

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

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14 Short title: Alternative reproductive tactics in black grouse

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17 **Summary**

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

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

32

33 **Introduction**

34 Individuals within populations often vary in the way they compete for access to mates.  
35 Such variation can include differences in morphological (e.g. colour polymorphism) and  
36 behavioural phenotypes (e.g. callers and satellites; Taborsky et al., 2008). Variation  
37 typically comes in two forms: strict *alternative reproductive strategies* with genetic  
38 polymorphisms underpinning distinct morphological or behavioural phenotypes (e.g. Lank  
39 et al., 1995; Sinervo & Lively, 1996), whereas *alternative reproductive tactics* refer to  
40 conditional or flexible behavioural patterns that are used as a part of a strategy where an  
41 individual's reproductive behaviour depends on environmental and/or genetic variation  
42 (Gross, 1996; Oliveira et al., 2008). While alternative reproductive tactics are more  
43 common and better studied than alternative reproductive strategies, the mechanisms  
44 underlying the variation in alternative reproductive tactics are unknown (Taborsky et al.,  
45 2008). Traditionally, the behavioural literature has separated alternative phenotypes into  
46 those due to genetic differences (e.g. polymorphisms) and those due to environmental or  
47 individual cues (e.g. conditional tactics; Brockmann, 2001).

48         Some of the classic systems with alternative reproductive strategies such as ruff  
49 (*Philomachus pugnax*) and side-blotched lizards (*Uta stansburiana*) have clear genetic  
50 polymorphism (Lank et al., 1995; Alonzo & Sinervo, 2001). In these cases, genotype  
51 frequencies underlying the alternative reproductive tactics are believed to be balanced by  
52 frequency-dependent selection, leading to equal fitness expectations of individuals using  
53 different tactics (Sinervo & Lively, 1996). In contrast, the vast majority of described cases  
54 of alternative reproductive tactics involve conditional responses of reproductive  
55 competitors (Gross, 1996). Conditional tactics can take two forms. For some species,  
56 individuals are forced to use an alternative tactic through their whole life if environmental  
57 conditions during development determine their ultimate characteristics. Drivers of these

58 differences include hormones (Hews et al., 1994) and food availability (Moczek & Emlen,  
59 1999). In such cases, individual males can "make the best of a bad job", by expressing  
60 behaviours which may lead to some (limited) fitness benefits (Myserud et al., 2008).  
61 Conversely, alternative reproductive tactics may occur at different life stages as an  
62 individual's transition between different states. For example, many organisms show age-  
63 specific patterns of early life improvement and late life senescence in trait expression  
64 (Kervinen et al., 2015; Hayward et al., 2015), which would suggest that age plays an  
65 important role in the expression of alternative reproductive tactics (Pianka & Parker,  
66 1975). In particular, the competitive ability of young and old males is generally lower than  
67 prime-aged males (Myserud et al., 2008; Mason et al., 2012). Alternative tactics in this  
68 context can include switching between dichotomous behaviours e.g. old damselflies switch  
69 from territorial to sneaking behaviour (Forsyth & Montgomery, 1987) or delaying onset of  
70 reproduction (Kervinen et al., 2012). However, few studies have looked at how age or  
71 body condition may impact the variation of a single behavioural tactic (though see Mason  
72 et al., 2012; Tennenhouse et al., 2012), despite many of these tactics showing considerable  
73 variation (e.g. Clutton-Brock et al., 1979; Hogg, 1984). In species where male-male  
74 competition is particularly intense, males engaging in reproductive effort typically have  
75 impaired body condition. This can happen through physical mass loss (Deustch et al.,  
76 1990; McElligott et al., 2003; Hämäläinen et al., 2012), injury (Clutton-Brock et al., 1979)  
77 or deterioration in the quality of important traits (e.g. vocal display: Vannoni & McElligott,  
78 2009). In such cases, individuals can take advantage of these declines by boosting their  
79 own display rates (Pitcher et al., 2014) or increasing their reproductive effort towards the  
80 end of the breeding season (Mason et al., 2012).

81         The black grouse (*Lyrurus tetrix*) is a lekking Galliform species that has strong  
82 sexual selection through male-male competition and female choice. Males express multiple

83 sexually-selected morphological and behavioural traits (summarised by Kervinen et al.,  
84 2015), and reproductive success is directly linked to investment in costly behaviours. In  
85 particular, fighting is an important part of male lekking behaviour (Höglund et al., 1997).  
86 Males that fight most frequently and have the highest rates of winning occupy and  
87 maintain a central territory on the lek (Hämäläinen et al., 2012), and males with central  
88 territories attract more females than peripheral males (Hovi et al., 1994). Gaining a  
89 dominant status and thus a central territory on the lek often demands several years of active  
90 display (Kokko et al., 1998). Large body mass is a key determinant of male reproductive  
91 success because it positively correlates with their fighting rate and thus with the male's  
92 mating success and dominance status (Hämäläinen et al., 2012). Hence, lighter males may  
93 invest differently in reproductive effort compared to heavier males. Body mass in black  
94 grouse is age-related (Kervinen et al., 2015); young males are lighter and less capable of  
95 coping with the costs of lekking (Siitari et al. 2007), so many males may delay the onset of  
96 reproduction into their second or even third year (Kervinen et al., 2012, 2016). Some  
97 yearlings do lek despite being lighter and, thus unlikely to gain dominance (Kervinen et al.,  
98 2012). However, it is unclear if the yearling males that lek have different reproductive  
99 tactics than adults within the lekking season. Using a long-term longitudinal dataset in  
100 male black grouse, we tested whether there was within-breeding season variation in  
101 individual investment in reproductive effort (measured by lek attendance and fighting rate)  
102 in relation to age and two measures of condition (body mass, lyre length). In addition, we  
103 also tested whether different patterns of reproductive effort were linked to different  
104 investment tactics as measured by mass loss over the breeding season. We predicted that  
105 yearlings will have lower investment in lekking than adults, but based on previous work  
106 (Mason et al. 2012), would increase their effort towards the end of the breeding season.  
107 We also predicted that body mass but not lyre length would positively impact investment

108 in lekking effort. Lastly we predicted that males with greater investment in reproductive  
109 effort would have greater mass loss.

110

## 111 **Material and Methods**

### 112 *Study population*

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

119 Birds were captured prior to the lekking season from January to March using walk-in  
120 traps baited with oats and some males were re-captured following the lekking season in 3  
121 years (2005–2007; full description of the re-captures in Lebigre et al. 2013). Birds were  
122 trapped soon after they arrived at the feeding site, typically close to sunrise. All the traps  
123 were sprung at the same time and immediately covered with dark clothes to reduce capture  
124 stress. Each bird was removed one at a time from traps and placed into a fabric bag and  
125 taken to a hide for handling. Each bird was fitted with an aluminium ID ring and three  
126 plastic colour rings for individual identification. Birds were weighed in fabric bags (to the  
127 nearest 10 g), and the left and right outermost lyre (tail) feathers were measured from base  
128 to tip (to the nearest 1.0 mm). Birds were aged as yearlings or older (hereafter adults) by  
129 plumage differences (Helminen, 1963). All birds were released at the site of capture after  
130 handling. This research was carried out in compliance with the current laws of Finland.  
131 Birds were captured under the permission of the Central Finland Environmental Centre

132 (permissions KSU-2003-L-25/254 and KSU-2002- L-4/254) and the Animal Care  
133 Committee of the University of Jyväskylä (ESLH-2009-05181/Ym-23).

134

### 135 ***Behavioural data***

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

151

### 152 ***Statistical analyses***

153 We restricted our data to males who held permanent territories throughout the study (i.e.  
154 who were present  $\geq 50$  % of observation days and thus had permanent territories (Kervinen  
155 et al. 2012). This allowed us to investigate individual variation within a strategy (i.e.

156 territoriality). Daily lek attendance and daily fighting rates are dependent on the absolute  
157 number of lekking days as well as the start, end and peak days of lekking. These vary both  
158 between years and between sites due to environmental factors (e.g. temperature; Ludwig et  
159 al., 2006). To avoid this confounding effect and to aid interpretation, the lekking periods  
160 were scaled so that on day 0,  $\geq 50$  % of all observed copulations had occurred. Thus day 0  
161 represents the peak of the lekking season. The amount of activity maps that are collected  
162 each day for the most attending male is important, since if these decline then other males'  
163 lek attendance may appear to increase. We tested whether the number of maps collected  
164 differed across the lekking season using a Poisson GLMM; we found no temporal effect on  
165 the number of activity maps collected for the top male (Poisson GLMER: day (linear),  
166  $z=0.68$ ,  $P=0.497$ ; day (quadratic),  $z=0.39$ ,  $P=0.696$ ).

167 To analyse differences in behavioural tactics we carried out a series of linear mixed  
168 effects models (LMM) using the *lmer* function from the R package *lmerTest* (Kuznetsova  
169 et al., 2014), run in R 3.0.2 (R Core Team, 2013). In all models, we included two random  
170 effects: year and individuals' ID nested within site. In the first models, we compared the  
171 effect of age (adults/yearlings) on daily lek attendance and daily fighting rate. In each  
172 model, we included the main effects age, day (linear and quadratic), and the interactions of  
173 day (linear and quadratic) with male age; non-significant interactions ( $\alpha > 0.05$ ) were  
174 removed in a stepwise fashion until only significant interactions or the fixed effects  
175 remained. We then tested whether males with different phenotypes had different daily lek  
176 attendance patterns and daily fighting rates. We used two morphological traits linked to  
177 individuals' body condition (body mass and lyre length). Previous studies showed that  
178 male body mass is critical to black grouse males' lek performance as dominant males are  
179 heavier and lose substantially more weight during the mating season than the other males  
180 (Hämäläinen et al., 2012; Lebigre et al., 2013). The lyre length is also a measure of body



181 condition as males with longer lyres have lower blood parasite load (microfilaria of  
182 *Onchocercidae* spp; Höglund et al., 1992), but it is unrelated to males' competitive ability  
183 on the lek and their lek attendance (Hämäläinen et al., 2012). Yearling and adult males  
184 were tested separately because yearling males have significantly lower trait body mass and  
185 tail length than adults (Siitari et al. 2007), meaning that analysing different-aged  
186 individuals in the same analysis (even when accounting for age-specific effects) would  
187 lead to overestimates of the association between male traits and differences in reproductive  
188 tactics (Kervinen et al., 2015). Again in each model, we included the interactions of linear  
189 and quadratic day with traits (body mass or lyre length); non-significant interactions ( $\alpha$   
190  $>0.05$ ) were removed in a stepwise fashion until only significant interactions or the fixed  
191 effects remained.

192 For a subset of adult males (N=15 males, 148 observations), we calculated their body  
193 mass loss over the lekking season (pre-lekking mass (g) – post-lekking mass (g)). Males  
194 were recaptured using the same walkin traps used during winter captures, baited with  
195 willow catkins. Captures took place a few days after the mating season. There was no  
196 significant relationship between initial mass and mass lost (Pearson's correlation:  $r=-0.14$ ,  
197  $P=0.601$ ), and no relationship between capture day post-lek and body mass (Lebigre et al.  
198 2013). We assessed whether males with differing resource investment (as measured by  
199 mass loss), showed differing patterns of daily lek attendance and daily fighting rate. In this  
200 model, we included the interactions of day (linear and quadratic) with mass loss as fixed  
201 effects; non-significant interactions ( $\alpha >0.05$ ) were removed in a stepwise fashion until  
202 only significant interactions or the fixed effects remained.

203 **Results**

204 *Age-specific variation in timing of reproductive effort*

205 There was a significant negative quadratic effect of the variable ‘day’ on daily lek  
206 attendance (Table 1) most likely due to a decline in daily lek attendance at the end of the  
207 lekking season (Figure 1a). Adult males had a consistent daily lek attendance across the  
208 lekking season, with a decline after the peak day of copulations (Figure 1a). Yearling  
209 males had lower daily lek attendance than adult males (yearlings: mean daily attendance  $\pm$   
210  $SD=0.61\pm0.35$ ; adults: mean daily attendance  $\pm$   $SD=0.85\pm0.26$ ). There was a significant  
211 interaction between the variable ‘day’ (linear) and males’ age (Table1) as yearling males  
212 increased their daily lek attendance during the season, but their daily attendance declined  
213 in a similar way as that of the adult males after the peak copulation days (Figure 1a).

214 There was an overall negative linear effect of day on males’ fighting rate meaning  
215 that daily fighting rate decreased towards the end of the lekking season (Table 1). Yearling  
216 males fought less often than adult males (yearlings: mean fighting rate  $\pm$   $SD=0.12\pm0.19$ ;  
217 adults: mean fighting rate  $\pm$   $SD=0.23\pm0.24$ ) and yearling males maintained low fighting  
218 rates while Yearling males in general maintained low fighting rates across the season  
219 whereas the daily fighting rate of adult males decreased towards the end of the lekking  
220 season as indicated by the significant interaction between day (linear) and age (Figure 1b;  
221 Table 1).

222

223 *Condition-dependence of reproductive effort*

224 For adult males, there were no significant interactions between morphological traits and  
225 day (linear) or day (quadratic) for either daily lek attendance or daily fighting rate (Table  
226 2). Instead, heavier males had higher lek attendance and fought more frequently than

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

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

241

## 242 **Discussion**

### 243 *Age-specific variation in timing of reproductive effort*

244 Across many species, age plays an important role in determining alternative reproductive  
245 tactics. Typically, prime-age males perform tactics that focus on male-male competition  
246 over access to females or defence of groups of females (John, 1993; Coltman et al., 2001;  
247 Saunders et al., 2005), whereas younger or older males may perform sneaking or satellite  
248 tactics (Forsyth & Montgomerie, 1987; John, 1993; Saunders et al., 2005). Young males  
249 may also show reduced levels of attendance at breeding sites (Deutsch et al., 1994;  
250 Kervinen et al., 2012). Our results show that as well as adopting completely different

251 behavioural tactics of lek attendance/non lek attendance (Kervinen et al. 2012), young  
252 males who do attend the lek can adapt their reproductive effort within a breeding season.  
253 Younger males had lower attendance overall, but their peak attendance was later and  
254 fighting rates higher at the end of the breeding season in comparison to adult males. Other  
255 studies have found older, more dominant males declining in reproductive effort late in the  
256 breeding season, with younger males increasing allocation to reproductive effort later in  
257 the breeding season (Mason et al., 2012) or showing no change (Tennenhouse et al., 2012).  
258 Such patterns are most likely explained by the declining body condition of the dominant  
259 males, their exhaustion and males' loss of motivation in reproductive display as the  
260 number of females' visits declines towards the end of the breeding season. By increasing  
261 reproductive effort later in the breeding season, yearling or young males have display rates  
262 of behaviour that are similar to adults and may therefore gain some reproductive success if  
263 females use these traits (indicators of their short term investment in reproduction) for mate  
264 choice.

265

### 266 *Condition-dependence of reproductive effort*

267 Many alternative reproductive tactics are condition- or state-dependent, irrespective of age  
268 (Leary et al., 2005; Lidgard et al., 2005; though see Alonso et al., 2010). Smaller males or  
269 those with less available resources may show a different behavioural phenotype e.g.  
270 satellite versus calling (Woodhouse's toads *Bufo woodhousii*: Leary et al., 2005), or may  
271 show reductions in the allocation of reproductive effort (Yuval et al., 1998; Eggert &  
272 Guyétant, 2003). In our study, allocation of effort in both fighting and lek attendance was  
273 driven by male condition both in adults and to a lesser extent in yearling males. This is  
274 perhaps unsurprising, as reproductive effort is typically very energetically costly in lekking

275 species (Vehrencamp et al., 1989), and nutritional reserves are crucial for determining  
276 participation (Yuval et al., 1998 Bachman & Widemo 1999). The non-significant trend in  
277 yearlings probably reflects the fact that lighter males did not attend the lek at all and  
278 delayed their age at first reproduction (Kervinen et al., 2012). Adult males attending the  
279 lek also tended to be heavier than non-territorial males (Hämäläinen et al., 2012), but our  
280 data show that even within these males, body mass is impacting reproductive effort.  
281 Despite this, we did not find any evidence of different reproductive tactics; lighter males  
282 did not differ in terms of the temporal pattern of fighting or lek attendance, but just carried  
283 out behaviours at a lower rate. In another lekking species, the great bustard, reproductive  
284 allocation was unrelated to body mass (Alonso et al., 2010). In black grouse, body mass is  
285 important in determining social rank through fighting (Hämäläinen et al., 2012), whereas  
286 in bustards, age seems to be more important for social ranking (Alonso et al., 2010).  
287 Hence, age and condition related patterns of reproductive allocation may act  
288 independently.

289         In contrast to body mass, tail length was unrelated to patterns of investment in  
290 reproduction. This was not surprising since previous tests looking at the relationship  
291 between fighting rates and other ornaments found no relationship (Hämäläinen et al.,  
292 2012). Tail length is an important part of female mate choice and is sexually-selected in  
293 black grouse (Höglund et al. 1994; Kervinen et al. 2016). Damage to the tail caused by  
294 fighting is important for mate choice particularly in sub-dominant males (Höglund et al.  
295 1994). In some species, tail length predicts the ability to hold resources indicating a role in  
296 male-male competition, possibly by signalling quality (Savalli 1994). Tail length in  
297 general is mainly used for signalling (Fitzpatrick 1998), so unlike body mass which is  
298 more directly linked to fighting outcome and allocable resources for lekking, it is perhaps  
299 not unexpected that tail length is unrelated to reproductive tactics.

300 Interestingly, we found evidence that alternative reproductive tactics may offer  
301 different outcomes in terms of body condition loss. As in many species (Deutsch et al.,  
302 1990), the loss of body condition in black grouse is considerable during the breeding  
303 season (Lebigre et al., 2013). We found that males investing in early lek attendance lost a  
304 greater amount of body mass than those who delayed their attendance. Such a result is  
305 similar to that found in fallow deer (*Dama dama*); fallow deer who invested most in certain  
306 rut behaviours had greatest mass loss (Jennings et al., 2010). However, in sage grouse  
307 (*Centrocercus urophasianus*), the most active displayers lost the least amount of weight  
308 (Vehrencamp et al. 1989). Sage grouse however are somewhat exceptional in that males  
309 forage on the lek and during the lekking season, something that other species do not do  
310 (Cowles & Gibson 2014). Therefore, the smaller body mass loss in active sage grouse  
311 displayers is probably explained by their better foraging abilities (Vehrencamp et al. 1989).  
312 Reproductive effort is costly in black grouse, with many males dying after reproducing or  
313 after peak reproductive effort (Alatalo et al., 1991; Kervinen et al., 2015, 2016). Our  
314 results suggest that selective allocation of reproductive effort may therefore be one way of  
315 minimising costs of lekking and ensuring survival to the following year. Managing within-  
316 breeding season reproductive effort may therefore have wider importance in the scheduling  
317 of reproduction across individuals' lifetimes.

318

### 319 **Conclusions**

320 Our results build on previous work showing age-specific differences in timing of  
321 reproductive effort (Mason et al., 2012; Tennenhouse et al., 2012), but we found no  
322 relationship between condition and timing. However, adult males with low or no mass loss  
323 had different timing of effort. Such patterns may arise for two reasons: firstly, males of  
324 lower competitive ability responding to declines in dominant males' condition and gain

325 some access to reproduction (Mason et al. 2012). Alternatively, males may be adjusting  
326 timing effort to reduce the costs of such effort. Either way, it seems that how or when  
327 males invest reproductive effort is important. It is likely that flexible timing of  
328 reproductive effort by males is widespread in many mating system,  
329

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- 459

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

464

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

470

471 Figure 3: Surface plot showing the interaction between individual daily lek attendance, day  
472 and the mass loss between pre- and post-lekking for adult males (N=15 males, 148  
473 observations). Mass loss is presented so that negative values indicate large mass loss  
474 and positive values indicate mass gain. Days have been scaled so that on day 0,  $\geq 50$   
475 % of all copulations have occurred.

476

477

478

479 Table 1. Temporal variation in daily lek attendance and daily fighting rate of males in  
 480 relation to age (yearling/adult). The interaction between day and age was included,  
 481 but deleted if non-significant. The parameter day is scaled so that on day 0,  $\geq 50\%$  of  
 482 all copulations have occurred. All parameter estimates are multiplied by 1000 to aid  
 483 interpretation.

484

<b>Model</b>	<b>Parameter</b>	<b>Estimate</b>	<b><math>\pm</math>SE</b>	<b><i>t</i></b>	<b><i>p</i></b>
Daily lek attendance (N=281 individuals/N observations 3875)	Intercept	219.60	23.19	9.471	<0.001
	Day (linear)	0.25	1.40	0.18	0.857
	Day (quadratic)	-1.36	0.23	-5.97	<0.001
	Age	-222.20	16.99	-13.08	<0.001
	Day (linear) x Age	14.93	3.52	4.24	<0.001
Daily fighting rate (N=281 individuals/N observations 3875)	Intercept	219.20	23.19	9.45	<0.001
	Day (linear)	-5.89	1.26	-4.68	<0.001
	Day (quadratic)	-0.16	0.20	-0.76	0.446
	Age	-98.18	13.91	-7.06	<0.001
	Day (linear) x Age	8.87	3.11	2.86	<0.001

485

486

487 Table 2. Temporal variation in daily lek attendance and daily fighting rate in relation to body mass and lyre length of adult ( $\geq 2$  year old) and  
488 yearling males (1 year old). The interaction between day and mass and lyre length was included, but deleted as non-significant. The  
489 parameter day is scaled so that on day 0,  $\geq 50$  % of all copulations have occurred. All parameter estimates are multiplied by 1000 to aid  
490 interpretation.

<b>Model</b>	<b>Parameter</b>	<i>Adults male</i>				<i>Yearling males</i>			
		<b>Estimate</b>	<b><math>\pm</math>SE</b>	<b><i>t</i></b>	<b><i>p</i></b>	<b>Estimate</b>	<b><math>\pm</math>SE</b>	<b><i>t</i></b>	<b><i>p</i></b>
Daily lek attendance <sup>a</sup>	Intercept	-3364.00	1348.00	-2.50	0.013	-9043.00	4627.00	-1.95	0.056
	Day (linear)	2.96	1.47	2.01	0.044	11.44	4.59	2.50	0.013
	Day (quadratic)	-0.98	0.25	-3.88	0.000	-2.30	0.83	-2.75	0.006
	Mass	592.70	188.60	3.14	0.002	1369.00	654.90	2.09	0.041
Daily lek attendance <sup>b</sup>	Intercept	572.70	174.50	3.28	0.001	1523.00	615.60	2.47	0.016
	Day (linear)	2.83	1.49	1.90	0.057	11.56	4.58	2.53	0.012
	Day (quadratic)	-0.94	0.25	-3.72	0.000	-2.26	0.83	-2.71	0.007
	Lyre length	1.32	0.77	1.72	0.086	-4.72	3.23	-1.46	0.149
Daily fighting rate <sup>a</sup>	Intercept	-2864.00	1110.00	-2.58	0.010	-5157.00	2427.00	-2.13	0.038
	Day (linear)	-5.84	1.42	-4.12	0.000	1.11	2.75	0.40	0.688
	Day (quadratic)	-0.35	0.24	-1.45	0.146	-0.12	0.50	-0.24	0.810
	Mass	431.60	155.30	2.78	0.006	746.60	343.50	2.17	0.034
Daily fighting rate <sup>b</sup>	Intercept	37.34	142.00	0.26	0.793	512.30	322.80	1.59	0.118
	Day (linear)	-5.84	1.44	-4.07	0.000	1.08	2.75	0.39	0.695
	Day (quadratic)	-0.32	0.24	-1.32	0.188	-0.10	0.50	-0.20	0.839
	Lyre length	0.82	0.62	1.31	0.190	-2.08	1.69	-1.23	0.223

491 <sup>a</sup>N=235 adult males, 2882 daily observations; 67 yearling, 511 daily observations

492 <sup>b</sup>N=230/2820 daily observations, 67 yearling, 511 daily observations

493

494

495

496 Table 3. Temporal variation in daily lek attendance and daily fighting rate of adult males in  
497 relation to the amount of weight lost over the lekking period (g). The interaction  
498 between day and mass loss was included, but deleted if non-significant. The  
499 parameter day is scaled so that on day 0,  $\geq 50\%$  of all copulations have occurred. All  
500 parameter estimates are multiplied by 1,000 to aid interpretation.

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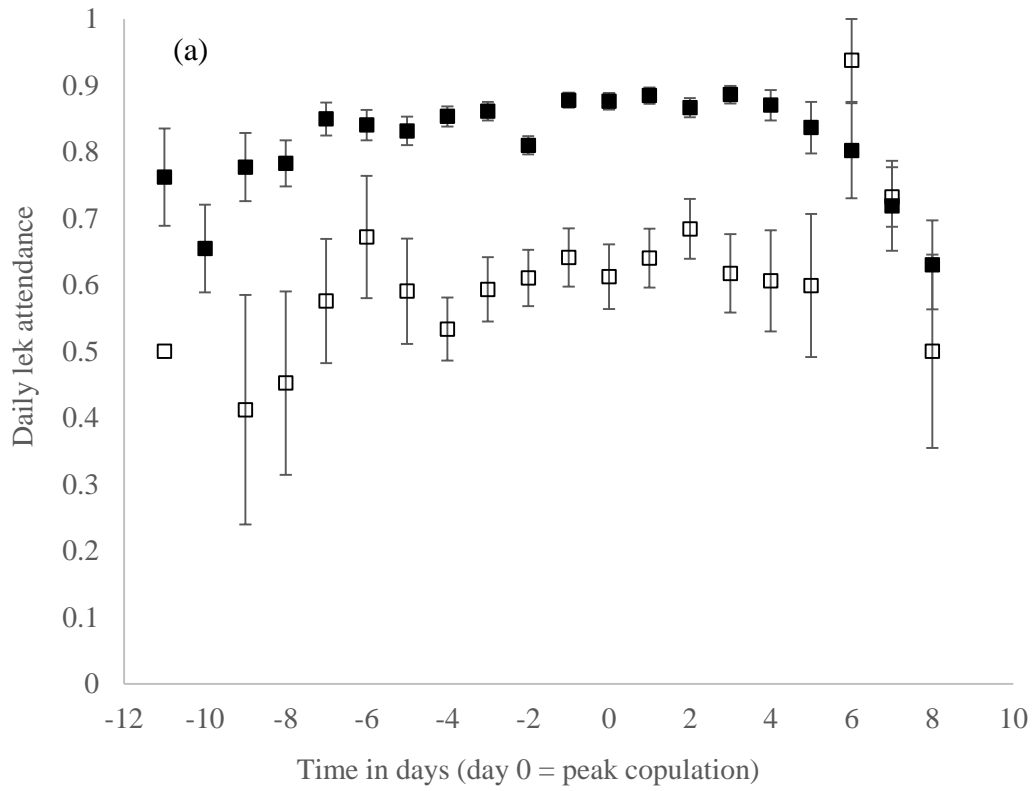
<b>Model</b>	<b>Parameter</b>	<b>Estimate</b>	<b>SE</b>	<b><i>t</i></b>	<b><i>p</i></b>
Daily lek attendance	Day (linear)	31.87	10.17	3.14	0.002
	Day (quadratic)	0.02	0.43	0.04	0.966
	Mass loss (g)	0.89	1.66	0.54	0.592
	Day (linear) x Mass loss	-0.27	0.11	-2.43	0.017
Daily fighting rate	Day (linear)	7.69	9.09	0.85	0.399
	Day (quadratic)	4.77	2.02	2.36	0.020
	Mass loss	-0.27	0.54	-0.49	0.628

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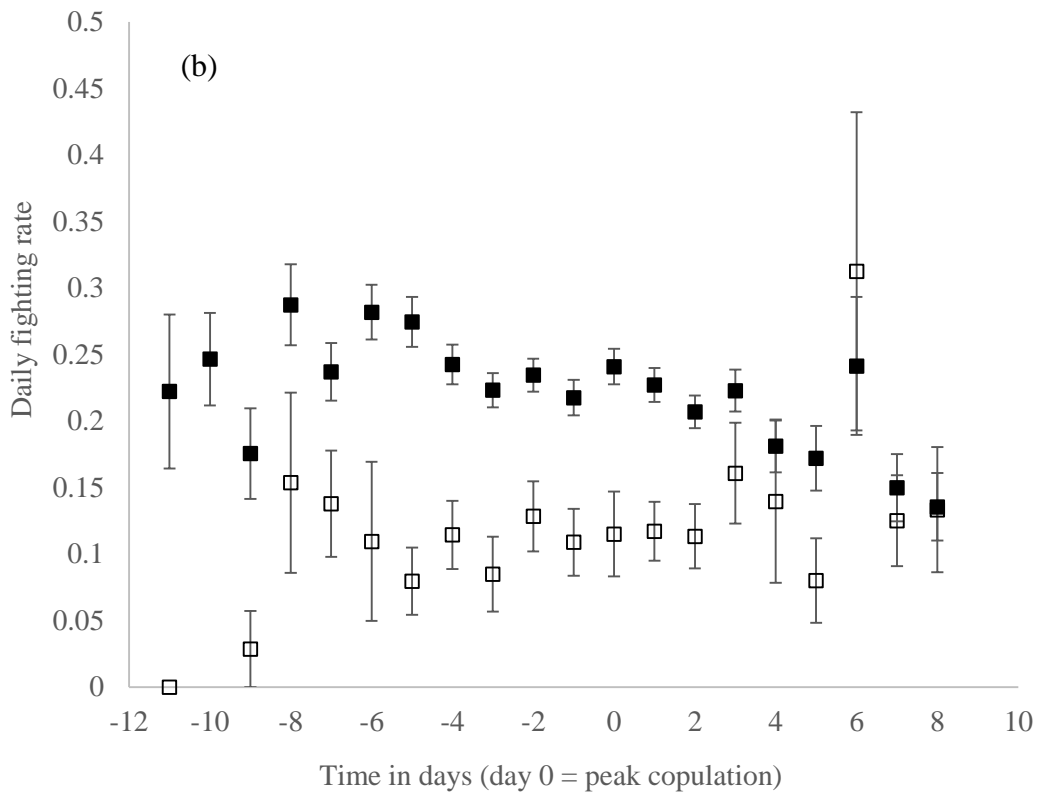
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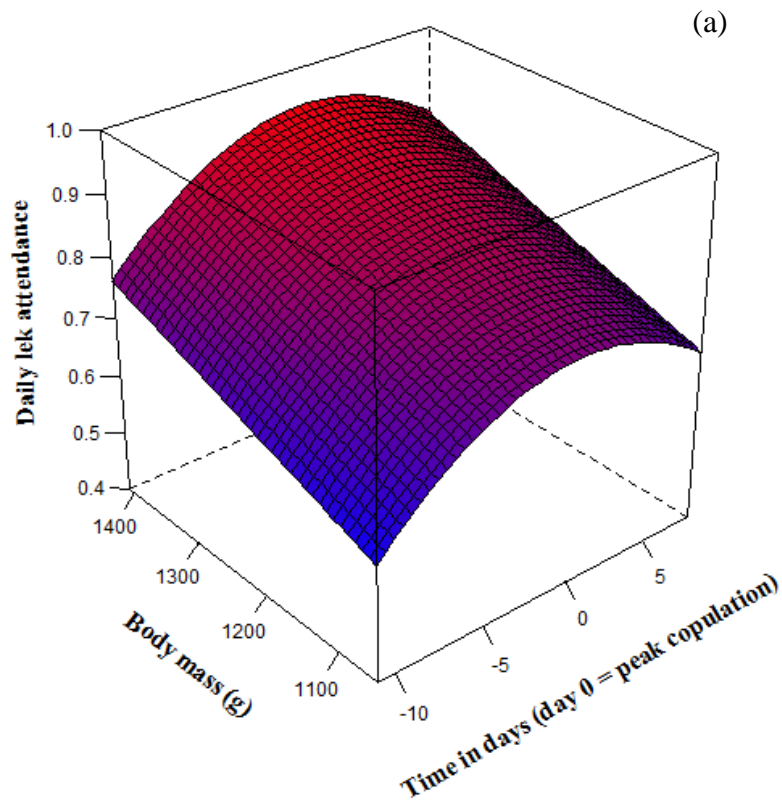
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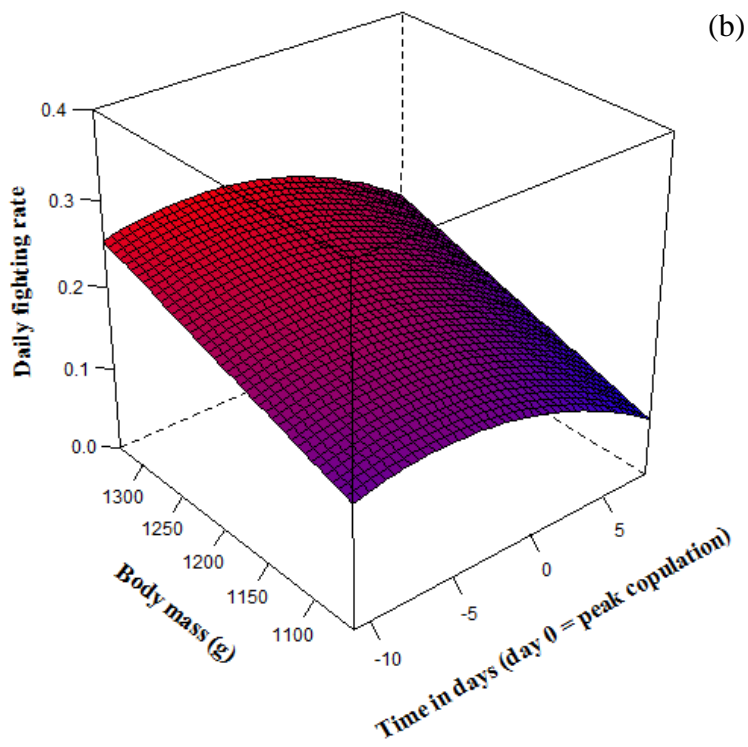
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508 **Figure 1**

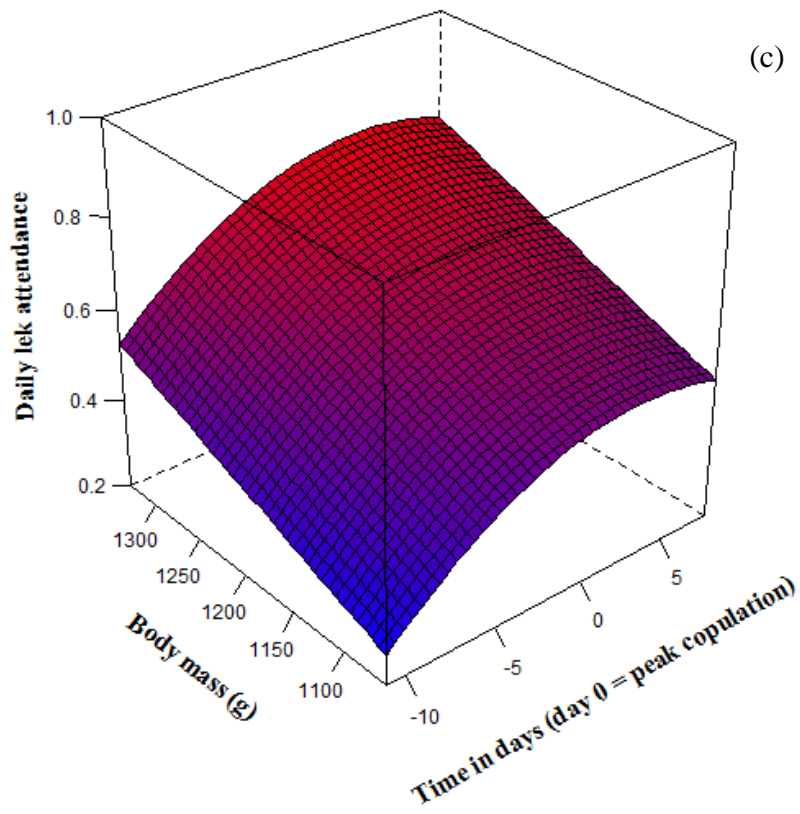
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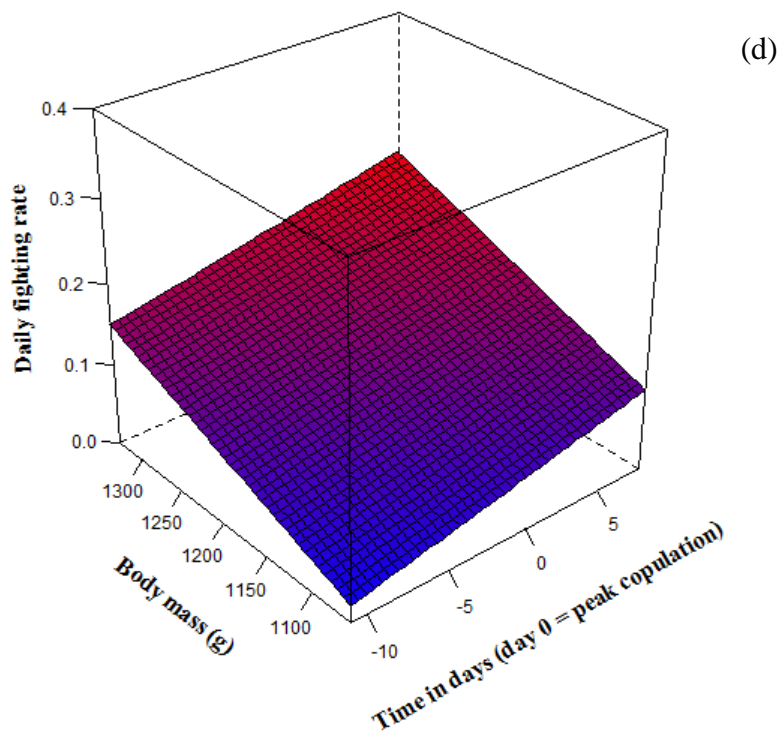
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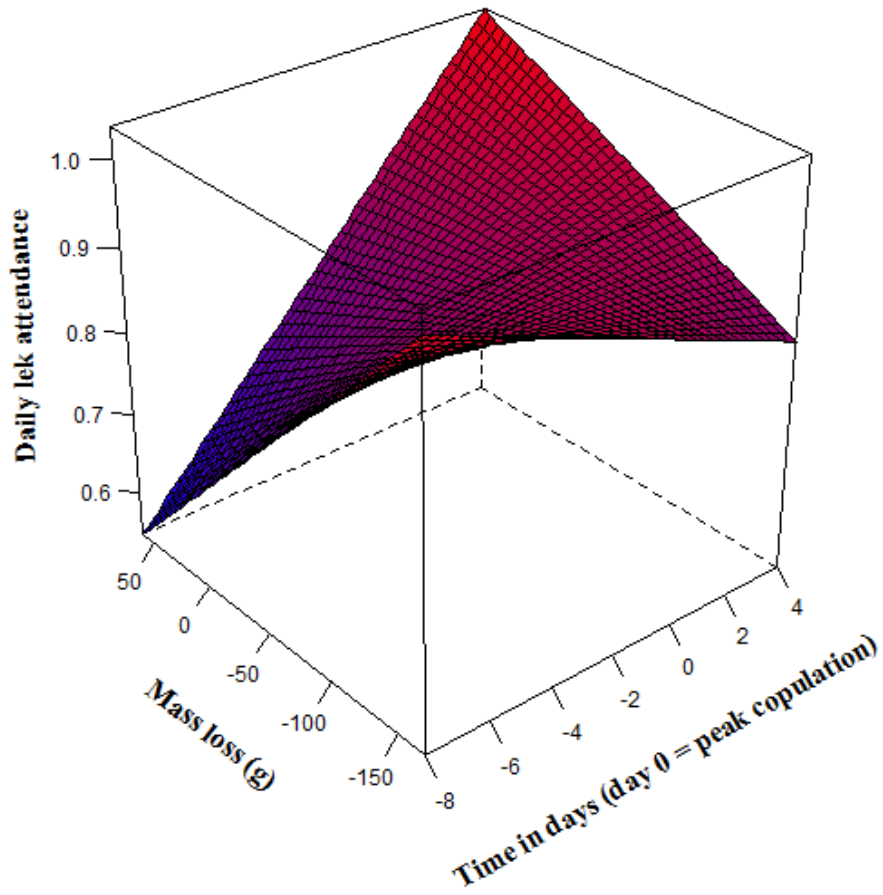


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Figure 2



514

515 **Figure 3**

516