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Author: Milonoff, Markku

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Delayed or instant copulation? Effect of female copying on male mating decisions

Markku Milonoff

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Observations of capercaillie, *Tetrao urogallus*, males that do not mate with soliciting females are rather common. Here I present circumstantial evidence that the delaying of copulation is voluntary and propose a hypothesis to explain it. Males of lekking species may delay copulation voluntarily if females copy the mate choice of others, i.e. females around a male may attract females arriving later at the lek. The benefits of delayed copulation depend on the tendency of females to copy each other and the males' risk of losing copulations. Widely scattered display territories in dense forests and longevity are factors that may promote the delaying behaviour of capercaillie and other species with similar characteristics.

Markku Milonoff, Evo Game Research Station, Kaitalammintie 75, FIN-16970 Evo, Finland

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Females may copy each other when choosing a mate. Pruett-Jones (1992) has clarified the definition of female copying as »a choice in which the probability that a female chooses a given male increases if other females have chosen that male and decreases if they have not«. To be real copying the change in the probability of choice should also be »strictly because of the actions of other females and not the consequences of those actions«. Copying has been suggested to occur in lek breeding birds (Van Rhijn 1973, Wiley 1973, Lill 1974, Bradbury 1981) and proposed to be a reason for the extreme unanimity in female mate choice (Bradbury & Gibson 1983). Theoretically, copying has been shown to be a feasible strategy whenever there is a cost of active mate choice (Losey et al. 1986, Pruett-Jones 1992). Consequences of female copying include increased variance in male mating success and a greater opportunity for sexual selection (Wade & Pruett-Jones 1990).

Female copying is most likely to occur in non resource-based harem and lek mating systems in which females are able to actively choose their mates and to assess the mate-choice decisions of others (Wade & Pruett-Jones 1990). Recently, the issue of possible copying has been raised frequently and, even though empirical data are hard to obtain, there is now growing evidence of the phenomenon (review in Pruett-Jones 1992, see also Clutton-Brock & McComb 1993, Dugatkin & Godin 1993). In lekking birds, female copying has been demonstrated in black grouse, *Tetrao tetrix*, (Höglund et al. 1990, Höglund et al. in Pomiankowski 1990) and in sage grouse, *Centrocercus urophasianus* (Gibson et al. 1991, review in Wiley 1991). The effects of female copying on male mating decisions have been discussed only briefly (Gibson et al. 1991). As copying seems to be rather common, males could be expected to take advantage of it by voluntarily delaying copulation and by promoting copying.

In this article, I present evidence of delayed copulation and review the literature. I concentrate on the large and

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highly dimorphic, lekking forest grouse, the capercaillie, *Tetrao urogallus*. The spring display of capercaillie lasts about three months, but females visit the lek during a period of only a few weeks (Pirkola & Koivisto 1970). Usually, one male performs most of the copulations on the lek (e.g. Lumsden 1961, Müller 1979, Moss 1980). During a period of about ten days, most females visit the territory of this male and show their willingness to mate by squatting. Females seem to mate only once and to leave the lek immediately thereafter (Pirkola & Koivisto 1970, Wegge & Larsen 1987). I also consider factors which may affect the occurrence of delaying behaviour in the capercaillie and other grouse species.

Material and methods

Data about the display behaviour of capercaillies were collected in 1985-90 on two display grounds near Evo Game Research Station (southern Finland, 61°10'N, 25°10'E). The observations were made during the period when most females mated. The whole display ground could not be monitored and therefore observing was concentrated on males that were expected to mate. In order not to miss any copulations of the males monitored, observers spent the whole night and the morning in hiding. As females could not be identified individually, the numbers of females are minimums. Observations usually covered consecutive days. Females were observed on 12 mornings. On seven mornings, at least one female solicited and altogether 10 copulations were observed in five mornings. In addition, observations from leks in Central Finland (see Valkeajärvi & Ijäs 1991) are considered.

Results

In the two capercaillie leks monitored in this study, it was characteristic for the males not to mate with soliciting females at first (Table 1). The males always delayed copulation by at least 30-120 min. from the time of the first soliciting. On four of five mornings, at least one soliciting female was ignored for the whole morning. On two of these four mornings, all the soliciting females left the lek without copulating. On one of these two mornings, the number of females ignored was at least five. In both cases, the number of soliciting females was either the same or higher in the following morning. Time between the first and last copulation in the same morning varied from 20 minutes to over three hours.

Table 1. Display behaviour of the capercaillie on two leks in southern Finland in five mornings when at least one female solicited and, in addition, two mornings after a morning when the male did not copulate at all (the exact number of copulations is not known). The number of soliciting females is the minimum of different individuals in that morning. Delaying time is the time lapse between the first soliciting and the first copulation.

No of soliciting females	No of copulations	Time between the first and last copulation	Delaying time	No of soliciting females the next morning
5	2	20 min.	30 min.	?
1	0	–	Whole morning	3
5	0	–	Whole morning	5
7	5	>180 min.	45 min.	?
3	3	20 min.	120 min.	?

Discussion

Occurrence of delayed copulation in capercaillie and other species

Ignoring soliciting females seems to be quite common also in other capercaillie leks (Pirkola & Koivisto 1970, Wiesner et al. 1973, Hauge 1974, Moss 1980, Avery 1984, Rolstad 1985, P. Valkeajärvi, pers. comm.). Some mornings no mating takes place at all, even though numerous, frequently squatting females gather around a male (five in this study, see also Moss 1980). Apparently, the same willing females seem to return to the same male the next morning (Moss 1980, Table 1). It is unclear how long this kind of behaviour may last, but females have been observed to offer themselves for up to four hours during one morning without result (Moss 1980). After delaying, the male may eventually mate with either a few of the squatting females or with all of them successively (P. Valkeajärvi, pers. comm.; Table 1).

The capercaillie is not the only species where males have been observed to ignore soliciting females. The same kind of behaviour has been observed in lekking sage grouse (Scott 1942, Wiley 1973, Gibson et al. 1991) and great bustards, *Otis tarda* (Cramp & Simmons 1980). The reason for this behaviour, however, is unknown.

Reasons for delayed copulation

One possibility could be that copulation is not delayed at all; females may just not be ready to mate, when they begin to solicit. Nevertheless, capercaillie males do not even try to copulate during delaying and the squatting behaviour of the females is apparently the same whether mating takes place or not (pers. obs.). Furthermore, males are fairly indifferent to the postures of the decoys with which they copulate (pers. obs.). In a crowd of females around a top male, squatting may be so vigorous and continuous that there can be no doubt about the willingness of the females (see also Moss 1980).

One reason for delaying could be that males are physiologically unable to mate immediately after encounter-

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ing females. However, the delaying behaviour is not restricted to the beginning of the mating period and, sometimes capercaillie males copulate instantly at the beginning of the mating period (P. Valkeajärvi, pers. comm.; pers. obs.). Also, if subordinate males manage to sneak in among soliciting females, they copulate immediately, despite the fact that they have had less contact with females than the top male (Moss 1980, pers. obs.). Moreover, males in captivity are able to mate instantly with females or with decoys at the very first meeting (pers. obs.).

Slow mating rates of males among lekking birds could be related to sperm depletion (Gibson et al. 1991), but there is little support for the occurrence of sperm depletion in wild birds on the whole (review in Birkhead & Møller 1992). Furthermore, at least among the capercaillie, delaying leads to situations in which the risk of depletion actually increases. If sperm depletion was a problem, the best strategy would be to copulate as soon as there was enough sperm. In a situation when soliciting females were available all the time, this would lead to a sequence of copulations early in the morning and then regularly after sperm storages had been replenished. However, the observed mating habits of capercaillies do not support this assumption (see also Wiesner et al. 1973). The distribution of copulations is very uneven and many of the copulations happen in rapid sequences after long delays (P. Valkeajärvi, pers. comm.; Table 1: three copulations in 20 minutes after a delay of two hours). The number of successively mated females may be large (e.g. 10 copulations in one hour, P. Valkeajärvi, pers. comm.). Males delay copulation even though they have not copulated earlier in the morning and even if there is only one female to inseminate (Moss 1980, Table 1).

Delaying could be a way to ensure undisturbed copulation. However, among the capercaillie, the top male is rarely disturbed during mating and delaying only seems to encourage other males to trespass (e.g. Hauge 1974, Moss 1980, Rolstad 1985). The best strategy to ensure copulations would probably be to mate instantly when females solicit; in this way large female clusters would not arise and the possibility that other males should steal matings would be limited.

As there seems to be no physiological or behavioural constraints that could explain the delaying, I put forward the hypothesis that the behaviour is voluntary and adaptive, as females around a male attract other females (see Höglund et al. 1990, incl. references). This may apply especially to young inexperienced females which, at least in some gallinaceous species, generally arrive late at the lek (Wiley 1973, incl. references, Höglund et al. 1990). Older females may already have gained experience with the males in previous years.

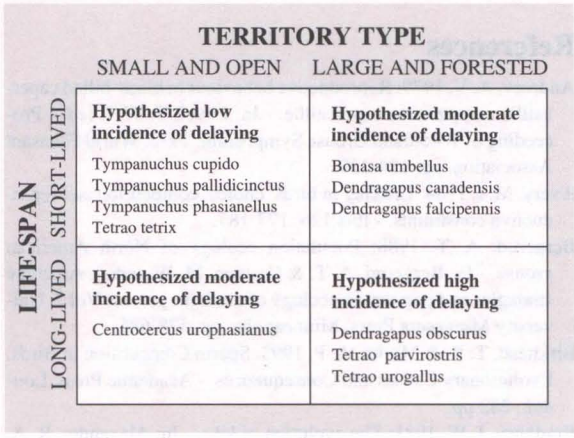

Figure 1. Ecological factors which may influence the development of delayed copulation in males. Promiscuous grouse species have been divided into four groups according to the theoretical occurrence of delaying. The territory types have been divided in accordance with Hjorth (1970) and the division into long- and short-lived species has been made in accordance with Bergerud (1988; average adult mortality rate lower or higher than 45%; mortality rates of capercaillie and black grouse from Lindén 1981). For details see the text.

Consequences of delaying

A clear conflict seems to exist between females willing to mate and unwilling males. For females it may be dangerous to stay on the display ground and withholding of mating may also delay egg-laying. Fights among females (e.g. Moss 1980) may arise because they are in a hurry to copulate. For a male, delaying is profitable only if »choosy« females do not copulate with other males, despite the delay. As this seems to be the case (Moss 1980), it indicates that experienced females are strongly attracted to specific characteristics in the males.

Delaying is risky for the male, too; he may die before the next opportunity to mate arises or some other male may copulate with the females. The top male must also compromise between attracting a large female group into his territory and losing copulations to intrusive males. The risk of losing copulation could explain why males in many cases finally begin to copulate after serious fights (Hauge 1974, Moss 1980, Rolstad 1985, P. Valkeajärvi, pers. comm.). Furthermore, delaying seems to be more frequent when only a few rivals are present (see Rolstad 1985).

In addition, delaying also has evolutionary consequences. Female copying per se increases the variance in male mating success and therefore the opportunity of sexual selection (Wade & Pruett-Jones 1990). The delaying of copulation increases the possibility of copying and, hence, increases the opportunity of sexual selection even more. It is interesting to note that the capercaillie, sage grouse and great bustard, among which the delaying be-

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haviour has been observed, belong to the bird species in which sex-linked dimorphism is most pronounced (see below).

Factors affecting the occurrence of delaying

Among traits that make delaying beneficial for a male are a low risk of losing copulations and the strong tendency of females to copy each other. Especially the capercaillie shows some ecological aspects that allow these conditions to be fulfilled: 1) the capercaillie holds large display territories (Hjorth 1970, Catusse 1993, for black-billed capercaillie, *Tetrao parvirostris*, see Andreev 1979) which may minimise the risk of sneak copulations; 2) the annual death-rate of adult capercaillies is the lowest among grouse (Wegge 1984, Bergerud 1988) and, thus, the probability that a capercaillie male or his females will die during delaying is probably low as well; 3) the female-biased sex ratio of capercaillie may even increase the possible benefits for a delaying male (see Lindén 1981).

Large display territories within forests may also promote female copying. Limited visibility and audibility make simultaneous comparison of capercaillie males difficult for females, which may hinder and prolong their selection of a male. If the choice is difficult, earlier experience will be valuable, and without it (e.g. young females), copying other females may be the best coping mechanism (see Dugatkin & Godin 1993).

Female copying may be a good strategy especially in long-lived species like the capercaillie (see Wegge 1984, Bergerud 1988). In long-lived species, age and experience are highly variable factors that may be very important for the fitness of both males and females (Halliday 1983, Manning 1985, see also Gibson et al. 1991, Petrie 1993). Furthermore, the copying behaviour of females inevitably increases the differences in fitness among males (Wade & Pruett-Jones 1990). All in all, this may lead to female groups - which grow in size year after year - around the oldest males (if they are still physically capable of defending their territories and mates). Therefore, a large female group around a male would also be a reliable indication of the age and fitness of the male in question. If distinct fitness differences among males exist, it may also be worthwhile for females to be faithful to the top male despite the delay in copulation.

Considering the above-mentioned factors, capercaillie as well as blue grouse, *Dendragapus obscurus*, would seem to be the most probable grouse species to have evolved delaying behaviour (Fig. 1). Sage grouse and the other promiscuous grouse species with dispersed males, *Dendragapus canadensis, Dendragapus falcipennis, Bonasa umbellus*, (Hjorth 1970) are also potential candidates. In other grouse species, the best strategy for a male is probably to mate instantly. The two species of grouse among which males are reported to occasionally ignore soliciting females support this assumption (Capercaillie: Pirkola & Koivisto 1970, Wiesner et al. 1973, Hauge 1974, Moss 1980, Avery 1984, Rolstad 1985, observations cited here; Sage grouse: Scott 1942, Wiley 1973, Gibson et al. 1991). Also the great bustard (Cramp & Simmons 1980) is long-lived and has widely spaced leks and, thus, should be counted among the species in which the delaying behaviour might have evolved.

Testing the above-mentioned hypotheses is difficult. To be profitable, the delay should increase the number of females mating with the top males. Theoretically, this would be an almost inevitable consequence of female copying. In regard to capercaillie, my own few observations do not contradict this; if the male did not copulate at all, the number of soliciting females would be the same or higher the following morning (Table 1). However, this might also be a direct consequence of the fact that the number of soliciting females increases as the mating season advances. Experiments with decoy females might be fruitful (see Höglund et al. in Pomiankowski 1990). In any case, observations of males which ignore soliciting females should not be immediately interpreted as cases of sperm depletion or abnormal behaviour.

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