Pushy males and choosy females: courtship disruption and mate choice in the lekking great snipe

Stein Are Sæther^{1*}, Peder Fiske^{1,2} and John Atle Kålås²

¹Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

²Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway

We studied the effects of male disruptive behaviour on female mate choice and male mating success in the great snipe, *Gallinago media*, a lekking bird. Harassment from neighbouring males, a widespread behaviour in lekking animals, was the most prevalent cause of females leaving a male territory. Several lines of evidence show that females did not prefer to mate with males able to protect them from harassment. Males that obtained mating success were no less likely to suffer disruptions and females were no less likely to be disrupted when with their preferred male. Females returned to the male they later mated with, despite being repeatedly chased away by neighbours. The probability that an individual female returned and solicited mating from a male was 15 times higher for the male she was chased away from compared to the neighbour that chased her away. Females returned as often or more to the territory owner after being disrupted, compared to after leaving the territory without being harassed. Our results suggest that female great snipes are extremely choosy, but also that females do not gain direct benefits (harassment avoidance) by mating with certain males. Females appear to have neither direct nor indirect preferences for dominance that could give them such benefits—females appeared choosy despite, not because of, harassment. If females gain indirect benefits (genetically superior offspring) by being choosy, this is also likely to be unrelated to any dominance among males.

Keywords: lek paradox; dominance; harassment; disruption; mate choice; *Gallinago media*

1. INTRODUCTION

Mating success varies greatly among males in many animals having a lek mating system (Bradbury *et al.* 1985; Wiley 1991; Höglund & Alatalo 1995; Mackenzie *et al.* 1995). This skew provides strong opportunity for sexual selection. Many lekking species are sexually dimorphic and this has been used as evidence that sexual selection is particularly strong. Several mechanisms that could generate mating skew on leks have been suggested, including female mate choice, male competition for mates, female copying and chance (Höglund & Alatalo 1995; Mackenzie *et al.* 1995). How much freedom females have to choose males in lekking species is controversial (see Balmford 1991; Wiley 1991; Höglund & Alatalo 1995; Carbone & Taborsky 1996; Clutton-Brock *et al.* 1996). Some have argued that female mate choice is free from interference from male competition for mates (e.g. Bradbury & Gibson 1983), while others have emphasized that male competition and male dominance relationships (e.g. Beehler & Foster 1988) constrain any female choice (at least within leks) or that females let males decide among themselves by inciting fights. This disagreement may or may not reflect variation between species. Separating the effects of female mate choice and male competition on male mating success might be difficult empirically. A

correlation between a male trait and mating success need not be due to a female preference for the trait, but rather because the trait gives males an advantage in interactions with other males.

(a) *Male competition, and direct and indirect female mate choice*

Teasing apart the effects of female mate choice and male competition on mating skew may not only be difficult, but in fact impossible. At least two reasons exist for the dichotomy between mate choice and competition being meaningless. First, females might show direct mate choice based on dominance (but see Qvarnström & Forsgren 1998). Females have been suggested to discriminate between males, e.g. by observing male–male interactions (see the references in Trail & Koutnik (1986)). Second, indirect mate choice will set the conditions for male competition (Wiley & Poston 1996). As an example, take the often-claimed (but seldom tested) preference of females for mating at central positions at a lek or the preference of female antelopes (Deutsch & Nefdt 1992) for mating at heavily used locations at leks. These female preferences will indirectly cause a relationship in males between success in male–male interactions and success in obtaining mates, because males compete over the positions preferred by females. The above arguments also apply to sexual selection. Partitioning sexual selection into intrasexual and intersexual may be impossible—the

*Author for correspondence (sas@alfa.itea.ntnu.no).

same trait can be both armament and ornament (Berglund *et al.* 1996) or female preferences can indirectly cause selection on traits favourable in competition between males (Wiley & Poston 1996).

Nevertheless, it is of interest (i) to learn how free females are to choose among the males at leks, (ii) whether females show direct preference for dominant males, and (iii) whether females show any indirect preferences (e.g. for territory positions or safety from harassment) that eventually cause dominance to be related to mating success.

(b) *Direct and indirect benefits of choice*

If females show direct or indirect preferences for dominant males, it is conceivable that females might gain direct benefits from mate choice at leks, e.g. by avoiding harassment from subordinate males. These benefits, although likely to be small, could outweigh the small costs of mate choice at leks. These costs are thought to be small, since comparing many potential mates in a short time may be relatively easy at leks. This scenario of 'small direct benefits–small costs' has been suggested to provide a solution to the lek paradox (Reynolds & Gross 1990). Mate choice at leks (or in other systems where females receive no material benefits from males) appears paradoxical because female preferences will be expected to disappear if preferences are for heritable traits. This is because genetical variation in male traits preferred by females will be expected to be lost and, hence, the reason for maintaining female preferences (indirect, genetic benefits) will also be lost. The lek paradox has been suggested as resolved by arguing that (i) females are not choosy after all, matings being instead determined by male interactions, (ii) mechanisms exist that maintain variation despite selection (Pomiankowski & Møller 1995; Rowe & Houle 1996), (iii) the benefits of choice are not genetic (indirect) but instead affect the female directly (Reynolds & Gross 1990; Kirkpatrick & Ryan 1991), or (iv) preferences vary among females (Brown 1997; Jennions & Petrie 1997; Widemo & Sæther 1999).

(c) *Disruptive behaviour, mate choice and the lek paradox*

One common aspect of male competition in lekking animals is disruptive behaviour, where males intrude and terminate female courtship visits to other males (Foster 1983). This is an interesting behaviour since it is 'the one direct means of thwarting female choice that is available to the males of lek species' (Trail 1985a, p. 778) as opposed to causally more indirect, difficult-to-observe and vaguely defined behaviour (in a territorial system) such as 'dominance'. In some lekking ungulates, females mating at leks may suffer less disruptions and harassment than outside leks (Nefdt 1995) and these direct benefits may explain the evolution of lekking itself in ungulates (Clutton-Brock *et al.* 1993). If females have direct or indirect preferences for dominant males, we expect males achieving mating success to be less likely to suffer disruption and mating success should be negatively related to the likelihood of suffering disruption. If females have direct preferences for dominant males, individual females will be expected to avoid males they are being disrupted from and possibly to prefer disrupters. Likewise, if

females gain direct benefits from mating with particular males that can protect them from harassment, females should prefer such males and we should expect to find a negative relationship between male mating success and the tendency to suffer disruptions.

The present investigation aimed at understanding the influence of male–male competition on female mating behaviour and male mating success in the lekking great snipe (*Gallinago media*). We show that, though common, disruptive behaviour by neighbouring males does not alter the mate choice of individual females and does not cause males suffering disruptions to be less successful. We argue that this provides clear evidence for the importance of direct female choice on male mating success and evidence against direct benefits of mate choice in the form of protection from harassment. Hence, direct benefits are unlikely to explain the lek paradox in this species.

2. METHODS

(a) *Field methods*

The great snipe is a relatively rare shorebird inhabiting mountainous marsh areas (in Scandinavia) or flood marshes (in the Baltic, Poland and former USSR), being formerly more widespread in Europe. The study site was in Gåvålia (62° 17' N, 9° 36' E), Norway (see Løfaldli *et al.* 1992). The study population occupies several leks where snipes have been caught in mist-nets and individually marked. The data presented here were collected in 1994 (leks 2, 5 and 12), 1995 (leks 2, 5 and 12) and 1996 (leks 2, 5 and 10) from mid-May to mid-June. One to four observers (depending on the number of males present) made observations at these leks from 23.00 to 02.30, the time when females visit leks (Kålås *et al.* 1995). Usually, no unoccupied space exists between male territories in this species and a male territory occupies *ca.* 100 m² on average (Fiske *et al.* 1994). The number of males at a lek is usually between ten and 25, but varies somewhat during the mating season and between leks (S. A. Sæther, P. Fiske and J. A. Kålås, unpublished data). Each observer continuously surveyed all visits by females to an assigned subset of the males, noted all copulations and solicitations by females and paid particular attention to when and how females departed a territory. These courtship visits could be terminated in one of the following ways: (i) the female walked out of the territory and into another male's territory or out of the lek; (ii) the female flew out of the territory; (iii) the male territory owner chased her out of the territory; (iv) another female chased her away; (v) the female disappeared to the observer in the *Carex*/*Salix* vegetation and the mode of departure was thus unknown; or (vi) another male chased her out of the territory. We call cases of this last category disruptions. These were usually caused by immediate neighbours of the territory owner intruding the territory and approaching the female. Often these attempts were put to a halt by the owner and only those attempts that caused the female to leave the territory are considered as disruptions here. In addition, it can be noted that several cases were observed when intruders were unsuccessful, in that a female refused to take off but instead squeezed herself down in the vegetation. Usually, the territory owner would soon arrive and chase away an intruder. However, neighbours often managed to chase away a female even if the male owner was nearby. A male intrusion was often followed by a fight within the territory and, if the female had not already been chased off, she often was during such fights. Disruptions seemed to be

directed at one specific female (or sometimes several) and, consequently, was not simply a side-effect of males intruding territories for other reasons. Since females that departed by flying away and in particular by being chased away were unlikely to go unnoticed, most cases of females disappearing in the vegetation probably involved females that eventually walked out of the territory.

Female great snipe solicit copulation by adopting an easily recognized squatting posture. Disruptions of soliciting females were rare (27 out of 1143 solicitations observed in 1994–1998, irrespective of whether the female left the territory when disrupted and including unidentified females). Because of the scarcity of such disruptions they were not dealt with further unless the disruption caused the female to leave the territory.

(b) *Material*

In this study, we pooled observations from leks and years and analysed relationships on a bird-year basis, counting each individual once a year. The study populations in 1994, 1995 and 1996 consisted of 86, 82 and 70 marked males, respectively, and 47, 44 and 39 marked females, respectively (238 male-years and 130 female-years). We made 815 observations of identified female visits to male territories in 1994–1996, involving 92 female-years (68 individual females). These observations lasted on average 13.8 min (s.d. = 19.3, median = 7, range = 1–162, $n = 734$). For 444 out of these 815 observations, we knew how the visit was terminated and in the rest of the cases the females disappeared in the vegetation.

(c) *Analyses*

We analysed the effect of disruptions on males and females in three basic ways.

- (i) First, we analysed whether the probability that males suffered disruption was related to their mating success. This probability was based on the number of female visits to a male terminated by disruption from third-party males, divided by the total number of female visits to the male. Only visits by marked and identified females were included in this and all subsequent analyses. Since individual females often mate several times in a mating season (Fiske & Kålås 1995) we did not simply sum up the total number of matings a male received as a measure of mating success. Instead, we tried to estimate the number of individual females that mated with the male. This was done by combining the records for identified females with the minimum number of different unmarked females mating with the male. This latter number was calculated by the criteria that an unmarked female could mate on three consecutive nights (Fiske & Kålås 1995). We could sometimes keep track of several unmarked females and, thus, distinguish between different unmarked females mating on the same night, but not across nights. However, most females were marked. We calculated mating success only for males that were observed territorial on at least five nights. A successful male is here defined as a male that obtained at least one mating in the specific season. Some females were only seen to solicit copulation and not actually to copulate. These females were also included in a male's mating success since they had probably mated with that male (Fiske & Kålås 1995).
- (ii) A more powerful and informative test of the effects of disruptions on male mating success is to analyse disruptions on an individual female basis. In other words, we asked

whether the probability that a female is disrupted is different when at the territory of the male she chooses to mate with compared with when at the territory of other males. We analysed this by computing the probability for each individual female that she suffered disruption when at the territory of the male she preferred compared with when at the territory of any other male. A preferred male is defined here as the male a specific female mated or solicited mating with in the specific season. If a female copulated with more than one male, only the male with whom she copulated the most was classified as her preferred male. We excluded females not seen to solicit mating and females not seen with non-preferred males. First, we made analyses simply using the proportion of visits disrupted when with each of the two groups of males. Second, it could be argued that what matters to a female is the likelihood of suffering disruption per time unit spent at a territory and this can differ between the two groups of males. Therefore, we also made analyses where, for each female, we divided the number of disruptions by the total number of minutes she was observed within the territories of each group of males. This sample was slightly smaller since, for a few females, we did not have observations where the length of the visits was known for both groups of visited males.

- (iii) 'Especially informative will be quantitative data on the success of interfering males following disruption...' (Foster 1983, p. 69). Therefore, we made a third group of analyses where the subsequent behaviour of a female following a disruption was focused upon. For each case of disruption we checked whether the female returned (later in the mating season) and, if so, if she also solicited mating. This was checked for the male that disrupted her, for the male she was disrupted from and for a randomly chosen neighbour. This neighbour was selected from the neighbours of the male suffering the disruption (excluding the disrupter) by means of a dice, for each disruption separately. The probability that a female returned (or also solicited) to each of these male categories was then calculated for each female as the average over all disruptions she suffered within a mating season. This allowed us to compare the probabilities of returning (and soliciting) to the male suffering disruption versus returning to the other males. We could also test whether performing disruptions implied benefits such as redirection of mate choice towards the disrupter (by comparing disrupter versus random neighbour). Finally, for each female we calculated the probability that she would subsequently visit (or solicit to) the territory owner after visits that were not terminated by disruption. This was done in order to compare this with the probability of returning to the territory owner after disruptions, to see whether females avoided males from which they were disrupted.

All statistical tests were non-parametric, although we preferred to present mean values and their 95% confidence limits in the figures. The p -values are two-tailed.

3. RESULTS

(a) *Causes of female departures from territories*

The overall proportion of female visits terminated by disruption was between 32.3% (figure 1, all observations) and 59.5% (excluding those with unknown mode of

Figure 1. The frequency of courtship disruption and the other ways in which females depart from male territories. Data are for identified females in 1994–1996.

departure). The true percentage was probably closer to the former figure since disruptions were less likely to go unnoticed by observers when females went out of sight compared with the other modes of departure such as walking out of the territory.

(b) *Disruptions of female visits to territories of successful versus unsuccessful males*

We observed 795 courtship visits by 68 identified females (92 female years) to identified males which were assigned as mating successes. Among males that mated at least once in a given year ($n=28$), 233 out of 694 female visits (33.6%) were disrupted by other males. For unsuccessful males ($n=29$) the proportion of disrupted visits was 26 out of 101. Analysed on a per male-year basis we found no significant difference between successful and unsuccessful males in the proportion of female visits that were disrupted (figure 2a; Mann–Whitney U -test $z = -1.47$, $p = 0.14$, only counting males that were visited at least once in a year). If anything, males that mated had a higher not lower probability of having female visits terminated by disruption (figure 2a). Within the group of males that mated, we found no significant relationship between mating success and proportion of visits disrupted (figure 2b; Spearman's $r = 0.28$, $n = 28$, $p = 0.072$). Again, if anything, the relationship was positive.

(c) *Disruptions of female visits to territories of preferred versus non-preferred males*

Individual females were more likely to be disrupted from the territory of their preferred male than from territories of other males (figure 3a; Wilcoxon's matched-pairs, signed-ranks test $z = -3.38$, $n = 51$, $p < 0.001$).

This result indicates that females do not discriminate against males whose territories they had been disrupted from. Analysed on a per time-unit basis, instead of per visit, we found no significant difference in the likelihood of being disrupted between visits to preferred and non-preferred males (figure 3b; Wilcoxon's matched-pairs, signed-ranks test $z = -0.75$, $n = 48$, $p = 0.47$), the observed difference being in the same direction as before.

Figure 2. (a) Probability (mean + 95% confidence limit) of female visits being terminated by disruption by other males for males with and without mating success. The probabilities were computed for each male as the proportion of visits that were disrupted. (b) Probability of female visits being disrupted by other males in relation to mating success (minimum number of different females mating) for males that obtained at least one mating.

(d) *Effects of disruptions on female behaviour*

A final approach was to look even more directly at the effects on individual males of disrupting individual females. We computed the probabilities that those individual females, after a disruption, would return (figure 4a) and solicit mating (figure 4b) with the disrupting male, a non-disrupting neighbour and the male from which she was disrupted.

Females did not return (figure 4a) or mate (figure 4b) with the disrupter more often than with a randomly chosen neighbour. This result strongly indicates that females do not prefer to mate with disrupters and that they do not redirect their mate choice to disrupters. On the contrary, females returned (figure 4a) and solicited mating (figure 4b) with much higher probability to the male that they had been disrupted from, compared to the disrupting male or the randomly chosen neighbour (Friedman's two-way ANOVA, returns $\chi^2 = 40.2$, $n = 53$, d.f. = 2, $p < 0.0001$ and solicitations $\chi^2 = 34.67$, $n = 39$, d.f. = 2, $p < 0.0001$). Females were as likely or more likely to return (figure 4a), and somewhat more likely to solicit (figure 4b; Wilcoxon's matched-pairs, signed-ranks test $z = -1.99$, $n = 35$, $p = 0.046$) with the territory owner after being disrupted

Figure 3. Probability (mean + 95% confidence limit) that a female is disrupted when at the territory of the male she mated with (her preferred male) compared with when at the territory of other males. (a) Analysed per visit. For each female these two probabilities were computed as the proportions of her visits to the respective males that were disrupted, based on 662 observations of courtship visits by 51 females (397 visits and 159 disruptions with a female's preferred male and 265 visits and 53 disruptions with a non-preferred male). Only females observed at least once with both their preferred and a non-preferred male are included. (b) Analysed per minute the visit lasts. This sample consisted of 614 observations of 48 females for a total of 8373 min.

compared with when they were not disrupted. This last result constitutes direct evidence that females do not avoid males with whom they suffer disruptions.

4. DISCUSSION

(a) *Females are choosy despite being harassed by males*

Disruptions were a common feature at great snipe leks. However, females did not avoid revisiting males they were chased away from and did not preferentially mate with disrupting males as suggested for another lekking species (Trail 1985b; Trail & Koutnik 1986). On the contrary, females were much more likely to return and mate with the male they were chased away from rather than with the disrupter or with other males. Therefore, we conclude that it is not important in the mate choice of a female whether she is disrupted or not from a potential

Figure 4. The effect of courtship disruption on subsequent female behaviour. (a) The probabilities (mean + 95% confidence limit) that females returned to different categories of males after a courtship disruption. Also shown is the probability of returning to the territory owner when the female visit was not terminated by disruption. DV, disrupted visits; NDV, non-disrupted visits. The values used are the means for each female (to avoid pseudoreplication) and only those visits where the female was later (on a subsequent, separate visit) observed at least once are included in the calculation of these probabilities. (b) As in (a) for the probability of females returning to solicit. Only those cases where the female was subsequently seen on at least one visit to solicit are included here.

mate. Female great snipe visit the leks for many nights before mating and usually mate with the male on more than one night (Fiske & Kålås 1995). The females seemed to have decided whom to mate with before actually mating and were not easily dissuaded by disrupters even when repeatedly disrupted. Thus, females were choosy despite not because of the high levels of harassment. This is evidence against direct benefits explaining the lek paradox in this species.

(b) *Dominance is not likely to be important in the distribution of matings within leks*

Disruptions may have an impact on female mating patterns with or without the presence of dominance relationships among males. However, because disruptive behaviour was so common and did not seem to have much impact on female mating patterns, dominance is unlikely to be important in influencing male mating

success. We do not think dominance is an important aspect of the behaviour of lekking great snipe males. We found no evidence that 'dominant' males can control 'subordinate's' reproduction, since the tendency to suffer disruption was higher for males obtaining mating success. Nor is there any evidence that females prefer central territories or specific locations at the lek that males could fight over (Höglund & Robertson 1990; Fiske *et al.* 1994; S. A. Sæther, P. Fiske and J. A. Kålås, unpublished data).

Neither the presence or absence of dominance precludes female choice on the basis of indirect benefits. An absence of dominance does preclude indirect benefits mediated by direct or indirect choice of dominant males, but not indirect benefits in general. We argue that the data suggest that there are no dominance relationships between males. Although that may not be true, if we assume that the tendency to suffer disruption is related to dominance, then the results at least indicate that females do not prefer dominant males and, therefore, do not obtain indirect benefits in this way. Whether they obtain indirect benefits in other ways is still an open question.

The existence of some sort of dominance hierarchy should not be taken for granted in any lekking species. We question its existence in the great snipe, although an earlier study (Höglund & Robertson 1990) claimed to find a linear dominance rank hierarchy using the outcome of fights to calculate dominance relationships. However, this is ambiguous because males are territorial. Asymmetries in ownership will therefore confound relationships between dominance rank based on fights and mating success. As acknowledged by Höglund & Alatalo (1995), this is precisely the case in this species because '... males often visited by females remained in their territories while unpopular males left their territories to attack males when the successful males had female visits' (p. 69). We think our approach addressing the effects of disruptions on female behaviour provides a more direct and reliable way of testing whether any dominance relationship can be important. In short, the results suggest that (i) females do not have direct preferences for dominant males, (ii) females do not have indirect preferences for dominant males within leks, (iii) the distribution of matings within leks is not influenced much by male competition for mates, and (iv) females are highly choosy and may possibly have direct preferences unrelated to dominance, for indirect benefits.

However, this is not to say that male competition for mates is unimportant in the distribution of matings in this species. There is an additional way in which indirect female mate choice may restrict their set of potential mates, although in a more trivial sense. Some males visit leks without establishing territories and this may be related to male-male competition (Gratson *et al.* 1991; Höglund & Alatalo 1995). In this way indirect female choice (Wiley & Poston 1996), because of a preference for mating at leks, may influence the distribution of matings by setting the conditions for competition.

Nevertheless, among those males that establish a territory and maintain it, there is apparently not much scope for third-party males to interfere with female mating

decisions, apart from delaying matings. The available evidence also suggests that female mating decisions are not based on male competitive behaviour. On the contrary, we think direct female choice of mates has seldom been so clearly demonstrated as in this species: despite frequent disruption of females' courtship visits, females returned to their preferred male and mated.

(c) *Why do males disrupt?*

The above arguments prompt the question, what is the benefit for males of performing disruptions? We will briefly mention four possibilities. We note from the outset the problem that even small benefits, which are difficult ones to detect, can make the behaviour worthwhile if the costs are low.

- (i) Females may sometimes find the delay caused by disruption in mating with the preferred male too costly. Hence, male interference might constrain female choice by introducing time costs. However, this seems unlikely to be very important, since females spend several days at the lek and usually mate more than once, although choosiness may be lower late in the season or vary among females. Disruptions seem to have a rather low influence on this potential trade-off between the costs of delaying breeding and mating with the preferred male, since females show a remarkable resoluteness to return after being disrupted. The potential benefit to disrupters of a small number of females mating with another male than her preferred may very well have to be shared with other non-disrupting males. Yet, it may pay off as long as females do not actively avoid previous disrupters. This may indeed be the case since there were no significant differences between the disrupter and the randomly chosen neighbour. Disrupters seem to be neither discriminated against nor favoured by females, simply ignored in most cases. We point out that the small numbers of females soliciting matings from their disrupters or neighbours (figure 4b) should not be interpreted as females having redirected their choice to these males. In these cases it could simply be that the female was being disrupted when at the territory of a non-preferred male.
- (ii) Another occasional benefit may occur for males if disruptions are actually attempts at forced copulations. Only limited anecdotal evidence exists on the possibility of males mating with non-soliciting females in this species: one female disrupted by a neighbour was pursued and got stuck in the vegetation, but managed to free herself as the male was seemingly about to attempt copulation. Males often pursue disrupted females out of the lek area for some time before returning to their territories. Although seeing what happens outside the lek can be difficult, we have no indications that females solicit matings outside lek territories.
- (iii) A related possibility is that disruptions may be attempts at copulation with females soliciting to the territory owner. Interruption of solicitations is infrequent (see § 2(a)) but we have four observations of males managing to mate with females inside other

males' territories. In two of these cases the disrupting male physically displaced the territory owner from the back of the female and copulated with the still soliciting female. However, since most disruptions involved females not soliciting mating, this seems inadequate as an explanation.

- (iv) A final possibility (which was suggested by a referee) is that the benefit lies not in mating with the female disruptee but, rather, in removing any opportunity to copy among females, who may otherwise be attracted to males with many females present. However, this seems unlikely since females may also be attracted by the increased activity caused by disruptions. Based on the distribution of matings in time, Fiske *et al.* (1996) argued that copying is unlikely to be important in great snipe mate choice.

Some questions remain. Why are visits to more successful males more likely to become disrupted? Why are females more likely to be disrupted when with their preferred male? Why are females more likely to solicit mating from the male after being disrupted than when not being disrupted? The answer to all these questions might be that, for some reason, the disrupting males are more interested in disrupting fertile females. If fertile females have finished mate sampling, they will be spending most of their time (when at the lek) with their preferred male. This will create a bias in the likelihood of females being disrupted with respect to both overall male mating success and status as preferred by the individual female. We suggest the reason why males are more interested in disrupting fertile females is that these females are more sensitive to time costs, as explained above.

(d) Conclusions

Scenarios where females obtain good genes from high-quality males by preferring dominant males directly do not seem to apply to the great snipe. Other studies have shown that such indirect benefits do not come from indirect preferences of dominance either (such as central positions or specific locations within leks; Höglund & Robertson 1990; Fiske *et al.* 1994; S. A. Sæther, P. Fiske and J. A. Kålås, unpublished data). It thus appears to be a conflict between female preferences and male competition for mates, in contrast to the more harmonious view that females might somehow use male competition to select genetically high-quality males (see also Qvarnström & Forsgren 1998).

However, the results presented also strengthen the possibility that female great snipes choose mates for genetic (indirect) benefits for their offspring rather than direct benefits. Our results suggest that the lek paradox is not solved by direct benefits of harassment avoidance in this species.

Thanks are due to F. Widemo, P. T. Smiseth and the referees for comments and to those who helped us in the field in 1994–1996, in particular T. Bretten, J. M. Gjøl, S. Kålås, P. T. Rintamäki and S. L. Svartaas.

REFERENCES

- Balmford, A. 1991 Mate choice on leks. *Trends Ecol. Evol.* **6**, 87–92.
- Beehler, B. M. & Foster, M. S. 1988 Hotshots, hotspots, and female preferences in the organization of lek mating systems. *Am. Nat.* **131**, 203–219.
- Berglund, A., Bisazza, A. & Pilastro, A. 1996 Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* **58**, 385–399.
- Bradbury, J. W. & Gibson, R. M. 1983 Leks and mate choice. In *Mate choice* (ed. P. Bateson), pp. 109–138. Cambridge University Press.
- Bradbury, J. W., Vehrencamp, S. L. & Gibson, R. 1985 Leks and the unanimity of female choice. In *Evolution: essays in honour of John Maynard Smith* (ed. P. J. Greenwood, P. H. Harvey & M. Slatkin), pp. 301–314. Cambridge University Press.
- Brown, J. L. 1997 A theory of mate choice based on heterozygosity. *Behav. Ecol.* **8**, 60–65.
- Carbone, C. & Taborsky, M. 1996 Mate choice or harassment avoidance? A question of female control at the lek. *Behav. Ecol.* **7**, 370–378.
- Clutton-Brock, T. H., Deutsch, J. C. & Nefdt, R. J. C. 1993 The evolution of ungulate leks. *Anim. Behav.* **46**, 1121–1138.
- Clutton-Brock, T. H., McComb, K. E. & Deutsch, J. C. 1996 Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky. *Behav. Ecol.* **7**, 373–378.
- Deutsch, J. C. & Nefdt, R. J. C. 1992 Olfactory cues influence female choice in two lek-breeding antelopes. *Nature* **356**, 596–598.
- Fiske, P. & Kålås, J. A. 1995 Mate sampling and copulation behaviour of great snipe females. *Anim. Behav.* **49**, 209–219.
- Fiske, P., Kålås, J. A. & Sæther, S. A. 1994 Correlates of male mating success in the lekking great snipe (*Gallinago media*): results from a four year study. *Behav. Ecol.* **5**, 210–218.
- Fiske, P., Kålås, J. A. & Sæther, S. A. 1996 Do female great snipe copy each other's mate choice? *Anim. Behav.* **51**, 1355–1362.
- Foster, M. S. 1983 Disruption, dispersion, and dominance in lek-breeding birds. *Am. Nat.* **122**, 53–72.
- Gratson, M. W., Gratson, G. K. & Bergerud, A. T. 1991 Male dominance and copulation disruption do not explain variance in male mating success on sharp-tailed grouse (*Tympanuchus phasianellus*) leks. *Behaviour* **118**, 187–213.
- Höglund, J. & Alatalo, R. V. 1995 *Leks*. Princeton University Press.
- Höglund, J. & Robertson, J. G. M. 1990 Female preferences, male decision rules and the evolution of leks in the great snipe *Gallinago media*. *Anim. Behav.* **40**, 15–22.
- Jennions, M. D. & Petrie, M. 1997 Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* **72**, 283–327.
- Kålås, J. A., Fiske, P. & Sæther, S. A. 1995 The effect of mating probability on risk taking: an experimental study in lekking great snipe. *Am. Nat.* **146**, 59–71.
- Kirkpatrick, M. & Ryan, M. J. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.
- Løfaldli, L., Kålås, J. A. & Fiske, P. 1992 Habitat selection and diet of great snipe *Gallinago media* during breeding. *Ibis* **134**, 35–43.
- Mackenzie, A., Reynolds, J. D., Brown, V. J. & Sutherland, W. J. 1995 Variation in male mating success on leks. *Am. Nat.* **145**, 633–652.
- Nefdt, R. J. C. 1995 Disruptions of matings, harassment and lek-breeding in Kafue lechwe antelope. *Anim. Behav.* **49**, 419–429.
- Pomiankowski, A. & Møller, A. P. 1995 A resolution of the lek paradox. *Proc. R. Soc. Lond. B* **260**, 21–29.
- Qvarnström, A. & Forsgren, E. 1998 Should females prefer dominant males? *Trends Ecol. Evol.* **13**, 498–501.

- Reynolds, J. D. & Gross, M. R. 1990 Costs and benefits of female mate choice: is there a lek paradox? *Am. Nat.* **136**, 230–243.
- Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* **263**, 1415–1421.
- Trail, P. W. 1985a Courtship disruption modifies mate choice in a lek-breeding bird. *Science* **227**, 778–780.
- Trail, P. W. 1985b Territoriality and dominance in the lek-breeding Guianan cock-of-the-rock. *Natl Geogr. Res.* **1**, 112–123.
- Trail, P. W. & Koutnik, D. L. 1986 Courtship disruption at the lek in the Guianan cock-of-the-rock. *Ethology* **73**, 197–218.
- Widemo, F. & Sæther, S. A. 1999 Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends Ecol. Evol.* **14**, 26–31.
- Wiley, R. H. 1991 Lekking in birds and mammals: behavioral and evolutionary issues. *Adv. Study Behav.* **20**, 201–291.
- Wiley, R. H. & Poston, J. 1996 Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**, 1371–1381.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.