BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston vanhassa juhlasalissa (S212)
joulukuun 2. päivänä 1995 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä,
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UNIVERSITY OF JYVÄSKYLÄ

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Editor
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Department of Biology and Environmental Science
University of Jyväskylä

URN:ISBN:978-951-39-8350-5
ISBN 978-951-39-8350-5 (PDF)
ISSN 0356-1062

ISBN 951-34-0647-4
ISSN 0356-1062

Jyväskylä University Printing
House and Sisäsuomi Oy, Jyväskylä
1995

ABSTRACT

Hovi, Matti
The lek mating system in the black grouse: the role of sexual selection
Jyväskylä: University of Jyväskylä, 1995, 30 p.
(Biological Research Reports from the University of Jyväskylä, ISSN 0356-1062; 48)
ISBN 951-34-0647-4
Yhteenveto: Teeren soidin: evoluutio ja seksuaalinen valinta
Diss.

The aim of this thesis was to study the mechanisms behind the evolution of black grouse leks, and to examine the nature of sexual selection on leks. It was found that the mating preferences of females had an important role in the evolution of this particular mating system. Female preference for central males on a lek was suggested by both observational data from field and experimental data from aviary. Females favoured central males irrespective of male identity, and this preference was strong enough to yield a *per capita* benefit for males to be in the center. Therefore, males with the tendency to form tight clusters have been selected for. Sexual selection operated in slightly different ways depending on the habitat of lekking. On bogs, the male aggregations were spatially stable, while on ice-covered lakes the leks were mobile. This mobility was due to the lack of landmarks by which the males establish their territories, and it had consequences for female mate sampling and sexual selection. Females could choose from fewer males on lakes than on bogs, and the distribution of male mating success was more skewed on lakes. The dominant males prevented females from visiting all males on lakes. Still, females tried to approach other males than the first one visited, which induced interactions between males, and provided the females with information on the dominance status of the males. In a playback experiment, females were not attracted to leks with supplemented male vocal display. Instead, the number of males increased in the playback sites. These results indicate that the possible effect of playback on females was probably overrun by fidelity to breeding sites. In males, the response was most likely caused by young males with low site fidelity, who were attracted to the leks perceived as suitable-sized for them. In a comparative analysis of lekking, male mating skew and sexual dimorphism in body size in birds, no general patterns appeared between any of the variables examined. Phylogenetic sources seemed to explain some of the variation in lek structure. It was concluded that with respect to these questions, intraspecific variation might offer more possibilities for studying adaptive processes.

Key words: Black grouse; leks; sexual selection; mate choice; dominance; mating skew.

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List of original publications

This thesis is based on the following articles, which are refered to by their Roman numerals in the text:

I Hovi, M., Alatalo, R. V., Höglund, J., Lundberg, A. & Rintamäki, P. T. 1994: Lek centre attracts black grouse females. - Proc. R. Soc. Lond. B 258: 303-305.

II Hovi, M., Alatalo, R. V. & Rintamäki, P. T.: Habitat differences and the variability in the lek mating system of black grouse. - Behaviour (in press).

III Hovi, M., Alatalo, R. V. & Siikamäki, P. 1995: Black grouse leks on ice: female mate sampling by incitation of male competition? - Behav. Ecol. Sociobiol. (in press).

IV Hovi, M., Alatalo, R. V., Höglund, J. & Lundberg, A.: Traditionality of black grouse leks. - Manuscript.

V Hovi, M., Alatalo, R. V., Halonen, M. & Lundberg, A.: Responses of male and female black grouse to male vocal display. - Manuscript (submitted).

VI Hovi, M.: A comparative analysis of lekking, mating skew and sexual size dimorphism. - Manuscript.

CONTENTS

1 INTRODUCTION

1.1 What are leks?

The concept of mating system refers to the way in which individuals acquire mates (Emlen & Oring 1977). In polygynous systems, one male may fertilize several females, and some of the males may not mate at all. A special case of polygyny is lekking, where males defend small display territories, that are more or less densely aggregated. These territories contain no resources for females except the males themselves. Thus, the only motivation for females to visit these aggregations is to copulate (Bradbury 1985, Clutton-Brock 1989, Davies 1991, Höglund & Alatalo 1995). As in most other mating systems, females are usually the choosy sex whereas males compete for fertilization success.

Mating success among males is distributed more unevenly on leks than in other polygynous systems (Bradbury & Gibson 1983, Wiley 1991). Since females in most cases are apparently free to choose their mates, intersexual selection has been though to account for much of the variation in male success (Bradbury & Gibson 1983, but see e.g. Beehler & Foster 1988). Nowadays it is appreciated that female choice and competition between males both are likely to shape mating patterns. Their relative importance may vary among species, among populations within a species, and also within a population as conditions change (Gibson & Bradbury 1986, 1987).

A typical character of all leks is male emancipation from parental duties, which has been regarded as an ecological prerequisite for lekking to evolve (Höglund & Alatalo 1995). Consequently, males are allowed to canalize all of their reproductive investment into mating. Lekking birds are very often precocial, and there is thus less, if any, need for biparental care. It is unclear, however, whether and how the patterns of parental care and lekking are causally related to each other (Höglund & Alatalo 1995).

A widely used criterion to distinguish between leks and other polygynous systems is the presence/absence of resources on the arena. In resource-defence polygyny males defend territories that contain some essential resources for females. However, no clear division between this system and pure leks can be made. Especially insects and some ungulates aggregate at the vicinity of a resource, for example, food, egg-laying substrate or cover from predators (insects: Otte 1974, Alexander 1975, Thornhill & Alcock 1983, ungulates: Gosling 1986, Clutton-Brock 1989). In the study of mating aggregations there is no need for strict classification, since every aspect of leks shows large variation across and within taxa, and the variation is of interest itself.

Leks vary sometimes within a species or a population with many respects. I compared in the second study (II) leks of black grouse in two different habitats. Leks on bogs are typically very stable, and territorial boundaries are clear, whereas on ice-covered lakes male aggregations are mobile and more dispersed. This is largely due to the homogeneous surface which does not allow the males to establish territorial boundaries. Possible effects of these differences to female mate choice are investigated (II).

1.2 Hypotheses for the evolution of leks

During the last three decades there has been much theoretical interest for explaining the origin and evolution of mating systems in terms of individual fitness consequences (e.g. Emlen & Oring 1977, Davies 1991). Earlier explanations emphasizing group selection-like mechanisms (Wynne-Edwards 1962) are nowadays regarded as irrelevant. Two questions may be asked regarding leks: 1) Why males aggregate ? and 2) Why females come to mate at these aggregations ? Most of the hypotheses assume that dispersion pattern of either sex has an influence on that of the other sex. A first set of explanations does not rely on female preferences of mating with aggregated males, but instead, stress several ecological factors behind the aggregation:

1) Predation risk per capita is lower for males displaying in groups compared to solitary individuals. This is theoretically plausible, in apparent analogy to grouping in general (Bertram 1978, Pulliam & Caraco 1984). However, empirical evidence favouring this explanation is scarce (but see e.g. Gosling & Petrie 1990).

2) Information on resources (food patches etc.) is gained from conspecifics at leks (Emlen & Oring 1977).

3) Females orientate themselves passively towards the strongest stimuli (Otte 1974). This is not likely to work with auditory stimuli since sound propagation can not increase disproportionally with lek size (Bradbury 1981, Cade 1981).

4) The habitat required by males for displaying or by females for breeding may be limited, which leads to formation of leks (Parker 1978). Even though female dispersion in several taxa is directly affected by the dispersion of suitable habitat patches (Parker 1978, Trail 1985), this hypothesis may

explain only a minor part of lek evolution (Bradbury & Gibson 1983, Höglund & Alatalo 1995).

5) Males choose their display sites in relation to the probability of encountering females ("hot spot" hypothesis, Bradbury & Gibson 1983, Bradbury et al. 1986). Clustering of males thus occurs when females are patchily distributed, for instance, around resources. Areas of high female density may also be found at the overlapping zones of female home ranges. Some authors have found empirical evidence for such patterns in more or less indirect tests (Bradbury et al. 1989, Westcott 1994, but see Höglund & Robertson 1990a).

6) Males benefit from being aggregated because of chances of a female entering onto their territory after leaving from other males' territories are higher than in solitary males ("black holes" hypothesis, Clutton-Brock et al. 1992, Stillman et al. 1993). Females prefer to mate on clusters, because they are less often harassed there. This might work in ungulates where females may be seriously injured if disturbed during mounting attempts.

Another group of hypotheses stresses the importance of female mating preferences as a selecting force in lek evolution:

7) Females may prefer to mate with aggregated over solitary males, or perhaps prefer large over small aggregations. There is some correlational evidence for increased mating success per male on average as lek size increases (Shelly 1990, Alatalo et al. 1992), which may level off after certain lek sizes (Bradbury et al. 1989). Experiments that would validate these results have been difficult to perform. In the ruff the results did support this explanation (Lank & Smith 1992), whereas in fruit flies they did not (Droney 1994). The advantages of mating on (large) leks could be related to lower predation risk to females or their nests (Wrangham 1980, Phillips 1990), easier comparison of males (Alexander 1975), or higher quality of the best or the average male compared to small leks (Beehler & Foster 1988, Alatalo et al. 1992). Finally, the preference of females may be non-adaptive and be selected along with the tendency of males to aggregate, if the traits are in a linkage disequilibrium (Queller 1987).

8) Females favour particular males. Then it pays for the less attractive males to aggregate around the preferred males in the hope of gaining part of the copulations (spatial spillover). This "hot shot" hypothesis implies that attractiveness of the hot shot male can be perceived and assessed by other males (Arak 1983, Beehler & Foster 1988). There is evidence that some males try to steal copulations from attractive males in the natterjack toad (Arak 1983), and one of the predictions of this hypothesis is thus supported.

The "hot shot" (8) and the "female preference" (7) hypotheses contrast particularly in the question of position effects on leks. In some lekking species males in the central territories enjoy higher mating success than the peripheral males (Kruijt et al. 1972, Wiley 1973; but see Lill 1974, Gibson & Bradbury 1985). If the "hot shot" mechanism works, the centrality of the successful males is just a consequence of their attractivity, because they are made central by other males. Under the "female preference" hypothesis, females favour the central males *because of* their position. I have focused on the evolution of black grouse leks in two studies (I, V). First (I), I have attempted to tease apart these two hypotheses with a choice experiment in aviary, and second (V), I performed a playback experiment to examine how females and males respond to male vocal display supplemented on lake leks.

1.3 The nature of sexual selection on leks

One main question for the studies of sexual selection during the last two decades has been to determine the relative importance of intersexual (mate choice) and intrasexual (mate competition) selection (Andersson 1994). Generally females of lekking species have been thought to have better possibilities to exercise choice, or reduced costs of choice, compared to non-lekking species (Alexander 1975, Bradbury & Gibson 1983, Reynolds & Gross 1990). However, some lek systems are characterized by strict dominance hierarchies between males, and the copulations are performed always by one dominant male (LeCroy et al. 1980, Foster 1981, McDonald 1989). Male dominance relationships may, if not totally prevent female choice, reduce the options for females. On the other hand, female choice for dominant males would be expected because of several direct and indirect benefits (Cox & LeBoeuf 1977, Alatalo et al. 1991). I have investigated the effects of dominance status on male mating success in black grouse in the fourth study (IV). The study was done on lake leks, where territorial boundaries are absent (I) and there are no asymmetries between territory owners and intruders, which confound the study of dominance relationships on bog leks. I was also interested whether females behave in an incitive way, i.e. do they encourage males to show their dominance (see Cox & LeBoeuf 1977).

The potential for sexual selection is higher on leks than in other mating systems, because the male mating success is strongly skewed (reviewed in Wiley 1991, Höglund & Alatalo 1995). Sexual selection is often manifested in sexual dimorphism in size or other traits (Fisher 1930, O'Donald 1980, Gibson & Bradbury 1985), because large male size or traits associated with it are under directional selection. Theoretically, if male and female size are genetically correlated, the evolution of size dimorphism could proceed in much slower rate (Lande & Arnold 1985). Darwin (1871) suggested that exaggeration in male traits would be typical of lekking species, which, however, was not verified by comparative analyses (Payne 1984, Höglund 1989, Höglund & Sillén-Tullberg 1994).

The wide variation in lek size and structure allows comparative studies, which relate lek characters to sexual dimorphism and male mating skew. In my last study (VI) I examined if there exist general patterns across several lek-breeding bird species by removing the confounding effects of phylogeny with independent contrast methods (Felsenstein 1985, Harvey & Pagel 1991). Specifically, I asked whether extreme mating skew and sexual size dimorphism occur more commonly in species with tightly clustered, "classical" leks, than in species with dispersed leks. I was also interested to which extent the evolution of the above mentioned characters are constrained by common history (Gould & Lewontin 1979, Cheverud et al. 1985), and to which extent do they have the possibility to evolve in an adaptive manner (Emlen & Oring 1977, Krebs & Davies 1991). At least some insight to these problems is gained by analyzing the variation in these traits among and between different monophyletic taxa (VI).

2 METHODS

2.1 The lekking habits of the study species

The black grouse (*Tetrao tetrix* L.), a medium-sized member of the family Tetraonidae, is one of the "classical" lek-breeding birds. The leks are situated on open habitats, like treeless bogs, peat bogs, agricultural fields and ice-covered lakes. Males either defend stable territories (bogs) or mobile display ranges (lakes) and females visit these aggregations on several mornings prior to mating. Most dominant males tend to have their territories in the center of the lek, and subordinates occupy the peripheral territories (Kruijt et al. 1972). This, however, is not so straighforward on mobile lake leks (II, III).

In Central Finland mating season of black grouse usually begins on the last week of April, peaks on the first week of May, and ceases gradually during May. Females that loose their nests may, however, remate as late as in June. Lake leks break up when the ice thaws, and lake males move to display on nearby bogs, or sometimes, stay in trees on the lake shore. Males gather at the arena before sunrise, and often the first females visit in the twilight, too. After a display period of few hours females stop visiting, males become passive and finally depart from the lek site.

2.2 General methods

2.2.1 Observations in the field

Field observations were done both on bogs and on lakes. On most bog sites, the arena was provided with 10x10 m grid made of sticks to enable mapping of the male positions. The observations were done from tents or blinds erected 30-100 m from the lek center. Most birds were individually color-banded to allow identification. Bands were easily readable with 20-60 x telescopes. Observations were started when first males arrived, and continued until the males left. Movements of females, as well as solicitations (squat-down, see Koivisto 1965) and copulations were recorded.

On lake leks, grid marking was not possible owing to fragile ice. Therefore two observers were needed to determine the exact positions of individual birds. The observers were 200 m apart and sighted the birds simultaneously with telescopes fitted with angular rulers. Communication over walkie-talkies enabled the coordinated observation. Scan-samples were taken with 1-5 min intervals and positions were recorded as angles. Common control points made it possible to transform the angles relative to each other, and later they were further transformed to map coordinates with a computer algorithm designed for this purpose. Individual identification on lakes was based on morphological differences (lyre length, damages and spottings on under tail coverts) between males, or age class (adult/yearling). The latter is determined from wing coloration (Helminen 1963). Females were mostly morphologically unidentifiable, but their identity was determined by closely watching their movements.

2.2.2 The aviary stock (I, V)

In 1992, eight clutches of black grouse eggs were collected from Petäjävesi, Central Finland (62°12′N, 25°05′E) and incubated at the Konnevesi Research Station. From the 58 hatched chicks 12 survived to next spring, most of the mortality occurring during the first two weeks of life. The chicks were fed with ant pupae and flour beetle larvae, adding vitaminized oats and commercial hen fodder pellets to the diet after the first three weeks. In autumn they were also given berries, twigs and other plant material, while oats stayed the main food onwards. Until the age of six weeks the chicks were kept in outdoor meshwire cages (3-6 chicks in each), which were provided with heating lamps and dishes with water and food. After that they were transferred to indoor rooms (only one bird per room), where they lived continuously and were removed only temporarily during experiments in April-May.

The original stock was reinforced two times during the study. In January 1993 four females and four males were captured with traps in Suomussalmi, Kainuu (64°50′N, 28°30′E) on a feeding site, and transported to Konnevesi. This procedure was repeated in the end of the year 1993, when eight females and four males were captured. Some of these birds did not, however, survive very long in captivity, and mortality took place especially in winter. Therefore, despite the introduction of new birds the number of males and females available in experiments did not increase, but rather, remained somewhat stable during the years.

2.3 The test of the hypotheses for the evolution of leks (I)

In this study I used a large data set collected in Petäjävesi during 1987-1993. Each male's mating success was plotted against his territory size and position on the lek. The latter was measured as three intercorrelated variables, which were combined into PC1 with a principal component analysis. Observational data were supplemented with a choice experiment in aviary, where females had the option of choosing between groups of two or four males. Males were randomly arranged and changed daily, so that each female had a different male constitution in the trial. The setup mimicked a natural situation where female is sampling males on a lek, and she perceives males on both sides of her. Since territories in the central parts of leks are smaller than in the peripheral parts, the males are more tightly clumped there. Thus, the two-male group mimicked lek periphery, and the four-male group mimicked lek center. Females were placed between the male groups and their preference was scored according to their proximity to either group. This kind of tests are widely used for demonstrating choice in behavioural ecology (e.g. Forsgren 1992).

To separate the female preference and hot shot hypothesis, preference scores were calculated per male. If preferences were higher for males in the larger group, it should rule out the hot shot hypothesis, which does not assume higher per male benefit in the larger group (center).

2.4 Comparison of leks on different habitats (II)

In this study, several aspects of lek organization were compared between leks on bogs and leks on ice-covered lakes. Data on bog leks were collected during 1987-1993 from eight sites in Petäjävesi, and on lake leks during 1987-1988 and 1991-1993 in Petäjävesi and Konnevesi. Except leks, the sites itself were compared in terms of openness, which might in some cases limit the mobility of the male aggregation, since black grouse favours open sites, probably because of predator detection (Koivisto 1965). Openness was quantified by calculating the mean of the distances between lekking site and lake shore (or the border between bog and forest), measured to four cardinal directions (N, E, S, W). Lek stability was estimated as the shift of the lek center during one morning from the start of the display to the departure of males, and as changes in the positions of males in relation to each other. Lek structure was measured as the mean distance between two nearest neighbouring males.

I also compared the possibilities for females to choose among males. For that purpose, the number of males that a given female visited, was counted. On bogs visits were observed as visits to different male territories, whereas on territory-free lakes a female being within 5 m from a male was regarded as a visit. This distance is justified because a female can be regarded as being under "control" of that male, and she has the option of copulating with him without being interrupted by other males (Alatalo et al. 1996). The number of males that received copulations or solicitations was compared to examine if the distribution of matings is different on the two habitats. Because bog leks were generally larger in our data than lake leks (I), only leks within the same size class were used in these comparisons.

2.5 Dominance and limited mate sampling on lake leks (III)

Lake leks were observed during 1991-1993 in order to get detailed information on the mate sampling behaviour of females in the absence of territories and absolute site effects. Movements of males and females were analyzed from maps drawn on the basis of angular values transformed to coordinates (2.2.1.). Aggressive interactions between males (fights, chases and retreats) were considered to reflect dominance relationships between them, and based on several interactions between males, a linear dominance rank was constructed. Because leks of different size were pooled, position in dominance rank had to be transformed to relative dominance value. For the analysis of female movements, the top quarter of males within each lek was termed as dominants, the rest being subordinates.

Directions of female movements in relation to males of different dominance status were tested against random expectations. Visits to males (as determined in 2.2), solicitations and copulations were used as evidence for the effect of dominance status on male mating success, and for the prospects for females of making choice.

2.6 Between-year correlations in lek sizes (IV)

I was interested whether particular leks are consistently larger than the other leks. I plotted male and female numbers of a given lek in a given year against the numbers of the same site in the previous year. The changes in population density were taken into account by relating the lek sizes of a given year to the mean lek size of that year. I also applied partial correlation techniques to allow for intercorrelations between the number of males and females.

2.7 Playback experiments (V)

Here I wanted to test whether females use auditory cues when searching for leks to visit. Additionally, I looked the response of males to the experimentally increased vocal display output. The field test was performed on lake leks in Konnevesi and Petäjävesi during 1993-1994. Eight pairs of closely-located (3-10 km) leks were chosen, trying to match them with respect to lek size (male numbers) as well as possible. Within each pair, one lek was randomly assigned as playback, while the remaining was control. The playback consisted of an endless 1-min tape which contained rookooing display by four males. The tape was compiled from four different tapes of individual males recorded in Petäjävesi in 1987-1988. The idea of the treatment was to make a small lake lek sound like a large lek. The tapes were played through loudspeakers, starting before the arrival of males and continuing until the departure of males, or at least 2-3 hours. Within each lek pair, playback and control sites were observed on alternative mornings, and male and female numbers were counted.

In the aviary, females were introduced into pens (1 x 1 x 0.6 m), and visual contact between them was prevented by fences made of plastic canvas. Each female was tested by erecting a player on both sides of her pen at the distance of 15 m. A tape with a single male rookooing was played from the other side, and a tape with four males (compiled as above) was played from the opposite side. Orientation of the female in the pen was used as an indication of her choice.

2.8 A comparative analysis of lekking, mating skew and sexual size dimorphism (VI)

In the last study (VI) I compared lekking bird species in order to establish any relationships between lek size, lek structure, male mating skew and sexual size dimorphism. Lek characters were defined as the mean number of males within a lek, and mean distance between nearest neighbours. In some cases this was calculated from male territory size, assuming circular shape and no space between territories. Male mating skew, which I assumed to represent the potential for selection, was calculated with two indices (Alatalo et al. 1992, Keller & Vargo 1993). Size dimorphism was measured from the regression of male body mass against female body mass (because of the positive allometry between them, Ranta et al. 1994), and residuals from that regression were used as indicative of the degree of dimorphism.

In comparative studies the phylogenetic relationships between species have to be taken into account, because related species do not represent independent data points. Therefore, I used the independent contrast methods for continuous variables (Felsenstein 1985, Harvey & Pagel 1991). I identified the contrasts from the phylogeny based on Sibley & Ahlquist (1990), constructed by Höglund (1989). I performed the analysis across all avian taxa with lek mating system, where information was available, because data were not sufficient for an analysis within coherent clades. I estimated the amount of phylogenetic variation by performing ANOVAs across orders and families, to see whether variation between groups on this level exceeds the variation within groups.

3 RESULTS AND DISCUSSION

3.1 Female preferences for central males (I)

In the field, male mating success (in terms of number of copulations) was significantly positively related to centrality of territory. Additionally, males with large territories gained more matings than males with small territories. Territories were generally smaller in the center, and the results imply that some males were able to maintain relatively large territories despite their central position. These males were most likely dominants, which were favoured by females (Alatalo et al. 1991). Territory centrality and size together explained one third of the total variation in male mating success.

In the aviary trials females favoured the four-male (mimicking center) group strongly enough to yield a per capita benefit for males in that group. Also, every male achieved higher preference scores when belonging to the four-male group. Active preference for dense male aggregation was also suggested by Kruijt et al. (1972) for black grouse, and by Lank & Smith (1992) for ruff. We found the preference for central males irrespective of male identity, which gives strong support for the "female preference" hypothesis for the evolution of leks (Alexander 1975, Bradbury 1981), and explains why males aggregate to form tight clusters.

There remains the possibility that some males are attracted by other males to join leks, as the hot shot hypothesis predicts. However, the consequences are not necessarily negative for the inherently attractive male: instead of losing some of the copulations to his satellites, he may increase his own attractivity by being surrounded by other males (cf. Spurrier et al. 1994).

3.2 Habitat differences and their consequences for lekking (II)

On homogeneous surfaces of ice-covered lakes the leks were not "classical" in the sense that they were mobile and more dispersed compared to bog leks. The spatial organization changed to some extent, in terms of positions of males in relation to each other, as indicated by the changes in nearest neighbours on lakes. These results are in good accordance with earlier findings in black grouse (Koivisto 1965), and also correspond with other northern grouse where unstable leks sometimes occur on snow-covered surfaces (Gibson & Bradbury 1986, 1987, Tsuji 1993). Most likely the instability was caused by the lack of landmarks, such as vegetation or microtopographical features, which serve as territory boundaries on bogs.

The loss of territorial structure and dispersion of males occurred probably through intense dominance competition between males (Foster 1983), and had consequences for female mate sampling. Females spend more time on their lek visits on lakes, but in spite of that ended up with fewer visited males compared to their counterparts on bogs. Still, females behaved in a similar manner on both habitats, i.e. as if they were making choice. In fact, movements of females seemed to be one of the proximate factors behind the mobility of males, since the males tended to follow walking females in order to court them. The skew in mating success among males was more pronounced on lakes compared to similar-sized bog leks. On lakes, the top male received, on average, 70 % of matings, while the corresponding proportion on bog leks was less than 50 %. This may indicate stronger selection for dominance-related traits on lakes (see also IV).

3.3 The effect of dominance hierarchy on male mating success and female mate sampling (III)

After having landed on the arena (typically on the peripheral areas outside the group of lekking males), females started their sampling by moving towards dominant males more often than randomly expected. This may mean that the females had a priori knowledge on the dominance relations of males. When being courted, females tried to approach other males, but failed to do so in most cases. Attempts to visit other males than the first one visited were followed by dominance interactions between the courting and the approached male. This kind of behaviour could be judged as incitation, where the female tries to encourage males to show their dominance relationships (Cox & LeBoeuf 1977, Byers et al. 1994). At least, black grouse females did not try to avoid causing interactions between males.

Male dominance status was a significant determinant of his mating success, while centrality was not. This is easily understood, since on mobile systems like lake leks, absolute (or even relative) positions do not play a role in mate sampling, because they change over time (II). On small leks as in this study, females may not perceive any males as central. Moreover, females were not free to sample between males, even if they prefered the ones which tended to be in the center (Kruijt et al. 1972, II). Probably the dominance status was not much affected by mating success (c.f. Sorenson & Derrickson 1994), since part of the observations on which the determination of dominance were done before first matings.

It is difficult to know what the motivation of females was when they approached other males than the nearest courting one. In any case, it made the dominance relationships between males very straightforward, and this information is used by females in mate selection on bog leks (Alatalo et al. 1991). Thus, even though (and because) mate sampling seems to be limited by male dominance competition on lake leks, the females will mate with the dominant males with greater probability.

3.4 Traditionality of leks (IV)

There was a significant positive association between male numbers of successive years on leks. The number of females tended to correlate with the lek size (number of males) in the same year, but not with past lek size or the number of females in the previous year. Thus, the strong traditionality seems to be generated by the tendency of adult males to occupy a territory on the same lek year after year. Additionally, young males may preferentially join leks with several adult males. Adult females also show high breeding-site fidelity (Willebrand 1988), but here the female counts between years were unrelated. One possible reason for the lack of this correlation may be the high annual mortality of females (Angelstam 1984).

3.5 Responses of males and females to supplemented vocal display (V)

Despite the effort to match the lek sizes within experimental pairs, the control leks happened to be larger in the beginning of the experiment. Therefore, I compared changes in male and female numbers from the first morning to the mean of the later mornings. The number of females did not increase significantly more on playbacks, while the effect on males was clear. On playback sites, the lek size increased somewhat, and on control sites, there was a tendency for lek size to decrease. In some cases it was possible that the playback attracted males from the nearby control sites.

In the aviary test, females did not orientate towards multi-male tapes as strongly as predicted, even though there was a tendency of choosing multi-male tapes in 1995. This result is ambiguous because of the small sample size, and consequently, low power of the test. In any case, females did not seem to use auditory cues when choosing which lek to visit. Visual contact to the males may be needed before the visiting decision of landing on the lek is made.

Moreover, females show strong fidelity to breeding sites after their first year (Willebrand 1988, see IV), and maybe a treatment like this is not strong enough to attract them to neighbouring leks. The potential responders, the yearling females, were not very numerous during the study.

The response of males, instead, was at first sight supportive for the "hot shot" hypothesis, which predicts that unattractive males should join the attractive ones (Arak 1983, Beehler & Foster 1988, Höglund & Robertson 1990b). In this case, the mobile males were most likely yearlings, which often display alone and are not attached to sites as strongly as older males (de Vos 1983). But, I can not rule out the possibility that they were interested in the whole lek, which they perceived as large, instead of gathering around an attractive male. If this is the case, then one might argue that the males came to the playback sites because they perceived them as being of size which females prefer, and where these young males might get occasional copulations.

3.6 Lekking, mating skew, and sexual size dimorphism in birds (VI)

Lek size or structure, as measured by inter-male distance, were not related to the skewness in male mating success, as measured by two different indices (Alatalo et al. 1992, Widemo & Owens 1995). Predictions regarding higher or lower inequality of male success with the increasing "degree of lekking" gain no support from general trends across taxa. The dimorphism in body mass, which should be the result of sexual selection on male size, was neither correlated with lek characters. Apparently the advantage of large body size in males is not a general pattern in lekking birds. A reason for the lack of any relationship may be due to some species having aerial, or otherwise energy-demanding display, which selects for small rather that large males (Andersson & Norberg 1981, Payne 1984).

Ideally this kind of analyses should be performed within clades that are monophyletic (derived from a common ancestor), but I did not find enough relevant data for such analyses. It is possible that there are lineage-specific correlations which may reflect adaptive responses for selective pressures within each lineage. However, when pooled together into same independent contrast analysis, trends of different direction are masked and can not be detected. The correlation between lek size and mating skew within the Tetraonidae hints at the possible existence of such specific trends.

A significant fraction of the variation in lek structure was explained by the family membership, which suggests a phylogenetic, historical component in the existing inter-male distances. However, even though constrained by phylogeny, the lek structure may be similar in related species because of common selective environment (Pagel & Harvey 1988).

4 CONCLUSIONS

In this thesis I studied how leks have evolved, and how sexual selection operates on leks, by using descriptive, comparative and experimental approaches. I have chosen to use the black grouse as a model organism in the first five studies, whereas the sixth study focuses on general patterns over all lekking bird species, allowing for phylogenetic relationships with the independent contrasts method.

The selective environment seems to be non-uniform for black grouse, as suggested here with the respect to sexual selection. Leks on lakes and leks on bogs may differ in the traits which are selected, and also how strongly they are selected. In the former habitat, selection on female mating preferences might be low, because nearly all females mate with the dominant males, irrespective what they prefer. But, if females favour dominant males, lakes are optimal habitat for them to get what they want. On bogs, females that use effectively several cues of male quality, or copy each other, may be successful in passing their genes to the next generation. Male traits connected with dominance are selected on both habitats, but obviously more strongly on lakes because of direct competition and more extreme mating skew.

The mechanism by which the habit of mating in aggregations has evolved was revealed in the choice experiment, where females favoured more densely clustered males. Although the experiment was conducted in a within-lek scale, the similar mechanism may also function in selection between leks, where males displaying in dense aggregations are favoured over those that are dispersed. The ancestral state of lekking in the lineage of the genus Tetrao may have been more dispersed than the present state, and females have started to mate preferentially with males who have neighbours nearby. This joint evolution of male clustering and female preference for clusters could proceed in a similar fashion as Fisherian runaway sexual selection in general, but also Zahavian indicator models may apply. Females may gain by being choosy, either through direct (avoidance of diseases or disruptions) or indirect benefits (high genetic quality for the offspring).

Hypotheses alternative to the "female preference" are not necessarily irrelevant, even in the case of black grouse. Their predictions may be valid, but they may provide answers to slightly different questions than the evolution of leks. For instance, the "hot shot" mechanism may work in the settlement of young (or otherwise poor) males. The fact that mobile males were attracted to the leks where vocal display was supplemented, supports this explanation. The lack of the response of females suggests that auditory cues do not provide enough information on lek quality, to be used by females when visiting the leks.

Any relationships between lek size or structure, male mating skew and sexual size dimorphism cannot be generalized across species. The lack of any correlations suggests that other aspects than lek size or structure contribute to the variation in mating skew, and selection does not need to drive male size in exaggeration. Moreover, the roles of different selective pressures are very likely to differ between species, leading to different adaptations. In part, the "solutions" may be limited by phylogenetic constraints, but similarities between related species may also indicate common selective environments.

Acknowledgements

This thesis is not a fulfillment of a predestined mission. Rather, it is the synergistic result of courageous ideas of my supervisor, Prof. Rauno Alatalo, good opportunities in the financial terms, and finally, my own investment of labour. Rauno has been keeping the reins, and at times the pace as well, though in a very subtle way, while my job has been only to keep on moving. His help has extended not only to the office, but also to the field. Part of the material I have used could not have been collected without a large team of co-workers, many of which appear as co-authors in the original papers. As a complementary project to the field studies, black grouse have been kept in captivity in Konnevesi Research Station, and the following persons have been involved in a way or another in this (sometimes desperate) business: J. Berg, M. Halonen, J. Höglund, L. Ijäs, A. Koljonen, R. Latvanen, A. Lundberg, H. Pöysä, J. Raatikainen, P. T. Rintamäki, P. Siikamäki, A. Sirkka and P. Valkeajärvi. In the final straight, E. Korpimäki and H. Lindén kindly read and commented the first written version of the thesis. An important influence on my scientific growth process was obtained during my stay at Uppsala University. An enthusiastic atmosphere in the office, and in Konnevesi, was created by the numerous colleagues, some of which eventually have become friends also outside office hours. I have also given great value for the leisure time activities and various sports exercised with the KOMU rtön. y. Further, I thank all the musicians at our department for good and Bad Company. Finally, surely more than anyone else, my dear wife Pirkko has helped me over troubled water, and with the support from her, and our families, the load has been lighter for me to carry.

Financially I have been supported by the Academy of Finland (also via R. V. A. and P. Helle), Societas Biologica Fennica Vanamo, NorFA, NKE, and Wihuri Foundation.

YHTEENVETO

Teeren soidin: evoluutio ja seksuaalinen valinta

Tutkin väitöskirjatyössäni teeren soitimen evoluutiomekanismeja, lajinsisäistä vaihtelua erityyppisten soidinten välillä, ja naaraan parinvalintamahdollisuuksia reviirittömässä soidinsysteemissä. Koiraiden parittelumenestys riippui siitä, kuinka lähellä soitimen keskustaa niiden reviiri sijaitsi. Reviirit ovat soidinkeskustassa varsin pieniä ja koiraat vastaavasti tiheästi ryhmittyneet. Naaraat suosivat tarhakokeissa selvästi tiheitä koirasryhmittymiä, minkä voidaan maastoaineistosta saatujen tulosten perustella päätellä olevan osoitus aktiivisesta valinnasta pariutua keskellä soidinta olevien koiraiden kanssa. Tällöin seksuaalinen valinta suosii tiheisiin ryhmittymiin pyrkiviä koiraita, mikä on todennäköisesti johtanut ryhmäsoitimen kehittymiseen teerellä.

Teeren soitimista osa sijaitsee järvien jäillä, osa avoimilla soilla. Nämä soidintyypit eroavat toisistaan mm. rakenteen ja vakauden suhteen. Jääsoitimilla koiraat sijaitsevat keskimäärin kauempana toisistaan ja soitimet ovat liikkuvia, mikä johtunee kiinteiden reviirien perustamiseen vaadittavien maamerkkien puuttumisesta. Soidinrakenteella on vaikutuksia naaraan parinvalintaan: järvien reviirittömillä soitimilla naaraan mahdollisuudet valita parittelukumppani ovat rajoitetut, sillä dominantit koiraat estävät naaraan vierailut muiden koiraiden läheisyydessä. Koiraiden väliset dominanssisuhteet ovat erittäin selvät varsinkin pienillä jääsoitimilla, joilla hallitsee usein yksi ainoa koiras. Naaraille ei todennäköisesti ole kuitenkaan haittaa valintamahdollisuuksien puuttumisesta, sillä dominantin koiraan kanssa parittelusta voi olla erilaisia suoria tai epäsuoria hyötyjä. Eräs mahdollinen hyöty voi olla koiraan elinkykyyn vaikuttavan geneettisen aineksen välittyminen naaraiden jälkeläisille.

Teerikoiraiden soidinäänet ovat kauaskantavia ja ilmaisevat aamuhämärässä soitimen sijainnin. Eräässä osatyössäni tutkin akustisen signaalin merkitystä naaraiden valintakäyttäytymiseen soittamalla osalla soitimista koiraiden soidinääniä kovaäänisten kautta. Tarhatut naaraat eivät valintakokeessa näyttäneet erottavan yksinäistä koirasta neljän koiraan ryhmästä. Maastossa keinotekoinen soidinäänten lisäys ei houkutellut naaraita paikalle, joten ilmeisesti pelkkä akustinen signaali ei riitä naaraille soidinpaikan valintaan, vaan koiraat täytyy myös nähdä, jolloin naaras saa tietoa soitimen koosta. Kovaäänisillä oli kuitenkin vaikutus koiraisiin: soidinäänten lisäys houkutteli kukkoja, jotka todennäköisesti olivat nuoria ja reviirittömiä. Tämä viittaa siihen, että nuorille koiraille on eduksi liittyä suurehkoon soitimeen, jossa naaraita käy enemmän kuin pienillä soitimilla ja mahdollisuudet satunnaisiin paritteluihin ovat olemassa.

Viimeinen osatutkimukseni on vertaileva analyysi soitimen rakenteen ja koon sekä sukupuoltenvälisen kokoeron ja paritteluvinouman (engl. mating skew) välisistä suhteista. Paritteluvinoumalla tarkoitetaan paritteluiden jakauman poikkeavuutta tasajakaumasta, ts. tilanteesta, jossa kaikki koiraat olisivat yhtä menestyksekkäitä. Käytin aineistona lintulajeja, joilla on joko ns. klassinen (koiraat lähellä toisiaan) tai ns. hajautunut (engl. dispersed) ryhmäsoidin. Soitimen rakenne ja koko eivät osoittautuneet merkittäviksi paritteluvinoumaan vaikuttaviksi tekijöiksi. Klassisilla ryhmäsoitimilla seksuaalinen valinta ei siis näyttäisi välttämättä olevan voimakkaampaa kuin hajautuneilla soitimilla. Soitimen tyypillä tai paritteluvinoumalla ei ollut myöskään yhteyttä sukupuolten väliseen kokoeroon, jota usein pidetään seksuaalisen valinnan ilmentymänä. Onkin todennäköistä, että eri lajien ja lajiryhmien väliset erot esim. elinympäristössä ja fylogeneettisessä historiassa peittävät mahdolliset yleiset trendit soidintyypin ja seksuaalisen valinnan välillä.

REFERENCES

Alatalo, R. V., Höglund, J. & Lundberg, A. 1991: Lekking in black grouse - a test of male viability. - Nature 352: 155-156.

Alatalo, R. V., Höglund, J., Lundberg, A. & Sutherland, W. J. 1992: Evolution of black grouse leks: female preferences benefit males in larger leks. - Behav. Ecol. 3: 53-59.

Alatalo, R. V., Burke, T., Dunn, J., Hanotte, O., Höglund, J., Lundberg, A., Moss, R. & Rintamäki, P. T. 1996: Paternity, copulation disturbance and female choice in lekking black grouse. - Anim. Behav. (in press).

Alexander, R. D. 1975: Natural selection and specialized chorusing behaviour in acoustical insects. - In: Pimentel, D. (ed.), Insects, science and society: 35-77. Academic Press, New York.

Andersson, M. 1994: Sexual selection. - 599 p. Princeton University Press, Princeton.

Andersson, M. & Norberg, Å. 1981: Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling flight performance. - Biol. J. Linn. Soc 15: 105-130.

Angelstam, P. 1984: Sexual and seasonal differences in the mortality of the black grouse Tetrao tetrix in boreal Sweden. - Ornis Scand. 15: 123-134.

Arak, A. 1983: Male-male competition and mate choice in anuran amphibians. - In: Bateson, P. (ed.), Mate choice: 181-210. Cambridge University Press, Cambridge.

Beehler, B. M. & Foster, M. S. 1988: Hotshots, hotspots, and female preferences in the organization of lek mating systems. - Am. Nat. 131: 203-219.

Bertram, B. C. R. 1978: Living in groups: predators and prey. - In: Krebs, J. R. & Davies, N. (eds), Behavioural ecology: an evolutionary approach: 64-96. Blackwell, Oxford.

Bradbury, J. W. 1981: The evolution of leks. - In: Alexander, R. D. & Tinkle, D. W. (eds), Natural selection and social behaviour: 138-169. Chiron Press, New York.

Bradbury, J. W. 1985: Contrasts between insects and vertebrates in the evolution male display, female choice and lek mating. - Fort. Zool. 31: 273-289.

Bradbury, J. W. & Gibson, R. M. 1983: Leks and mate choice. - In: Bateson, P. (ed.), Mate choice: 109-138. Cambridge University Press, Cambridge.

Bradbury, J., Gibson, R. M. & Tsai, I. M. 1986: Hotspots and the dispersion of leks. - Anim. Behav. 34: 1694-1709.

Bradbury, J. W., Gibson, R. M., McCarthy, C. E. & Vehrencamp, S. L. 1989: Dispersion of displaying male sage grouse. II. The role of female dispersion. - Behav. Ecol. Sociobiol. 24: 15-24.

Byers, J. A., Moodie, J. D. & Hall, N. 1994: Pronghorn females choose vigorous mates. - Anim. Behav. 47: 33-43.

Cade, W. H. 1981: Field cricket spacing and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. - Z. Tierpsychol. 55: 365-375.

Cheverud, J. M., Dow, M. M. & Leutenegger, W. 1985: The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. - Evolution 39: 1335-1351.

Clutton-Brock, T. H. 1989: Mammalian mating systems. - Proc. R. Soc. Lond. B. 236: 339-372.

Clutton-Brock, T. H., Price, O. F. & MacColl, A. D. C. 1992: Mate retention, harassment and the evolution of ungulate leks. - Behav. Ecol. 3: 234-242.

Cox, C. R. & LeBoeuf, B. J. 1977: Female incitation of male competition: A mechanism in sexual selection. - Am. Nat. 111: 317-335.

Darwin, C. 1871: The descent of man and selection in relation to sex. - 490 p. Murray, London.

Davies, N. B. 1991: Mating systems. - In: Krebs, J. R. & Davies, N. B. (eds), Behavioural ecology: an evolutionary approach, 3rd. ed: 263-294. Blackwell, Oxford.

de Vos, G. J. 1983: Social behaviour of black grouse: an observational and experimental field study. - Ardea 71: 1-103.

Droney, D. C. 1994: Tests of hypotheses for lek formation in a Hawaiian Drosophila. - Anim. Behav. 47: 351-361.

Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection, and the evolution of mating systems. - Science 197: 215-223.

Felsenstein, J. 1985: Phylogenies and the comparative method. - Am. Nat. 125: 1-15.

Fisher, R. A. 1930: The genetical theory of natural selection. - 272 p. Clarendon Press, Oxford.

Forsgren, E. 1992: Predation risk affects mate choice in a gobiid fish. - Am. Nat. 140: 1041-1049.

Foster, M. S. 1981: Cooperative behaviour and social organization of the swallow-tailed manakin (Chiroxiphia caudata). - Behav. Ecol. Sociobiol. 9: 167-177.

Foster, M. S. 1983: Disruption, dispersion, and dominance in lek breeding birds. - Am. Nat. 122: 53-72.

Gibson, R. M. & Bradbury, J. W. 1985: Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. - Behav. Ecol. Sociobiol. 18: 117-123.

Gibson, R. M. & Bradbury, J. W. 1986: Male and female mating strategies on sage grouse leks. - In: Rubenstein, D. I. & Wrangham, R. W. (eds), Ecological aspects of social organization: 379-398. Princeton University Press, Princeton.

Gibson, R. M. & Bradbury, J. W. 1987. Lek organization in sage grouse. Variations on a territorial theme. - Auk 104: 77-84.

Gosling, L. M. 1986: The evolution of mating strategies in male antelopes. - In: Rubenstein, D. I. & Wrangham, R. W. (eds), Ecological aspects of social organization: 244-281. Princeton University Press, Princeton.

Gosling, L. M. & Petrie, M. 1990: Lekking in topi: a consequence of satellite behaviour by small males at hotspots. - Anim. Behav. 40: 272-287.

Gould, S. J. & Lewontin, R. C. 1979: The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. - Proc. R. Soc. Lond. B. 205: 581-598.

Harvey, P. H. & Pagel, M. D. 1991: The comparative method in evolutionary biology. - 239 p. Oxford University Press, Oxford.

Helminen, M. 1963: Composition of the Finnish populations of Capercaillie, Tetrao urogallus, and Black Grouse, Lyrurus tetrix, in the autumns of 1952-1961, as revealed by a study of wings. - Pap. Game Res. 23: 1-124.

Höglund, J. 1989: Size and plumage dimorphism in lek-breeding birds: a comparative analysis. - Am. Nat. 134: 72-87.

Höglund, J. & Alatalo, R. V. 1995: Leks. - 249 p. Princeton University Press, Princeton.

Höglund, J. & Robertson, J. G. M. 1990a: Spacing of leks in relation to female home ranges, habitat requirements and male atractiveness in the great snipe (Gallinago media). - Behav. Ecol. Sociobiol. 26: 173-180.

Höglund, J. & Robertson, J. G. M. 1990b: Female preferences, male decision rules and the evolution of leks in the great snipe Gallinago media. - Anim. Behav. 40: 15-22.

Höglund, J. & Sillén-Tullberg, B. 1994: Does lekking promote the evolution of male-biased size dimorphism in birds? On the use of comparative approaches. - Am. Nat. 144: 881-889.

Keller, L. & Vargo, E. L. 1993: Reproductive strategies and reproductive roles in colonies of eusocial insects. - In: Keller, L. (ed.), Queen number and sociality in insects: 16-44. Oxford University Press, Oxford.

Koivisto, I. 1965: Behaviour of the black grouse, Lyrurus tetrix (L.) during the spring display. - Finn. Game Res. 26: 1-60.

Krebs, J. R. & Davies, N. B. 1991: Behavioural ecology: an evolutionary approach, 3rd ed. - 482 p. Blackwell, Oxford.

Kruijt, J. P., de Vos, G. J. & Bossema, I. 1972: The arena system of the black grouse Lyrurus tetrix (L.). - Proc. Int. Ornithol. Congr. 15: 399-423.

Lande, R. & Arnold, S. J. 1985: Evolution of mating preference and sexual dimorphism. - J. Theor. Biol. 117: 651-664.

Lank, D. B. & Smith, C. M. 1992: Females prefer larger leks: field experiments with ruffs (Philomachus pugnax). - Behav. Ecol. Sociobiol. 30: 323-329.

LeCroy, M., Kulupi, A. & Peckover, W. S. 1980: Goldie's bird of paradise: display, natural history, and traditional relationships of the people to the bird. - Wilson Bull. 92: 289-301.

Lill, A. 1974: Sexual behaviour of the lek-forming white-bearded manakin (Manacus manacus trinitatis Hartert). - Z. Tierpsychol. 36: 1-36.

McDonald, D. B. 1989: Cooperation under sexual selection: age-graded changes in a lekking bird. - Am. Nat. 134: 709-730.

O'Donald, P. 1980: Genetic models of sexual selection. - 250 p. Cambridge University Press, Cambridge.

Otte, D. 1974: Effects and functions in the evolution of signalling systems. - Ann. Rev. Ecol. Syst. 5: 385-417.

Pagel, M. D. & Harvey, P. H. 1988: Recent developments in the analysis of comparative data. - Q. Rev. Biol. 63: 413-440.

Parker, G. A. 1978: Searching for mates. - In: Krebs, J. R. & Davies, N. B. (eds), Behavioural ecology: an evolutionary approach: 214-244. Blackwell, Oxford.

Payne, R. B. 1984: Sexual selection, lek and arena behaviour, and sexual size dimorphism in birds. - Ornithol. Monogr. 33: 1-52.

Phillips, J. B. 1990. Lek behaviour in birds: do displaying males reduce nest predation? - Anim. Behav. 39: 555-565.

Pulliam, H. R. & Caraco, T. 1984: Living in groups: Is there an optimal group size? - In: Krebs, J. R. & Davies, N. B. (eds), Behavioural ecology: an evolutionary approach, 2nd ed: 122-147. Blackwell, Oxford.

Queller, D. C. 1987: The evolution of leks through female choice. - Anim. Behav. 35: 1424-1432.

Ranta,. E., Laurila, A. & Elmberg, J. 1994: Reinventing the wheel: analysis of sexual dimorphism in body size. - Oikos 70: 313-321.

Reynolds, J. D. & Gross, M. R. 1990: Costs and benefits of female mate choice: Is there a lek paradox? - Am. Nat. 136: 230-243.

Shelly, T. E. 1990: Waiting for mates: variation in female encounter rates within and between leks of Drosophila conformis. - Behaviour 107: 34-48.

Sibley, C. G. & Ahlquist, J. E. 1990: Phylogeny and classification of birds: a study in molecular evolution. - 1008 p. Yale University Press, New Haven.

Spurrier, M. F., Boyce, M. S. & Manly, B. F. J. 1994: Lek behaviour in captive sage grouse Centrocercus urophasianus. - Anim. Behav. 47: 303-310.

Stillman, R. A., Clutton-Brock, T. H. & Sutherland, W. J. 1993: Black holes, mate retention, and the evolution of ungulate leks. - Behav. Ecol. 4: 1-6.

Thornhill, R. & Alcock, J. 1983: The evolution of insect mating systems. - 547 p. Harvard University Press, Cambridge, Mass.

Trail, P. W. 1985: Territoriality and dominance in the lek-breeding Guianan cock-of-the-rock. - Nat. Geogr. Res. 1: 112-123.

Tsuji, L. J. S. 1993: Snowfall causes lek movement in the sharp-tailed grouse. - Wilson Bull. 104: 188-189.

Westcott, D. A. 1994: Leks of leks: a role for hotspots in lek evolution? - Proc. R. Soc. Lond. B. 258: 281-286.

Widemo, F. & Owens, I. P. F. 1995: Lek size, male mating skew, and the evolution of lekking. - Nature 373: 148-151.

Wiley, R. H. 1973: Territoriality and non-random mating in sage grouse, Centrocercus urophasianus. - Anim. Behav. Monogr. 6: 87-169.

Wiley, R. H. 1991: Lekking in birds and mammals: behavioural and evolutionary issues. - Adv. Study Behav. 20: 201-291.

Willebrand, T. 1988: Demography and ecology of a black grouse (Lyrurus tetrix L.) population. - 44 p. Ph D thesis, Uppsala University, Uppsala.

Wrangham, R. W. 1980: Female choice of least costly males: a possible factor in the evolution of leks. - Z. Tierpsychol. 54: 357-367.

Wynne-Edwads, V. C. 1962: Animal dispersion in relation to social behaviour. - 653 p. Oliver & Boyd, Edinburgh.

ORIGINAL PAPERS

I

Lek centre attracts black grouse females

by

Matti Hovi, Rauno V. Alatalo, Jacob Höglund, Arne Lundberg & Pekka T. Rintamäki

Proc. R. Soc. Lond. B. 258: 303-305, 1994

https://doi.org/10.1098/rspb.1994.0177

II

Habitat differences and the variability in the lek mating system of black grouse

by

Matti Hovi, Rauno V. Alatalo & Pekka T. Rintamäki

Behaviour (in press), 1996

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https://doi.org/10.1163/156853996X00215

III

Black grouse leks on ice: female mate sampling by incitation of male competition?

by

Matti Hovi, Rauno V. Alatalo & Pirkko Siikamäki

Behav. Ecol. Sociobiol. (in press), 1995

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https://www.jstor.org/stable/4601139

https://doi.org/10.1007/BF00177408

IV

Traditionality of black grouse leks

by

Matti Hovi, Rauno V. Alatalo, Jacob Höglund & Arne Lundberg

Manuscript

https://lintulehti.birdlife.fi:8443/pdf/artikkelit/450/tiedosto/of_73_119-123_artikkelit_450.pdf

V

Responses of male and female black grouse to male vocal display

by

Matti Hovi, Rauno V. Alatalo, Matti Halonen & Arne Lundberg

Manuscript (submitted)

https://doi.org/10.1111/j.1439-0310.1997.tb00145.x

VI

A comparative analysis of lekking, mating skew and sexual dimorphism

by

Matti Hovi

Manuscript

A COMPARATIVE ANALYSIS ON LEKKING, MATING SKEW AND SEXUAL SIZE DIMORPHISM IN BIRDS

by

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ABSTRACT

A comparative analysis across bird taxa with lek mating system was performed, in order to examine possible relationships between lek size and structure, skewness in male mating success and sexual dimorphism in body mass. The method of independent contrasts was used for removing the confounding effects of phylogenetic relationships between species. There appeared to be no general relationships between lek size and male mating skew or sexual body mass dimorphism. Nor was the lek structure, in terms of inter-male distance, associated with mating skew or sexual dimorphism. Moreover, species with extreme mating skew, and thus, high potential for sexual selection, did not have disproportionally large males. Phylogenetic relations explained part of the variation in lek size and inter-male distance. It was concluded that interspecific variation in lekking and body mass dimorphism cannot be understood with these factors, and rather, intraspecific analyses of the variation might be more fruitful for the study of adaptations involved in lek mating systems.

INTRODUCTION

As a mating system, leks are characterized by highly uneven distribution of mating success among males. It has been suggested that the extreme polygyny found on leks would have been responsible for large male size in relation to female size (Darwin 1871, Payne 1984). Even though large body size seems to offer a selective advantage for males in diverse taxa (reviewed in Andersson 1994), comparative evidence for general patterns is controversial (Höglund 1989, Oakes 1991). On the other hand, Trail (1990) predicted no sexual dimorphism in lekking species because of the social selection on both sexes. Earlier analyses have questioned whether lekking species are more dimorphic than non-lekking species, whereas dimorphism among lek-breeders has not been investigated in a fashion that takes the phylogenetic relationships into account.

Leks vary widely with respect to, for instance, the degree of male clustering. At the one extreme, there are tightly clumped "classical" leks (e.g. ruff, Philomachus pugnax, Hogan-Warburg 1966), which gradually turn into "dispersed" leks as the distance between individual males increases (e.g. Lawe's parotia, Parotia lawesii, Pruett-Jones and Pruett-Jones 1990). Because sexual selection should be stronger in lekking than in non-lekking species, as indicated by more skewed distribution of mating success on leks (Bradbury and Gibson 1983, Wiley 1991), there could also exist a relationship between the degree of male clustering and the strength of selection. One possible reason for strong selection on clumped leks is the possibility for females to copy each other's mate choice, which is likely to increase the mating skew (Wade and Pruett-Jones 1990). Male traits correlated with body size (or size itself) being likely targets of selection, species with tightly clustered male aggregations should show most extreme sexual dimorphism.

Foster (1983) discussed a possibility where inter-male distance may increase when aggressiveness in males, or the traits associated with it, is selected for. This could occur when aggressive males disrupt matings of their neighbours, which occurs with varying frequency in most lek systems (e.g. Trail 1985, Nefdt 1995). If this is a general trend, species with most extreme mating skew and strongest selection should not be most tightly clustered because inter-male distance would be a compromise between benefits from female visits and costs from disruption of matings (Foster 1983).

In addition to aggregation, there is also wide variation in lek size, i.e. the number of males that are displaying at the same lek. A minimum size of a lek is two males displaying close to each other, and at the other extreme, there are leks of hundreds of males (e.g. sage grouse, Scott 1942). Since leks have been regarded as selecting male secondary sexual traits more strongly than other mating systems do (Darwin 1871, Payne 1984), we might expect species with larger leks showing more extreme mating skew and sexual size dimorphism compared to species with small leks. With different arguments, Beehler and Foster (1988) also predicted lek size to be a positive function of mating skew. Contrary to this, it has been argued that mating skew should decrease as lek size increases (Alatalo et al. 1992, Widemo and Owens 1995) due to e.g. disturbance of copulations, or larger set of acceptable males on larger leks.

Variation in leks and its consequences for sexual selection have been studied mainly in the intraspecific context. In this paper I examine whether there exists general, interspecific relationships between lek size and structure, male mating skew, and sexual dimorphism by comparative methods. Mating skew and its measurement is a topic under recent debate (Keller and Vargo 1993, Widemo and Owens 1995, Mackenzie et al. 1995), and while using different approaches in my analyses I will examine if the results are dependent on the way of measurement. I also try to estimate the extent to which the existing patterns reflect historical constraints rather than adaptive plasticity (Prum 1994). I seek answer for this question by analyzing if and how much of the variation is explained by the membership of higher taxa considered as monophyletic (orders and families).

METHODS

The Material

Of the 9000 bird species in the world, about one per cent are considered as lekking (Höglund and Alatalo 1995), and detailed descriptions are available for only a fraction of these. This analysis is based on 38 species that breed either on classical leks (arenas) or on dispersed/exploded leks (Table 1.). However, information on all aspects of leks was not found for all species. The species belong to five orders and 12 families, applying the taxonomic divisions of Howard and Moore (1991).

Lek Characteristics

I obtained data on lek size (as the number of attending males) and spatial structure (as the distance between nearest neighbouring males) from original publications and in some cases, from Cramp and Simmons (1980, 1983). If mean lek sizes or nearest neighbour distances of a species were not given, I calculated them when data allowed, or used multiple sources when available. It is notable that within species, the variation in e.g. lek size was pronounced, but it was reduced into one average value, which I hoped was presentative for the species in question (Table 1.). Data on lek sizes were available for 37 species. Information on lek size were missing mainly for exploded or dispersed leks. In some papers distances between nearest males were not given, but instead, sizes of the male territories were indicated. In these cases I calculated the distance between the centers of two adjacent territories of average size, assuming that the territories are round-shaped. In the case of species that cooperatively display on courts (e.g. manakins of genus Chiroxiphia, e.g. Foster 1977, 1981, Prum 1994), I estimated the nearest neighbour distance by dividing the court area by the mean number of males that occupy a court.

Body mass and sexual dimorphism

Data on body mass were obtained from original publications or from Dunning (1992). If body masses were given separately for different sexes, their mean was used as a value for a given species. In such cases it was also possible to calculate the magnitude of sexual dimorphism. Because of the positive allometry between body mass and dimorphism, I calculated the residuals of the slope of female mass-male mass (Ranta et al. 1994). Body masses were also used for allowing for a relationship between male-male distance and body size. Nearest neighbour distance was regressed against body mass, and the residuals were used for further analyses. In both of the above cases, the residuals were roughly normally distributed.

Male mating skew

Data on the distribution of mating success in terms of copulations was available for 18 species. The distribution of mating success was either given for a single lek, separately for different leks/lek-years, or occasionally, pooled across leks (e.g. Andersson 1989). When mating skew could be estimated for different leks (or from different sources), their mean was used in the analysis. Following Keller and Vargo (1993), I calculated the ratio of the observed skew to maximum possible skew, "KV". In this index, unity means extreme skew while zero indicates equal distribution of matings among males. However, this index may have some unwanted properties (Mackenzie et al. 1995). Because of the possible biases in skew particularly on small leks, I used additionally the proportion of copulations achieved by the top 20% of males of all copulations ("A", Alatalo et al. 1992), which should be unbiased measure of the mating inequality. In the results, correlations based on both indices are reported.

Phylogenetic analyses

The fact that different species share a common ancestor prevents one from treating them as independent data points (e.g. Harvey and Pagel 1991). Therefore, the part of the variation which is due to phylogeny has to be removed from the total variation in the variables in question. The independent comparisons method (Felsenstein 1985, Harvey and Pagel, 1991) is an effective way to use all information available in hierarchical taxonomical levels. I assumed the punctuated equilibrium model of evolution, and thus, I ignored differences in branch lengths in these analyses. I used the phylogenetic tree of Höglund and Sillén-Tullberg (1994) based on Sibley and Ahlquist (1990) to find taxon pairs for comparison. Despite incomplete phylogeny at lower levels (genera) of the hierarchy, it was possible to construct a bifurcating tree, because even in genera with unsolved phylogeny data were typically available for two species at most only, which formed the pair for comparison. When testing specific predictions I correlated (Spearman rank correlation) the contrasts of two variables to each other. Additionally, I counted the numbers of negative versus positive comparisons and tested them with Sign test.

I also tested to which extent the variation in male mating skew, lek size, lek structure (inter-male distances) and sexual dimorphism was explained by phylogeny. This was done by performing ANOVAs across families and orders. I only took into account taxa that included at least two species with information available (four orders and eight families). Furthermore, I correlated the variables within families (Tetraonidae, and for one test also Pipridae) that included at least five species with appropriate data available to examine if any trends exist among lineages. In these comparisons, phylogeny was not allowed for due to small sample sizes. Statistical tests were done with SPSS software, and all probability values are for two-tailed tests.

RESULTS

Lek characteristics and male mating skew

The contrasts between inter-male distance and male mating skew did not show a predicted negative association (Fig. 1a, KV: $r_s=-0.17$, n=18, NS, A: $r_s=0.04$, n=18, NS). There were equal amounts of positive and negative contrasts. Likewise, there was no significant association between lek size and male mating skew (Fig. 1b, KV: $r_s=0.05$, n=16, NS, A: $r_s=0.18$, n=16, NS), and the number of positive versus negative contrasts did not deviate from random expectation, either. Thus, the observed skew in male mating success did not seem to be related either to the degree of male clustering or the number of males on lek. This was also the case among manakins (Pipridae), where no association between lek size and mating skew existed (KV: $r_s=0.2$, n=5, $p>0.1$). However, within Tetraonidae, there was a significant positive correlation between these characters (KV: $r_s=0.90$, n=5, $p<0.05$).

Lek characteristics and sexual size dimorphism

There was a trend, though non-significant, of sexual dimorphism in body mass to increase with the distance between males (Fig. 2a, $r_s=0.39$, n=13, NS). In addition, the number of positive contrasts tended to be greater than expected (10 positive versus 3 negative contrasts, Sign test: p=0.092), which suggests that there might exist a positive relationship between these attributes. Thus, species with tightly clustered males seem to be less dimorphic than species with dispersed leks. Size dimorphism was not related to lek size (Fig. 2b, $r_s=0.07$, n=14, NS), and positive and negative contrasts were represented equally (9 versus 5, Sign test: NS). In grouse, there was no association between sexual dimorphism and either of the two lek characters.

Sexual dimorphism and male mating skew

As predicted, there was a positive trend between male mating skew (as measured with both indices) and sexual dimorphism, suggesting that species with highly unequal distribution of matings among males are also most dimorphic. The relationship was, however, non-significant (Fig. 3, KV: $r_s=0.42$, n=10, NS, A: $r_s=0.32$, n=10, NS), and positive and negative contrasts were presented equally. The data from Tetraonids agree with the general finding of no significant association.

Phylogenetic sources of variation

At the family level, there was significant variation only in inter-male distance (Table 2, F=2.10, df=7, 35, $p<0.05$). Family membership explained 37 % of the variation in lek structure. This indicates that male dispersion patterns were more similar within families than randomly expected. Variation in all other variables (lek size, mating skew and dimorphism) was not attributable to phylogeny at this level, and only 12-29 % of the variation was explained by family membership. At higher level, only variation in ln-transformed lek size tended to occur between orders (Table 2, F=2.34, df=3, 30, $p<0.10$, 19 % of variation explained) while other variables showed more variation within orders. The proportion of variation explained by order membership varied between 2-20 %.

DISCUSSION

Contrary to the expectation, lek social organization in terms of inter-male distances was not related to the skew in male mating success. It seems that even if lek structure had an effect on mating patterns, other factors are far more important and contribute more to the variation. Simultaneously, the possibility of reversed causality is not supported: mating skew (indicative of the strength of selection) is not a significant factor affecting lek structure. One possible alternative would be that the intensity of male dominance competition and the risk of disturbance of copulations dictate the optimal distances between males (Foster 1983). Similarly, there was no association between mating skew and lek size, which leaves the prediction by Widemo and Owens (1995) without support. They found that mating skew was negatively correlated with lek size in the ruff (*Philomachus pugnax*), probably because of the inability of the top male to monopolize the females, and the resulting spillover of matings (but see Mackenzie et al. 1995). Also, in the black grouse (*Tetrao tetrix*) the distribution of matings was less pronounced on larger leks (Alatalo et al. 1992). However, this pattern does not seem to be general across different taxa.

Also, sexual size dimorphism was not related to the degree of male clustering or lek size, which gives additional support for Höglund's (1989) finding that lekking species are not more dimorphic than the non-lekking ones (see also Oakes 1992 and Höglund and Sillén-Tullberg 1994 for the discussion on the same topic). Even though sexual selection may be the most important reason behind large male size in relation to female size, other aspects than spatial organization of leks seem to be responsible for it. The male mating skew was not related to the degree of sexual size dimorphism, which seems to be in accordance with Björklund's (1990) study on dimorphism among polygynous and monogamous passerines. He found no size differences between the species exhibiting different mating systems (but see Webster 1992 for different results and conclusions). It is noteworthy, that the target traits of sexual selection need not always be related to body size. Even if they were, small size may be selected for, like in birds with flight display, where small size improves aerial agility (Andersson and Norberg 1981, Payne 1984).

One factor, which will weaken the correlations between lek properties, mating skew and sexual size dimorphism, if there are any, may be the heterogeneity of the data. Parameters regarding lek size and structure may be based on small samples, which produces confounding noise to the data set. Further, body mass shows large temporal fluctuation in most species, and therefore, may not be the best indicator of body size. In most studies, mating distributions were available for one lek only, and if these intensively studied leks were not typical for the species in question in some respect, the indices of mating skew (Table 1) may be misleading. The results were not dependent on the use of the two different indices. But, if the index by Keller and Vargo (1993) overestimates the skew on small leks, as suggested by Mackenzie et al. (1995), then the relationship between skew and lek size should turn to positive direction, when the other index (Alatalo et al. 1992) is used. Indeed, this was the case (Fig. 1b.), but the change was not strong enough to yield a significant correlation. After all, the two indices yielded very similar results, because they were strongly correlated to each other ($r_s=0.85$, $n=21$, $p<0.001$). Therefore, only "KV" was used in all of the figures and all of the tests in Table 2.

My analysis was performed across very different avian taxa, which may be separated by long evolutionary time. Perhaps the tests would be more powerful if they were done within monophyletic clades. Unfortunately the data were too few to allow proper within-clade analyses. A simple correlation among Tetraonidae suggests a positive relationship between lek size and mating skew, and trends of unknown direction may exist also within other lineages. When several groups with different lineage-specific trends are pooled into one analysis, the result may be a zero correlation. This could be proved with a more comprehensive data set.

Some understanding to the variation in male mating skew and body size dimorphism might be obtained if the lekking species were examined casewise. For instance, the behavioral performance at leks may set limits for a directional selection on body size, if the display consists of energy-demanding movements, as is the case for waders. Further, the mating skew in such species may be less extreme, if the top males get exhausted during the mating season, and matings are gained successively by several males. In large-bodied species, such as the capercaillie (Tetrao urogallus), the leks are characterized by rather stable spatial organization, which is based on dominance hierarchy of males. This allows male body size to increase further, and gives rise to the positive allometry between body size and size dimorphism. In peafowl (Pavo cristatus), the accumulation of mating success to particular males is probably partly prevented by females, who guard their mates by copulating repeatedly with him (Petrie et al. 1992). Very high values of mating skew in Chiroxiphia manakins are related to the rigid dominance-based cooperatively display system (Foster 1977, 1981, McDonald 1990), where one male dominates at each court at a time. Dominance hierarchy also seems to be the reason for the extreme skew in some other species. (e.g. capuchinbird, Perissocephalus tricolor, Trail 1990).

Finally, the large variation between different taxa does not necessarily form any general trend between the characters studied. Common phylogenetic history seemed to explain part of the variation in the lek structure, and perhaps, also in lek size. However, similarities among related species may not necessarily reflect only phylogenetic constraints, but also common selective environment, which has lead to similar adaptations (Pagel and Harvey 1988).

Analyses of intraspecific variation might shed more light on the evolution of leks, sexual selection and sexual dimorphism.

APPENDIX

Sources in Table 1: 1) Beck & Braun 1978, 2) Wiley 1973, 3) Alatalo et al. 1992, 4) Johnsgard 1983, 5) Catusse 1993), 6) Wegge & Rolstad 1986, 7) Hamerstrom & Hamerstrom 1960, 8) Ballard & Robel 1974, 9) Robel 1966, 10) Schroeder 1990, 11) Baydack 1988, 12) Landel 1989, 13) Moules & Boag 1981, 14) Rippin & Boag 1974, 15) Davison 1981, 16) Petrie et al. 1991, 17) Höglund et al. 1993, 18) Lank & Smith 1987, 19) Pruett-Jones 1988, 20) Höglund & Lundberg 1987, 21) Höglund & Robertson 1990, 22) Merton et al. 1984, 23) Snow 1973, 24) Stiles & Wolf 1979, 25) Snow 1974, 26) Snow 1977, 27) Wiley 1971, 28) Westcott 1993, 29) Schwartz & Snow 1978, 30) Robbins 1983, 31) Robbins 1985, 32) Snow 1963, 33) Théry 1992, 34) Lill 1976, 35) Skutch 1969, 36) Lill 1974a, 37) Lill 1974b, 38) McDonald 1990. 39) Foster 1981, 40) Trail & Koutnik 1986, 41) Snow 1970, 42) Snow 1972, 43) Stiles & Whitney 1983, 44) Brosset 1982), 45) Andersson 1989, 46) Andersson 1992, 47) Barnard & Markus 1989, 48) Shaw 1984, 49) Payne & Payne 1984, 50) Pruett-Jones & Pruett-Jones 1982, 51) Borgia 1985, 52) Pruett-Jones & Pruett-Jones 1990, 53) Pruett-Jones et al. 1990, 54) Beehler & Pruett-Jones 1983, 55) LeCroy et al. 1980, 56) Beehler 1983, 57) Pruett-Jones & Pruett-Jones 1986, 58) Dinsmore 1970, 59) Gilliard 1969, 60) Beehler 1988, 61) LeCroy 1981.

ACKNOWLEDGEMENTS

I would like to thank R. V. Alatalo and J. Höglund for helpful advice during the work, and E. Korpimäki for comments on the manuscript. H. Högmander and J. Merilä provided valuable information. Financially I was supported by the Academy of Finland.

REFERENCES

Alatalo, R. V., Höglund, J., Lundberg, A. & Sutherland, W. J. 1992: Evolution of black grouse leks: female preferences benefit males in larger leks. Behav. Ecol. 3: 53-59.

Andersson, M. 1994: Sexual selection. Princeton University Press, Princeton.

Andersson, M. & Norberg, Å. 1981: Evolution of reversed sexual size dimorphismand role partitioning among predatory birds, with a size scaling flight performance. Biol. J. Linn. Soc. 15: 105-130.

Andersson, S. 1989: Sexual selection and cues for female choice in leks of Jackson's widowbird Euplectes jacksoni. Behav. Ecol. Sociobiol. 25: 403-410.

Andersson, S. 1992: Lek mating and sexual selection in Jackson's widowbird Euplectes jacksoni. PhD Thesis, University of Göteborg, Göteborg.

Ballard, W. B. & Robel, R. J. 1974: Reproductive importance of dominant male greater prairie chickens. Auk 91: 75-85.

Barnard, P. & Markus, M. B. 1989: Male copulation frequency and female competition for fertilizations in a promiscuous brood parasite, the pin-tailed whydah Vidua macroura. Ibis 131: 421-425.

Baydack, R. K. 1988: Characteristics of sharp-tailed grouse (Tympanuchus phasianellus) leks in the parklands of Manitoba. Can. Field-Nat. 102: 39-44.

Beck, T. D. I. & Braun, C. E. 1978: Weights of Colorado sage grouse. Condor 80: 241-243.

Beehler, B. M. 1983: Lek behavior of the lesser bird of paradise. Auk 100: 992-995.

Beehler, B. M. 1988: Lek behavior of the raggiana bird of paradise. Nat. Geogr. Res. 4: 343-358.

Beehler, B. M. & Foster, M. S. 1988: Hotshots, hotspots, and female preferences in the organization of lek mating systems. Am. Nat. 131: 203-219.

Beehler, B. M. & Pruett-Jones, S. G. 1983: Display dispersion and diet of birds of paradise: a comparison of nine species. Behav. Ecol. Sociobiol. 13: 229-238.

Björklund, M. 1990: A phylogenetic interpretation of sexual dimorphism in body size and ornament in relation to mating system in birds. J. Evol. Biol. 3: 171-183.

Borgia, G. 1985: Bower quality, number of decorations and mating success of male satin bowerbirds (Ptilonorhyncus violaceus): an experimental analysis. Anim. Behav. 33: 266-271.

Bradbury, J. W. & Gibson, R. M. 1983: Leks and mate choice. In Mate choice (ed. P. Bateson), pp. 109-138. Cambridge University Press, Cambridge.

Brosset, A. 1982: The social life of the African forest yellow-whiskered greenbul Andropadus latirostris. Z. Tierpsychol. 60: 239-255.

Catusse, M. 1993: Spatial and temporal plasticity of a capercaillie (Tetrao urogallus) arena in the French Pyrenees. Ethol. Ecol. Evol. 5: 145-156.

Cramp, S. & Simmons, K. E. L. 1980, 1983: Handbook of the birds of Europe, the Middle East and North Africa. Vols. 2 & 3. Oxford University Press, Oxford.

Darwin, C. 1871: The descent of man, and selection in relation to sex. Murray, London.

Davison, G. W. H. 1981: Sexual selection and the mating system of Argusianus argus (Aves: Phasianidae). Biol. J. Linn. Soc. 15: 91-104.

Dinsmore, J. J. 1970: Courtship behavior of thegreater bird of paradise. Auk 87: 305-321.

Dunning, J. B. 1992: Handbook of avian body masses. CRC Press, U. S. A.

Felsenstein, J. 1985: Phylogenies and the comparative method. Am. Nat. 125: 1-15.

Foster, M. S. 1977: Odd couples in manakins: a study of social organization and cooperative breeding in Chiroxiphia linearis. Am. Nat. 111: 845-853.

Foster, M. S. 1981: Cooperative behaviour and social organization of the swallow-tailed manakin (Chiroxiphia caudata). Behav. Ecol. Sociobiol. 9: 167-177.

Foster, M. S. 1983: Dispersion, disruption, and dominance in lek-breeding birds. Am. Nat. 122: 53-72.

Gilliard, E. T. 1969: Birds of paradise and bowerbirds. Natural History Press, New York.

Hamerstrom, F. N., Jr. & Hamerstrom, F. 1960: Comparability of some social displays of grouse. Proc. 12th Int. Orn. Congr., 274-293.

Harvey, P. H. & Pagel, M. D. 1991: The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hogan-Warburg, A. J. 1966: Social behaviour of the ruff, Philomachus pugnax (L.). Ardea 54: 109-229.

Howard, R. & Moore, A. 1991: A complete checklist of the birds of the world, 2nd ed. Academic Press, London.

Höglund, J. 1989: Size and plumage dimorphism in lek-breeding birds: a comparative analysis. Am. Nat. 134: 72-87.

Höglund, J. & Alatalo, R. V. 1995: Leks. Princeton University Press, Princeton.

Höglund, J. & Lundberg, A. 1987: Sexual selection in a monomorphic lek-breeding bird: correlates of male mating success in the great snipe Gallinago media. Behav. Ecol. Sociobiol. 21: 211-216.

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.

Höglund, J. & Sillén-Tullberg, B. 1994: Does lekking promote the evolution of male-biased size dimorphism in birds? On the use of comparative approaches. Am. Nat. 144: 881-889.

Höglund, J., Montgomerie, R. & Widemo, F. 1993: Costs and consequences of variation in the size of ruff leks. Behav. Ecol. Sociobiol. 32: 31-39.

Johnsgard, P. A. 1983: The grouse of the world. Croom Helm, Kent.

Keller, L. & Vargo, E. L. 1993: Reproductive strategies and reproductive roles in colonies of eusocial insects. In: Queen number and sociality in insects (ed. Keller, L.), pp. 16-44. Oxford University Press, Oxford.

Landel, H. 1989: A study of female and male mating behavior and female mate choice in the sharp-tailed grouse Tympanuchus phasianellus. PhD. Thesis, Purdue University, West Lafayette.

Lank, D. B. & Smith, C. M. 1987: Conditional lekking in the ruff (Philomachus pugnax). Behav. Ecol. Sociobiol. 20: 137-145.

LeCroy, M. 1981: The genus Paradisaea: display and evolution. Am. Mus. Nat. Hist. Novit. 2714: 1-52.

LeCroy, M., Kulupi, A. & Peckover, W. S. 1980: Goldie's bird of paradise: display, natural history and traditional relationships of the people to the bird. Wilson Bull. 92: 289-301.

Lill, A. 1974a: Sexual behavior in the lek-forming white-bearded manakin, M. manacus trinitatis Hartert. Z. Tierpsychol. 36: 1-36.

Lill, A. 1974b: Social organization and space utilization in the lek-forming white-bearded manakin, M. manacus trinitatis. Z. Tierpsychol. 36: 513-530.

Lill, A. 1976: Lek behavior in the golden-headed manakin, Pipra erythrocephala in Trinidad (West Indies). Z. Tierpsychol. Suppl. 18: 1-84.

Mackenzie, A., Reynolds, J. D. & Sutherland, W. J. 1995: Measuring sexual selection. Nature 376: 471.

McDonald, D. B. 1990: Correlates of male mating success in a lekking bird with male-male cooperation. Anim. Behav. 37: 1007-1022.

Merton, D. V., Morris, R. V. & Atkinson, I. A. E. 1984: Lek behaviour in a parrot: the kakapo, Strigops habroptilus, of New Zealand. Ibis: 126: 277-283.

Moyles, D. L. J. & Boag, D. A. 1981: Where, when and how male sharp-tailed grouse establish territories on arenas. Can. J. Zool. 59: 1576-1581.

Nefdt, R. J. C. 1995: Disruptions of matings, harassment and lek-breeding in Kafue lechwe antelope. Anim. Behav. 49: 419-429.

Oakes, E. J. 1992: Lekking and the evolution of sexual dimorphism in birds: comparative approaches. Am. Nat. 140: 665-684.

Pagel, M. D. & Harvey, P. H. 1988: Recent developments in the analysis of comparative data. Q. Rev. Biol. 63: 413-440.

Payne, R. B. 1984: Sexual selection, lek and arena behaviour, and sexual size dimorphism in birds. Ornithol. Monogr. 33: 1-52.

Payne, R. B. & Payne, K. 1977: Social organization and mating success in local song populations of village indigobirds, Vidua calybeata. Z. Tierpsychol. 45: 113-173.

Petrie, M., Hall, M., Halliday, T., Budgey, H. & Pierpoint, C. 1992: Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male more than once? Behav. Ecol. Sociobiol. 31: 349-358.

Petrie, M., Halliday, T. & Sanders, C. 1991: Peahens prefer peacocks with elaborate trains. Anim. Behav. 41: 323-332.

Pruett-Jones, M. A. & Pruett-Jones, S. G. 1982: Spacing and distribution of bowers in Macgregor's bowerbird (Amblyornis macgregoriae). Behav. Ecol. Sociobiol. 11: 25-32.

Pruett-Jones, S. G. 1988: Lekking versus solitary display: temporal variations in dispersion in the buff-breasted sandpiper. Anim. Behav. 36: 1740-1752.

Pruett-Jones, S. G. & Pruett-Jones, M. A. 1986: Altitudinal distribution and seasonal activity patterns of birds of paradise. Nat. Geogr. Res. 2: 87-105.

Pruett-Jones, S. G. & Pruett-Jones, M. A. 1990: Sexual selection through female choice in Lawe's parotia, a lek-mating bird of paradise. Evolution 44: 486-501.

Pruett-Jones, S. G., Pruett-Jones, M. A. & Jones, H. I. 1990: Parasites and sexual selection in birds of paradise. Am. Zool. 30: 287-298.

Prum, R. O. 1994: Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). Evolution 48: 1657-1675.

Ranta, E., Laurila, A. & Elmberg. J. 1994: Reinventing the wheel: analysis of sexual dimorphism in body size. Oikos 70: 313-321.

Rippin, A. P. & Boag, D. A. 1974: Spatial organization among male sharp-tailed grouse on arenas. Can. J. Zool. 52: 591-597.

Robbins, M. B. 1983: The display repertoire of the band-tailed manakin (Pipra fasciicauda). Wilson Bull. 95: 321-504.

Robbins, M. B. 1985: Social organization of the band-tailed manakin (Pipra fasciicauda). Condor 87: 449-456.

Robel, R. J. 1966: Booming, territory size and mating success of the greater prairie chicken (Tympanuchus cupido pinnatus). Anim. Behav. 14: 328-331.

Schroeder, M. A. 1990: Movement and dispersion of greater prairie-chickens in northeastern Colorado. PhD Thesis, Colorado State University, Fort Collins.

Schwartz, P. & Snow, D. W. 1978: Display and related behaviour of the wire-tailed manakin. Living Bird 17: 51-78.

Scott, J. A. 1942: Mating behaviour of the sage grouse. Auk 59: 477-498.

Shaw, P. 1984: The social behavior of the pin-tailed whydah Vidua macroura in northerh Ghana. Ibis 126: 463-473.

Sibley, C. G.& Ahlquist, J. E. 1990: Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven.

Skutch, A. F. 1969: Life histories of Central American birds III. Pacific Coast Avifauna 35.

Snow, B. K. 1970: A field study of the bearded bellbird in Trinidad. Ibis 112: 299-329.

Snow, B. K. 1972: A field study of the calfbird, Perissocephalus tricolor. Ibis 114: 139-162.

Snow, B. K. 1973: The behaviour and ecology of hermit hummingbirds in the Kanaku mountains, Guyana. Wilson Bull. 85: 163-177.

Snow, B. K. 1974: Lek behaviour and breeding of Guy's hermit hummingbird Phaethornis guy. Ibis 116: 278-297.

Snow, B. K. 1977: Comparison of the leks of Guy's hermit hummingbird Phaethornis guy in Costa Rica and Trinidad. Ibis 119: 211-214.

Snow, D. W. 1963: The display of the orange-headed manakin. Condor 65: 44-48.

Stiles, F. G. & Whitney, B. 1983: Notes on the behavior of the Costa Rican sharpbill (Oxyruncus cristatus frater). Auk 100: 117-125.

Stiles, F. G. & Wolf, L. L. 1979: Ecology and evolution of lek mating behaviour in the long-tailed hermit hummingbird. Orn. Monogr. 27: 1-77.

Théry, M. 1992: The evolution of leks through female choice: differential clustering and space utilization in siz sympatric manakins. Behav. Ecol. Sociobiol. 30: 227-237.

Trail, P. W. 1985: Courtship disruption modifies mate choice in a lek-breeding bird. Science 227: 778-780.

Trail, P. W. 1990: Why should lek-breeders be monomorphic? Evolution 44: 1837-1852.

Trail, P. W. & Koutnik, D. L. 1986: Courtship disruption at the lek in the Guianan cock-of-the-rock. Ethology 73: 197-213.

Wade, M. J. & Pruett-Jones, S. G. 1990: Female copying increases the variance in male mating success. Proc. Nat. Acad. Sci. USA 87: 5749-5753.

Webster, M. S. 1992: Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). Evolution 46: 1621-1641.

Wegge, P. & Rolstad, J. 1986: Size and spacing of capercaillie leks in relation to social behaviour and habitat. Behav. Ecol. Sociobiol. 19: 401-408.

Westcott, D. 1993: Habitat characteristics of lek sites and their availability for the ochre-bellied flycatcher, Mionectes oleagineus. Biotropica 25: 444-451.

Widemo, F. & Owens, I. P. F. 1995: Lek size, male mating skew, and the evolution of lekking. Nature 373: 148-151.

Wiley, R. H. 1971: Song groups in a singing assembly of little hermits. Condor 73: 28-35.

Wiley, R. H. 1973: Territoriality and non-random mating in sage grouse, Centrocercus urophasianus. Anim. Behav. Monogr. 6: 87-169.

Wiley, R. H. 1991: Lekking in birds and mammals: behavioural and evolutionary issues. Adv. Study Behav. 20: 201-291.

Table 1. Summary of the species and variables used in the comparison. The classification follows Howard and Moore (1991) and Prum (1992). Each value is assumed to roughly estimate the mean value of the characters. Lek size expresses the mean number of attending males. Inter-male distance is an average distance between two nearest neighbouring males. Mating skew describes the skewness in mating success among males: index "A" is the proportion of matings obtained by the top 20 % of males (Alatalo et al. 1992), while "KV" is based on the formula by Keller and Vargo (1993, see also Widemo and Owens 1995). Values of dimorphism are residuals from a regression of male body mass on female body mass (see Ranta et al. 1994).

	Lek size	Inter-male distance (m)	Mating skew "A"	Mating skew "KV"	Dimorphism	Sources
Phasianidae						
Centrocercus urophasianus	45	7	1.00	0.920	1.14	1-2
Tetrao tetrix	13	11	0.81	0.653	-0.26	3
T. mlokosiewiczi	10	-	-	-	-	4
T. urogallus	12	165	-	-	1.91	5-6
Tympanuchus cupido	11	12	0.75	0.880	-0.63	7-10
T. phasianellus	11	10	0.94	0.811	-1.19	11-14
Argusianus argus	-	375	-	-	-0.80	15
Pavo cristatus	10	9	0.54	0.273	-0.35	16
Scolopacidae						
Philomachus pugnax	6	1.3	0.65	0.714	1.45	17-18
Tryngites subruficollis	7	38	0.71	0.698	-	19
Gallinago media	13	11	0.56	0.557	-2.56	20-21
Psittacidae						
Strigops habroptilus	50	100	-	-	0.30	22
Trochilidae						
Phaethornis superciliosus	15	9	-	-	-0.31	23-24
P. guy	10	16	-	-	-	25-26
P. ruber	36	-	-	-	-	23
P. longuemareus	19	11	-	-	-	27
Tyrannidae						
Mionectes oleaginus	3	30	-	-	-	28

Pipridae						
P. fulicauda	-	25	-	-	-	29
P. fascicauda	21	6	-	-	-	30-31
P. aureola	3	35	-	-	-	32
P. pipra	3	30	-	-	-	33
P. erythrocephala	10	5	0.34	0.285	-	33-34
Lepidothrix serena	6	6	-	-	-	33
L. coronata	5	29	-	-	-	35
Manacus manacus	8	2.2	0.86	0.711	-	33, 36-37
Chiroxiphia linearis	-	18	1.00	0.975	-0.13	38
C. caudata	5	80	0.76	0.700	-	39
Corapipo gutturalis	7	33	1.00	1.000	-	33
Cotingidae						
Rupicola rupicola	55	1.5	0.88	0.598	-	40
Procnias averano	4	180	-	-	-	41
Perissocephalus tricolor	8	6	1.00	1.000	-0.87	42
Oxyruncidae						
Oxyruncus cristatus	-	150	-	-	-	43
Pycnonotidae						
Pycnonotus latirostris	20	15	-	-	-	44
Ploceidae						
Euplectes jacksoni	15	205	0.74	0.629	0.49	45-46
Vidua macroura	-	100	0.80	0.746	-	47-48
V. chalybeata	-	300	0.95	0.709	-	49
Ptilonorhyncidae						
Amblyornis mcgregoriae	-	170	-	-	-	50
Ptilonorhyncus violaceus	-	-	0.63	0.532	-	51
Paradisaeidae						
Parotia lawesii	20	60	0.87	0.736	-	52-53
Cicinnurus regius	2	64	-	-	-	54
Paradisaea decora	9	2.5	-	-	-	55
P. minor	-	-	0.98	0.963	0.88	56
P. rudolphi	-	310	-	-	-	57

P. apoda	-	64	-	-	-	58
P. raggiana	4	10	-	-	0.80	54, 59-60
P. rubra	10	-	-	-	-0.02	61

Table 2. Effects of order and family levels on the variation in lek size (ln-transformed), inter-male distance (body size-corrected), sexual dimorphism (body size-corrected) and mating skew ("KV").

		Order			Family	
	F	df	P	F	df	P
Lek size	2.34	3, 33	0.093	1.63	6, 31	0.180
Inter-male distance	1.47	3, 38	0.239	2.10	7, 35	0.049
Dimorphism	0.21	3, 15	0.889	0.25	6, 15	0.950
Mating skew "KV"	0.20	2, 19	0.823	0.29	6, 19	0.930

Legends to figures:

Fig. 1. a) The contrasts between male mating skew, as measured by the index of Keller and Vargo (1993, "KV"), and body size-corrected inter-male distance on leks.

b) The contrasts between male mating skew, as measured by both "KV" (filled circles, solid line) and "A" (Alatalo et al. 1992, open circles, dashed line), and ln-transformed lek size.

Fig. 2. a) The contrasts between sexual dimorphism in body size (residuals from male body mass-female body mass-regression, Ranta et al. 1994) and body size-corrected inter-male distance on leks.

b) The contrasts between sexual body size dimorphism and ln-transformed lek size.

Fig. 3. The contrasts between sexual size dimorphism and male mating skew ("KV").

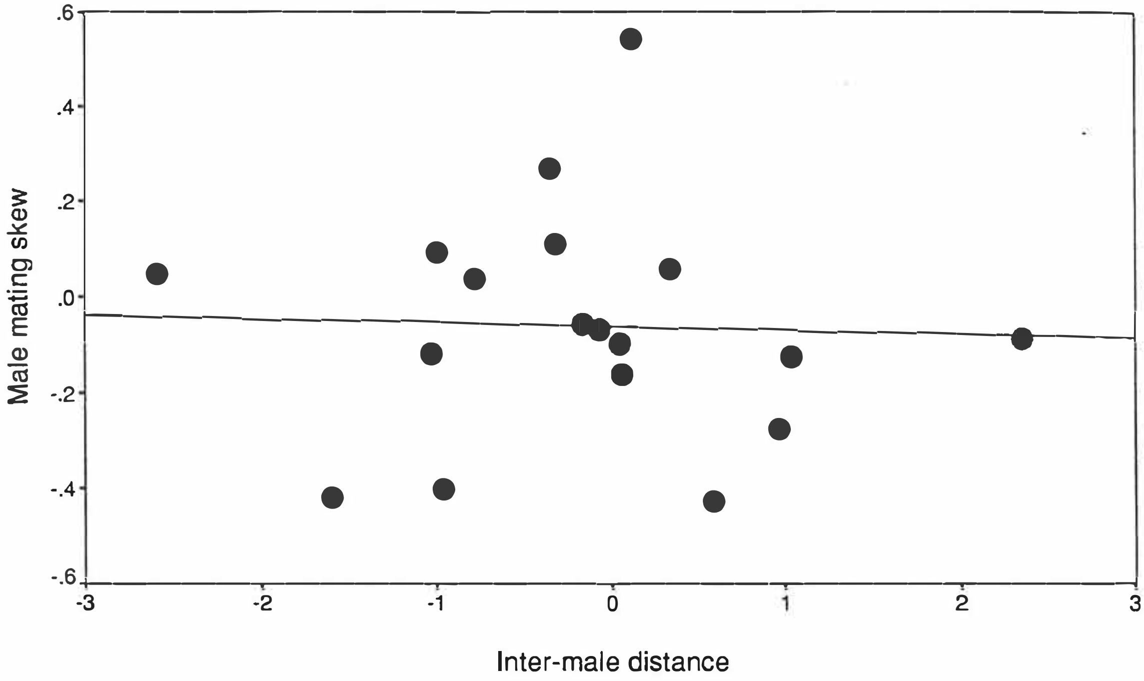

Fig. 1a.

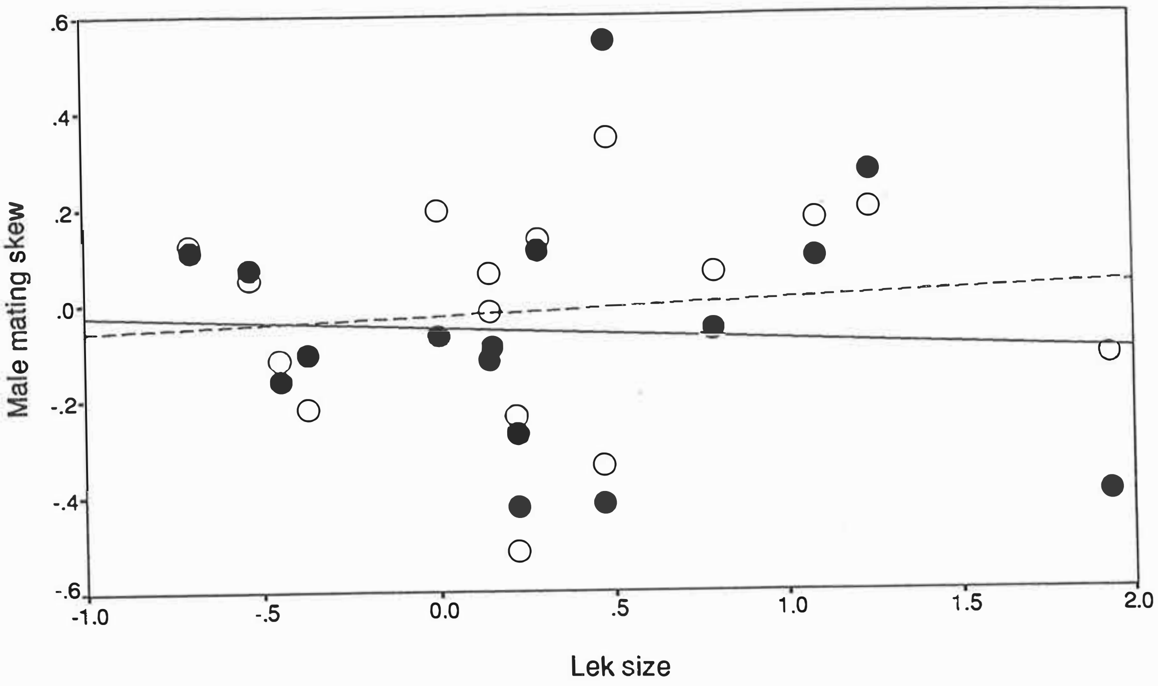

Fig. 1b.

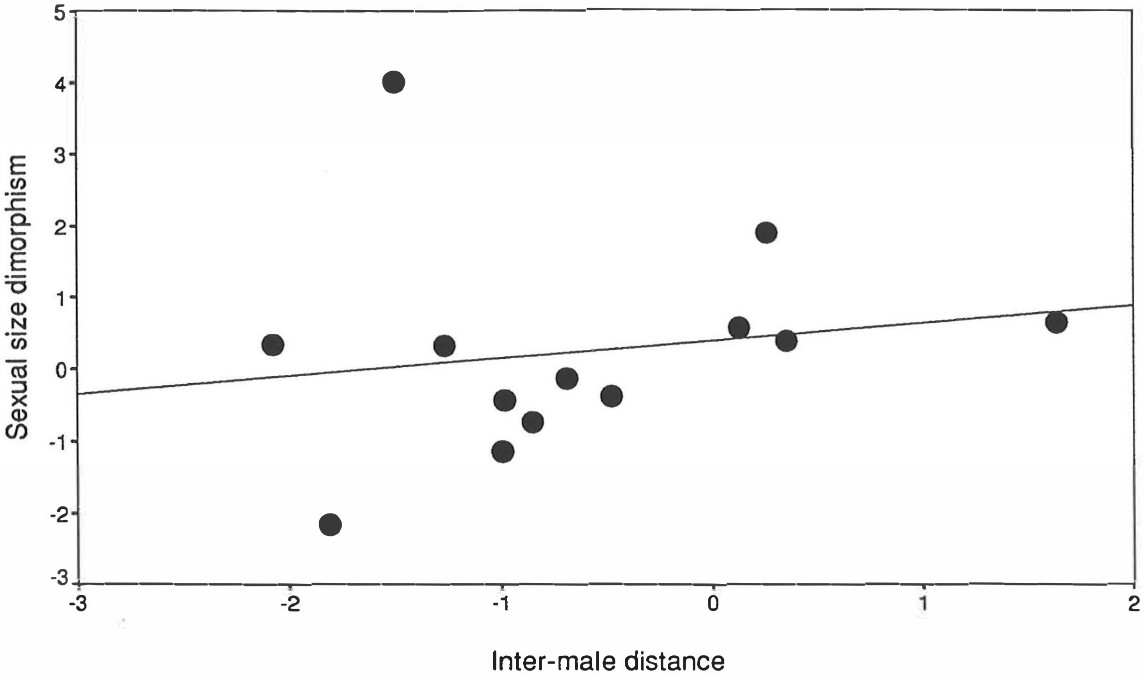
Sexual size dimorphism
5
4
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
Inter-male distance

Fig. 2a.

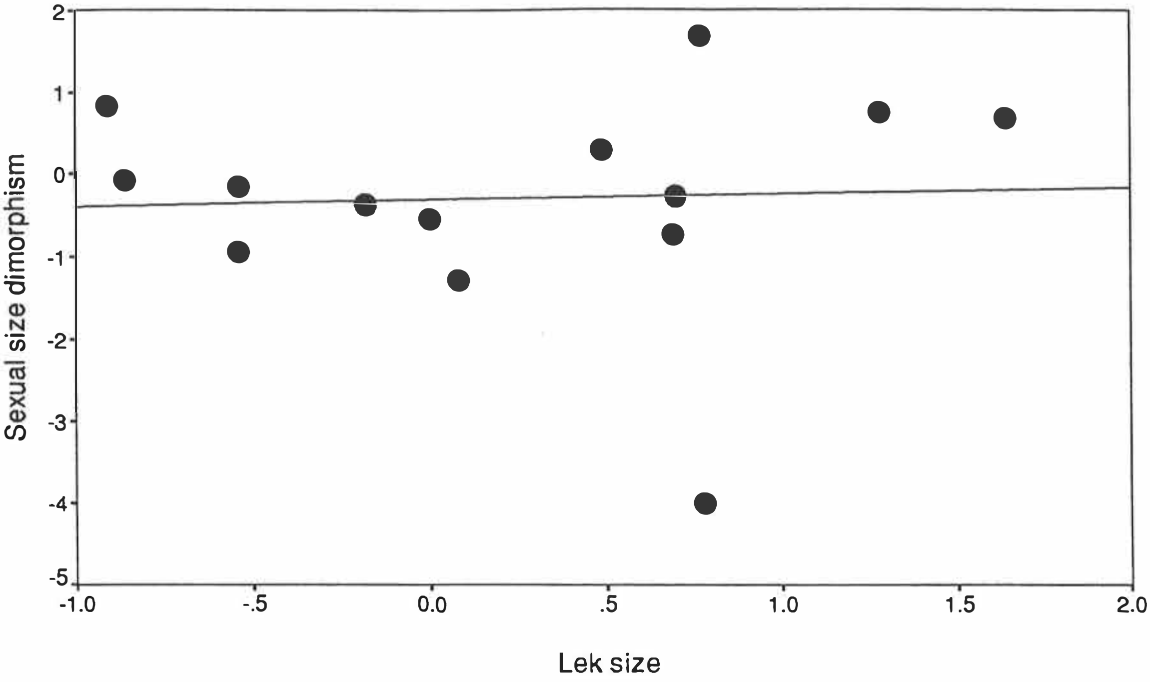

Fig. 2b.

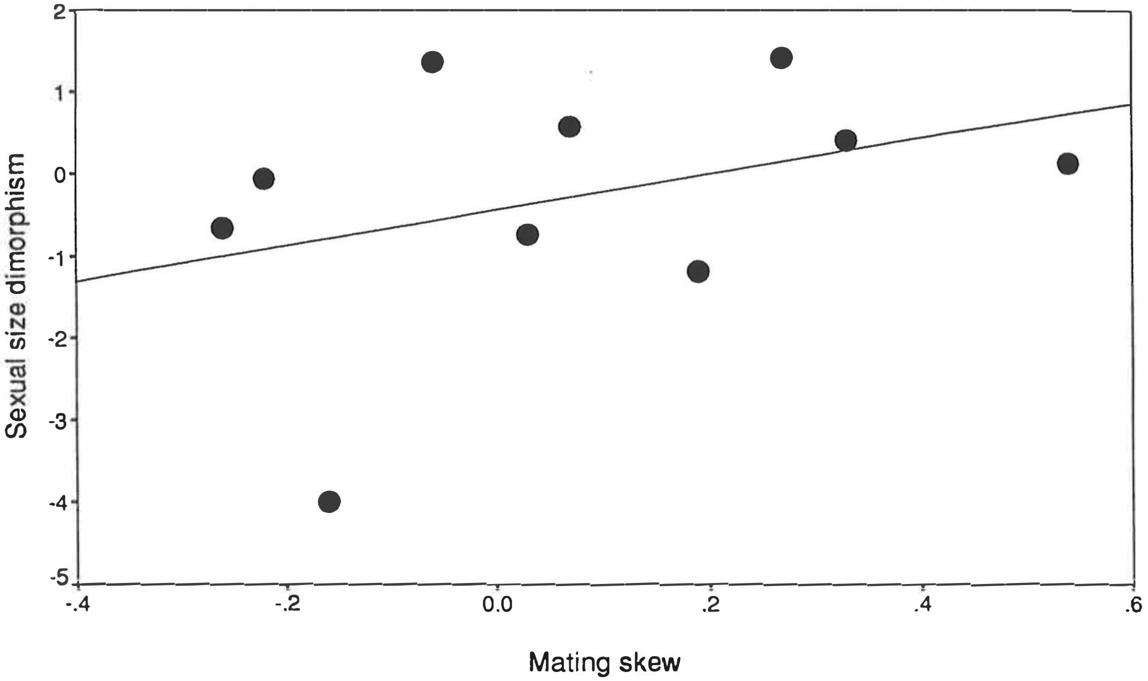

Fig. 3.