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

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Abstract :

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

Introduction

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

Integumentary ornament size is typically mediated by androgens, which can act as immunosuppressants or oxidative stressors, making the signal physiologically or energetically costly to express (Folstad and Karter 1992, von Schantz et al. 1999, Alonso-Alvarez et al. 2007, Mougeot et al. 2009 and references therein). This suggests that only high quality males are able to mediate these costs, especially in combination with other factors influencing their current condition; for example food availability or parasite burden. The ability to cope with these costs and, as such, the resources available for investment into sexual interactions may vary further with age (Yoccoz et al. 2002, Nieminen et al. 2016). For example, in younger males, investment may be allocated instead to growth or development

(Nussey et al. 2009, Kervinen et al. 2015). Due to the costs involved with expressing such traits, these ornaments are usually only largest when dominance is more important, i.e. during the breeding season (e.g. the bill knob of mute swans *Cygnus olor*: Horrocks, Perrins and Charmantier 2009). However, many species interact outside of the breeding season, often particularly intensively in the months or weeks leading up to the period of maximum trait expression; these interactions can lead to differences in dominance status and reproductive success (e.g. Marra and Holmes 2001, Yoshino and Goshima 2002, Pryke et al. 2002, Mougeot et al. 2005 a, c, Poisbleau et al. 2006, Reudink et al. 2009). Despite this, most investigations focus on peak expression or discrete periods before and during breeding (e.g. Forstmeier 2002, Faivre et al. 2003, Jawor et al. 2004, Miller and Brooks 2005, Mougeot, Redpath and Pieltney 2006, Dobson et al. 2008, Murphy et al. 2009).

Research shows that developing larger static (e.g. bone-based such as antlers) traits is costly (Walther and Clayton 2005). It therefore follows that developing such traits earlier in the lead-up to, or during, the breeding season is likely to come at a higher physiological and energetic cost (e.g. Møller 1994, Lantz and Karubian 2001, Peters, Astheimer, Cockburn 2001). The claim that costly ornaments honestly signal quality thus needs to be understood in a dynamic context, particularly for more transient signals (i.e. integumentary or skin-based), as this may only be true in some phases of growth; modelling suggests that higher quality individuals should delay growth until closer to breeding (Rands, Evans and Johnstone 2011). For example, the red grouse *Lagopus lagopus scotica* has two seasonal ornament growth peaks; autumn and spring. Those with the largest combs during autumn become more dominant and are able to establish a territory, whilst those failing to do this do not survive to see the breeding season (Mougeot et al. 2005a, Mougeot et al. 2003a, c). We also know that developing the largest or most elaborate ornament may be facilitated by periods of earlier and more accelerated growth (e.g. Barnard 1995, Bartoš and Losos 1997, Dunn and Cockburn 1999, Ninni et al. 2004, Siefferman, Hill and Dobson 2005, Lee, Monaghan and Metcalfe 2012). Expression of these signals and the information conveyed by their interactions can change dramatically before the breeding season, for example due to shifts in social status (Kitaysky, Wingfield and Piatt 1999, Setchell and Dixson 2001, Oliveira 2004), and conspecifics may dynamically assess this (Torres and Velando 2003) and implement flexible patterns of reproductive effort (Nieminen et al. 2016). The period prior to the breeding season itself may even determine the ultimate size of the ornament, as well as its costliness, i.e. its condition-dependence (Bartoš and Losos 1997, Rands, Evans and Johnstone 2011). Thus,

taking a snapshot of ornaments, that may be partially developed, prior to breeding may be misleading (Rands, Evans and Johnstone 2011).

The black grouse *Lyrurus tetrix* is a lekking Galliform species with strong intersexual and intrasexual selection, in which copulations are skewed towards a few superior males (Alatalo, Höglund and Sutherland 1992, Kokko and Lindström 1996, Kervinen et al. 2016). Males have a number of morphological and behavioural traits that are used for both intersexual and intrasexual signalling (Hovi et al. 1994, Höglund, Johansson and Pelabon 1997, Rintamäki et al. 1997, 2000, 2001, Siitari et al. 2007, Hämäläinen et al. 2012, Lebigre, Alatalo and Siitari 2013). Of these, their testosterone-dependent red eye combs are the most variable in size (Rintamäki et al. 2000, Kervinen et al. 2015), peaking during the breeding season (Fig 1). However, male dominance is acquired and maintained through multi-annual, year-round interactions (Kokko et al. 1998, Rintamäki et al. 1999, Siitari et al. 2007), similar to the patterns shown in red grouse (Mougeot et al. 2005a, Mougeot et al. 2003a, b), suggesting that the top males should have larger eye combs at all times. The breeding season occurs over approximately 2 weeks during spring, but winter flocking and dominance-related interactions begin up to 3-5 months before this (Alatalo, Höglund and Lundberg 1991, Lebigre et al. 2012). During this period, physiological stress levels increase in red grouse, and likely enforce the honesty of signals (Bortolotti et al. 2009). Those in better condition or phenotypic quality are likely to cope more successfully with prolonged periods of expressing larger eye combs. As resources available for investment and, accordingly, dominance vary across an individual's lifetime, we also investigated the relationship between age and ornament expression. Using a longitudinal dataset of individual eye comb size across multiple years, we tested whether condition or dominance were related to eye comb sizes before and during the breeding season, and how this varied with age.

Material and Methods

Data collection

Black grouse were studied at 5 protected lek sites in central Finland (centred around Petäjävesi: lat. 62°25'N, long. 25°18'E) from January-May, 2001-13 and 2015. Individuals were caught (during January-May) with oat-baited walk-in traps, using standard protocols (see Siitari et al. 2007, Lebigre et al. 2012). Each individual was banded, weighed (to nearest 10g) and aged as adult (≥ 2 years old) or younger (1 year old), based on plumage differences (Helminen 1963). Eye combs were recorded on a digital video camera with a 1cm scale

reference. The area of each eye comb (cm^2) was calculated using ImageJ software (Rasband 2012), and then summed to get total eye comb area for each individual (cm^2). Repeatability for these measurements was calculated using ICC function (Wolak et al. 2012) in R (ICC=0.986, 95% CI=0.97/0.99, n=50), with a margin of error in estimated comb size of only 1%.

Behavioural data

During the mating season (ca. 2 weeks in late April - early May) behaviours of ringed males were recorded daily, at regular intervals from 03:00 to 08:00 am as this is primary period of activity and when copulations occur. Behaviours (fighting, hissing, rookooing, inactive; Höglund et al. 1997) and the spatial location of each male were scan sampled at regular intervals (documented as 'activity maps'). Total number of copulations, lek attendance (proportional to the highest attending male on the same lek that year), and the centre of each male's territory (median coordinates of observations) were calculated for all males. Distance from lek centre was calculated as the linear distance of each male's territory centre from the lek centre (median coordinates of all observations of all males). There is strong sexual selection on male behavioural traits of which lek attendance, distance from lek centre and number of copulations achieved accurately capture male dominance (Kervinen et al. 2016).

Statistical Analysis

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

We tested for correlations between eye comb size and the following four dominance- and condition-related measures for both age groups: (a) distance from lek centre, as dominant males hold territories closer to the lek centre (Rintamäki et al. 1997); (b) lek attendance, as dominant males attend the lek most often (Alatalo et al. 1996); (c) copulations, as only the dominant males reproduce (Alatalo et al. 1991); (d) body mass (g), a measure of condition (e.g. Alatalo et al. 1996) as heavier males have more resources (condition-dependence) to

invest both in ornament growth and dominance-related activities (Willebrand and Marcström 1989, Rintamäki et al. 2001, Nieminen et al. 2016). Lek attendance was included as a binary factor, based on high ($\geq 80\%$) and low ($< 80\%$) attendance, because of a sharp increase in mating success for those with $\geq 80\%$ attendance (Kervinen, Lebigre and Soulsbury 2016). All models had a Gaussian error structure and used total eye comb size (combined area of left and right eye comb) as the dependent variable. In all models, individual identity, year and site were included as random effects to control for repeated measures, cohort and differences between sites, such as resources.

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

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

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

Results

Age differences in eye comb growth

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

Total eye comb size was significantly related to the linear and quadratic terms of Julian date (linear: Estimate \pm SE = -0.04 ± 0.002 , $t = -14.30$, $P < 0.001$; quadratic: Estimate \pm SE = $6.57 \times 10^{-4} \pm 2.46 \times 10^{-5}$, $t = 26.67$, $P < 0.001$). Adult males had larger eye combs than younger males (Estimate \pm SE = 1.80 ± 0.06 , $t = 30.49$, $P < 0.001$), and there was a significant interaction between age 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 Julian date. Adult males always had larger eye combs and the increase in size of eye combs was faster than in younger males (Fig 1c).

Adult males and dominance-related eye comb growth-scheduling

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

Younger males and dominance-related eye comb growth-scheduling

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

Changing status and eye comb growth

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

Discussion

Age differences in eye comb growth

Younger males are typically lighter than adult males and presumably have fewer resources available for allocation to ornament expression (Kervinen et al. 2015). Accordingly, younger black grouse males have been shown to rank lower on the lek, achieving little reproductive success, with only a minority participating in dominance-related activities such as fighting and lek attendance (Brittas and Willebrand 1991, Alatalo et al. 1992, Kokko and Lindström 1996, Kervinen et al. 2012). In line with these results, we found that younger males had consistently smaller eye combs than adult males. This result is similar to those reported in other taxa, for example in male red deer (*Cervus elaphus*) investment into rutting and antler growth (both required for dominance) is lower in young males than healthy adult males (Nussey et al. 2009; see Balbontín et al. 2007, Evans, Gustafsson and Sheldon 2011 for additional examples). Low younger investment is also unsurprising as younger males that significantly invest in early, prolonged ornament growth may incur costs of reduced future success in ornament expression, reproduction and survival (Stearns 1989, Hunt et al. 2004, Siitari et al. 2007, Kervinen et al. 2015, see Metcalfe and Monaghan 2001 for a review). Hence, delayed ornament expression until full maturity may be beneficial to male lifetime reproductive success (Kokko 1997, Kervinen et al. 2015).

Adult males and dominance-related eye comb size

Heavier adult males had larger eye combs before and during the breeding season. Previous studies have demonstrated that ornament expression is condition-dependent (Holzer, Jacot and Brinkhof 2003, Cotton, Fowler and Pomiankowski 2004, Poisbleau et al. 2006, Emlen et al. 2012, but see Badyaev and Duckworth 2003). High testosterone levels allow males to express larger eye combs and be more reproductively successful but also result in trade-offs between ornament expression and immune function or oxidative defence (Alatalo et al. 1996, Rintamäki et al. 2000, Mougeot et al. 2009, Martínez-Padilla et al. 2014). As such, similarly to the red grouse, heavier black grouse males, i.e. those in better condition, are more likely to

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be able to cope with pressures on condition, such as parasite burden, whilst sustaining the physiological investment required to maintain growth and expression of a larger ornament (Höglund, Alatalo and Lundberg 1992, Mougeot, Evans and Redpath 2005b, Mougeot et al. 2009, Yang et al. 2013).

We also found that those males spending the most time on the lek and those achieving the most copulations expressed larger eye combs both before and during the breeding season. In many species, dominance status is accrued or maintained through extended time periods, not just during the breeding season (Andersson 1989, Höglund, Johansson and Pelabon 1997, McElligott et al. 1998, McGraw et al. 2001, Friedl and Klump 2005, Poisbleau et al. 2006). In black grouse, dominance-related interactions begin up to 3-5 months before breeding season, when males and female live in mixed-sex wintering flocks (Alatalo, Höglund and Lundberg 1991, Lebigre et al. 2012). Hence, ornament expression outside the breeding season has a function in social competition and future reproductive success. For example, in red grouse, the outcome of dominance-related interactions during the autumn heavily influences breeding success the following spring, and dominance is closely related to eye comb size in red grouse (Mougeot et al. 2003a, b).

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

Younger males and dominance-related eye comb size

Eye comb size was also related to dominance in younger males. The key difference between adults and younger males was that variation in eye comb size across younger males occurred later on and much closer to the breeding season. Younger males may be physiologically constrained from producing larger eye combs because they cannot produce high levels of

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testosterone, or may have fewer resources to allocate to ornament growth or maintenance. This may mean they should delay expressing larger ornaments until later in the season, in line with findings that younger males increase reproductive effort as adult male effort declines (Nieminen et al. 2016) or possibly not participate in dominance-related interactions until they have become an adult (Kokko 1997). Experimentally increased testosterone in younger males led to an increase in eye comb size (Siitari et al. 2007), but even then eye combs were not as large as adults, suggesting that physiological constraint may only be partly important. Since heavier younger males had large eye combs at all times, it seems that higher quality or better condition individuals are more likely to have the resources available to invest in ornament growth. As those younger males that participate in dominance behaviours are shown to invest in larger eye combs but later than adults, i.e. only as the breeding season approaches, it may also be that resource availability is a limiting factor (Lindström et al. 2009, Kervinen et al. 2012, see Dmitriew 2011 for a review). There is also evidence for this pattern in younger males of other avian species (e.g. house finches *Haemorrhous mexicanus*, Badyaev and Duckworth 2003, bearded reedlings *Panurus biarmicus*, Surmacki, Stepniewski and Stepniewska 2015), suggesting that timing of investment in younger males is critical. Hence, whilst condition-dependent ornament expression is continuous across both age groups, there are differences in eye comb growth patterns towards the breeding season. These differences may be due to resource-based or physiological constraints in younger males, limiting their ability to grow large eye combs, which may also link to evidence of young males increasing reproductive effort with decline in adult male investment (Nieminen et al. 2016).

Conclusions

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

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Figure Legends

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

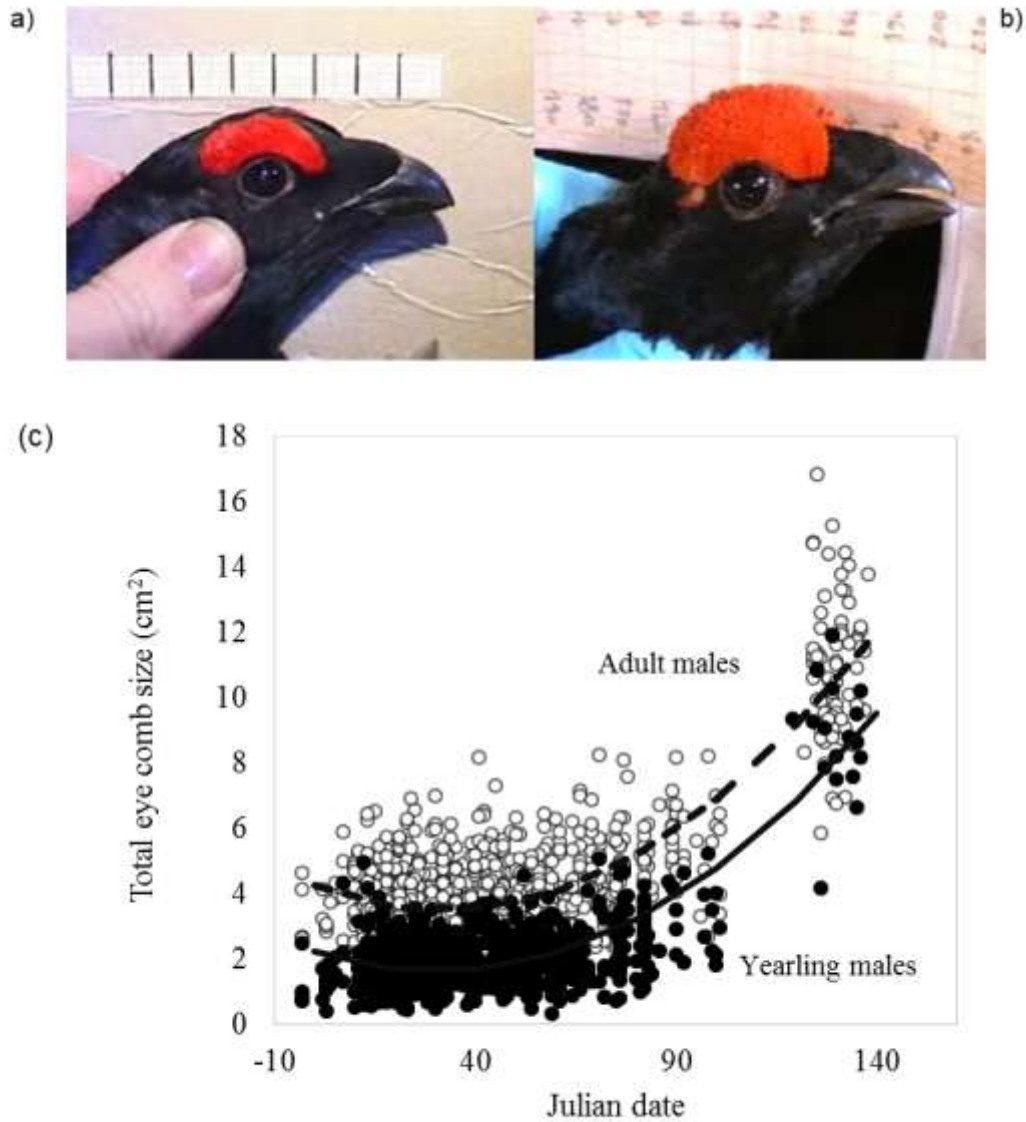


Figure 2: The relationship between adult eye comb growth, Julian date and (a) log body mass (dashed line = heavy (1400g) male, solid line = light (1100g) male), (b) lek attendance (dashed line = high attender, solid line = low attender) and (c) mating success (dashed line = males mating with high success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

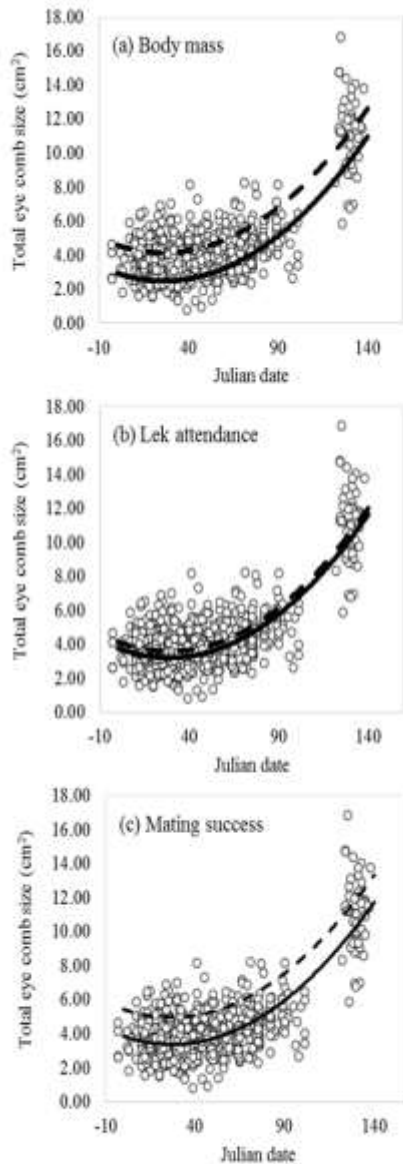


Figure 3: The relationship between younger male eye comb growth, Julian date and (a) log body mass (dashed line = heavy (1400g) male, solid line = light (1100g) male), (b) lek attendance (dashed line= high attender, solid line = low attender), (c) distance from lek centre (dashed line= male close to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

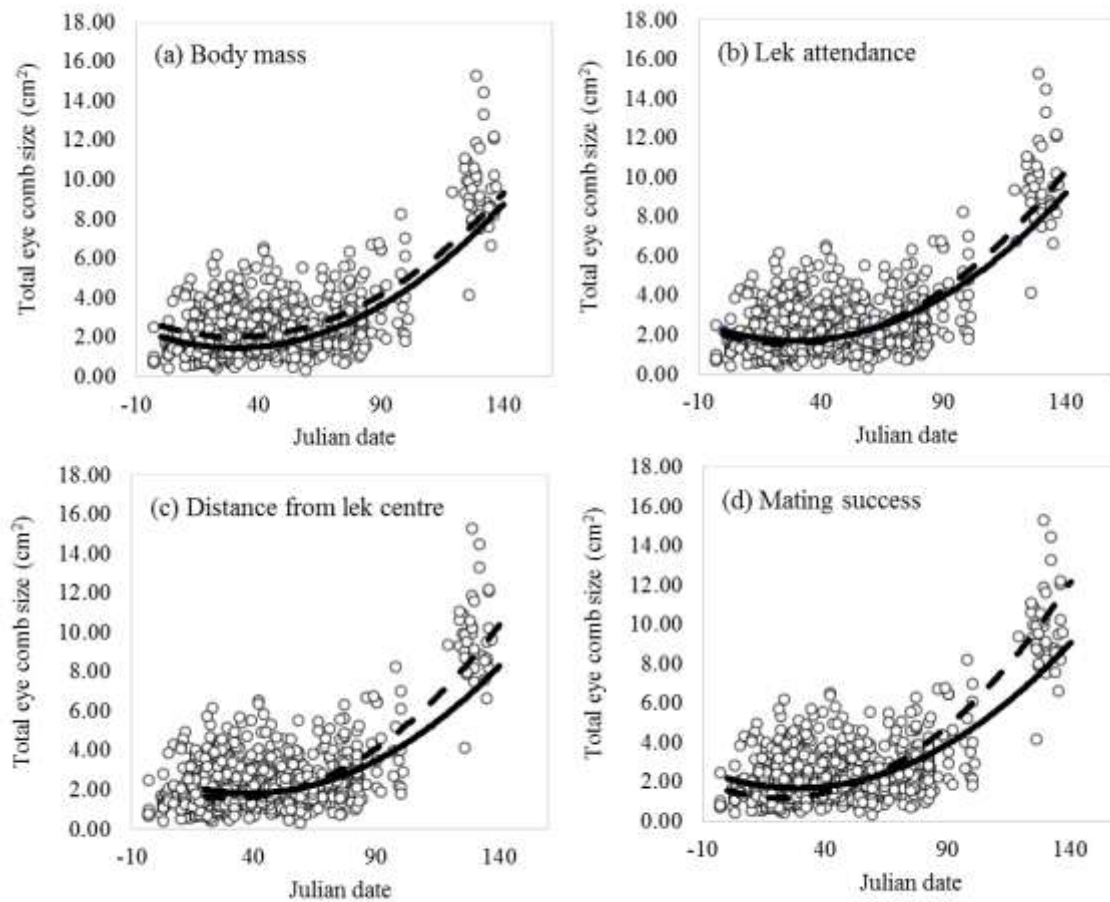


Figure 4: Adult male eye comb area in relation to Julian date and between-year changes in lek attendance.

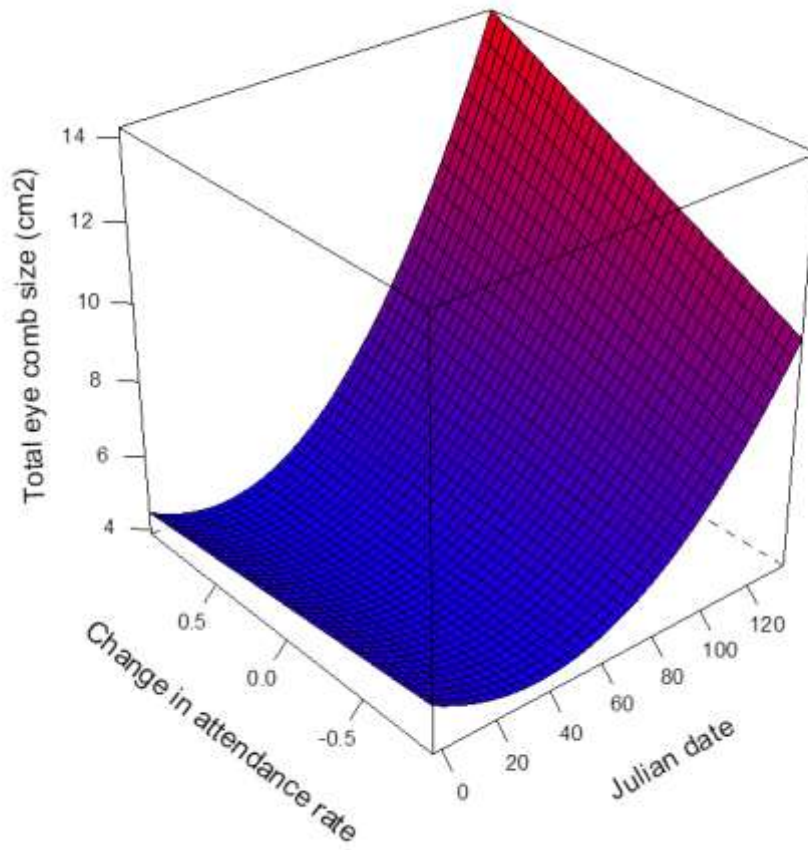


Table Legends

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

Model	Variable	<i>Younger males</i>				<i>Adult males</i>			
		Estimate	±SE	<i>t</i>	<i>P</i>	Estimate	±SE	<i>t</i>	<i>p</i>
Body mass				-				-	
Younger males (751 observations)	Intercept	-12.65	4.03	3.14	<0.001	-46.25	6.53	7.07	<0.001
males/759 observations)	Julian date (linear)	-0.04	0.01	11.33	<0.001	-0.04	0.01	7.65	<0.001
Adults (542 males/796 observations)	Julian date (quadratic)	6.11x10 ⁻⁴	2.82x10 ⁻⁵	21.68	<0.001	6.56x10 ⁻⁴	3.40x10 ⁻⁵	19.29	<0.001
	Body mass	2.12	0.57	3.72	<0.001	7.02	0.92	7.66	<0.001
Lek attendance				9.93	<0.001	3.79	0.25	15.09	<0.001
Younger males (209 observations)	Julian date (linear)	-0.04	0.01	6.07	<0.001	-0.04	0.01	6.58	<0.001
males/225 observations)	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 observations)	Lek attendance	-0.21	0.18	1.38	0.230	0.38	0.11	3.35	<0.001
	Julian date	-	-	-	-	-	-	-	-

males/5 39 observat ions)	(linear) * lek attendance Julian date (quadratic) * lek attendance	6.74x 10 ⁻⁵	2.82x 10 ⁻⁵	2.3 9	0.01 8	-	-	-	-
Distance from the lek centre	Intercept	2.24	0.29	7.6 5	<0.0 01	4.25	0.26	16. 48	<0.0 01
Younger males (161 males/1 72 observat ions)	Julian date (linear) Julian date (quadratic) Distance from lek centre	-0.05	0.01	6.7 9	<0.0 01	-0.04	0.01	6.6 8	<0.0 01
Adults (288 males/5 05 observa tions)	Julian date (linear) * distance from lek centre Julian date (quadratic) * distance from lek centre	-	-	-	-	-	-	-	-
Copulatio ns	Intercept	2.18	0.22	10. 12	<0.0 01	3.85	2.55	14. 99	<0.0 01
Younger males (210 males/ 224 observat ions)	Julian date (linear) Julian date (quadratic) Copulations	-0.03	0.01	5.9 9	<0.0 01	-0.04	0.01	5.4 7	<0.0 01
Adults	Copulations	-0.08	0.06	1.3 1	0.18 2	0.04	0.01	3.1 8	0.00 2

(290	Julian date								
males/49	(linear)*copulations	-	-	-	-	-	-	-	-
3	observations								
observati	Julian date	2.36x	5.95x	3.9	<0.0				
ons)	(quadratic)*copulations	10^{-5}	10^{-6}	7	01	-	-	-	-

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
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
	Julian date (quadratic)	6.44×10^{-4}	8.54×10^{-5}	7.53	<0.001
	Distance from lek centre	3.41×10^{-3}	5.27×10^{-4}	0.65	0.519
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
	Julian date (quadratic)	6.95×10^{-4}	7.74×10^{-5}	8.98	<0.001
	Lek attendance	-0.04	0.04	-1.08	0.283
	Julian date (quadratic)*Lek attendance	1.70×10^{-4}	6.02×10^{-5}	2.82	0.006