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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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 tetrix* − 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 tetrix*

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

3

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*

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

We used longitudinal data describing male mating success and the expression of multiple sexually-selected morphological and behavioural traits to quantify changes in mating success with male age and determine the relative contribution of the age-specific trait expression to this pattern. We first tested the hypothesis that the variation in male mating success is age-dependent by quantifying the effects of age, age of first lek attendance (AFL), lifespan and terminal investment on males' annual mating success (AMS). This enabled us to separate the effects of within-individual improvement and senescence on AMS from selective appearance and disappearance 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$^2$ 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$^2$ 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 γ were nonsignificant, β 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 ($s_j$ and γ) 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 $s_i$, $s_j$, β and

287   γ 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

## AGE EFFECTS ON MATING SUCCESS

349

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

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

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

Siitari 2013). The stronger sexual selection differentials found on male behaviour

(such as lek attendance, fighting rate and territory centrality) might be explained by

their extreme variation and strong relationship with males' current body condition

(Hämäläinen *et al.* 2012; Lebigre, Alatalo & Siitari 2013), which is itself age-

dependent in this species (Kervinen et al. 2015). Moreover, multiple traits together

might provide a better overall measure of quality than each cue alone in this system

(redundant signal hypothesis; see Candolin 2003). Indeed, it usually takes years for a

male to obtain a central territory on a lek (Kokko *et al.* 1998, 1999; DuVal 2012).

Therefore, female preference for males displaying on central territories (Höglund &

Lundberg 1987; Hovi *et al.* 1994; Kokko *et al.* 1998, 1999; Bro-Jørgensen & Durant

2003), indicates that both males' short- and long-term phenotypic quality matters

(viability, long-term lekking effort). Although it is also possible that there are

uninvestigated components of male phenotype that are important for female choice,

our analysis shows that behavioural traits are under age-independent sexual selection

but that these traits themselves may not be enough for females to discriminate the

quality of males at certain ages. As a consequence, morphological traits (body mass,

lyre length) may be used as additional cues to supplement female choice (Møller &

Pomiankowski 1993). Morphological traits may also have a dual utility, by serving as

honest signals of male fighting ability or dominance (Berglund, Bisazza & Pilastro

1996), but previous evidence suggests this is unlikely in black grouse (Rintamäki *et*

*al.* 2000).

We found evidence of non-linear sexual selection gradients ($\gamma$) for several traits

which are commonly interpreted as evidence of balancing (negative $\gamma$) or disruptive

(positive $\gamma$) selection (Stinchcombe *et al.* 2008; Hunt *et al.* 2009). However, the

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 ≥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

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747

*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 ± 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
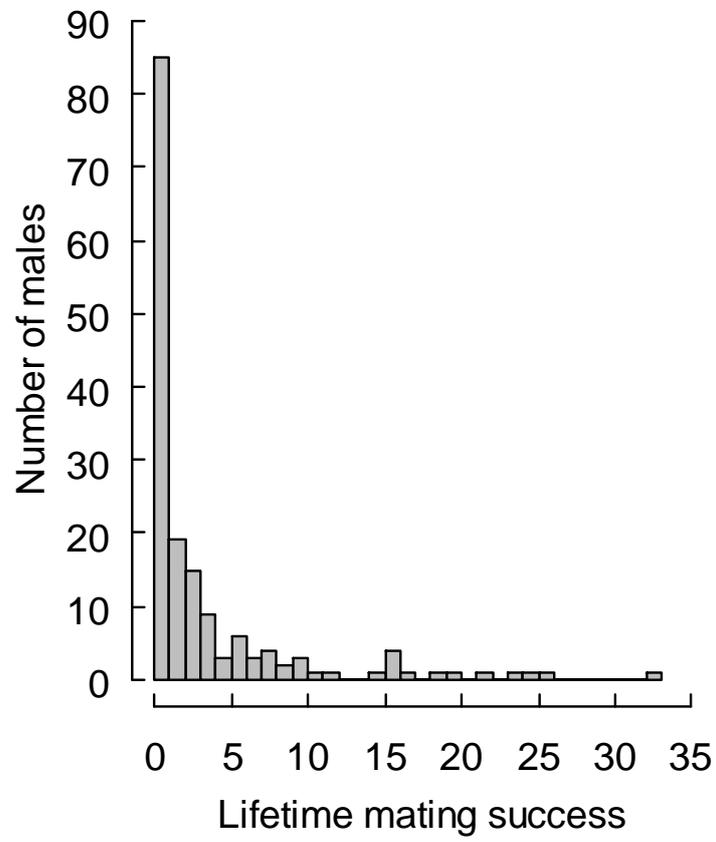
772    sharply increases. All parameters were standardised to account for the variation lek

773    size and the total number of copulations on the lek (see Materials and methods).
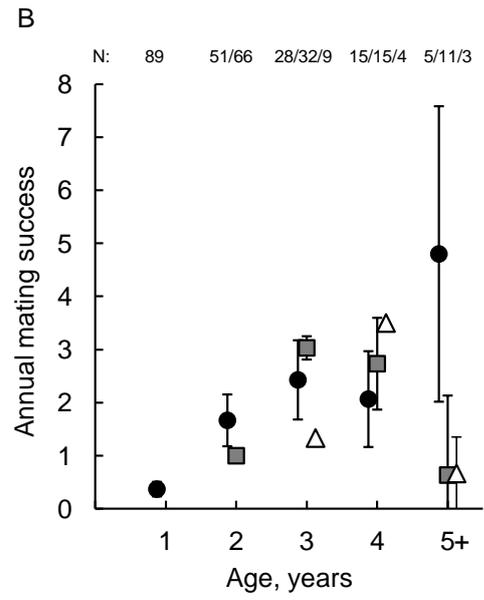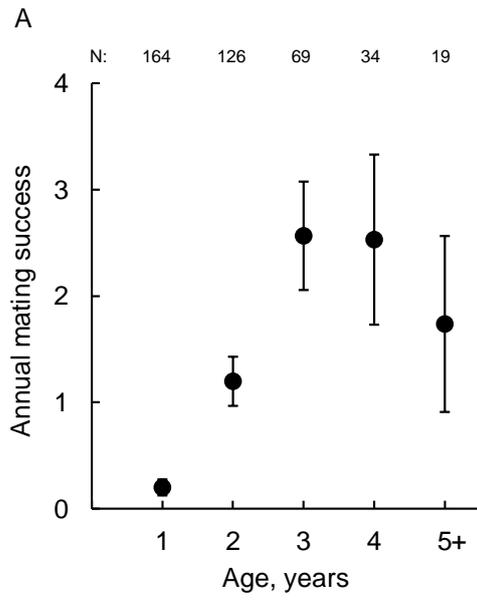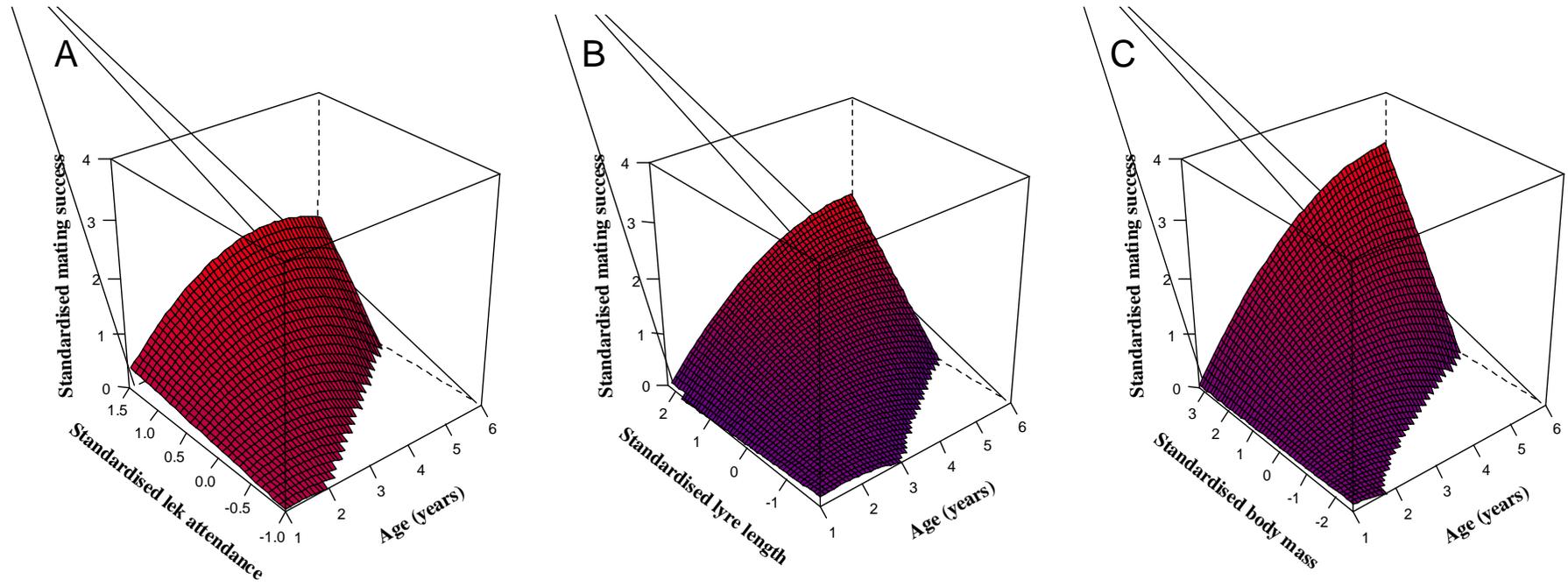
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**Figures**

779    Figure 1.
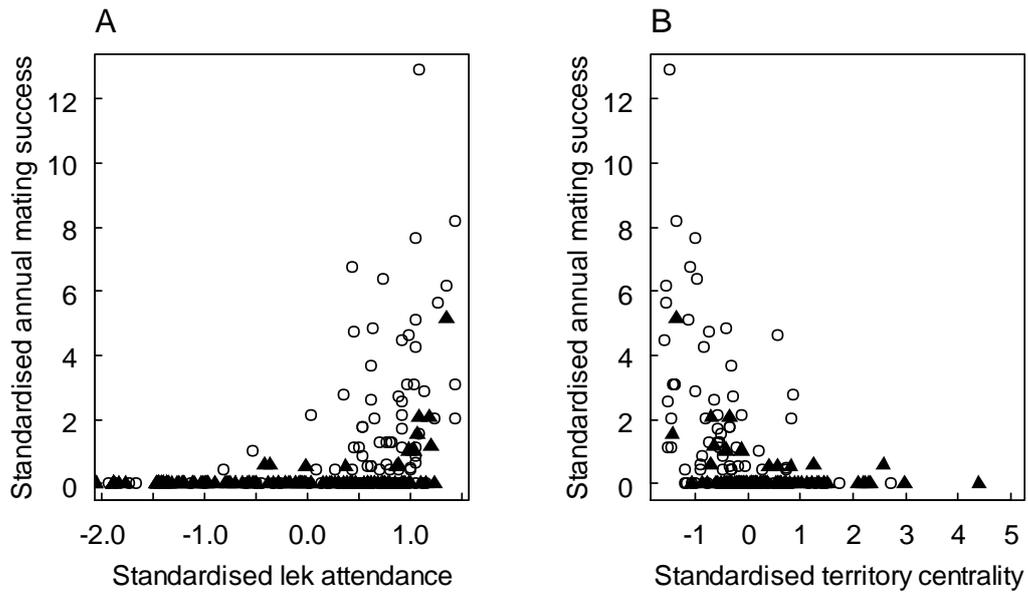
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781     Figure 2.

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785    Figure 3.

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787    Figure 4.

788 **Tables**

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790 Table 1. A suite of pre-selected biologically relevant candidate models predicting the effects of age, $age^2$, 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 $AIC_c$ values, model weights ($w_i$), 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 | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | Cum. $w_i$ | ER |
|---|---|---|---|---|---|---|---|---|
| 1 | Age + $Age^2$ + 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 + $Age^2$ + AFL + Age*AFL | 12 | −858.03 | 1740.85 | 1.14 | 0.15 | 0.63 | 1.77 |
| 4 | Age + $Age^2$ + 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 + $Age^2$ + AFL + LS + TE | 13 | −858.01 | 1742.94 | 3.23 | 0.05 | 0.87 | 5.03 |
| 7 | Age + $Age^2$ + AFL + LS + TE + Age*AFL + Age*LS + Age*TE | 16 | −855.08 | 1743.53 | 3.83 | 0.04 | 0.91 | 6.77 |
| 8 | Age + $Age^2$ + AFL + LS + TE + Age*AFL | 14 | −857.54 | 1744.15 | 4.44 | 0.03 | 0.93 | 9.21 |
| 9 | Age + $Age^2$ | 10 | −862.01 | 1744.56 | 4.86 | 0.02 | 0.96 | 11.34 |
| 10 | Age + $Age^2$ + TE + Age*TE | 12 | −860.60 | 1745.98 | 6.27 | 0.01 | 0.97 | 23.05 |
| 11 | Age + $Age^2$ + 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$^2$ + LS + TE | 12 | −861.81 | 1748.41 | 8.70 | 0.00 | 1.00 | 77.52 |
| 16 | Age + Age$^2$ + 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$^8$ |

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797    Table 2. The relative importance and averaged coefficient estimates with unconditional standard errors and 95% unconditional confidential

798    intervals of age, age$^2$, 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$^2$ | 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 | **0.763 ± 0.206** | 0.129 ± 0.077 | 0.332 ± 0.249 | **−0.366 ± 0.136** | 0.034 ± 0.113 | **0.728 ± 0.301** | **0.209 ± 0.050** | **0.222 ± 0.074** | 0.133 ± 0.069 | **0.208 ± 0.088** |
| Lyre length | −0.520 ± 0.285 | −0.161 ± 0.163 | **0.743 ± 0.376** | −0.075 ± 0.085 | −0.053 ± 0.115 | 0.783 ± 0.438 | **0.208 ± 0.055** | 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 | **0.150 ± 0.067** | −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 | **0.193 ± 0.043** | 0.040 ± 0.058 | 0.092 ± 0.060 | −0.005 ± 0.061 |
| Behavioural traits | | | | | | | | | | |
| Lek attendance | 0.129 ± 0.110 | **0.455 ± 0.078** | **0.471 ± 0.172** | 0.131 ± 0.113 | **1.367 ± 0.334** | 0.398 ± 0.346 | **0.450 ± 0.045** | **0.508 ± 0.077** | 0.189 ± 0.114 | **1.301 ± 0.337** |
| Fighting rate | **0.186 ± 0.066** | −0.080 ± 0.121 | 0.055 ± 0.160 | 0.098 ± 0.062 | −0.026 ± 0.108 | −0.198 ± 0.182 | **0.252 ± 0.065** | −0.121 ± 0.122 | 0.103 ± 0.063 | −0.048 ± 0.109 |
| Territory centrality* | **−0.552 ± 0.080** | **0.342 ± 0.066** | −0.323 ± 0.181 | −0.049 ± 0.064 | 0.134 ± 0.075 | −0.358 ± 0.243 | **−0.620 ± 0.078** | **0.370 ± 0.066** | **−0.225 ± 0.102** | **0.155 ± 0.075** |

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

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