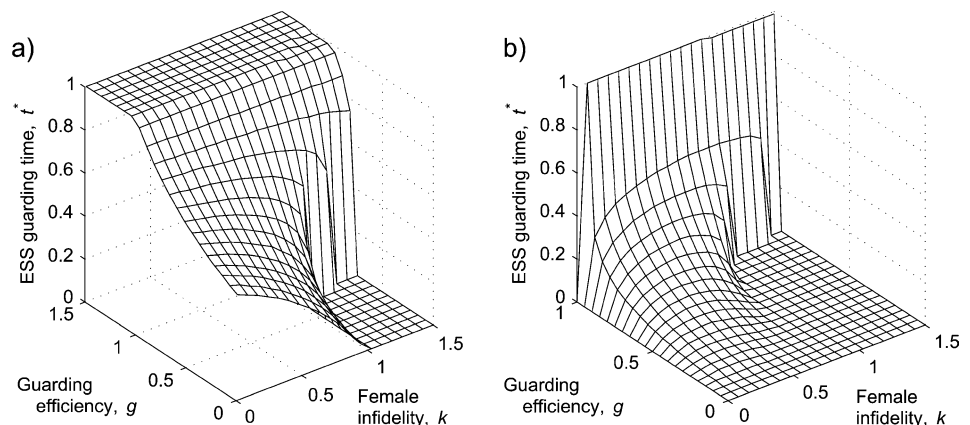
RESULTS

Guarding intensity might be expected to increase with the tendency of females to seek extrapair copulations (k). However, it turns out that this is not necessarily the case: the relationship is nonlinear and depends on the particular assumptions made regarding the shape of the trade-off between guarding and extrapair activities. Mate-guarding behavior is most intense when it is efficient (i.e., high g), but the effects of female infidelity vary depending on the exact assumptions made (Figure 2a,b). The paternity Function 1a predicts *less* guarding when females have a strong tendency for infidelity (Figure 2a). The Function 1b, on the other hand, predicts an initial increase in guarding time with increasing infidelity and then a decrease (Figure 2b).

Males that behave optimally clearly trade off the fitness gains obtained at home with gains elsewhere. If females never seek extrapair copulations, the time invested in guarding does

Figure 2

Evolutionarily stable mate-guarding effort as a function of female infidelity k and mate-guarding efficiency g , with within-pair paternity obeying (a) Equation 1a or (b) Equation 1b. Note that responses to infidelity differ between model assumptions. All males are assumed to be of equal quality ($a = 1$, identical k values among males).



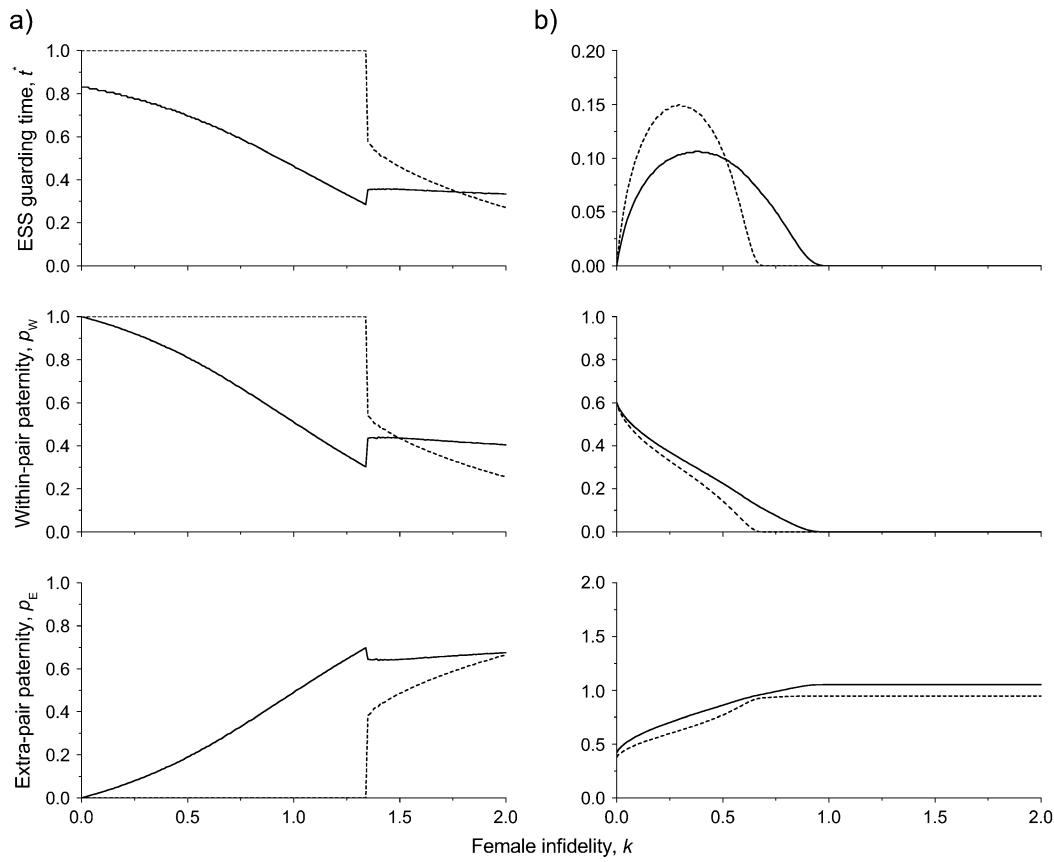


Figure 3

The impact of increasing female infidelity (k) on the evolutionary stable proportion of time invested in guarding, within-pair paternity, and extrapair paternity, according to the different model formulations (a or b, referring to paternity Functions 1a or 1b, respectively). Solid lines show time invested and paternity gained by attractive males, broken lines show guarding time and paternity gained by unattractive males. Parameter values used: (a), $x = 0.5$, $g = 0.8$, $a = 0.9$, $k_1 = k$ as indicated on the x-axis, $k_2 = 2k$; (b), $x = 0.5$, $g = 0.6$, $a = 0.9$, $k_1 = k$ as indicated on the x-axis, $k_2 = 1.5k$.

not have any fitness consequences for the male in our model where the investment trades off with extrapair activities only (and not with, e.g., foraging). In this case it is selectively neutral. With increasing infidelity, the importance of mate guarding increases, but so does the lost opportunity cost of mate guarding. This is because higher female infidelity implies higher potential fitness benefits to the male, provided by extrapair females. Additionally, the efficiency of mate guarding in ensuring paternity deteriorates when females seek extrapair activities very intensely, and this explains why mate guarding becomes less intense, or vanishes, at high values of k .

When males vary in their ability to attract extrapair females and ensure paternity at home, further complications are possible. Observed within-pair paternity levels arise through an interaction between the tendency of females to seek extrapair mates and the guarding behavior of males. A typical result of this interaction is that attractive males guard less than unattractive males (Figure 3): being attractive both improves the paternity a male gains at home gained when he guards little and enhances his success when he spends time elsewhere. In some cases (Figure 3a, low to moderate k), unattractive males spend all their time mate guarding and forego the chance of any extrapair paternity. For attractive males, the trade-off is different: higher chances of gaining paternity away from home, together with their social mate being less inclined to seek extrapair offspring, means that the optimal time attractive males spend guarding is less.

However, this argument does not always hold, due to possible nonlinear relationships between time spent guarding and its effectiveness in deterring extrapair activities. With high values of female infidelity (k) in Figure 3a,b, unattractive males are not able to secure much paternity at home regardless of their guarding effort. Consequently, they may guard less than attractive males or cease guarding altogether. Attractive males may still spend some time guarding, unless infidelity k increases further to make guarding inefficient for these males too (Figure 3b).

The exact patterns clearly depend on how a male's attractiveness influences his success at securing paternity at home versus elsewhere. Despite these complications, attractive males are often predicted to guard less, given their higher success outside the pair bond. Does this also mean that they gain less paternity at home, or is reduced guarding fully compensated by their attractiveness (such that their social mate does not tend towards infidelity as strongly as females of other males)? The former possibility predicts that within-pair and extrapair paternity gained by a male should correlate negatively, whereas the latter predicts a positive relationship.

Our model predicts that either scenario is possible. In the example of Figure 3a, compensation is nowhere near complete: attractive males suffer from lower within-pair paternity when they spend less time mate guarding than unattractive males, except for a small region at high-infidelity values where guarding times are almost identical. They enjoy much higher extrapair paternity, however. Interestingly, they

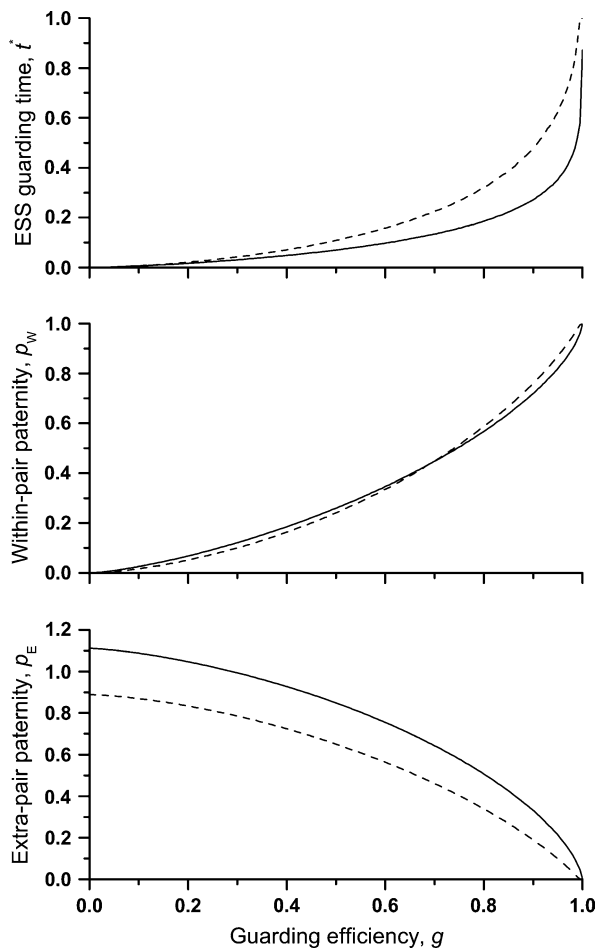


Figure 4
Evolutionarily stable guarding times t^* , as well as within-pair and extra-pair paternity for attractive and unattractive males, as a function a , the relative success of the less attractive males, when they are attempting extra-pair copulations. This example uses within-pair paternity Function 1a with parameter values $x = 0.5$, $k_1 = 0.5$, $k_2 = 0.8$, $g = 0.1$.

are able to cuckold other attractive males, as unattractive males spend 100% of their time guarding, which totally protects their within-pair paternity interests. In the example of Figure 3b, on the other hand, we have assumed that full-time guarding does not guarantee full paternity. Consequently, guarding is less intense, paternities are more evenly distributed, and attractive males win on both fronts: they gain more paternity both at home and elsewhere.

Thus, attractiveness can sometimes compensate for reduced mate guarding at home, but it does not always do so. This is illustrated by varying the relative attractiveness of unattractive males (Figure 4). When unattractive males have very low success elsewhere (small a), their guarding becomes so intense that their within-pair paternity improves beyond that of attractive males. As the relative attractiveness of unattractive males approaches that of attractive ones (high a , Figure 4), the males that gain more extra-pair paternity gain more at home too. Finally, the sign of the correlation between within-pair and extra-pair paternity may also depend on the efficiency of guarding, g . In the example of Figure 5, the higher guarding effort by unattractive males almost perfectly compensates for their social mate's stronger tendency to cuckold them. When guarding is very efficient (high g), it overcompensates, and unattractive males end up with higher

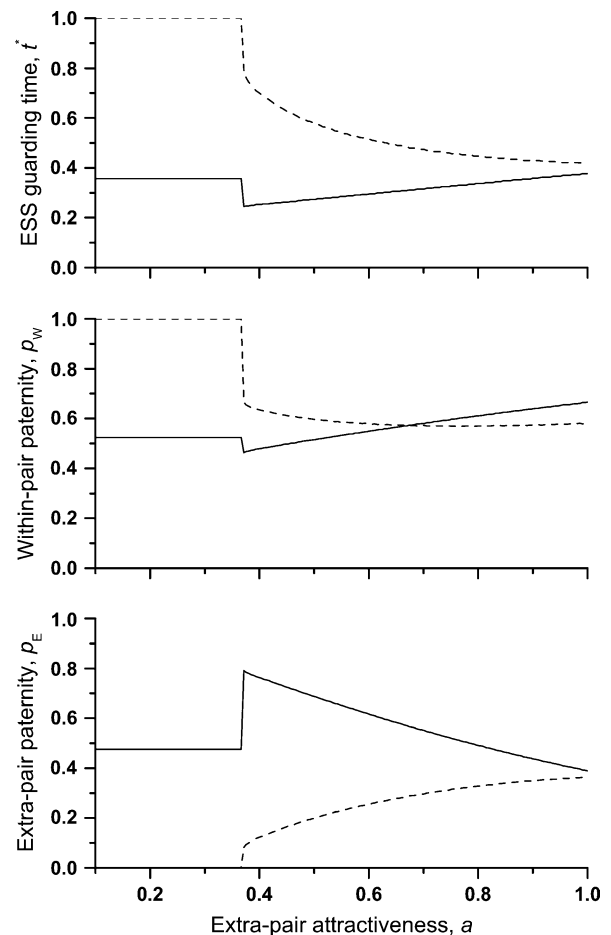


Figure 5
Evolutionarily stable guarding times t^* , as well as within-pair and extra-pair paternity for attractive and unattractive males, as a function of the efficiency of guarding g . This example uses within-pair paternity Function 1b with parameter values $x = 0.5$, $k_1 = 0.3$, $k_2 = 0.4$, $a = 0.8$.

within-pair paternity p_w than attractive males. When guarding is less efficient (low g), it undercompensates.

DISCUSSION

Our modeling shows that mate guarding can substantially alter paternity patterns from what would be expected based solely on how much females are assumed to benefit from extra-pair fertilizations. The extent of mate guarding in a particular mating system, however, is difficult to predict for a number of reasons. First, as the female tendency to seek extra-pair copulations increases, there is more reason for the male to mate guard, but at the same time any particular level of mate guarding becomes less efficient, thus forming a disincentive to mate guard (see Morrell, 2004, for a related argument in a different context). Second, if mate guarding intensity is based on a trade-off between paternity at home and elsewhere, increasing female infidelity implies larger fitness gains for males who spend more time away from home looking for additional matings. This explains why mate guarding ceases if females become very unfaithful (or very good at escaping male mate-guarding attempts) and highlights the importance of taking into account population-level feedbacks in a self-consistent way when developing models of

mating systems (Houston and McNamara, 2002; Kokko and Jennions, 2003; Queller, 1997; Webb et al., 1999).

The curvilinear relationship between female infidelity and optimal level of mate guarding also complicates the relationship between mate guarding and observed within-pair and extrapair paternity. We investigated the consequences of two different assumptions on biologically feasible relationships between guarding and within-pair paternity, and in both cases the outcomes depend on details such as the efficiency of guarding and the eagerness of females to seek extrapair copulations. This may help explain why it is difficult to detect an overall association between mate guarding and paternity in an interspecific comparison (Møller and Ninni, 1998). For example, low mate-guarding intensity can be equally well predicted under conditions that yield low paternity (guarding is of little use if expected paternity remains low no matter how much the male guards) or under conditions that yield high paternity (if females do not gain much benefit from extrapair offspring, there is little need to guard, as suggested for the purple sandpiper; Pierce and Lifjeld, 1998). Across species, least mate guarding occurs in highly polygynous taxa (Møller and Birkhead, 1991), which fits in well with our results that predict cessation of mate guarding at highest values of infidelity k .

If females vary in their behavior depending on the attractiveness of their mate, we can also expect complications in the relationship between male attractiveness and his paternity with his social mate. Attractive males are often predicted to guard less in our model, yet an attractive male does not necessarily suffer a great fitness loss through cuckoldry in his own nest, if his attractiveness makes his social mate less prone to mate with extrapair males. However, in other cases we predict that unattractive males guard so much more intensely than attractive males that the within-pair paternity of the latter remains smaller. Such cases are reflected as a negative correlation between paternity at home and elsewhere, and we predict this to be particularly likely when variation in male attractiveness is high (low a in the model) and when females do not pay disproportionate attention to their own social mate's attractiveness when "deciding" whether to engage in extrapair activities. Another requirement for a negative correlation is that mate guarding is sufficiently efficient to limit free expression of female mating preferences because this allows the inferior males to maintain high within-pair paternity.

Is there evidence supporting our result that it can sometimes pay attractive males to reduce mate guarding to such a degree that their paternity at home suffers? A meta-analysis (Møller and Ninni, 1998) implies that male birds with more extravagant secondary sexual characters generally enjoy higher paternity in their own nests, but this study did not explicitly quantify if the same males also had elevated success elsewhere. Both positive and negative correlations can be found in the literature. For example, older Bullock's orioles *Icterus galbula bullockii* lost less within-pair paternity and gained more extrapair fertilizations than did yearling subadult males (Richardson and Burke, 1999). Similarly, most extrapair males in the blue tit *Parus caeruleus* did not lose paternity themselves (Kempnaers et al., 1997), and in this species poor-quality males who guard lose paternity to good-quality males despite their more intense mate-guarding behavior (Kempnaers et al., 1995). But in the yellow warbler *Dendroica petechia*, known extrapair sires were just as likely to be cuckolded themselves as any male in the population (Yezerinac et al., 1995), and for the pied flycatcher *Ficedula hypoleuca*, it has been reported that attractive black males are cuckolded more than brown unattractive ones (Lifjeld et al., 1997)—although these authors did not find mate guarding an adequate

explanation for the pattern. Only a handful of studies exist that document relationships between male mate guarding and other aspects of the mating system. Black-throated blue warbler *Dendroica caerulescens* males with many extrapair opportunities have been shown to guard less and consequently end up with less paternity in their own broods (Chuang-Dobbs et al., 2001). Other species in which guarding correlates negatively with paternity at home include blue-throats (Johnsen et al., 1998b) and purple martins (Wagner et al., 1996). In wheatears *Oenanthe oenanthe*, on the other hand, good body condition seems to aid paternity at home as well as improves success elsewhere (Currie et al., 1999).

In the example of the wheatear, the positive correlation may be partly explained by adaptive time allocation: males guard intensely when the female is close to laying (Currie et al., 1998), which may allow the best males to escape the strict trade-off and achieve high paternity at home as elsewhere. In our model, we assumed that males could not escape the trade-off; if they do so (at least partly), the likelihood of positive correlations between within-pair and extrapair paternity will increase. In any case, late-breeding wheatears are documented to use direct guarding more than early-breeding ones (Currie et al., 1998), a pattern predicted by our study if the early-arriving birds are better competitors (Kokko, 1999). Similarly, in penduline tits *Remiz pendulinus*—a species in which neither mate guarding nor cuckoldry is particularly intense—males who guarded most were more likely to suffer cuckoldry (Schleicher et al., 1997).

Like all models, ours makes some simplifying assumptions. Firstly, we have examined only two families of biologically plausible paternity functions (Equations 1a and 1b). Reality could, of course, provide us with a larger set of possibilities. However, most of our current conclusions point out that a limited set of functions can produce diverse outcomes. Adding more functions to this list could only increase the diversity, thus only strengthening the generality of our conclusions. A second assumption is that the model is based on the assumption that females pursue extrapair copulations (infidelity parameter k). While there is some consensus that this is indeed the case, studies that detail the costs and benefits of such behavior are rare (reviewed in Westneat and Stewart, 2003). We have also assumed that the parameter k , which summarizes female behavior, is fixed for a given species. Given this lack of empirical knowledge, it may be premature to suggest that a model should consider the coevolution of both female and male behaviors. Nevertheless, such a co-evolutionary scenario could have interesting implications, and might help to focus on the most likely ones of the multitude of scenarios that the current modeling effort has produced. Such future studies should also consider the possibility that females gain by resisting extrapair copulation attempts by some males (Gavrilets et al., 2001; Westneat and Stewart, 2003).

The extent to which female control over extrapair fertilizations is restricted by mate guarding requires much more study. The above results give the impression that examples where less attractive males gain more paternity at home (due to extensive and efficient mate guarding) seem quite rare. If this proves to be true generally, mate guarding does not appear a very strong evolutionary force in shaping mating systems. But if females regularly escape mate-guarding attempts, we face an enigma: why does mate guarding evolve, if it is so inefficient? Currently, we do not have a general answer to this question. Studies on paternity rarely present data in a form that allows direct comparison of within-pair and extrapair paternity, and direct data on mate guarding is usually lacking. Such data are crucial before general conclusions can be made about the importance of mate

guarding in shaping genetic parentage in socially monogamous species.

Thus, we can only point to a surprising lack of knowledge on natural systems regarding the various theoretical possibilities: the relationship between male attractiveness and mate guarding may mean that sexual selection uniformly favors attractive males both in their own brood as well as elsewhere, or, alternatively, less attractive males perform relatively well under social monogamy, due to their mate-guarding efforts. In the latter case, mate guarding diminishes the intensity of sexual selection arising through female choice. Even in the cases where mate guarding can be shown to be efficient in restricting female infidelity (as has been shown experimentally for the Seychelles warbler *Acrocephalus sechellensis*, Komdeur et al., 1999, and black-throated blue warblers, Chuang-Dobbs et al., 2001), between-individual variation can allow for a variety of different relationships between guarding and paternity. These patterns remain to be investigated in wild populations, as do those that arise from the interaction between mate guarding and alternative paternity guards, such as frequent copulations (Møller and Birkhead, 1991).

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