

Pekka Rintamäki

Male Mating Success
and Female Choice in
the Lekking Black Grouse

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1995

Pekka Rintamäki

Male Mating Success
and Female Choice in
the Lekking Black Grouse

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Liikunnan salissa (L304)
kesäkuun 17. 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,
in Auditorium L304, on June 17, 1995 at 12 o'clock noon.



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1995

Male Mating Success
and Female Choice in
the Lekking Black Grouse

Pekka Rintamäki

Male Mating Success
and Female Choice in
the Lekking Black Grouse



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1995

URN:ISBN:978-951-39-9331-3
ISBN 978-951-39-9331-3 (PDF)
ISSN 0356-1062

Jyväskylän yliopisto, 2022

ISBN 951-34-0551-6
ISSN 0356-1062

Copyright © 1995, by Pekka Rintamäki
and University of Jyväskylä

Jyväskylä University Printing House
and Sisäsuomi Oy, Jyväskylä 1995

To Eevi and Queen Jasmina

ABSTRACT

Rintamäki, Pekka

Male mating success and female choice in the lekking black grouse

Jyväskylä: University of Jyväskylä, 1995, 23 p.

(Biological Research Reports from the University of Jyväskylä,

ISSN 0356-1062; 45)

ISBN 951-34-0551-6

Yhteenveto: Koiraan lisääntymismenestykseen vaikuttavat tekijät ja naaraan valintakäyttäytyminen teeren soitimella.

Diss.

Behaviour of lekking black grouse males and females were studied during years 1987-1994 in Central Finland. Most of the observed birds had been measured and colour-ringed. Females prefer central, clustered males. However, females do not favour specific sites within the central area of the lek. Over the seasons successful males did not change their territory position but unsuccessful males tried to gain some benefit by gathering around these attractive males. Males gather to lek and defend their territories also in autumn. This lekking activity is likely to be adaptive behaviour for ensuring possibilities to achieve copulations in the spring. Less successful males at the edge of the lek were most asymmetrical in tarsus length suggesting poor condition among these males. Male behavioural traits did not predict particularly well male mating success, even if lek attendance and lyre posture had significant effects. Among the morphological traits, size had some impact so that larger males were more successful. Black grouse females did not sample males randomly, since they targeted their visits to central males. Females are free to sample several males simultaneously which suggests the pool comparison tactic. Heavy females visited more males than lighter females suggesting that sampling includes some costs even in this lekking species.

Key words: Sexual selection; mate choice; lekking; black grouse.

P.Rintamäki, Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland.

LIST OF ORIGINAL PUBLICATIONS

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

- I Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg A. 1995: Male territoriality and female choice on black grouse leks. - *Anim. Behav.* 49:759-767.
- II Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg, A. 1995: Mate sampling behaviour of black grouse females (*Tetrao tetrix*). - *Behavioral Ecology and Sociobiology* (in press).
- III Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg, A. : Factors determining male mating success on black grouse leks . - Manuscript (submitted).
- IV Rintamäki, P.T. & Karvonen, E.: Effects of autumn lekking on male mating success on black grouse leks. - Manuscript.
- V Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg, A. : Fluctuating asymmetry and mating success in lekking black grouse. - Manuscript (submitted).

CONTENTS

1	Introduction	7
1.1	Lekking as a mating system	7
1.2	Mating system of the black grouse - a general overview	8
2	Material and methods	10
2.1	Study sites	10
2.2	Bird capturing and measurements	10
2.3	Lekking observations	11
3	Results and discussion	13
3.1	Male territoriality and female choice (I,III,IV)	13
3.2	Male behaviour and female choice (III,IV)	14
3.3	Fluctuating asymmetry and female choice (V)	15
3.4	Female mate sampling behaviour (II)	15
4	Conclusions	17
	Acknowledgements	18
	Yhteenveto	19
	References	21

1 INTRODUCTION

1.1 Lekking as a mating system

Among the several mating systems (monogamy, polygamy etc.) one specific mating system is called "lekking" or "arena display". Lekking behaviour is not simple to define, because more or less similar behaviour have been described in several taxa. The most favoured definition has been suggested by Bradbury (1981) and it includes four criteria:

- 1) There is no bond between the male and the female apart from the brief copulation and there is no paternal care.
- 2) Displaying males are highly aggregated within the space suitable for display at traditional mating arenas which females visit for mating.
- 3) Male territories provide absolutely no external resources that influence female future breeding success and females breed outside the lek.
- 4) Females are always free to choose any of the males for copulation.

These criteria are not perfectly valid except among very few species, and therefore Höglund & Alatalo (1995) developed a more general definition of the lek. In this definition lek is "aggregated male display that females attend primarily for the purpose of fertilisation". This definition emphasises one important feature; in lekking species males do not seem to offer females anything else than genes (sperm). Thus lekking is considered to express more intersexual selection than to intrasexual selection.

Höglund & Alatalo (1995, in press) summarised the lekking species in mammals, birds and other taxa such as insects and reptiles. This compilation brings out one important thing; the huge variability of lekking taxa. Thus it is reasonable also to predict variability in mechanisms that determine mating success.

Factors that explain mating success can be divided to those that operate *between* and *within* leks. Within lek studies, as in this thesis, allow us to receive detailed information of the operation of sexual selection on leks. This includes selection on males and male strategies to enhance their mating success. It is essential also to consider female choice strategies in the same context. When understanding sexual selection and female strategies we may have the background to explain evolution of lekking. In this thesis I will study how male territoriality, behaviour and morphology both in the mating season in spring and also in autumn are connected to male mating success. In addition, I will focus on the question how females sample among the males.

1.2 Mating system of the black grouse - a general overview

The black grouse is one of the most intensively studied lekking species. Several articles considering lekking behaviour and sexual selection have been published by Finnish (Koivisto 1965, Alatalo et al. 1991, 1992, Hovi et al. 1995, Rintamäki et al. 1995), Swedish (Hjorth 1970, Höglund et al. 1990, 1993, 1994) and Dutch (Kruijt & Hogan 1967, Kruijt et al. 1972, de Vos 1979, 1983, Kruijt & de Vos 1988) researchers.

Black grouse has the mating system that can be considered as the "classical" lekking. Males gather in mating season on specific display sites, i.e. open bogs, fields and ice-covered lakes to defend their territories and to persuade incoming females to mate. It is also typical that males lek more or less actively already in autumn.

Lek size (i.e. no. of males) varies considerably between areas and years depending on annual mortality and breeding success of previous years. In our study areas lek size over 10 males is rare - usually leks consist of fewer males and it is not rare that "lek" includes only one or a few males. Lek sites situate usually some 2 km away from each other and are thus audible to each other. On larger leks territories are tightly clumped and thus males have to defend their territories constantly. Usually this aggregation leads to dominance hierarchy among males: subdominant, usually younger males position themselves at the edge of the lek while central males are usually older. Yearlings seldom establish permanent territories and thus do not achieve many copulations. In black grouse, as well as in many other lekking species, matings are considerably skewed. In smaller leks usually only one dominant male gets all the matings and on larger leks 2-3 males get over two thirds of the copulations (Alatalo et al., 1992).

Male display behaviour is called "rookooing" (Hjorth 1970). This conspicuous bubbling "song" is produced in specific air sacs and is used to attract females to leks and to male territories. Apart from the rookooing behaviour, males also present "hissing" and "flutter-jumps". These are calls and jumping advertisement that males use when females are near or passing by the lek. Fighting is common at territory boundaries. Usually males only threaten each other (activity called "sparring") but occasionally they also have

intense physical combats. Because females decide their mating partner, males try to attract females inside their territories where matings usually occur. If female is willing to copulate, she allows the male to circle around it. During male circling female lays down and if stayed long enough in that position, male jumps on the female's back and copulates. Even if the copulation lasts only a few seconds, it is easy to observe because the male has to flap wings conspicuously to maintain his balance.

2 MATERIAL AND METHODS

2.1 Study sites

During years 1987-1994 we studied a total of 21 leks that were situated mostly in Petäjävesi, Keuruu and Uurainen, in Central Finland. Parts of the leks were situated on open bogs or peat bogs (13) and rest on ice-covered lakes. The data are mainly collected from bogs because in many study years ice melted the before main mating season. One of the leks was studied in all the years, three leks during 3 years and two during 2 years. The other leks were studied only on one year.

Vegetation on the lek sites on open bogs includes mainly different mosses (*Sphagnum spp.*), sedges (*Carex spp.*), cotton grass (*Eriophorum vaginatum*) and some Scots pine (*Pinus sylvestris*). All leks were situated on open areas where predators (goshawk, *Accipiter gentilis* and fox *Vulpes vulpes*) usually can not kill the birds. The lek studied in most detail was situated on a nature reserve without hunting, while on other leks annual mortality was influenced by hunting in the autumn.

2.2 Bird capturing and measurements

We captured a total of 225 males from 6 leks. Most of the males (80 %) were caught from our main study lek that was situated on a winter feeding site. These birds were captured by using walk-in-traps and cannon-nets. In total 175 females were caught of which 78 % were trapped on the main lek. Both females and males were caught mainly in winter, but some were captured also during the mating season at the turn of April and May. We do not have any indications that trapping would disturb later lekking behaviour of the

birds.

Males and females were aged (Helminen 1963) and individually marked with one aluminium ring and two or three plastic colour-rings on the legs. In males we avoided to use red and orange rings because these colours resemble too much male eye-combs and therefore may affect male behaviour. Plastic rings were glued to avoid them from opening afterwards. A total of 113 females were radio-tagged on neck (Biotrack UK necklace mounts, weight approximately 1.5 % of female body mass).

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 mm and tarsus length (the distance from the heel to the bending points of the toes including the tarso-metatarsal bone) to the nearest 0.1 mm with a caliper. Wing length was measured from the carpal joint to the tip of the longest primary feather (to the closest mm). Lyre was measured as the length of the longest outer tail feather from the base to the tip after flattening the feather. Body mass was measured with a Pesola spring balance to the closest 10 g. To study fluctuating asymmetry (FA), we measured also both sides of tarsus and outermost tail feathers.

2.3 Lekking observations

Leks were observed from blinds (a tent or a hovel) erected close to lek sites. We used mainly binoculars (8-12x), telescopes (16-60x), light intensified binoculars and occasionally video cameras to identify and observe individuals. Colour-ringed birds were easy to identify and if not ringed, we separated different birds by using individual plumage characters (damages on plumage and variability in black spots on white undertail coverts) and territory position. Juvenile birds were rather easy to distinguish from adults even at distance because their lyre is considerably shorter and because tertials, primary and secondary coverts are brownish.

Territory size and position was determined by using 10 x 10 meter grid system on each lek. Positions were mapped to the closest 1 m on the two-dimensional area. We observed both behaviour and territory position at 5-20 minutes intervals when females were not present on the lek. Observations were not made if all the males were simultaneously inactive (usually late morning).

A) Behavioural observations consist of following variables:

Attendance: proportional value how faithfully male was visiting the lek arena (100 % = male was always seen on the active lek).

Rookooing: proportion of observations when the male was displaying vocally.

Fighting: proportion of observations when the male was interacting with other males.

Passivity: proportion spent in other activities (eating, sleeping, preening,

feeding etc.)

Lyre posture: ranges from 0 to 2 from totally folded tail to totally erected tail.

B) Territorial observations consist of following variables:

Territory size: we estimated the average diameter that includes 50 % of the most central locations of each male on his territory.

Number of neighbours: amount of neighbours around male territory.

Proportion of the territory encircled (= territorial pressure): proportional value (max. 100 %) describing how tightly surrounded by other territories the male territory was.

Distance to lek center: distance from each male's territory median location to the lek center (= median of the all observation locations).

In the study of female sampling behaviour we concentrated on observing female positions on each day at one minute intervals. Observations were done on the most detailed studied lek, where females were easier to capture and observe. Positions were taken by the help of the grid system and also with help of male territories visited by females. Female was thought to be on specific male's territory if it was clearly inside the territory. Before landing on the lek arena, females usually sit on treetops near lek and therefore we tried also to identify the presence of such females.

3 RESULTS AND DISCUSSION

3.1 Male territoriality and female choice (I, III, IV)

Male territoriality seems to be very crucial for black grouse female choice and some models have been recently suggested to explain mating success. Firstly, spatial spillover- mechanism (or attractive male or "hotshot" model, e.g. Arak 1988, Höglund & Robertson 1990) that suggests that females for some reason prefer certain males, then neighbouring males gain some copulations by theft, female-female competition or by female mistakes. Secondly, temporal spillover- model suggests that females tend to copulate on historically successful territories or sites (e.g. Wiley 1973, Gibson 1992). Our results suggest that black grouse females do not prefer specific mating sites over the seasons, but for some reason favour attractive males. Furthermore, unsuccessful males try to establish their territories closer to the lek centre than the centre of the matings which suggests that males get some benefit by stealing copulations from attractive, "hotshot" males. In addition, successful males do not change their territories between seasons.

Territorial traits were important prediction of male mating success in spring or in autumn. In multivariate analyses spatial features (central position of the territory, the number of surrounding neighbours) were most important in explaining male mating status.

In previous studies in lekking species, correlations between male territoriality and male mating success have been established (Koivisto 1965, Lill 1974, Gibson & Bradbury 1985, Höglund & Lundberg 1987, Clutton-Brock et al. 1989, Trail & Adams 1989, Gosling & Petrie 1990). In recent years these correlations have been considered to be more a consequence of other preferred traits and not the targets for mate choice. However, our empirical results and experimental studies (Hovi et al. 1995) suggest that females really choose males by using territorial position as a criterion. Support to this comes also from the lekking observations in autumn. They clearly

emphasise the role of territorial defence. This sexual activity outside breeding season has been observed in a few grouse species in North America and in Europe (see e.g. Johnsgard 1983). Male attendance in autumn cannot be explained only as a reflection of hormonal activity after moulting season. In black grouse autumn lekking is essential for territory defence and initial establishment of territories.

3.2 Male behaviour and female choice (III, IV)

Several morphological (e.g. Andersson 1989, Gibson et al., 1991, Petrie et al., 1991) and behavioural (e.g. Höglund & Lundberg 1987, Clutton-Brock et al. 1988, Pruett-Jones & Pruett-Jones 1991) traits have explained male mating success in lekking birds. In partial correlation analyses male size was correlated with black grouse mating success. Male attendance and lyre posture were the behavioural traits that were positively correlated with matings.

Why these are the only traits that are correlated with mating success, while for example extravagant lyre length and noticeable rookooing behaviour are not? All the correlated traits are connected with territorial traits, in particular attendance is essential for maintaining the territory. Lyre length may not be any target for female choice anymore although tail condition does have some impact (Höglund et al. 1994). Furthermore, females can separate juveniles and adults easily by comparing tail lengths. Even if females may prefer more audible and probably therefore also larger leks (Gibson 1989, Alatalo et al. 1992), lack of correlation with rookooing probably arises because males at the edge of the lek mainly use this display. Instead, the successful central males, besides rookooing, must fight much more to maintain their territories. It seems that the importance of rookooing is probably to attract females to the lek.

In previous studies in lekking birds morphological traits male mating success has been mainly found to be correlated with elaborated tails (e.g. Andersson 1989, Petrie et al. 1990) and spectral call parameters (e.g. Kruijt et al. 1988, Robertson 1990, Gibson et al. 1991) while other traits such as male body mass has not been important. Male behavioural features as criteria for female choice have largely concentrated on male attendance on the lek (e.g. Lank & Smith 1987, Apollonio et al. 1989), but also on display rate (e.g. Clutton-Brock et al. 1988, McDonald 1989). It is likely that dominance relationships between males are important (Alatalo et al. 1991), but they cannot be measured directly and it is possible that the role of behavioural traits have been underestimated in lekking studies.

3.3 Fluctuating asymmetry and female choice (V)

Fluctuating asymmetry (FA), where normally symmetrical bilateral traits are for some reason more or less asymmetrical, has recently been discussed widely in sexual selection studies (e.g. Møller & Höglund 1991, Møller 1992, Swaddle & Cuthill 1994, Watson & Thornhill 1994). FA has been considered to reflect male inability to tolerate environmental stress and therefore it is likely to be an indicator of male genetic quality. Thus, in sexual selection context, FA may be an indicator of "good genes" (Zahavi 1975, Hamilton & Zuk 1982). Possible trait differences between bilateral organisms may exist either in ornaments or non-ornamented traits.

Black grouse males were studied in order to compare both ornament (lyre) and non-ornament (tarsus) symmetry and mating success. Lyre asymmetry was not correlated with mating success, but instead, males that had more asymmetrical tarsus, got fewer copulations. Earlier studies in black grouse have verified that territorial factors are important for female choice. Males that were more surrounded by neighbouring males, were also most symmetrical and therefore also more successful in achieving matings.

3.4 Female mate sampling behaviour (II)

Despite the many sexual selection studies of lekking species in recent years (see Gross 1994, Wiley 1991), not much attention has been paid to study female mate sampling process, i.e. how females make their mate choice (but see Trail & Adams 1989, Petrie et al. 1992, Fiske & Kålås 1994). Problems arise because searching evidently involves costs that may affect general sexual selection models (Kirkpatrick 1987, Pomiankowski 1988, Pomiankowski 1989, Pomiankowski et al. 1991).

Sampling behaviour was studied in order to find out how many males females check and how do they sample males in relation to many models suggested (Janetos 1980, Wittenberger 1983, Real 1990). We also addressed the question how searching behaviour among earlier studies in other lekking and non-lekking species is comparable to our studies.

Females sampled, on average 4 different males before making their mate decision, but the final mate choice was rather independent of the order in which males had been visited. This kind of searching behaviour fits best to the pool comparison tactic (best-of-n- tactic). This is to be expected for lekking species, where females are able to compare males simultaneously. Furthermore, visited males were not chosen non-randomly because in multivariate analyses visitations (53 %) are explained better by male traits than is the mating success itself (33 %). Also, experienced females seem to choose their mate from the previous year. Studies on lekking sage grouse (Gibson & Bachman 1992) emphasise that costs of choice are probably negligible in lekking species. Possible direct costs may be meaningless (for

example risk of predation). Even if black grouse females spend a relatively short time (typically less than one hour) actively on the lek arena, correlation between female weight and the number of males visited suggests some costs. These costs may be indirect such as increasing copulation disruption risk and the risk of not being fertilised at the right time (Trail & Adams 1989). Comparisons between lekking and non-lekking species surprisingly do not provide any clear differences in female search strategies. Similar studies made in lekking peacock (Petrie et al. 1992) and great snipe (Fiske & Kålås 1994) are not clearly supportive of effective pool-comparison of males.

4 CONCLUSIONS

Territorial traits such as distance to lek center and the number of neighbours are essential for male mating success. Although territory is important, females do not choose specific locations per se, but favour some of these central males. Successful males do not change their territories over the seasons while new males tried to establish their territories closer to copulation centre than the centre of the lek. Males defend actively their territories also in autumn that also suggests that territorial position is important alone, not only as a consequence of other traits. Capability to establish the territory might reflect male genetic quality, since it was the most symmetrical males that had access to central territories.

Behavioural and morphological traits do not explain mating success particularly well, even if male attendance on the lek and male size have some importance. It is possible that active display behaviour is important in persuading females to lek, but not as much a primary target for females in their mate choice.

Females seem to observe and sample males for a relatively short time that suggests that sampling is not costly. Still, differences in sampling behaviour between females of different body mass suggests some costs. Direct costs are probably negligible but indirect costs, such as copulation disturbance risk and risk of not being fertilised at the right time, may be important. Female sampling is also non-random in that successful males on the centre of the males received many visits while edge males were not even visited at all. Female sampling behaviour fits best the pool-comparison tactic, where females gain benefits by comparing several males simultaneously. Female behaviour to mate with previous year mate suggests some benefits for faithfulness.

Acknowledgements

This work is part of the black grouse project started in 1987 by Rauno Alatalo, Jacob Höglund and Arne Lundberg. Firstly, not according to alphabetical order, I thank my encouraging supervisor Rauno that both provided me possibility to make this thesis and also helped in many ways in the field and on the desk. Co-authors in most studies in this thesis (also JH and AL) understandably helped in the field and both planning and checking the papers. Furthermore, this dissertation would not have been possible without sacrificing help in the field by Harri Hakkarainen, Matti Halonen, Esa Huhta, Jukka Jokimäki, Simo Jokinen, Pirkko Siikamäki, Jukka Suhonen, William J. Sutherland and Staffan Thorman. Special thanks I direct to my grouse- colleague Matti Hovi, to helpful Osmo Rätti and to Pentti Valkeajärvi and Lauri Ijäs for providing help. In addition I am pleased to thank several people that have in a way or another helped me to make this thesis ready: Tapio Aalto, Antti Isokallio, Ari Jäntti, Pekka Kauppinen, Janne Kilpimaa, Lasse Kosonen, Janne Kotiaho, Johanna Mappes, Tapio Mappes, Silja Parri, Jyrki Pusenius, Veikko Salonen, Heikki Setälä, Sinebrychoff, Pekka Sintonen, Tapani Syrjälä, Jouni Taskinen, Esa Valkila and Hannu Ylönen. Kimmo Hirvonen kindly drew grouse drawings.

My warmest regards I owe to my mother who never tried to prevent my emerging love to observe and study phenomena nature. I am also grateful to my closest support Eevi Karvonen and to our more than lovely dog, Queen Jasmina for both helpful comments and background facilities.

Study was done by the financial support of Emil Aaltonen foundation and Nordisk Forskerutdanningsakademi (NorFA).

Yhteenveto

Koiraan lisääntymismenestykseen vaikuttavat tekijät ja naaraan valintakäyttäytyminen teeren soitimella

Seksuaalivalinnan tutkimus on tällä hetkellä yksi suosituimmista käyttäytymisekologian tutkimuskentistä. Pyrkimyksenä on selvittää eri eliöillä, mitkä seikat vaikuttavat yksilön päätökseen valita tietty pariutumiskumppani. Lähes kaikilla lintu- ja nisäkäslajeilla, joilla seksuaalivalintaa on eniten tutkittu, naaras on se sukupuoli, joka valitsee koiraan. Mielenkiinnon kohteena on siten, mitkä koiraan tarjoamat tekijät ovat merkityksellisiä naaraille. Pariutumisjärjestelmistä tavallisimpia ovat yksiavioisuus (monogamia) ja erityisesti koiraiden moniavioisuus (polygamia). Tällaisilla lajeilla seksuaalivalintaan vaikuttavia tekijöitä on usein hankala tutkia, koska monien eri tekijöiden vaikutusta voi olla vaikea erottaa. Tällaisia seikkoja ovat esimerkiksi reviiirin laatu, pesäpaikka, pesäpaikan suojaisuus ja koiraan laatu.

Teeren pariutumisjärjestelmä, ryhmäsoidin (engl. lek), poikkeaa muista pariutumissysteemeistä erityisesti siinä, että koiraat tarjoavat naaralle vain sperman eli geeninsä. Koiraat nimittäin eivät osallistu mitenkään esimerkiksi haudontaan tai jälkeläistenhuoltoon eivätkä myöskään tarjoa naaralle resursseja sisältävää reviiiriä. Naaraan katsotaan siten joutuvan tekemään pariutumispäätöksensä pelkästään koiraan ominaisuuksien perusteella. Tällaiseen vertailuun tarjoaakin soidin, missä koiraat kerääntyvät yleensä jollekin avoimelle paikalle samanaikaisesti, erinomaisen mahdollisuuden. Tutkimme vuosina 1987-1994 teeren soidinkäyttäytymistä Petäjaveden ympäristössä Keski-Suomessa. Tarkoituksenamme oli selvittää, miten koiraan morfologia, käyttäytyminen ja reviiiritekijät vaikuttavat koiraan parittelumenestykseen. Teeret soivat myös syksyllä, ja siksi selvitimme reviiiri- ja käyttäytymistekijöiden vaikutusta myös syksyn ja kevään välillä. Lisäksi havainnoimme naaraiden valintakäyttäytymistä soidinarenalla. Yksilöiden tunnistamisen helpottamiseksi linnut pyydystettiin talvella ja merkittiin yksilöllisesti värirenkain, osa naaraista myös radiolähtimillä. Samalla linnuilta mitattiin pyrstön (lyyran), nilkan ja rintalastan pituus sekä paino. Pyrstön ja nilkan pituudet mitattiin molemmista puoliskoista epäsymmetrisyyden selvittämiseksi. Käyttäytymisen havainnointi keskittyi aktiivisuuden havainnointiin (taistelut, pulputtaminen, joutenolo ja paikallaoloaktiivisuus), ja lintujen sijaintien avulla saatiin tietoa koiraan liikkeistä reviiirillään ja koko soitimella. Reviiiritekijöistä tärkeimmät seikat olivat koiraan reviiirin etäisyys soitimen keskusta, koirasta ympäröivien toisten koiraiden lukumäärä sekä reviiirin pinta-alan koko.

Morfologiatekijöistä kookkaammat koiraat olivat menestyksekkäimpiä. Yllättäen teeren pyrstön pituudella ei ollut merkitystä vanhojen koiraiden parittelumenestykseen vaikkakin naaraat voivatkin sen pituuden avulla helposti erottaa nuoret koiraat vanhoista. Käyttäytymistekijöistä koiraan paikallaolo oli merkittävä, mutta ei esimerkiksi pulputusinnokkuus. Pulputuksen tarkoituksena onkin ilmeisesti lähinnä houkutella naaraita soidinpaikalle, mutta se ei ole sinänsä seksuaalivalinnan kohde. Kaikkein selkeimmin koiraan menestystä selitti koiraan reviiirin sijainti. Keskellä soitimen keskustaa muiden koiraiden ympäröiminä olleet kukot olivat selvästi suosituimpia parittelu-

kumppaneita. Nämä koiraat joutuvat myös puolustamaan reviiriään muilta koirailta aktiivisimmin, ja siksi soidinpulputukseen jäävä aika on vähäisempi kuin mitä vähemmän aktiivisesti tappelevilla reunakoirailta. Reviirin merkitys korostuu myös syysoitimen merkityksellä: menestyäkseen koiraiden on yksinkertaisesti jatkuvasti puolustettava reviiriään. Lisäksi menestyneet koiraat eivät muuta enää reviiriään, kun taas huonosti menestyneet tai uudet koiraat pyrkivät perustamaan reviirinsä lähellä suosittuja koiraita. Lyyran epäsymmetrisyydellä ei ollut vaikutusta parittelumenestykseen, mutta sen sijaan koiraat, joilla oli epäsymmetrisimmät nilkat, menestyivät heikommin. Naaraat eivät todennäköisesti valitse koiraita niiden nilkkojen perusteella, mutta niiden epäsymmetrisyys voi kertoa epäsuorasti kukon laadusta. Koiraiden, joiden nilkkojen epäsymmetria oli suurin, reviirit sijaitsivatkin todennäköisimmin soitimen reunaosissa.

Soidin tarjoaa naaraille hyvän mahdollisuuden vertailla eri koiraita samanaikaisesti. Tästä ilmeisesti johtuu se, että naaraat viettävät sangen vähän aikaa koiraita tarkkaillen (keskimäärin alle tunnin). Tämä ei viittaa suoriin kustannuksiin (esim. saaliisijoutumisriskiin), koska vain hyvin harvoin kanahaukka onnistuu saalistamaan menestyksellisesti soidinalueelta. Kun kuitenkin painavimmat naaraat käyvät useimpien koiraiden reviireillä, saattavat kustannukset olla epäsuoria. Tällaisia kustannuksia voivat olla parittelujen häirintäriski tai se, ettei hedelmöittyminen tapahdu oikea-aikaisesti. Lisäksi naaraat käyvät vain tiettyjen, soitimen keskellä sijaitsevien koiraiden reviireillä. Ilmeisesti jotakin hyötyä on myös uskollisuudella, sillä naaraat näyttävät suosivan edellisvuoden parittelukumppaniaan.

REFERENCES

- Alatalo, R.V., Höglund, J. & Lundberg, A. 1991. Lekking in black grouse - a test of male viability. - *Nature (London)* 352: 155-156.
- Alatalo, R.V., Höglund, J., Lundberg, A. & Sutherland, W.J. 1992: Evolution of the black grouse leks - Female preferences benefit males in larger leks. - *Behav. Ecol.* 3: 53-59.
- Andersson, S. 1989: Sexual selection and cues for female choice in leks of Jackson's widowbird *Euplectes jacksoni*. -*Behav. Ecol. Sociobiol.* 25: 403-410.
- Arak, A. 1988: Female mate selection in the natterjack toad: active choice or passive attraction ? - *Behav. Ecol. Sociobiol.* 22: 317-327.
- Beehler, B.M. & Foster, M.S. 1988: Hotshots, hotspots and female preferences in the organization of lek mating systems. - *Am. Nat.* 131: 203-219.
- Bradbury, J.W. 1981: The evolution of leks. - In: R.D. Alexander & D.W. Tinkle (eds), *Natural Selection and Social Behaviour. An integrated approach*: 138-169. New York & Concord: Chiron Press.
- Bradbury, J.W. & Gibson, R.M. 1983: Leks and mate choice. -In: P.Bateson (ed.), *Mate choice*: 109-138. Cambridge, Cambridge Univ. Press.
- Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S.D. 1988: Passing the buck: resource defence, lek breeding and mate choice in fallow deer. - *Behav. Ecol. Sociobiol.* 23: 281-296.
- Clutton-Brock, T.H., Hiraiwa-Hasegawa, M. & Robertson, A. 1989: Mate choice on fallow deer leks. - *Nature (London)* 340: 463-465.
- Deutsch, J.C. & Nefdt, P. 1992: Olfactory cues influence female choice in two lek-breeding antelopes. - *Nature (London)* 356: 596-598.
- Fiske P. & Kålås, J.A. 1994: Mate sampling behaviour of great snipe females. - *Anim. Behav.*
- Gibson, R.M. 1989: Field playback of male display attracts females in lek breeding sage grouse. - *Behav. Ecol. Sociobiol.* 24: 439-433.
- Gibson, R.M. 1992: Lek formation in sage grouse: the effect of female choice on male territory settlement. - *Anim. Behav.* 43: 443-450.
- 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: D.I. Rubenstein & R.W. Wrangham (eds), *Ecological aspects of social organization*: 379-398. Princeton, Princeton Univ. Press.
- Gibson, R.M., Bradbury, J.W. & Vehrencamp, S.L. 1991: Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. - *Behav. Ecol.* 2: 165-180.
- Gibson, R.M. & Bachman, G.C. 1992: The costs of female choice in a lekking bird. - *Behav. Ecol.* 3: 300-309.
- Gilliard, E.T. 1962: On the breeding behaviour of the cock-of-the-rock (*Aves, Rupicola rupicola*). - *Bull. Am. Mus. nat. Hist.* 124: 31-68.
- Gosling, L.M. & Petrie, M. 1990: Lekking in topi: a consequence of satellite

- behaviour by small males at hotspots. - *Anim. Behav.* 40: 272-287.
- Gross, M.R. 1994: The evolution of behavioural ecology. - *TREE* 9: 358-360.
- Hjorth, I. 1970: Reproductive behaviour in Tetraonidae. *Swedish Wildlife (Viltrevy)* 7: 190-596.
- 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., Alatalo, R.V. & Lundberg, A. 1990: Copying the mate choice of others? Observations on female black grouse. - *Behaviour* 114: 221-231.
- Höglund, J., Alatalo, R.V., Lundberg, A. & Rätti, O. 1994: Context-dependent effects of tail-ornament damage on mating success in black grouse. *Behav. Ecol.* 5: 182-187.
- Höglund, J. & Alatalo, R.V. 1995. *Leks*. Princeton, Princeton Univ. Press - in press.
- Hovi, M., Alatalo, R.V., Höglund, J., Lundberg, A. & Rintamäki, P. 1995: Lek center attracts black grouse females. - *Proc. R. Soc. Lond. (B)* 258: 303-305.
- Janetos, A.C. 1980. Strategies of female choice: a theoretical analysis. - *Behav. Ecol. Sociobiol.* 7: 107-112.
- Kirkpatrick, M. 1987: Sexual selection by female choice in polygynous animals. - *Ann. Rev. Ecol. Syst.* 18: 43-70.
- Koivisto, I. 1965: Behaviour of the black grouse, *Lyrurus tetrix* (L.), during the spring display. - *Finnish Game Res.* 26: 5-60.
- Kruijt, J.P., de Vos, G.J. & Bossema, I. 1972: The arena system of the black grouse. - *Proc. 15th Int. Orn. Congr.:* 399-423.
- 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.
- Møller, A.P. & Pomiankowski, 1993: Fluctuating asymmetry and sexual selection. - *Genetica* 89:267-279.
- Petrie, M., Hall, M., Halliday, H. Budgey, H. & Pierpoint, C. 1992: Multiple mating in a lekking bird: why do peahens mate more than one male and with the same male more than once. - *Behav. Ecol. Sociobiol.* 31: 349-358.
- Pomiankowski, A. 1988: The evolution of female preferences for male genetic quality. - *Oxford Surv. Evol. Biol.* 5: 136-184.
- Pomiankowski A., Iwasa, Y. & Nee, S. 1991: The evolution of costly preferences. I Fisher and biased mutation. - *Evolution* 45: 1422-1430.
- Pruett-Jones, S.G. & Pruett-Jones, M.A. 1991: Sexual selection through female choice in Lawe's parotia, a lek mating bird of paradise. - *Evolution* 44: 486-501.
- Real, L. 1990: Search theory and mate choice. I. Models of single sex discrimination. - *Am. Nat.* 136: 376-405.

- Ryan, M.J. 1980: Female mate choice in a Neotropical frog. - *Science* 209: 523-525.
- Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg, A. 1995. Male territoriality and female choice on black grouse leks. - *Anim. Behav.* 49: 759-767.
- Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg, A. 1995. Female mate sampling behaviour on black grouse leks -*Behav. Ecol. Sociobiol.* (in press).
- Trail, P.W. & Adams, E.S. 1989: Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. - *Behav. Ecol. Sociobiol.* 25: 283-292.
- van Rhinj, J.G. 1991: *The ruff*. London, T. & A.D. Poyser.
- Warner, R.R. 1987: Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. - *Anim. Behav.* 35: 1470-1478.
- Wiley, R.H. 1973: Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. - *Anim. Behav. Monogr.* 6: 87-169.
- Wittenberger, J.F. 1983: Tactics of mate choice. - In: P.Bateson (Ed.), *Mate choice*: 435-447. Cambridge, Cambridge University Press.

I

**MALE TERRITORIALITY AND FEMALE CHOICE
ON BLACK GROUSE LEKS**

by

Pekka T. Rintamäki, Rauno V. Alatalo, Javob Höglund
& Arne Lundberg

Animal Behaviour 1995

[https://doi.org/10.1016/0003-3472\(95\)80208-8](https://doi.org/10.1016/0003-3472(95)80208-8)

Reproduced with permission of The Association for the Study of Animal
Behaviour

II

MATE SAMPLING BEHAVIOUR OF BLACK GROUSE
FEMALES
(*Tetrao tetrix*)

by

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

Behav. Ecol. Sociobiol. (in press) 1995

<https://doi.org/10.1007/BF00176719>

Reproduced with permission of Springer-Verlag, Heidelberg

III

**FACTORS DETERMINING MALE MATING SUCCESS ON
BLACK GROUSE LEKS**

by

Pekka T. Rintamäki, Rauno V. Alatalo, Jacob Höglund
and Arne Lundberg

<https://www.jstor.org/stable/23735755>

Manuscript (submitted)

IV

**EFFECTS OF AUTUMN LEKKING ON MALE MATING
SUCCESS ON BLACK GROUSE LEKS**

by

P.T. Rintamäki, E. Karvonen, R.V. Alatalo

Manuscript

V

**FLUCTUATING ASYMMETRY AND MATING SUCCESS IN
LEKKING BLACK GROUSE**

by

P.T. Rintamäki, R.V. Alatalo, Jacob Höglund
& Arne Lundberg

<https://doi.org/10.1006/anbe.1996.0434>

Manuscript (submitted)