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Costs and consequences of variation in the size of ruff leks

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Summary. We studied 13 ruff leks in a small region on the island of Gotland (Sweden) to investigate the effect of lek size on the costs and benefits of lekking for individual males. Male ruffs occur in two behaviourally and morphologically distinct forms, "independents" ("residents" plus "marginals") and "satellites", whose costs and benefits we have assessed separately. These ruff leks had from 1–10 resident (territory-holding) males and were visited daily by satellites, marginals and females from 5–25 May, when most copulations occurred. We used the average number of independent males, counted during censuses taken every 5 min during 2-h observation periods at each lek, as an index of mean lek size. Per independent male, the numbers of both satellites and females increased significantly with mean lek size. Female arrival rate and attendance (total female-minutes) also increased significantly with mean lek size as did the average per capita rate of mating success for resident males (that of satellites was not quite significant). Thus, the dispersion of both of these male categories did not appear to fit an ideal free distribution with respect to mating success. In addition, the number of independent-independent fights per independent and the rate of satellite-resident dyad formation per resident increased significantly with mean lek size. These results suggest that ruffs on larger leks enjoy higher mating success than those on smaller leks but also that costs increase with lek size. We suggest that independent males distribute themselves so as to maximize their own net benefits and that this factor can account for both the occurrence of ruff leks and the variation in their size.

Introduction

Although many hypotheses have been proposed to explain lek evolution (for reviews see Bradbury and Gibson 1983; Arak 1984; Bradbury and Davies 1987), some aspects of lekking have, until recently, not been well studied. One important factor that has long been overlooked is the possibility that the average male fitness varies with lek size. If males are more successful on leks than during solitary display and if average male fitness increases with lek size, the habit of joining aggregations of males would be selected for and could explain why leks exist. Recently, some evidence indicates that there is such a fitness gain to males in larger leks (e.g. Alatalo et al. 1991; Lank and Smith 1992; Svensson and Pettersson 1992).

If mean male fitness does increase with lek size, why do we find considerable variation in lek size, even within a limited area that would be accessible to all males (e.g. Bradbury et al. 1989; van Rhijn 1991)? One possible reason is that costs as well as benefits covary with lek size. In lekking black grouse (*Tetrao tetrix*), the per capita fighting rate increased with lek size, indicating a higher cost for males on larger leks (Alatalo et al. 1992). If attendance at larger leks is generally associated with higher costs (e.g. injury, interference and increased energy expenditure that might reduce their access to females), we should expect males to trade the potential fitness gains that they might accrue on larger leks against those costs. If males differ in quality, the optimal solution for each individual would depend on the qualitiy of the other males present on a lek. Thus, males should be expected to distribute themselves according to models of ideal free distributions of unequal competitors (Fretwell and Lucas 1970; Sutherland 1983; Sutherland and Parker 1985; Parker and Sutherland 1986; Houston and McNamara 1988). Such models predict that high quality males will attend the best lek sites (e.g. where female encounter rate is highest). Low quality individuals will consequently gather at sites where the gain rate is low but where costs are also low.

Male ruffs (*Philomachus pugnax*) display on leks that vary both in size and the rate of female visitation (van Rhijn 1991). This species is therefore ideally suited for examining the costs and benefits associated with displaying on leks of different sizes. In addition, ruff leks are

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usually relatively small (<30 males in attendance) and many leks are often clustered in a small geographical area such that they are easily accessible to all males of females in the local population. This latter characteristic is especially important when assessing models of ideal free distributions (Fretwell and Lucas 1970). Also, because males have extremely polymorphic plumage, they can often be individually identified without capturing and colour-ringing and, as a result, the mating success of particular males can be readily assessed.

In this study, we examine how the numbers and behaviour of male and female ruffs varied over 13 different lek sites studied in one season in a small area in southeastern Sweden. We explicitly designed this study to address the following questions: (1) do females tend to visit males on larger rather than smaller leks, (2) is male mating success higher on larger leks, and (3) is it more costly for males to attend larger leks?

Methods

Study area. We observed ruff leks from 4 May to 10 June 1990 on a 90-ha study area comprising two adjacent peninsulas on the southern part of the island of Gotland (57° 10′N, 18° 20′E), Sweden, in the Baltic Sea. This area consisted mainly of shore meadows grazed by sheep and cattle, interspersed with cultivated fields and thickets (Fig. 1). Ruffs attended lek sites and nested only on the meadows.

In 1990, we found 13 different ruff leks on the study area (Table 1), usually on slightly raised ridges near small bodies of water (Fig. 1). Thorough surveys of the study area indicated that these were the only ruff leks present that year. Some of these lek sites have been active for many years and are well-known to local farmers. For example, we briefly observed many of these leks in May–June 1988 and, during a short survey in 1989, found all but one lek that was active in 1990. The average numbers of males counted on the 12 leks sampled both years were highly correlated (Spearman rank correlation, $r_s = 0.76$, $P < 0.01$), suggesting that the relative sizes of these leks have been stable in recent years.

Individual identification. On a few leks, some of the males were ringed with unique colour combinations, but the plumage polymorphism in this species made it possible to recognize and individually identify almost all unmarked males as well (see also Hogan-Warburg 1966). We drew a "mug shot" of each male to facilitate individual identification from day to day and when males moved between leks. Each lek was usually watched by the same observer for several consecutive days. Plumage variation among females was usually too slight to permit individual identification but most females could be followed during a single visit so that their arrival and departure times and mating success could be recorded accurately.

Following Hogan-Warburg (1966), we classified males as either "independents" or "satellites" by their plumage coloration and behaviour. Usually satellites had white head tufts and light-coloured ruffs whereas independents had head tufts that ranged from grey to brown to black with a variety of markings (see also Hogan-Warburg 1966; van Rhijn 1983). Independents were further classified as "residents" or "marginals" depending upon their behaviour – each resident remained mostly at one lek where it defended a small display court whereas marginal males travelled from lek to lek, often with satellites and/or females. When marginals visited a lek, they did not defend display courts and usually stayed on the periphery of the main display arena. Satellites also travelled among leks but they displayed distinctive behaviour when interacting with resident males (see Hogan-Warburg 1966).

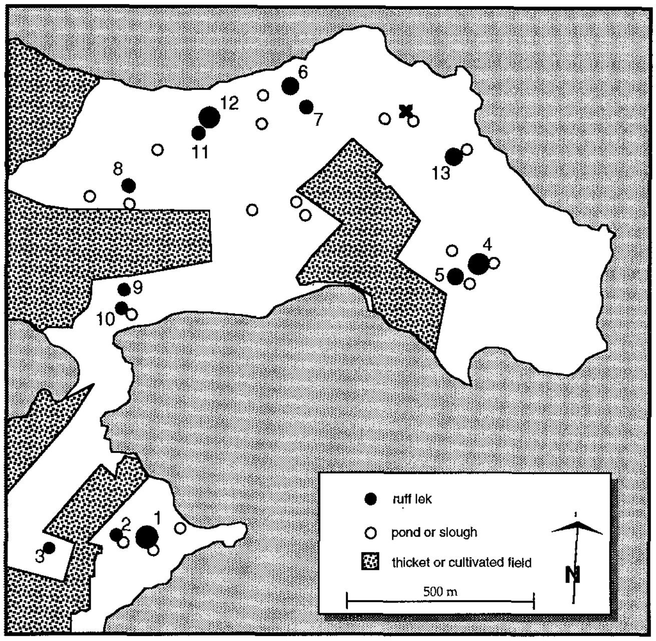

Fig. 1. Map of the study area showing the location of leks and small bodies of water. The sizes of the *dots* for the different leks are proportional to the number of residents associated with each lek. One lek (marked ×) on the study site was not observed because we could not gain access to the land

Table 1. Characteristics of the 13 ruff leks studied

Lek	Observation periods		Total observation time (h)	Mean no. of			Residents
	No.	Dates (May)		I	S	F	
1	14	5–25	27.8	7.34	1.10	0.98	10
2	7 (3)[a]	9–19 (9–13)[a]	14.0 (6.0)[a]	0.83	0.05	0.07	2
3	9	10–25	18.0	0.80	0.02	0.04	1
4	18	6–24	36.9	6.09	0.72	1.20	9
5	9	9–22	14.6	3.41	0.71	0.21	5
6	15	5–25	28.9	3.18	0.31	0.33	6
7	5	11–17	10.0	1.91	0.12	0.05	3
8	10	6–17	18.7	2.05	0.34	0.27	3
9	11	8–24	22.0	1.04	0.08	0.15	2
10	10	8–24	20.0	0.87	0.02	0.07	2
11	8	5–18	14.5	2.31	0.14	0.21	3
12	8	8–23	15.3	3.56	0.59	0.56	9
13	7	12–25	13.8	5.26	1.09	0.67	6

[a] For 4 observation periods (8.0 h) only 5-min counts were recorded

Mean numbers of independents (I), satellites (S) and females (F) were calculated from 5-min counts during each observation period. "Residents" represents the total number of individual males that behaved as residents on each lek. Data shown here are only for those observation periods analysed

Unlike marginals, satellites are often accepted within the territories of residents and habitually form short-term associations (which we called "dyads") with the residents. In a dyad, resident and satellite squat facing each other, the resident often holding his bill over the head of the satellite. Especially in the presence of females, the resident may perform ritualized pecking directed at the head of the satellite, sometimes actually hitting the satellite's head. Satellites were usually submissive, not reacting to the resident's behaviour, but sometimes this pecking action seemed to cause the satellite to leave the resident's display court.

Observation periods. We attempted to watch leks for 2-h observation periods on all but 4 days late in the study period in 1990. Occasionally observation periods were cut short when leks were disturbed by grazing livestock. Each lek was watched using binoculars and telescope from blinds or observation posts (behind stone walls or nearby buildings) <100 m away. Once observers had entered a blind or arrived at a concealed observation post, their presence did not seem to influence the behaviour of the birds.

We attempted to observe each lek at least once every 3 days after at least one resident became established on a display court. We sampled most of the large leks more frequently than smaller leks (Table 1) so that we could obtain comprehensive information on the mating behaviour of individual males (unpublished data) – mating activity was rare on the smaller leks. Even on days when we did not conduct observations at small leks, we usually checked them briefly to ensure that nothing unusual was happening at those sites.

Even though male ruffs were usually present on leks from sunrise (0400–0500 hours local time, GMT-2) to sunset (2030–2130 hours), there tended to be more activity in the early morning hours (see also Lank and Smith 1987). Thus, when there was more than one observation period on a lek on a given day, we used only the earliest period in all analyses. Our conclusions are unaffected by restricting analyses to data from the early morning periods.

During each observation period at a lek, we attempted to record the time of arrival and departure of all females and males. We also tried to determine the identity of participants in all fights and independent-satellite dyads (see below). Fights occurred most often between independent males and involved either kicking with the legs and feet (see Hogan-Warburg 1966 for description) or aggressive chases, often with pecking and bodily contact. Since males are sometimes injured during fights (personal observation) and both fighting and the forming of dyads can interfere with a male's access to females (Hogan-Warburg 1966), we assume that these activities represent costs to resident males.

Individual females typically visit leks for 2–3 consecutive days before egg-laying and may solicit and copulate repeatedly with the same or different males during these periods (Lank and Smith 1987). Though Lank and Smith (1987) documented copulations away from lek sites in their study area in Finland, we observed none during our study and we believe that the overwhelming majority of matings in our study population occurred at the leks we studied. We defined a failed copulation as those instances when a male attempted to mount or did mount a female but did not achieve cloacal contact, either because the pair was interrupted by another male or because the female terminated the interaction. We defined a successful copulation as a mounting involving cloacal contact, and a mating as one or more consecutive successful copulations between the same male and female during the female's visit to the lek. Hence, a female that successfully copulated with more than one male during the same visit to a lek was assigned one mating for each bout of copulations with each male. For example, one female who successfully copulated four consecutive times with one male, then twice with a different male, was scored as successfully copulating six times and mating twice during that lek visit. We define mating success as the number of matings per male per hour.

In addition to the continuous observations made at each lek, we counted the number of independents, satellites and females present every 5 min to provide indices of lek size and the presence of satellites and females. During these counts, it was sometimes not possible to distinguish between the two kinds of independents (marginals and residents). However, since marginal males visited the leks infrequently and irregularly, the number of independents counted provides a reasonable index of the number of residents present on each lek. Even though each resident male was associated mainly with only one lek (Table 1), there was considerable variation in the amount of time that each resident spent on his lek (see Results). Thus, we define mean lek size as the average number of independents present (i.e. the mean of the means from 5-min counts for each observation period at a lek). Since we were particularly interested in the response of females and satellites to variation in lek size, this "mean lek size" provides an useful index of the average lek size that would be perceived by these visitors during the study period. Because total attendance time of marginals was only 5.8% of that of all independents (mean value from 13 leks, range 0–10%), we estimate that our mean lek size index would have overestimated the mean number of residents present by only about 5%, on average.

Statistical analyses. We used Sokal and Rohlf (1981) for statistical tests, notation and P values. We used nonparametric analyses throughout because many of our variables are proportions and rates whose underlying distributions could not be accurately determined from the relatively small sample size of leks in this study. Thus, particularly for correlation analyses, we have analysed only in trends in the data, rather than the shapes of those relationships. We used proportions and rates for many variables to control for differential sampling effort and so that we could compare the per capita costs and benefits to males, in particular.

Data from two leks were not included in any analyses of behaviour (lek attendance and both intra- and intersexual interactions): at lek 8, tall grass often obscured observations and made it difficult to positively identify individuals at all times; at lek 2, detailed observations were made only during three observation periods early in the season – after 13 May, 5-min counts for this lek were made during four observations periods at lek 1, which was nearby. For leks 2 and 8, we used data from the 5-min counts only.

Since all but 4 of the 169 successful copulations ($n=11$ leks) that we observed occurred from 5 to 25 May, we restricted all our analyses to that period. During this period, each lek site was occupied by at least one resident male, and satellites and/or females visited each lek during most (88%) of the 131 observation periods analyzed. After 24 May, few copulations were observed, some lek sites were occasionally unoccupied for long periods, and the visitation rate of females and satellites declined markedly.

Two small leks (leks 7 and 11) were abandoned by their residents in the middle of our study period, being last observed on 17 and 18 May, respectively (Table 1). Though the total numbers of residents and copulations on leks were lower at the beginning and end of our study period (e.g. Fig. 1), sampling at all but these two leks occurred throughout this period and was therefore not biased with respect to the peak period of activity. Since those two leks were abandoned when the copulation rate had already begun to decline, our estimates of mating success and females visitation rates at those leks might be slightly overestimated relative to leks sampled throughout the study period. Restricting all of our analyses to the period 5–17 May, however, had no effect on any of our conclusions, but provides data that are more representative of male mating success throughout the breeding season.

Results

Lek size

The 13 leks that we studied varied in mean size from 0.80 to 7.34 independent males, with 1–10 different resident males associated with each site (Table 1). Mean lek size (calculated from 5-min counts) was highly correlated with the total number of resident males at each lek ($r_s = 0.97$, $P < 0.001$, $n=13$ leks). In most cases, however, mean lek size was smaller than the number of residents (Table 1) associated with a site because residents were

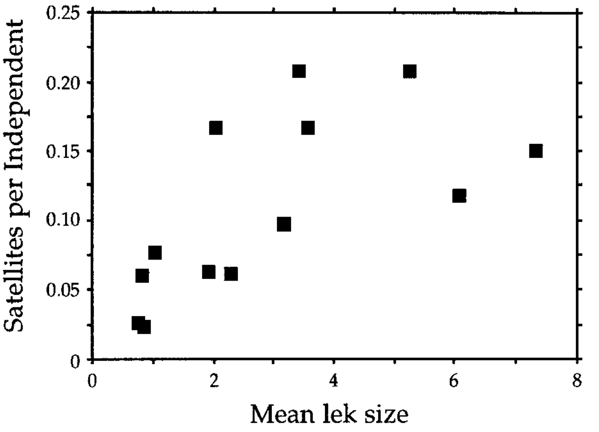

Fig. 2. Relationship between mean lek size and the average number of satellites per independent male present. See Methods and Table 1 for sample sizes for this and subsequent Figures

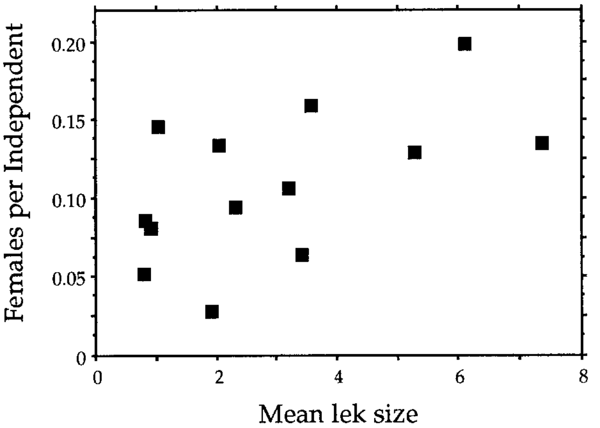

Fig. 3. Relationship between mean lek size and the average number of females per independent male present

sometimes away from the lek site during 5-min counts. On average, residents spent 53% of their daytime on their leks ($n=13$ lek means). Some residents often spent entire observation periods on a lek and the mean proportion of observation periods that a resident did this increased significantly with mean lek size ($r_s=0.81$, $P<0.005$, $n=11$). Despite this, the average percentage of time that a resident spent on his lek was not related to mean lek size ($r_s=0.05$, $P>0.50$, $n=11$), probably because lek attendance times by residents were highly variable.

Lek attendance by females and satellite males

The mean numbers of both satellites and females counted at leks increased significantly with mean lek size (satellites: $r_s=0.96$, $P<0.001$; $n=13$; females: $r_s=0.92$, $P<0.001$, $n=13$). Per independent male present, the numbers of satellites ($r_s=0.75$, $P<0.005$, $n=13$, Fig. 2) and females ($r_s=0.60$, $P<0.05$, $n=13$, Fig. 3) also increased significantly with mean lek size. Thus, both satellites and females were distributed nonrandomly with respect to lek size, associating more often with larger leks.

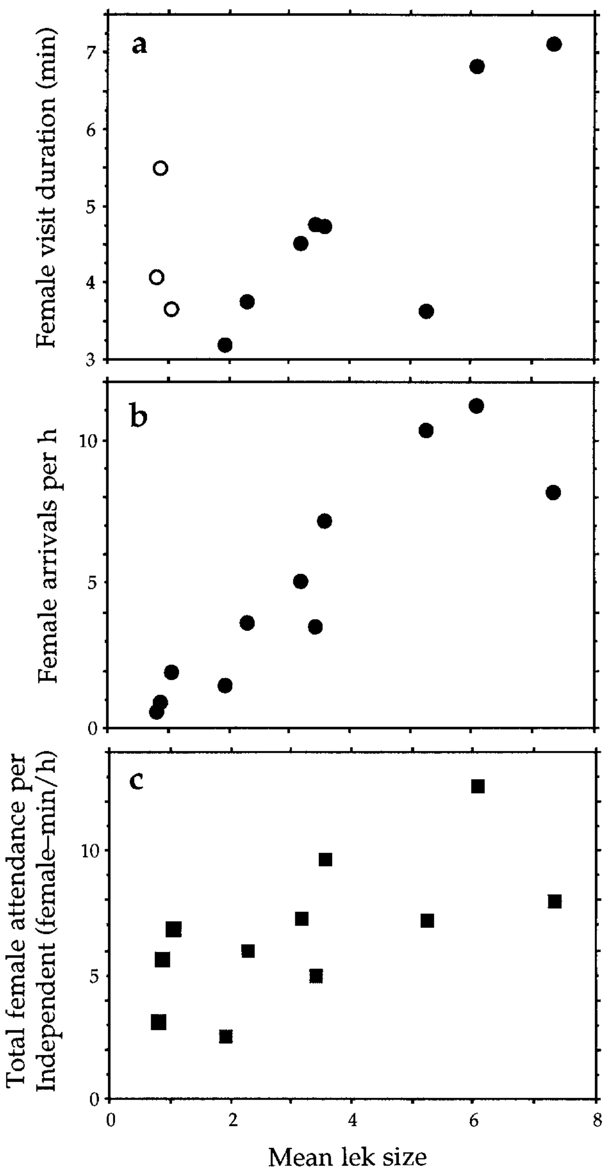

Fig. 4a–c. Relationship between mean lek size and **a** the mean duration of female visits (*open circles* are leks with ≤2 residents), **b** the average mean female arrival rate, and **c** total female attendance per independent male present. Female attendance is expressed as female-minutes per observation-hour to standardize for observation periods of different length

The behaviour of females also illustrates their tendency to visit larger leks. For example, the mean duration of a female visit increased with lek size ($r_s=0.43$, $P=0.20$, $n=11$, Fig. 4a), though the correlation is not significant (note that, in this and subsequent analyses, leks 2 and 8 are not included – see Methods). Females, however, tended to loiter at the lek periphery on their infrequent visits to the smallest leks, suggesting that their visit duration at those leks was not related to any possible preference for the residents there. When the three smallest leks, with only one or two resident males, were removed from the analysis, the duration of female visits increased significantly with mean lek size ($r_s=0.74$, $P=0.05$, $n=8$, see Fig. 4a). Female arrival rates ($r_s=0.94$,

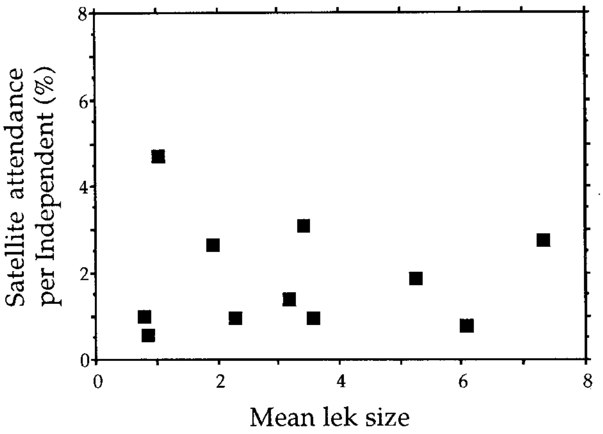

Fig. 5. Relationship between mean lek size and and the average satellite attendance per independent male present. Satellite attendance was measured as the proportion of observation time that each satellite attend a lek, averaged over all satellites at that lek

$P<0.001$, $n=11$, Fig. 4b) and the total amount of time spent by females on a lek ($r_s=0.96$, $P<0.001$, $n=11$) also both increased significantly with mean lek size as did total female attendance, defined as the total number of female minutes per observation hour, per independent male ($r_s=0.75$, $P=0.01$, $n=11$, Fig. 4c). Thus individual independent males on larger leks had the opportunity to encounter females at a higher rate than those on smaller leks.

Satellite attendance also increased with lek size. To analyse this, we calculated the mean proportion of time that individual satellites were present on a lek during every observation period, then averaged these means over all observation periods for each lek. This measure of lek attendance by satellites increased significantly with mean lek size ($r_s=0.67$, $P<0.05$, $n=11$). Satellite male attendance per independent male present, however, was independent of lek size ($r_s=0.10$, $P>0.50$, $n=11$, Fig. 5). Thus satellites appeared to remain longer on larger leks but the amount of time that they spent per independent present did not increase with lek size.

Male-male interactions

The rate that fights occurred per independent male increased significantly with mean lek size ($r_s=0.64$, $P<0.05$, $n=11$, Fig. 6a). Per independent male, fighting rates increased with mean lek size, both among independents ($r_s=0.63$, $P<0.05$, $n=11$) and between independents and satellites ($r_s=0.55$, $0.10>P>0.05$, $n=11$), though the latter correlation is not statistically significant. The resident-satellite fighting rate per satellite, however, was not correlated with mean lek size ($r_s=0.01$, $P>0.50$, $n=11$, Fig. 6b). Similarly, the number of satellite-independent dyads formed per independent male per hour increased significantly with mean lek size ($r_s=0.72$, $P<0.02$, $n=11$) though the number of such dyads per satellite per hour did not ($r_s=0.41$, $P>0.20$, $n=11$). Thus, independent males on the larger leks interacted both with satellites and with other independents at a higher rate than those on smaller leks whereas the interaction rates for satellites were independent of lek size. Virtually all of the these male-male interactions involved at least one resident male; marginal-marginal fights and marginal-satellite dyads were very rare. Thus, the fighting and dyad formation rates that we have documented for independents largely represent costs for residents rather than for marginals.

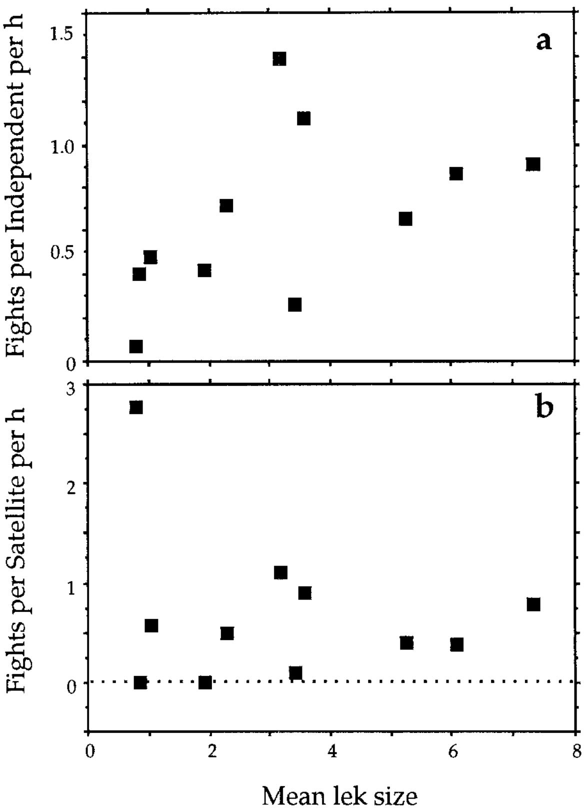

Fig. 6a, b. Relationship between mean lek size and **a** the number of fights per independent male present and **b** the number of fights per satellite male present. Fights are expressed as a rate (per observation-hour) to standardize for observation periods of different length

Male mating success

The per capita rate of male mating success (matings/male per hour) increased with mean lek size for both resident ($r_s=0.91$, $P<0.001$, $n=11$, Fig. 7a) and satellite males ($r_s=0.56$, $0.10>P>0.05$, $n=11$, Fig. 7b), though the correlation for satellites is not quite significant. Marginal males did not even attempt copulations and are thus not analysed here. Despite the fact that the male mating rate was higher on larger leks, total female attendance (female-min) per mating was not correlated with mean lek size for matings with either independents ($r_s=-0.64$, $0.20>P>0.10$, $n=7$) or satellites ($r_s=0.50$, $P=0.50$, $n=5$) or all male pooled ($r_s=-0.43$, $P>0.20$, $n=7$). Thus the amount of time required for females to choose mates and copulate with them was not influenced by the higher rates of male-male interactions at larger leks.

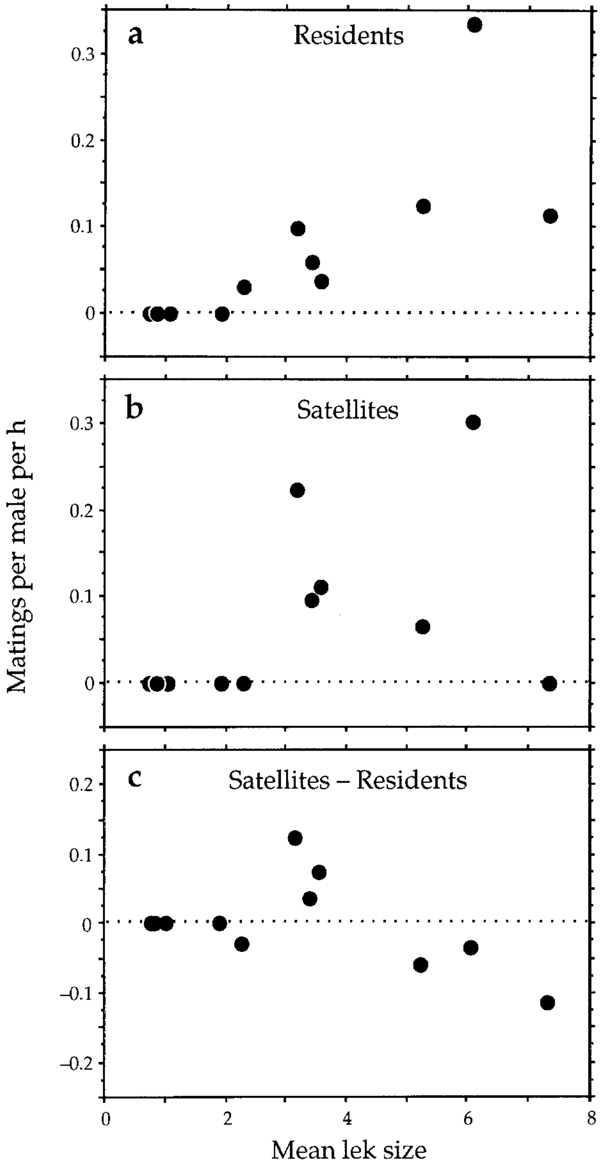

Fig. 7a–c. Relationship between mean lek size and the matings obtained by **a** resident and **b** satellite males, and **c** the difference between the rate of mating by satellites and residents. Matings are expressed as a rate (per observation-h) to standardize for observation periods of different length

Although the per capita success of both residents and satellites both increased with lek size, the number of matings obtained by the average satellite in the whole study population was significantly lower than that of the average resident – 23% of the 119 males that we studied were satellites but they acquired only 9% of the 135 matings observed ($G = 8.2$, $df = 1$, $P = 0.008$). Satellites obtained matings at approximately the same rate as independents on the five smallest leks, at higher rates on the three medium-sized leks and at lower rates on the three largest leks (Fig. 7c). Thus, although the malting success of the average satellite increased with lek size, satellites were proportionately less successful than independents on the three largest leks.

Despite the increased fighting rate on larger leks, copulation success rate (i.e. the percent of copulation attempts that were successful) of residents increased significantly with mean lek size ($r_s = 0.78$, $P < 0.05$, $n = 9$, Fig. 8a), excluding two leks where the residents did not attempt to copulate. For satellites, on the other hand, copulation success rate decreased with mean lek size ($r_s = -0.35$, $P > 0.50$, $n = 6$, Fig. 8b), though the correlation is far from significant. These trends show that the copulation attempts of residents were less likely to fail on larger leks, either terminal by females or disturbed by other males. Copulation attempts by satellites, on the other hand, may be more successful on smaller leks but more work will be needed to confirm this relation.

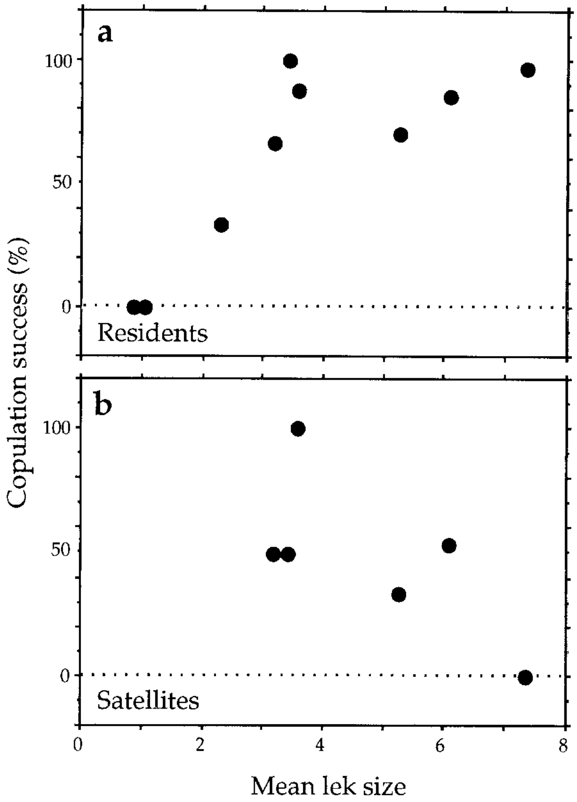

Fig. 8a, b. Relationship between mean lek size and the copulation success of **a** resident and **b** satellite males. Copulation success is expressed as the percent of copulation attempts that were successful (i.e. involved cloacal contact; see Methods)

To determine the mating skew among the territory-holding resident males on leks where copulations occurred, we calculated the proportion of copulations obtained by the top 25th percentile of resident males ranked in order of success. When the total number of residents was not evenly divisible by 4, the number of copulations obtained by the male of the 25th percentile was adjusted proportionately. This skew decreased significantly with lek size ($r_s = -0.86$, $P < 0.05$, $n = 7$). Thus, on smaller leks, the few males that obtained copulations seem to have been better able to monopolize females.

Discussion

Male benefits related to lek size

Female ruffs were more likely to visit larger leks as shown by the nonrandom distribution of females, and their arrival rates (Fig. 4b). Female visit durations also increased with mean lek size (Fig. 4a). As a result, females spent more time on larger leks. Females moved frequently and freely among lek sites in our study area, so it is reasonable to assume that they had ample opportunity to sample all of the lek sites that we studied. Moreover, because females did not appear to compete for access to males, it does not appear that the distribution of females among leks could have been influenced by female-female competition. Female attendance was also nonrandom per independent male present such that independents on larger leks had more opportunity to interact with females.

Resident males on larger leks were more successful in obtaining matings than males on smaller leks, as shown by the positive correlation between per capita mating rates and lek size (Fig. 7a). Since female attendance time per mating was not positively correlated with lek size, we assume that increases in female attendance were not due to an increase either in the time required to choose a mate or the extra time required for courship and copulation. We conclude, therefore, that female attendance was positively correlated with lek size simply because females preferred to mate with males on larger leks and thus visited them more often. These conclusions are supported by a recent experimental study (Lank and Smith 1992) showing that female ruffs can perceive differences in lek size at a distance and prefer to visit larger leks.

Satellite males also visited larger leks more often, and appeared to benefit from these visits (Fig. 7b). It seems, however, that satellite mating success was relatively better on medium-sized leks when compared to that of the residents there (Fig. 7c). On one of the three largest leks, satellites achieved their highest absolute mating rate but on another they obtained no matings. Further work is obviously needed before we can be certain that satellites maximize their mating rate on medium-sized leks. If they do, then their apparent preference for visiting larger leks, even per capita independent male (Fig. 2), will be difficult to explain.

Increased male mating success on larger leks has also been found in a few recent studies of other lekking species. In *Drosophila conformis*, for example, larger leks had higher female visitation rates (Shelly 1990) and in the stink bug, *Megacopta punctatissimum*, females courted males in aggregations more often than they courted solitary males (Hibino 1986). In the behaviourally sex-role-reversed dance fly, *Empis borealis*, where females lek, average female mating success increased with the size of female swarms and visiting males mated more often in larger swarms, (Svensson and Pettersson 1992). In the Uganda kob (*Kobus kob thomasi*), a lekking antelope, mean ejaculation rate per male also increased with lek size (Balmford 1990). In black grouse, larger leks had more female visits, more copulations per male and individual females were more likely to mate when they visited larger leks (Alatalo et al. 1991). Thus the tendency of females to mate more often on larger leks may be a general phenomenon.

Male costs related to lek size

If males benefit from joining larger leks, the fact that many leks are relatively small suggests that attending large leks must also be relatively costly. Indeed, this seems to be the case for independent (Fig. 6a) and but not for satellite males (Fig. 6b). Independent males (mainly residents) on larger leks fought both satellites and other independents at higher rates than those on smaller leks. In addition to fighting, independents on larger leks also formed dyads with satellites more frequently. Thus, the main cost to residents is that a territory needs to be defended if they are to maintain their position on the lek and obtain matings.

Even though the attendance time of resident males did not vary with lek size we found that residents on larger leks were present during entire observation periods more often than residents on smaller leks. We interpret this result as a possible additional cost to residents on larger leks. Thus residents on larger leks more often spent long periods (>2 h) on their leks without foraging and might, as a result, have been under greater food stress than residents at smaller leks who more frequently left their courts to visit foraging areas nearby.

While the benefits to satellites on larger leks appear to be similar to those for residents (Fig. 7a, b), it is less obvious that the costs are. Since satellites do not defend territories, it is not surprising their their fighting rate does not increase with lek size. The main disadvantage for satellites visiting large leks may simply be that they are less likely to obtain access to females – the fact that their mating success was relatively lower than residents on large leks (Fig. 7c) supports this. One possible explanation for this reduction in mating success might be that the most successful residents on the largest leks were of such high quality that they allowed satellites access to their territories less often than residents on smaller leks. This explanation is compatible with our finding of a reduced mating skew on larger leks only if there was a relatively higher proportion of top quality males present on those largest leks. Further research will be needed to test this possibility.

As in the ruff (present study), the fighting rate per male black grouse also increased with lek size (Alatalo et al. 1991). To the best of our knowledge such data are not available for any other lekking species. As we have noted earlier, however, it is necessary to assess both the costs and benefits of joining leks of different sizes if we are to understand the evolution of leks.

Relevance to models of lek evolution

Models proposed to explain the evolution of lekking behaviour (for reviews see Bradbury and Gibson 1983; Arak 1984; Bradbury and Davies 1987) may be divided into "no-preference models" and "preference models". No-preference models are generally of three types. First, in the hotspot model (Bradbury and Gibson 1983; Bradbury et al. 1986), males simply settle in those sites where their expected rate of encountering females is highest. By this site choice alone, males would be expected to settle according to an ideal free distribution (Bradbury et al. 1986, 1989). Second, predator avoidance models propose that males and/or females aggregate to maximize the probability of detecting predators (Lack 1968; Wittenberger 1978). The numbers of males and females on each lek are expected to be random and thus proportional to their frequency in the population. On average, then, an ideal free distribution of males would be expected. Third, in the passive attraction models (Otte 1974), females simply go to the lek closest to their home range, or if more than one site is nearby, to the site providing the largest stimulus. As shown by Bradbury (1981), the number of females per male predicted by this model can at best be proportional to the number of males and thus should if an ideal free distribution.

From our study, it is clear that resident and perhaps also satellite males gained a mating advantage at larger leks and thus the distribution of these males was not ideal free. We can, therefore, reject all of the no-preference models as primary explanations for variation in the size of ruff leks. Recent work on the black grouse (Alatalo et al. 1991) has shown that no-preference models are not likely to explain to evolution of lekking in that species either. While we can reject no-preference models as being of primary importance in these cases, it seems likely that these models can tell us something about lekking behaviour at a different level of explanation. The fact that ruff leks in our study site often were situated next to ponds (Fig. 1), which females use for drinking and bathing, suggests that leks are often near places of high female traffic, as predicted by the hotspot model. Thus, the hotspot model may help to explain where leks are initially located even though it does not explain subsequent male dispersion among lekking sites. In addition, a simulation study has recently shown that if a female preference is involved, further male clumping is enhanced and males will display on fewer sites than when there is no female preference (Gibson et al. 1990). Thus, a hotspot model may explain only the initial establishment of lekking sites in a population and not their subsequent maintenance. Certainly, on our study area, a few potential hotspots near small bodies of water visited by females had no leks nearby (Fig. 1).

Models based on female preference come in two classes. First, the hotshot model assumes that females prefer to mate with the highest quality males in a population and thus travel to wherever those males are lekking. Low quality males simply join the hotshots in order to parasitize high quality males by stealing copulations. Thus, hotshots should not only be attractive to females but also to low quality males (Beehler and Foster 1988; Arak 1988; Höglund and Robertson 1990). Second, many anothers have suggested that females simply prefer to visit aggregated males for various reasons unrelated to individual male quality and attractiveness (e.g. Alexander 1975; Borgia 1979; Bradbury 1981; Queller 1987).

Our study provides some clear support for these preference models – both females and satellites visited larger leks more often and residents on larger leks had more opportunity to encounter females and mated more frequently with them. We do not yet known, however, why female ruffs prefer larger leks and experimental tests will have to be performed in order to convincingly distinguish among the alternatives. If females simply go to larger leks because that is where they are likely to find the highest quality males, as predicted by the hotshot model, we would expect a larger proportion of low quality males and satellites on larger than on smaller leks. It is difficult to assess resident male quality, but satellites were indeed more common on the larger leks. This pattern, however, is also predicted if females prefer larger leks for some other reason, such as the average male quality being higher at these sites. Theoretically, it can be shown that if females only prefer the hotshot, and are able to recognize him, it would pay the hotshot to move to another site (W.J. Sutherland in prep.). Hence, we would expect lek size and male residency to be unstable. We found the opposite pattern – leks were fairly stable in numbers both within and between years and especially successful residents in our population showed a high site tenacity (unpublished data).

In an extension of the ideal free distribution model, Sutherland and Parker (1985) considered cases where individual differed in competitive ability (see also Parker and Sutherland 1986; Houston and McNamara 1988). In this model for the ideal free distribution of unequal competitors, males should trade the benefits of being at a site with high gain rates against the costs. For example, low quality individuals would suffer more from interference than high quality individuals. It can be shown that the ESS for each individual male depends his competitive ability. Thus, low quality males maximize their net benefit by attending sites where their gain rate is lower but where they suffer less from interference. This may explain why some male ruffs displayed on small leks in spite of the lowered probability of encountering females and mating there. Only the best competitors should stay at sites with the highest number of females (W.J. Sutherland and J. Höglund in prep.).

Under this model, further aggregation is enhanced when females prefer to visit the largest leks. This can occur if females prefer high quality males and lek size provides an index of male quality. Females also probably have to trade off the travel time and other costs associated with male fighting and interference on larger leks against the costs of mating with males of inferior quality on smaller leks. This may explain why some female ruffs occasionally mated on smaller leks.

This and other recent studies of other lekking animals strongly suggest that female choice has been an important force in the evolution of lek mating systems. These studies, however, have only begun to unravel the complex interactions that seem to influence lek size. The results of this study suggest that two different kinds of information will be essential if we are to critically test models of lek evolution based on the ideal free distribution of unequal competitors. First, it will be essential to gather data, as we have done, on the mating success rates of males on different lek sizes within a single breeding population during a period when females have equal access to all leks (e.g. during one breeding season). Without such information it is impossible to determine whether the distribution of males and females is nonrandom. Second, information is needed on the relative competitive abilities and attractiveness of lekking males as well as on the costs of defending courts (or territories) on leks of different size. Some of our indirect measures of male quality and costs suggest that both increase with lek size but more direct measures [e.g. survivorship (Alatalo et al. 1992) and energetic costs (Vehrencamp et al. 1989)] are clearly preferable.

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