Correlates of male mating success on black grouse (*Tetrao tetrix* L.) leks

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Sexual selection in black grouse was studied through multivariate analyses of possible correlates of mating success using data from an eight year study of 10 different leks. Body size was weakly correlated with mating status (0 or ≥ 1 mating) and tail length was significantly correlated with mating success (total number of copulations) even after controlling for the effects of age and body size. Among several behavioural variables, having a high attendance, being more active and having the tail lyre-feathers erected more often were significantly related to high mating success also when age and the other factors were controlled for. In addition, there were strong relationship between a combined measure of territorial centrality and territory size and their interaction such that males that held relatively large central territories had higher mating success. Males that spent more time rookooing (display) had lower mating success. This last somewhat counter-intuitive result could be explained by a significant interaction between rookoo and centrality; central and successful males were engaged in more interactions with neighbours, and therefore were not allowed to display as often as peripheral unsuccessful males. Display activity indeed turned out to be a significant factor of mating success when we controlled for territory position. All of the significant variables are likely to reflect male motivation and/or competence. The results thus indicate that successful males are signified by being healthy, active and capable to defend relatively large central territories on the leks. We conclude that sexual selection in black grouse is most likely mediated both by male-male competition and female preference.

Introduction

Sexual selection was defined by Darwin (1871) as "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction". During the last decades the study of sexual selection has recieved considerable attention and numerous field studies have been devoted to study sexual selection in the wild (*see* Bradbury & Andersson 1987, Andersson 1994). One commonly addressed topic in these studies is: which traits correlates with male mating success in wild populations? If any particular trait can be shown to covary with mating success, such a trait is a likely target for sexual selection and may thus show micro-evolutionary response if heritable. Traits that are believed to have evolved through sexual selection are often called secondary sexual traits or ornaments.

Lekking is a mating system where displaying males form aggregations (called leks) which females visit primarily to mate. This makes lekking species highly amenable for studies of sexual selection since large data sets relating male traits to mating success can be collected with relative ease. A typical feature of leks is the high variance in male mating success (e.g., Kruijt & de Vos 1988, Wiley 1991, Höglund & Alatalo 1995). However, so far sexual selection studies have largely concentrated on identification and experimental verification of female choice on a single male secondary sexual trait. In reality, several traits may be under selection simultaneously, and it has been suggested that sexual selection is likely to involve one strongly favoured male "handicap" trait together with several weakly favoured Fisherian traits (Pomiankowski 1987, Møller & Pomiankowski 1993).

Male mating success on vertebrate leks has been found to be related to traits such as morphological ornaments (Andersson 1989, Höglund *et al*. 1990, Petrie *et al*. 1991, Pruett-Jones & Pruett-Jones 1991) and spectral call parameters (Ryan 1980, Kruijt & de Vos 1988, Robertson 1990, Gibson *et al*. 1991, Fiske *et al*. 1994, Fiske *et al*. 1998). In many cases, successful males are behaviourally active in terms of display rate (Sullivan 1983, Gibson & Bradbury 1985, Höglund & Lundberg 1987, Clutton-Brock *et al*. 1988, Andersson 1989, McDonald 1989, Pruett-Jones & Pruett-Jones 1991) and attendance at the lek (Lank & Smith 1987, Apollonio *et al*. 1989, Hill 1991, Fiske *et al*. 1994, Fiske *et al*. 1998). A third set of factors that may be related to male mating success are territorial features such as micro-habitat (Shelly 1987, Deutsch & Nefdt 1992, Deutsch & Weeks 1992) and centrality of the territory (Clutton-Brock *et al*. 1988, Kruijt & de Vos 1988, Gosling & Petrie 1990, Gratson *et al*. 1991, van Rhijn 1991, Fiske *et al*. 1994, Hovi *et al*. 1994, Rintamäki *et al*. 1995a, Fiske *et al*. 1998). It has also been shown that male mating success may vary because of stochastic events such as variation in mean male mating success among leks (Mackenzie *et al*. 1995).

Studies of correlates of male mating success in lekking species have used Spearman and Pearson correlations (Apollonio *et al*. 1989), multiple regression (Hill 1991), and selection differentials and multiple regression (Fiske *et al*. 1994). While many factors related to male mating success have been identified, only few studies have enough large data sets to consider each of them simultaneously in multivariate analyses. Many of the more comprehensive studies suggest rather low degrees of explanation in the proposed multivariate model (Gibson & Bradbury 1985, Höglund & Lundberg 1987, Andersson 1989, Gosling & Petrie 1990). Furthermore, given the great variability in lek-systems with respect to the degree of male aggregation, the impact of resource proximity and the degree to which females are free to choose between males, it is not surprising that the relative importance of morphological, behavioural and territorial features seems to vary between species (Fiske *et al*. 1998).

We have studied several black grouse (*Tetrao tetrix*) leks over a period of eight years, which allows a particular potential for a detailed multivariate analysis. Previous studies on this species have suggested that vocal activity (Kruijt & de Vos 1988), centrality of territories (Kruijt & Hogan 1967, de Vos 1983, Kruijt & de Vos 1988, Hovi *et al*. 1994, Rintamäki *et al*. 1995a), male dominance (Alatalo *et al*. 1991) and the condition of tail ornaments (Höglund *et al*.

1994) are single factors that are related to the mating success. Furthermore, male mating success is positively associated with male viability (Alatalo *et al*. 1991) and also related to males' previous territory history (Kokko *et al*. 1998), attendance in the non-breeding season (Rintamäki *et al*. 1999), and lifetime lekking performance (Kokko *et al*. 1999). In this species, males lekking on larger leks on open bogs have rather strict territory boundaries, and therefore females are relatively free to choose any of the males for copulation (Rintamäki *et al*. 1995b). However, also male-male competition is likely to be a factor which is important for differences in male mating success. In this study, we will analyse to which degree male mating success is related to various aspects of morphology, behaviour and territorial features.

Material and methods

Study sites

The study was carried out during 1987–1994 in central Finland, where we annually followed one to ten leks. Lek size varied from 5 to 18 territorial males (mean = 8.0) thus representing medium sized or large lek in Finland. One lek was studied in all eight years, five in two to three years and others in one year (summarised in Table 1). In our analyses we did not use smaller leks (< 5 males), because for such we had very incomplete data.

Leks were situated both on bogs (*n* = 7) and lakes (*n* = 3). There is evidence that male territoriality varies depending on where the lek is situated (i.e., on a sphagnum bog or an ice-covered lake, Hovi *et al*. 1996). Despite this fact, we included all types of leks into the analyses because we want to express overall correlations from the leks observed. Still, our results are biased towards bog leks (*see* Table 1). Lek number one was situated in a nature reserve where shooting is prohibited. The main predators on adult black grouse are goshawks (*Accipiter gentilis*) and foxes (*Vulpes vulpes*). Shooting is an additional cause of mortality and can be high on non-reserved leks (Rintamäki *et al*. 1995b).

Male capture

We succeeded to catch a total of 225 different males from six leks (Table 1). Lek number one was studied in more detail, because it was situated at a winter feeding site and thus offered better conditions to catch the birds. This is why most birds were from this lek (78.2%). Birds were caught during winter or early April in walk-in-traps, feeding traps (baited with willow buds or oats) or, occasionally, by cannon netting. We have no indications that capturing influences male mating success or any other variable.

Males were aged (as yearlings or older according to Helminen 1963) and individually marked with one aluminium ring and two or three coloured rings on the legs. This allowed us to identify males at a distance. On leks where males remained uncaught we identified them by using individual plumage characteristics (black spots on the white under tail-coverts and plumage damages).

Morphological measurements

For each captured male we measured sternum-, tarsus-, wing- and lyre length and body mass. Sternum length (the keel of the breastbone from the anterior to the posterior tip) was measured to the nearest 1 mm and tarsus length (the distance

Table 1. Summary of the leks used in analyses during years 1987–1994. Beh = behavioural observations, Mor = morphological measurements and Ter = territorial observations. Leks 2–4 were lake leks.

Lek code	Study years	Average lek size	Beh	Mor	Ter	*n* males
1	8	14	8	8	8	176
2	1	7	1	–	–	–
3	2	5.5	2	–	–	–
4	2	6	2	–	–	–
12	3	8	2	2	3	13
13	3	10	2	3	3	25
14	1	7	1	1	1	1
16	1	10	–	–	1	–
19	3	8	2	2	3	7
20	1	5	1	1	1	3

from the heel to the extreme bending points of the toes thus including some of the tibiotarsal bone) to the nearest 0.1 mm with a calliper. Wing length was measured from the carpal joint to the tip of the longest primary (to the nearest 1 mm). Lyre was measured as the length of the longest outer tail feather from the base to the tip after flattening it. Body mass was measured with a Pesola spring balance to the closest 10 g.

Observations

Leks were observed from blinds (tents or small huts) erected close to lek sites. We observed the birds with the help of binoculars (8–12×) and telescopes (16–60×). On larger leks we used two to three observers to guarantee reliable observations; on smaller leks one person was capable of observing behaviours, movements and copulations. Observations were started before the males arrived at the lek-sites at dawn (0200–0400 hours) and stopped after male departure (0800–0900 hours).

Behavioural observations

Black grouse males are rather fearless when displaying, and we have no indications that the observations disturbed the birds. Most females mate within seven to ten days in each year (Alatalo *et al.* 1992). Copulation success of a male was scored as the number of females observed copulating with. Copulations are conspicuous because the male flutters it's wings in a typical manner when copulating. Most females (80%) copulate only once during the mating season and there is consistent correspondence between observed copulations and true parentage (Alatalo *et al.* 1996). Therefore it is unlikely that we have missed many copulations.

We observed each male's behaviour using a scan sampling scheme approximately every 5–20:th min. Behavioural observations included (a) *attendance* (percent scans when present on the lek, i.e. 100% = male was always seen on the lek), (b) *rookoo* (percent scans when a male was performing a stereotyped vocal display), (c) *fighting* (percent scans when a male was in-

volved in fighting), (d) *lyre posture* (value from 0–2 which describes whether males had folded (0), semi-folded (1) or erected (2) lyre feathers and the value entered in following analyses is the mean for each male of all scans), and (e) *passivity* (percent scans when a male was involved in one of the following behaviours: eating, sleeping, preening, or feeding).

Male behaviour was determined both in the absence and presence of females. On smaller leks, however, where female visits are scanty, observations where largely collected when females were not present. This is a way how data on lekking species have commonly been collected (*see* meta-analysis of Fiske *et al.* 1998).

Territorial features

Spatial variables were recorded simultaneously with the behavioural scan-samples. The position of each male on the lek-site during scan-sampling was determined by using a 10 × 10-meter grid system on each lek and positions were mapped to the closest 1 m on the grid. *Territory size* was determined for each male as the length in metres of the 25%–75% percentiles of all observations vertically and horizontally on the grid. We then summed both axes and divided by two to obtain an estimate of the diameter of the territory. This value, which was entered in subsequent analyses, is highly correlated with actual territory size ($r_s = 0.78$, $n = 105$, $p < 0.001$). We also calculated to what extent each male's territory was encircled by other males. This was done by counting the number of neighbours and determining the proportion of the territory encircled by others. *Distance* (meters) *to the lek centre* (median of the all mapped points), was calculated from each male's territory centre (median points).

Statistical analyses

For males that occurred in several years we chose the year where the data were most complete (or one year randomly if not decided by the first criterion) to avoid pseudoreplication (*see* e.g. Heffner *et al.* 1996). Thus each male is only

included once in the following analyses.

To reduce the number of variables to be included in the analyses, we combined the effects of morphology and body mass in to a composite variable. *Size* is the first principal component ($PC1_a$, Table 2) of the logged values for each of sternum-, tarsus-, and wing length and body mass. All these are highly intercorrelated and have positive eigenvalues. We also combined the effects of distance from the lek centre, no. of neighbours and circumference of territory encircled in a similar manner. In this case a high value of the first principal component means being close to the lek centre, having many neighbours and much of the territory circumference surrounded (Table 2). This variable will be referred to as *Territory*.

The data on copulation success and several other variables (territory size, attendance, and lyre posture) were not normally distributed. Furthermore, analyses of skewness and homoscedasity of the errors in linear regressions indicated violations of the assumptions for traditional linear regression. We have, therefore, analysed the data using generalised linear models with the package Genstat 5 (Genstat 5 Committee 1993). We first determined the simple univariate correlation between copulation success and any other variate using a logarithmic link function and a poisson error distribution. We then performed multiple regressions for several models either using the same link function and error distribution or transformed the response variable from copulation numbers to a binomial variate: copulation success (where 0 is no copulations and 1 is ≥ 1 copulation). In the latter case, we used a logistic link function. We tested alternative link functions but the logarithmic one performed best in all cases. To choose among alternative models we performed analyses of deviance (*see* e.g., Hosmer & Lemeshow 1989). To examine if the parameter estimate of each variable was significantly different from 0 we used *t*-tests where the standard errors were based on a dispersion parameter of 1.

Results

Morphological traits

Both size (PC1 of body mass, tarsus, sternum, wing length) and lyre length showed strong age effects. In simple correlation analyses only lyre length was correlated with male mating success (Table 3). When controlling for age, lyre length was still significant when mating success was a

Table 2. Factor loadings of four size (sternum, tarsus, wing and body mass) and three territory (distance from the lek centre, no. of neighbours, circumference of territory encircled) traits for the principal components ($PC1_a$ and $PC1_b$, respectively).

Trait	$PC1_a$	Trait	$PC1_b$
1. Sternum	–0.49	1. Distance from the lek centre	–0.54
2. Tarsus	–0.61	2. No. of neighbours	0.57
3. Wing	–0.35	3. Territory circumference	0.62
4. Body mass	–0.52		
Eigenvalues	1.85		2.56
% of total variance explained	46.3		85.4

Table 3. Simple correlations between different variates and male mating success (= total seasonal no. of copulations). Significance tests are based on the deviance from a model including the constant only. Age effects are not accounted for. * = significant at $p < 0.05$ after table-wide correction for multiple tests. F^{**} = deviance ratio when term removed from model.

	r	df	F^{**}	p
Morphology				
Size ($PC1_a$)	0.20	94	4.0	0.03
Lyre length	0.32	101	11.7	< 0.001*
Behavioral traits				
Attendance	0.53	155	59.1	< 0.001*
Rookoo	0.07	124	0.6	0.21
Fighting	0.15	140	3.2	0.04
Lyre posture	0.28	146	12.6	< 0.001*
Passivity	–0.21	116	5.43	0.01
Spatial variables				
Territory ($PC1_b$)	0.51	132	45.5	< 0.001*
Territory size	0.02	106	0.04	0.42

continuous variable (Table 4) while size was significant in the logistic regression (Table 5).

Behavioural traits

In the simple correlation analyses, attendance and lyre position (Table 3) were significantly positively correlated with male mating success whereas rookoo, being active (1 – passivity) and fighting were not. These results were largely unaffected in the partial analyses where also age was included as a factor. When mating success was allowed to vary continuously, attendance, lyre posture and proportion scans being active were significant with largely unaffected parame-

ter estimates. Significant interactions between lyre posture and being active (1 – passivity), rookoo and fighting indicate that successful males at the centre of the lek face a different time allocation problem as compared to successful males at the edge of the leks. This interpretation is further strengthened by the significant negative relationship between rookoo and mating success (*see* below). In the logistic regression, lyre posture was not significant but showed a positive trend ($p < 0.10$). The most important behavioural trait in all analyses was attendance.

Spatial variables

Among the spatial variables territory position ($PC1_b$) was significant in the univariate analyses and showed high deviance ratios (Table 3). Instead, territory size was not correlated with male mating success in the univariate analyses

Table 4. Partial correlations of different variates and male mating success (= total seasonal no. of matings). Significance tests are based on the deviance from a model including all the main effects except one. A model were run for each of the main categories morphology, spatial variables and behavioural traits respectively. Age (yearling or older) were included as a term in each model. We ran full models including all possible two-way interactions and subsequently dropped these if non-significant until only significant interactions remained. * = significant at $p < 0.05$ after table-wide correction for multiple tests. e = estimate.

	e	df	t	p
Morphology				
Age	0.88	90	2.19	0.03
Size ($PC1_a$)	0.21	90	1.97	0.05
Lyre length	0.19	90	2.95	0.003*
No interactions				
Behavioral traits				
Attendance	5.10	115	5.23	< 0.001*
Rookoo	–75.0	115	3.42	< 0.001*
Fighting	–46.6	115	2.63	< 0.009
Lyre posture	25.0	115	2.80	0.005*
Passivity	–48.7	115	3.42	0.004*
Rookoo ×				
Lyre posture	39.4	115	12.0	0.001*
Passivity ×				
Lyre posture	25.7	115	2.78	0.005*
Spatial variables				
Territory ($PC1_b$)	0.20	104	1.24	0.20
Territory size	0.03	104	3.54	< 0.001*
$PC1_b$ × Size	0.03	104	3.71	< 0.001*

Table 5. Partial correlations (r_p) between different variates and male mating status (= 0 is no copulations and 1 is ≥ 1 copulation). Significance tests are based on the deviance from a model including all the main effects except one. A model were run for each of the main categories morphology, spatial variables and behavioural traits respectively. Age (yearling or older) were included as a term in each model. [x]For morphological variables, lyre length was first dropped from a model including age, size and lyre lenght. The effect of size was then checked together with age. * = significant at $p < 0.05$ after table-wide correction for multiple tests. F^{**} = deviance ratio when term removed from model.

	r_p	df	F^{**}	p
Morphology[x]				
Size ($PC1_a$)	0.18	196	6.5	0.006*
Lyre length	0.06	195	0.8	0.20
Behavioral traits				
Attendance	0.39	107	19.4	< 0.001*
Rookoo	0.15	107	2.4	0.06
Fighting	0.15	107	2.4	0.06
Lyre posture	0.16	107	2.8	0.05
Passivity	0.15	107	2.3	0.06
Spatial variables				
Territory ($PC1_b$)	0.40	99	18.5	< 0.001*
Territory size	0.05	99	0.24	0.31

(Table 3) Interestingly, however, the multivariate analyses revealed that there is a complex relationship between territory size and proximity to the lek centre as there was a significant interaction between these variables. Our interpretation of this interaction is that birds that held relatively large central territories are the most successful ones (Table 4 and 5).

When we analysed rookoo and proximity to the lek centre in a joint model we found that birds that had a high rookoo value were more successful when controlling for age and proximity to the lek centre. We also found an interaction between rookoo and proximity to the lek centre such that birds that had a high rookoo rate at the centre of the lek were more successful (Table 6).

Discussion

Morphological traits

Some, but certainly not all, previous studies of single lekking species have emphasised correlations between morphological traits, such as ornaments, and mating success (e.g., Ryan 1983, Höglund & Lundberg 1987, Petrie *et al.* 1991, Pruett-Jones & Pruett-Jones 1991). In the black grouse, we could not find any clear effects of overall body size on male mating success, although composite body size was a significant predictor of male mating status (0 vs. ≥ 1 copulation). This may arise because larger males may be more powerful when competing for territories and there may thus be a covariation with such males being found in favoured territories.

In this data, the lyre length was correlated with male mating success when controlling for body size and age, indicating that the trait at present is under directional selection. This fits with the observation that in the black grouse, the lyre is sexually dimorphic: males have on average 79% longer outermost tail feathers as compared with females. Additional evidence that morphological characters are likely under weak selection come from the study by Höglund *et al.* (1994). In an experiment where the white under tail-coverts were manipulated, the mating suc-

cess of peripheral males but not of central males was affected. This result suggests that morphological traits such as tail feathers may be important cues for female choice, but that the relative importance of different traits may be masked in a correlation study. Since juvenile males have shorter outermost tail feathers (on average 17% of that of adults), females and/or males could also use lyre length as an indicator of age.

Assuming the reason for the evolution of extravagant tail is female preference, such traits have either been suggested to have evolved because of a Fisherian run-away- process (Fisher 1930) or females seeking "good genes" (Zahavi 1975, Hamilton & Zuk 1982). It is very speculative to discuss which theory, if any, explains the evolution of the lyre. A Fisherian process may have been involved. Alternatively or additionally, the lyre is used in dominance status signalling among males. Under this scenario, it is predicted that males in good condition and with high status optimize lyre length annually (Höglund & Sheldon 1998). In conclusion, the lyre may offer information both competing males and choosy females.

Behavioural observations

In several lekking species male behaviour, especially display rate, has been found to be correlated with male mating success (Gibson & Bradbury 1985, Höglund & Lundberg 1987, Clutton-

Table 6. Partial correlations between rookoo, territorial centrality and male mating success (= total seasonal no. of matings). Significance tests are based on the deviance from a model including all the main effects except one. Age (yearling or older) were included as a term in each model. We ran full models including all possible two-way interactions and subsequently dropped these if non-significant until only significant interactions remained. * = significant at *p* < 0.05 after table-wide correction for multiple tests.

	e	df	*t*	*p*
Territory (PC1$_b$)	1.24	68	3.89	< 0.001*
Rookoo	1.87	68	2.81	< 0.005*
PC1$_b$ × Rookoo	−2.43	68	3.42	< 0.001*

Brock *et al.* 1988, McDonald 1989, Pruett-Jones & Pruett-Jones 1991, Fiske *et al.* 1998). In a simple correlation analysis, the display activity (i.e. the proportion of scans when a male was rookooing) does not seem to correlate with mating success. Similar results were obtained by Kruijt and de Vos (1988) even if they got a positive relationship when they analysed spectral aspects of the rookoo. In a smaller but more detailed data set, rookoo was also negatively related to mating status (Höglund *et al.* 1997). However, the territory position on the lek-arena may affect how a male can behave. Clearly, central males are most likely to be forced to fight more because their territories are the ones most encircled by other males (e.g., Kruijt *et al.* 1972). In fact, disclosed by the analyses made here, proportionally higher rookooing display of central males was found to predict higher mating success. This hints that active rookooing between fighting may be judged by females. Rookoo in the black grouse may also serve a function such that low ranking and/or novice males may rookoo to attract more males to the lek (Hovi *et al.* 1997, *see* also Widemo & Owens 1995). Under any of these explanations, the rookoo behaviour is probably not a primary target of sexual selection but may instead affect the attraction of males and females to the lek as such (Alatalo *et al.* 1992, Hovi *et al.* 1997).

On black grouse leks in our study area, male attendance on the lek arena was essential for achieving copulations. This result agrees with findings in a few other lekking species (Payne & Payne 1977, Lank & Smith 1987, Apollonio *et al.* 1989) and a meta-analysis of lekking species (Fiske *et al.* 1998). In this context Mackenzie *et al.* (1995) pointed out that the variation in male mating success on leks can be ascribed to a range of factors including chance events, variation in male quality, female copying the choice of other females and variation in attendance. They furthermore suggested that if these factors were additive the different variance components could be partitioned. At this point we would like to emphasize that the variation in male attendance in the black grouse is probably not directly related to the variance in mating success (i.e. that by being absent a male looses opportunities to mate, but *see* de Vos 1983: 89), because the variation in attendance when females are present is probably very close to zero since absent males return to the lek-site and thus practically all males are present during female visits (de Vos 1983, own observations). Furthermore, the effects of attendance and quality aspects are multiplicative as evidenced by a relationship between territory and attendance (deviance ratio = 36.62, $p < 0.001$). Thus variation in attendance probably reflects variations in motivation and/or competence among males during the copulation period and the whole life (Kokko *et al.* 1999).

There are probably more male behavioural aspects that are important but difficult to obtain data on. For instance, dominance relationships could not be estimated here, and the data include observations when females were not present at lek. Other studies suggest that an active male courtship behaviour is an important difference between successful and unsuccessful males (Höglund *et al.* 1997). This aspect has also been verified in a study of male eye-comb size effects on male mating success, where it was found that males showed larger combs during the presence of females (Rintamäki *et al.* 2000). Hence the variation of the results seen in studies of mating success of lekking species (*see* Fiske *et al.* 1998) may also indicate differences how the data have been collected.

Territorial features

Territorial traits have also been found to be a target of selection in lekking species (Kruijt & Hogan 1967, Wiley 1973, Höglund & Lundberg 1987, Apollonio *et al.* 1989, Gratson *et al.* 1991, van Rhijn 1991, Deutsch & Nefdt 1992, Fiske *et al.* 1998). We found that males that were positioned close to lek centre, had many neighbours and whose territories were surrounded by others, received more copulations (*see also* Koivisto 1965, de Vos 1983, Kruijt & de Vos 1988). Furthermore, and most importantly, being central is not enough, the territory also needs to be large for it's central position (Hovi *et al.* 1994, Höglund *et al.* 1997). The ultimate reason for why central males are more successful has been a continuous debate subject. It is not clear if males ultimately are (1) central because they are

successful or (2) successful because they are central (e.g., Höglund & Robertson 1990, Hovi *et al.* 1994; note that females may still use any aspect of male centrality, such as the level of aggregation, under any of these two hypotheses). Experimental studies made in the field (Kruijt *et al.* 1972) and in captivity (Hovi *et al.* 1994) suggest that females do prefer clustered males as such, although there is no unequivocal experimental evidence that the female preference for clusters is solely due to the preference for aggregated males. However, detailed analyses of male territory settlement and territory organisation within and between years suggest that males relocate around particularly attractive males and that the lek-centre shifts in space from year to year (Rintamäki *et al.* 1995a). It could thus be that females use the level of male aggregation as a rule of thumb when selecting males. Attractive males are under natural conditions always found in the lek centre because of male relocations due to high mortality of territorial males (Rintamäki *et al.* 1999) and even queuing of desirable territories on the centre of the lek arena (Kokko *et al.* 1998). The importance of territory location is additionally supported by the fact that females already in autumn (when matings do not occur) prefer the same territories they mate in the following spring (Rintamäki *et al.* 1999).

Conclusions

In conclusion, body size, when controlled for age effects, had some but minor influence on male mating success. The lyre length is positively related to male mating success when controlling for body size and age effects. In agreement with previous findings from studies of black grouse, and a meta-analysis of other lekking species (Fiske *et al.* 1998), centrally located territories are good correlates of male mating success but the territories need to large for their central position in order for the male to be successful. Evidence from other studies suggest that black grouse females prefer central males and that males relocate around particular males thus making them more central (Kokko *et al.* 1998). Among behavioural traits, attendance and

lyre posture were both significant correlates of mating success. Similar results were also suggested in a meta-analysis of lekking species (Fiske *et al.* 1998) and in a long-term study of attendance on mating success of black grouse males (Kokko *et al.* 1999). Interestingly, male display activity (rookooing) became important when territory location was controlled for. Lyre posture and attendance are believed to reflect general activity levels. Attendance and mating success are probably not related to one another in a simple manner, i.e. males may loose matings by not being present, because male attendance is probably close to 100% when females are present. We summarise that it is not possible to unambigously discern which of the two processes of sexual selection, male-male competition and/or female preference, that mediate the correlations observed in this paper but it is likely that both processes are involved and that both favour healthy and active males.

Acknowledgements

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