Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*)

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Summary. Preference by females for choosing mates at male aggregations has been hypothesized as the primary selective pressure favoring the formation of leks, but alternative hypotheses account for lek formation without invoking female preference. Observational studies to determine whether male mating success increases with lek size, as predicted under the female preference hypothesis, have produced inconsistent results, possibly due to covariation of lek size with other variables or to male-male or intersexual conflict over lek size. We tested whether females prefer larger leks in a field experiment with ruffs (*Philomachus pugnax*), a lekking sandpiper, in which male group size, composition, and location were controlled. Wild females chose the larger of two adjacent groups often enough such that males in larger groups had significantly higher per capita rates of female visitation (Table 3). Such behavior would probably lead to higher per male mating rates at larger leks, which is generally considered a necessary condition for female choice to select for lek display (Fig. 2). Lek size in nature will reflect both female preference for larger leks and competition among males, which may favor smaller lek size. All else being equal, however, female ruffs preferred to visit larger groups strongly enough to maintain lekking by males.

Introduction

There is no consensus among biologists as to why males of certain species display to females in groups called leks. One school of thought favors female choice as the driving force in lek evolution. Females might benefit from mating at leks through easier location of males, discrimination among males, increased safety from predators, less disturbance at nest sites, or other reasons (Alexander 1975; Emlen and Oring 1977; Parker 1978; Wrangham 1980; Bradbury 1981; Bradbury and Gibson 1983; Trail 1987; Phillips 1990; Reynolds and Gross 1990). Female choice could select for lekking even if

the only benefits to females were genetic (Queller 1987). A second school of thought proposes that direct advantages to males are sufficient to account for the evolution of leks without female choice. Displaying males may aggregate at places where encounter probabilities with females are high because of female movement patterns independent of male distribution (Lill 1976; Emlen and Oring 1977; Bradbury and Gibson 1983; Bradbury et al. 1986; Lank and Smith 1987), lekking may lower the predation risk to males (Koivisto 1965; Wiley 1974), or leks may form when males cluster around certain highly attractive individuals (Waltz 1982; Arak 1983; Beehler and Foster 1988; Höglund and Robertson 1990; Gosling and Petrie 1990). These hypotheses and others are not mutually exclusive, and much current research aims at quantifying the importance of each in lekking species.

Despite the wealth of theory, no studies have yet tested whether female preference for mating at leks is strong enough to compensate males for the intrinsic penalty of competition from other males incurred when joining a lek. The critical criterion for assessing this is usually considered to be whether per male mating rate attributable to female choice increases with lek size (Bradbury 1981; Queller 1987). In an experimental study, Kruijt et al. (1972) reported that female black grouse (*Tetrao tetrix*) visited a cluster of 6 model male grouse 16 times compared with 3 visits to an adjacent cluster of 3 models. Statistical analysis confirms a preference for visiting the larger group (null hypothesis that p and $q = 0.5$, binomial $p = 0.002$), but the data are insufficient to show a higher per capita visitation rate for models in the larger group (null hypothesis that $p = 0.67$, $q = 0.33$, 1-tailed binomial $p = 0.095$).

Two types of observational studies have been presented as tests of the importance of female preference in the evolution of lekking. The first type asks directly whether per capita male fitness increases with lek size. Most of these studies failed to find such a relationship, either in terms of visits by females (Koivisto 1965; van Rhijn 1983; Bradbury et al. 1989), or copulation success [Hamerstrom and Hamerstrom 1955; Lill 1976; de Vos

1983 (our analysis of data in his Table 45); Pruett-Jones 1985]. These studies involved post hoc analyses of data collected for other purposes, with the exception of Pruett-Jones (1985). On the other hand, three studies specifically designed to address male mating success as a function of lek size found advantages for males in larger groups. Female visits per male increased with chorus size in a neotropical frog (Ryan et al. 1981), black grouse males have higher mating rates at larger leks (Alatalo et al. in press), and similar results have been found in ruff (*Philomachus pugnax*) (Höglund, Montgomerie, and Widemo, personal communication).

The second type of observational study tested Bradbury's (1981; Bradbury and Gibson 1983) deduction that the importance of female choice might be assessed by measuring interlek distances relative to female prebreeding home-range size. It has become clear that assumptions about the strength of female preference, differences in male quality (Höglund and Robertson 1990; Alatalo et al. 1991) and/or mating skew as a function of lek size [see de Vos 1983 (data in his appendix 3); Pruett-Jones 1985; Bradbury et al. 1986; Alatalo et al. in press], female search costs, and other parameters (Bradbury and Gibson 1983; Beehler and Foster 1988; Gibson et al. 1990) confound the interpretation of such tests. While the direct comparison of male success across lek sizes makes fewer assumptions than studies of lek spacing, other variables may covary with lek size, such as the size of breeding habitat patches from which leks might draw females (Wegge and Rolstad 1986), the nature of male-male interactions on the leks, and the attractiveness of individual males. Lack of information on, or controls for, such covariates confounds interpretation of the results with respect to female preference for lekking. If older males occur disproportionately on larger leks, for example, as in black grouse (Alatalo et al. in press), higher mating rates on larger leks may reflect female preference for older males, rather than preference for larger leks per se.

To examine female preferences for visiting different-sized groups of males when other factors were controlled, we performed an experiment similar to that of Kruijt et al. (1972). We provided wild female ruffs, a shorebird species in which males form dense leks, with the opportunity to respond to and choose between two captive groups of males. Twin aviaries were built in breeding habitat, stocked with males, and the behavior of passing ruffs recorded. We thus asked directly whether females preferred to visit the larger group, and whether any such preference would be strong enough to favor lekking by males.

Methods

Lekking in ruff. Certain aspects of ruff leks suggested that it might be possible to create and monitor two artificial leks within a manageable space and produce meaningful results. Ruff leks are compact; display courts are 1–1.5 m apart. Leks frequently occur within 100 m of each other, and leks of 3–6 males are common (Andersen 1948; Hogan-Warburg 1966; van Rhijn 1983, 1991; Scheufler

and Stiefel 1985; Lank and Smith 1987). While certain lek sites are used for years, new ones are also established annually. Individual females commonly visit more than one lek, and nesting females almost never do (Lank and Smith, personal observations); thus, visitors will be potentially mating females, and choice among leks is a real possibility. Intrasexual and intersexual displays occur on or near the ground. Long-distance advertising is done through highly conspicuous visual "greeting" displays. When potential visitors are sighted in the air, males flap their wings and may hover low over their courts (Hogan-Warburg 1966). There are no acoustic displays which might complicate interpretation of the responses of passing birds.

Experimental lek configuration. Experiments were conducted within a 50–150 m wide band of ruff breeding habitat located along the shore of Liminganlahti, ca. 50 km south of Oulu, Finland, at the height of the breeding season in the springs of 1986 (22 May–2 June) and 1987 (22–31 May). Lank and Smith (1987) provide a seasonal phenology of ruff breeding and a further description of the study site. Two rectangular aviaries (5.8 × 1.8 × 2 m) were constructed 35 m apart (Fig. 1). The aviaries were quite transparent, made with black plastic "berry netting" strung on twine and stretched between 4 thin wooden corner posts. Captive male ruffs were placed in each aviary. Observers recorded the behavior of the captive males and of passing wild ruffs from a blind placed ca. 45 m to one side of a line between the aviaries (Fig. 1).

In 1986, the aviaries were positioned along a man-made dike running perpendicular to the shoreline, producing a shoreward and a landward aviary. The dike was physically similar to one used by wild ruffs as a lek site 1.3 km away. Since nearly all approaching ruffs flew along the shoreline, most potential visitors first encountered the shoreward aviary. In 1987, the aviaries were constructed at a different site, in flat nesting habitat, along a line parallel to the shore (Fig. 1). The aviary sites were built up ca. 0.20 m with dead, dried *Phragmites* stems, to eliminate pools of water and create more visual uniformity to the sites. Natural piles of *Phragmites* stems left by spring tides are used as male display sites. At the 1987 site, there was no consistent pattern to which aviary was first encountered by visitors. The closest active lek site was ca. 200 m away.

Attributes and behavior of captive males. Adult males were caught near the study site and held throughout each year's study. All had fully developed neck ruffs, head tufts, and facial wattles typical of mature males, but they nonetheless differed in appearance. Male ruffs have a complex breeding plumage polymorphism which is associated with a dimorphism in lekking behavior (Hogan-Warburg 1966; van Rhijn 1973). Lighter-plumaged "satellite" males circulate among and co-occupy courts with darker-plumaged territorial "resident" males. Only resident males were used in 1986. In 1987, the number of satellites (1–2) in each aviary was the same in all tests reported here.

Captive males were held in the aviaries only during trials, and food and a small water bath were available to them. Males typically lost mass during their first week in captivity, and then stabilized. Midway through the experiments, males had lost a mean of 23 g (range −66 to +2), or about 11% of their mass when captured. Capture and maintenance in captivity seriously affected the males' physiology and probably also their behavior in the aviaries.

We recorded the behavior of captives by scan sampling every 5 min. The mean activity budget of males in the aviaries was 63% standing, 18% maintenance, 13% walking, 6% "fly-ups" (see below), and 1% agonistic, similar to the time budget of males at leks early in the lekking season (Lank and Smith 1987). Prior to visits, "standing" caged males were a reasonable approximation of lekking males. However, caged males did not show normal courtship behavior when visitors arrived, and visitors often appeared more interested in the captives than vice versa. To control for potential effects of particular males, we shuffled the composition of the groups between trials. Aviary choice by visitors was

not associated with the presence of any individual male (contingency tables of the aviary preferred by visitors vs. whether or not the aviary contained a particular male, G-statistics, all $p > 0.10$).

We tallied the number of times males flew up and hovered in the aviary. "Fly-ups" were superficially similar to "greeting" displays (see above), and thus were a priori the most likely behavior pattern to attract passing birds. However, aviary preference was independent of the presence or absence of fly-ups during the 5-min period preceding a visit, both in control trials with equal group sizes and in trials in which group sizes differed (control tests: fly-up categories = both, aviary 1 only, aviary 2 only; choice categories = no preference, aviary 1, aviary 2; $n = 9$, $G = 3.00$, 4 d.f., $p = 0.55$; group size tests: fly-up categories = both, aviary with more males only, aviary with fewer males only; choice categories = no preference, aviary with fewer males, aviary with more males; $n = 52$, $G = 0.50$, 4 d.f., $p = 0.77$). In summary, no measured aspect of male morphology or behavior correlated with visitor choice.

Classification of the behavior of wild ruffs. The passage of a ruff or flock of ruffs within 100 m of the aviaries was termed an *encounter*. From the blind (Fig. 1), observers described the behavior of all wild ruffs encountering the aviaries on microcassette recorders. Immediately following encounters, observers depicted visitor behavior in flight and on the ground on maps outlining the aviaries and the blind. The outcome of each encounter was determined subsequently from tape transcriptions and maps without knowledge of the group sizes in the aviaries.

Encounters were first dichotomized as showing *no response*, if a ruff or flock of ruffs flew by without obvious hesitation or deviation of 90° or more in flight path, or as a *visit*, if the passing ruff or ruffs appeared to change flight path to inspect the aviaries. This distinction was in all cases unambiguous. The outcome of each visit was categorized as showing an *initial preference* for one aviary or another or *no preference*, based on the visitor's nearest proximity to the aviaries. A preference was tallied if a visitor approached within 7.5 m of an aviary. Approaching birds often suddenly veered away, presumably when they perceived the netting surrounding the males. Because of this artifact, we made an a priori decision to combine analysis of visits where passing birds landed and those in which they circled or made a pass at an aviary. There was in fact no difference in the pattern of male group size preference between landing and fly-by visits ($n = 102$, $G = 0.13$, 1 d.f., $p = 0.72$). Cases in which visitors first approached one aviary but landed near the other were scored as a preference for the second aviary. *No preference* was scored if visiting birds flew or landed between aviaries (more than 7.5 m away from both) or circled both aviaries and continued their flight. Because our 7.5-m cutoff criterion was arbitrary and conservative, no preference visits were excluded from our critical tests of per capita visitation rates. Use of a more liberal criterion allows assignment of a preference for all but two responding flocks and increases the significance levels of the results.

Each encounter by a ruff or flock of ruffs was treated as one independent, equally weighted data point. On two occasions, visiting flocks split into subflocks with different preferences; each subflock was treated as a separate visit, a conservative procedure which biases against establishing any aviary preference. We tested whether male group size preference differed with the size of the visiting flock. Flocks of shorebirds appear to make group decisions about flight direction in migratory contexts (Lank 1983; Alerstam et al. 1990), and any bias would affect the female visitation rate per visit per male. Flocks choosing the larger or smaller group did not differ in the number of females in either year (1986: $t = 0.65$, 14 d.f., NS; 1987: $t = 0.65$, 30 d.f., NS), and thus flock size does not complicate the results.

Experimental design and hypothesis testing. We tested the relative attractiveness of groups of males in a series of trials. For each trial, we placed a group of males in each aviary. The number of captive males per trial ranged from 4–7 in 1986; and 6–8 in
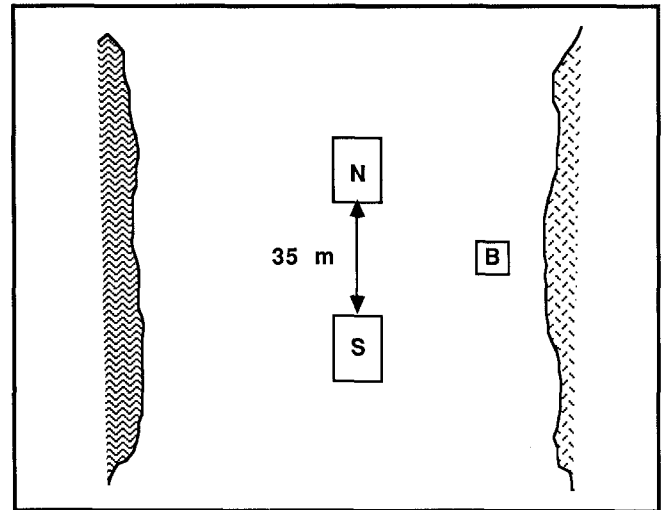

Fig. 1. The configuration of the experimental aviaries (N, S), and the observer's blind (B) in 1987. Breeding habitat was bounded by the shoreline to the left and *Phragmites* stands to the right

1987. To control for possible intrinsic aviary biases, we conducted paired sets of trials with the same groups of males in opposite aviaries. As an additional control, we ran pairs of trials with equal numbers of males in each aviary. We attempted to equalize the encounter rate per trial by varying the length of trials between 2 and 6 h, running longer trials if encounter rates had been low the previous day. Despite this procedure, the number of encounters per trial ranged from 1 to 23, with a mean of 10.3 ± 7.2 (SD).

The strength of group-size preference was tested by comparing the proportion of choices between aviaries to the male group size ratio during the trial. Captive group size ratios ranged from 1:1 in control trials to 3:1. On some visits, a wild, visiting male or males was already at the aviary (within 3 m) when additional ruffs arrived ($n = 23$). These males were added to the group size for that aviary. The group size preference of newly arriving ruffs did not differ with respect to the presence or absence of visiting males [multidimensional contingency analysis (Sokal and Rohlf 1981) of group size preference (larger, smaller), visiting male (presence, absence), and visitor sex (M, F, M+F); G of preference × visiting male term = 2.65, 2 d.f., $p = 0.265$]. When mixed-sex flocks visited, the arriving males were not included in male group size ratio, since group size prior to female arrival was being tested. A female was present prior to 9 visits, and visitors chose the aviary with the female in 8 of these cases. These 9 visits were excluded from the analyses.

Group size preferences of visitors were tested against (1) the null hypothesis of no preference (probability of choice = 0.5 for each group of males), and (2) the null hypothesis of proportional, or equal per-male, visitation, as predicted under an "ideal-free" distribution (Fretwall and Lucus 1970) of males with female encounter probability (Bradbury 1981). The expected value for proportional visitation was the ratio of males in the two aviaries, expressed as the fraction of total males per trial present in each group. For example, if the male group size ratio were 2:1 (e.g., 6 and 3 males), the expected value for proportional visitation would be 0.67 to the larger and 0.33 to the smaller. Statistical significance was assessed by computing the exact binomial probability of obtaining the observed and more extreme values versus expected values. One-tailed probabilities were used when the null hypothesis was that females preferred the larger group.

A graphical framework for interpreting the results of this two-choice experiment is shown in Fig. 2. The proportion of visits to the larger group is plotted against the proportion of total males comprising the larger group. Above the horizontal line, females prefer larger groups; below it females prefer smaller groups. Along
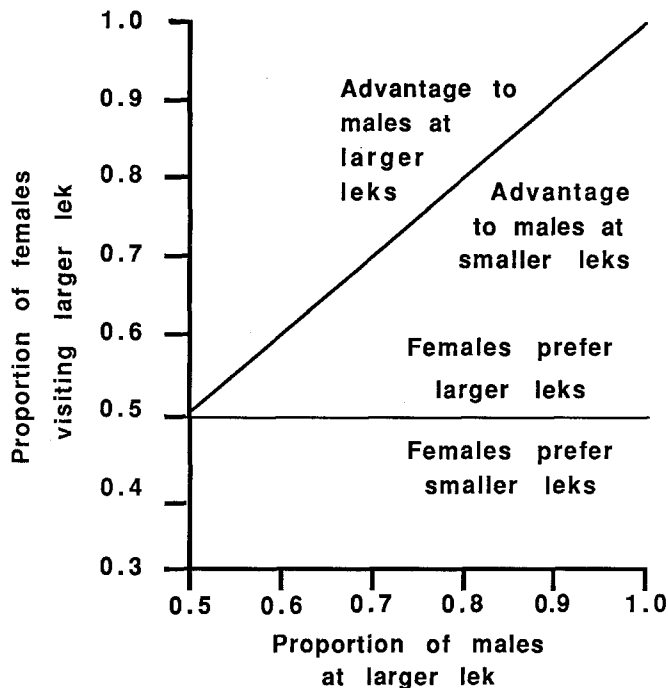
Fig. 2. A conceptual framework for interpretation of the results of the choice experiment; see Methods for explanation

the diagonal, all sites are visited in proportion to male group size in ideal-free manner. Above the diagonal, female preference is strong enough to select for lekking by males. Points between the diagonal and horizontal line appear to be evolutionarily unstable or represent male-female conflict over male group size.

One might argue that the overall preference per trial, rather than each visit, should be treated as an independent data point ("pseudoreplication"; Hurlbert 1984). While we believe this overstates the case, we present our results on both a per-trial and a per-visit basis for critical tests of female preference of male group size. While our primary interest was with the responses of females, we present data on the choices of males and mixed-sex flocks for comparison.

Results

Response rates of passing ruffs

In 1986, all 10 individual females or female flocks encountering the aviaries responded, as did 6 of 8 mixed-sex flocks. The response rate of females was thus almost maximal, even though only 4–7 males were in the trials. Only 70% of passing males and male flocks visited the aviaries ($n = 51$). In 1987, the response rate of females or flocks containing females increased with the number of males used in the trial: 54% when 6 males were present ($n = 70$), 70% with 7 males ($n = 20$), and 87.5% with 8–10 males ($n = 8$) [Mantel-Haenszel χ^2 analyzing trends in categorical data (SAS 1985), $p = 0.022$]. Males encountering the aviary did not show as strong a group size effect, but the trend was similar (63%, 82%, 88% responding for the same males/trial categories, $n = 76$, $p = 0.09$).

Table 1. Aviary preferred by visiting ruffs in 1986. "Neither" indicates a passing flock visited but showed no preference. No female-only or mixed-sex flocks visited when group sizes were equal

Aviary with more males	Number of choices		
	Shore	Neither	Inland
Females only			
Shore	5	0	0
Inland	1	0	4
Mixed-sex flocks			
Shore	2	0	1
Inland	1	0	2
Males only			
Shore	7	3	1
Equal	5	0	0
Inland	8	6	9

Preferences between group sizes

In 1986, 9 of 10 individual female visitors and flocks preferred the aviary with the larger group of males (Table 1, 1-tailed binomial probability of 9 or more out of 10 against a 0.5 expectation: $p = 0.011$). Unanimity of choice would be needed to have shown greater than proportional visitation with this sample size (mean male group size ratio when females visited $= 2.2$; under proportional visitation the expected proportion of visits to the larger group $= 0.685$, 1-tailed binomial $p = 0.127$ for 9 out of 10). Four of 6 mixed-sex flocks preferred the larger group (expected 0.5: $p = 0.343$; expected 0.672: $p = 0.638$). Using all visits including females, mean male group size ratio was 2.1:1, compared with the female visit ratio of 4.3:1; thus, males in the larger group received about twice as many visits per capita as did those in the smaller group. Despite the size of this difference, the data are sufficient to reject the null hypothesis of no preference ($p = 0.011$), but not proportional visitation ($p = 0.120$).

Visiting males in 1986 apparently showed both a preference for the larger group and a bias towards choosing the shoreward aviary, which was nearly always encountered first as flocks approached the site (Table 1). When the larger group was towards the shore, the visitation rate was 7:1 for the shoreward group. However, when the larger group was inland, the ratio was 9:8 for the larger group ($G = 3.13$, 1 d.f., $p = 0.077$). When group sizes were equal, all visitors chose the shoreward aviary (binomial p against $0.5 = 0.03$) providing further evidence of a bias.

In 1987, the choice of aviary by responding birds of both sexes was independent of approach direction, even in control tests where the number of captive males in the aviaries was equal ($n = 29$, approaches classified as north, south, or east-west, preference classed as north, south, or none; $G = 2.23$, 4 d.f., $p = 0.69$). Nor was one aviary favored over the other in general (2-tailed binomial test, $p = 1.00$). The 1987 results are thus presented

directly relative to male group size rather than aviary location (Table 2).

Females (20 out of 27) and mixed flocks (5 out of 5) preferred the larger group (binomial probabilities against 0.5: females $p=0.009$, mixed flocks $p=0.031$), but data were insufficient to reject proportional visitation, despite unanimous choice for the larger aviary by the mixed flocks (females: expected $=0.630$, $p=0.16$; mixed-flocks: expected $=0.663$, $p=0.125$). The mean male group size ratio when females visited was $1.9:1$, compared with the female visit ratio of $3.6:1$. Thus, as in 1986, males in the larger group received about twice as many visits per capita as did those in the smaller group. As in 1986, however, proportional visitation was

still not rejected for the sample of all visits with females (observed $=0.78$, expected $=0.658$, $p=0.097$).

In 1987, visiting males failed to show a significant preference for the larger group ($p=0.100$ against 0.5). As in 1986, male preferences appeared to be weaker than those of females.

To increase statistical sensitivity, we pooled data from 1986 and 1987. We tabulated the proportion of responses in which visitors preferred the larger male group by the 6 male group size ratios tested (Table 3, top). For females and mixed sex flocks combined, 5 of the 6 proportions are higher than the male group size ratios, while the 6th, with a sample size of 2 visits, is lower. Thus, 5 of 6 points fall above the diagonal line in Fig. 2, in the region where female choice selects for lekking by males. For all visits including females, the proportion of visitors which preferred the larger group is higher than expected under both the null hypothesis of no group size preference and proportional visitation. Males significantly preferred the larger group, but not strongly enough to reject proportional visitation, even when mixed-sex flocks are included with the male totals. Overall, male preference appeared to be weaker than that of females (65% vs. 78% of visits to the larger lek); these visits include the apparent shoreward bias of males from the 1986 trials. Male data scatter around the diagonal ideal-free line

Table 2. Aviary preferred by visiting ruffs in 1987. "Neither" indicates a passing flock visited but showed no preference

Visiting group composition	Number of choices		
	Larger	Neither	Smaller
Females only	20	6	7
Mixed-sex flocks	5	3	0
Males only	19	7	11

Table 3. The proportion of visits (*top*) and trials (*bottom*) in which visitors chose the larger group (C_L), at each male group size ratio (M_L). For ease of comparison with visitation proportions, size ratio is expressed as no. of males in the larger group/total no. of males per trial. Equal per capita visitation occurs if $C_L = M_L$. Both the null hypothesis of no group size preference ($P_{0.50}$) and that of equal per capita visitation (P_{ML}) were tested with binomial tests. Sample-size weighted mean M_Ls ($\bar{x}_L$) were used as expected values in tests against P_{ML}. $n=$ number of visits (top) or trials (bottom)

M_L	Visitor sex									
	Females only		Mixed-sex flocks		All visits with females		Males only		All visits with males	
	C_L	n	C_L	n	C_L	n	C_L	n	C_L	n
Number of visits										
0.57	1.00	3	1.00	2	1.00	5	0.60	5	0.71	7
0.60	1.00	4	0.00	1	0.80	5	0.54	13	0.50	14
0.63	0.50	2	–	0	0.50	2	0.00	1	0.00	1
0.67	0.63	16	0.86	7	0.70	23	0.65	23	0.70	30
0.71	0.88	8	–	0	0.88	8	0.67	3	0.67	3
0.75	1.00	4	1.00	1	1.00	5	0.89	9	0.90	10
All	0.78	37	0.82	11	0.79	48	0.65	54	0.68	65
$\bar{x}_L$	0.67		0.65		0.66		0.66		0.66	
$P_{0.50}$	<0.001		0.033		<0.001		0.020		0.002	
P_{ML}	0.090		0.202		0.039		0.490		0.416	
Number of trials										
0.57	1.00	2	1.00	1	1.00	4	0.75	4	0.75	4
0.60	1.00	3	0.00	1	1.00	2	0.67	3	0.50	4
0.63	0.50	2	–	0	0.50	2	0.00	1	0.00	1
0.67	0.60	5	1.00	4	0.75	8	0.67	9	0.86	7
0.71	1.00	4	–	0	1.00	4	1.00	1	1.00	1
0.75	1.00	3	1.00	1	1.00	3	1.00	5	1.00	5
All	0.84	19	0.86	7	0.87	23	0.74	23	0.76	22
$\bar{x}_L$	0.69		0.66		0.66		0.66		0.69	
$P_{0.50}$	0.002		0.063		<0.001		0.017		0.013	
P_{ML}	0.122		0.242		0.022		0.283		0.315	

in Fig. 2. A direct test for a sex difference in preference, however, is not significant (males vs. females plus mixed-sex flocks: $G = 2.61$, 1 d.f., $p = 0.11$).

Pooling over years also allowed analysis of the data using the outcome of each trial, rather than each visit, as an independent data point, thereby lessening the potential problem of pseudoreplication. Analyses of trials showed an identical statistical outcome to those of visits (Table 3, bottom). Females preferred the larger group on a significantly higher number of trials than expected under proportional visitation; males showed a significant preference for the larger group but not significantly higher than proportional visitation.

Discussion

Our experiments showed that when other factors are controlled, females prefer to visit larger groups of males. Unless a female's propensity to mate is negatively correlated with visitation rate or male group size, this visitation preference would result in a per capita mating advantage for males at larger leks, and thus would select for lekking by males.

Do our data indicate female choice for visiting larger groups in the context of mate choice? Larger groups might be perceived at greater distances and thus "passively" attract additional visitors. This hypothesis predicts a bias towards visiting the group closest to the direction of approach. While males were biased at the 1986 site, females were not, nor was either sex at the 1987 site. If conspicuousness were an important variable, we might also predict a correlation between choice and conspicuous male behavior, which was not found (see Methods). Could visitor motivation have been related to foraging, rather than mating, behavior? The 1986 test site, where the response rate of passing flocks was higher, was well suited to display but was not foraging habitat. Aviary males were rarely foraging when potential visitors encountered the aviaries, and we doubt that this was an important aspect of the males' attraction for visitors. Finally, a general attraction for conspecifics could favor lek formation regardless of the original reason for the attraction.

Lek size in nature: male-female conflict?

Female preference for visiting and mating at larger leks, acting alone, should result in the formation of single, large leks within a suitable habitat (Oring 1982) or, more precisely, in leks spaced one female home-range apart (Bradbury 1981). This does not describe lek distribution and sizes in ruffs. Even within a continuous nesting habitat, clusters of small ruff leks are the rule (see Introduction), lek size can change considerably within seasons in relation to female mating activity, and even solitary displaying males may mate (Lank and Smith 1987). Lek formation in this species must be strongly influenced by factors other than the female preference for larger groups demonstrated in our experiments. The most interesting possibility is that male interests conflict with those of females to produce smaller leks.

In general, hypothesized benefits to females of mating at leks will increase with group size, although they probably approach asymptotes, and certain costs to females may also increase with lek size (Ryan et al. 1981; Bradbury 1981; Trail 1987). Although we found increased per capita visitation for males in larger groups, male benefits cannot increase indefinitely. Per capita benefits must decrease if all passing females visit and mate at a lek, but a decrement is likely to occur prior to that point. In our experiments, for example, 85%–95% of passing females visited when 5–9 males were present. From an average male's point of view, the most advantageous lek size might be in this range. This line of reasoning predicts that established males at very small leks might attempt to recruit additional members and thereby draw in more females per capita, while those at larger leks should attempt to limit lek size. Behavioral differences in ruffs as a function of lek size suggest that this may occur (Hogan-Warburg 1966).

A male's choice is further complicated by differences in competitive ability and/or attractiveness towards females. Our analysis and discussion has been based on the mean reproductive return for males at different-sized leks. However, since males differ in competitive ability, their decisions to join a lek are more complex than the per capita advantage rule suggests (c.f. Pulliam and Caraco 1984). If males of different quality distribute themselves among leks of different sizes in an ideal-free manner, then observations of a per capita male advantage in nature will indeed select for lek formation. However, if quality also differs with lek size, as in black grouse (Alatalo et al. in press), and as predicted if males follow an ideal-free distribution of unequal competitors (Sutherland and Parker 1985; Parker and Sutherland 1986), use of the per capita rule is inadequate. For example, less competitive males may have a greater chance of obtaining matings at smaller leks, despite a lower female visitation rate on average. Such considerations will tend to disperse males among smaller leks, contrary to selection from female preference.

Our results provide direct information on the strategy of lek exploration used by males which were not yet established on leks. Visiting male ruffs were largely, but not exclusively, younger, presumably less competitive birds (Hogan-Warburg 1966; Lank and Smith 1987). These males significantly preferred to visit larger groups, but less strongly than females, as shown in 3 separate analyses. In 1986, males were biased by the physical position of the aviaries, but females were not. In 1987, females, but not males, showed a positive trend in response rate when more males were in the aviaries. Finally, no analysis of male responses showed greater-than-proportional visitation, despite larger sample sizes than those for females. Our best assessment (Table 3) is that male behavior fell on or slightly below the proportional visitation line in Fig. 2. This suggests that unestablished males, at least, were exploring leks of different sizes in approximately an ideal-free manner. If new males settled in proportion to their visits, lek sizes would be smaller than those favored by female choice.

The experimental approach taken in this study shows that the hypothesized preference by females for larger

leks exists and can be measured. However, our controlled approach precluded assessment of the strength of this preference relative to other factors. Continued careful fieldwork, including experiments, will be needed to elucidate how individual decisions result in the distribution of displaying males and the formation of leks. All else being equal, however, female preference for visiting males in groups is strong enough to favor lekking by males.

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