

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

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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 (Myerud 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 (Myerud 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 (Deutsch 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 ≥ 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, ≥ 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 (α
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 $SD=0.61\pm 0.35$; adults: mean daily attendance \pm $SD=0.85\pm 0.26$). There was a significant
211 interaction between the variable ‘day’ (linear) and males’ age (Table 1) 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 $SD=0.12\pm 0.19$;
217 adults: mean fighting rate \pm $SD=0.23\pm 0.24$) 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, ≥ 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, ≥ 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, ≥ 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

Model	Parameter	Estimate	\pmSE	<i>t</i>	<i>p</i>
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 (≥ 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, ≥ 50 % of all copulations have occurred. All parameter estimates are multiplied by 1000 to aid
490 interpretation.

Model	Parameter	<i>Adults male</i>				<i>Yearling males</i>			
		Estimate	\pmSE	<i>t</i>	<i>p</i>	Estimate	\pmSE	<i>t</i>	<i>p</i>
Daily lek attendance ^a	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 ^b	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 ^a	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 ^b	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 ^aN=235 adult males, 2882 daily observations; 67 yearling, 511 daily observations

492 ^bN=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.

501

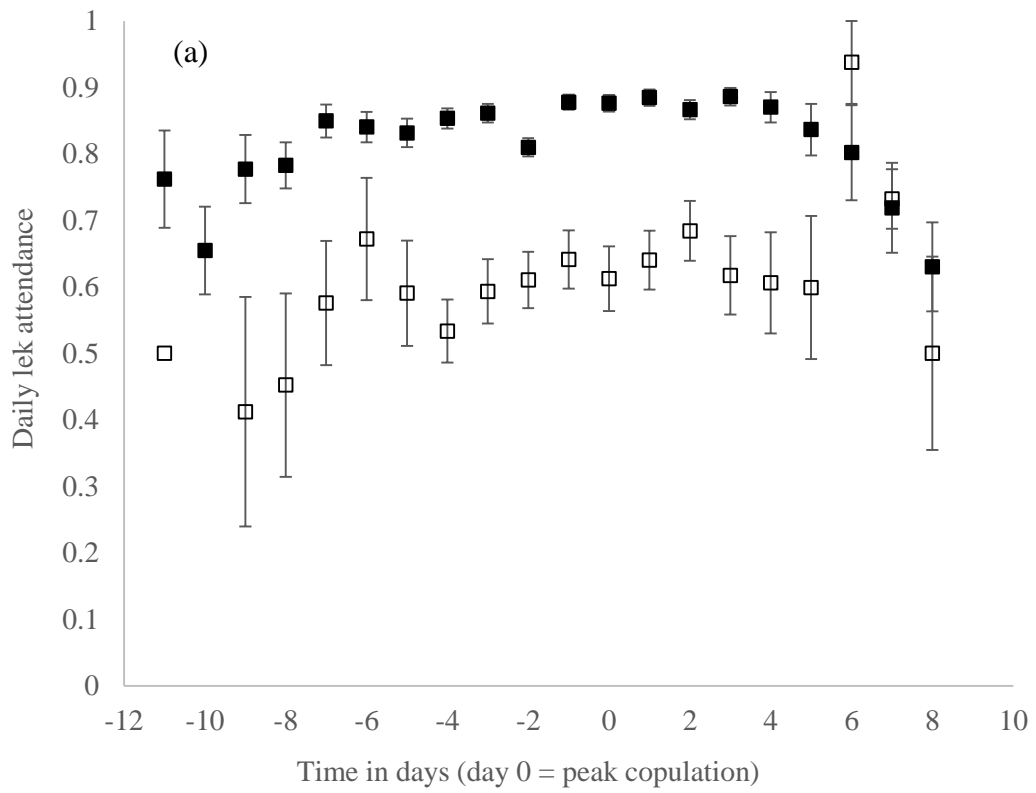
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Model	Parameter	Estimate	SE	<i>t</i>	<i>p</i>
Daily lek attendance	Day (linear)	31.87	10.17	3.14	0.002
	Day (quadratic)	0.02	0.43	0.04	0.966
	Mass loss (g)	0.89	1.66	0.54	0.592
	Day (linear) x Mass loss	-0.27	0.11	-2.43	0.017
Daily fighting rate	Day (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

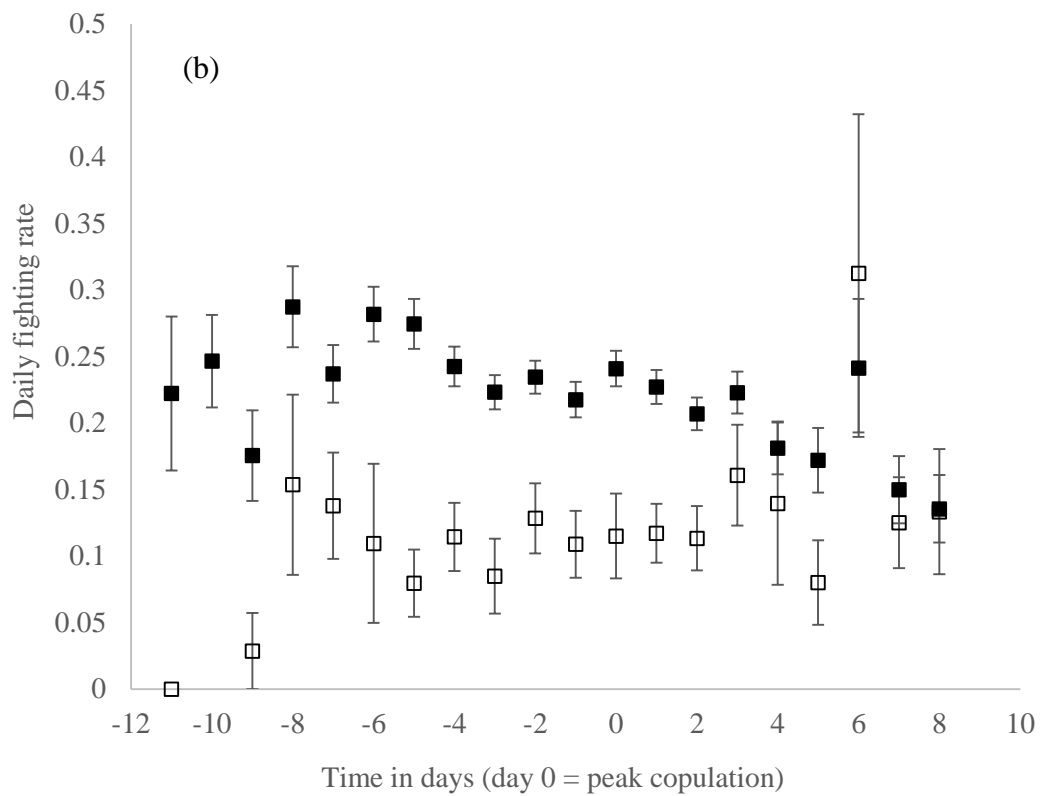
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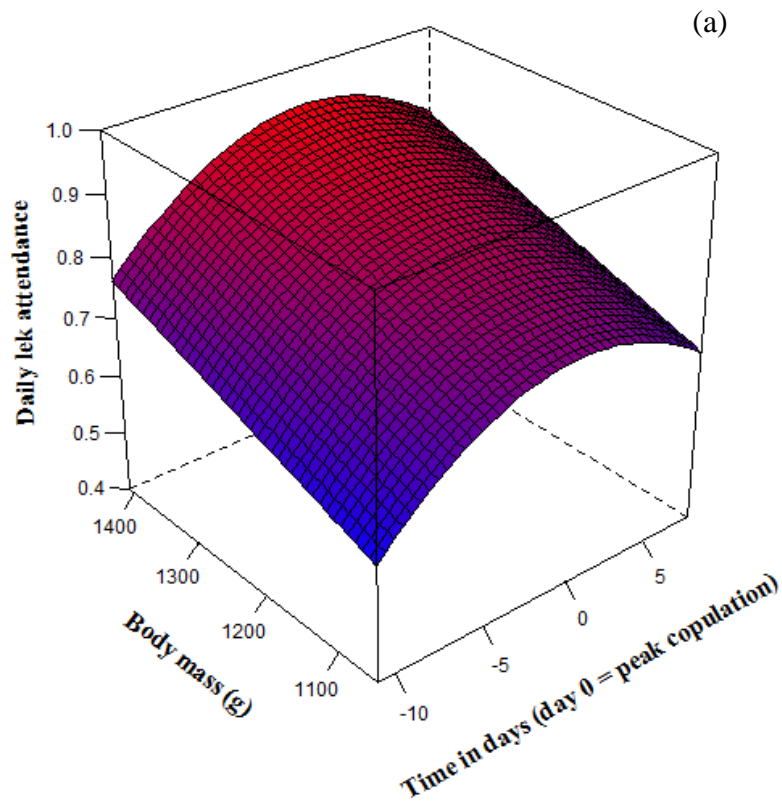
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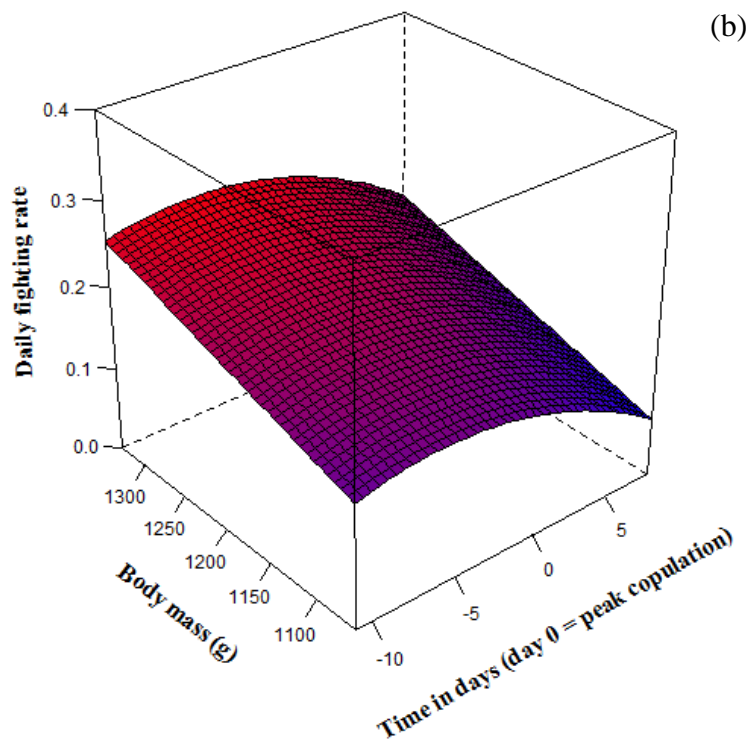
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508 **Figure 1**

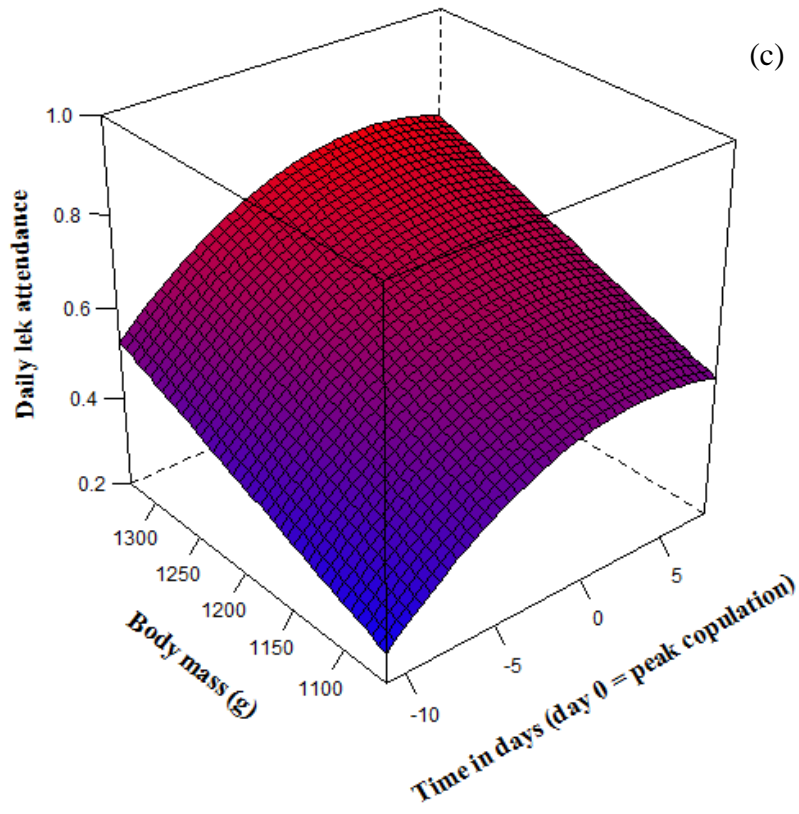
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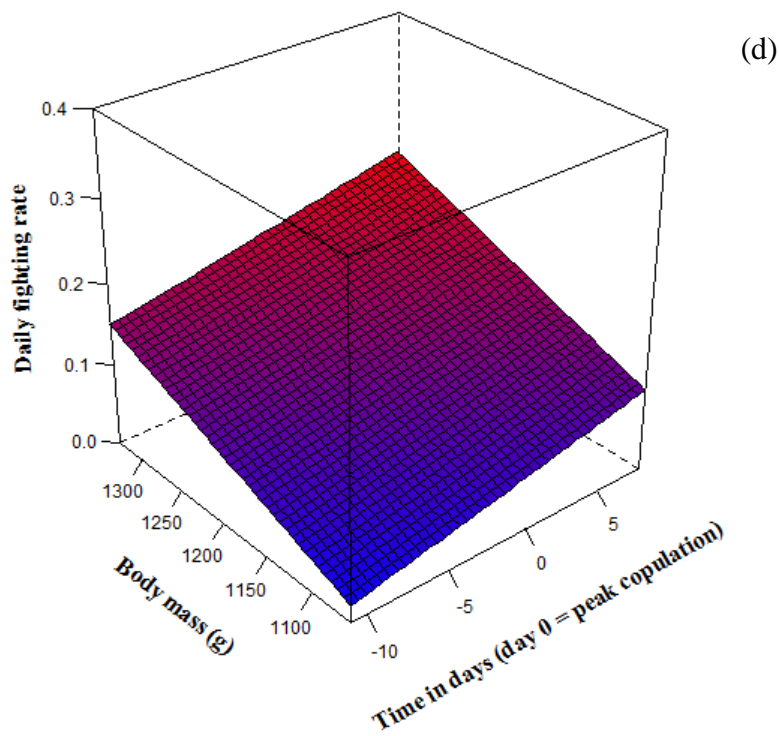
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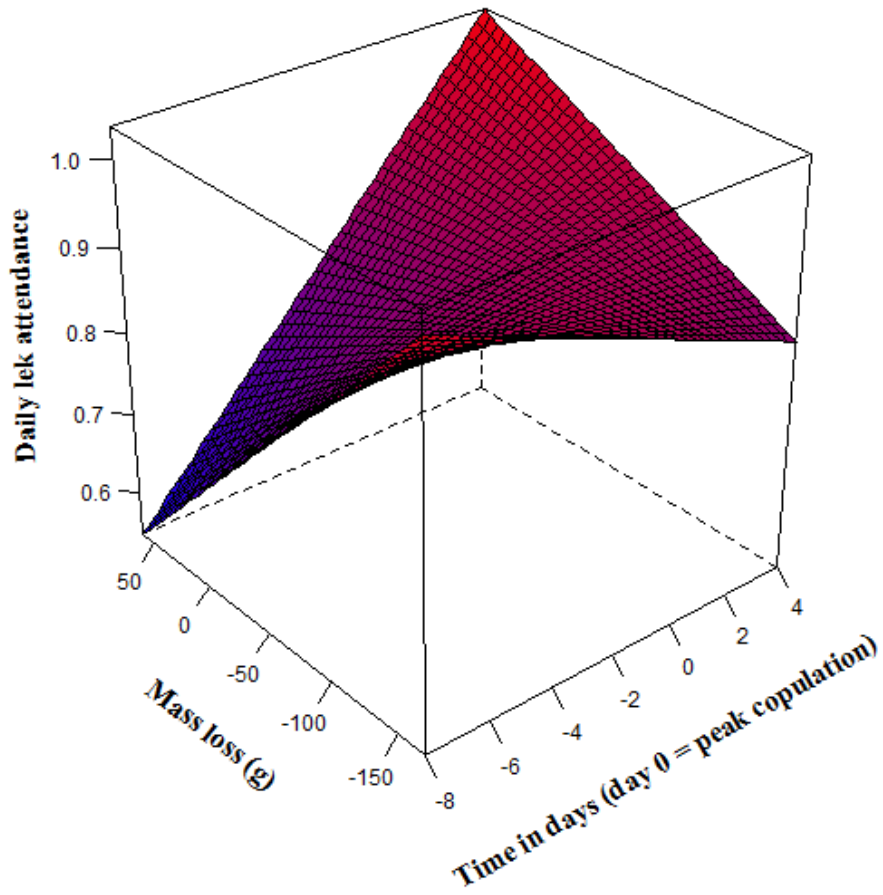


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Figure 2



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515 **Figure 3**

516