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Mate guarding as a key factor in the evolution of parental care in birds

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Abstract. The evolution of male parental care in vertebrates with internal fertilization must have been preceded by a stage in which males profit by staying with the female after copulation. This paper discusses the results of a series of computer simulations to determine the pay-off to post-copulatory mate guarding under various conditions. Guarding is promoted by asynchrony in fertility of the females, high copulation frequencies of females, preference of females for males using the guarding strategy, and mate fidelity of guarded females. Moreover, it is demonstrated that, under several conditions, apparently those operating in a natural environment, the success of the guarding strategy is inversely related to its frequency in the population. This implies that both the guarding and the non-guarding strategy can be maintained in the same population. This phenomenon is put forward as a key factor determining the pathways in the evolution of parental care.

The origin of parental care in birds was probably closely related to the acquisition of body temperature regulation, because this could also require regulation of egg temperature. Parental care must have been preceded by a stage without prolonged care after egg laying and could be established as soon as individuals succeeded in rearing more surviving offspring by incubation or other care, than simply by leaving the eggs to their fate. Parental care might have originated in three alternative ways.

First, both parents, female and male, could have evolved the ability to care for their offspring. There are two reasons why such transition from no care at all to biparental care cannot simply be rejected: (1) males and females possess almost the same set of genes, and thus are almost equally affected by natural selection for parental care, and (2) continuous regulation of egg temperature is not very easy for one parent, especially as foraging for its own needs takes a lot of time. However, there is at least one very important hindrance to the evolution of biparental care in species with internal fertilization (reptiles, birds and mammals): females and males experience quite different circumstances at the time of egg laying. Mothers are necessarily present when the eggs are laid, but fathers are not (Maynard Smith 1977). Another obstacle to the sudden appearance of biparental care is the slow rate of change in the course of evolution in the need for parental care by the offspring. It is therefore difficult to imagine how the aid of a second parent would further increase the number of surviving offspring in species evolving from a stage without parental care. Their young may still be adapted to survive without care at all. Evidence for evolution of biparental care via a stage of care by one parent has also been presented by Gittleman (1981) by pedigree analysis for fish. Thus, the idea of a direct transition, from a stage without parental care to a stage with biparental care, does not seem to be very realistic.

Second, the female could have evolved the ability to care for her offspring. This possibility seems to be rather plausible because the female lays the eggs. The evolution of prolonged care of the eggs by the female requires, as a matter of course, that a new (mutant) type of female, who performs some care, arises in the population. It also requires that this investment results in more surviving offspring than the same investment in prolonged laying or the same investment in extra reserves for the eggs. If these conditions are fulfilled, natural selection should, after a number of generations, result in all females having the ability to care for their offspring. Thus, the idea of a transition from a stage

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without parental care to a stage with parental care by the female seems to be associated with simple conditions. However, in birds the female allocates considerable reproductive effort in the formation of eggs. It has been argued that this effort was even greater in the common ancestor of birds, probably before it performed any prolonged parental care (Elzanowski 1985). It is reasonable to suggest that extra investment in care after laying necessarily leads to lower investment in reserves before laying, and possibly to fewer surviving offspring. This could have been an obstacle in the evolution of parental care by the female, which possibly facilitated the evolution of male parental care.

Thus, third, the male could have evolved the ability to care for his offspring. This possibility might have occurred if there was any other reason for the male to stay after copulation with the female, at least until egg laying. There seems to be at least one situation in which it is advantageous to the male to stay with the female. If females tend to copulate with many different males for the same clutch of eggs, and if males are able to keep other males away from females, the reproductive success of a male may increase when he guards females after insemination until egg laying. Such a male would ensure that his inseminations fertilize the eggs. This is, in fact, the beginning of a monogamous pair-bond. The establishment of such a bond may be the basis for the evolution of male parental care.

MATE GUARDING

The possibility of the evolution of male parental care depends on the benefits and costs of post-copulatory mate guarding. The benefits of the guarding strategy may be described as an increase in the efficiency of insemination (e.g. Birkhead et al. 1987). Guarding raises the probability that copulations with a certain female lead to fertilization. However, this strategy may also incur considerable costs for the male. During mate guarding a male is less able than non-guarding males to court other females and, thus, to copulate with them. This may lead to a lower reproductive success than for non-guarding males. The costs of the guarding strategy may thus be described as a decrease in the number of females who can be inseminated. In cases where the benefits outweigh the costs, natural selection should promote the evolution of guarding. Where costs exceed benefits, natural selection should not promote mate guarding.

The cost and benefits of guarding for an individual are closely related to the frequency of guarding in the population (van Rhijn 1984). If the guarding strategy is rare, implying that the majority of males try to copulate with any female, the benefits of guarding are high, because many copulation attempts by other males can be prevented. The costs, however, are also high, because the guarding male has to refrain from many copulation opportunities with other females. If, however, guarding is common, it may be difficult for a male to find an unguarded female. This implies that the costs of guarding are comparatively low: the time needed to find a female is long in comparison with the time needed for guarding. It also implies that the benefits of guarding are low: the probability of an unguarded female copulating for a second time is much lower than in the situation with mainly non-guarding males. This could mean that both guarding and non-guarding strategies can be maintained in the same population as a mixed evolutionarily stable strategy (ESS; e.g. Maynard Smith 1982).

Earlier theoretical work, however, suggests that precopulatory mate guarding, a kind of guarding promoting future access to receptive females, evolves only as a pure ESS (Grafen & Ridley 1983; Ridley 1983). This should occur if females permit males to copulate for a very short period of their reproductive cycle, provided that males are able to judge the female's reproductive state. In contrast, models of post-copulatory mate guarding (Yamamura 1986; Yamamura & Tsuji 1989), primarily developed for insects, suggest that guarding and non-guarding strategists may coexist in the same population. The differences between the outcomes of these models might indicate that pre-copulatory and post-copulatory guarding are fundamentally distinct, or instead, that the assumptions do not correspond. Clearly, we do not yet understand how mate guarding might have evolved. In this paper, I use computer simulations to study the costs and benefits of post-copulatory mate guarding, especially under conditions that apply to vertebrates with internal fertilization of eggs.

PROCEDURES

My experimental subjects belonged to a hypothetical species without parental care. Two different types of male mating strategies could occur in this species: mate guarding and non-guarding. Males with the least complex non-guarding strategy started to court females (searching) to test whether they were willing to copulate, copulated as soon as they found a receptive female, and, subsequently, continued to search. Males with the more complex non-guarding strategy also started to search and court to test whether a female was willing to copulate, copulated as soon as they found a receptive female, then stayed with that inseminated female and prevented copulations with other males up to the end of her fertile period, after which they started to search again.

To investigate what could happen in such a species, I composed small populations, mostly consisting of 20 males and 20 females. Then I determined the properties of the individuals in these populations. In most cases I assumed that the females in the population produced one clutch of eggs per reproductive season. This is a simplification of reality which does not seem to affect the data in an essential way, because a few trials with successive clutches gave similar results. The duration of the fertile period of a female was considered to be similar for all individuals, the onset of the fertile period was considered to differ between females, and the distribution of onsets over time was considered to be normal. By this combination of assumptions I could create a greater or lesser extent of overlap between the fertile periods of different females. Finally, all eggs were considered to be fertilized by sperm received from the male copulating last during the fertile period of the female concerned. This assumption seems to approach the normal situation for the separate eggs of birds, although earlier copulations may contribute also, but to a lesser extent (McKinney et al. 1984; Birkhead 1988). I programmed the computer to give details about the copulations in such populations with previously determined properties. This was done for 100 successive simulation trials. On the basis of the final copulations of 20 females in each of these 100 trials (2000 copulations) the relative success of males with the guarding strategy was determined by dividing the average number of such copulations per guarder by the average number of such copulations per non-guarder. Simulations were based on a model with a discrete time scale. They were performed with various values for: (1) duration of the female's fertile period; (2) variance in the onset of the fertile periods of the different females; (3) copulation frequency; and (4) proportion of males with the guarding strategy in the population. All simulation programs were run on an IBM compatible personal computer, using Turbo Pascal as the programming language.

I use the following terminology in this paper. Males with the non-guarding strategy are 'non-guarders' (NG), and males with the guarding strategy 'guarders' (G). A 'guard' is a guarder that actually accompanies a particular female after having copulated with her. 'Searching' is the courtship activity of non-guarders under all circumstances and of guarders when these do not accompany females inseminated by them.

SIMULATION RESULTS

Receptivity Determined by Females

In the first set of simulations I assumed that receptivity was determined only by the female. She copulated at least once at previously determined time units in her fertile period. The probability of a particular time unit being chosen was constant over the whole fertile period, and thus independent of the number of searching males. The probability that an unguarded female copulated with a male displaying the guarding strategy was determined by the frequency of such males among those searching. Thus, that probability was low when the majority of these males were guarding. In all simulations the females were programmed to copulate 1·8 times on average (copulation frequency, $C=1{\cdot}8$) and there were 10 guarders and 10 non-guarders ($G/NG=10/10$). When the duration of the fertile periods is increased, and all other properties of the population are held constant, the relative success of males with the guarding strategy decreases (Fig. 1). In contrast, an increase in the variance on the onset of fertile periods leads to an increase in the relative success of guarders (Fig. 2). The results shown in Figs 1 and 2 suggest that the relative success of the guarding strategy decreases when females have long fertile periods and when they tend to synchronize fertility (low variance).

The relative success of males with the guarding strategy further seems to depend on the number of copulations accepted by the female. An increase in the number of copulations leads to a considerable increase in the success of guarders (Fig. 3). The relative success of the guarding strategy is also related to the relative frequency in the population of males with the guarding strategy (Fig. 4). In one example in Fig. 4, when the duration of the fertile

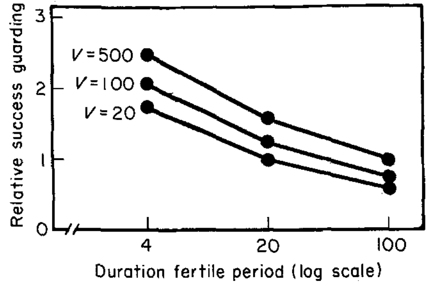

Figure 1. Copulation at pre-determined times: influence of variable durations of the female's fertile period on the relative success of guarding, for different variances (V) in the onset of fertile periods. Copulation frequency $C=1{\cdot}8$; Proportion of guarders G/NG = 10/10. A relative success below 1 indicates that the proportion of guarders is expected to be lower in the next generation. A relative success above 1 indicates that this proportion will be higher.

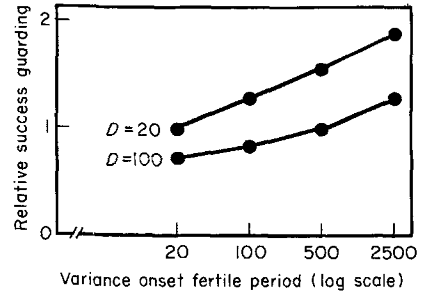

Figure 2. Copulation at pre-determined times: influence of variable variances in the onset of the fertile periods of the females on the relative success of guarding, for two different durations (D) of the fertile period. Copulation frequency $C=1{\cdot}8$; proportion of guarders G/NG = 10/10.

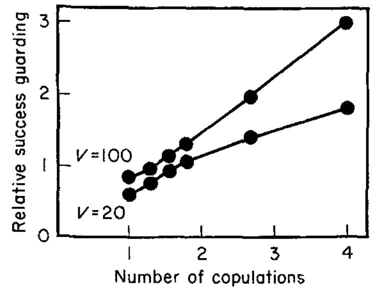

Figure 3. Copulation at pre-determined times: influence of variable copulation frequencies on the relative success of guarding, for two different variances (V) in the onset of fertile periods. Duration of fertile period $D=20$; proportion of guarders G/NG = 10/10.

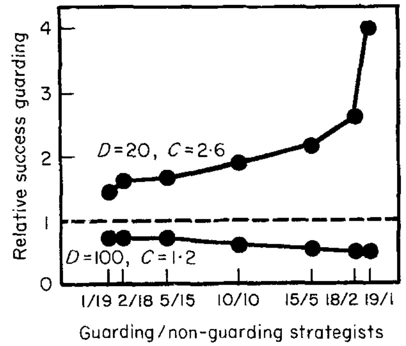

Figure 4. Copulation at pre-determined times: influence of variable proportions of guarders in the population on the relative success of guarding, for rather short fertile periods with moderate numbers of copulations ($D=20$, $C=2{\cdot}6$) and long fertile periods with few copulations ($D=100$, $C=1{\cdot}2$). Variance in the onset of fertile periods $V=100$. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

period is 20 and the average number of copulations 2·6, a change in relative frequencies of males leads to a change in relative success, but at all frequencies guarders remain more successful than non-guarders. In the other example (duration = 100, number of copulations = 1·2) a change in relative frequencies also leads to a change in relative success, but in all cases guarders remain less successful than non-guarders. In spite of many trials in this series of simulations, I could not find any example in which a change in relative frequencies resulted in a change from less successful to more successful, or vice versa. Thus, assuming that the properties of a population remain constant, it does not seem that guarders and non-guarders can co-exist in the same population.

The initial assumptions for the fictitious population were perhaps not very realistic. Females did not discriminate between guarders and non-guarders, and guarders were thought to be fully capable of preventing the female, guarded by them, from copulating with other males. The guarding strategy may even be maintained when females tend to prefer non-guarding males for copulation, provided that they accept a large number of copulations (Fig. 5). The guarding strategy may also be maintained when guards (guarding guarders) are not fully capable of preventing other copulations, provided that females accept a large number of copulations and that guarded females mostly select their guard for copulation (Fig. 6). When the guard has a 200-fold or 20-fold advantage the guarding strategy

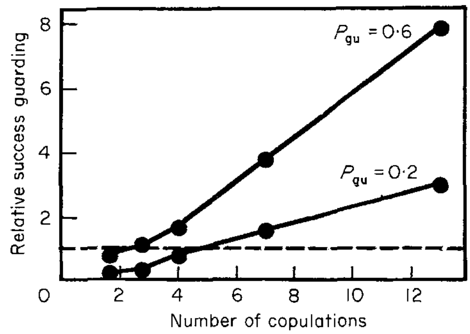

Figure 5. Copulation at pre-determined times: influence of variable copulation frequencies on the relative success of guarding when non-guarded females prefer non-guarders over searching guarders for copulation, for two different relative disadvantages (P_{gu}) of guarders compared with non-guarders. Duration of fertile period $D = 20$; variance in the onset $V = 100$; proportion of guarders G/NG = 10/10. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

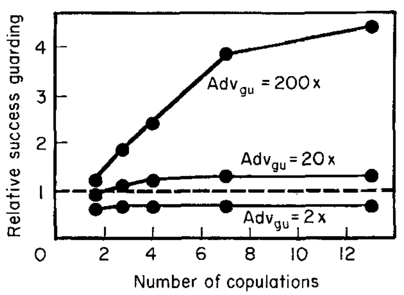

Figure 6. Copulation at pre-determined times: influence of variable copulation frequencies on the relative success of guarding when guards are not fully capable of preventing other copulations, for various relative advantages (Adv_{gu}) of guards compared to other searching males. Duration of fertile period $D = 20$; variance in the onset $V = 100$; proportion of guarders G/NG = 10/10. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

may become fixed, but the two-fold advantage of guards seems to be too low to maintain the strategy.

This first set of simulations suggests that the guarding strategy is promoted by the following factors: (1) short fertile periods; (2) asynchrony in fertility of the females (high variance); (3) many copulations per female per fertile period; (4) a preference of females for copulating with males using the guarding strategy; and (5) mate fidelity of the guarded females.

It is not very likely that, in species without parental care, natural selection would favour the last two possibilities: females who copulate with males using the guarding strategy, or females who are faithful to their mate. In such species females should select the best males, and the best males should not waste time by guarding. Yet, there remain sufficient other possibilities for the evolution of mate guarding in species without parental care by the male. The present approach, however, offers no support for the idea that the guarding and non-guarding strategies may coexist permanently within the same population.

Receptivity Determined by Males

The assumption that the probability of copulating is independent of the number of searching males is somewhat unrealistic. For that reason I proceeded with a second set of simulations, in which receptivity of the female was determined by males. The probability of a female accepting a copulation during a particular time unit was assumed to depend on courtship activity, a function of the number of searching (non-guarding) males and on the types of males around her. For each simulation run I determined five probabilities, which could all be different: (1) the probability (s) per time unit that a searching male copulates with an unguarded female (this probability may be different for males using the guarding strategy and those using the non-guarding strategy); (2) the probability (f) per time unit that a guard performs a subsequent copulation; and (3) to take account of the possibility that guarding is not a fully effective mechanism for preventing copulations by other males, I defined the probability (k) per time unit that a searching male kleptoparasitizes a guarded female; this probability may also be different for males using the guarding strategy and those using the non-guarding strategy.

Figure 7 shows an example of the results of these simulations. When the probability (s) that any searching male copulates with an unguarded female is increased, while all other variables are held constant, the relative success of guarders also increases. These results also show again that the relative success of guarding is positively influenced by asynchrony of fertility (V). In all these simulations the probabilities of copulating were similar for males using the guarding strategy and those with the non-guarding strategy. Fertile periods of all females were 20 time units in length ($D = 20$). There

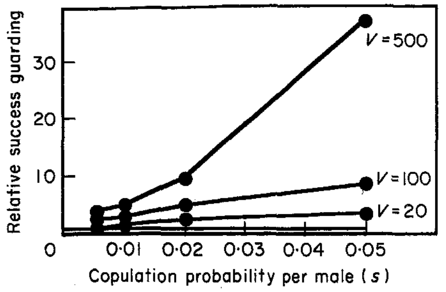

Figure 7. Copulation dependent on courtship activity: influence of variable copulation probabilities per male on the relative success of guarding, for different variances (V) in the onset of fertile periods. Duration of fertile period $D=20$; proportion of guarders G/NG = 10/10; no subsequent copulations by guard $f=0$; no kleptoparasitism $k=0$. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

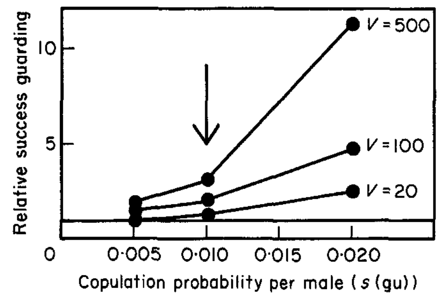

Figure 8. Copulation dependent on courtship activity: influence of variable copulation probabilities of searching guarders on the relative success of guarding at constant copulation probabilities of non-guarders (s(ng) = 0·01), for different variances (V) in the onset of fertile periods. Duration of fertile period $D=20$; proportion of guarders G/NG = 10/10; no subsequent copulations by guard $f=0$; no kleptoparasitism $k=0$. The arrow indicates where searching guarders and non-guarders have equal copulation probabilities. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

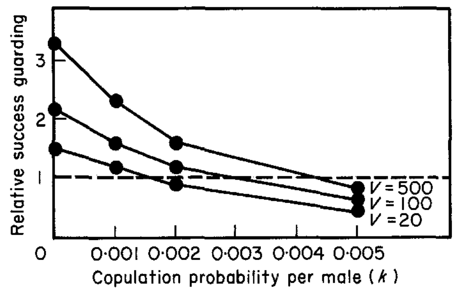

Figure 9. Copulation dependent on courtship activity: influence of variable copulation probabilities of searching males with guarded females (kleptoparasitism), for different variances (V) in the onset of fertile periods. Duration of fertile period $D=20$; proportion of guarders G/NG = 10/10; copulation probability $s=0{\cdot}01$; no subsequent copulations by guard $f=0$. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

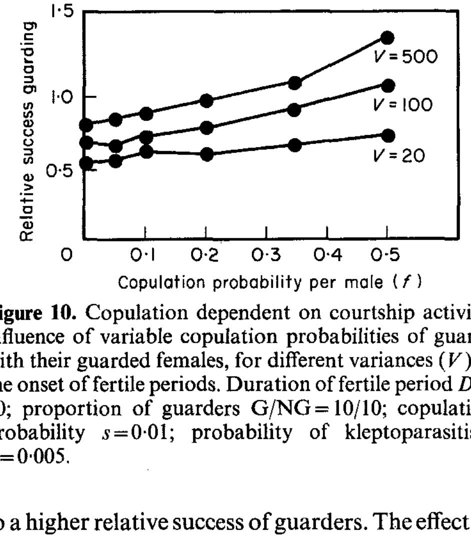

Figure 10. Copulation dependent on courtship activity: influence of variable copulation probabilities of guards with their guarded females, for different variances (V) in the onset of fertile periods. Duration of fertile period $D=20$; proportion of guarders G/NG = 10/10; copulation probability $s=0{\cdot}01$; probability of kleptoparasitism $k=0{\cdot}005$.

were always 10 males present with the guarding strategy and 10 with the non-guarding strategy (G/NG = 10/10). Females did not continue to copulate with their guards ($f=0$), but guarding was always fully effective in preventing copulations with other males ($k=0$).

Differences in the preference of females for guarding and non-guarding males also influence the relative success of the guarding strategy (Fig. 8). An increase in the copulation probability (s_{gu}) leads to a higher relative success of guarders. The effect of kleptoparasitism is demonstrated in Fig. 9. When the probability (k) of any searching male copulating with a guarded female is increased, and the other variables are held constant, the relative success of guarding decreases. The effect of continuation of copulation with guards is shown in Fig. 10. When the probability (f) of a guarding male copulating again with the same female is increased, the relative success of guarding also increases, provided that guarding is not fully successful and that the copulation probability of the guarding male is much higher than the probability of kleptoparasitism by each of the searching males ($k=0{\cdot}005$).

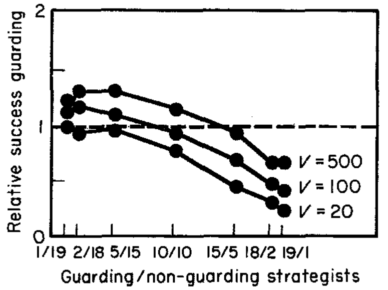

Figure 11. Copulation dependent on courtship activity: influence of variable proportions of guarders in the population on the relative success of guarding at low copulation probabilities of searching guarders (s(gu) = 0·005) and higher copulation probabilities of non-guarders (s(ng) = 0·20), for different variances (V) in the onset of fertile periods. Duration of fertile period $D = 20$; no subsequent copulations by guard $f = 0$; no kleptoparasitism $k = 0$. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

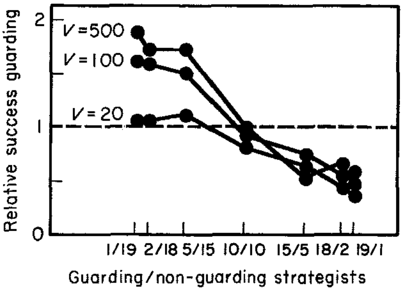

Figure 12. Copulations dependent on courtship activity: influence of variable proportions of guarders in the population on the relative success of guarding at low rates of kleptoparasitism ($k = 0·005$), for different variances (V) in the onset of fertile periods. Duration of fertile period $D = 20$; copulation probability $s = 0·05$. On the horizontal line (relative success = 1) guarders and non-guarders are equally successful.

The relationships in Figs 7–10 could have been anticipated by common sense reasoning. This is hardly the case for the relationships shown in Figs 11 and 12. Under particular conditions, for instance when females prefer non-guarders for copulation (Fig. 11), the relative success of guarding is inversely related to the proportion of guarders in the population. When males using the guarding strategy are rare, they are most successful, but when males using the guarding strategy are common, they are least successful. This implies that both strategies can be maintained in the same population in a stable equilibrium. A similar relationship was found when guarding is not fully effective in preventing copulations by other males (Fig. 12).

This second set of simulations suggests that the guarding strategy is promoted by the following factors: (1) asynchrony in fertility of the females; (2) many copulations per female per fertile period; (3) a preference of females for copulating with males using the guarding strategy; (4) mate fidelity of the guarded females; and (5) a low frequency of males with the guarding strategy in the population.

Reversed frequency dependence of the relative success of guarding did not occur in every situation. It was most distinct (1) when males with the non-guarding strategy were preferred by females for copulation, or (2) when guarded females did occasionally accept copulations by other males. It may be argued that these conditions are rather common in natural populations.

To explain a preference of females for males with the non-guarding strategy (1), one might consider a population in which attractiveness of males is variable and then reverse the argument. It is not adaptive for a very attractive male to guard, and thus to lose copulation opportunities. Attractive males should not waste time guarding females.

Imperfect effectiveness of guarding (2) is likely to occur during the first stages of its evolution. Moreover, although mate guarding seems to be rather effective in most species of birds (Birkhead et al. 1987), extra-pair copulations do occur in quite a number of species despite guarding (e.g. McKinney et al. 1984). Imperfect effectiveness of guarding may also be inferred from the occurrence of changes of mates during the reproductive period (e.g. Baeyens 1981; van Rhijn & Groothuis 1987). Finally, relaxation of the initial assumption, that eggs are considered to be fertilized only by the last male copulating, to a more realistic one of fertilization mainly by the last male copulating (Birkhead 1988), also causes imperfect effectiveness of guarding.

IMPLICATIONS OF THIS STUDY

Postcopulatory mate guarding may be considered as the initial step in the evolution of monogamy and male parental care. Since the success of the guarding strategy seems to be inversely related to its frequency under many, perhaps most, natural conditions, one may expect both guarding and non-guarding strategies to be maintained in the same population as a mixed ESS. This conclusion is supported by recent studies on post-copulatory mate guarding in birds (e.g. Møller 1985; Morton 1987).

Coexistence of guarders and non-guarders might imply that, before copulating, females cannot obtain reliable information about whether the male will stay to guard. This also means that the male's monogamous and parental tendencies are not fully certain at the time of copulation, and probably neither at the time of fertilization of the eggs. Thus, some females may be deserted before the eggs are laid. Consequently, in a pure male parental care system prolonged care of the offspring is not guaranteed. This condition may promote the evolution of female parental care (e.g. Lazarus 1990), and may lead to a situation in which the male cares for the offspring, but, in those cases where the male deserts, the female has to take over all parental duties. This change would imply that male and female have the same set of parental abilities at their disposal.

Whereas the evolution of similar parental roles is plausible from a situation with pure male parental care, its appearance seems very unlikely from a pure female care system (van Rhijn 1990). Since biparental care with similar or almost similar roles of both parents is the most common system in recent species of birds, the bird's common ancestor's parental care was probably not a pure female task. I have argued already that an initial step from no prolonged parental care after laying towards biparental care is rather improbable. This leaves only one remaining possibility, namely an initial step from no prolonged parental care after laying towards male parental care. Thus, on the basis of these theoretical considerations pure male parental care might represent the first phase in the evolution of parental care in birds (see also: van Rhijn 1990), in spite of the fact that pure male parental care is extremely rare among birds (e.g. Ridley 1978).

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