

Pro Gradu –tutkielma

**Fighting performance as a predictor of mating success in
male black grouse**

Anni Hämäläinen



Jyväskylän yliopisto

Bio- ja ympäristötieteiden laitos

Ekologia ja ympäristönhoito

UNIVERSITY OF JYVÄSKYLÄ, Faculty of Mathematics and Science

Department of Biological and Environmental Science

Ecology and Environmental Management

HÄMÄLÄINEN, A.: Fighting performance as a predictor of mating success in male black grouse

Master of Science Thesis: 25 p.

Supervisors: Docent Heli Siitari, Prof. Rauno Alatalo

Inspectors: Prof. Mikko Mönkkönen, Prof. Janne Kotiaho

April 2010

Key Words: centrality, dominance, female selection, lek, male-male competition, parasites, physical characteristics, winning

ABSTRACT

As a consequence of certain conflicting evolutionary interests of males and females, the sexes have taken on different reproductive roles. In many species, where females invest more in the production of offspring, males compete for the opportunities to reproduce and females attempt to choose the highest quality males to sire their offspring. Males of different species signal their quality in a variety of ways, including physical cues such as color signals or exaggerated secondary sexual characters, behavioral signals and acquisition of a dominance status through aggression towards other males. In the lekking black grouse only a few males manage to copulate and active fighting is required for a male to defend a territory which is a prerequisite for mating. Central territories and various physical signals have previously been associated with male mating success and in this study the connection of these factors to male fighting activity was studied. Fights between males were videotaped and examined in detail to determine the specific components of their fighting behavior. The number of fights engaged in, the total number of opponents fought with, fighting intensity and the winning of fights (characterized by the male turning his back to the opponent after a fight) were recorded from the tapes. These characteristics were examined in relation to the male's mating success as well as physical measures and parasite counts obtained by capturing the males before the lekking season. Males that fought more often, more intensively and with a higher number of males won their fights more often. Each of the fighting characteristics as well as fight winning predicted mating success reliably. Physical traits, on the other hand, were connected to male age but were not found to relate to fighting behaviors nor to correlate with mating success in these data. Territory position had no direct connection to mating success, but central males spent more time fighting or engaged in a higher number of fights. The results of this study imply that active fighting and dominance combined with age-revealing physical traits reliably signal male quality and may be used by females as mate selection criteria.

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos

Ekologia ja ympäristöhoito

HÄMÄLÄINEN, A.: Tappelukäyttäytyminen teerikoiraiden parittelumenestyksen ennustajana

Pro Gradu –tutkielma: 25 s.

Työn ohjaajat: Dosentti Heli Siitari, Prof. Rauno Alatalo

Tarkastajat: Prof. Mikko Mönkkönen, Prof. Janne Kotiaho

Huhtikuu 2010

Hakusanat: dominanssi, fyysiset piirteet, koiras-koiraskilpailu, loiset, naaraan valinta, reviirin keskeisyys, soidin, voittaja

TIIVISTELMÄ

Naaraiden ja koiraiden välisten evolutiivisten ristiriitojen johdosta sukupuolet ovat omaksuneet erilaiset lisääntymisroolit. Useissa lajeissa, joissa naaraat panostavat poikastuotantoon koiraita enemmän, koiraat kilpailevat keskenään parittelumahdollisuuksista ja naaraat pyrkivät valitsemaan parittelukumppanikseen hyvälaatuisen koiraan. Eri lajien koirailta on vaihtelevia tapoja viestiä laadustaan, esimerkiksi fyysiset ominaisuudet kuten värisignaalit tai näyttävät toissijaiset sukupuolisignaalit, käyttäytymispiirteet ja aggressiivisella käyttäytymisellä hankittu dominanssistatus. Teeren soitimella vain pieni osa koiraista parittelee ja koiraiden on taisteltava aktiivisesti ylläpitääkseen parittelujen saamisen kannalta oleellista reviiriä. Reviirin sijainti soitimen keskustassa ja useat fyysiset piirteet on aiemmin liitetty koiraiden parittelumenestykseen ja tässä tutkimuksessa pyrittiin selvittämään näiden muuttujien suhdetta tappelukäyttäytymisen piirteisiin. Koiraiden välisiä tappeluita videoitiin ja tarkkailtiin yksityiskohtaisesti koiraiden taistelukäyttäytymisen hahmottamiseksi. Koiraiden käymien tappeluiden määrä, vastustajien kokonaismäärä, tappelun intensiteetti sekä tappeluiden voittaminen (toisen koiraan kääntyminen pois päin vastustajasta tappelun päätteeksi) poimittiin videomateriaalista. Näitä piirteitä verrattiin koiraiden tappelumenestykseen sekä fyysisiin ominaisuuksiin ja loismääriin, jotka selvitettiin pyytämällä koiraat ennen soitimen alkua. Koiraat, jotka tappelivat eniten, intensiivisimmin ja useampien vastustajien kanssa voittivat tappelunsa useammin. Kaikki tappelukäyttäytymisen piirteet ja tappeluiden voittaminen ennustivat luotettavasti parittelumenestystä. Fyysiset piirteet puolestaan liittyivät koiraan ikään, mutta eivät tässä aineistossa korreloineet parittelumenestyksen tai tappelukäyttäytymisen kanssa. Reviirin sijainnilla ei ollut suoraa yhteyttä parittelumenestykseen, mutta keskeiset koiraat käyttivät suuremman osan ajastaan tappelemiseen tai kävivät useampia tappeluita. Tämän tutkimuksen perusteella aktiivinen tappeleminen ja dominanssiasema yhdistettyinä iän paljastaviin fyysisiin ominaisuuksiin viestivät luotettavasti koiraan laadusta ja voivat toimia parinvalintakriteereinä teerinaaraille.

CONTENTS

1	INTRODUCTION.....	5
1.1	Theory on sexual selection: male competition and female choice	5
1.2	Fighting.....	6
1.3	Physical condition and parasites	6
1.4	The lek as a mating system.....	7
1.5	The black grouse mating system.....	8
1.5.1	Black grouse leks	8
1.5.2	Indicators of male quality	9
1.5.3	Female choice	10
1.6	Research questions for this study.....	11
2	METHODS.....	11
2.1	Recording of behavioral data on leks.....	11
2.2	Data collection from tapes	12
2.3	Collection of physical data	13
2.4	Statistical analysis	13
3	RESULTS	13
3.1	Lekking sites.....	13
3.2	Fighting behavior	13
3.3	Physical characteristics and parasite loads	17
4	DISCUSSION	17
4.1	Fighting activity	17
4.2	Territory position	19
4.3	Physical traits and parasites	20
4.4	The significance of fighting for black grouse males.....	21
	ACKNOWLEDGEMENTS	21
	REFERENCES.....	22

1 INTRODUCTION

1.1 Theory on sexual selection: male competition and female choice

Males and females confront each other in the strive to pass forth their own genes to the next generation and improve their overall fitness. While the choosier sex attempts to select the best available partner, representatives of the other sex compete for a chance to get coupled, whether it is by fighting their peers, manipulating or convincing the opposite sex of their quality. Usually, where these kinds of forces are at play, females choose their mates and males struggle for female attention. Males may sometimes be able to force copulations, but in some, especially avian species, females are able to regulate who they mate with.

Females are also commonly the sex that directly invests more in the production and care of offspring both in time and energy and it is not unusual for the female to care for the young alone, receiving little or no assistance from the father. Consequently, the less paternal care or other benefits to the female are offered by the male, the more the female is expected to invest in choosing a mate that maximizes the received benefits and minimizes the costs of mating. It is of utmost significance especially when the mate provides them with nothing besides the sperm to fertilize their eggs (Höglund & Alatalo 1995). Female choosiness regularly leads to direct strategies by males to gain access to females.

Indeed, the mating success of males in a range of animal species is defined through some form of male-male –competition. Males may engage in direct aggressions over females, or maintain their status by more consistently fighting or intimidating other males. Through such encounters, males can gain social dominance, which according to Qvarnström and Forsgren (1998) can be defined as success in contests. Dominant males may enhance their reproductive prospects by preventing lower ranked individuals from accessing mates or resources. Dominance hierarchies are maintained by differences in aggressiveness, fighting ability, body size or weaponry. Fighting may sometimes be reduced by status badges or by signals of condition or fighting ability, allowing subdominant individuals to avoid engaging in a fight which they are likely to lose. A specific type of aggressive interaction between males is the disruption of matings by another male, which in many studies has been used as the sole measure of dominance (e.g. Gratson 1991, Saether *et al.* 1999). Dominance, along with the appropriate status signals, is commonly thought to be linked to male quality. It should thus signal male superiority to females, making it a reasonable assumption that females should primarily choose dominant males for mates. Many studies have been able to demonstrate a clear relation between male mating and reproductive success and male dominance rank (e.g. Alatalo *et al.* 1991, Klinkova *et al.* 2005).

Recent research suggests, however, that the relationship between male dominance and female choice is not always straight-forward. Although discrimination over mates is expected to yield benefits by increasing the chances of pairing with a high quality partner, it may also carry costs in terms of time, energy, and increased risk of predation (Reynolds & Gross 1990). Females may even avoid mating with dominant males if interaction with them would potentially incur costs to them due to male aggression (Ophir & Galef 2003, Moore & Moore 1999) or manipulation (Moore *et al.* 2003). For example, female Japanese quail (*Coturnix japonica*) favor losers of aggressive male-male fights in order to avoid injury by aggressive courtship behaviors by the dominant males (Ophir & Galef 2003). On the other hand, male dominance does not always honestly signal male quality (for a review, see Qvarnström & Forsgren 1998). Dominance has been found to in some species correlate

with for instance inferior paternal care (collared flycatcher: Qvarnström 1997, dark-eyed junco: Ketterson 1992), sperm depletion due to multiple copulations (Harris *et al.* 2005, Pitnick & Markow 1994), worse offspring quality (jackdaw: Verhulst & Salomons 2004), male aggression toward the female (northern elephant seal: Le Boeuf & Mesnick 1990) and increased disease and parasite transmission rate (mice: Freeland 1981, birds: Sheldon 1993).

Perhaps due to these factors, male dominance status does not always predict mating success, or has no detectable influence on female choice. For example Saether *et al.* (1999) argue that female choice is not affected by male dominance, measured as the amount of harassment the male was able to ward off. Moreover, individuals may have different mate preferences due to their own age, experience, size or genotype. These factors may encourage poor competitors to solicit lower quality partners in order to avoid costs of competition for high-quality mates (Fawcett & Johnstone 2003).

1.2 Fighting

When male competition takes the form of fighting, the value of the resource (such as access to mating partners) must be higher than the costs of engaging in agonistic behavior. Therefore, males are expected to learn to assess the potential costs of fighting versus benefits. Rutte *et al.* (2006) reviewed research done on fighting decisions and fight winning and losing and came up with several hypotheses on the causes of such behaviors. Males may be able to assess their situation by estimating their own and/or the opponent's strength and fighting skills. Hence they can either initiate a fight to gain further dominance or resources or avoid the conflict to minimize potential costs in energy and risk of injury. For instance, jumping spider (*Phidippus clarus*) males that have won previous fights are more likely to also win subsequent fights and likewise males that previously lost a fight continue to lose (Kasumovic *et al.* 2010). The loser effect was found to last longer than winner effect but in both, winners and losers, prior fighting experience improved the male's fighting ability.

Fighting requires extensive allocation of energy and the more aggressive the fight, the more exhausting it is for the fighters. Winning males have been shown to suffer less from the exertion or recover faster than losing males, which may indicate their better quality (studies mainly on invertebrates, reviewed in Briffa & Sneddon 2006). The loser of a fight may also avoid subsequent confrontations if they have suffered costs or an injury in previous encounters and are therefore in an even poorer condition to fight (Rutte *et al.* 2006). For instance, female crayfish have been shown by Aquiloni & Gherardi (2010) to directly select the winners of male-male fights for mates.

The regulation of continued aggression may also be influenced by some physiological mechanism that functions during fights, such as hormonal activity (e.g. testosterone levels or stress hormones) which enforce the winner or loser effect. Furthermore, environmental and social variables may influence the level of aggression (Rutte *et al.* 2006). Fight winners may be also determined by species-specific characteristics such as body size, body weight, size of weaponry (e.g. antlers or mandibles), age or physical condition (reviewed in Arnott & Elwood 2009).

1.3 Physical condition and parasites

Genetic and environmental effects determine the male's phenotype, behavior and thereby success. As suggested above, males successful in competing against other males may possess qualities that females (given the opportunity to make the choice) value. Females are likely to look for reliable indicators of male fitness in their behavior or appearance, such as courtship intensity or the secondary sexual characteristics displayed. For instance,

food availability has in some cases been shown to predict courtship intensity by males (e.g. Jennions & Backwell 1998, Wagner & Hoback 1999) and would therefore honestly indicate good male condition and foraging skills that could benefit the female or her offspring. In fact, Gontard-Danek & Möller (1999) propose that on average 9-10% of male mating success can be explained by variation in visible secondary sexual characters typical to the species.

Parasites are known to affect the health and fitness of individuals and may also be apparent in the expression of male secondary sexual traits. For instance, Hamilton and Zuk (1982) found blood parasites to affect male song and brightness in their classical study on North American passerines. Again, pied flycatcher males infected with *Trypanosoma* tended to have on average a lower reproductive success possibly because the parasite affected their general condition and therefore their moult, causing a decrease in the size of males' tail and wing ornaments (Rätti *et al.* 1993). Lower quality males may also have been in poor condition for some other reason and therefore easily infected, while high quality males were able to defend against an infection. High quality males may therefore even be more heavily burdened by parasites yet suffer less from them than lower quality males. Females may evaluate such characteristics when choosing a mate, as they may signal genetic resistance to disease as well as health and vigor.

An "immunocompetence-handicap hypothesis" has been proposed by Folstad *et al.* (1992) upon reviewing studies that demonstrate a decrease in male parasite infections due to castration, and an increase in parasite infections due to the administration of testosterone supplements. According to this hypothesis, the males' responses to parasite infections are self-regulatory through an endocrinological process. Hence male testosterone levels would vary in response to their condition, to either invest in the development and maintenance of secondary sexual characteristics or to boost their immune system by inducing lower testosterone levels. Individuals would therefore suffer a significant decrease in their fitness and lifetime reproductive success if their sexual signals were improved with the expense of their immune defense. This hypothesis emphasizes the reliability of the role of sexual signals as honest signals of viability. Roberts *et al.* (2004), however, point out that in certain species testosterone is not responsible for the expression of sexual traits. Likewise, the role of testosterone may be more ambiguous than shown by Folstad *et al.* (1992), as various other hormonal and immunological factors may appear connected to testosterone levels.

1.4 Lek as a mating system

Lek is a mating system where male-male competition and female choice are explicit: the males assemble into territorial groups during lekking season and matings occur on the lek (Höglund & Alatalo 1995). Males compete over the females, while the latter observe the males and choose their mates. No paternal care is provided by the male, and the territories generally offer females no benefits in the form of shelter, nesting site or food. The only benefit a female gains, then, would be the male's genes for their offspring (Bradbury 1981) and mate choice is thus of great importance. Leks occur in many taxonomic groups (see Höglund & Alatalo 1995 for a review) but avian leks will be the focus of this study. In Finnish avian species, lekking is common in capercaillie, black grouse, ruff and great snipe (Rintamäki *et al.* 1997).

Group leks are thought to have evolved due to reasons of predator avoidance, patchiness of appropriate mating places, settlement on sites where habitats of many females meet (Höglund & Alatalo 1995), better possibilities for females to compare males (Rintamäki *et al.* 1997) or due to *temporal* or *spatial spillover* (compared in Rintamäki *et al.* 1995a).

The *temporal spillover* hypothesis suggests that females copulate on historically successful sites and so lek sites persist over the years, and territories remain in place as long as their resident males survive. The *spatial spillover* hypothesis, on the other hand, implies that as females prefer certain males, neighboring males also receive a few matings by theft, female-female aggression or female mistake, making it useful for weaker males to seek proximity of “hotshots” or attractive males. This may lead to the centrality observed in some leks, e.g. those of black grouse, where central males are usually the most successful (Rintamäki *et al.* 1995, but see Saether *et al.* 2005 who find no effect of centrality on great snipe leks). The most important requirement for the sustainability of a lek is, however, female choice. Females must seek out leks and deliberately arrive to observe and mate with males at the lekking site, while temporal and spatial spillovers perhaps amplify the size and stability of the lek.

Kin selection has also been suggested by Höglund *et al.* (1999) as a possible contribution to the evolution of leks, as males on black grouse leks were found to be more closely related than expected by chance. Black grouse males are philopatric, which may contribute to this finding. Non-successful males may be induced to join leks even when they have little chance of achieving matings themselves, as they thereby increase the size of the lek. Larger leks are favored by females, so this could improve the success of their higher quality relatives and thereby advance the spread of their genes. In a more extensive genetic analysis, however, Lebigre *et al.* (2008) found evidence only of male philopatry but not higher relatedness within leks: males in the area were more closely related than females but there was no proof of lekking specifically with relatives. Kin selection is therefore unlikely to be the cause of lekking behavior, at least in the black grouse.

Fiske *et al.* (1998) found in their meta-analysis that the mating success in males of lekking species correlates positively with lek attendance, display activity, level of aggression, age and the size of exaggerated sexual signals. Territory centrality also predicted better mating success (but see Saether *et al.* 2005), while territory size and male body size showed only a weak positive effect.

1.5 The black grouse mating system

1.5.1 Black grouse leks

The black grouse (*Tetrao tetrix*) is a species in which lekking is the sole reproductive strategy. Leks take place on bogs, fields, lake surfaces or other open grounds, and the position of a lek is usually quite stable throughout years. Matings occur over a short period of time at the turn of April and May, most activity taking place in the early hours of mornings, and before sunset. Females arrive alone or in groups after males and spend about an hour on a few mornings watching males, possibly evaluating them at distance. They then tour male territories, choose a male, copulate usually only once with their chosen mate and lay eggs after a few days. Males cannot force females to copulate, making the matings entirely dependent on female choice (Rintamäki *et al.* 1995b).

Males exhibit characteristic behaviors on the lek, categorized as follows (Koivisto, I. 1965: Behavior of the black grouse, *Lyrurus tetrix* (L.), during the spring display. *Finn. Game Res.*, 26, 5–60, referred in Höglund *et al.* 1997): *Rookooing* is the most concurrent behavior by lekking males, where they stand still, body tilted forward, lyre erect and eye-combs inflated, and produce a well audible whistling sound. In *hissing*, males stand up tall and blow air through their air-sacs producing a hissing sound. Occasionally, males *flutter*, leaping into the air and beating their wings. *Fighting* behavior includes different levels of aggression towards opposing males from sparring to highly aggressive encounters where physical harm is done. When females are present, males may *circle* females, moving

around them to guide them towards the center of their territory, *copulate* (mounts a female, flapping his wings briefly) or *solicit* (attempt to copulate but female walks away) females. When not engaging in the mentioned lekking displays and encounters, males may also feed, walk or stand without displaying.

Males often display at the lek arenas also in the fall season. Rintamäki *et al.* (1999) suggest that this happens for the males to establish their territories already in the fall and maintain their position through constant activity for the spring lek. It may also be of some mate choice significance since females can use the opportunity to evaluate males early.

1.5.2 Indicators of male quality

Usually up to half of all lekking males manage to mate, while only a few of them score the vast majority of the matings (Rintamäki *et al.* 1997, Alatalo *et al.* 1992, Krujtit & de Vos 1988). Successful males attend the lek regularly and spend much of their time at the site; hence they are present more often during female visits (Höglund *et al.* 1997). Besides attendance, acquired dominance status and territory position seem to predict mating success. Dominance is gained over a timescale of several years through consistent effort by the male and territories are defended in a way that the central areas of a lek are most popular and require consistent fighting to hold (Hovi *et al.* 1994, Rintamäki *et al.* 1995a). The effort is necessary as holders of central territories have been shown to get more copulations (Alatalo *et al.* 1991).

Various physical and behavioral components relate to black grouse males' dominance ranks, including male size, eye comb size and redness, blueness of feathers, lek attendance and fighting activity. Territorial (attendance, centrality and territory size) and display cues (fighting activity, tail posture and vocal activity) were found by Alatalo *et al.* (manuscript) to be more variable than morphological traits, and out of these centrality, lek attendance and dominance as a yearling seem to best explain male dominance. High testosterone level, on the other hand, predicts a more central territory and more matings (Alatalo *et al.* 1996b).

Dominance also predicts male viability and fighting ability is indicated by intact ornaments, hence signaling good genes to the females (Alatalo *et al.* 1991). Höglund *et al.* (1997) showed that successful males spend more of their time fighting, both when females are present on the lek and when they are not, while unsuccessful males do more displaying and rookooing. The role of rookooing itself is unclear and contradicting results on the connection of rookooing activity to mating success exist (Rintamäki *et al.* 1997, Koivisto 1965). It may for instance announce male presence reducing fights or attract other individuals (male and female) to the lek, but it is thought to have little significance in female choice.

Although lekking behavior may be more significant in securing matings, black grouse males also signal their fitness with their several distinct sexual ornaments. These include a red eye comb, blue structural color in the feathers and long tail feathers (lyre). The red comb is further positively affected by the elevated testosterone levels observed during the mating season (Alatalo *et al.* 1996b). All these ornaments are displayed by males in lekking activities.

As the color ornaments respond readily to stress, they are a reliable indicator of the male's past stress resistance and potentially of male genetic quality (Siitari *et al.* 2007). The structural blue chroma of the breast feathers of males has been found to correlate positively with mating success and the red color of the comb and wattles may signal fitness through condition dependence. The red coloration is carotenoid-based and nutrition may affect its brightness and in previous studies, carotenoid-based colors have been associated with male health and condition as carotenoids are also required for the benefit of

immunocompetence. The size and color of the red ornaments can therefore function as reliable signals of male condition (e.g. McGraw & Ardia 2003). Siitari *et al.* (2007) found that adult black grouse males had larger and brighter colored combs than juveniles. They also showed that the sexual ornamentation is condition dependent through administering a testosterone treatment to young birds, which significantly reduced the strength of their sexual ornamentation in the following year, whereas vital traits such as wing length and body mass were unaffected by the treatment. Black grouse males are also capable of altering the size of their combs within seconds and display large combs during lekking especially when females are present (Rintamäki *et al.* 2000).

Young males have shorter tail feathers (lyre) which may be an important indication of male age for females. Lyre length is also diminished by *Microfilaria* infection (Rintamäki *et al.* 1992) and its condition is related to overall male health (Rintamäki *et al.* 1997). Hence lyre can be thought of as a reliable indicator of male condition and may reflect in the number of matings a male acquires. The condition effect is of more significance to young males but affects central males little, which implies that it is a secondary cue mainly used when more reliable quality indicators are lacking (Höglund *et al.* 1994). Furthermore, the tail is kept upright with muscle strength when actively lekking, which also requires energy and possibly communicates male quality. Alatalo (1991) found that top males manage to keep their tail ornament intact over the lekking season more often than unsuccessful males.

1.5.3 Female choice

Accurate choice of a high quality male is of great importance, and females are expected to use all available cues to choose well – including the behavioral and physical traits listed above. The direct advantages of successful mate choice to female can be expected to include good quality sperm, predator avoidance and disease or parasite avoidance. These in turn enhance female survival, may improve offspring quality or produce more fertile offspring. It has not been studied in black grouse whether male dominance correlates with female or hatchling survival or condition, in response to disease, parasites or sperm quality. Clutch size or likelihood of fertilization are likely to be irrelevant for the black grouse, as sperm seems to be enough for all fertilizations even among the most dominant males (Alatalo *et al.* 1996a). Polyandry and multiple matings are uncommon and the entire clutch is usually fathered by a single male (Lebigre *et al.* 2007).

Black grouse females do not seem to seek undisturbed copulations as they prefer larger leks where disturbance is more common (Alatalo *et al.* 1992). Although Alatalo *et al.* (1991) saw as many as 16.7 % of the copulations disturbed by another male, the female never mated with the male causing the harassment. Larger leks in fact have a higher total number of matings as well as a higher number of copulations per male (Alatalo *et al.* 1992, Rintamäki *et al.* 1997). Hovi *et al.* (1995) have suggested that on lake ice leks, females may even incite fights between males to assess their dominance.

Females may copy other females' mate choices, amplifying the success rate of the best males (Höglund *et al.* 1990). Copying can be especially useful for young females who have recently immigrated into the area and do not know the males, or have arrived later, which creates a time constraint for observing males. The top male and old females have been shown to mate earlier than other males and young females, which gives newcomers a chance to observe others' choices. Choosing the top male may be difficult and hence costly for females, making copying an efficient strategy.

Black grouse exhibit no strict couple bond, but if the male a female mated with the previous year is alive, then the female chooses the same male again next year (Rintamäki *et al.* 1995a, Rintamäki *et al.* 1997). If not, she mates with the top cock or a male

occupying the territory previously occupied by her previous mate (Rintamäki *et al.* 1995a). Alatalo *et al.* (1991) found the most popular cocks to live longer than unsuccessful ones.

1.6 Research questions for this study

In black grouse, dominance seems to predict mating success and as dominance essentially signifies success in fighting other males, this study addresses male-male fighting behavior in the lek over the mating season. The aim is to gain better understanding of the criteria that females use in their mate choice.

Male dominance has previously been assessed in a study by Alatalo *et al.* (1991) through feeding experiments with yearling males and by observing fights over taxidermic female grouse dummies at the territory border of two males. Additionally, territory centrality (Hovi *et al.* 1994) and time allocation to fighting (Höglund *et al.* 1997) have been associated to dominance. In this study, fights in real lekking situations were observed and the winner of a fight was thought to be the first male to turn away from their opponent. The male that leaves the fight first is likely to be stronger and has demonstrated his dominance to the opposing male. The victorious male may turn safely with little risk of the opponent attacking him from behind and pulling out tail feathers since it could be detrimental for a poorer fighter to get into a new fight with a stronger opponent. If turning behavior is a valid way of evaluating victories, central and successful males are predicted to be the first turner more often.

Besides fighting success, also fighting frequency and intensity are considered: males that invest a lot to territory defense are expected to have better control over their area and therefore succeed in maintaining a central position on the lek. Fighting activity and success are also compared to physical traits and to mating success: good fighters are likely to be in good physical condition to be able to perform well on lek. The study aimed to distinguish the features of fighting behavior that characterize a) a dominant male and b) a male successful in mating, by answering the following specific questions:

- Does fighting frequency or fighting intensity predict turning behavior or mating success?
- Does the number of opponents predict turning behavior or mating success?
- Does the turning behavior predict mating success?
- Do certain physical characteristics or parasite infection correlate with fighting behavior or mating success?
- Does territory centrality relate to fighting behavior or mating success?

2 METHODS

2.1 Recording of behavioral data on leks

The research was conducted as observation of fights between males at four lek sites in central Finland during the spring lek of 2006 in the last weeks of April through to the beginning of May. Prior to the lekking season, video material from the leks in years 2001-2004 was used to formulate hypotheses as to which components of fighting ability are most likely to be significant and to plan the videotaping and procedure for spring 2006.

The research was implemented as part of the research group's yearly lek watch. An observer was present in a hide usually between the hours 2am – 9am, ideally arriving before the males arrived and leaving after the males had departed. The observers drew location and activity maps of the lek every 5 minutes throughout each morning's lekking session, marking the location and current activity of each of the attending birds. Observing the individual behavior of the grouse was enabled as most of the males and many females

are individually marked with distinctive series of colored leg bands, in addition to which some females carry radio transmitters. Time, place and partner in mating were recorded for each mating event. Mating is conspicuous and easily detected though of short duration, as the male mounts a female and flaps his wings briefly.

Additionally, observers videotaped fights between males and identified the fighting males, aiming to get versatile coverage of the interactions. The best coverage in video material is usually from 3-4 am forward as the better light levels made filming easier.

The location and activity data were later tabulated and the males' territory coordinates, attendance and centrality information were obtained from this data. Lek attendance was calculated for each male from the activity maps: the number of sightings for each male were compared to the male for which there were most observations, and males were given an attendance rating as proportion of the attendance of the male that was most often present. The centrality of each male was calculated as the distance of his territory center to the lek center. The center of each male's territory was determined as the median of the coordinates of all observations for that male and the lek center was the median of coordinates of all male sightings over the observation period.

2.2 Data collection from tapes

After the lekking season, the video material of spring 2006 was searched for individual fights between two males, the fights observed in detail, and the features of the fights recorded. The identities of each of the fighters, fighting intensity, and the ending of the fight were studied. Specific attention was paid to the "turning behavior" that finished most fights. Turning behavior was interpreted as follows: as the fight draws to an end, one of the opposing males will usually turn its tail to its opponent. This male was thought to be dominant, as there is less danger of the other male attacking him across the territory border. If, however, the more subordinate male comes to turn around first, the dominant may attack and tear feathers off the opponent's tail. A damaged tail has been recorded to lower the mating success of males (Höglund *et al.* 1994). The winner was therefore considered to be the one who turned away from the fight first.

The confrontations were categorized as follows to three levels depending on the fighting intensity:

Level 1= Threatening: males stand facing each other and there is some stepping back and forth. The fight can last a fairly long time. Fights often take place on the outskirts of lek, among non-mating males, or in the very early or late hours of the day's lekking activities. Turning is often obscure or happens simultaneously.

Level 2= Males may jump against each other but generally there is no physical harm done. The fight often recedes to a "stand-around" resembling fight level 1. Fight may be prolonged and often one male begins to turn but movement of the other male stops it from doing so, and confrontation continues. Turning is usually clearly first by a certain male when confrontation ends.

Level 3= A level 3 fight entails a very aggressive attack where males jump up against each other and attempt to peck the other with their beak and pull feathers out. The confrontation is generally of short duration, and the first turner is usually clear.

Every fight was recorded according to the fight participants and intensity level. The first turner (winner of the fight) was assigned score 1 and loser score 0, or if the result was considered to be a tie with both males turning at the same time, both were given score 0.5. From the fight table, the number of fights per male and the relative winning score were counted. A cross tabulation was then made to compare each pair of males: their common fights and the relative victories and losses altogether. Fighting intensities, numbers of opponents per day and in total for each male were also counted. Further analyses were

done in SPSS: correlations between fighting success and number of fights as well as position on lek and mating success.

2.3 Collection of physical data

In the winter months before the lekking season, males were captured with walk-in traps for ringing and physiological measures at the lek sites, where winter feeding had also been organized. For a detailed description, see Lebigre (2008). All captured birds were weighed and their wing, tarsus and lyre lengths measured (see Siitari *et al.* 2007 for more details) and blood samples obtained in the field. Any blood parasites (mainly *Trypanosoma* and microfilaria) were counted from the blood samples (see Lebigre 2008 for more details).

2.4 Statistical analysis

Two of the lekking sites, Teerisuo and Saarisuo bogs, were included in the analysis. These two sites had the most video material available and the filming was most consistent among the trapping bogs. Video data was gained for 27.4.-6.5.2006 for Teerisuo and 28.4.-7.5.2006 for Saarisuo. Only tapes from the dates 28.4.-6.5. (9 days) were thereby included in the analyses for each of the bogs. Mating success over the entire lekking period was still considered in the analysis, i.e. also copulations seen on 7.5.2006 in Saarisuo.

Independent samples t-test was used for physical characteristics and Spearman's correlation coefficient (r_s) and Mann-Whitney U-test for fighting parameters and Microfilaria-counts. The Bonferroni adjustment (multiplying all p-values with the number of tested outcomes in the correlation table) was used to correct significance levels in multiple correlations. The data was split for male age and site when appropriate.

3 RESULTS

3.1 Lekking sites

The selected sites, Teerisuo and Saarisuo, both have naturally occurring leks on open bogs. Teerisuo is an undisturbed bog while Saarisuo has been influenced by peat harvesting. Some features of the two sites are listed in Table 1.

Table 1: Characteristics of the leks at Teerisuo and Saarisuo bogs.

	Teerisuo	Saarisuo	Total
No. of males associated with the lek	30	33	63
No. of fighting males (from taped fights)	17	10	27
No. of successful males (one or more matings)	7	4	11
No. of copulations recorded	23	38	61
Proportion of all matings by top male	0.35	0.87	
Proportion of level 3-fights recorded (from taped fights)	0.18	0.09	
Total no. of fights taped	842	632	1474

The sites differ somewhat in the number of males present and their activity. However, the differences between the males lekking at different bogs were generally not statistically significant. For the examined behavioral traits (mating success, number of fights, time allocation to fighting, fight intensity, fight winning, number of opponents, distance to lek center), physical characteristics (body mass, tarsus length, lyre length, total size of red eye combs, wing length) and parasite loads (only Microfilaria prevalence considered due to sample size restrictions), adult males did not differ significantly between

sites (all P-values ≥ 0.086). Therefore the males from both sites were combined in all analyses for adult males.

Among young males (born previous summer) the sites differed somewhat in respect to the proportion of fights won (only 3 young males in Teerisuo won any fights, none in Saarisuo, Mann-Whitney U: $Z = -2.216$, $N = 33$, $P = 0.027$), proportion of time spent fighting ($Z = -2.263$, $N = 9$, $P = 0.024$) and Microfilaria count ($Z = -2.281$, $N = 33$, $P = 0.023$), but other characteristics did not significantly differ between sites (P-values ≥ 0.059). For young males the sites were analysed separately only if they differed with respect to the characteristic under analysis.

For analyzing the significance of the various variables to male mating success (mating success: 0= no matings, 1= one or more matings), binary logistic regression was used to show that site has no interaction with the above listed fighting parameters or centrality when considering mating success (binary logistic regression, all interactions with site: $P \geq 0.447$). Therefore, the sites were combined also for the analysis of mating success.

3.2 Fighting behavior

Fights were usually most intense and frequent in the hours 3-5 am, when also most females visited. The vast majority of the recorded fights were between adult males, with only a few young males involved in fights (mean number of fights over the lekking period: adults= 49.4, young= 1.8). Only two young males managed to mate in Teerisuo and no young male mated in Saarisuo. The successful yearlings in Teerisuo were also very active fighters compared to other young males, which created a significant skew among young males.

The recorded number of fights, number of opponents, fighting intensity (as proportion of the highest intensity, level 3 fights out of all the male's fights), fighting success (victories as indicated by turning behavior) and lek attendance all correlated with each other strongly (shown separately for young and adult males in Table 2).

Table 2: Correlations (Spearman's rho, r_s) between the various fighting parameters (total number of recorded fights, total number of opponents, fight intensity and fight winning) and lek attendance in the different age groups of black grouse males in spring lek 2006. For young males, * indicates that values refer to data from Teerisuo only, since none of the young males in Saarisuo won fights. All P-values are Bonferroni-adjusted.

		Adult males (N=30)	Young males (N=33)
Total fights recorded vs. total victories (fights where male turned away first)	r_s	0.913	0.741*
	P	<0.001	<0.001
Total fights vs. total opponents	r_s	0.846	0.999
	P	<0.001	<0.001
Total fights vs. intensity (proportion of level 3 fights)	r_s	0.793	0.838
	P	<0.001	<0.001
Total victories vs. total opponents	r_s	0.901	0.734*
	P	<0.001	<0.001
Total victories vs. intensity	r_s	0.791	0.820*
	P	<0.001	<0.001
Total opponents vs. intensity	r_s	0.869	0.838
	P	<0.001	<0.001
Attendance vs. total fights	r_s	0.865	0.649
	P	<0.001	<0.001
Attendance vs. total victories	r_s	0.832	0.566*
	P	<0.001	<0.001
Attendance vs. total opponents	r_s	0.706	0.651
	P	<0.001	<0.001
Attendance vs. intensity	r_s	0.800	0.671
	P	<0.001	<0.001

Due to the strong intercorrelations of the behavioral parameters and the significant skew in mating success among males, the connections of each of the variables to mating success were determined separately using the Mann-Whitney U-test. The skew is especially strong among young males: only two young males mated during the season and the values for mating success for young males relate to the characteristics of those two individuals.

Males that managed to mate fought more frequently (adults: $Z = -2.467$, $N = 30$, $P = 0.014$, Figure 2A, young: $Z = -3.478$, $N = 33$, $P = 0.001$) and with a significantly higher number of opponents than unsuccessful males (adults: $Z = -2.620$, $N = 30$, $P = 0.009$, Figure 2B, young: $Z = -3.478$, $N = 33$, $P = 0.001$). Successful males also engaged in more high intensity fights (proportion of level 3-fights: adults: $Z = -2.697$, $N = 33$, $P = 0.007$, Figure 2C, young: $Z = -3.859$, $N = 33$, $P < 0.001$).

Finally, a higher proportion of fights won by the male (determined by turning behavior) predicts its mating success (adults: $Z = -2.651$, $N = 30$, $P = 0.008$, Figure 2D, young (only Teerisuo): $Z = -2.937$, $N = 13$, $P = 0.003$).

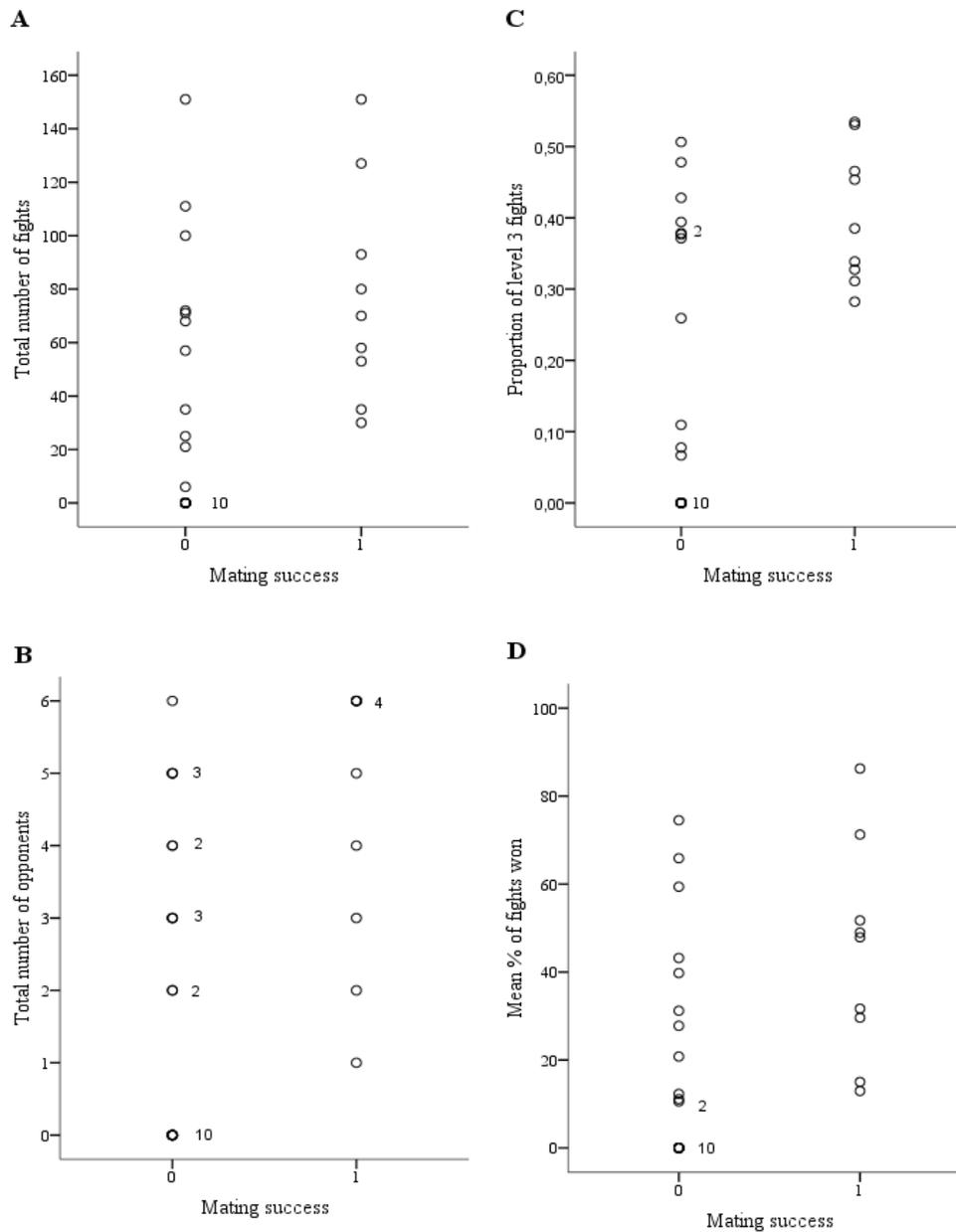


Figure 2: The influence of adult males' fighting behavior characteristics (Figure A: Total number of fights for each male, Figure B: Total number of opponents for each male, C: Fight intensity as proportion of level 3 fights, D: mean % of fights won by the male) on their mating success (0= no matings, 1= male has mated at least once). The numbers beside the circles indicate the number of males with the same result; when there is no number, there is only one male with such result. The figures are for adult males only.

The distance to lek center was calculated for 25 males (Teerisuo: adults= 13, young= 3, Saarisuo: adults= 6, young= 3) that held territories. Centrality did not correlate consistently with any of the fighting parameters or with mating success. However, when analyzing the sites separately, centrality was found to predict a higher total number of fights among adults at Saarisuo lek (distance to lek center vs. total number of recorded fights: $r_s = -0.928$, $N = 6$, $P = 0.008$) while this trend did not exist in Teerisuo ($r_s = -0.212$,

$N= 13$, $P= 0.487$). On the other hand in Teerisuo, the proportion of time spent fighting (observations when male was seen fighting, calculated from the activity maps) was found to correlate negatively with distance to lek center ($r_s= -0.661$, $N= 10$, $P= 0.038$) but in Saarisuo there was no statistically significant connection ($r_s= -0.800$, $N= 5$, $P= 0.104$).

3.3 Physical characteristics and parasite loads

23 males were captured for measurements in Teerisuo (13 young, 10 adults) and 33 in Saarisuo (20 young, 13 adults) before the lekking season. Significant differences in physical traits and parasite infections were found between adult and young males, but when age was controlled for, physiological conditions had little effect on male fighting or mating success, except in the young age class in Teerisuo.

Young males differed from adults (Independent samples t-test, P value for each of the following < 0.001) in weight ($t= -5.267$, $N= 53$), eye comb size (sum of left and right comb size: $t= -6.936$, $N= 54$), wing length ($t = -5.977$, $N= 54$) and mean lyre feather length ($t = -10.602$, $N= 38$). Adult males also had higher *Microfilaria* counts than young males (Mann Whitney U: $Z= -4.939$, $N= 56$, $P< 0.001$). No difference was found between the age groups in tarsus length or infection by other parasites.

Among young males in Teerisuo bog (3 actively lekking young males), body mass seemed to correlate positively with attendance, total number of opponents, total number of recorded fights, fighting intensity and proportion of fights won but after applying the Bonferroni correction, none of these correlations were significant (adjusted P-values all ≥ 0.100). In adult males and young males in Saarisuo such trends were missing.

Microfilaria, *Leucocytozoon* or *Trypanosoma* infections did not correlate with mating success, centrality, total number of fights, number of opponents, proportion of level 3 fights, nor with each other in this data set (no effect of age groups and sites, all Bonferroni-corrected P-values ≥ 0.612).

4 DISCUSSION

4.1 Fighting activity

In this study, behavioral characteristics were found to be consistently more relevant for dominance and mating success than physical traits or parasites. Active fighters showed most persistent aggression, maintained good control over their territory and received most of the copulations. Correlations between fighting frequency, fight intensity, the number of opponents and fight winning seem to indicate that dominant males have to allocate copious amounts of time and energy to territory defense. Physical characteristics and parasite infection were found to have little effect on any fighting parameters or on mating success in this study. Territory centrality was connected to a higher number of fights or more time spent fighting but, unlike in previous studies, centrality did not directly predict mating success. The results do, however, support the findings of earlier research that dominant males are more popular among females and have a higher reproductive success.

Measures of fight winning (determined by the sequence of fight participants turning away from the fight) and evaluation of fighting intensity were approximations done by naked eye but as all were done by the same person, they should be consistent. In cases where two males fought each other frequently, it might imply that they were more equal in dominance – where confrontations were rare, the weaker individual may have suffered from the attack and recognized its subordination, causing it to avoid further fights with the dominant male. The winner of a fight was not always the same unless the opponents represented very different levels of the dominance hierarchy. Therefore, multiple

observations of the fights between males are necessary for the dominance status to be deduced from the fighting behavior.

Winner effects may increase the winner's willingness to fight and aid in winning fights, while loser effects are likely to reinforce a losing male's withdrawal from fights or poor success in them (e.g. Rutte *et al.* 2006). Winner and loser effects are possible also on black grouse leks but this is difficult to ascertain in means similar to previous studies, where fight success has mainly been tested with naïve fighters in laboratory conditions. The observed skew in mating success may, however, be enforced by winner-loser effects since dominant males fight more and win more fights and females seem to select active, dominant fighters as mates. The study by Höglund *et al.* (1990) implies that the mating success of certain males may also be further enhanced through the copying behavior of females.

Successful males have been found by Höglund *et al.* (1997) to spend more time fighting, both when females are present on the lek and when they are not. In the present study, active fighters were also successful in mating and males near the center fought generally more. Some factors about the data collection may have enhanced this effect: there may have been a skew towards recording fights by central males as they were closer to the observer, more easily visible and fought relatively more than peripheral males. Males further away or not visible due to natural barriers (e.g. forest in Teerisuo) may have caused observers to overlook some fights among peripheral males. Nevertheless, the fighting was clearly more intense towards the central areas of the lek and therefore such error is likely to be irrelevant for this study, especially since the males further away from the lek center very rarely get any matings. The variation between leks and between individuals due to any differences in lek characteristics or taping caused by different video tapers was considered in the analyses and the differences were not statistically significant.

The fight numbers used in the analyses are not absolute since not all fights over the whole lekking season (males lek from February to the end of May) were recorded. However, the lek observation was conducted during the active mating season, which is the most significant period for the lekking males. The males are most active during this time, and it is crucial for the top males to successfully defend their territories during this period, since territory holders may change even during the mating season if top males are not in proper condition to maintain sufficient control over their territories.

Turning behavior (which was thought to represent winning of fights) was a relevant indicator of the male's overall control of his territory and mating success. Keeping the tail ornament intact (and upright with muscle strength) is of significance as it has been shown by Alatalo *et al.* (1991) to predict mating success, and attractive males manage to keep their tails undamaged with none or very few feathers torn off their tale ornament in fights. In their study, the male preferred by females on each lek spent more time fighting than other males, and the males successful in mating were able to keep other males further away in the presence of females than those that were unsuccessful. Furthermore, successful males were twice more likely to survive the next 6 months, which implies their greater viability. Such indications of viability connected to a better lyre condition make the lyre possibly relevant for female choice for good genes. Lyre length is also a good indication of male age (Siitari *et al.* 2007, this study). Due to the importance of the intact lyre as a signal of viability, turning behavior is likely to serve as a reliable indication of dominance status between the males.

Since the number of actively lekking young males that held territories and engaged in fighting was low, some analyses could not be performed on young males. Juveniles were on average quite passive with only a few exceptions in Teerisuo. These active young males even managed to mate, which influenced the overall results. However, the yearling males

that mated in Teerisuo were not seen lekking the following year and probably died between the mating seasons. Differences in motivation between males may cause their various behaviors and differences in energy allocation (Kokko 1998), so that poorer quality males that have a weakened chance of survival until the next opportunity to reproduce may benefit from investing all their strength into the present mating season.

Bog topography on each site may also have influenced which males were visible and most often recorded on tape, hence affecting the number of fights observed. Differences between the bogs in fine scale topography could also account for some of the observed differential distribution of matings. As the leks are naturally occurring, there were some differences between the sites. Teerisuo is an undisturbed bog while Saarisuo has a number of ditches due to peat harvesting that may have had some influence on male interactions. Males were capable of jumping over the ditches, but fights may have been less frequent between males from different strips. The great proportion of copulations to one male in Saarisuo may indicate that others have difficulty disrupting or courting the attending females when approaching is more difficult. On the other hand, the difficulty of approaching could have provided an opportunity for a distribution of the matings among several males. The high number of matings for one male therefore could indicate strong female preference.

The principles of a lekking system are not foolproof: local circumstances may also have influence on the outcome. For instance, the center of the Teerisuo lek appears to be shifting slightly from year to year, possibly due to the growth of new trees and the varying quantities of standing water on the site. Lek center may move and mix the male dynamics as old males stay in the same territories in consecutive years if successful. In Saarisuo, feeders used in the winter feeding and equipped with seeds were within top male territories, which may increase the mating skew in their favor if feeders attract females. Furthermore, a seemingly lower quality male in Teerisuo got many matings although it held a territory at the edge of the lek (but removing this male from the analyses had no effect on the results). Feeders were located in his territory and females frequently spent time there to feed. Natural leks are not generally good foraging sites at all, hence the significance of food resources in the study area is not known. Males, however, do not seem to prefer lekking at established feeding sites *per se*. Feeders are placed on naturally occurring lekking sites to improve the accumulation of the winter flock to a certain location for winter capturing.

If the feeding opportunities did, however, somehow attract females to certain territories, the males lekking near feeders may have a mating advantage. Alatalo *et al.* (1991) have showed that when females are within the male's territory, the territory holder is in a strong position regardless of his dominance status. When a female grouse dummy was placed at a territory boundary of two males, fights over the dummy were usually won by the male more attractive to females also in real life, but when the dummy was inside a territory, a territory holder of any status managed to defend the dummy. Previous site knowledge or time of ownership may also increase the value of a resource (such as territory) to an individual, increasing their determination to defend the resource (Qvarnström & Forsgren 1998). Therefore, males who attracted females originally with the feeders in their territory may then have been able to court and guard the females and win fights when females were present in their territory.

4.2 Territory centrality

In many previous studies, territory centrality has been linked to higher dominance status and better mating success (e.g. Hovi *et al.* 1994), but in the data examined here, territory location could not be directly linked to either. This lack of connection could result from

insufficient data, movement of lek centers or random factors and outliers. Alternatively, the effects of centrality may result from some other factor which has not yet been identified.

Implications of the theoretical significance of centrality are provided through a model by Kokko *et al.* (1998) which concludes that the distribution of territories among males is non-random. The model shows that a central territory is generally possessed by an older than average male, which has a history of high fighting rates. Since successful males do not usually try to move their territories closer to the center of the lek, a certain amount of “queue-jumping” also occurs, giving less successful males access towards the center. Territories near the lek center are generally smaller than those at the edges, but when the location is controlled for, the successful males tend to have larger territories than unsuccessful ones even near the center (Hovi *et al.* 1994, Höglund *et al.* 1997). The lek on Teerisuo bog has been drifting in space noticeably over the years, while males that were successful in previous years have apparently continued displaying on the same territory in consequent years. This may contribute to the lack of top males in the current lek center.

Various explanations have been put forward to explain the higher mating success of central males recorded in earlier studies. These include the following: best males are surrounded by worse individuals in hopes of chance copulations; central position requires good fighting ability, and only the best males can hold this position; females favor tight groups of males, searching for the best males (which happen to be in the middle) or the central males (which happen to be the best) (Rintamäki *et al.* 1997, Alatalo *et al.* 1991, Hovi *et al.* 1994). Ultimately, males occupying territories in lek centre have more males around their territories and end up with a higher number of proximate fighting partners. Males closer to lek center in this study were found to engage in more fights or spend more time fighting than peripheral males but central males were not themselves preferred by females. This suggests that the connection of centrality to male fighting activity may be the reason for the higher mating success of central males seen in other studies. Further research would be required to get conclusive evidence of this connection.

4.3 Physical traits and parasites

When secondary sexual characteristics function as honest indicators of the male's condition and inheritable quality, female choice can enhance the quality of their offspring. Møller & Alatalo (1999) found that male secondary sexual characteristics do indeed explain on average 1.5 % of the variation in offspring quality among species, the effect being often stronger in birds. Although the percentage is small, it may influence female choice and population fitness in the evolutionary scale. In addition, the decreased variance may be caused by female choice for the desired traits: the lek paradox expects continual directional selection to deplete genetic variation, reducing diversity between males (Taylor & Williams 1982).

Although the comb size was not found to be significant in this study, it has been found to predict success in earlier research. Rintamäki *et al.* (2000) show that the bright red comb and wattle ornaments of the black grouse males show variability in their size and brightness between males and found the comb size (in captured males) to correlate significantly with testosterone levels. Among the males that received copulations, the comb size also correlated with mating success. Differences in comb size were not detected during fights between successful and unsuccessful males, suggesting that the comb is less significant in male-male interactions.

Parasite infections (measured before the lek) were not found to correlate with fight frequency, number of opponents, the intensity of fights, mating success nor with each other in this data set. However, in a more extensive study on black grouse male physical

condition and parasites (Lebigre 2008), male weight was found to decrease and parasite counts increase over the lekking season (measures before and after the lek). The most successful males were found to lose more weight than others, which indicates a higher cost of lekking and loss of muscle to top males and signals their fitness.

Parasite infection levels were not found to correlate with fighting or mating success among these study populations. Likewise, Höglund *et al.* (1992) found no connection between parasitic infection and mating success or male survival but top males in their data seemed to be less often infected with the protozoan *Leucocytozoon lovati* than other males. Black grouse body weight also correlated negatively with the parasite load in their study.

4.4 The significance of fighting for black grouse males

When choosing mates, black grouse females seem to pick mainly old, dominant males that invest a great deal of energy to lekking and show consistent good control of their territory. Such males must maintain a high physical condition in order to survive the strain of the lek and still survive to the next mating season. By mating with these top males, the female's offspring might also be of higher quality and have higher fitness.

Although the central position of a male on the lek has been thought to be highly significant, the results of this study suggest that fighting activity and dominance are more important for male success than centrality *per se*. Such were also the implications of a study by Hovi *et al.* (1995) on ice leks, where territories are not fixed in space. There females seem to directly assess the males' fighting success: they may even incite fights between males and mate with the winner. Males successful in fighting off competing males were more often successful in securing matings.

High quality males can avoid overinvesting in reproduction in a way that it would reduce their survival given they have the sufficient quality and resources (Grether 1997). In a variety of species the male characteristics that predict mating success also relate to the longevity of adult males, the effect being the strongest in lekking species (reviewed by Jennions *et al.* 2001). Successful black grouse males have been shown to live longer (Alatalo *et al.* 1991), thereby supporting this view. In order to maximize one's lifetime reproductive success, a male is therefore expected to allocate energy to reproductive efforts only in proportion to its condition. Some exceptions are found in young males that lek actively in their first year but die soon after.

To conclude, although physiological characteristics of males seem to have less direct significance on black grouse male mating success than continuous lekking performance, the male must be in good condition in order to gain dominance. It appears that fighting behavior in combination with age-revealing and condition-related physical characteristics such as lyre length signal male quality well. If females are able to read these signs, they should be able to pick out the highest quality mates. After all, large leks – where behavioral aspects of males are important and interactions between males can be observed by females – have been favored over males displaying alone in the evolution of the species.

ACKNOWLEDGEMENTS

I want to thank my supervisors Heli Siitari and Rauno Alatalo, Christophe Lebigre for data and advice and the observers and videotapers at leks in spring 2006. Funding for the study was received from the Academy of Finland and Societas Biologica Fennica Vanamo. Data collection was financed by the Finnish Centre of Excellence in Evolutionary Ecology (2001-2006) and Evolutionary Research (2007-2012) funded by the Academy of Finland.

REFERENCES

- Alatalo, R.V., Burke, T., Dann, J., Hanotte, O., Höglund, J., Lundberg, A., Moss, R., Rintamäki, P.T. 1996a: Paternity, disturbance and female choice in lekking black grouse. – *Anim. Behav.* 52: 861-873
- Alatalo, R.V., Höglund J., Lundberg A., Rintamäki P.T., Silverin B. 1996b: Testosterone and male mating success on the black grouse leks. *Proc.R.Soc.Lond. B.* 263: 1697-1702
- Alatalo, R.V., Höglund, J., Lundberg, A. 1991: Lekking in the black grouse – a test of male viability. *Nature* 353
- Alatalo, R.V., Höglund, J., Sutherland, W.J. 1992: Evolution of black grouse leks: female preferences benefit males in larger leks. *Behav. Ecol.* 3: 53-59
- Aquiloni L. & Gherardi F. 2010: Crayfish females eavesdrop on fighting males and use smell and sight to recognize the identity of the winner. *Anim. Behav.* 79:265-269
- Bradbury, J.W. 1981: The evolution of leks. In R.D. Alexander & D.W. Tinkle, eds.: Natural selection and social behaviour. pp 138-169. New York and Concord: Chiron Press
- Fawcett, T.W. & Johnstone, R.A. 2003: Mate choice in the face of costly competition. *Behav. Ecol.* 14: 771–779
- Fiske P., Rintamäki P.T., Karvonen E. 1998: Mating success in lekking males: a meta-analysis. *Behav. Ecol.* 9:382-338
- Folstad, I. & Karter, A.J. 1992: Parasites, bright males, and the immunocompetence hypothesis. *Am. Nat.* 139: 603–622
- Freeland, W.J. 1981: Parasitism and behavioural dominance among male mice. *Science* 213: 461-462
- Gontard-Danek M.C: & Möller A.P. 1999: The strength of sexual selection: a meta-analysis of bird studies. *Behav. Ecol.* 10:476-486.
- Gratson M.W. 1991: Male-dominance and copulation disruption do not explain variance in male mating success on sharp-tailed grouse (*Tympanuchus phasianellus*) leks. *Behaviour* 118: 187-213
- Grether G.F. 1997: Survival cost of an intrasexually selected ornament in damselfly. *Proc.R.Soc.Lond. B* 264:207-210
- Hamilton W.D. & Zuk M. 1982: Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Harris W.E. & Moore P. J. 2005: Female Mate Preference and Sexual Conflict: Females Prefer Males That Have Had Fewer Consorts. – *Am. Nat.* 165

- Hovi M., Alatalo R.V., Höglund J., Lundberg A., Rintamäki, P.T. 1994: Lek center attracts black grouse females. – *Proc. R. Soc. Lond. B* 258: 303-305
- Hovi M., Alatalo R., Siikamäki P. 1995: Black grouse leks on ice: Female mate sampling by incitation of male competition? – *Behav. Ecol. Sociobiol.* 37:283-288
- Höglund J., Alatalo R.V., Lundberg A. 1990: Copying the mate choice of others? Observations on female black grouse. – *Behaviour* 114:1-4
- Höglund J., Alatalo R.V., Lundberg A. 1992: The effects of parasites on male ornaments and female choice in the lek-breeding black grouse (*Tetrao tetrix*). *Behav. Ecol. Sociobiol.* 30:71-76
- Höglund J., Alatalo R.V., Lundberg A., Rintamäki P.T., Lindell J. 1999: Microsatellite markers reveal the potential for kin selection on black grouse leks. *Proc. R. Soc. Lond. B* 266: 813-816
- 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 University Press
- Höglund J., Johansson T., Pelabon C. 1997: Behaviourally mediated sexual selection: characteristics of successful male black grouse, *Anim. Behav.* 54:255-264
- Jennions M.D. & Backwell P.R.Y. 1998: Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behav. Ecol.* 9:605-611
- Jennions M.D., Møller A.P., Petrie M. 2001: Sexually selected traits and adult survival: a meta-analysis. *Q Rev Biol* 76: 3-36
- Kasumovic M.M., Elias D.O., Sivalingham S., Mason A.C., Andradea M.C.B. 2010: Examination of prior contest experience and the retention of winner and loser effects. *Behav. Ecol.* 21:404-409
- Ketterson E.D., Nolan V. Jr., Wolf L., Ziegenfus C. 1992: Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). – *Am. Nat.* 140: 980-999
- Klinkova E.J., Hodges K., Fuhrmann K., de Jong T., Heistermann M. 2005: Male Dominance Rank, Female Mate Choice and Male Mating and Reproductive Success in Captive Chimpanzees. *Int J Primatol* 26, No. 2
- Kokko H. 1998: Good genes, old age and life-history trade-offs. *Evol Ecol* 12:739-750
- Kokko H., Lindstrom J., Alatalo R.V., Rintamaki P.T. 1998: Queuing for territory positions in the lekking black grouse (*Tetrao tetrix*). *Behav. Ecol.* 9: 376-383

- Krujtit J.P. & de Vos G.J. 1988: Individual variation in reproductive success in male black grouse, *Tetrao tetrix* L. In T.H. Clutton-Brock, ed.: Reproductive success. Studies of individual variation in contrasting breeding systems. pp. 279-290. Chicago: University of Chicago Press.
- Lebigre C., Alatalo R.V., Siitari H., Parri S. 2007: Restrictive mating by females on black grouse leks. *Mol. Ecol.* 16:4380-4389
- Lebigre C. 2008: Mating behaviour of the black grouse: genetic characteristics and physiological consequences. *Jyväskylä Studies in Biological and Environmental Science* 196:1-32
- Lebigre C., Alatalo R.V., Forss H.E., Siitari H. 2008: Low levels of relatedness on black grouse leks despite male philopatry. *Mol. Ecol.* 17:4512-4521
- Le Boeuf, B.J. & Mesnick, S. 1990: Sexual behaviour of male northern elephant seals: I. Lethal injuries to adult females. – *Behaviour* 116: 143-162
- McGraw K.J. & Ardia D.R. 2003: Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *Am. Nat.* 162: 704-712
- Møller A.P. & Alatalo R.V. 1999: Good-genes effects in sexual selection. *Proc. R. Soc. Lond. B* 266:85-91
- Moore A.J. & Moore P.J. 1999: Balancing sexual selection through opposing mate choice and male competition. *Proc. R. Soc. Lond. B* 266:711-716
- Ophir A.G. & Galef B.G. 2003: Female Japanese quail that 'eavesdrop' on fighting males prefer losers to winners. *Anim. Behav.* 66: 399-407
- Pitnick S. & Markow T.A. 1994: Male gametic strategies: sperm size, testis size, and the allocation of the ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. – *Am Nat.* 143: 785-819
- Qvarnström A. 1997: Experimentally increased batch size increases male competition and reduces male paternal care in the collared flycatcher. *Proc. R. Soc. Lond. B* 264: 1225-1231
- Qvarnström A. & Forsgren E. 1998: Should females prefer dominant males? *Trends Ecol Evol* 13:498-501
- Reynolds J.D. & Gross M.R. 1990. Costs and benefits of female mate choice: is there a lek paradox? *Am. Nat.* 136:230–243
- Rintamäki P.T., Alatalo R.V., Höglund J., Lundberg A. 1995a: Male territoriality and female choice on black grouse leks. *Anim. Behav.* 49: 759-767
- Rintamäki P.T., Alatalo, R.V., Höglund, J., Lundberg, A. 1995b: Mate sampling behavior in black grouse females. *Behav. Ecol. Sociobiol.* 37:209-215

- Rintamäki P.T., Hovi M., Alatalo R.V. 1997: Miten seksuaalivalinta toimii teeren soittimella. *Suomen Riista* 43: 48-55
- Rintamäki P., Höglund J., Karvonen E., Alatalo R.V., Björklund N., Lundberg A., Rätti O., Vouti J. 2000: Combs and sexual selection in black grouse (*Tetrao tetrix*) *Behav. Ecol.* 5:465-471
- Rintamäki P.T., Karvonen E., Alatalo R.V., Lundberg A. 1999: Why do black grouse perform on lek sites outside the breeding season? *J Avian Biol* 30:359-366
- Roberts M.L., Buchanan K.L., Evans M.R. 2004: Testing the immunocompetence handicap hypothesis: a review of the evidence. *Anim. Behav.* 68: 227–239
- Rutte C., Taborsky M. & Brinkhof M.W.G. 2006: What sets the odds of winning and losing? *Trends Ecol Evol* 21:16-21
- Rätti O., Dufva R., Alatalo R.V. 1993: Blood parasites and male fitness in the pied flycatcher. *Oecologia* 96:410-414
- Sæther S.A., Baglo R., Fiske P., Ekblom R., Höglund J., Kålås J.A. 2005: Direct and Indirect Mate Choice on Leks. *Am. Nat.* 166: 145–157
- Saether S.A., Fiske P., Kalas J.A. 1999: Pushy males and choosy females: courtship disruption and mate choice in the lekking great snipe. *Proc.R.Soc.Lond. B.* 266: 1227-1234
- Sheldon B.C. 1993: Sexually transmitted disease in birds: occurrence and evolutionary significance. *Philos. Trans. R. Soc. London Ser. B* 339: 491-497
- Siitari H., Alatalo R.V., Halme P., Buchanan K.L., Kilpimaa J. 2007: Color Signals in the Black Grouse (*Tetrao tetrix*): Signal Properties and Their Condition Dependency. *Am. Nat.* 169: supplement 81-92
- Verhulst S. & Salomons H.M. 2004. Why fight? Socially dominant jackdaws, *Corvus monedula*, have low fitness. *Anim. Behav.* 68: 777-783
- Wagner W.E. & Hoback W.W. 1999: Nutritional effects of calling behavior in the variable field cricket. *Anim. Behav.* 57:89-95