Flexible timing of reproductive effort as an alternative mating tactic in black grouse (*Lyrurus tetrix*) males

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Short title: Alternative reproductive tactics in black grouse
Summary

Alternative reproductive tactics often take the form of dichotomous behavioural phenotypes. Focusing attention on such obvious dichotomy means that flexible patterns of behaviour within tactics is largely ignored. Using a long-term dataset of black grouse *Lyrurus tetrix* lek behaviours, we tested whether there were fine-scale differences in reproductive effort (lek attendance, fighting rates) and whether these were related to age and phenotype. Yearling males increased their lek attendance and fighting rate to a peak when adult male effort was declining. Adults and yearlings allocated reproductive effort according to their body mass but this was unrelated to differences in timing of effort. In adult males, different patterns of lek attendance were associated with different costs of reproduction, measured by mass loss or gain. Overall, our work demonstrates that individuals can use flexible patterns of reproductive effort both in terms of their own condition, their age and the likely costs of behaviours.

Key words: alternative reproductive tactics, costs of reproduction, lekking, phenotype
Introduction

Individuals within populations often vary in the way they compete for access to mates. Such variation can include differences in morphological (e.g. colour polymorphism) and behavioural phenotypes (e.g. callers and satellites; Taborsky et al., 2008). Variation typically comes in two forms: strict alternative reproductive strategies with genetic polymorphisms underpinning distinct morphological or behavioural phenotypes (e.g. Lank et al., 1995; Sinervo & Lively, 1996), whereas alternative reproductive tactics refer to conditional or flexible behavioural patterns that are used as a part of a strategy where an individual’s reproductive behaviour depends on environmental and/or genetic variation (Gross, 1996; Oliveira et al., 2008). While alternative reproductive tactics are more common and better studied than alternative reproductive strategies, the mechanisms underlying the variation in alternative reproductive tactics are unknown (Taborsky et al., 2008). Traditionally, the behavioural literature has separated alternative phenotypes into those due to genetic differences (e.g. polymorphisms) and those due to environmental or individual cues (e.g. conditional tactics; Brockmann, 2001).

Some of the classic systems with alternative reproductive strategies such as ruff (Philomachus pugnax) and side-blotched lizards (Uta stansburiana) have clear genetic polymorphism (Lank et al., 1995; Alonzo & Sinervo, 2001). In these cases, genotype frequencies underlying the alternative reproductive tactics are believed to be balanced by frequency-dependent selection, leading to equal fitness expectations of individuals using different tactics (Sinervo & Lively, 1996). In contrast, the vast majority of described cases of alternative reproductive tactics involve conditional responses of reproductive competitors (Gross, 1996). Conditional tactics can take two forms. For some species, individuals are forced to use an alternative tactic through their whole life if environmental conditions during development determine their ultimate characteristics. Drivers of these
differences include hormones (Hews et al., 1994) and food availability (Moczek & Emlen, 1999). In such cases, individual males can "make the best of a bad job", by expressing behaviours which may lead to some (limited) fitness benefits (Mysterud et al., 2008). Conversely, alternative reproductive tactics may occur at different life stages as an individual’s transition between different states. For example, many organisms show age-specific patterns of early life improvement and late life senescence in trait expression (Kervinen et al., 2015; Hayward et al., 2015), which would suggest that age plays an important role in the expression of alternative reproductive tactics (Pianka & Parker, 1975). In particular, the competitive ability of young and old males is generally lower than prime-aged males (Mysterud et al., 2008; Mason et al., 2012). Alternative tactics in this context can include switching between dichotomous behaviours e.g. old damselflies switch from territorial to sneaking behaviour (Forsyth & Montgomery, 1987) or delaying onset of reproduction (Kervinen et al., 2012). However, few studies have looked at how age or body condition may impact the variation of a single behavioural tactic (though see Mason et al., 2012; Tennenhouse et al., 2012), despite many of these tactics showing considerable variation (e.g. Clutton-Brock et al., 1979; Hogg, 1984). In species where male-male competition is particularly intense, males engaging in reproductive effort typically have impaired body condition. This can happen through physical mass loss (Deustch et al., 1990; McElligott et al., 2003; Hämäläinen et al., 2012), injury (Clutton-Brock et al., 1979) or deterioration in the quality of important traits (e.g. vocal display: Vannoni & McElligott, 2009). In such cases, individuals can take advantage of these declines by boosting their own display rates (Pitcher et al., 2014) or increasing their reproductive effort towards the end of the breeding season (Mason et al., 2012).

The black grouse (Lyrurus tetrix) is a lekking Galliform species that has strong sexual selection through male-male competition and female choice. Males express multiple
sexually-selected morphological and behavioural traits (summarised by Kervinen et al., 2015), and reproductive success is directly linked to investment in costly behaviours. In particular, fighting is an important part of male lekking behaviour (Höglund et al., 1997). Males that fight most frequently and have the highest rates of winning occupy and maintain a central territory on the lek (Hämäläinen et al., 2012), and males with central territories attract more females than peripheral males (Hovi et al., 1994). Gaining a dominant status and thus a central territory on the lek often demands several years of active display (Kokko et al., 1998). Large body mass is a key determinant of male reproductive success because it positively correlates with their fighting rate and thus with the male’s mating success and dominance status (Hämäläinen et al., 2012). Hence, lighter males may invest differently in reproductive effort compared to heavier males. Body mass in black grouse is age-related (Kervinen et al., 2015); young males are lighter and less capable of coping with the costs of lekking (Siitari et al. 2007), so many males may delay the onset of reproduction into their second or even third year (Kervinen et al., 2012, 2016). Some yearlings do lek despite being lighter and, thus unlikely to gain dominance (Kervinen et al., 2012). However, it is unclear if the yearling males that lek have different reproductive tactics than adults within the lekking season. Using a long-term longitudinal dataset in male black grouse, we tested whether there was within-breeding season variation in individual investment in reproductive effort (measured by lek attendance and fighting rate) in relation to age and two measures of condition (body mass, lyre length). In addition, we also tested whether different patterns of reproductive effort were linked to different investment tactics as measured by mass loss over the breeding season. We predicted that yearlings will have lower investment in lekking than adults, but based on previous work (Mason et al. 2012), would increase their effort towards the end of the breeding season. We also predicted that body mass but not lyre length would positively impact investment
in lekking effort. Lastly we predicted that males with greater investment in reproductive effort would have greater mass loss.

Material and Methods

Study population

Field data was gathered between 2003–2013 from three lekking sites located in Central Finland (ca. 62°15’N; 25°00’E) of which two are peat harvesting areas and one is a protected bog in a natural state. Lek sizes in the study sites varied between 6–56 territorial males (mean±SD: Site 1=30.7±12.7 males, Site 2 =21.5±7.1, Site 3=12.8±5.0). Local hunting clubs refrained from hunting in these sites and their nearby areas so the age structure of black grouse populations of the research areas was considered to be natural.

Birds were captured prior to the lekking season from January to March using walk-in traps baited with oats and some males were re-captured following the lekking season in 3 years (2005–2007; full description of the re-captures in Lebigre et al. 2013). Birds were trapped soon after they arrived at the feeding site, typically close to sunrise. All the traps were sprung at the same time and immediately covered with dark clothes to reduce capture stress. Each bird was removed one at a time from traps and placed into a fabric bag and taken to a hide for handling. Each bird was fitted with an aluminium ID ring and three plastic colour rings for individual identification. 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 (Helminen, 1963). All birds were released at the site of capture after handling. This research was carried out in compliance with the current laws of Finland. Birds were captured under the permission of the Central Finland Environmental Centre.
(permissions KSU-2003-L-25/254 and KSU-2002- L-4/254) and the Animal Care Committee of the University of Jyväskylä (ESLH-2009-05181/Ym-23).

**Behavioural data**

Behavioural data was gathered from late April to early May during the lekking period when the majority of copulations occur. Each lek was observed daily for the entire lekking period from hides. Observers were in place before grouse arrived at the lek at sunrise and recorded lek observations until the grouse left (the observation period was therefore typically 03:00 to 09:00 am). Behaviours (fighting, hissing, rookoing, inactive, Höglund et al., 1997) and the spatial location of each individual male and female was recorded using scan sampling (documented as ‘activity maps’). Maps were drawn every ~5 minutes. If a male was observed at a lek at least once during the observation morning, it was recorded to be present. Total number of copulations for each individual and the highest number of females observed at the same time at a lek were also recorded. Daily attendance of each male (hereafter *daily lek attendance*) was calculated as a proportion of the attendance of the male most present on each morning (lek attendance = number of the individual’s activity maps / number of maps of the most attendant male on that lek). The daily fighting rates (hereafter *daily fighting rate*) were calculated as the proportion of time each male spent fighting on each morning.

**Statistical analyses**

We restricted our data to males who held permanent territories throughout the study (i.e. who were present ≥50 % of observation days and thus had permanent territories (Kervinen et al. 2012). This allowed us to investigate individual variation within a strategy (i.e.
territoriality). Daily lek attendance and daily fighting rates are dependent on the absolute number of lekking days as well as the start, end and peak days of lekking. These vary both between years and between sites due to environmental factors (e.g. temperature; Ludwig et al., 2006). To avoid this confounding effect and to aid interpretation, the lekking periods were scaled so that on day 0, ≥50 % of all observed copulations had occurred. Thus day 0 represents the peak of the lekking season. The amount of activity maps that are collected each day for the most attending male is important, since if these decline then other males’ lek attendance may appear to increase. We tested whether the number of maps collected differed across the lekking season using a Poisson GLMM; we found no temporal effect on the number of activity maps collected for the top male (Poisson GLMER: day (linear), z=0.68, P=0.497; day (quadratic), z=0.39, P=0.696).

To analyse differences in behavioural tactics we carried out a series of linear mixed effects models (LMM) using the lmer function from the R package lmerTest (Kuznetsova et al., 2014), run in R 3.0.2 (R Core Team, 2013). In all models, we included two random effects: year and individuals’ ID nested within site. In the first models, we compared the effect of age (adults/yearlings) on daily lek attendance and daily fighting rate. In each model, we included the main effects age, day (linear and quadratic), and the interactions of day (linear and quadratic) with male age; non-significant interactions (α >0.05) were removed in a stepwise fashion until only significant interactions or the fixed effects remained. We then tested whether males with different phenotypes had different daily lek attendance patterns and daily fighting rates. We used two morphological traits linked to individuals’ body condition (body mass and lyre length). Previous studies showed that male body mass is critical to black grouse males’ lek performance as dominant males are heavier and lose substantially more weight during the mating season than the other males (Hämäläinen et al., 2012; Lebigre et al., 2013). The lyre length is also a measure of body
condition as males with longer lyres have lower blood parasite load (microfilaria of *Onchocercidae* spp; Höglund et al., 1992), but it is unrelated to males’ competitive ability on the lek and their lek attendance (Hämäläinen et al., 2012). Yearling and adult males were tested separately because yearling males have significantly lower trait body mass and tail length than adults (Siitari et al. 2007), meaning that analysing different-aged individuals in the same analysis (even when accounting for age-specific effects) would lead to overestimates of the association between male traits and differences in reproductive tactics (Kervinen et al., 2015). Again in each model, we included the interactions of linear and quadratic day with traits (body mass or lyre length); non-significant interactions ($\alpha >0.05$) were removed in a stepwise fashion until only significant interactions or the fixed effects remained.

For a subset of adult males (N=15 males, 148 observations), we calculated their body mass loss over the lekking season (pre-lekking mass (g) – post-lekking mass (g)). Males were recaptured using the same walkin traps used during winter captures, baited with willow catkins. Captures took place a few days after the mating season. There was no significant relationship between initial mass and mass lost (Pearson’s correlation: $r=-0.14$, $P=0.601$), and no relationship between capture day post-lek and body mass (Lebigre et al. 2013). We assessed whether males with differing resource investment (as measured by mass loss), showed differing patterns of daily lek attendance and daily fighting rate. In this model, we included the interactions of day (linear and quadratic) with mass loss as fixed effects; non-significant interactions ($\alpha >0.05$) were removed in a stepwise fashion until only significant interactions or the fixed effects remained.
Results

Age-specific variation in timing of reproductive effort

There was a significant negative quadratic effect of the variable ‘day’ on daily lek attendance (Table 1) most likely due to a decline in daily lek attendance at the end of the lekking season (Figure 1a). Adult males had a consistent daily lek attendance across the lekking season, with a decline after the peak day of copulations (Figure 1a). Yearling males had lower daily lek attendance than adult males (yearlings: mean daily attendance ± SD=0.61±0.35; adults: mean daily attendance ± SD=0.85±0.26). There was a significant interaction between the variable ‘day’ (linear) and males’ age (Table 1) as yearling males increased their daily lek attendance during the season, but their daily attendance declined in a similar way as that of the adult males after the peak copulation days (Figure 1a).

There was an overall negative linear effect of day on males’ fighting rate meaning that daily fighting rate decreased towards the end of the lekking season (Table 1). Yearling males fought less often than adult males (yearlings: mean fighting rate ± SD=0.12±0.19; adults: mean fighting rate ± SD=0.23±0.24) and yearling males maintained low fighting rates while Yearling males in general maintained low fighting rates across the season whereas the daily fighting rate of adult males decreased towards the end of the lekking season as indicated by the significant interaction between day (linear) and age (Figure 1b; Table 1).

Condition-dependence of reproductive effort

For adult males, there were no significant interactions between morphological traits and day (linear) or day (quadratic) for either daily lek attendance or daily fighting rate (Table 2). Instead, heavier males had higher lek attendance and fought more frequently than
lighter males throughout the lekking season (Table 2a; Figure 2a & 2b), but there were no relationship with lyre length. The same pattern was true for yearling males with no significant interactions between morphological traits and day (linear) or day (quadratic) for either daily lek attendance or daily fighting rate. Heavier yearling males attended the lek more frequently and fought more frequently than lighter males throughout the lekking season (Table 2, Figure 2c and 2d), but no other trait was related to lek attendance or fighting rates.

The mass loss of adult males during the lekking period had a significant interaction with day (linear) (Table 3). Males with the greatest mass loss showed high daily lek attendance early in the lekking season but their attendance subsequently declined. Males with no mass loss or even an increase in mass, had low initial daily lek attendance, but their attendance increased towards the end of the lekking season (Figure 3). In contrast, there were no effects of mass loss on fighting rate on its own or in interaction with day (linear) or day (quadratic; Table 3).

Discussion

Age-specific variation in timing of reproductive effort

Across many species, age plays an important role in determining alternative reproductive tactics. Typically, prime-age males perform tactics that focus on male-male competition over access to females or defence of groups of females (John, 1993; Coltman et al., 2001; Saunders et al., 2005), whereas younger or older males may perform sneaking or satellite tactics (Forsyth & Montgomerie, 1987; John, 1993; Saunders et al., 2005). Young males may also show reduced levels of attendance at breeding sites (Deutsch et al., 1994; Kervinen et al., 2012). Our results show that as well as adopting completely different
behavioural tactics of lek attendance/non lek attendance (Kervinen et al. 2012), young males who do attend the lek can adapt their reproductive effort within a breeding season. Younger males had lower attendance overall, but their peak attendance was later and fighting rates higher at the end of the breeding season in comparison to adult males. Other studies have found older, more dominant males declining in reproductive effort late in the breeding season, with younger males increasing allocation to reproductive effort later in the breeding season (Mason et al., 2012) or showing no change (Tennenhouse et al., 2012). Such patterns are most likely explained by the declining body condition of the dominant males, their exhaustion and males’ loss of motivation in reproductive display as the number of females’ visits declines towards the end of the breeding season. By increasing reproductive effort later in the breeding season, yearling or young males have display rates of behaviour that are similar to adults and may therefore gain some reproductive success if females use these traits (indicators of their short term investment in reproduction) for mate choice.

**Condition-dependence of reproductive effort**

Many alternative reproductive tactics are condition- or state-dependent, irrespective of age (Leary et al., 2005; Lidgard et al., 2005; though see Alonso et al., 2010). Smaller males or those with less available resources may show a different behavioural phenotype e.g. satellite versus calling (Woodhouse's toads *Bufo woodhousii*; Leary et al., 2005), or may show reductions in the allocation of reproductive effort (Yuval et al., 1998; Eggert & Guyétant, 2003). In our study, allocation of effort in both fighting and lek attendance was driven by male condition both in adults and to a lesser extent in yearling males. This is perhaps unsurprising, as reproductive effort is typically very energetically costly in lekking
species (Vehrencamp et al., 1989), and nutritional reserves are crucial for determining participation (Yuval et al., 1998 Bachman & Widemo 1999). The non-significant trend in yearlings probably reflects the fact that lighter males did not attend the lek at all and delayed their age at first reproduction (Kervinen et al., 2012). Adult males attending the lek also tended to be heavier than non-territorial males (Hämäläinen et al., 2012), but our data show that even within these males, body mass is impacting reproductive effort. Despite this, we did not find any evidence of different reproductive tactics; lighter males did not differ in terms of the temporal pattern of fighting or lek attendance, but just carried out behaviours at a lower rate. In another lekking species, the great bustard, reproductive allocation was unrelated to body mass (Alonso et al., 2010). In black grouse, body mass is important in determining social rank through fighting (Hämäläinen et al., 2012), whereas in bustards, age seems to be more important for social ranking (Alonso et al., 2010). Hence, age and condition related patterns of reproductive allocation may act independently.

In contrast to body mass, tail length was unrelated to patterns of investment in reproduction. This was not surprising since previous tests looking at the relationship between fighting rates and other ornaments found no relationship (Hämäläinen et al., 2012). Tail length is an important part of female mate choice and is sexually-selected in black grouse (Höglund et al. 1994; Kervinen et al. 2016). Damage to the tail caused by fighting is important for mate choice particularly in sub-dominant males (Höglund et al. 1994). In some species, tail length predicts the ability to hold resources indicating a role in male-male competition, possibly by signalling quality (Savalli 1994). Tail length in general is mainly used for signalling (Fitzpatrick 1998), so unlike body mass which is more directly linked to fighting outcome and allocable resources for lekking, it is perhaps not unexpected that tail length is unrelated to reproductive tactics.
Interestingly, we found evidence that alternative reproductive tactics may offer different outcomes in terms of body condition loss. As in many species (Deutsch et al., 1990), the loss of body condition in black grouse is considerable during the breeding season (Lebigre et al., 2013). We found that males investing in early lek attendance lost a greater amount of body mass than those who delayed their attendance. Such a result is similar to that found in fallow deer (*Dama dama*); fallow deer who invested most in certain rut behaviours had greatest mass loss (Jennings et al., 2010). However, in sage grouse (*Centrocercus urophasianus*), the most active displayers lost the least amount of weight (Vehrencamp et al. 1989). Sage grouse however are somewhat exceptional in that males forage on the lek and during the lekking season, something that other species do not do (Cowles & Gibson 2014). Therefore, the smaller body mass loss in active sage grouse displayers is probably explained by their better foraging abilities (Vehrencamp et al. 1989).

Reproductive effort is costly in black grouse, with many males dying after reproducing or after peak reproductive effort (Alatalo et al., 1991; Kervinen et al., 2015, 2016). Our results suggest that selective allocation of reproductive effort may therefore be one way of minimising costs of lekking and ensuring survival to the following year. Managing within-breeding season reproductive effort may therefore have wider importance in the scheduling of reproduction across individuals’ lifetimes.

**Conclusions**

Our results build on previous work showing age-specific differences in timing of reproductive effort (Mason et al., 2012; Tennenhouse et al., 2012), but we found no relationship between condition and timing. However, adult males with low or no mass loss had different timing of effort. Such patterns may arise for two reasons: firstly, males of lower competitive ability responding to declines in dominant males’ condition and gain
some access to reproduction (Mason et al. 2012). Alternatively, males may be adjusting
timing effort to reduce the costs of such effort. Either way, it seems that how or when
males invest reproductive effort is important. It is likely that flexible timing of
reproductive effort by males is widespread in many mating system,

Acknowledgement

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References


success in great bustard leks: the effects of age, weight, and display effort. — Behav.

Alonzo, S.H. & Sinervo, B. (2001) Mate choice games, context-dependent good genes, and
Sociobiol.49: 176-186.

and alternative reproductive tactics in a lekking sandpiper, the ruff (*Philomachus

Behav. 30: 1-51.


Figure 1. Mean ± SE individual daily lek attendance (a) and daily fighting rates (b) of males across the lekking season. Filled squares represent adult males and open squares yearling males. Days have been scaled so that on day 0, ≥50 % of all copulations have occurred.

Figure 2: Surface plot showing the individual daily lek attendance in relation to the day and body mass of (a) adult males and (c) yearling males and the individual daily fighting rate in relation to the day and body mass (b) adult males and (c) yearling males. Days have been scaled so that on day 0, ≥50 % of all copulations have occurred.

Figure 3: Surface plot showing the interaction between individual daily lek attendance, day and the mass loss between pre- and post-lekking for adult males (N=15 males, 148 observations). Mass loss is presented so that negative values indicate large mass loss and positive values indicate mass gain. Days have been scaled so that on day 0, ≥50 % of all copulations have occurred.
Table 1. Temporal variation in daily lek attendance and daily fighting rate of males in relation to age (yearling/adult). The interaction between day and age was included, but deleted if non-significant. The parameter day is scaled so that on day 0, ≥50 % of all copulations have occurred. All parameter estimates are multiplied by 1000 to aid interpretation.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>±SE</th>
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<th>p</th>
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<td>3.52</td>
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<td>Daily fighting rate (N=281 individuals/N observations 3875)</td>
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Table 2. Temporal variation in daily lek attendance and daily fighting rate in relation to body mass and lyre length of adult (≥2 year old) and yearling males (1 year old). The interaction between day and mass and lyre length was included, but deleted as non-significant. The parameter day is scaled so that on day 0, ≥50 % of all copulations have occurred. All parameter estimates are multiplied by 1000 to aid interpretation.

<table>
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<tr>
<th>Model</th>
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<td>3.23</td>
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<td>0.010</td>
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<sup>a</sup>N=235 adult males,2882 daily observations; 67 yearling, 511 daily observations

<sup>b</sup>N=230/2820 daily observations, 67 yearling, 511 daily observations
Table 3. Temporal variation in daily lek attendance and daily fighting rate of adult males in relation to the amount of weight lost over the lekking period (g). The interaction between day and mass loss was included, but deleted if non-significant. The parameter day is scaled so that on day 0, ≥50 % of all copulations have occurred. All parameter estimates are multiplied by 1,000 to aid interpretation.

<table>
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<tr>
<th>Model</th>
<th>Parameter</th>
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Figure 1
Figure 2
Figure 3