

Forum

Mate choice or harassment avoidance? A question of female control at the lek

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*Recent studies on the reproductive behavior of fallow deer, *Dama dama*, propose that harassment from nonterritorial males has a major influence on female movements and mate selection, leading ultimately to the evolution of lek mating in this species. In order to support this statement, one must demonstrate that female movements between lek and isolated territories, and among lek males, lead to a reduction in levels of harassment. We argue that current evidence in favor of this view is inconclusive. A quantification of the total harassment costs experienced by females in lek and isolated territories has never been made. In addition, female movements within the lek may actually lead to higher levels of disruption and harassment: The rate at which females join male territories increases with harem size (the number of females present in the territory), even though harems are disrupted increasingly with size due to a higher frequency of intrusions by nonterritorial males. Females also join male territories at a higher rate while these males are engaged in copulatory sequences, but copulatory sequences are again associated with high levels of disruption and harem instability. In the above studies it is argued that females are nonselective in their mating preferences. This assessment is based on the finding that males that adopt different reproductive strategies do not differ in their mating rates. Here mating rate is measured as the number of copulations received per female-hour. There are a number of reasons, however, why females exhibiting mating preferences might remain longer with preferred males, and so the above preference measure cannot be used to exclude the possibility that females are selective. More research is required to identify the major factors influencing patterns of mate selection and the evolution of leks in this species. We suggest a number of field tests that may help to identify these factors.*

The question of which factors influence the process of female mate selection is one of long-standing debate in the areas of sexual selection and the evolution of mating systems (for review, see Balmford, 1991; Balmford and Read, 1991; Bateson, 1983; Clutton-Brock et al., 1993; Kirkpatrick, 1987; Kirkpatrick and Ryan, 1991; Pomiankowski and Sheridan, 1994). Mating systems can vary considerably depending on, for example, the type and density of resources, predation risk, and animal densities (Apollonio et al., 1989; Balmford et al., 1992; Clutton-Brock et al., 1993; see Emlen and Oring, 1977, for interspecific comparisons). To understand variation in mating systems, we need to know about the mating strategies of each sex and the impact each sex has on the behavioral strategies of the other. This can be described in terms of the conflict between the sexes over the control of reproductive benefits, and recent discussions have stressed the need for a better understanding of female reproductive strategies (Ahnesjö et al., 1993; Gowaty, 1994; Warner, 1990).

This article outlines several models used to explain lek evolution before reviewing data on the mating system in fallow deer, *Dama dama* (Apollonio et al., 1989, 1990, 1992; Clutton-Brock et al., 1988, 1989, 1992; Langbein and Thirgood, 1989;

Pemberton and Balmford, 1987; Schaal and Bradbury, 1987; Thirgood, 1991). Clutton-Brock et al. (1992) used data from this species to support the view that male harassment and the risk of predation are the main factors influencing mate selection and ultimately the evolution of fallow deer leks (see also Clutton-Brock and McComb, 1993; McComb and Clutton-Brock, 1994). We find considerable evidence that is inconsistent with this view and argue that the evidence suggests that female behavior is motivated by mating preferences. We recommend a number of analyses using field data which could be used to test these alternatives.

The models

Some models used to explain the evolution of leks assume that males have an overriding influence on patterns of female mate selection, with females exhibiting simple mating rules (Beehler and Foster, 1988) and little or no preference for different male characteristics (Clutton-Brock et al., 1992; Foster, 1983; Wittenberger, 1978). Beehler and Foster (1988) suggest that dominant lek males may control female mate selection by restricting the courtship activities of neighboring males. Clutton-Brock et al. (1992) focus on the impact of harassment from nonterritorial males that chase and attempt to copulate with the females. Females are assumed to move to areas offering the greatest protection from harassment, and the clustered distribution of lek territories are thought to offer greater protection than isolated territories. The tendency for females to prefer males with large harems (group of females within the territory) is then interpreted as a defensive "grouping" strategy (Clutton-Brock and McComb, 1993; Clutton-Brock et al., 1992, 1993; McComb and Clutton-Brock, 1994). Although Clutton-Brock et al. (1992) refer to the possible influence of predation on lek evolution, the main focus of their research is on the impact of male harassment, and so we refer to this as the "harassment avoidance" model.

Another group of models assumes that females have access to different areas of the lek and the ability to select particular males. We refer to these as the "preference" models (Kirkpatrick and Ryan, 1991). Mate selection is assumed to be based on some form of comparison of male characteristics (Pruett-Jones and Pruett-Jones, 1990). Females are thought to be attracted to leks because they offer an increased likelihood of getting a good-quality or attractive mate. This might result either from the ability to assess a number of males in close proximity or because lek males tend to be more mature, of higher quality, or dominant to other males (Alatalo et al., 1992; Bradbury, 1981; Bradbury and Gibson, 1983). Unanimity of female preference for particular lek males can be explained either in terms of independent female choice or copying as a strategy to reduce the costs of mate assessment (Bradbury and Gibson, 1983; Dugatkin, 1992; Dugatkin and Godin, 1993; Gibson and Bradbury, 1991; Gibson and Höglund, 1992; Pruett-Jones, 1992).

In many lekking species, some males in a population may also defend isolated territories. Under these circumstances, the process of female mate selection can occur at two levels. Females select between lek or isolated territorial males and, within leks, among different lek males. Models used to describe lek evolution often explain both levels but may assume that different factors influence female movements at each level (see, e.g., Beehler and Foster, 1988).

Mating behavior in fallow deer

Fallow deer have a highly variable mating system. In the rutting season, males may follow females, defend nonstationary female groups, or defend isolated or lek territories (see Langbein and Thirgood, 1989, for a review). Nonestrous females are known to stay in mixed-sex herds of approximately 20 individuals. In populations where males form leks, females exhibit strong preference for these aggregations. In one study, 94% of all copulations were performed with lek males (Clutton-Brock et al., 1988, Langbein and Thirgood, 1989). Females typically come into estrus within 1–12 h after their arrival on the lek and visit a number of males during their stay [approximately 4/h (Clutton-Brock et al., 1989)]. Females preferentially visit males with large harems. Nonterritorial males make intrusions into lek territories and harass females by chasing and attempting to mate with them. Almost all the females mate only once and then leave the lek shortly afterward (Apollonio et al., 1990; Clutton-Brock et al., 1988, 1989). Reproductive success among lek males is highly skewed and is associated with male characteristics such as antler and hind foot length, fighting success, and groan rates (Clutton-Brock et al., 1988, 1989) and territory location (Apollonio et al., 1989, 1990).

Review of the data

Support for the harassment avoidance model

If the preference for leks represents a harassment avoidance strategy, one would expect females to experience reduced harassment costs in lek territories. Clutton-Brock et al. (1992) found that females on lek territories actually experience higher rates of intrusion by nonterritorial males than they do on isolated territories, although females visiting isolated territories were chased for longer distances once they had been separated from the territorial male. The distance females were chased was considered more important than the intrusion rate, and it was argued, therefore, that the costs of harassment were higher on isolated territories (Clutton-Brock et al., 1992, 1993). The evidence nonetheless remains inconclusive because there was no attempt to quantify the overall costs of harassment on different territory types.

Clutton-Brock et al. (1992) argue that although females visit a number of males within the lek, movements between territories are mostly initiated by disruption from nonterritorial males, and so are not necessarily motivated by mate choice (see also Clutton-Brock et al., 1993). However, female movements within leks do not appear to result in reduced levels of harassment. The rate at which females join male territories increases proportionally with harem size. Although Clutton-Brock et al. (1993) and Clutton-Brock and McComb (1993) argue that this is because the per capita rate of intrusion declines with harem size, there appears to be no published evidence in support of this statement. The rate of intrusion by nonterritorial males increases in proportion to the number of females in the harem [i.e., the intrusion rate per capita remains constant (Clutton-Brock et al., 1989 : Figure 3)]. In addition, it appears that intrusions against large harems result in higher levels of disruption and harassment than is suggested by the per capita rate. This is because territorial males are unable to defend against the high rates of intrusion associated with large harems. Consequently, harems with eight or more females are frequently disrupted and are highly unstable (Clutton-Brock et al., 1988, 1989, 1992).

The rate at which females join male territories is also higher while males are copulating with other females, sometimes leading to several females being mated in quick succession (Clutton-Brock et al., 1988). These serial copulations again

attract the attention of nonterritorial bucks and neighboring territorial males, which also increase harem instability (Clutton-Brock et al., 1988: Figure 7; Clutton-Brock et al., 1993).

Thus, both female preference for large harems and the tendency to join males during copulatory sequences increase levels of disruption within the territory and apparently lead to the female experiencing higher levels of harassment.

Support for preference models

Although recent studies identify harassment as having a major influence on the fallow deer mating system, earlier papers describe this system in a way that is consistent with preference models. Clutton-Brock et al. (1989) state “the observation that bucks rarely interfered with their neighbors’ harems and females moved freely between bucks suggests that females choose their mates on the basis of male phenotype rather than territory type or location.” Females were also found to exhibit a high degree of unanimity in their selection of particular lek males. For example, over a 2-year period, the most successful male copulated with 15% of all females visiting the lek, whereas 50% of lek males did not copulate at all (Clutton-Brock et al., 1988). In addition, experimental manipulation of male position on the lek was not found to alter male mating success, suggesting that male characteristics were the most important factor influencing mating success (Clutton-Brock et al., 1989).

In fallow deer, female preference for leks could be explained in terms of the opportunity to compare several males simultaneously (as mentioned above). Alternatively, females may prefer lek males because only older males or males of superior quality may be able to afford the high costs associated with maintaining lek territories (see, e.g., Apollonio et al., 1989). This appears to be the case in Uganda kob (*Kobus kob*), in which male body weight was the main factor influencing the ability to defend lek territories (Balmford et al., 1992).

Within the lek, preference for large harems could represent a form of mate-choice copying, as described earlier. Alternatively, females may move to unstable harems to induce territorial behavior in the male to test his rank, levels of vigor, and other aspects of his quality (e.g., Cox and Le Boeuf, 1977).

Measuring female preference

The above interpretation conflicts with recent suggestions by Clutton-Brock et al. (1992), Clutton-Brock and McComb (1993), McComb and Clutton-Brock (1994), and Sillman et al. (1993) that females do not exhibit preferences or are “no more likely” to mate with particular males. These statements are based on the finding that males adopting different mating strategies do not have different mating rates based on the measure “number of copulations/female-hour” (the sum of the time that females spend on the territory before mating with the male).

This preference measure is intended to indicate female readiness to mate and control for skews in mating success that might arise for other reasons. For example, even if females are nonselective and mate with all males with the same probability, the chance of a female mating with a particular male will increase with the time spent on a male’s territory.

The above preference measure, however, cannot be used to rule out the existence of strong mating preferences. A number of mate-choice processes might produce a positive correlation between female preference and the time spent with the preferred male. For example, the mean copulation duration in fallow deer is 4 min, excluding initial courtship (Clutton-Brock et al., 1988). Females may have to wait, therefore, for the opportunity to mate with males with a number of associated females. In addition, the time required to initiate court-

ship may be greater for successful males because of the higher rates of intrusion from nonterritorial males associated with large harems. Alternatively, females may stay longer with the males they finally mate with because of the time required to discriminate reliable cues of male quality. In the cock-of-the-rock (*Rupicola rupicola*), for example, females make a number of successive comparisons, returning to some males a number of times (Trail and Adams, 1989). By either mechanism, preferred males may acquire more female hours than average.

The issue of whether this is an appropriate measure of preference is important because it has led Clutton-Brock et al. (1993) to conclude that the "evidence of female mating preferences on mammalian leks is equivocal" [this includes analyses on Kafue lechwe (*Kobus lechwe*) and Uganda kob (see also Clutton-Brock et al., 1992; Clutton-Brock and McComb, 1993; Stillman et al., 1993)]. This statement seems misleading in light of the fact that skews in mating success in ungulates are stronger than those found in a number of lekking bird species (see Clutton-Brock et al., 1993).

Ideally, one should justify the use of a particular preference measure. Given mate assessment may require time with the preferred male and there may be delays associated with mating with males that are popular, we recommend using the number of copulations per unit time males are on the lek as the measure.

Captive choice experiments

In an attempt to determine, under controlled conditions, which factors motivated mate selection in fallow deer, Clutton-Brock and McComb (1993) and McComb and Clutton-Brock (1994) conducted a series of captive choice experiments. One of the main objectives of these experiments was to test whether females are motivated by the need for safety (represented by female groups) rather than by the need to select a mate. The females were given progesterone implants and estrus was induced in some of these individuals by removing the implants 2 to 3 days before the experiments began. Pairs of females were placed in a choice arena consisting of a central lane surrounded by four paddocks containing the individuals to be chosen. The options included, for example, a male alone against a male with a group of females or a male with a group of females against a group of females without a male. The female's position in relation to the paddocks and her sniff rate toward the paddocks were used as indicators of preference.

Although we appreciate the need to control for confounding effects, we believe that these experiments have a number of potential problems. First, this type of comparison cannot be performed in a properly controlled manner because the options of seeking safety and selecting a mate differ in a number of ways—not just by one factor. This makes interpretation of the results difficult. Standard choice experiments assess preferences for males that differ (predominantly) by one characteristic.

Second, the experimental conditions may be too artificial to adequately represent the conditions at the lek, potentially leading to behavioral patterns that do not occur in natural conditions. For example, the choice females in these experiments were not allowed to interact directly with the males. This may explain why females showed no preference for male characteristics such as age and antler size or previous copulatory success and harem size, all of which influence female preference in the wild (Clutton-Brock et al., 1989).

Finally, nervousness in the choice females (referred to in Clutton-Brock and McComb, 1993; McComb and Clutton-Brock, 1994) will tend to favor defensive behaviors like group-

ing while reducing mating tendencies. Although McComb and Clutton-Brock (1994) found that the grouping tendency in estrous females was more pronounced than that of nonestrous females, it is not clear whether the process of removing these implants caused the females to react more nervously (nonestrous females were not similarly handled) or whether estrous females may exhibit a higher stress response, making them more temperamental under experimental conditions. It is difficult to judge, therefore, whether these results are representative of female behavior under natural conditions at the lek.

Future research

Given our concerns with these experiments, we favor an approach that relies on a detailed analyses of field data obtained primarily from female behavior. We suggest the following areas of investigation.

1. Preference for leks and levels of harassment: a) the total costs of harassment (e.g., in terms of energetic costs or risk of injury) incurred by females in lek and isolated territories need to be quantified using activity budgets and rates and forms of harassment received; b) the time required to travel to isolated and lek territories could also be used to estimate the degree of exposure to unprotected nonterritorial areas. Based on the harassment avoidance model, we would predict that females visiting leks would experience lower overall levels of harassment.

2. Preference for particular lek males and large harems: a) the patterns of female movement within the lek should be examined in relation to levels of harassment experienced and the characteristics of the males visited; b) the effectiveness of male territorial defense and the corresponding levels of disturbance experienced by the female needs to be examined for different-sized harems; along with c) an analysis of the male's ability to maintain the harem and his subsequent reproductive success (suggested also by Clutton-Brock et al., 1993). Harem maintenance could be represented by the departure rate of females from the territory per intrusion by nonterritorial males. Based on the harassment avoidance model, we would expect females to avoid frequently disrupted areas of the lek. The existence of repeated visits to the same male despite the high levels of harassment, or the male's inability to maintain the harem, suggests females are not simply avoiding harassment. Alternatively, we would predict, based on the preference models, that females would be attracted to particular males within the lek (e.g., Clutton-Brock et al., 1989). Patterns of visitation may represent a form of mate sampling. Where the benefits of choice exceed the costs of harassment, mate sampling may lead to the female experiencing higher levels of harassment (e.g., Balmford et al., 1992; Petrie et al., 1991; Trail, 1985; Trail and Adams, 1989; Trail and Koutnik, 1986).

3. Preference measures: a) the time component for the measure number of copulations per female hour needs to be described in more detail. Is the time accrued over repeated visits to the territory? What is the average duration of visits to successful and unsuccessful males? Such information would provide a greater understanding of whether females remain with certain males because these males are more effective at defending the females; b) given the potential for disruption and delays before courtship, there is a need for a reassessment of mate preference using the number of copulations per unit time males are on the lek.

Conclusion

Support for the harassment avoidance model is inconclusive. The total costs of harassment have not been quantified for

females visiting lek and isolated territories. Within leks, female behavior may result in increased levels of harassment. We believe that the available data on fallow deer provide greater support for preference models of lek evolution.

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Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky

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The initial, but superficial, paradox of lek mating systems is why males should defend mating territories in clusters instead of distributing themselves throughout female ranges. In most lek systems, the answer is obvious: Receptive females collect at clusters of mating territories so that males holding territories in clusters typically show higher mating success than males holding isolated territories (Höglund and Alatalo, 1995; Wiley, 1991). This answer uncovers a second, underlying para-