

1 **Age, condition and dominance-related sexual ornament size before and** 2 **during the breeding season in the black grouse *Lyrurus tetrrix***

3 **Abstract**

4 Male ornaments function as honest cues of male quality in many species and are subject to intra-
5 and intersexual selection. These ornaments are generally studied during peak expression,
6 however their size outside the breeding season may determine ultimate ornament size and
7 costliness, and as such reproductive success. We investigated whether male black grouse *Lyrurus*
8 *tetrrix* eye comb size was related to age, condition and measures of male dominance before and
9 during the breeding season. Total combined eye comb size began to increase ~70 days before the
10 start of the breeding season. Adult males (aged ≥ 2 years old) had consistently larger eye combs
11 than younger males (1 year old) both before and during the breeding season. Heavier and more
12 dominant adult males (attending the lek more frequently and successfully reproducing) had larger
13 eye combs. For younger males, those that were heavier had larger eye combs. Additionally, males
14 that spent more time on the lek showed increased eye comb size as the breeding season
15 approached. Overall we find that ornament size is positively related to dominance and condition
16 before and during the breeding season. Since dominance is accrued through year-round
17 interactions in many species, the ability to maintain larger signals over prolonged periods,
18 including outside of the breeding season, is likely to be beneficial for adults. For younger males, it
19 is likely that they cannot sustain or are constrained from producing larger eye combs over long
20 periods of time. They therefore prioritise growth of their ornaments later, and according to the
21 amount of time they spend on the lek.

22

23 **Key words:** ornament, age, dominance, pre-breeding, condition-dependence, sexual selection

24 **Introduction**

25 Males of many species display elaborate ornaments that function as honest indicators of individual
26 quality if ornament production or maintenance comes at a cost to the bearer (Zahavi 1975,
27 Andersson 1994). These ornaments may function as intersexual signals, whereby females can
28 assess and choose potential mates (Hill 1991), intrasexual signals, whereby males can assess
29 dominance in conspecific males (Chaine and Lyon 2008), or both (Griggio et al. 2007). The
30 expression of sexually-selected traits during an individual's lifespan is extremely dynamic,
31 increasing or decreasing with age (e.g. Kervinen et al. 2015) and going through cycles of renewal
32 as, for example, deer annually shed and regrow antlers, and birds moult and replace brightly
33 coloured plumage (e.g. Kierdorf, Li and Price 2009, Saino et al. 2013). Thus, many ornaments are
34 not displayed continuously, but grown expressly for the breeding season, and then moulted or
35 contracted when no longer required (Jenni and Winkler 2011). For example, a bird's plumage-
36 based displays reflect quality during moult thus reflecting previous condition (e.g. McGraw et al.
37 2002, Serra et al. 2007, Harms et al. 2015). In contrast, some traits, including behaviours, may
38 dynamically reflect current condition (e.g. vocalisations: Vannoni and McElligott 2009). Skin-based
39 (integumentary) ornaments are one such example of this, and are widespread throughout the
40 animal kingdom (fish: Pike et al. 2010; birds: Prum and Torres 2003, Rosenthal et al. 2012;
41 reptiles: Langkilde and Boronow 2010). These structures have been shown to vary in colour and
42 size and can fluctuate to reflect changes in condition rapidly; for example skin colouration in the
43 blue-footed booby (*Sula nebouxii*) can change according to nutritional condition in as little as 48
44 hours (Velando, Beamonte-Barrientos and Torres 2006; also see Doucet and Mennill 2009, Butler
45 and McGraw 2011). This suggests integumentary traits may act as cues of current phenotypic
46 quality (Perez-Rodriguez 2008, Hill, Hood and Huggins 2009).

47 Integumentary ornament size is typically mediated by androgens, which can act as
48 immunosuppressants or oxidative stressors, making the signal physiologically or energetically
49 costly to express (Folstad and Karter 1992, von Schantz et al. 1999, Alonso-Alvarez et al. 2007,
50 Mougeot et al. 2009 and references therein). This suggests that only high quality males are able to

51 mediate these costs, especially in combination with other factors influencing their current condition;
52 for example food availability or parasite burden. The ability to cope with these costs and, as such,
53 the resources available for investment into sexual interactions may vary further with age (Yoccoz
54 et al. 2002, Nieminen et al. 2016). For example, in younger males, investment may be allocated
55 instead to growth or development (Nussey et al. 2009, Kervinen et al. 2015). Due to the costs
56 involved with expressing such traits, these ornaments are usually only largest when dominance is
57 more important, i.e. during the breeding season (e.g. the bill knob of mute swans *Cygnus olor*.
58 Horrocks, Perrins and Charmantier 2009). However, many species interact outside of the breeding
59 season, often particularly intensively in the months or weeks leading up to the period of maximum
60 trait expression; these interactions can lead to differences in dominance status and reproductive
61 success (e.g. Marra and Holmes 2001, Yoshino and Goshima 2002, Pryke et al. 2002, Mougeot et
62 al. 2005 a, c, Poisbleau et al. 2006, Reudink et al. 2009). Despite this, most investigations focus
63 on peak expression or discrete periods before and during breeding (e.g. Forstmeier 2002, Faivre
64 et al. 2003, Jawor et al. 2004, Miller and Brooks 2005, Mougeot, Redpath and Piertney 2006,
65 Dobson et al. 2008, Murphy et al. 2009).

66 Research shows that developing larger static (e.g. bone-based such as antlers) traits is
67 costly (Walther and Clayton 2005). It therefore follows that developing such traits earlier in the
68 lead-up to, or during, the breeding season is likely to come at a higher physiological and energetic
69 cost (e.g. Møller 1994, Lantz and Karubian 2001, Peters, Astheimer, Cockburn 2001). The claim
70 that costly ornaments honestly signal quality thus needs to be understood in a dynamic context,
71 particularly for more transient signals (i.e. integumentary or skin-based), as this may only be true in
72 some phases of growth; modelling suggests that higher quality individuals should delay growth
73 until closer to breeding (Rands, Evans and Johnstone 2011). For example, the red grouse
74 *Lagopus lagopus scotica* has two seasonal ornament growth peaks; autumn and spring. Those
75 with the largest combs during autumn become more dominant and are able to establish a territory,
76 whilst those failing to do this do not survive to see the breeding season (Mougeot et al. 2005a,
77 Mougeot et al. 2003a, c). We also know that developing the largest or most elaborate ornament

78 may be facilitated by periods of earlier and more accelerated growth (e.g. Barnard 1995, Bartoš
79 and Losos 1997, Dunn and Cockburn 1999, Ninni et al. 2004, Siefferman, Hill and Dobson 2005,
80 Lee, Monaghan and Metcalfe 2012). Expression of these signals and the information conveyed by
81 their interactions can change dramatically before the breeding season, for example due to shifts in
82 social status (Kitaysky, Wingfield and Piatt 1999, Setchell and Dixson 2001, Oliveira 2004), and
83 conspecifics may dynamically assess this (Torres and Velando 2003) and implement flexible
84 patterns of reproductive effort (Nieminen et al. 2016). The period prior to the breeding season itself
85 may even determine the ultimate size of the ornament, as well as its costliness, i.e. its condition-
86 dependence (Bartoš and Losos 1997, Rands, Evans and Johnstone 2011). Thus, taking a
87 snapshot of ornaments, that may be partially developed, prior to breeding may be misleading
88 (Rands, Evans and Johnstone 2011).

89 The black grouse *Lyrurus tetrix* is a lekking Galliform species with strong intersexual and
90 intrasexual selection, in which copulations are skewed towards a few superior males (Alatalo,
91 Höglund and Sutherland 1992, Kokko and Lindström 1996, Kervinen et al. 2016). Males have a
92 number of morphological and behavioural traits that are used for both intersexual and intrasexual
93 signalling (Hovi et al. 1994, Höglund, Johansson and Pelabon 1997, Rintamäki et al. 1997, 2000,
94 2001, Siitari et al. 2007, Hämäläinen et al. 2012, Lebigre, Alatalo and Siitari 2013). Of these, their
95 testosterone-dependent red eye combs are the most variable in size (Rintamäki et al. 2000,
96 Kervinen et al. 2015), peaking during the breeding season (Fig 1). However, male dominance is
97 acquired and maintained through multi-annual, year-round interactions (Kokko et al. 1998,
98 Rintamäki et al. 1999, Siitari et al. 2007), similar to the patterns shown in red grouse (Mougeot et
99 al. 2005a, Mougeot et al. 2003a, b), suggesting that the top males should have larger eye combs
100 at all times. The breeding season occurs over approximately 2 weeks during spring, but winter
101 flocking and dominance-related interactions begin up to 3-5 months before this (Alatalo, Höglund
102 and Lundberg 1991, Lebigre et al. 2012). During this period, physiological stress levels increase in
103 red grouse, and likely enforce the honesty of signals (Bortolotti et al. 2009). Those in better
104 condition or phenotypic quality are likely to cope more successfully with prolonged periods of

105 expressing larger eye combs. As resources available for investment and, accordingly, dominance
106 vary across an individual's lifetime, we also investigated the relationship between age and
107 ornament expression. Using a longitudinal dataset of individual eye comb size across multiple
108 years, we tested whether condition or dominance were related to eye comb sizes before and
109 during the breeding season, and how this varied with age.

110

111 **Material and Methods**

112 **Data collection**

113 Black grouse were studied at 5 protected lek sites in central Finland (centred around Petäjavesi:
114 lat. 62°25'N, long. 25°18'E) from January-May, 2001-13 and 2015. Individuals were caught (during
115 January-May) with oat-baited walk-in traps, using standard protocols (see Siitari et al. 2007,
116 Lebigre et al. 2012). Each individual was banded, weighed (to nearest 10g) and aged as adult (≥ 2
117 years old) or younger (1 year old), based on plumage differences (Helminen 1963). Eye combs
118 were recorded on a digital video camera with a 1cm scale reference. The area of each eye comb
119 (cm^2) was calculated using ImageJ software (Rasband 2012), and then summed to get total eye
120 comb area for each individual (cm^2). Repeatability for these measurements was calculated using
121 ICC function (Wolak et al. 2012) in R (ICC=0.986, 95%CI=0.97/0.99, n=50), with a margin of error
122 in estimated comb size of only 1%.

123

124 **Behavioural data**

125 During the mating season (ca. 2 weeks in late April - early May) behaviours of ringed males were
126 recorded daily, at regular intervals from 03:00 to 08:00 am as this is primary period of activity and
127 when copulations occur. Behaviours (fighting, hissing, rookooing, inactive; Höglund et al. 1997)
128 and the spatial location of each male were scan sampled at regular intervals (documented as
129 'activity maps'). Total number of copulations, lek attendance (proportional to the highest attending

130 male on the same lek that year), and the centre of each male's territory (median coordinates of
131 observations) were calculated for all males. Distance from lek centre was calculated as the linear
132 distance of each male's territory centre from the lek centre (median coordinates of all observations
133 of all males). There is strong sexual selection on male behavioural traits of which lek attendance,
134 distance from lek centre and number of copulations achieved accurately capture male dominance
135 (Kervinen et al. 2016).

136

137 **Statistical Analysis**

138 We tested the idea that males of differing age, condition and dominance status would vary in the
139 timing of eye comb size change. This was analysed using linear mixed-effect models (LMMs). In
140 each model, the linear and quadratic terms of Julian date were included to account for possible
141 non-linearity of ornament growth. A polynomial linear regression was used as it is appropriate for
142 investigating the increasing exponential growth leading to the breeding season. Black grouse
143 males forage in the forests surrounding the lek sites after the breeding season, meaning they
144 cannot be captured so we lack data on the decline of eye comb size.

145 We tested for correlations between eye comb size and the following four dominance-and
146 condition-related measures for both age groups: (a) distance from lek centre, as dominant males
147 hold territories closer to the lek centre (Rintamäki et al. 1997); (b) lek attendance, as dominant
148 males attend the lek most often (Alatalo et al. 1996); (c) copulations, as only the dominant males
149 reproduce (Alatalo et al. 1991); (d) body mass (g), a measure of condition (e.g. Alatalo et al. 1996)
150 as heavier males have more resources (condition-dependence) to invest both in ornament growth
151 and dominance-related activities (Willebrand and Marcström 1989, Rintamäki et al. 2001,
152 Nieminen et al. 2016). Lek attendance was included as a binary factor, based on high ($\geq 80\%$) and
153 low ($< 80\%$) attendance, because of a sharp increase in mating success for those with $\geq 80\%$
154 attendance (Kervinen, Lebigre and Soulsbury 2016). All models had a Gaussian error structure
155 and used total eye comb size (combined area of left and right eye comb) as the dependent

156 variable. In all models, individual identity, year and site were included as random effects to control
157 for repeated measures, cohort and differences between sites, such as resources.

158 In order to test for differences in eye comb size across the time period before and during
159 the breeding season, each variable was first tested in interaction with Julian date (linear and
160 quadratic). The interaction terms were subsequently removed in a backward stepwise manner if
161 non-significant. We first quantified the differences in eye combs size between adults (≥ 2 years old)
162 and younger males (< 1 year old), identified because the majority of morphological and behavioural
163 trait development occurs between 1 and 2 years old in black grouse, with mating being largely
164 unsuccessful until 2 years old (Alatalo et al. 1992, Kervinen et al. 2012). Any significant
165 interactions between age and Julian date would indicate a difference in the eye comb growth
166 patterns between groups. We then tested relationships with dominance- and condition-measures.
167 For these analyses adults and younger males were analysed separately, as only a minority of
168 younger males participate in dominance-related behaviours, and strong age-dependency in
169 morphological and behavioural traits may over or under emphasise patterns (Kervinen et al. 2012,
170 2015).

171 Lastly, we tested whether changes in dominance between years led to differences in
172 growth of eye combs. To this end, we subtracted the value of individuals' dominance measures
173 (lek attendance, distance from lek centre) from the previous year's values, respectively. A negative
174 value for distance from lek centre would therefore indicate that a male was moving closer to the lek
175 centre and becoming more dominant. Conversely, a positive value for lek attendance indicated
176 more time spent at the lek and greater dominance. We carried out a LMM with total eye comb size,
177 Julian date (linear and quadratic) and the between-year differences as fixed factors. Similarly to
178 the condition and dominance analyses; identity, age and year were included as random effects
179 and backward stepwise removal of interactions was carried out. We used only adult males for this
180 analyses to avoid the change in traits between younger and adults confounding results (Kervinen
181 et al. 2015). Models were run using the lme4 function (Bates, Maechler and Bolker 2015) along

182 with the lmerTest function (Kuznetsova, Brockhoff and Christensen 2015). All models were run in
183 R version 3.1.2 (R Development Core Team 2012).

184

185 **Results**

186 **Age differences in eye comb growth**

187 In total, we measured 577 adult males a total of 830 times, with individual adults measured
188 between 1 and 8 times across their lifetimes. Within each year, most males were sampled once
189 (704 times), but some were measured multiple times within a year (two measures = 98 measured
190 twice, 18 measured three times, 10 measured four times). We measured 800 younger males, with
191 most being measured once (753) and few being measured twice or more (41 measured twice, 6
192 measured three times).

193 Total eye comb size was significantly related to the linear and quadratic terms of Julian
194 date (linear: Estimate \pm SE = -0.04 ± 0.002 , $t = -14.30$, $P < 0.001$; quadratic: Estimate \pm SE =
195 $6.57 \times 10^{-4} \pm 2.46 \times 10^{-5}$, $t = 26.67$, $P < 0.001$). Adult males had larger eye combs than younger males
196 (Estimate \pm SE = 1.80 ± 0.06 , $t = 30.49$, $P < 0.001$), and there was a significant interaction between age
197 and quadratic Julian date (Estimate \pm SE = $3.78 \times 10^{-5} \pm 1.33 \times 10^{-5}$, $t = 2.84$, $P = 0.005$), but not linear
198 Julian date. Adult males always had larger eye combs and the increase in size of eye combs was
199 faster than in younger males (Fig 1c).

200

201 **Adult males and dominance-related eye comb growth-scheduling**

202 For adult males, heavier males always had larger eye combs (Table 1; Fig 2a). Similarly, males
203 that attended the lek more frequently (Fig 2b) had higher mating success (Fig 2c) and larger eye
204 combs. There was a non-significant trend for black grouse with territories closer to the lek centre to
205 have larger eye combs.

206

207 **Younger males and dominance-related eye comb growth-scheduling**

208 Younger males that were heavier had consistently larger eye combs (Table 1; Fig 3a). In addition,
209 those males that; attended the lek frequently (Fig 3b), had territories closer to the lek centre (Fig
210 3c) and those that had higher mating success (Fig 3d) grew larger eye combs close to the
211 breeding season (Table 1). However, these more dominant males did not grow larger eye combs
212 early on, prior to the breeding season.

213

214 **Changing status and eye comb growth**

215 Adult males that increased their lek attendance between years significantly increased eye comb
216 size, especially closer to the breeding season (Table 2; Fig 4), but there was no effect of moving
217 closer to the lek centre (Table 2).

218

219 **Discussion**

220 **Age differences in eye comb growth**

221 Younger males are typically lighter than adult males and presumably have fewer resources
222 available for allocation to ornament expression (Kervinen et al. 2015). Accordingly, younger black
223 grouse males have been shown to rank lower on the lek, achieving little reproductive success, with
224 only a minority participating in dominance-related activities such as fighting and lek attendance
225 (Brittas and Willebrand 1991, Alatalo et al. 1992, Kokko and Lindström 1996, Kervinen et al. 2012).
226 In line with these results, we found that younger males had consistently smaller eye combs than
227 adult males. This result is similar to those reported in in other taxa, for example in male red deer
228 (*Cervus elaphus*) investment into rutting and antler growth (both required for dominance) is lower
229 in young males than healthy adult males (Nussey et al. 2009; see Balbontín et al. 2007, Evans,
230 Gustafsson and Sheldon 2011 for additional examples). Low younger investment is also
231 unsurprising as younger males that significantly invest in early, prolonged ornament growth may
232 incur costs of reduced future success in ornament expression, reproduction and survival (Stearns

233 1989, Hunt et al. 2004, Siitari et al. 2007, Kervinen et al. 2015, see Metcalfe and Monaghan 2001
234 for a review). Hence, delayed ornament expression until full maturity may be beneficial to male
235 lifetime reproductive success (Kokko 1997, Kervinen et al. 2015).

236

237 **Adult males and dominance-related eye comb size**

238 Heavier adult males had larger eye combs before and during the breeding season. Previous
239 studies have demonstrated that ornament expression is condition-dependent (Holzer, Jacot and
240 Brinkhof 2003, Cotton, Fowler and Pomiankowski 2004, Poisbleau et al. 2006, Emlen et al. 2012,
241 but see Badyaev and Duckworth 2003). High testosterone levels allow males to express larger eye
242 combs and be more reproductively successful but also result in trade-offs between ornament
243 expression and immune function or oxidative defence (Alatalo et al. 1996, Rintamäki et al. 2000,
244 Mougeot et al. 2009, Martínez-Padilla et al. 2014). As such, similarly to the red grouse, heavier
245 black grouse males, i.e. those in better condition, are more likely to be able to cope with pressures
246 on condition, such as parasite burden, whilst sustaining the physiological investment required to
247 maintain growth and expression of a larger ornament (Höglund, Alatalo and Lundberg 1992,
248 Mougeot, Evans and Redpath 2005b, Mougeot et al. 2009, Yang et al. 2013).

249 We also found that those males spending the most time on the lek and those achieving the
250 most copulations expressed larger eye combs both before and during the breeding season. In
251 many species, dominance status is accrued or maintained through extended time periods, not just
252 during the breeding season (Andersson 1989, Höglund, Johansson and Pelabon 1997, McElligott
253 et al. 1998, McGraw et al. 2001, Friedl and Klump 2005, Poisbleau et al. 2006). In black grouse,
254 dominance-related interactions begin up to 3-5 months before breeding season, when males and
255 female live in mixed-sex wintering flocks (Alatalo, Höglund and Lundberg 1991, Lebigre et al.
256 2012). Hence, ornament expression outside the breeding season has a function in social
257 competition and future reproductive success. For example, in red grouse, the outcome of
258 dominance-related interactions during the autumn heavily influences breeding success the

259 following spring, and dominance is closely related to eye comb size in red grouse (Mougeot et al.
260 2003a, b).

261 Our results also show that between-year changes in dominance status are associated with
262 larger eye combs. Males that attended the lek more frequently in the following year had larger eye
263 combs near to the breeding season. A similar pattern but within-season has been observed in
264 other species, such as the jungle fowl *Gallus gallus* in which changes in dominance led to changes
265 in comb size (Cornwallis and Birkhead 2008). Similarly, changes in male dominance status in
266 fallow deer (*Dama dama*) affects antler growth rate (Bartoš and Losos 1997, Ciuti and Apollonio
267 2011, also see Tibbetts and Safran 2009, Lantz and Karubian 2016). This indicates that those
268 individuals able to increase their dominance can alter the expression of ornaments accordingly,
269 and that having larger eye combs reflects dominance both before and during the breeding season
270 (Rintamäki et al. 1999, Kokko et al. 1999).

271

272 **Younger males and dominance-related eye comb size**

273 Eye comb size was also related to dominance in younger males. The key difference between
274 adults and younger males was that variation in eye comb size across younger males occurred later
275 on and much closer to the breeding season. Younger males may be physiologically constrained
276 from producing larger eye combs because they cannot produce high levels of testosterone, or may
277 have fewer resources to allocate to ornament growth or maintenance. This may mean they should
278 delay expressing larger ornaments until later in the season, in line with findings that younger males
279 increase reproductive effort as adult male effort declines (Nieminen et al. 2016) or possibly not
280 participate in dominance-related interactions until they have become an adult (Kokko 1997).
281 Experimentally increased testosterone in younger males led to an increase in eye comb size
282 (Siitari et al. 2007), but even then eye combs were not as large as adults, suggesting that
283 physiological constraint may only be partly important. Since heavier younger males had large eye
284 combs at all times, it seems that higher quality or better condition individuals are more likely to

285 have the resources available to invest in ornament growth. As those younger males that participate
286 in dominance behaviours are shown to invest in larger eye combs but later than adults, i.e. only as
287 the breeding season approaches, it may also be that resource availability is a limiting factor
288 (Lindström et al. 2009, Kervinen et al. 2012, see Dmitriew 2011 for a review). There is also
289 evidence for this pattern in younger males of other avian species (e.g. house finches *Haemorhous*
290 *mexicanus*, Badyaev and Duckworth 2003, bearded reedlings *Panurus biarmicus*, Surmacki,
291 Stępniewski and Stępniewska 2015), suggesting that timing of investment in younger males is
292 critical. Hence, whilst condition-dependent ornament expression is continuous across both age
293 groups, there are differences in eye comb growth patterns towards the breeding season. These
294 differences may be due to resource-based or physiological constraints in younger males, limiting
295 their ability to grow large eye combs, which may also link to evidence of young males increasing
296 reproductive effort with decline in adult male investment (Nieminen et al. 2016).

297

298 **Conclusions**

299 In summary, we found clear differences in eye comb size between ages and between dominant
300 and subordinate males. In adults, dominant males had larger eye combs both before and during
301 the breeding season. Males that increased their dominance between years increased their eye
302 comb sizes. Younger males had smaller eye combs than adult males, and showed similar
303 dominance-related patterns. The main difference between younger and adult males related to
304 timing of eye comb size increase, with variation in younger male eye comb size occurring much
305 later than in adults. We suggest this is due to physiological or resource-based constraints. Our
306 results suggest that, since dominance is accrued through year-round interactions in many species,
307 the ability to maintain larger signals over prolonged periods and outside of the breeding season is
308 likely to be beneficial, especially for adults.

309

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318

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593 Table 1: Outputs for LMM models testing the variation in relationship between eye comb area (dependent variable) and Julian date according to 4
 594 condition and dominance-related morphological and behavioural traits.

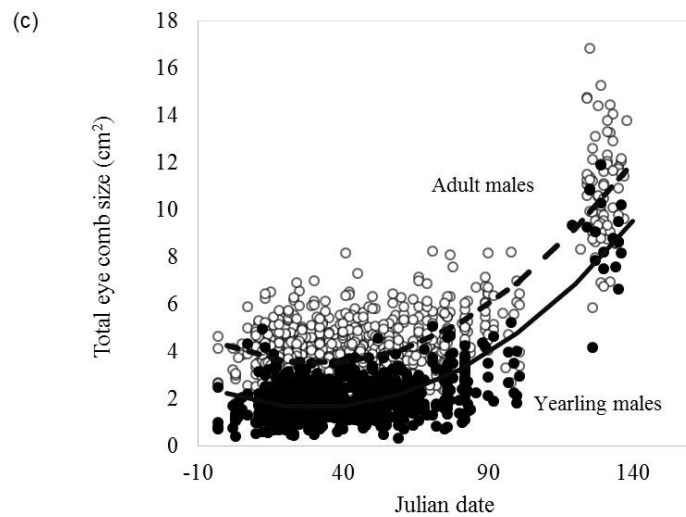
595

Model	Variable	Younger males				Adult males			
		Estimate	±SE	t	P	Estimate	±SE	t	p
Body mass	Intercept	-12.65	4.03	-3.14	<0.001	-46.25	6.53	-7.07	<0.001
Younger males (751 males/759 observations)	Julian date (linear)	-0.04	0.01	-	<0.001	-0.04	0.01	-7.65	<0.001
	Julian date (quadratic)	6.11x10 ⁻⁴	2.82x10 ⁻⁵	21.68	<0.001	6.56x10 ⁻⁴	3.40x10 ⁻⁵	19.29	<0.001
Adults (542 males/ 796 observations)	Body mass	2.12	0.57	3.72	<0.001	7.02	0.92	7.66	<0.001
Lek attendance	Intercept	2.22	0.24	9.93	<0.001	3.79	0.25	15.09	<0.001
Younger males (209 males/225 observations)	Julian date (linear)	-0.04	0.01	-6.07	<0.001	-0.04	0.01	-6.58	<0.001
	Julian date (quadratic)	6.16x10 ⁻⁴	4.57x10 ⁻⁵	13.46	<0.001	6.82x10 ⁻⁴	4.19x10 ⁻⁵	16.30	<0.001
Adults (302 males/539 observations)	Lek attendance	-0.21	0.18	-1.38	0.230	0.38	0.11	3.35	<0.001
	Julian date (linear) * lek attendance	-	-	-	-	-	-	-	-
	Julian date (quadratic) * lek attendance	6.74x10 ⁻⁵	2.82x10 ⁻⁵	2.39	0.018	-	-	-	-
Distance from the lek centre	Intercept	2.24	0.29	7.65	<0.001	4.25	0.26	16.48	<0.001
Younger males (161 males/172 observations)	Julian date (linear)	-0.05	0.01	-6.79	<0.001	-0.04	0.01	-6.68	<0.001
	Julian date (quadratic)	7.80x10 ⁻⁴	5.20x10 ⁻⁵	14.99	<0.001	7.04x10 ⁻⁴	4.45x10 ⁻⁵	15.82	<0.001
Adults (288 males/505 observations)	Distance from lek centre	-0.01	0.00	1.18	0.240	-0.01	0.00	-1.89	0.059
	Julian date (linear) * distance from lek centre	-	-	-	-	-	-	-	-
	Julian date (quadratic) * distance from lek centre	-1.57x10 ⁻⁶	7.23x10 ⁻⁷	-2.18	0.031	-	-	-	-
Copulations	Intercept	2.18	0.22	10.12	<0.001	3.85	2.55	14.99	<0.001
Younger males (210 males/ 224 observations)	Julian date (linear)	-0.03	0.01	-5.99	<0.001	-0.04	0.01	5.47	<0.001
	Julian date (quadratic)	5.96x10 ⁻⁴	4.29x10 ⁻²	13.88	<0.001	6.54x10 ⁻⁴	4.48x10 ⁻⁵	14.61	<0.001
Adults (290 males/493 observations)	Copulations	-0.08	0.06	-1.31	0.182	0.04	0.01	3.18	0.002
	Julian date (linear)*copulations	-	-	-	-	-	-	-	-
	Julian date (quadratic)*copulations	2.36x10 ⁻⁵	5.95x10 ⁻⁶	3.97	<0.001	-	-	-	-

596 Table 2: LMM model outputs for the relationship between eye comb size and Julian date and changes in dominance-related traits in male black grouse.

	Model	Variable	Estimate	SE	T	p
597	Change in distance from lek centre (91 individuals/152 data points)	Intercept	4.45	0.36	12.36	<0.001
		Julian date (linear)	-0.03	0.12	-2.62	0.010
598		Julian date (quadratic)	6.44 x10 ⁻⁴	8.54 x10 ⁻⁵	7.53	<0.001
		Distance from lek centre	3.41 x10 ⁻³	5.27 x10 ⁻⁴	0.65	0.519
599	Change in lek attendance (93 individuals/167 data points)	Intercept	4.07	0.33	14.14	<0.001
		Julian date (linear)	-0.04	0.01	-3.74	<0.001
600		Julian date (quadratic)	6.95 x10 ⁻⁴	7.74 x10 ⁻⁵	8.98	<0.001
		Lek attendance	-0.04	0.04	-1.08	0.283
601		Julian date (quadratic)*Lek attendance	1.70 x10 ⁻⁴	6.02x10 ⁻⁵	2.82	0.006

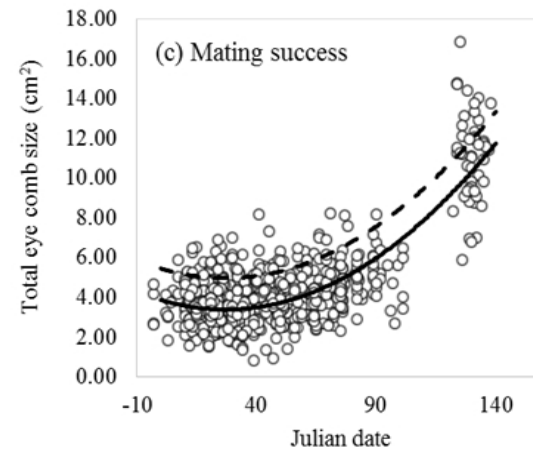
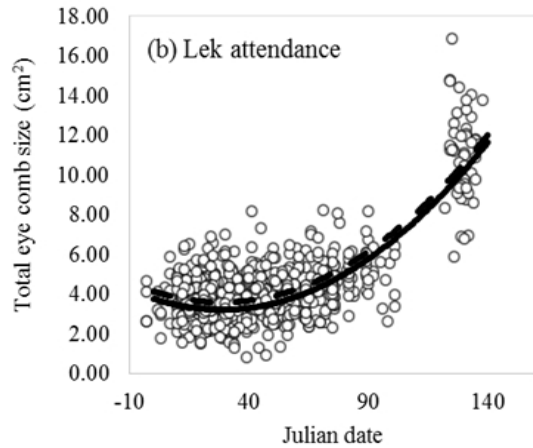
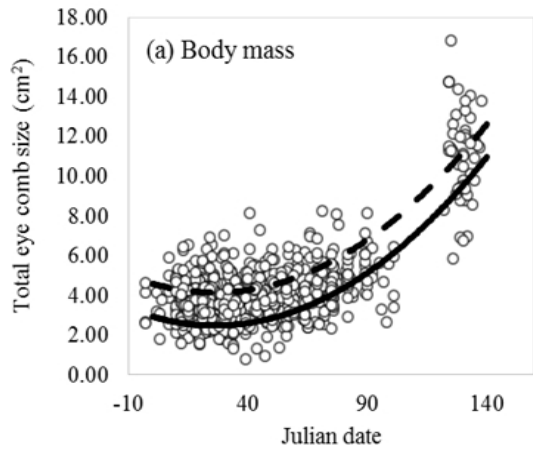
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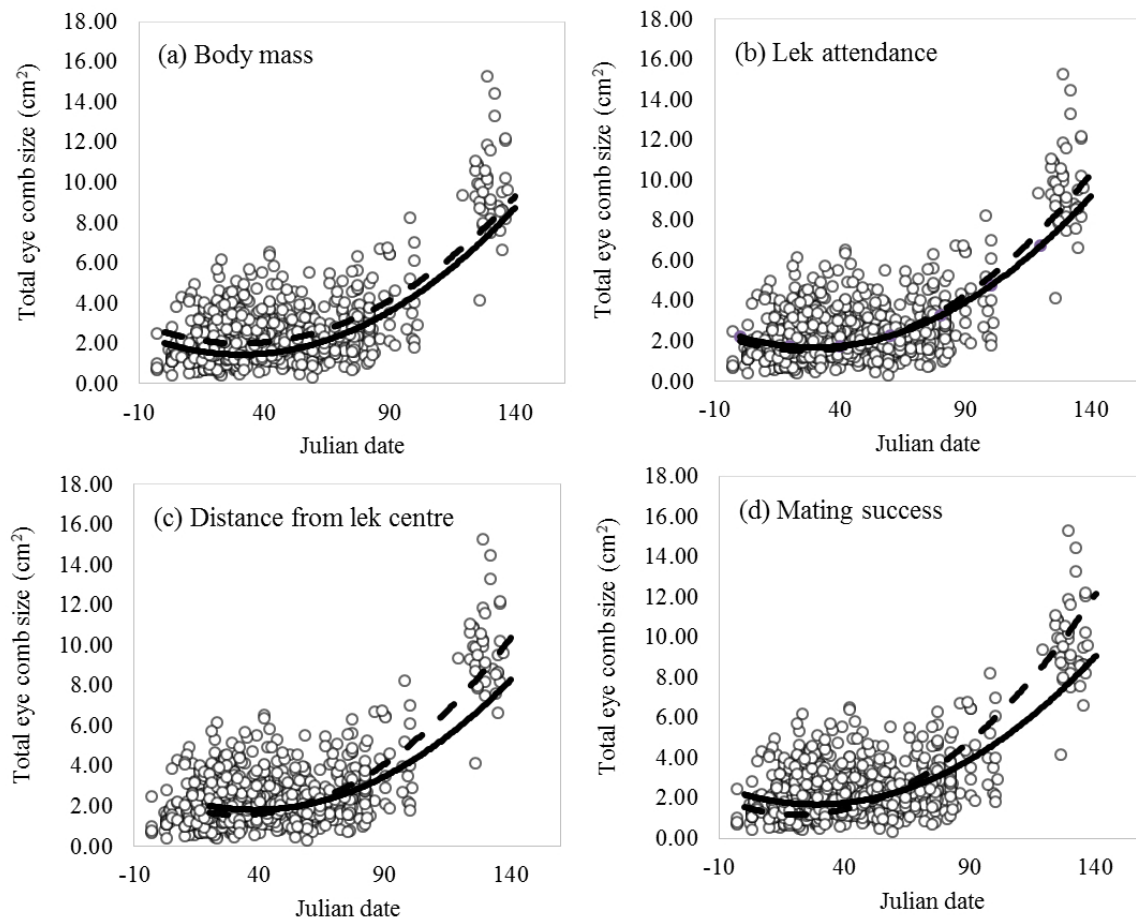
604 **Figure 1.** Supra-orbital red eye combs of black grouse. Photographs show an adult male caught in the (a) before the breeding season (30 January) and again (b)
605 during the breeding season (16 May). (c) Supra-orbital eye comb size for adult males (dashed line, open circles) and younger (solid line, solid points) male black
606 grouse before and during the breeding season. Individual data points are shown.

607

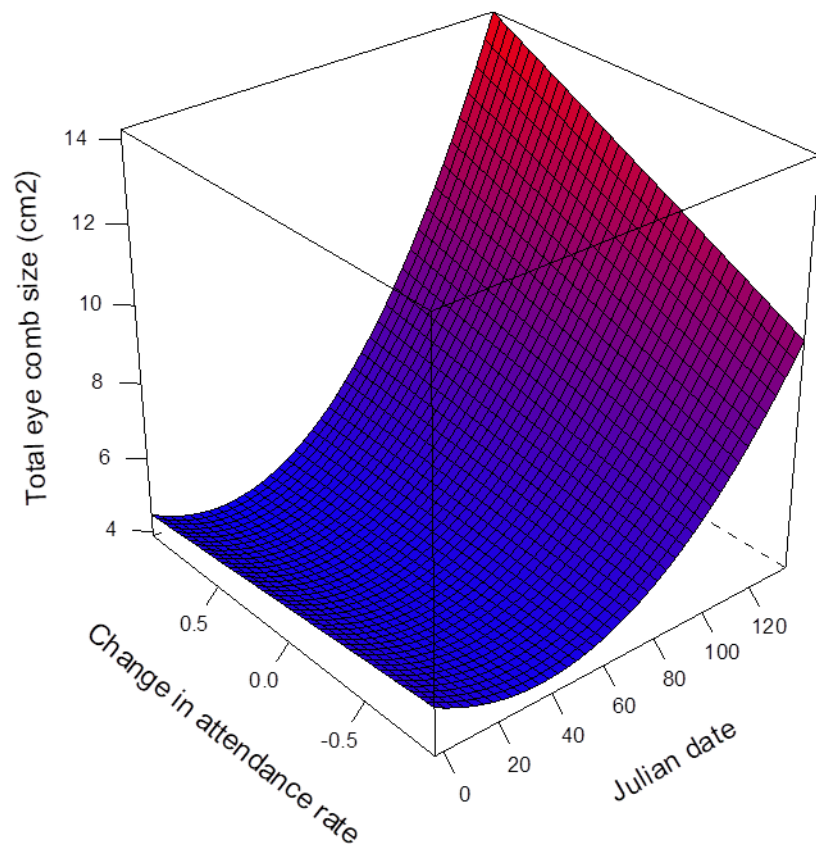


608 **Figure 2.** The relationship between adult eye comb growth, Julian date and (a) log body mass
 609 (dashed line=heavy (1400 g) male, solid line=light (1100 g) male), (b) lek attendance (dashed
 610 line=high attender, solid line=low attender) and (c) mating success (dashed line=males mating with
 611 high success (> 5 copulations), solid line=males unsuccessful (0 copulations) in mating).
 612 Individual data points are shown and illustrative fitted lines represent dominant and subordinate
 613 individuals.

614



615 **Figure 3.** The relationship between younger male eye comb growth, Julian date and (a) log body mass (dashed line=heavy (1400 g) male, solid line=light (1100 g)
 616 male), (b) lek attendance (dashed line= high attender, solid line=low attender), (c) distance from lek centre (dashed line= male close to lek centre (≤ 20 m), solid
 617 line= male far from lek centre (≥ 80 m)) and (d) mating success (dashed line=successful male (5 copulations), solid line=males unsuccessful (0 copulations) in
 618 mating). Individual data points are shown and illustrative fitted lines represent dominant and subordinate individuals.
 619



620 Figure 4. Adult male eye comb area in relation to Julian date and between-year changes in lek attendance.