

1       **Age-dependent and age-independent sexual selection on**  
2       **multiple male traits in the lekking black grouse (*Lyrurus***  
3                       ***tetrix*)**

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14  
15   Running headline: Age-(in)dependent sexual selection in *L. tetrix*

16  
17   **Summary**

- 18           1. Individuals' reproductive success is often strongly associated with their  
19                            age, with typical patterns of early life reproductive improvement and late  
20                            life senescence. These age-related patterns are due to the inherent trade-  
21                            offs between life history traits competing for a limited amount of resources  
22                            available to the organisms. In males, such trade-offs are exacerbated by the  
23                            resource requirements associated with the expression of costly sexual

24 traits, leading to dynamic changes in trait expression throughout their  
25 lifespan.

26 2. Due to the age-dependency of male phenotypes, the relationship between  
27 the expression of male traits and mating success can also vary with male  
28 age. Hence, using longitudinal data in a lekking species with strong sexual  
29 selection – the black grouse *Lyrurus tetrrix* – we quantified the effects of  
30 age, lifespan and age of first lek attendance (AFL) on male annual mating  
31 success (AMS) to separate the effects of within-individual improvement  
32 and senescence on AMS from selective (dis)appearance of certain  
33 phenotypes. Then, we used male AMS to quantify univariate and  
34 multivariate sexual selection gradients on male morphological and  
35 behavioural traits with and without accounting for age and age-related  
36 effects of other traits.

37 3. Male AMS increased with age and there was no significant reproductive  
38 senescence. Most males never copulated and of the ones that did, the  
39 majority had only one successful year. Lifespan was unrelated to AMS, but  
40 early AFL tended to lead to higher AMS at ages 1 to 3. AMS was related  
41 to morphological and behavioural traits when male age was ignored.  
42 Accounting for age and age-specific trait effects (i.e. the interaction  
43 between a trait and age) reduced the magnitude of the selection gradients  
44 and revealed that behavioural traits are under consistent sexual selection,  
45 while sexual selection on morphological traits is stronger in old males.

46 4. Therefore, sexual selection in black grouse operates primarily on male  
47 behaviour and morphological traits may act as additional cues to  
48 supplement female choice. These results demonstrate the multifaceted

49 influence of age on both fitness and sexual traits and highlight the  
50 importance of accounting for such effects when quantifying sexual  
51 selection.

52

53 **Key-words:** ARS, mating success, lek, long-term data, LRS, selection differential,  
54 selection gradient, senescence, *Tetrao tetrrix*

55

## 56 **Introduction**

57

58 Sexual selection underpins the evolution of extravagant male ornaments either  
59 through female preference for higher expression of these traits (e.g. colourful feathers)  
60 or through the competitive advantage they offer during male-male competition (e.g.  
61 male weaponry, Andersson 1994). Therefore, direct relationships between male traits  
62 and mating success are generally interpreted as evidence for sexual selection on male  
63 traits. However, mating success in a particular year of a male's life may not accurately  
64 reflect the association between the trait and fitness, since individual mating success  
65 typically increases in early life and decreases at later ages (Jones *et al.* 2008; Nussey  
66 *et al.* 2013).

67 Age-dependent mating and reproductive success are typically explained by the  
68 inability to simultaneously maximise competing life history traits (e.g. growth,  
69 reproductive investment, survival), due to the limited amount of resources available to  
70 the organisms (Stearns 1992). Such trade-offs are responsible for the constraints on  
71 reproductive effort in early ages, when resources are allocated to growth, leading to  
72 shorter (reproductive) lifespan (Curio 1983; Forslund & Pärt 1995; Descamps *et al.*  
73 2006; Reed *et al.* 2008). Therefore, individuals might delay the onset of breeding until

74 their condition allows them to display intensively and compete for mates and thus  
75 reduce the fitness costs associated with an earlier onset of breeding (Curio 1983;  
76 Beauchamp & Kacelnik 1990; Forslund & Pärt 1995). Apparent age-dependent  
77 reproductive success may also arise due to selection acting against individuals in poor  
78 condition leading to an increase in the proportion of 'high quality' individuals within a  
79 cohort (selective appearance of good reproducers / selective disappearance of bad  
80 reproducers; van de Pol & Verhulst 2006), or due to the negative effects of ageing on  
81 individuals' physiological condition, which leads to a reduction in reproductive  
82 success, i.e. senescence (Stearns 1992; Williams *et al.* 2006; Bouwhuis *et al.* 2010;  
83 Nussey *et al.* 2013). All these mechanisms can explain the association between male  
84 age and their ability to mate and hence produce offspring. Thus, fully understanding  
85 the variation in individuals' fitness requires quantifying the temporal dynamics in  
86 reproductive success that emerges from life history trade-offs.

87         In males of species with strong sexual selection, the allocation of resources to  
88 reproduction embodies the expression of costly sexual traits that underlie males'  
89 competitive ability and attractiveness (Andersson 1994; Höglund & Sheldon 1998).  
90 Males' age has been shown to associate with the size and quality of sexual traits such  
91 as antler size, tail feathers and plumage colouration (e.g. Nussey *et al.* 2009; Evans,  
92 Gustafsson, & Sheldon 2011; Kervinen *et al.* 2015) most probably through changes in  
93 body condition throughout individuals' lifespan (Höglund & Sheldon 1998; Emlen *et*  
94 *al.* 2012). Therefore, quantifying the effect of the expression of a specific trait on  
95 male mating success requires accounting for direct and indirect age-specific effects of  
96 other traits.

97         Studies quantifying sexual selection on male traits while also accounting for age  
98 are still relatively scarce (Coltman *et al.* 2002; Kruuk *et al.* 2002; Freeman-Gallant *et*

99 *al.* 2010), with the majority examining single traits (though see Freeman-Gallant *et al.*  
100 2010). One reason for the paucity of such studies is that accurate measures of male  
101 mating success are difficult to collect in natural populations, because copulations can  
102 be difficult to observe and animals move in and out from the study area (Coltman *et*  
103 *al.* 1999; Kruuk *et al.* 2002). Molecular markers can be used to deduce female mating  
104 behaviour and male mating success, but the accuracy of such methods will strongly  
105 depend on our ability to quantify accurately male mating success and to identify  
106 multiple matings, as well as on the occurrence of post-copulatory sexual selection  
107 (Eberhard 1996; Birkhead 1998; Birkhead & Møller 1998). Therefore, better  
108 understanding the magnitude of sexual selection acting on male traits requires using  
109 study systems in which male mating success can reliably be measured and related to  
110 the expression of the multiple traits across their entire lifespan (Clutton-Brock &  
111 Sheldon 2010).

112       In the lekking black grouse (*Lyrurus tetrix*, formerly *Tetrao tetrix*), male mating  
113 success can easily be recorded since copulations are very conspicuous and most  
114 copulations take place on leks (Lebigre *et al.* 2007). Females usually mate only once  
115 with one male and the parentage analyses demonstrated a very high concordance  
116 between observed mating success and genetic reproductive success (in 94% of the  
117 cases, the presumed father sired all the hatchlings of the brood; Lebigre *et al.* 2007).  
118 Males are very faithful to the leks where they initially established their territories and  
119 rarely switch lek sites (Rintamäki *et al.* 1995; Höglund *et al.* 1999; Lebigre *et al.*  
120 2008). Hence, we can monitor the mating success of the same individuals over their  
121 whole lifespan, as all males holding central territories and >90% of all territorial  
122 males were ringed. Male mating skew is substantial due to the intense male-male  
123 competition and clear female choice (Alatalo, Höglund & Lundberg 1991; Alatalo *et*

124 *al.* 1992). In theory, males with no mating success could gain indirect fitness benefits  
125 by increasing the mating opportunities of their close relatives, but such kin selected  
126 benefits amount only to *ca.* 3% of a copulation in this study system (Lebigre *et al.*  
127 2014). Contrary to most previous studies that focused on one or two sexually-selected  
128 traits, male black grouse express multiple morphological and behavioural traits that  
129 are related to male mating success (these traits are partially correlated; see  
130 Supplementary Table S1). Lyre length and quality (Höglund *et al.* 1994, Rintamäki *et al.*  
131 *al.* 2001), the size of testosterone-dependent red eye combs (Rintamäki *et al.* 2000),  
132 body mass (Rintamäki *et al.* 2001, Lebigre, Alatalo & Siitari 2013) and blue chroma  
133 colouration of breast feathers (Siitari *et al.* 2007) are all positively correlated with  
134 male mating success. Moreover, females prefer mating with males that have high lek  
135 attendance (Alatalo *et al.* 1992), fight frequently and successfully against other males  
136 (Hämäläinen *et al.* 2012), and occupy central territories on leks (Hovi *et al.* 1994).  
137 However, a substantial amount of the variation in all these traits is explained by male  
138 age (Kervinen *et al.* 2015; unconditional  $R^2$  range in this study: 0.18–0.78, see  
139 Nakagawa & Schielzeth 2013 for detailed methods).

140         We used longitudinal data describing male mating success and the expression of  
141 multiple sexually-selected morphological and behavioural traits to quantify changes in  
142 mating success with male age and determine the relative contribution of the age-  
143 specific trait expression to this pattern. We first tested the hypothesis that the variation  
144 in male mating success is age-dependent by quantifying the effects of age, age of first  
145 lek attendance (AFL), lifespan and terminal investment on males' annual mating  
146 success (AMS). This enabled us to separate the effects of within-individual  
147 improvement and senescence on AMS from selective appearance and disappearance  
148 of certain phenotypes in the population. We then quantified the effect of each

149 morphological and behavioural trait on male AMS while accounting for other  
150 unmeasured age-specific effects using univariate sexual selection differentials and  
151 multivariate sexual selection gradients with male age as a covariate. We tested  
152 whether these sexual selection gradients were age-specific by including an interaction  
153 term between male age and trait expression. Finally, we re-quantified the univariate  
154 sexual selection differentials and multivariate sexual selection gradients without male  
155 age as a covariate to determine whether accounting for age effects (and hence the  
156 expression of other age-related traits not directly used as covariates in the models)  
157 changes the strength of sexual selection acting on the measured traits.

158

## 159 **Materials and methods**

160

### 161 **STUDY POPULATION AND FIELD METHODS**

162

163 During 2002–2013, we collected longitudinal data describing male mating success  
164 and multiple sexual traits in five study sites in Central Finland (peat bogs with high  
165 visibility, *ca.* 62°15'N; 25°00'E). In addition, males were monitored during the  
166 mating season in spring 2014 to ensure the use of complete cohorts (no ringed males  
167 alive) in the analyses. Each study site is a local main lek with 5–40 territorial males,  
168 and as local hunting clubs have refrained from hunting on these areas, the age  
169 structure of the study population can reasonably be assumed to be natural.

170 Data on morphological traits were collected from the study sites annually in  
171 January–March by catching birds from the winter flocks with oat-baited walk-in traps  
172 (for methods, see Kervinen *et al.* 2012; Lebigre *et al.* 2012). Each captured individual  
173 was aged as yearling or older according to plumage characteristics and individually

174 ringed for future identification with an aluminium tarsus ring with a unique serial  
175 number and three coloured tarsus rings. All captured birds were blood sampled (for a  
176 parallel study) and measured for body mass, lyre (i.e. tail) length, eye comb size and  
177 blue chroma colouration of breast feathers (Siitari *et al.* 2007; Lebigre *et al.* 2012).

178 Male mating success and lekking behaviour were recorded on the study sites  
179 (leks) annually during the peak mating season (the period in late April – early May  
180 when virtually all copulations take place, Ludwig *et al.* 2006). During this period,  
181 typically lasting 1 to 2 weeks depending on the weather conditions, all study leks were  
182 monitored daily from *ca.* 3:00 to 8:00 a.m. by observers located in hides near the lek  
183 arenas (for detailed methods, see Kervinen *et al.* 2012; Lebigre *et al.* 2012). Male  
184 behaviour was scan sampled at regular intervals and categorised as rookooing, hissing  
185 (the two main vocal displays), fighting or inactive (methods and behaviours are  
186 described in detail in Höglund, Johansson & Pelabon 1997). Lek attendance  
187 (proportional to the most commonly present male on the same lek), the relative  
188 proportion of each behaviour, and males' territory distances from the lek centre  
189 (hereafter "territory centrality"; see Lebigre *et al.* 2012) were calculated for all  
190 individually identifiable males from the records (see Rintamäki *et al.* 1995; Alatalo *et*  
191 *al.* 1996). Finally, we documented the occurrence of copulations, which are easy to  
192 observe, as males flap their wings conspicuously when mounting females, their  
193 location and the individuals involved.

194

## 195 DATA VALIDATION

196

197 In these analyses, we only included the males that were first caught as yearlings and  
198 could therefore be precisely aged. The data consisted of records of AMS, lekking



199 behaviour (lek attendance, fighting rate, territory centrality) and morphological traits  
200 (body mass, lyre length, blue chroma, eye comb size) for 164 male black grouse with  
201 known year of hatching (2001–2008), known AFL (at age 1: N = 89, at age 2: N = 66,  
202 at age 3: N = 9) and known lifespan of 1 to 6 years (412 records in total); no males  
203 with detailed life history survived >6 years old. Due to male philopatry for their initial  
204 lekking site (Rintamäki *et al.* 1995; Höglund *et al.* 1999; Lebigre *et al.* 2008), lifespan  
205 was defined as the age at which the male was last time seen on the lek. Complete  
206 cohorts (i.e. no ringed males of the cohort alive in spring 2014) were available for  
207 males hatched in 2001–2008. Cohorts hatched 2009 onwards were excluded because  
208 of large proportions (>10%) of individuals being still alive in spring 2014.

209

## 210 STATISTICAL ANALYSES

211

212 All analyses were run in R 3.0.3 (R Development Core Team 2014). We used  
213 generalised linear mixed effects models (GLMM) to test the effects of age, AFL,  
214 lifespan and terminal investment on AMS following the procedure detailed in van de  
215 Pol & Verhulst (2006). We used varIdent variance error structure from Poisson  
216 distribution ('gls' function from the R package 'nlme') to account for the  
217 overdispersion in the data. Age and age<sup>2</sup> represented the linear and quadratic within-  
218 individual change in AMS with age. A significant positive effect of AFL on AMS can  
219 be interpreted as evidence for selective appearance of good reproducers. A significant  
220 negative effect of lifespan (i.e. age at last lek) on AMS, in turn, can be interpreted as  
221 evidence for selective disappearance of poor reproducers. The interactions of AFL  
222 and lifespan with age were also introduced as fixed effects to account for potential life  
223 history differences (e.g. reproduction at early ages and short lifespan vs. long lifespan

224 and reproduction at older ages). A binary fixed effect 'terminal event' (TE, indicates  
225 whether it was the male's last year alive or not) and its interaction with age was  
226 included to account for potential terminal investment in reproduction, as this can  
227 affect the interpretation of evidence of senescence (Rattiste *et al.* 2004; Hammers *et*  
228 *al.* 2012). Individual identity nested within study site was fitted as a random effect in  
229 all models to account for multiple measures from the same individuals and locations.

230 Model selection was carried out for the pre-selected set of biologically relevant  
231 candidate models following the AIC-IT procedure (Table 1), and models within 95%  
232 cumulative model weight (*ca.*  $\Delta AIC_c < 6$ ) were averaged (Burnham, Anderson &  
233 Huyvaert 2011; Grueber *et al.* 2011). Then, the relative importance and model-  
234 averaged coefficient estimates with unconditional SE and unconditional 95% CI were  
235 calculated for each parameter in the averaged models (R package 'AICcmodavg' v.  
236 2.0-1, Mazerolle 2014). As random slopes cannot be fitted in *gls* models, we repeated  
237 the same analysis using '*lme*' function from the R package 'nlme' with individual  
238 identity nested within study site fitted as the random intercept and its interaction with  
239 age fitted as the random slope to reduce the risk of potential type I and type II errors  
240 (Schielzeth & Forstmeier 2009). However, as including random slopes did not  
241 significantly change the interpretation of the results (Supplementary Table S2, S3, S4  
242 and S5) and as the *gls* models better accounted for the overdispersion in the data  
243 (based on the model residuals), we present the results of the initial *gls* approach.

244 Measures of senescence that do not account for within-individual age effects  
245 (random slopes) may mask within-individual patterns of ageing and mix together  
246 individuals with differing life history strategies (Bouwhuis *et al.* 2009). As including  
247 random slopes did not significantly alter the interpretation of our results, we could  
248 ignore variation in within-individual patterns of ageing. Thus, we carried out a

249 Poisson GLMM on AMS data after the age at which AMS showed its statistical peak  
250 with age and AFL fitted as linear effects only and individual identity nested within  
251 study site fitted as a random effect. In this additional analysis, a significant negative  
252 effect of age can be considered as evidence of senescence (Bouwhuis *et al.* 2009).

253 To quantify age-specific sexual selection, we first standardised male AMS by  
254 dividing each male's AMS by the annual mean AMS of all males on the same lek: the  
255 total number of copulations on the lek varied between sites and years (mean  $\pm$  SD =  
256  $30.84 \pm 20.18$ , N = 49), but it was not correlated with individual AMS (Spearman's  $r =$   
257  $0.05$ ,  $p = 0.323$ , N = 412). We then standardised (i.e. zero-centred: mean = 0, SD = 1)  
258 each morphological and behavioural trait using the yearly population mean as the  
259 reference and related each standardised trait and their quadratic terms to male  
260 standardised AMS using age and age<sup>2</sup> as covariates to obtain linear and nonlinear  
261 sexual selection differentials ( $s_i$  and  $s_j$ ). In addition, the models included the  
262 interaction of male age and trait expression to determine whether the magnitude and  
263 direction of sexual selection on a specific trait changes with age. When the interaction  
264 term or  $s_j$  were nonsignificant,  $s_i$  was quantified in the absence of these terms.  
265 Univariate selection differentials measure both direct selection acting on each trait and  
266 indirect selection resulting from selection acting on other traits with which the focal  
267 trait is correlated. Therefore, we also carried out multivariate selection analyses where  
268 multiple correlated (see Supplementary Table S1) traits and their quadratic terms were  
269 used simultaneously to quantify linear ( $\beta$ ) and nonlinear ( $\gamma$ ) sexual selection gradients.  
270 In the multivariate analysis, the parameter estimate for each trait accounts for the  
271 selection acting on the other correlated traits, and hence allows direct comparison of  
272 the relative contribution of each trait to the variance in male mating success. The  
273 interactions of male age and trait expressions were included in the model, and when

274 the interaction term or  $\gamma$  were nonsignificant,  $\beta$  was quantified in the absence of these  
275 terms. Due to our relatively limited sample size and the large number of parameters  
276 (two parameters for age, seven parameters for directional selection, seven parameters  
277 for nonlinear selection, seven interaction terms and the random effect term), the  
278 multivariate analysis was conducted separately for male morphological and  
279 behavioural traits which are partly independent (Rintamäki *et al.* 2001; Lebigre *et al.*  
280 2012; Kervinen *et al.* 2015). Therefore, using age as a covariate in the models relating  
281 for instance male mating success to the expression of the various morphological  
282 ornaments enables us to account partially for the expression of the age-related  
283 behavioural traits and other potentially unmeasured traits. Coefficients of the  
284 quadratic terms ( $s_i$  and  $\gamma$ ) were doubled to measure balancing and disruptive selections  
285 respectively (Stinchcombe *et al.* 2008). Finally, for comparison and to estimate the  
286 age-(in)dependency of sexual selection acting on male traits, we quantified  $s_i$ ,  $s_j$ ,  $\beta$  and  
287  $\gamma$  as described above but without accounting for individual age.

288

## 289 **Results**

290

### 291 AGE EFFECTS ON MATING SUCCESS

292

293 There was substantial variation in LMS as 52% (85/164) of the males did not mate,  
294 whilst the top 12 males accounted for 50% of all observed copulations ( $N = 480$ ;  
295 maximum LMS = 32, Fig. 1). Most males reproduced only in a single year (68%;  
296 54/79) and of these, 74% (40/54) died after this reproductive event. Of those 25 males  
297 that reproduced in multiple years, 16 males survived after the year of their maximum

298 AMS and 20 males received >50% of their LMS in a single year (Supplementary Fig.  
299 S1).

300 Nine of the pre-selected candidate models of AMS were within 95%  
301 cumulative model weight which led to multimodel inference (Table 1). Age was  
302 included in all and AFL in all but one of the averaged models and thus they had the  
303 highest relative importance (Table 2). Moreover, age and AFL were the only variables  
304 for which the 95% CI of the averaged coefficient estimate did not overlap 0. AMS  
305 increased with age until the statistical maximum at age of 3.7 years after which it  
306 levelled off but did not decrease significantly towards the end of life (GLMM:  $-0.709$   
307  $\pm 0.878$ ,  $t = -0.807$ ,  $P = 0.423$ ; Fig. 2 a). In addition to these direct age effects, males'  
308 AFL was important; males lekking at age 1 tended to have higher AMS at age 2 than  
309 males that began lekking at age 2, and males that began lekking at age 1 or 2 tended to  
310 have higher AMS at age 3 than males that began lekking at age 3 (Fig. 2 b). Among  
311 males known to be territorial in our study leks, these differences were absent at older  
312 ages and all strategies led to similar LMS (mean  $\pm$  SE:  $2.71 \pm 0.60$ ,  $3.20 \pm 0.69$  and  
313  $3.11 \pm 1.62$  for males with AFL = 1 (N = 89), AFL = 2 (N = 66) and AFL = 3 (N = 9),  
314 respectively; ANOVA:  $F_{1,162} = 0.242$ ,  $P = 0.623$ , N = 164). Lifespan was not  
315 correlated with AMS and there was no clear evidence of terminal investment in  
316 reproduction (Table 2). Lastly, there was a significant positive relationship between  
317 AFL and lifespan ( $r_s = 0.40$ , N=164,  $P < 0.001$ ), indicating that males starting to lek  
318 older had longer lifespans.

319

320 SEXUAL SELECTION ON MALE TRAITS

321

322 Sexual selection operated on all behavioural traits but not on all morphological traits  
323 when accounting for males' age. The significant interactions of lek attendance and  
324 lyre length with age indicated that the magnitude of sexual selection operating on  
325 these traits increased with age (Table 3 a, Fig. 3 a, b). Males' AMS increased non-  
326 linearly ( $s_j$ ) with lek attendance and territory centrality (Fig. 4 a, b) and linearly ( $s_i$ )  
327 with fighting rate (Table 3 a). Conversely, males' AMS increased linearly with body  
328 mass but for other morphological traits  $s_i$  and  $s_j$  were nonsignificant. When accounting  
329 for age and the expression of other morphological or behavioural traits (multivariate  
330 sexual selection gradients), we found a significant interaction of age with body mass  
331 on AMS, indicating stronger sexual selection on body mass in older males (Table 3 a;  
332 Fig. 3 c). Moreover, males' AMS increased non-linearly ( $\gamma$ ) with lek attendance and  
333 linearly ( $\beta$ ) with body mass (Table 3 a).

334         When not accounting for male age, the magnitude of univariate sexual selection  
335 differentials increased and the sexual selection gradients became significant on  
336 morphological traits. Specifically, AMS increased significantly linearly ( $s_i$ ) with lyre  
337 length and eye comb size and non-linearly ( $s_j$ ) with blue chroma (Table 3 b). For body  
338 mass, the age-corrected and age-independent sexual selection differentials changed  
339 from significantly linear ( $s_i$ ) to significantly non-linear ( $s_j$ ), probably as a result of  
340 within-age differences in AMS and body mass relationship. For behavioural traits  
341 there were no substantial differences in the significance of  $s_i$  and  $s_j$  whether  
342 accounting for age or not. Controlling for the expression of other morphological or  
343 behavioural traits but not for age revealed that males' AMS increased significantly  
344 non-linearly ( $\gamma$ ) with body mass, lek attendance and territory centrality (Table 3 b).

345

## 346 **Discussion**

347

348 AGE EFFECTS ON MATING SUCCESS

349

350 Males' AMS was strongly associated with their age, as it first increased linearly until  
351 reaching a peak or plateau at age 3 or 4 and levelling off until death. Terminal effects,  
352 i.e. individuals investing differently in their last breeding attempt, could alter  
353 conclusions about age-specific breeding success (Rattiste 2004). Reproductive effort  
354 can increase when residual reproductive value decreases, i.e. towards the end of life  
355 (*sensu* terminal investment: Williams 1966; Pianka & Parker 1975; Clutton-Brock  
356 1984). Indeed, terminal investment in female reproduction has been documented in  
357 many species (Creighton, Heflin & Belk 2009; Fisher & Blomberg 2011), but  
358 evidence in birds and especially for males are scarce (but see e.g. Velando,  
359 Drummond & Torres 2006). In addition, several studies have found increased  
360 reproductive effort and/or sexual signalling towards the end of life (e.g. moose *Alces*  
361 *alces*: Mysterud, Solberg & Yoccoz 2005; mealworms *Tenebrio molitor*: Sadd *et al.*  
362 2006), including in black grouse (Kervinen *et al.* 2015). However, we found here that  
363 this recently documented late life increase in reproductive effort and sexual signalling  
364 did not lead to changes in mating success towards the end of life in male black grouse.  
365 Therefore, either these two processes are disconnected and females discriminate  
366 against old and very active males in a similar way as they discriminate against very  
367 active yearling males (Siitari *et al.* 2007; Kervinen *et al.* 2012) or, the previously  
368 documented terminal investment in reproductive effort (Kervinen *et al.* 2015)  
369 dampens a potential decline in mating success. The alternative to an increase in  
370 reproductive effort is a decline in fitness, i.e. senescence. However, we did not detect  
371 significant reproductive senescence in male black grouse in contrast to previous long-

372 term studies (e.g. Bouwhuis *et al.* 2009; reviewed in Nussey *et al.* 2013). This is  
373 because most males that had any mating success reproduced only once and tended to  
374 die directly after reproducing. This means that their highest AMS was in their last  
375 year of life. Such high mortality possibly stems from the high energetic or  
376 physiological costs of reproductive effort (Lebigre, Alatalo & Siitari 2013). However,  
377 not all males had their highest AMS in their last year of life, but for those males that  
378 bred more than once, most copulations still occurred in a single year and there were  
379 sharp declines in AMS after this. This means that across the population, terminal  
380 effects went in both directions depending on the number of reproductive episodes,  
381 contributing to a lack of either terminal investment or reproductive senescence being  
382 detected.

383         Male lifespan had low relative importance and its averaged coefficient estimate  
384 was positive, but nonsignificant, indicating that short- and long-lived males did not  
385 differ in their age-specific AMS. Previously we found significant positive effects of  
386 lifespan on male morphological and behavioural traits (Kervinen *et al.* 2015). Our  
387 results suggest that the trajectories of expression of male traits are partially  
388 independent from male mating success, and that the outcome of sexual selection  
389 cannot be directly linked to the expression of each trait separately. This is perhaps not  
390 unexpected since age-specific trajectories typically vary across multiple traits (e.g.  
391 Hayward *et al.* 2015), meaning that phenotypic, reproductive and survival traits may  
392 be decoupled (Evans *et al.* 2011; Bouwhuis *et al.* 2012). However, relatively little is  
393 known about age-specific trade-offs between sexually-selected traits and reproductive  
394 traits (Cornwallis, Dean & Pizzari 2014). The fact that there are differences in trait  
395 trajectories, strongly suggest that no single process underlies these patterns, but there



396 is critical need to quantify the physiological basis for such potential trade-offs  
397 (Cornwallis, Dean & Pizzari 2014).

398         Across the males that became territorial in the studied leks, there was a  
399 significant negative effect of AFL on AMS, indicating that males that began lekking  
400 at ages 1 or 2 tended to have higher age-specific AMS at ages 2 or 3 than the males  
401 that were on their first lek at ages 2 or 3, respectively. This confirms a previous study  
402 of the same black grouse population, but without accurate age estimates, which  
403 showed that lekking experience is positively correlated with mating success (Kokko *et*  
404 *al.* 1998). Thus, males with low AFL had higher age-specific AMS either because  
405 they defended more central territories, or because they were better able to fight  
406 against their neighbours due to their past experience in displaying with other males.  
407 However, due to the high mortality among territorial yearling and 2-year-old males,  
408 AFL was unrelated to LMS, which provides a mechanism to help maintaining the  
409 coexistence of multiple male life history strategies in this population (Kervinen *et al.*  
410 2015).

411

## 412 SEXUAL SELECTION ON MALE TRAITS

413

414 Given that both male mating success (this study) and the expression of a multitude of  
415 male morphological and behavioural traits (Kervinen *et al.* 2015) depend on age, our  
416 aim was to quantify whether accounting for such age effects (and hence indirectly for  
417 the effect of age-related traits not used in the selection gradients) affected our  
418 estimates of sexual selection operating on the morphological and behavioural traits.  
419 We found that sexual selection operated strongly on most morphological and  
420 behavioural traits when not accounting for male age but these effects strongly

421 declined when accounting for age. A similar effect has been found in common terns  
422 (*Sterna hirundo*) in which accounting for age decreased the magnitude of viability  
423 selection associated with individuals' trait expression (Zhang *et al.* 2015). Univariate  
424 sexual selection differentials indicated sexual selection acting more generally on male  
425 lekking behaviour than on male morphological traits when accounting for males' age.  
426 This might primarily be due to age-specific sexual selection acting on body mass, lyre  
427 length and lek attendance. Indeed, young males have low mating success regardless of  
428 their body mass, lyre length, as they lack lekking experience and central territories. In  
429 contrast, in prime age males and very old males that have the experience, high body  
430 mass is selected for as it enables successful lekking performance (Lebigre, Alatalo &  
431 Siitari 2013). To our knowledge, only two studies on ungulates have quantified age-  
432 specific sexual selection gradients; one showed that sexual selection in horn length of  
433 big horn sheep increased with age (Coltman *et al.* 2002), and the other reported strong  
434 selection for antler size in red deer during peak reproductive age (Kruuk *et al.* 2002).  
435 In general, such age effects are not due to age *per se* but are most likely due to the  
436 expression of other age-related traits that are not accounted for when quantifying the  
437 selection gradient.

438 Multiple sexual signals can convey different messages about male quality over a  
439 range of time periods (Doucet & Montgomerie 2003) leading to variation in female  
440 choice or mate choice errors which may dampen or even mask sexual selection  
441 (Chaine & Lyon 2008). This is very likely to apply to black grouse males'  
442 morphological traits as lyre length and blue chroma reflect male condition during  
443 moult which occurs shortly after the previous mating season (Siitari *et al.* 2007) while  
444 body mass and eye comb size are more plastic and reflect shorter-term male condition  
445 (Pérez-Rodríguez & Viñuela, 2008; Hämäläinen *et al.* 2012; Lebigre, Alatalo &

446 Siitari 2013). The stronger sexual selection differentials found on male behaviour  
447 (such as lek attendance, fighting rate and territory centrality) might be explained by  
448 their extreme variation and strong relationship with males' current body condition  
449 (Hämäläinen *et al.* 2012; Lebigre, Alatalo & Siitari 2013), which is itself age-  
450 dependent in this species (Kervinen *et al.* 2015). Moreover, multiple traits together  
451 might provide a better overall measure of quality than each cue alone in this system  
452 (redundant signal hypothesis; see Candolin 2003). Indeed, it usually takes years for a  
453 male to obtain a central territory on a lek (Kokko *et al.* 1998, 1999; DuVal 2012).  
454 Therefore, female preference for males displaying on central territories (Höglund &  
455 Lundberg 1987; Hovi *et al.* 1994; Kokko *et al.* 1998, 1999; Bro-Jørgensen & Durant  
456 2003), indicates that both males' short- and long-term phenotypic quality matters  
457 (viability, long-term lekking effort). Although it is also possible that there are  
458 uninvestigated components of male phenotype that are important for female choice,  
459 our analysis shows that behavioural traits are under age-independent sexual selection  
460 but that these traits themselves may not be enough for females to discriminate the  
461 quality of males at certain ages. As a consequence, morphological traits (body mass,  
462 lyre length) may be used as additional cues to supplement female choice (Møller &  
463 Pomiankowski 1993). Morphological traits may also have a dual utility, by serving as  
464 honest signals of male fighting ability or dominance (Berglund, Bisazza & Pilastro  
465 1996), but previous evidence suggests this is unlikely in black grouse (Rintamäki *et*  
466 *al.* 2000).

467         We found evidence of non-linear sexual selection gradients ( $\gamma$ ) for several traits  
468 which are commonly interpreted as evidence of balancing (negative  $\gamma$ ) or disruptive  
469 (positive  $\gamma$ ) selection (Stinchcombe *et al.* 2008; Hunt *et al.* 2009). However, the  
470 significant positive  $\gamma$  and  $s_j$  values found in this study more likely suggest “threshold”

471 values for male lek attendance and territory centrality as male mating success sharply  
472 increases when males have a lek attendance  $\geq 0.8$ , and defend territories within *ca.* 20  
473 metres from the lek centre. Other species show similar nonlinear “threshold”  
474 relationships between mating success and both physical (e.g. bighorn rams *Ovis*  
475 *canadensis* and horn length: Coltman *et al.* 2002) and behavioural traits (e.g. topi  
476 bulls *Damaliscus korrigum* and territory centrality: Bro-Jørgensen & Durant 2003). In  
477 black grouse, territory centrality and lek attendance are strongly related and the  
478 threshold values found in this study may reflect the difference between the dominant  
479 males displaying very actively on central territories and the other, less successful  
480 males that hold territories further away from the lek centre. It is important to note that  
481 the relationship between lek attendance and mating success is not due to missed  
482 mating opportunities of the males attending less to the lek, because copulations take  
483 place on the leks when all territorial males are present (Kokko *et al.* 1999; Lebigre *et*  
484 *al.* 2007).

485

## 486 CONCLUSIONS

487

488 This study shows that the overall variation in male black grouse mating success is  
489 strongly related to male age with substantial nonlinear increase over individuals’  
490 lifespan without a significant decrease at the end of life. Hence, age-related changes in  
491 male trait expression explains a substantial amount of the total variation in male  
492 mating success. Age of first lek attendance was negatively related to age-specific  
493 mating success, but unrelated to males’ lifetime mating success. Young age of first lek  
494 attendance was also associated with shorter lifespan, indicating that different male life  
495 history strategies coexist in this population. Sexual selection seemed to operate on

496 both morphological and behavioural traits when male age was not used to measure the  
497 sexual selection gradients. However, when accounting for the effect of other age-  
498 related traits, males' mating success was directly related only to behavioural traits, but  
499 was related to male body mass, lyre length and lek attendance in an age-specific  
500 manner (i.e. selection acted on these traits in old males only). Hence, sexual selection  
501 in this species primarily operates on male behaviour and morphological traits are used  
502 as additional cues to supplement female choice. This study shows that the complex  
503 dynamics of the expression of males' sexual traits with age needs to be accounted for  
504 and failing to do so might lead to an overestimation of the magnitude of sexual  
505 selection acting on these traits and of their potential microevolutionary changes.

506

### 507 **Data Accessibility**

508

509 We will archive the data associated with this manuscript to Dryad Digital Repository  
510 (<http://datadryad.org/>) should the manuscript be accepted.

511

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513

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523

## 524 **References**

525

526 Alatalo, R.V., Höglund, J. & Lundberg, A. (1991) Lekking in the black grouse – a test  
527 of male viability. *Nature*, 352, 155–156.

528 Alatalo, R.V., Höglund, J., Lundberg, A., Rintamäki, P.T. & Silverin, B. (1996)  
529 Testosterone and male mating success on the black grouse leks. *Proceedings of*  
530 *the Royal Society B: Biological Sciences*, 263, 1697–1702.

531 Alatalo, R.V., Höglund, J., Lundberg, A. & Sutherland, W.J. (1992) Evolution of  
532 black grouse leks – female preferences benefit males in larger leks. *Behavioral*  
533 *Ecology*, 3, 53–59.

534 Andersson, M. (1994) *Sexual selection*. Princeton University Press, Princeton, New  
535 Jersey.

536 Beauchamp, G. & Kacelnik, A. (1990) On the fitness functions relating parental care  
537 to reproductive value. *Journal of Theoretical Biology*, 146, 513–522.

538 Berglund, A., Bisazza, A. & Pilastro, A. (1996) Armaments and ornaments: an  
539 evolutionary explanation of traits of dual utility. *Biological Journal of the*  
540 *Linnean Society*, 58, 385–399.

541 Birkhead, T.R. (1998) Cryptic female choice: Criteria for establishing female sperm  
542 choice. *Evolution*, 52, 1212–1218.

543 Birkhead, T.R. & Møller, A.P. (1998) *Sperm competition and sexual selection*.  
544 Academic Press, London.

545 Bouwhuis S., Charmantier A., Verhulst S. & Sheldon B.C. (2010) Individual variation  
546 in rates of senescence: natal origin effects and disposable soma in a wild bird  
547 population. *Journal of Animal Ecology*, 79, 1251–1261.

548 Bouwhuis, S., Sheldon, B.C., Verhulst, S. & Charmantier, A. (2009) Great tits  
549 growing old: selective disappearance and the partitioning of senescence to  
550 stages within the breeding cycle. *Proceedings of the Royal Society B: Biological  
551 Sciences*, 276, 2769–2777.

552 Bouwhuis, S., Choquet, R., Sheldon, B.C. & Verhulst, S. (2012) The forms and  
553 fitness cost of senescence: age-specific recapture, survival, reproduction, and  
554 reproductive value in a wild bird population. *American Naturalist* 179, E15–  
555 E27.

556 Bro-Jørgensen, J., & Durant, S.M. (2003) Mating strategies of topi bulls: getting in  
557 the centre of attention. *Animal Behaviour*, 65, 585–594.

558 Burnham, K.P, Anderson, D.R. & Huyvaert, K.P. (2011) AIC model selection and  
559 multimodel inference in behavioral ecology: some background, observations,  
560 and comparisons. *Behavioural Ecology and Sociobiology*, 65, 23–35.

561 Candolin, U. (2003) The use of multiple cues in mate choice. *Biological Reviews*, 78,  
562 575–595.

563 Chaine, A.S. & Lyon, B.E. (2008) Adaptive plasticity in female mate choice dampens  
564 sexual selection on male ornaments in the lark bunting. *Science* 319, 459–462.

565 Clutton-Brock, T.H. (1984) Reproductive effort and terminal investment in  
566 iteroparous animals. *American Naturalist*, 123, 212–229.

567 Clutton-Brock, T.H. & Sheldon, B.C. (2010) Individuals and populations: the role of  
568 long-term, individual-based studies of animals in ecology and evolutionary  
569 biology. *Trends in Ecology and Evolution*, 25, 562–573.

570 Coltman, D.W., Bancroft, D.R., Robertson, A., Smith, J.A., Clutton-Brock, T.H. &  
571 Pemberton, J.M. (1999) Male reproductive success in a promiscuous mammal:  
572 behavioural estimates compared with genetic paternity. *Molecular Ecology*, 8,  
573 1199–1209.

574 Coltman D.W., Festa-Bianchet M., Jorgenson J.T. & Strobeck C. (2002) Age-  
575 dependent sexual selection in bighorn rams. *Proceedings of the Royal Society B:*  
576 *Biological Sciences*, 269, 165–172.

577 Cornwallis, C.K., Dean, R. & Pizzari, T. (2014) Sex-specific patterns of aging in  
578 sexual ornaments and gametes. *American Naturalist*, 184, E66–E78.

579 Creighton, J.C., Heflin, N.D. & Belk, M.C. (2009) Cost of reproduction, resource  
580 quality, and terminal investment in a burying beetle. *American Naturalist*, 174,  
581 673–684.

582 Curio, E. (1983) Why do young birds reproduce less well? *Ibis*, 125, 400–404.

583 Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.M. (2006) Best squirrels trade a  
584 long life for an early reproduction. *Proceedings of the Royal Society of London*  
585 *B: Biological Sciences*, 273, 2369–2374.

586 Doucet, S.M. & Montgomerie, R. (2003) Multiple sexual ornaments in satin  
587 bowerbirds: ultraviolet plumage and bowers signal different aspects of male  
588 quality. *Behavioral Ecology*, 14, 503–509.

589 DuVal, E.H. (2012) Variation in annual and lifetime reproductive success of lance-  
590 tailed manakins: alpha experience mitigates effects of senescence on siring  
591 success. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1551–  
592 1559.

593 Eberhard, W.G. (1996) Female control: Sexual selection by cryptic female choice.  
594 Princeton University Press, Princeton, New Jersey.



595 Emlen, D.J., Warren, I.A., Johns, A., Dworkin, I. & Corley Lavine, L. (2012) A  
596 mechanism of extreme growth and reliable signaling in sexually selected  
597 ornaments and weapons. *Science*, 337, 860–864.

598 Evans, S.R., Gustafsson, L. & Sheldon, B.C. (2011) Divergent patterns of age-  
599 dependence in ornamental and reproductive traits in the collared flycatcher.  
600 *Evolution*, 65, 1623–1636.

601 Fisher, D.O. & Blomberg, S.P. (2011) Costs of reproduction and terminal investment  
602 by females in a semelparous marsupial. *PloS ONE*, 6, e15226.

603 Forslund, P. & Pärt, T. (1995) Age and reproduction in birds – hypotheses and tests.  
604 *Trends in Ecology and Evolution*, 10, 374–378.

605 Freeman-Gallant, C.R., Taff, C.C., Morin, D.F., Dunn, P.O., Whittingham, L.A. &  
606 Tsang, S.M. (2010) Sexual selection, multiple male ornaments, and age- and  
607 condition-dependent signalling in the common yellowthroat. *Evolution*, 64,  
608 1007–1017.

609 Grueber, C.E., Nakagawa, S., Lawis, R.J. & Jamieson, I.G. (2011) Multimodel  
610 inference in ecology and evolution: challenges and solutions. *Journal of*  
611 *Evolutionary Biology*, 24, 699–711.

612 Hämäläinen, A., Alatalo, R.V., Lebigre, C., Siitari, H. & Soulsbury, C.D. (2012)  
613 Fighting behaviour as a correlate of male mating success in black grouse *Tetrao*  
614 *tetrix*. *Behavioral Ecology and Sociobiology*, 66, 1577–1586.

615 Hammers, M., Richardson, D.S., Burke, T. & Komdeur, J. (2012) Age-dependent  
616 terminal declines in reproductive output in a wild bird. *PLoS ONE*, 7, e40413.

617 Hayward, A.D., Moorad, J., Regan, C.E., Berenos, C., Pilkington, J.G., Pemberton,  
618 J.M. & Nussey, D.H. (2015) Asynchrony of senescence among phenotypic traits  
619 in a wild mammal population. *Experimental Gerontology*, 71, 56–68.

620 Höglund, J., Alatalo, R.V., Lundberg, A., Rintamäki, P.T. & Lindell, J. (1999)  
621       Microsatellite markers reveal the potential for kin selection on black grouse  
622       leks. *Proceedings of the Royal Society B: Biological Sciences*, 266, 813–816.

623 Höglund, J., Alatalo, R.V., Lundberg, A. & Rätti, O. (1994) Context-dependent  
624       effects of tail-ornament damage on mating success in black grouse. *Behavioral*  
625       *Ecology*, 5, 182–187.

626 Höglund, J., Johansson, T. & Pelabon, C. (1997) Behaviourally mediated sexual  
627       selection: Characteristics of successful male black grouse. *Animal Behaviour*,  
628       54, 255–264.

629 Höglund J. & Lundberg A. (1987) Sexual selection in a monomorphic lek-breeding  
630       bird: correlates of male mating success in the great snipe *Gallinago media*.  
631       *Behavioural Ecology*, 21, 211–216.

632 Höglund, J. & Sheldon, B.C. (1998) The cost of reproduction and sexual selection.  
633       *Oikos*, 83, 478–483.

634 Hovi, M., Alatalo, R.V., Höglund, J., Lundberg, A. & Rintamäki, P.T. (1994) Lek  
635       center attracts black grouse females. *Proceedings of the Royal Society B:*  
636       *Biological Sciences*, 258, 303–305.

637 Hunt, J., Breuker, C.J., Sadowski, J.A. & Moore, A.J. (2009) Male–male competition,  
638       female mate choice and their interaction: determining total sexual selection.  
639       *Journal of Evolutionary Biology*, 22, 13–26.

640 Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H.,  
641       Bize, P., Brommer, J., Charmantier, A., Charpentier, M., Clutton-Brock, T.H.,  
642       Dobson, F.S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., Jones, C.G.,  
643       Lillard, B.-G., McCleery, R., Merilä, J., Neuhaus, P., Nicoll, M.A.C., Norris,  
644       K., Oli, M.K., Pemberton, J., Pietiäinen, H., Ringsby, T.H., Roulin, A., Saether,

645 B.E., Setchell, J.M., Sheldon, B.C., Thompson, P.M., Weimerskirch, H.,  
646 Wickings, E.J. & Coulson, T. (2008) Senescence rates are determined by  
647 ranking on the fast-slow life-history continuum. *Ecology Letters*, 11, 664–673.

648 Kervinen, M., Alatalo, R.V., Lebigre, C., Siitari, H. & Soulsbury, C.D. (2012)  
649 Determinants of yearling male lekking effort and mating success in black grouse  
650 (*Tetrao tetrix*). *Behavioral Ecology*, 23, 1209–1217.

651 Kervinen, M., Lebigre, C., Alatalo, R.V., Siitari, H. & Soulsbury, C.D. (2015) Life  
652 history differences in age-dependent expressions of multiple ornaments and  
653 behaviors in a lekking bird. *American Naturalist*, 185, 13–27.

654 Kokko, H., Lindström, J., Alatalo, R.V. & Rintamäki, P.T. (1998) Queuing for  
655 territory positions in the lekking black grouse (*Tetrao tetrix*). *Behavioral*  
656 *Ecology*, 9, 376–383.

657 Kokko, H., Rintamäki, P.T., Alatalo, R.V., Höglund, J., Karvonen, E. & Lundberg, A.  
658 (1999) Female choice selects for lifetime lekking performance in black grouse  
659 males. *Proceedings of the Royal Society B: Biological Sciences*, 266, 2109–  
660 2115.

661 Kruuk, L.E.B., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F. & Clutton-  
662 Brock, T.H. (2002) Antler size in red deer: Heritability and selection but no  
663 evolution. *Evolution* 56, 1683–1695.

664 Lebigre, C., Alatalo, R.V., Forss, H.E. & Siitari, H. (2008) Low levels of relatedness  
665 on black grouse leks despite male philopatry. *Molecular Ecology*, 17, 4512–  
666 4521.

667 Lebigre, C., Alatalo, R.V., Kilpimaa, J., Staszewski, V. & Siitari, H. (2012)  
668 Leucocyte counts variation and measures of male fitness in the lekking black  
669 grouse. *Journal of Ornithology*, 153, 95–102.

670 Lebigre, C., Alatalo, R.V. & Siitari, H. (2013) Physiological costs enforce the honesty  
671 of lek display in the black grouse (*Tetrao tetrix*). *Oecologia*, 172, 983–993.

672 Lebigre, C., Alatalo, R.V., Siitari, H. & Parri, S. (2007) Restrictive mating by females  
673 on black grouse leks. *Molecular Ecology*, 16, 4380–4389.

674 Lebigre, C., Alatalo, R.V., Soulsbury, C.D., Höglund, J. & Siitari, H. (2014) Limited  
675 indirect fitness benefits of male group membership in a lekking species.  
676 *Molecular Ecology* 23, 5356–5365.

677 Ludwig, G.X., Alatalo, R.V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. (2006).  
678 Short- and long-term population dynamical consequences of asymmetric climate  
679 change in black grouse. *Proceedings of the Royal Society B: Biological*  
680 *Sciences*, 273, 2009–2016.

681 Mazerolle, M.J. (2014) Package 'AICcmodavg': Model Selection and Multimodel  
682 Inference Based on (Q)AIC(c). Version 2.0-1. [http://cran.r-project.org/web/  
683 packages/AICcmodavg/AICcmodavg.pdf](http://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf)

684 Møller, A.P. & Pomiankowski, A. (1993) Why have birds got multiple sexual  
685 ornaments? *Behavioural Ecology and Sociobiology*, 32, 167–176.

686 Mysterud, A., Solberg, E. J. & Yoccoz, N.G. (2005) Ageing and reproductive effort in  
687 male moose under variable levels of intrasexual competition. *Journal of Animal*  
688 *Ecology*, 74: 742–754.

689 Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining  $R^2$   
690 from generalized linear mixed-effects models. *Methods in Ecology and*  
691 *Evolution*, 4, 133–142.

692 Nussey, D.H., Froy, H., Lemaitre J.F., Gaillard, J.M. & Austad, S.N. (2013)  
693 Senescence in natural populations of animals: Widespread evidence and its  
694 implications for bio-gerontology. *Ageing Research Reviews*, 12, 214–225.

695 Nussey, D.H., Kruuk L.E.B., Morris, A., Clements, M.N., Pemberton, J.M. &  
696 Clutton-Brock, T.H. (2009) Inter- and intrasexual variation in aging patterns  
697 across reproductive traits in a wild red deer population. *American Naturalist*,  
698 174, 342–357.

699 Pérez-Rodríguez, L. & Viñuela, J. (2008) Carotenoid-based bill and eye ring  
700 coloration as honest signals of condition: an experimental test in the red-legged  
701 partridge (*Alectoris rufa*). *Naturwissenschaften*, 95, 821–830.

702 Pianka E.R. & Parker W.S. (1975) Age-specific reproductive tactics. *American*  
703 *Naturalist*, 109, 453–864.

704 R Development Core Team. 2014. R: A language and environment for statistical  
705 computing. R Foundation for Statistical Computing. Vienna, Austria.

706 Rattiste, K. (2004) Reproductive success in presenescent common gulls (*Larus*  
707 *canus*): the importance of the last year of life. *Proceedings of the Royal Society*  
708 *B: Biological Sciences*, 271, 2059–2064.

709 Reed, T.E., Kruuk, L.E., Wanless, S., Frederiksen, M., Cunningham, E.J. & Harris,  
710 M.P. (2008) Reproductive senescence in a long-lived seabird: rates of decline in  
711 late-life performance are associated with varying costs of early reproduction.  
712 *American Naturalist*, 171, E89–E101.

713 Rintamäki, P.T., Alatalo, R.V., Höglund, J. & Lundberg, A. (1995) Male territoriality  
714 and female choice on black grouse leks. *Animal Behaviour*, 49, 759–767.

715 Rintamäki, P.T., Höglund, A., Alatalo, R.V. & Lundberg, A. (2001) Correlates of  
716 male mating success on black grouse (*Tetrao tetrix* L.) leks. *Annales Zoologici*  
717 *Fennici*, 38, 99–109.

718 Rintamäki, P.T., Höglund, J., Karvonen, E., Alatalo, R.V., Björklund, N., Lundberg,  
719 A., Rätti, O. & Vouti, J. (2000) Combs and sexual selection in black grouse  
720 (*Tetrao tetrix*). *Behavioral Ecology*, 5, 465–471.

721 Sadd, B., Holman, L., Armitage, H., Lock, F., Marland, R. & Siva-Jothy, M.T. (2006)  
722 Modulation of sexual signalling by immune challenged male mealworm beetles  
723 (*Tenebrio molitor*, L.): evidence for terminal investment and dishonesty.  
724 *Journal of Evolutionary Biology*, 19, 321–325.

725 Schielzeth, H. & Forstmeier, W. (2009) Conclusions beyond support: overconfident  
726 estimates in mixed models. *Behavioral Ecology*, 20, 416–420.

727 Siitari, H., Alatalo, R.V., Halme, P., Buchanan, K.L. & Kilpimaa, J. (2007) Color  
728 signals in the black grouse (*Tetrao tetrix*): Signal properties and their condition  
729 dependency. *American Naturalist*, 169, S81–S92.

730 Stearns, S.C. (1992) *Evolution of life histories*. Oxford University Press, Oxford.

731 Stinchcombe, J.R., Agrawal, A.F., Hohenlohe P.A., Arnold, S.J. & Blows, M.W.  
732 (2008) Estimating nonlinear selection gradients using quadratic regression  
733 coefficients: double or nothing? *Evolution*, 62, 2435–2440.

734 van de Pol, M. & Verhulst, S. (2006) Age-dependent traits: a new statistical model to  
735 separate within- and between individual effects. *American Naturalist*, 167, 765–  
736 773.

737 Velando, A., Drummond, H. & Torres, R. (2006) Senescent birds redouble  
738 reproductive effort when ill: confirmation of the terminal investment hypothesis.  
739 *Proceedings of the Royal Society B: Biological Sciences*, 273, 1443–1448.

740 Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement  
741 of Lack's principle. *American Naturalist*, 100, 687–690.

- 742 Williams, P.D., Day, T., Fletcher, Q. & Rowe, L. (2006) The shaping of senescence in  
743 the wild. *Trends in Ecology and Evolution*, 21, 458–463.
- 744 Zhang, H., Vedder, O., Becker, P.H. & Bouwhuis, S. (2015) Contrasting between- and  
745 within-individual trait effects on mortality risk in a long-lived seabird. *Ecology*,  
746 96, 71–79.
- 747

748 **Figure legends**

749

750 Figure 1. The distribution of lifetime mating success (LMS) in male black grouse (N  
751 = 164). Mating skew was substantial: most males never mated at all, whereas the top  
752 12 males accounted for roughly the half (238/480) of all copulations.

753

754 Figure 2. Variation in mean annual mating success (AMS, mean  $\pm$  SE) with age for a)  
755 all males (N = 164) and b) separately for males that started lekking at age 1 (black  
756 circles, N = 89), at age 2 (grey squares, N = 66) or at age 3 (white triangles, N = 9). N  
757 denotes the age-specific sample sizes. Note the different scales on the vertical axes.  
758 For the figure, ages 5 and 6 were combined to age class 5+. The high mean AMS with  
759 large SE at age 5+ of the males that began lekking at age 1 is largely affected by one  
760 male that had 15 copulations at age 6.

761

762 Figure 3. The interactions of age with a) lek attendance, b) lyre length and c) body  
763 mass on annual mating success (AMS), indicating that the strength of sexual selection  
764 on these traits increased with age. All parameters were standardised to account for the  
765 variation lek size and the total number of copulations on the lek (see Materials and  
766 methods).

767

768 Figure 4. Annual mating success (AMS) of yearling (filled triangles) and older (ages 2  
769 to 6 years; open circles) male black grouse in relation to a) lek attendance and b)  
770 territory centrality (analysed as the male's territory distance from the lek centre).  
771 Significant  $s_j$  and  $\gamma$  values on these traits suggested thresholds after which AMS



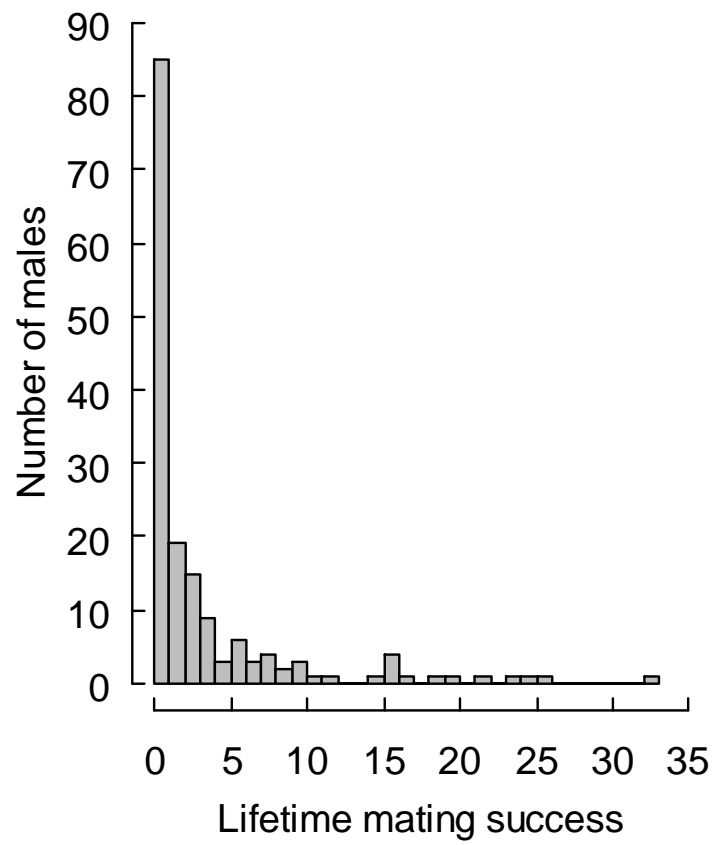
772 sharply increases. All parameters were standardised to account for the variation lek  
773 size and the total number of copulations on the lek (see Materials and methods).

774

775

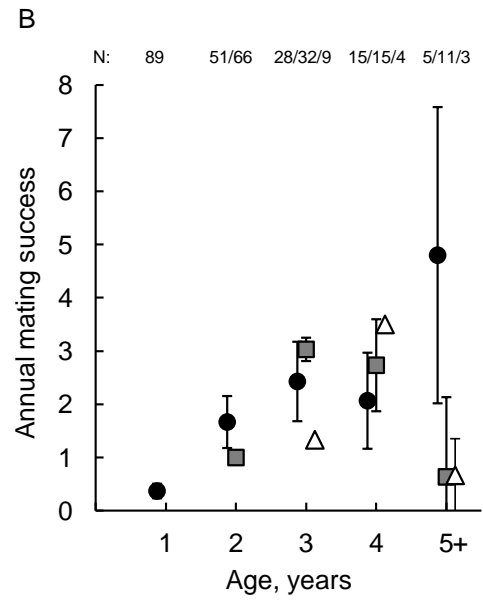
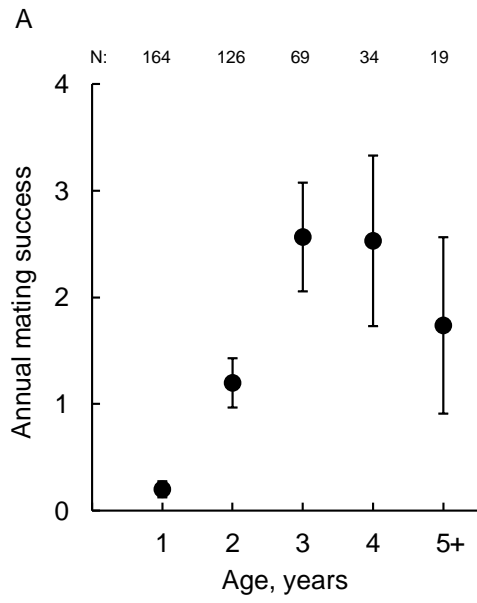
776 **Figures**

777



778

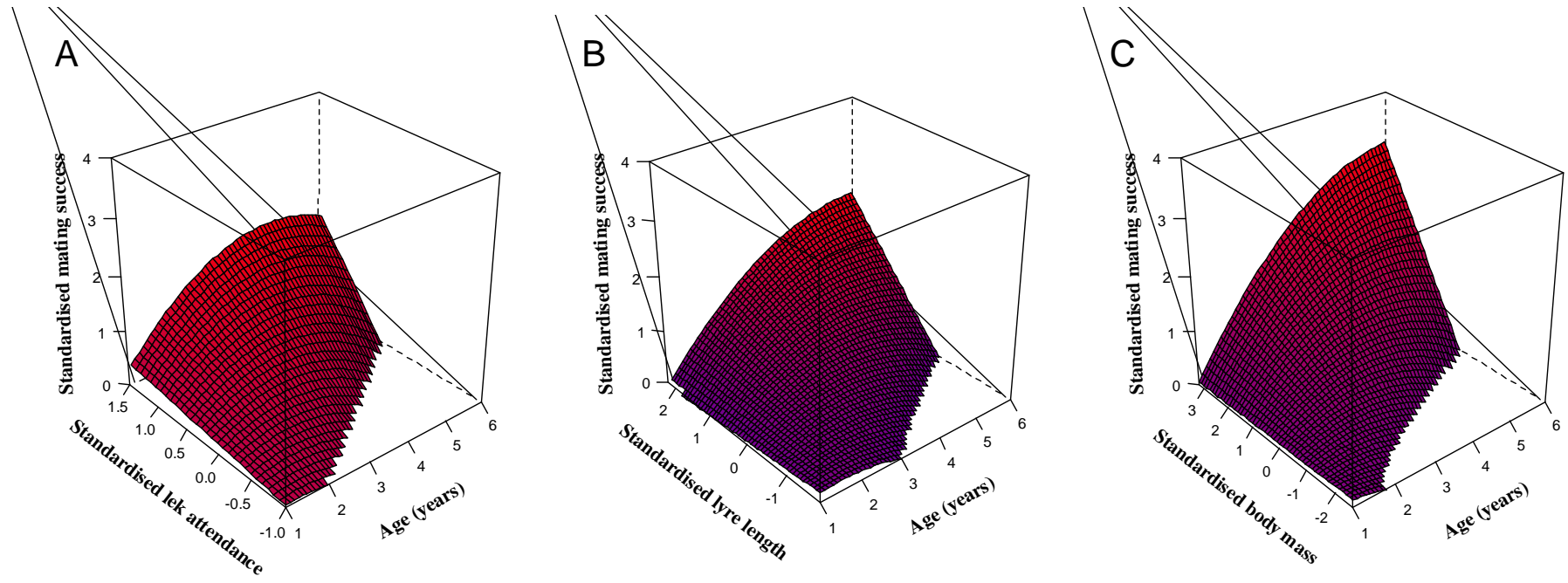
779 Figure 1.



780

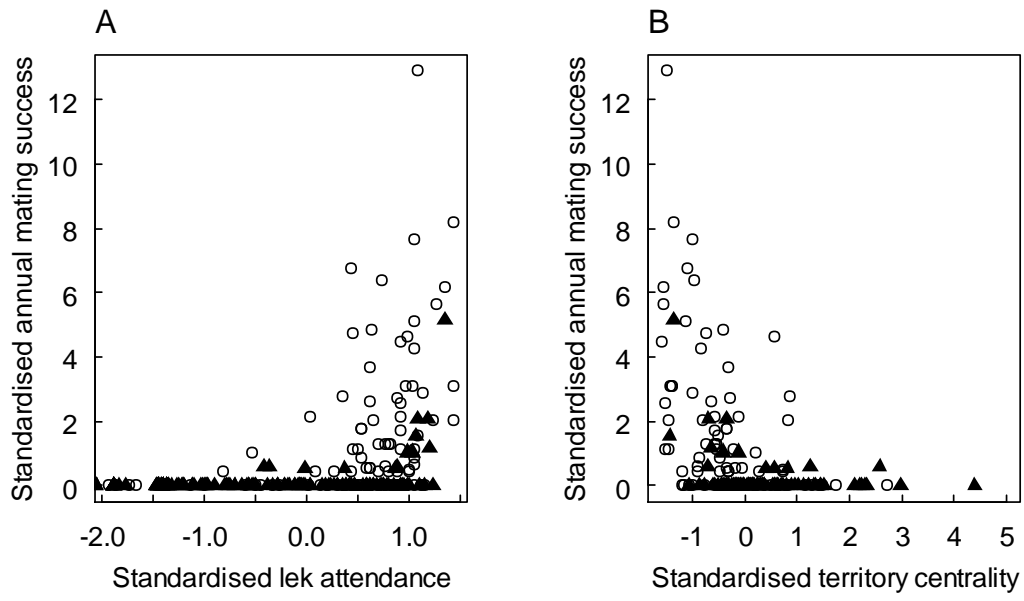
781 Figure 2.

782



783  
784

785 Figure 3.



786

787 Figure 4.

788 **Tables**

789

790 Table 1. A suite of pre-selected biologically relevant candidate models predicting the effects of age, age<sup>2</sup>, age of first lek attendance (AFL),  
 791 lifespan (LS) and terminal event (TE; binary, indicates if it was the male's last year alive or not) on annual mating success in male black grouse,  
 792 with the number of estimated parameters for each model (k), Log-likelihood and AIC<sub>c</sub> values, model weights (w<sub>i</sub>), cumulative model weights  
 793 and evidence ratios (ER). Individual identity nested within study site was fitted as a random factor in all the models. Candidate models within  
 794 95% cumulative model weight were averaged (see Table 2).

Rank	Model	k	LogLik	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	Cum. w <sub>i</sub>	ER
1	Age + Age <sup>2</sup> + AFL	11	-858.52	1739.71	0.00	0.27	0.27	
2	Age + LS + TE + AFL + Age*LS + Age*TE	14	-855.56	1740.19	0.48	0.21	0.48	1.27
3	Age + Age <sup>2</sup> + AFL + Age*AFL	12	-858.03	1740.85	1.14	0.15	0.63	1.77
4	Age + Age <sup>2</sup> + AFL + LS + TE + Age*LS + Age*TE	15	-855.28	1741.77	2.06	0.10	0.72	2.81
5	Age + AFL + LS + TE + Age*AFL + Age*LS + Age*TE	15	-855.34	1741.90	2.20	0.09	0.81	3.00
6	Age + Age <sup>2</sup> + AFL + LS + TE	13	-858.01	1742.94	3.23	0.05	0.87	5.03
7	Age + Age <sup>2</sup> + AFL + LS + TE + Age*AFL + Age*LS + Age*TE	16	-855.08	1743.53	3.83	0.04	0.91	6.77
8	Age + Age <sup>2</sup> + AFL + LS + TE + Age*AFL	14	-857.54	1744.15	4.44	0.03	0.93	9.21
9	Age + Age <sup>2</sup>	10	-862.01	1744.56	4.86	0.02	0.96	11.34
10	Age + Age <sup>2</sup> + TE + Age*TE	12	-860.60	1745.98	6.27	0.01	0.97	23.05
11	Age + Age <sup>2</sup> + TE	11	-861.98	1746.61	6.91	0.01	0.98	31.63
12	Age + LS + TE + Age*LS + Age*TE	13	-860.30	1747.52	7.82	0.01	0.98	49.82
13	Age + AFL	10	-863.69	1747.93	8.22	0.00	0.99	60.99

14	Age + AFL + Age*AFL	11	-862.82	1748.30	8.60	0.00	0.99	73.65
15	Age + Age <sup>2</sup> + LS + TE	12	-861.81	1748.41	8.70	0.00	1.00	77.52
16	Age + Age <sup>2</sup> + LS + TE + Age*LS + Age*TE	14	-860.00	1749.05	9.35	0.00	1.00	107.08
17	Age + AFL + LS + TE	12	-863.38	1751.55	11.85	0.00	1.00	373.39
18	Age + AFL + LS + TE + Age*AFL	13	-862.54	1752.00	12.29	0.00	1.00	467.29
19	Age	9	-866.88	1752.20	12.50	0.00	1.00	517.40
20	Age + TE	10	-866.80	1754.15	14.44	0.00	1.00	1366.80
21	Age + TE + Age*TE	11	-866.73	1756.13	16.42	0.00	1.00	3685.64
22	Age + LS + TE	11	-866.74	1756.13	16.43	0.00	1.00	3687.43
23	Null	8	-880.90	1778.15	38.45	0.00	1.00	2.23 x 10 <sup>8</sup>

795  
796

797 Table 2. The relative importance and averaged coefficient estimates with unconditional standard errors and 95% unconditional confidential  
 798 intervals of age, age<sup>2</sup>, age of first lek attendance (AFL), lifespan (LS) and terminal event (TE; binary, indicates if it was the male's last year alive  
 799 or not) and their relevant interactions on annual mating success in male black grouse.

Parameter	Relative importance	Estimate	Unconditional SE	95% unconditional CI
Age	1.00	2.15	0.49	1.19, 3.11
AFL	0.98	-0.37	0.16	-0.67, -0.06
Age <sup>2</sup>	0.66	-0.24	0.12	-0.48, 0.01
LS	0.52	0.22	0.20	-0.18, 0.61
TE	0.52	-0.46	0.38	-1.20, 0.28
Age:LS	0.44	-0.30	0.17	-0.63, 0.04
Age:TE	0.44	0.10	0.26	-0.41, 0.60
Age:AFL	0.31	-0.13	0.15	-0.43, 0.17



800 Table 3. Standardised linear ( $s_i$ ) and nonlinear ( $s_j$ ) univariate sexual selection differentials and linear ( $\beta$ ) and nonlinear ( $\gamma$ ) multivariate sexual  
801 selection gradients in male black grouse with and without controlling for individual age. Estimates are provided with their standard errors. Bold  
802 indicates significance at  $P < 0.05$ . Individual identity nested within study site was fitted as a random factor in all the models.

Trait	a) Controlled for individual age						b) Not controlled for individual age			
	$s_i$	$s_j$	age*trait	$\beta$	$\gamma$	age*trait	$s_i$	$s_j$	$\beta$	$\gamma$
Morphological traits										
Body mass	<b>0.763 ± 0.206</b>	0.129 ± 0.077	0.332 ± 0.249	<b>-0.366 ± 0.136</b>	0.034 ± 0.113	<b>0.728 ± 0.301</b>	<b>0.209 ± 0.050</b>	<b>0.222 ± 0.074</b>	0.133 ± 0.069	<b>0.208 ± 0.088</b>
Lyre length	-0.520 ± 0.285	-0.161 ± 0.163	<b>0.743 ± 0.376</b>	-0.075 ± 0.085	-0.053 ± 0.115	0.783 ± 0.438	<b>0.208 ± 0.055</b>	0.198 ± 0.104	0.064 ± 0.074	0.027 ± 0.114
Blue chroma	-0.028 ± 0.040	0.110 ± 0.069	0.076 ± 0.119	-0.028 ± 0.042	0.098 ± 0.072	0.132 ± 0.171	0.076 ± 0.039	<b>0.150 ± 0.067</b>	-0.010 ± 0.042	0.098 ± 0.072
Eye comb size	0.048 ± 0.061	0.012 ± 0.059	0.170 ± 0.177	0.023 ± 0.066	-0.033 ± 0.064	0.336 ± 0.227	<b>0.193 ± 0.043</b>	0.040 ± 0.058	0.092 ± 0.060	-0.005 ± 0.061
Behavioural traits										
Lek attendance	0.129 ± 0.110	<b>0.455 ± 0.078</b>	<b>0.471 ± 0.172</b>	0.131 ± 0.113	<b>1.367 ± 0.334</b>	0.398 ± 0.346	<b>0.450 ± 0.045</b>	<b>0.508 ± 0.077</b>	0.189 ± 0.114	<b>1.301 ± 0.337</b>
Fighting rate	<b>0.186 ± 0.066</b>	-0.080 ± 0.121	0.055 ± 0.160	0.098 ± 0.062	-0.026 ± 0.108	-0.198 ± 0.182	<b>0.252 ± 0.065</b>	-0.121 ± 0.122	0.103 ± 0.063	-0.048 ± 0.109
Territory centrality*	<b>-0.552 ± 0.080</b>	<b>0.342 ± 0.066</b>	-0.323 ± 0.181	-0.049 ± 0.064	0.134 ± 0.075	-0.358 ± 0.243	<b>-0.620 ± 0.078</b>	<b>0.370 ± 0.066</b>	<b>-0.225 ± 0.102</b>	<b>0.155 ± 0.075</b>

803 \* Territory centrality was analysed as the male's territory's distance from the lek centre.

804