Master of Science Thesis

Timing of reproductive effort as an alternative mating strategy in young black grouse (*Tetrao tetrix*) males

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ABSTRACT

Sexual selection generates competition over mates producing differences in reproductive success between individuals. The life history theory predicts that because of scarce resources individuals face the problem in allocating energy to different functions such as growth, survival, and reproduction. As a consequence, older age, large body size, and impressive sexual ornaments are the common characters of dominant individuals, who are often superior in competition over mates thus enjoying the highest reproductive success. Nevertheless, young or unfit individuals may have alternative mating strategies which assist them to avoid competition with superior individuals and increase their reproductive success. In this study timing of reproductive effort as a potentially alternative mating strategy of young lekking black grouse (*Tetrao tetrix*) males was investigated. The behavioural (lek attendance and fighting rate) features of yearling and adult males were compared, and the effect of morphological (body mass and tail length) traits on the behaviour were studied. The large long-term dataset was gathered in years 2003–2013 from three study sites, and analysed by generalized linear mixed effects models (GLMM). Yearling males, who were the most present on the lek arena, scheduled their reproductive effort later in the lekking season compared to adult males. The yearling males showing this alternative mating strategy proved to be of a high quality: compared to other yearlings, they were diligently present on the lek arena, fought actively and had larger body mass. Probably they were able to invest substantially more to the lekking season than most of the yearlings, but less than adults, and therefore profited from the alternative mating strategy. Later timing of effort in yearling males may also set more selection pressure for adult males by delaying the decrease of intensive competition in the end of the lekking season. Hence, this study supports indirectly the idea that endurance rivalry may operate on black grouse leks.

TIIVISTELMÄ

Seksuaalivalinta aiheuttaa yksilöiden välille kilpailua parittelukumppaneista, minkä johdosta osa yksilöistä lisääntyy toisia enemmän. Elinkiertoteorian mukaan yksilöt eivät niukkojen resurssien vuoksi pysty tehokkaasti kohdentamaan energiaa samanaikaisesti useisiin toimintoihin, kuten kasvuun, selviytymiseen ja lisääntymiseen. Ikä, suuri koko ja näyttävät seksuaaliornamentit ovat seksuaalivalinnassa menestyvän yksilön merkkejä, sillä tällaisilla yksilöillä riittää energiaa elintärkeiden toimintojen lisäksi myös lisääntymiseen. Tavallisesti ne menestyvätkin parhaiten kilpailussa parittelukumppaneista. Nuoret tai huonokuntoiset yksilöt voivat kuitenkin turvautua vaihtoehtoisiin lisääntymisstrategioihin välttääkseen suoraa kilpailua dominoivien yksilöiden kanssa ja parantaakseen lisääntymismenestystään. Tässä tutkimuksessa perehdyttiin nuorten teerikukkojen (*Tetrao tetrix*) soidinvireyden ajoittamiseen vertaamalla 1-vuotiaiden ja aikuisten kukkojen soidinkäyttäytymistä eli läsnäoloa ja tappeluaktiivisuutta, sekä morfologisten ominaisuuksien eli ruumiinpainon ja pyrstön pituuden vaikutusta soidinkäyttäytymiseen. Mittava pitkäaikaisaineisto kerättiin vuosina 2003–2013 kolmelta keskisuomalaiselta soitimelta. Aineisto analysoitiin lineaarisia sekamalleja (GLMM) hyväksikäyttäen. Eniten soitimella läsnä olleiden nuorten kukkojen havaittiin ajoittavan soidinvireytensä aikuisia kukkoja myöhemmin. Tätä vaihtoehtoista lisääntymisstrategiaa noudattavat nuoret kukot olivat paitsi ahkerasti läsnä soitimella, myös aktiivisia tappelijoita ja kooltaan suurempia kuin muut 1-vuotiaat kukot. Todennäköisesti nämä nuoret kukot pystyivät panostamaan soidinkauteen huomattavasti ikätovereitaan enemmän, mutta kuitenkin aikuisia kukkoja vähemmän, minkä johdosta ne ehkä hyötyivät myöhemmästä soidinvireyden ajoituksesta eniten. Nuorten kukkojen vaihtoehtoinen lisääntymisstrategia voi asettaa lisää valintapaineita myös aikuisille kukoille hidastamalla kilpailun vähenemistä soidinkauden lopulla. Tämä tutkimus osoittaakin epäsuorasti, että niin sanotulla kestävyyskilpailulla ("endurance rivalry") voi olla sijansa teeren seksuaalivalinnassa.

Contents

1. INTRODUCTION

1.1. Basics of sexual selection

Sexual selection is based on competition over mates leading to situation where some individuals receive more copulations and produce more offspring than others (Darwin 1859). Mechanisms operating on competition over mates may be based on a competition within a sex (intrasexual selection) or on a mate choice between sexes (intersexual selection, Andersson 1994). Intrasexual selection occurs mostly between males, whereas intersexual selection is typically a female choice of available males. This pattern is explained by the factors that generally limits genders' reproductive success: males are typically limited by access to females, whereas females are limited by access to resources (Davies et al. 2012). Males generally have greater reproductive potential than females since they are able to produce more offspring in a given time than females are. Consequently, males invest in increasing the number of their partners, whereas females invest in quality of offspring and in parental care. This makes females generally more selective ones in choosing a partner since a partner of a high quality is able to offer more resources and/or better genes for a female and her offspring than is a male of a low quality.

Sexual selection is one process that has led to sexual dimorphism between genders in many species (Darwin 1871). Dimorphism can be divided in three parts. Primary sexual traits are differences in copulatory organs of males and females, while ecological sexual traits refer to ecological differences between sexes such as distinct foraging manners. These two parts of dimorphism are beneficial purely from the survival point of view: different copulatory organs ensure reproduction mechanically, and ecological differences such as different foraging manners decrease competition between genders (Andersson 1994). However, the third part of dimorphism, secondary sexual traits such as large body size, behaviour, ornaments, or weaponry seem to have developed just because of sexual selection (Darwin 1871, Andersson 1994, Savalli 1995). Nowadays it is widely accepted that secondary sexual traits have developed to act as weapons and signals in mate competition and in mate choice (Andersson 1994).

Mechanisms of intrasexual selection have traditionally been separated broadly in two forms: pre- and post-copulatory sexual selection (Andersson 1994). Within that, there are four forms: sperm competition, scramble competition, endurance rivalry, and contests. Sperm competition is based on males' ability to displace competitors' sperm, produce sperm frequently, and guarding the females from other males. In scramble competition, it is crucial that males locate females before other males, leading e.g. to highly evolved sense organs of males in many arthropod species. In endurance rivalry, males able to maintain mating behaviour or other sexual traits through the whole mating season receive more opportunities to copulate than less durable competitors. The most successful males of contests have traits such as weapons, large body size, or threat signals which help them to win, and consequently increase their mating opportunities.

1.2. The function of secondary sexual traits in sexual selection

1.2.1. Intersexual selection

Secondary sexual traits have an important role in female mate choice by acting as signals of a male's quality (Berglund et al. 1996). Two major theories have explained this pattern. Firstly, according to Fisher's reinforcing theory males with an extreme feature survive better than other males (Fisher 1930 quoted by Andersson 1994). Females favouring the

males with such feature would produce offspring that have a survival advantage. The theory assumes that both the males' better survival and females' interest in such males are heritable, and as the consequence the amount of such males and females increases in the population. The feature of males evolves over the time until it has become so exaggerated it begins to reduce males' survival. This begins to restrict the selection process. Another theory is called indicator mechanism theory (e.g. Williams 1966 and Zahavi 1975 quoted by Andersson 1994). Accordingly, secondary sexual traits may reduce males' survival and thus act as cues of males' genetic quality for females since males able to live with such feature may pass on their quality to offspring.

Inconsistent with both the major theories, it is debated whether secondary sexual traits really reduce survival of their bearer since there is limited empirical evidence (Kotiaho 2001). Furthermore, there is evidence of males with the most impressive traits having greater longevity than males with smaller traits, and secondary sexual traits thus signalling males' prevailing condition (Jennions & Møller 2001). However, there is no doubt that females often prefer partners with impressive secondary sexual traits (e.g. Höglund & Alatalo 1995, Berglund et al. 1996, Davies et al. 2012, but see Qvarnström & Forsgren 1998). There is also some evidence of offspring fathered by impressive males being more viable than offspring fathered by less impressive males (e.g. Norris 1993, von Schantz et al. 1993). Furthermore, studies concerning species with paternal care such as house finch (*Carpodacus mexicanus*, Hill 1991) and blue grosbeak (*Guiraca caerulea*, Keyser & Hill 2000) have shown that impressive males are the most capable of offering resources for females and offspring. Thus, secondary sexual traits may indicate a male's quality as a parent and maybe also his genetic quality, but the mechanisms behind these patterns are a lot more complex than both the reinforcing theory and indicator mechanism theory assume.

1.2.2. Intrasexual selection

Secondary sexual traits are crucial in male competition over females. Weapons such as antlers and spurs are themselves beneficial in straight combats, well-developed sense organs help to find a mate in scramble competition, large testicles ensure success in sperm competition, and high body mass assists endurance (Andersson 1994). However, secondary sexual traits may also act as signals of a male's social dominance revealing his good condition and competitiveness. Consequently, inferior competitors are able to avoid contact with superior competitors which saves energy and time, and decreases the probability of getting injured.

Often social hierarchies of males determine their reproductive success as females prefer to copulate with dominant males (e.g. Andersson 1994, Berglund et al. 1996). Features acting as signals in male contests are multiple: they may be morphological such as ornaments or weapons, behavioural such as intimidation, related to a male's age or body size, or mixture of these (Berglund et al. 1996). In several studies signals have been found to be honest, as well. For example, collared flycatcher (*Ficedula albicollis*) males with relatively large forehead patches win territory contests more likely, and have a female in a shorter time than males with smaller patches (Pärt & Qvarnström 1997). Furthermore, calls of baboon (*Papio cynocephalus ursinus*) males change with their dominance rank dominant males calling more frequently, more loudly, and for longer than inferior ones (Fischer et al. 2004).

In several species, body size and age are the major features determining males' success in contest competition, and thus also in reproduction (Briffa & Sneddon 2007). For example, in species such as northern elephant seal (*Mirounga angustirostis*) and red deer (*Cervus elaphus*) reproductive success increases with larger body mass (reviewed by

Andersson 1994). Furthermore, the reproductive success of both elephant seal males and red deer stags is the highest in prime age. Smaller males avoid direct interactions with dominant males: in elephant seals the body size and in red deer the size of antlers are the most important signals in estimating the competitiveness of a contestant.

Body size is also strongly connected with a male's endurance. Male bullfrogs (*Rana catesbeiana*) with greater body mass in the beginning of the mating season are able to show dominant behaviour longer than lighter individuals (Judge & Brooks 2001). They lose their weight slower during the season, but have lost more of their weight by the end of the season than lighter males. Similar pattern have been detected e.g. in elephant seals (*Mirounga* spp., Deutsch et al. 1990 quoted by Andersson 1994, Galimberti et al. 2007), and in red deer in which prime-aged males having the highest reproductive success lose more of their body mass than younger or older individuals (Yoccoz et al. 2002).

1.3. Alternative mating strategies

According to the life history theory individuals are exposed to trade-offs as they need to allocate energy between different functions (Stearns 1992). Reproduction today may reduce growth or survival of an individual, weaken its condition, or damage its future reproduction. Consequently, not only species but also individuals within species have different reproductive strategies. Generally, males of larger size and with more conspicuous morphological traits are more successful in male competition over females than are smaller and inconspicuous males (Andersson 1994). However, in several species males of inferior competitive skills have been detected to resort to alternative mating strategies to avoid direct competition and to increase their mating success.

Alternative mating strategies may be determined through two mechanisms of which the first one is genetic (Davies et al. 2012). In this case there exist two or more genetic morphs of males in a population, all the morphs having equal average fitness. The classic example are side-blotched lizard (*Uta stansburiana*) males which have three morphs differing in the colour of throats and territorial behaviour (Sinervo & Lively 1996). All the morphs, and thus all the strategies are under frequency-dependent selection fluctuating in a population.

The second mechanism operates through a male's current condition (Davies et al. 2012). Males of e.g. smaller size resort to an alternative strategy until they have grown larger because they are facing the problem in allocating energy between growth and reproduction (Stearns 1992). As small individuals they are forced to "make the best of a bad job" and often reproduce less than bigger males (Davies et al. 2012). Such behaviour have been detected e.g. in ungulates (Mysterud et al. 2008, Mason et al. 2012, Tennenhouse et al. 2012) and in anurans (Andersson 1994). In some species such as dung beetle (*Onthophagus taurus*) some males are forced to use an alternative strategy through their whole life since environmental conditions during developmental stages determine characteristics of a male (Emlen & Nijhout 1999).

Age is often one of the major factors affecting body size and morphological traits of males (Clutton-Brock 1988). For example, young Alpine chamois (*Rupicapra rupicapra*, Mason et al. 2012) and red deer (Mysterud et al. 2008) males are inferior competitors compared to older ones. The alternative mating strategy used by young stacks is scheduling their reproductive effort later in the rutting season than adult males do.

1.4. Lek as a mating system

Sexual selection plays especially visible role in lekking species because of the lek having many unusual characteristics compared to other mating systems. As a consequence,

lekking species have received a lot attention in the research of sexual selection (Andersson 1994, Höglund & Alatalo 1995).

The traditional definition of the lek as a mating system contains four preconditions (Bradbury 1981). Firstly, males of lekking species do not offer paternal care for their offspring. The only thing they provide for the next generation are genes. Secondly, the leks are arenas where most of the matings occur, and where males aggregate although it offers no resources such as food or cover for them. Thirdly, for females the lek offers just one significant resource: males. Lastly, females are able to choose their partner on the lek arena. However, the four requirements should not be interpreted too strictly, but preferably as a continuum (Höglund & Alatalo 1995). Rare species fill the criteria fully, but many other are reasonable close to them.

Sexual selection among males is rather strong not only in the lek, but also in many other polygynous mating systems (Höglund & Alatalo 1995). Strong selection and competition cause one of the most peculiar features of the leks: highly skewed mating success of males. In lekking species generally 10–20 % of males receive 70–80 % of all copulations (Mackenzie et al. 1995).

1.5. The goals of the study

Black grouse (*Tetrao tetrix*) is a lekking species of order Galliformes. Leks of black grouse consist of dense clustered males defending their territories (Hovi et al. 1994). Mating skew of males is substantial: the top male receives 50–100 % of all copulations of the certain lek (Alatalo et al. 1992), and altogether < 10 % of males receive half of all copulations (Kervinen 2013). Males are not able to force females to copulate, so the final decision of mating is made by a female (Rintamäki et al. 1995). However, males can increase their mating success through several ways. Successful males are regularly present and active fighters on the lek arena (Höglund et al. 1997). Active fighting is a precondition for occupying and maintaining the central territory on the lek arena (Hämäläinen et al. 2012), and central territorial males, again, are more popular amongst females than are peripheral males (Alatalo et al. 1991, Hovi at al. 1994, Rintamäki et al. 1995, Hämäläinen et al. 2012). Gaining on the dominant status and thus the central territory on the lek arena often demands males' contribution of several years (Kokko et al. 1998). A large body mass correlates positively with the fighting rate of males, and thus indirectly affects males' mating success and dominance status (Hämäläinen et al. 2012). From three morphological traits, the size of eye combs, the length of a lyre (tail), and the amount of blue chroma in breast feathers, only the amount of blue chroma has detected to correlate positively with males' mating success (Siitari et al. 2007). In summary, contests between males typically determine males' dominance status, the position of a territory, and thus also probabilities for mating, whereas female choice defines males' mating success (Höglund & Alatalo 1995).

Age has a considerable meaning in mating success of black grouse males. Eye combs, lyres, and blue chroma of plumage of adult males are more impressive than those of young males (Kervinen et al. 2014). These ornaments are together with the dominance status cues of a male's higher age revealing that a male has got through viability selection (e.g. Kokko 1997). Hence, young males are inferior competitors in male-male competition comparing to adults, and less attractive to females than adult males.

Black grouse males seem to have different life history strategies: males who display on the lek and are territorial already in their first year are shorter lived than males who start displaying not until in their second year (Kervinen et al. 2014). Because of superiority of adult males in male competition, yearling males taking part to the lek may have tactics to avoid competition. As most of the copulations take place on the leks (Alatalo et al. 1996,

Lebigre et al. 2007) and females prefer to mate with central territorial males (Alatalo et al. 1991, Hovi at al. 1994, Rintamäki et al. 1995, Hämäläinen et al. 2012), the only way for yearling males to avoid competition would be scheduling their reproductive effort differently from that of adult males. Such pattern has been found in some lekking ungulates (e.g. Alpine chamois, Mason et al. 2012, and red deer, Mysterud et al. 2008), but not in any lekking bird species.

To study the question, firstly changes in attendance and fighting rate of males over the whole season were quantified as these two are the major factors determining a male's mating success (Höglund et al. 1997, Hämäläinen et al. 2012). Secondly, the repeatability of behaviour of males of different ages was calculated. Thirdly, males' response in terms of attendance and amount of fighting in presence of females and the total number of copulations were investigated. Lastly, changes in attendance and fighting rate of males in relation to body mass and length of lyre were quantified as it is known that body mass correlates positively with a male's fighting rate (Hämäläinen et al. 2012), and that the role of a lyre is still uncertain in sexual selection (e.g. Rintamäki et al. 2001, Siitari et al. 2007, Hämäläinen et al. 2012).

2. MATERIALS AND METHODS

2.1. Study population

Field data was gathered in 2003–2013 from 3 lekking sites located in Central Finland (ca. 62º15´N; 25º00´E). Two of the sites were peat harvesting areas and one was a protected bog in a natural state. The lek sizes in the study sites varied between 6–56 territorial males. Local hunting clubs refrained from hunting in the bogs and nearby areas so the age structure of black grouse populations of the research areas was considered to be natural.

2.2. Winter captures, morphological measurements and behavioural data

Birds were captured from January to March using walk-in traps baited with oats. All the traps were sprung at the same time and after that immediately covered with dark clothes to calm down birds. Every bird was individually removed from the traps to fabric bags and taken to a hide hut for handling. After handling birds were set free.

Each bird was leg banded with an aluminium ID ring and 3 plastic colour rings to make it possible to identify them on the lek from distance. Birds were weighed in fabric bags (to the nearest 10 g), and the left and right outermost lyre (tail) feathers were measured from base to tip (to the nearest 1.0 mm). Birds were aged as yearlings or older (hereafter adults) by plumage differences. Yearlings have more brownish colouration in their plumage and their first primaries are sharper than those of adults (Helminen 1963).

Behavioural data was gathered in the turn of April and May, when the majority of copulations occur. Leks were observed from hides between 3 and 9 a.m. Attendance and fights of males were recorded in activity maps. Drawing activity maps focused on moments, when no females were present on the lek arena. If a male was observed on the lek arena at least once during the observation morning, it was recorded to be present. The total number of copulations and the highest number of females observed at the same time on the lek arena were recorded, as well. Based on the activity maps, daily lek attendance of each male (hereafter attendance) was calculated as a relative percentage value of the so called top male's attendance, who was the male most present (100 %) on each morning. Daily fighting rates (hereafter fighting rate) were calculated as a relative percentage values of time which each male fought of its own attendance on certain mornings.

2.3. Statistical analyses

Males, who were present ≥ 50 % of lekking days and thus had permanent territories, were selected for the analyses. Both age classes were divided further into two groups by attendance: highly attending males had been present on the lek arena ≥ 80 % of the top male's attendance on each day, and lowly attending males < 80 % of the top male's attendance on each day. The threshold value of 80 % was selected as males with < 80 % lek attendance over the lekking season typically have very low if any mating success, whereas after the threshold mating success increases rapidly (Kervinen 2013).

Lekking days were scaled so that on the day 0 ≥ 50 % of all observed copulations had occurred. Thus the day 0 represents the copulation peak.

To investigate the repeatability or better known as the intraclass correlation coefficient (ICC) of males' attendance, the following formula was used:

$$ICC = \frac{S_A^2}{S_A^2 + S_W^2}$$

Here S_A^2 is the between group variance and S_W^2 the within group variance (Wolak et al. 2012). The variance of the whole data including all adult and yearling males was used as the between group variance. ICC-values were calculated for 10 groups: all adult males and all yearling males, highly and lowly attending adults and yearlings, copulated adults and yearlings, and not copulated adults and yearlings (Appendix 1).

All modelling was done using generalised linear mixed effects models (GLMM). The identity of each male was nested with the year in which a male had been observed on the lek to separate observations of a same male being on the lek in consecutive years. The identity was used as a random effect in all models. The lekking site was not used as a variable in models as behaviour of males does not vary between sites.

All the statistical analyses were done by using R 3.0.2 (R Core Team 2013). The effect of lekking days (hereafter day) on attendance and fighting rate was modelled for the whole data (Appendix 1, function lmer from the R package lmerTest, Kuznetsova et al. 2014). The interaction between day and age of a male was included in the models. The effect of the number of females and total copulations on attendance and fighting rates of males were modelled separately for highly and lowly attending adults, and for highly and lowly attending yearlings (Appendix 1) using 80 % threshold value as a binary variable (0 = males attending < 80% of the top male's attendance and 1 = males attending ≥ 80 % of the top male's attendance, function glmer from the R package lme4, Bates et al. 2014). The effect of morphological traits (body mass and length of lyre) on attendance and fighting rates were modelled separately for all adults and for all yearlings (Appendix 1, function lmer from the R package lmerTest, Kuznetsova et al. 2014). The interaction between morphological traits and day was modelled, but in every case AIC values were lower for models without the interaction term.

3. RESULTS

3.1. Temporal variation in male behaviour

There was the negative quadratic effect of day on attendance (Table 1) meaning that attendance was lower at the end of the lekking season (Figure 1A). Yearling males were less present than adult males. A significant linear interaction between day and age indicated that yearling males increased their attendance during the season, but showed a similar amount of decline as adult males.

There was the negative linear effect of day on fighting rate (Table 1) meaning that fighting rate decreased towards the end of the lekking season (Figure 1B). Yearling males fought less than adult males. The significant linear interaction between day and age indicated that yearling males increased their fighting rate, whereas the fighting rate of adult males decreased towards the end of the lekking season.

Table 1. Temporal variation in attendance and fighting rate of males. Parameter day is scaled so that on the day $0 \geq 50$ % of all copulations have occurred. Values of estimates and SE have been multiplied by 1000 to help the interpretation.

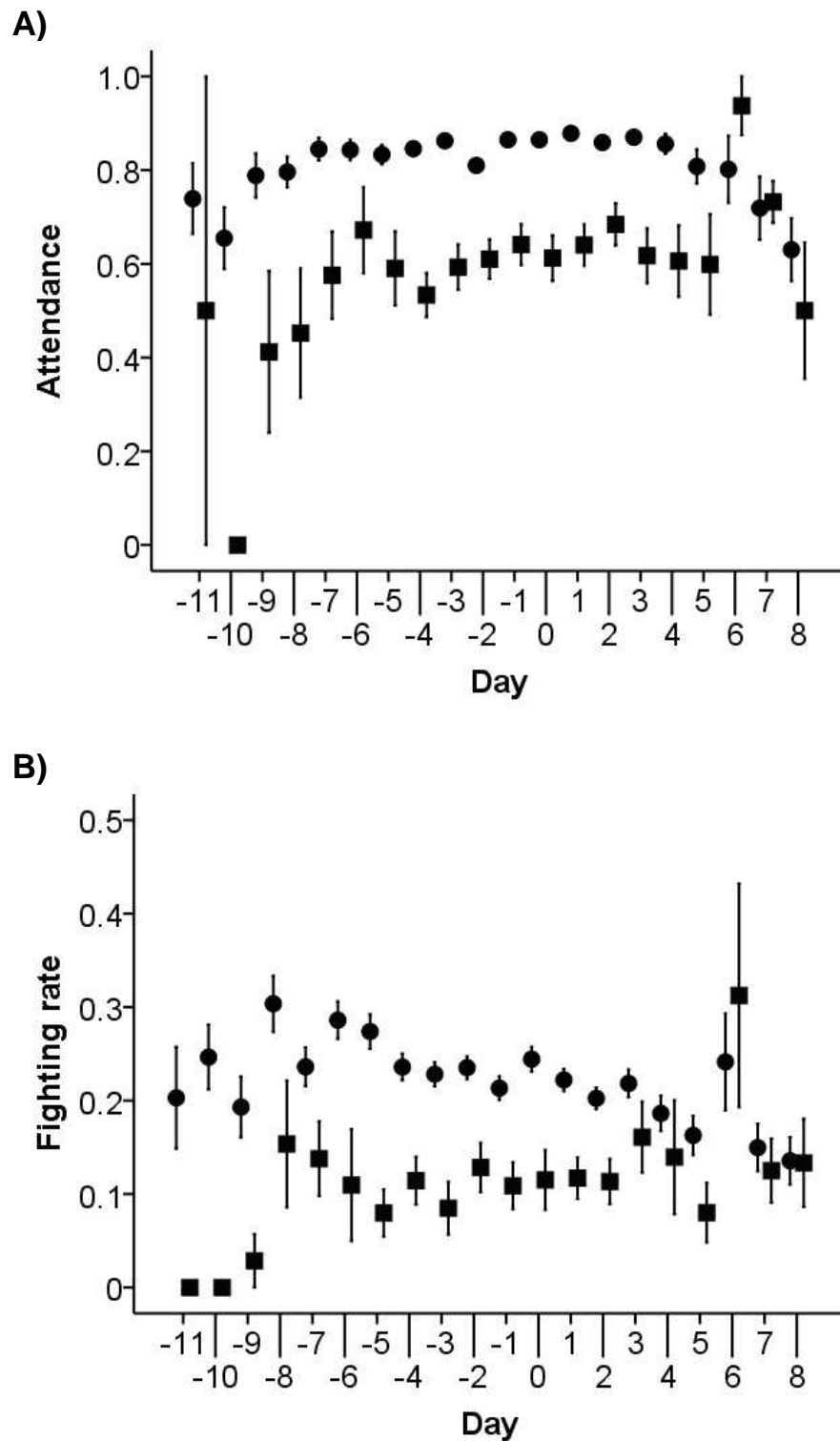| Parameter	Attendance				Fighting rate			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	859.04	8.96	95.87	<0.001	222.03	6.97	31.86	<0.001
Day	0.59	1.33	0.44	0.658	−5.78	1.20	−4.83	<0.001
Day^2	−1.10	0.23	−4.87	<0.001	−0.27	0.20	−1.31	0.189
Age juv	−231.28	24.82	−9.32	<0.001	−103.38	19.35	−5.34	<0.001
Day:age	10.95	3.87	2.83	0.005	7.72	3.47	2.22	0.026
Day^2:age	−1.13	0.70	−1.61	0.107	0.17	0.63	0.27	0.786

A)

B)

Figure 1. Attendance (A, mean ± SE) and fighting rates (B, mean ± SE) of males. Circles represent adult males and squares yearling males. Days have been scaled so that on the day $0 \geq 50\%$ of all copulations have occurred.

3.2. Repeatability of attendance

Attendance of adult males was more repeatable than that of yearling males (Table 2). Attendance of adult males that received copulations, was more repeatable than that of adult males which did not get any copulation. Furthermore, highly attending adult males were present in a more repeatable way than lowly attending adult males. Amongst yearling males the patterns were similar, but the repeatability of attendance was in general lower than that of adult males. Especially yearlings that did not receive any copulation and that were lowly attending had low values of the repeatability.

Table 2. Repeatabilities (ICC) of attendance of adult and yearling males. Highly attending males were present on the lek arena $\geq$ 80 % of the top male's time and lowly attending males < 80 % of the top male's time. A male was recorded as mated if it had received at least one copulation.

Adults	ICC
All	0.43
Highly attended	0.58
Lowly attended	0.43
Copulated	0.54
Not copulated	0.36
Yearlings	
All	0.30
Highly attended	0.50
Lowly attended	0.26
Copulated	0.43
Not copulated	0.28

3.3. The effect of female presence on male behaviour

Both the highly attending adult males and lowly attending adult males were less present on the lek arena when the number of females increased (Table 3, Figure 2A). Similar pattern was found in yearling highly attending males although not quite statistical significantly, but not in lowly attending yearling males (Table 3, Figure 2B).

Highly attending yearling males fought more when the number of females on the lek arena increased (Table 3, Figure 3). The number of females did not have effect on fighting rate of adults and lowly attending yearlings (Table 3).

Table 3. The effect of the number of females and copulations on attendance and fighting rate of males. Values of estimates and SE have been multiplied by 1000 to help the interpretation.

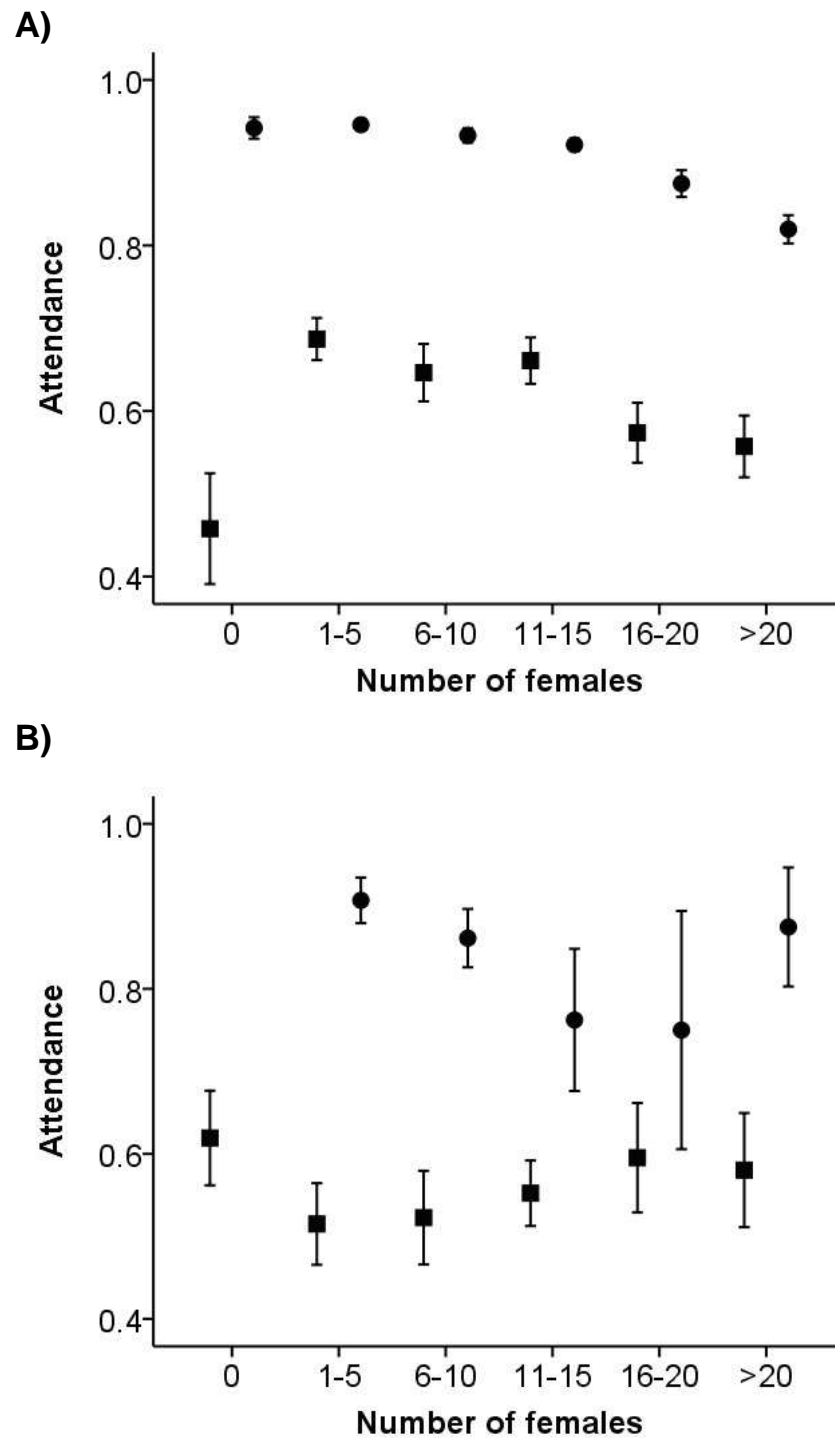|	High attendance				Low attendance			
Attendance								
Adults	Estimate	SE	Z	p	Estimate	SE	Z	p
Intercept	2667.31	154.75	17.24	<0.001	−123.84	169.23	−0.73	<0.001
No. of fem.	−64.46	10.43	−6.18	<0.001	−36.34	13.18	−2.76	0.006
Intercept	2446.65	101.84	24.02	<0.001	−277.48	114.49	−2.42	0.015
No. of cops	−50.93	13.56	−3.76	<0.001	−23.68	17.23	−1.38	0.169
Yearlings								
Intercept	1412.70	530.63	2.66	0.008	−1218.40	329.32	−3.70	<0.001
No. of fem.	−79.14	46.11	−1.72	0.086	9.34	23.28	0.40	0.688
Intercept	1273.84	324.81	3.92	<0.001	−1507.28	215.17	−7.01	<0.001
No. of cops	−46.58	50.75	−0.92	0.359	60.20	28.98	2.08	0.038
Fighting rate								
Adults								
Intercept	−1168.12	59.08	−19.77	<0.001	−1574.78	123.11	−12.79	<0.001
No. of fem.	−1.66	3.94	−0.42	0.674	3.43	9.02	0.38	0.704
Intercept	−952.84	45.95	−20.74	<0.001	−1456.43	102.37	−14.23	<0.001
No. of cops	−27.55	5.18	−5.32	<0.001	−27.94	13.63	−2.05	0.040
Yearlings								
Intercept	−1712.04	269.47	−6.35	<0.001	−2000.45	250.05	−8.00	<0.001
No. of fem.	57.48	25.26	2.28	0.023	4.60	16.07	0.29	0.775
Intercept	−1638.27	268.10	−6.11	<0.001	−2064.74	205.05	−10.07	<0.001
No. of cops	69.47	28.37	2.45	0.014	−27.18	23.43	−1.16	0.246

Figure 2. The effect of the number of females on adult (A) and yearling (B) males' attendance (mean ± SE). Circles represent highly attending and squares lowly attending males.
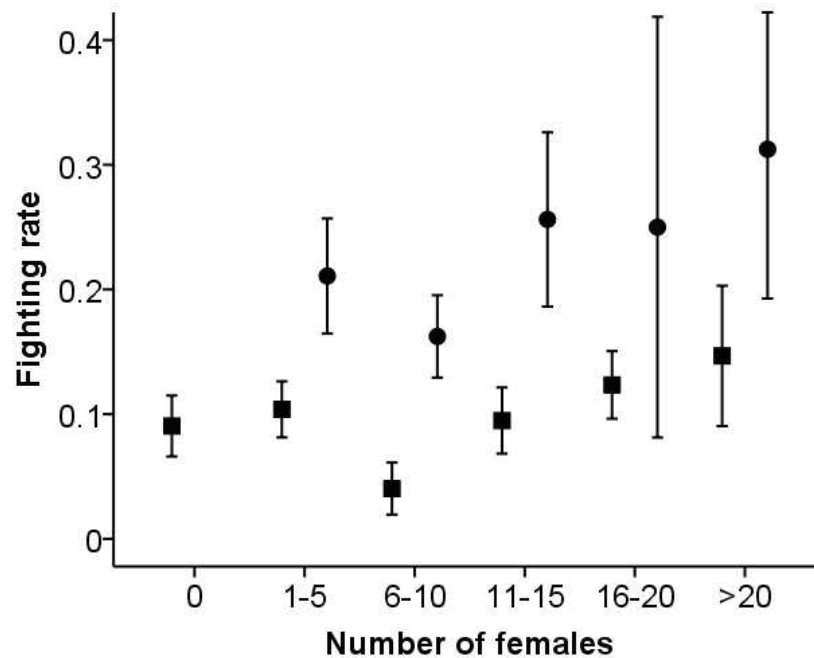
Figure 3. The effect of the number of females on fighting rate (mean ± SE) of yearling males. Circles represent highly attending yearlings and squares lowly attending yearlings.

3.4. The effect of the total number of copulations on male behaviour

Highly attending adult males were less present on the lek arena in days, when the total number of copulations was high (Table 3, Figure 4A). Instead, lowly attending yearling males were more actively present on days, when the total number of copulations was high (Table 3, Figure 4B). The number of copulations did not affect attendance in lowly attending adults or in highly attending yearlings.

Both the highly attending and lowly attending adult males fought less in days when most of the copulations occurred (Table 3, Figure 5A). Instead, highly attending yearling males fought more in days when most of the copulations occurred (Table 3, Figure 5B). Fighting rate of lowly attending yearlings was low and unchanging despite the number of total copulations.
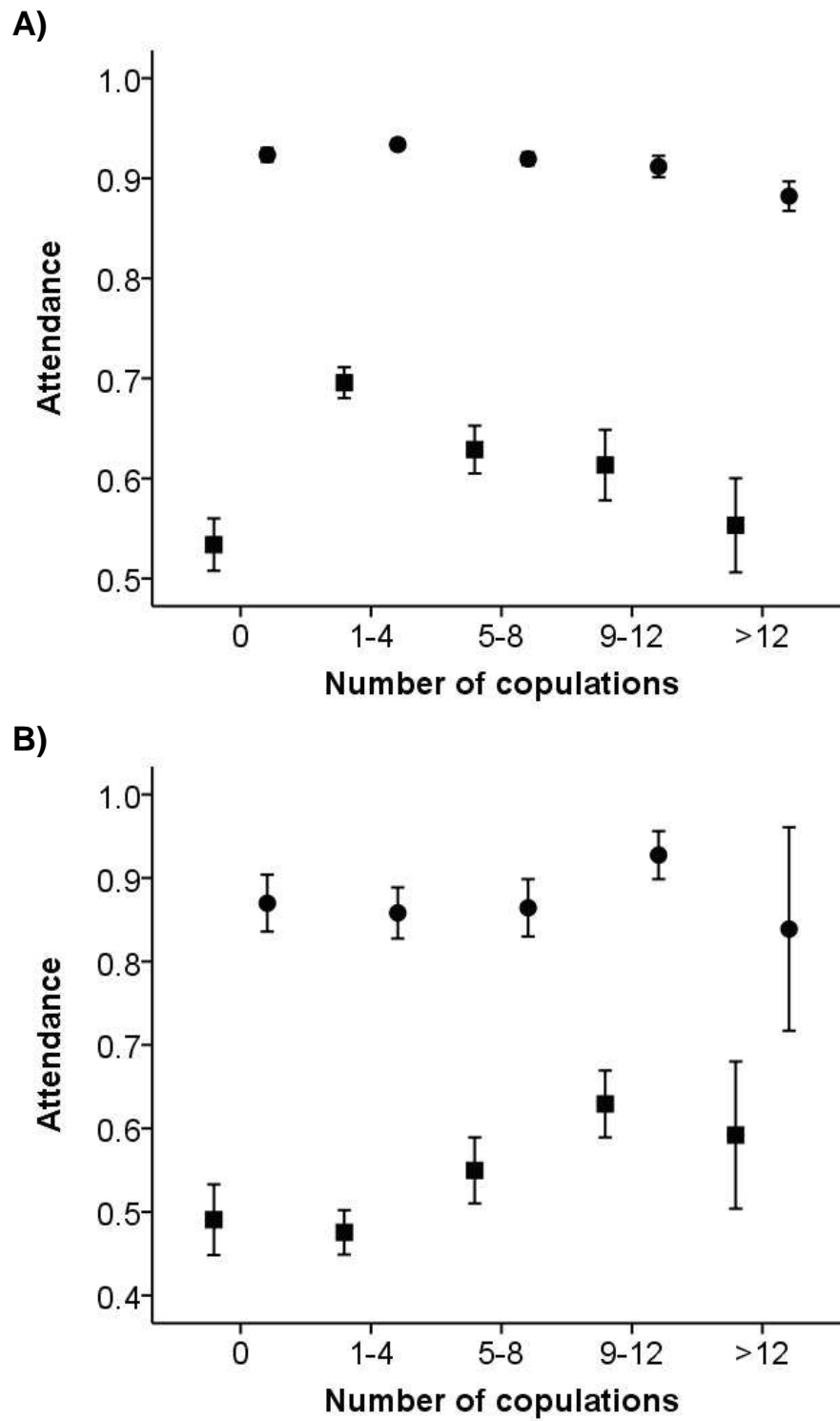
Figure 4. The effect of the total number of copulations on attendance (mean ± SE) of adult (A) and yearling (B) males. Circles represent highly attending and squares lowly attending males.
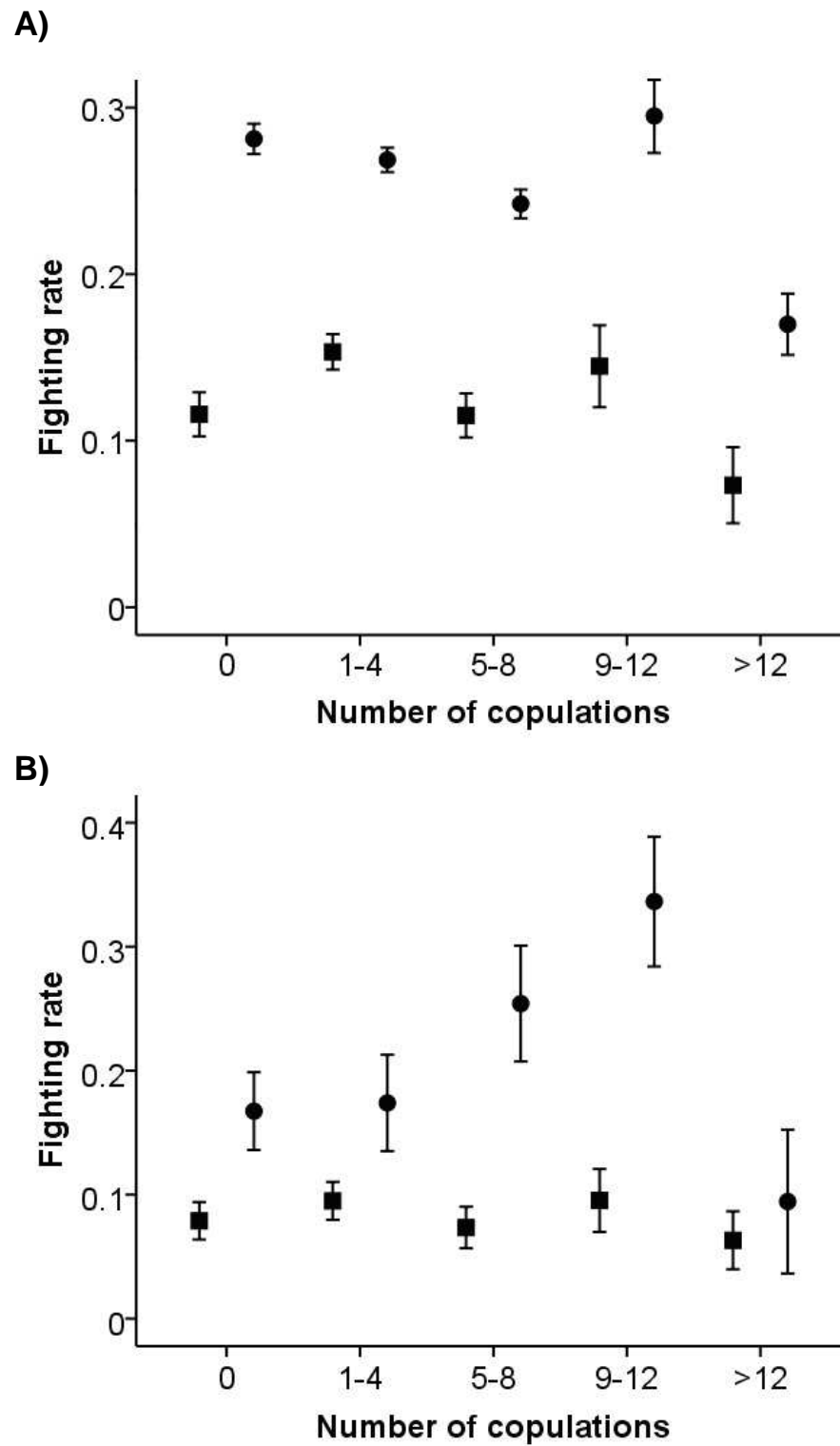
A)

B)

Figure 5. The effect of the total number of copulations on fighting rate (mean ± SE) of adult (A) and yearling (B) males. Circles represent highly attending and squares lowly attending males.

3.5. The effect of morphological traits on male behaviour

Attendance and fighting rate of heavier males were higher than those of lighter males through the whole lekking season (Figure 6). Among age classes, heavier adult males were more present on the lek arena than lighter ones (Table 4, Figure 7A), but in yearling males the pattern was not quite statistically significant. Heavier adult males also fought more than lighter ones (Table 4, Figure 7B), but body mass did not have effect on fighting rate of yearling males. Length of lyre did not have effect on attendance or fighting rate of either adult or yearling males (Table 4).

Table 4. The effect of body mass and length of lyre on attendance and fighting rate of males. Parameter day has been scaled so that on the day $0 \geq 50$ % of all copulations have occurred. Values of estimates and SE have been multiplied by 1000 to help the interpretation.

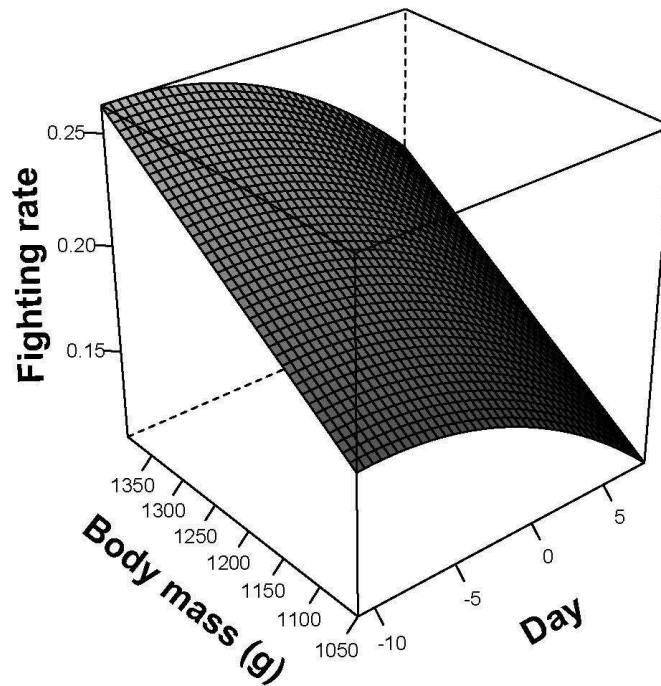|		Attendance				Fighting rate			
Adults	Parameter	Estimate	SE	t	p	Estimate	SE	t	p
	Intercept	362.59	204.04	1.77	0.077	−242.51	175.00	−1.39	0.167
	Day	2.07	1.45	1.43	0.153	−5.92	1.37	−4.32	<0.001
	Day^2	−1.12	0.25	−4.53	<0.001	−0.45	0.23	−1.91	0.056
	Mass	0.40	0.16	2.48	0.014	0.37	0.14	2.68	0.008
	Intercept	780.47	175.89	4.44	<0.001	103.84	151.98	0.68	0.495
	Day	2.18	1.46	1.49	0.136	−5.85	1.39	−4.23	<0.001
	Day^2	−1.06	0.25	−4.24	<0.001	−0.41	0.24	−1.72	0.086
	Lyre	0.38	0.79	0.48	0.629	0.55	0.68	0.80	0.424
Yearlings									
	Intercept	−612.75	646.46	−0.95	0.347	−421.66	349.60	−1.21	0.233
	Day	11.97	4.61	2.60	0.01	1.81	2.75	0.66	0.511
	Day^2	−2.27	0.84	−2.71	0.007	−0.17	0.50	−0.34	0.736
	Mass	1.06	0.55	1.92	0.060	0.46	0.30	1.55	0.127
	Intercept	1533.62	616.25	2.49	0.016	510.08	333.16	1.53	0.131
	Day	11.86	4.62	2.57	0.011	1.72	2.75	0.63	0.532
	Day^2	−2.25	0.84	−2.69	0.007	−0.16	0.50	−0.31	0.756
	Lyre	−4.78	3.24	−1.48	0.145	−2.06	1.75	−1.18	0.245

A)
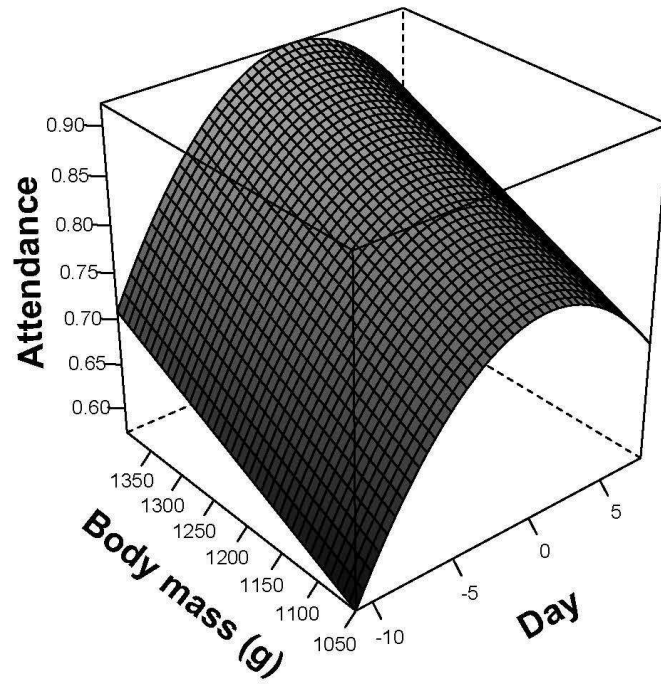
B)

Figure 6. The effect of body mass (g) on attendance (A) and on fighting rate (B) of males. Days have been scaled so that on the day $0 \geq 50$ % of all copulations have occurred.
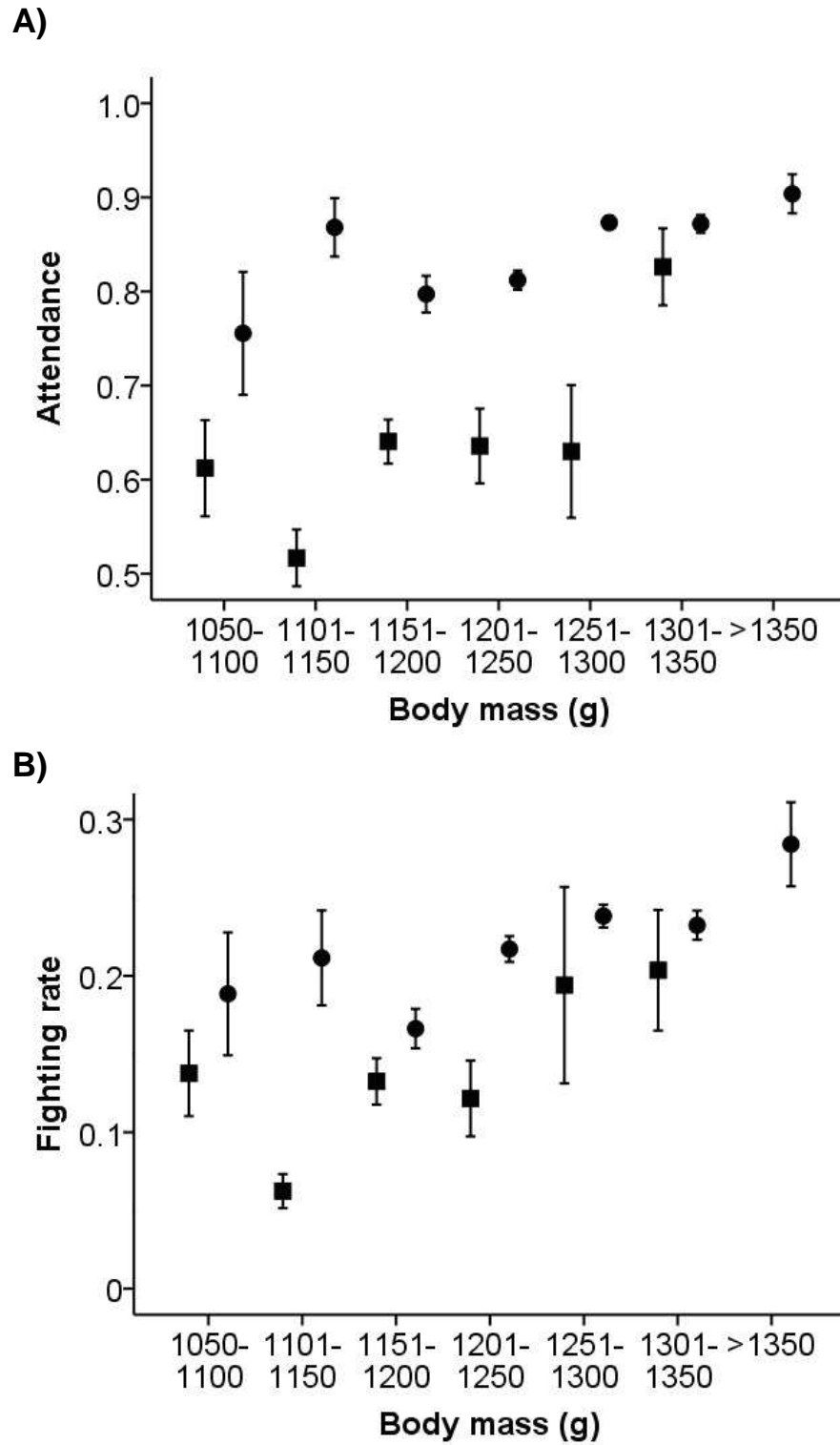
A)

B)

Figure 7. The effect of body mass (g) on attendance (A, mean ± SE) and on fighting rate (B, mean ± SE) of males. Circles represent adult males and squares yearling males.

4. DISCUSSION

4.1. Timing of reproductive effort

According to the life history theory individuals are forced to allocate their energy between different functions because of scarce resources (Stearns 1992). Hence, individuals are not able to maintain e.g. maximal growth and reproduction simultaneously. In male competition over females, males of the most impressive sexual ornaments, large body size, and high dominance status are often the winners which females generally prefer to copulate with (e.g. Andersson 1994, Höglund & Alatalo 1995, Berglund et al. 1996, but see Qvarnström 1998). In many species age is one of the most common factors connected to above-mentioned features, and thus improves a male's reproductive success (Clutton-Brock 1988). Full-grown males in a good condition are able to allocate energy to non-vital functions such as secondary sexual traits (Stearns 1992). Often young males are inferior competitors in relation to adults (e.g. ungulates, Mysterud et al. 2008, Mason et al. 2012, Tennenhouse 2012, pinnipeds, Deutsch et al. 1990 quoted by Andersson 1994, and birds, Alonso et al. 2010), but alternative mating strategies offer them a way to avoid direct interaction with superior males, and thus increase their mating success (Andersson 1994).

    All yearling black grouse males do not take part on the lek in their first year (Kervinen et al. 2012), but for those who do there seems to be a different mating strategy from that of adult males. In this study it was found that adult males invested more than yearlings during most of the season. Attendance of both adult and yearling males seemed first to increase toward the copulation peak, whereas fighting rate started to decrease after the first few days of the lekking season (Figure 1). In the very beginning of the season males compete with each other and solve borders of territories which explain the increase in fighting rate in the first few days. A reduction in fighting rate towards the copulation peak occurs probably because males concentrate more on rookooing and attracting females, who circle on the lek arena already days before the copulation peak. However, after the peak and especially on the few last days of the season the effort of adults and yearlings seemed to turn to more similar due to opposite trends in both attendance and fighting rate. Adults seemed to be less present and less active fighters, whereas yearlings seemed to retain or even increase their attendance and fighting activity. The reduction in activity of adult males after the copulation peak is probably a sign of exhaustion and a response to the decreasing number of females as the most active phase of the season passes by. Yearlings, instead, are usually unable to compete against adult males, and they seldom mate (Kervinen et al. 2012). Males lekking already in their first year live on average a shorter life than males starting lekking in their second year (Kervinen et al. 2014). Additionally, over half of all males do not receive any copulation in their whole life (Kervinen 2013), so every opportunity for mating is of a high importance for yearling males. Competition decreases towards the end of the season along with adults being less present and reducing fighting, so it is cost-effective for yearlings to increase their activity. Although the majority of females are receptive just over the few days of the copulation peak, some single females may mate in later days, and these rare mating opportunities in the end of the season may be the only chance for yearling males to pass their genes to the next generation. Yearling black grouse males seem to follow "the best of a bad job" strategy as they are not able to bear the costs of more successful mating strategy (Isvaran 2005), which would be defending central territories on the lek arena (Alatalo et al. 1991, Hovi at al. 1994, Rintamäki et al. 1995, Hämäläinen et al. 2012). Similar delayed reproductive effort of lekking young males is found also e.g. in red deer (Mysterud et al. 2008) and in Alpine chamois (Mason et al. 2012).

However, it needs to be taken into account that a significant quadratic effect *per se* does not tell about significant increases or decreases in attendance. The beginning and the end of the season should be tested separately to find out whether the trends in Figure 1A are significant (Keller et al. 2008). Furthermore, the retention and even the slight increase in attendance and fighting rate of yearlings on the last few days of the season may be due to the small sample size: just four yearlings, all observed in 2008, displayed and fought in the last three days of the season. Nevertheless, the amount of yearling territorial males correlates positively with the population density which was high in 2008 (Kervinen et al. 2012). Thus, the alternative mating strategy used by young black grouse males may possibly appear just when the density is high and competition between males as its most extreme. Further investigations are needed to solve this question.

4.2. Differences in behaviour of adult and yearling males

Variation in lekking behaviour between age groups has been found e.g. from ungulates and birds. For example, old big horn (*Ovis canadensis*) rams defend females from other rams and court them, whereas young rams block females from the tending area or try to pass the old dominant rams to get an access to females (Coltman et al. 2001). Old lekking great bustard (*Otis tarda*) males, contrary to young ones, are able to display more alone which probably increases their mating success (Alonso et al. 2010). Instead, black grouse males receiving copulations need to be actively present on the lek as females mate preferably with males who have territories in the centre of the lek, and keeping the central territory demands defending it from intruders (Hämäläinen et al. 2012). Attendance behaviour of adult males proved to be more repeatable than that of yearlings supporting the idea of adults being more regularly present, and thus desirable partners for females. Furthermore, inside the both age groups patterns were similar: behaviour of males being highly attended and receiving copulations was more repeatable.

Results concerning proportion of attendance of males when more females arrived and more copulations occurred, were surprising. Intuitively, attendance of males should increase during the copulation peak, but the behaviour of adults did not follow this assumption. Instead, attendance of all adults decreased when number of females increased (Figure 2A). Highly attending adult males were less present also when lots of copulations occurred (Figure 4A). One explanation is that especially highly attending adults have been invested a lot already in the very beginning of the lekking season, and when the strain of the lek is at its highest, some of these males may already be slightly exhausted. Not just occupying the central territory by active presence and fighting, but also keeping it through the season are the tests of a black grouse male's quality (Senior Lecturer Carl Soulsbury, University of Lincoln, personal communication), and the latter also a sign of a male's endurance.

Attendance behaviour of highly attending yearlings seemed to follow the pattern detected in all adults (Figures 2B and 4B), but statistical significance was not found (Table 3). This supports the results of highly attending yearlings showing the different mating strategy from that of adults. However, lowly attending yearlings were clear exceptions among all other males: they were more present during the copulation peak (Figure 4B). These yearlings may invest their slender effort exactly on the moments when the lek is in its most active phase. Their opportunities for mating are really scarce, but trying is still better than nothing. Additionally, young males are more attracted to loud and large leks (Alatalo et al. 1992), so continuous rookooing of other males in the most active phase of the lekking season may just tempt all the territorial lowly attending yearlings being present simultaneously.

However, there is also the possibility that the data concerning attendance is slightly biased: in mornings when the lek has been in its most active phase, drawing activity maps has focused on the end of the morning, when copulations are rare, and when some of the males may have already left the lek arena. This could maybe change attendances of males to seem lower than they really are. On the other hand, the number of yearling lowly attending males may be overrepresented: they may stay till later morning on the lek arena than adult males, who may have experience of females copulating almost without exceptions in early hours.

Fighting behaviour differed among adult and yearling males. Highly attending yearlings fought more when the number of females and copulations increased (Figures 3 and 5B), whereas all adult males fought less when plenty of copulations occurred (Figure 5A). Highly attending yearlings have not probably been as much present on the lek in the beginning of the season as adult males, so they do not have as high quality territories in spatial sense as adult males have. To enhance their mating opportunities, highly attending yearlings may try to weaken adult males by active fighting: adults being a bit tired during the copulation peak are easier to overtake from the territories. Similarly adult males having peripheral territories may try to replace the central territorial males; sometimes the top male receiving the most of the copulations has changed in the middle of the season (Kervinen 2013).

Decreasing fighting rate of adult males during the copulation peak may be due to concentrating on courting females (Höglund et al. 1997). Territorial adults may have established their position on the lek so they do not need to fight as actively as in the beginning of the season. Instead, low fighting rate of lowly attending yearlings is explained by their territories located on sides of the lek where competition between males is minor.

In summary, constant attendance behaviour and increasing fighting rate of highly attending yearling males during the copulation peak supports the results of yearlings showing the alternative mating strategy. In some species with long lifespan such as Alpine chamois the alternative strategy appears clearly after certain age (Mason et al. 2012). Black grouse being relatively short lived species (Kervinen et al. 2014), the alternative mating strategy can be seen only amongst the yearlings of high attendance as they have better ability to allocate resources to the lekking season than lowly attending males have. This explains the opposite trends in behaviour of highly and lowly attending yearlings.

4.3. The morphological traits

A breeding season is known to be very energetically costly for males of many species such as elephant seals (Deutsch et al. 1990 quoted by Andersson 1994, Galimberti et al. 2007), bullfrog (Judge & Brooks 2001), red deer (Yoccoz et al. 2002), and black grouse, as well (Lebigre et al. 2013). Unsurprisingly, heavier black grouse males were able to attend more on the lek and fight more actively than males with lower body mass (Figure 6). The same pattern recurred also in attendance of the both age groups (Figure 7A) and in fighting rate of adult males (Figure 7B). The highly attending yearlings were also the heaviest ones (Figure 7A) as can be expected according to restricted possibilities of energy allocation (Stearns 1992), and due to previous studies (Kervinen et al. 2012). Nevertheless, fighting rate of yearlings did not increase along with body mass (Figure 7B). The dispersion in fighting rate amongst yearlings was greater than that of adults especially among high weight classes. The reason may be related to differences in experience and motivation of adult and yearling males; yearlings are not as experienced fighters, and may thus avoid direct interaction more than adults. Again, yearlings of the highest weight class fought almost as much as adult males of the same class which further tells about their ability to invest more in the lekking season and bear the costs of it. The heaviest young males are

also probably the most successful in terms of reproduction as it has been found that high body mass correlates positively with yearling male territoriality (Kervinen et al. 2012).

Black grouse males with high mating success lose more of their body mass during the lekking season than males with lower mating success (Lebigre et al. 2013). Body mass measures used in this study are measured in winter, and therefore reveal the initial body condition of males before the lekking season. Heavy males regardless of their age are in a good condition which enables them to allocate more energy to costly behaviour (Stearns 1992): spending a lot of time on the lek arena and maintaining their territories by fighting.

Length of lyre did not have effect on either attendance or fighting rate of males. The role of the lyre in black grouse leks is unclear as females seem to prefer males with longer (Rintamäki et al. 2001) and undamaged lyres (Alatalo et al. 1991), but on the other hand length of lyre does not correlate with male fighting behaviour (Hämäläinen et al. 2012) which determines strongly the territory centrality, and thus a male's mating success (Alatalo et al. 1991, Hovi at al. 1994, Rintamäki et al. 1995, Hämäläinen et al. 2012). However, the lyre is one of the sexual ornaments which size is determined by a male's condition during moult soon after the lekking season. Lekking being energetically costly for males (Lebigre et al. 2013), they may be in a poor condition during moulting, but get better by the next lekking season. Thus, males are not able to affect length of lyre during the season, but are able to modify their behaviour according to their current condition (Hämäläinen et al. 2012). As a consequence, males with shorter lyres may be as regularly present and as active fighters than males with longer lyres.

It is known that the size of eye combs and the amount of blue chroma have roles in sexual selection of black grouse (Siitari et al. 2007). In this study they were not taken into account. Blue chroma reflectance begins to decrease at the latest after a male's third living year, while the size of eye combs grows till fourth year (Kervinen et al. 2014). It demands further research to find out, how those traits affect attendance and fighting rate of males, and whether there are differences between adult and yearling males.

The positive effect of higher body mass of adult males on both to attendance and fighting rate, and increased fighting rate of highly attending yearlings during the copulation peak are indirect supports of endurance rivalry operating on black grouse leks. Durable adult males are probably heavier ones as can be predicted on the grounds of the life history theory and energy allocation (Stearns 1992). Thus, they are probably the ones best tolerating attacks of other males and keeping their territories through the whole lekking season preventing other males from mating, and being themselves successful in reproduction. Furthermore, there are evidences of the top male having changed in the middle of the lekking season as the previous top male has worn out (Kervinen 2013). It is possible that the male of extreme endurance may dominate the whole season and maybe also afterwards, when the very last females arrive to copulate.

4.4. Conclusions

This study shows that based on attendance and fighting behaviour, yearling black grouse males of high lek attendance seem to have the alternative mating strategy, which is to schedule their reproductive effort later in the lekking season than adult males do. Male competition decreases along with adults showing slight signs of exhaustion already during the copulation peak, and this may offer the rare and unique opportunities of mating for yearling males (see e.g. Alatalo 1991, Kervinen et al. 2012). In addition to high lek attendance, active fighting and great body mass are the characteristics of yearling black grouse males showing the alternative strategy. As can be interpreted on the grounds of the life-history theory (Stearns 1992), these yearlings are probably able to allocate more resources to the lekking season than lowly attending yearlings, but still less than adults.

Possibly another mechanism such as the structure of males' dominance hierarchy demanding the rise of several years (Kokko et al. 1998) prevents yearlings being equal competitors with adults. As a consequence, the alternative strategy is limited to this particular group of males which probably profits the most of it.

Female choice and male contests are known to operate in black grouse leks (Höglund & Alatalo 1995), but this study suggests of endurance rivalry having a role, as well. Yearling males scheduling their effort later in the lekking season prevents the decrease of total competition and extends the period of which adult top males should stay dominants. As a consequence, not just the most dominant, but at the same time the most durable males will have the highest reproductive success. However, this study supports endurance rivalry on black grouse leks only indirectly. More research is needed to find out, how strong mechanism the alternative mating strategy of yearling males is, and how it possibly affects individual reproduction and sexual selection operating on black grouse leks.

ACKNOWLEDGEMENTS

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APPENDIX

Appendix 1. Sample sizes of the analyses. The keys of letters representing the analyses are following: A. ICC; B. the effect of day on attendance and fighting rate; C. the effect of the number of females and total copulations on attendance and fighting rate; D. the effect of morphological traits on attendance and fighting rate.

Analysis	Age	Group	n individuals	n observations
A	Adults	All	443	3623
		Highly attended	321	2660
		Lowly attended	122	963
		Copulated	210	1727
		Not copulated	238	1944
	Yearlings	All	68	511
		Highly attended	16	126
		Lowly attended	52	385
		Copulated	13	98
		Not copulated	56	421
B	Adults and yearlings	All	514	4190
C	Adults	Highly attended	189	1478
		Lowly attended	76	539
	Yearlings	Highly attended	8	56
		Lowly attended	31	212
D	Adults	All	349	2857
	Yearlings	All	67	503