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# Life-History Differences in Age-Dependent Expressions of Multiple Ornaments and Behaviors in a Lekking Bird

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ABSTRACT: Age is a major factor explaining variation in life-history traits among individuals with typical patterns of increasing trait values early in life, maximum trait expression, and senescence. However, age-dependent variation in the expressions of sexually selected traits has received less attention, although such variation underpins differences in male competitive abilities and female preference, which are central to sexual selection. In contrast to previous studies focusing on single traits, we used repeated measures of seven sexually selected morphological and behavioral traits in male black grouse (*Tetrao tetrix*) to quantify the effects of age and life span on their expressions and quantified this variation in relation to male reproductive effort. Trait expression increased with age, but long-lived males had a slower increase and delayed maxima in trait values compared with short-lived males. There was evidence of terminal investment (increasing trait values during the last breeding season) in some traits and senescence in all traits. These trait dynamics were largely explained by the timing of male peak lekking effort. This study shows that fully understanding the variation in sexually selected traits and fitness benefits associated with sexual selection requires accounting for the complex interaction among individual age, life span, and the timing of individuals' investment in reproduction.

*Keywords:* aging, individual improvement, lek, life span, long-term data, senescence.

## Introduction

Age-dependent variation in life-history traits, secondary sexual traits, and behavior is widespread, with typical patterns of increasing trait values early in life, maximum trait expression, and senescence (Manning 1985; Andersson 1994; Brooks and Kemp 2001; Jones et al. 2008; Nussey et al. 2013). The variation in the duration of each stage and/or the shape of individual trajectories often depend on species' life history and might result from differences in individuals' allocation strategies. Despite the increasing understanding of the age-dependent variation in trait expression, little is known about the mechanisms underlying such variation and their implications for sexual selection (Bonduriansky et al. 2008; Monaghan et al. 2008; Nussey et al. 2013).

Until recently, longitudinal studies of age-dependent variation in individual performance and trait expression have been scarce, as long-term data with repeated measures of individuals are extremely laborious to collect (Clutton-Brock and Sheldon 2010). However, only longitudinal studies can separate within-individual (i.e., phenotypic plasticity, individual improvement, senescence) and between-individual (i.e., selective appearance or disappearance of certain phenotypes) effects of age on trait expression (van de Pol and Verhulst 2006; van de Pol and Wright 2009). As individual trajectories can be hidden by demographic heterogeneity (Bouwhuis et al. 2009; van de Pol and Wright 2009; Evans et al. 2011), neglecting within-individual effects might lead to incorrect conclusions about the effects of aging on life histories.

The application of mixed models to longitudinal data has bypassed this major limitation and revealed that within- and between-individual effects can differ in many situations and that both can result in a positive association between age and trait expression at the population level (van de Pol and Verhulst 2006; van de Pol and Wright 2009; Rebke et al. 2010). Most longitudinal studies published to date have analyzed key life-history traits, such as reproductive success (e.g., Dugdale et al. 2011; Froy et al. 2013) and survival (e.g., Bouwhuis et al. 2012), but there is growing interest in age-dependent variation in secondary sexual traits (Balbontín et al. 2011; Evans et al. 2011) and behavior (Mainguy and Côté 2008; Nussey et al. 2009). This is crucial because secondary sexual traits act as honest indicators of individuals' overall genetic quality if their elaboration and maintenance are associated with fitness costs, which in turn depend on individual body condition

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(Zahavi 1975; Kotiaho 2001). Moreover, life-history theory predicts that when resources are limited, all fitness components cannot be maximized simultaneously due to trade-offs. Individuals are consequently expected to adjust their trait expression according to their condition, and excess allocation on sexual traits or behavior can trade off with survival or reproductive success (Stearns 1992; Reznick et al. 2000). Hence, only longitudinal studies can reliably quantify the degree to which variation in the expressions of these traits with age can explain a large proportion of the variation in individual fitness.

Although longitudinal studies of age-dependent variation in trait expression are accumulating across a wide range of taxa (e.g., Coltman et al. 2002; Hoikkala et al. 2008; Nussey et al. 2009; Massot et al. 2011; Vande Velde 2011), the mechanisms behind these patterns are often not thoroughly understood (Monaghan et al. 2008; Nussey et al. 2013). In particular, previous studies have focused on socially monogamous birds with limited potential for sexual selection (e.g., Balbontín et al. 2011; Evans et al. 2011; Bouwhuis et al. 2012; Froy et al. 2013). However, since male-male competition and female choice can dampen or strengthen the effects of aging on life histories (Bonduriansky et al. 2008), patterns of age-dependent trait expression in these species with low variation in male mating success may differ substantially from those observed in species with strong sexual selection. Moreover, many previous studies have focused on single sexually selected traits (e.g., antler size [Nussey et al. 2009] and tail feather length [Balbontín et al. 2011]). However, sexual selection is clearly a multifaceted process, so investigating multiple traits simultaneously is needed to unravel the constraints and trade-offs acting on these traits (Evans et al. 2011) and to accurately quantify the overall fitness costs of trait expression (Kotiaho 2001; Lecomte et al. 2010). Finally, age-dependent expressions of sexual traits has not yet been quantified in relation to temporal scheduling of individual reproductive effort, where peak reproductive effort is expected to differ among individuals depending on their current body condition and, hence, may be the only opportunity during which all traits are expressed at their maximum. Therefore, to fully understand the effects of age on individual trait expressions and their consequences for sexual selection, long-term studies of species with multiple sexual traits and quantification of the age-dependent expressions of these traits in relation to the timing of reproductive effort are needed.

The black grouse (*Tetrao tetrix*) is a relatively short-living lekking galliform (<2% of recruited individuals live 5 years or longer) with intense male-male competition, and female choice is a major factor driving the evolution of the expressions of multiple male sexual traits (Alatalo et al. 1991, 1992). In particular, females prefer mating with males that are most present on the leks (Alatalo et al. 1992), fight frequently and successfully against other males (Hämäläinen et al. 2012), and occupy central territories (Hovi et al. 1994). Males with the greatest body mass loss during the lek have the highest fighting rate (Hämäläinen et al. 2012), the highest mating success, and the most central territories (Lebigre et al. 2013), indicating that strong physiological costs of male display mediate the honesty of these traits. Furthermore, lyre (i.e., tail) length and quality (the amount of damage to the white under tail feathers; Höglund et al. 1994), the size of the testosterone-induced red eye combs (Alatalo et al. 1996), and blue chroma coloration of breast feathers (Siitari et al. 2007) are all positively correlated with male mating success. The distribution of male annual mating success is highly skewed, with few dominant males monopolizing nearly all copulations, whereas the majority of males, especially yearlings, do not mate (Alatalo et al. 1992; Kervinen et al. 2012). Consequently, male lifetime mating success is similarly skewed, and most males fail to contribute genetically to the next generation. Therefore, the lekking black grouse is an outstanding natural system to study the age-dependent expressions of multiple morphological traits and behaviors in relation to sexual selection.

We tested the hypothesis that male trait expression depends on both male age and life span, and we expected that males with high early life trait expressions would have shorter life spans. We therefore quantified the age-dependent expressions of multiple morphological and behavioral traits. We separated the effects of within-individual improvement and senescence from selective appearance and disappearance of certain phenotypes in the population. To compare the relative magnitude of the change in morphological and behavioral traits, we replicated this analysis using the dimensionless relative rates of change in trait expression. We then determined whether there was senescence in these secondary sexual traits by testing the hypothesis that trait expression declines following their maximum expression. Finally, we introduced a novel peak-centering analysis, where the expressions of morphological traits and behaviors were related to male peak lekking effort, to test the hypothesis that trait expression depends on the individual timing of reproductive effort, independently from male age per se.

## Material and Methods

### Study Population

Five black grouse leks were monitored in Central Finland (approximately 62°15′N, 25°00′E) during the period 2002–2013. Each lek is the local main lek, holding 5–40 territorial males. The age structure of our study population was as-

sumed to be natural, as local hunting societies have refrained from hunting on these leks and in their close surroundings. During the study period, the local population density varied from 6.2 to 14.6 individuals per square kilometer of woodland (autumn wildlife triangle censuses, organized by the Finnish Game and Fisheries Research Institute), which was consistent with the observed age structure and the total number of males in the studied winter flocks and leks (fig. S1, available online).

### Morphological Data

Morphological data were collected on lek sites annually during January–March by catching black grouse with oat-baited walk-in traps (for methods, see Lebigre et al. 2012). Each bird captured for the first time was marked for future identification with a unique combination of an aluminum tarsus ring (with an individual serial number) and three colored plastic tarsus rings. Body mass (to the nearest 10 g), tarsus (to the nearest 0.1 mm), and lyre length (the longest tail feather from base to tip, to the nearest 1.0 mm) of each male were measured. If a male had lost his tail feathers and the new molted feathers were still clearly growing, lyre length was considered a missing data point. A sample of breast feathers was taken from each male, and the reflectance of the feathers' blue chroma coloration was measured in the laboratory (soon after the field season during 2002–2008 and collectively in 2011 for data from 2009 to 2011; not measured during 2012–2013, $N = 7$) with an Avantes spectrophotometer (GS 3100; EG&G Gamma Scientific, San Diego, CA; details are provided in Siitari et al. 2007). Eye combs were recorded against a scale with a digital video camera, and the total eye comb area (hereafter, eye comb size) was measured from snapshots using ImageJ software (ver. 1.46r; Rasband 2012).

### Behavioral Data

Behavioral data were collected at the study leks annually during the mating season (typically lasting 8–12 days in late April and early May). During this period, each lek was monitored daily approximately from 0300 to 0800 hours from a hide next to the lek (males also display to some extent before sunset, but copulations occur in the morning; R. V. Alatalo, C. Lebigre, and H. Siitari, personal observation). Male behavior was categorized as rookooing, hissing (the two main vocal displays), fighting, or inactive (details are provided in Höglund et al. 1997), and the location (x- and y-coordinates) of all ringed males (all males holding central territories; overall, >90% of the territorial males were ringed) on the lek were recorded at regular intervals. The time and location of all copulations and the identity of the male and female involved were also

recorded. Lek attendance (proportional to the highest attending male on the same lek that year) and the center of each male's territory (median coordinates of observations) were calculated for all territorial males (see Alatalo et al. 1996). Similarly, the location of the lek center (median coordinates of all observations of all males) and the linear distance of each male's territory center from the lek center were calculated. The relative proportion of each behavior was calculated for each male, but as these behaviors are mutually exclusive, only fighting rate was used in the analyses, as it likely has the greatest impact on male mating success (Hämäläinen et al. 2012).

### Male Age and Life Span

All captured unringed males were aged as yearlings or older according to their plumage characteristics (Helminen 1963). Only males captured for the first time as yearlings were included in the data, as older males ($\geq 2$ years) cannot be reliably aged on the basis of morphological traits (Helminen 1963). Including males with uncertain age in the analyses would thus hinder the accurate quantifications of the effect of age on trait expression. As male black grouse are philopatric to their lekking site, adult dispersal is rare (Caizergues and Ellison 2002; Lebigre et al. 2008), and because ringed males visiting our study leks have a virtually 100% probability of being observed, territorial males no longer observed were assumed to have died, and their last observations either on the lek (for behavioral traits) or during capture (for morphological traits) were used to determine their life span.

### Data Validation

The data consisted of records of morphological traits (body mass, lyre length, blue chroma, eye comb size) and lekking behavior (lek attendance, fighting rate, territory distance from the lek center) for 164 male black grouse with known year of hatching (2001–2008) and known life span of 1–6 years (totaling 423 records; table S1; tables S1–S6 are available online). For the analyses, ages 5 and 6 years were pooled into a single age class, and average trait values were used for the 7 males that were 6 years old. In case of missing data from age 5 years in these males, the trait values from age 6 years were used. Complete cohorts were available for males hatched in 2001–2006 and 2008, but 2 of the 130 ringed males hatched in 2007 were still alive in the spring of 2013. Since only 2 males of >1,200 ringed males hatched between 2000 and 2006 reached age 7 years, all males of the 2007 cohort were assumed not to have survived after the lekking season of 2013, and the whole 2007 cohort was included in the analyses. Cohorts hatched from 2009 on-

**Table 1:** Age-dependent expressions of morphological (pts. a–e) and behavioral (pts. f–h) traits in male black grouse

| Model | Parameter | Relative importance | Estimate | SE | Effect size, $r$ (95% CI) |
|---|---|---|---|---|---|
| a. Body mass, $n = 164$ | (Intercept) | ... | 1,271.66 | 11.45 | ... |
| id : site variance = 1,310 | **Age** | **1.00** | **90.10** | **13.71** | **.31 (.21, .39)** |
| residual variance = 1,296 | **Age$^2$** | **1.00** | **−234.57** | **35.08** | **−.31 (−.39, −.22)** |
| | LS | 1.00 | −.86 | 16.54 | −.00 (−.10, .09) |
| | TE | 1.00 | 21.89 | 13.58 | .08 (−.18, .17) |
| | Cohort | .76 | ... | ... | ... |
| | **Age : LS** | **1.00** | **103.14** | **38.02** | **.13 (.04, .22)** |
| | **Age : TE** | **1.00** | **80.32** | **27.90** | **.14 (.04, .23)** |
| | **Age$^2$ : LS** | **1.00** | **120.16** | **27.52** | **.21 (.11, .30)** |
| | Age$^2$ : TE | .61 | −44.13 | 25.18 | −.09 (−.18, .01) |
| b. Lyre length, $n = 163$ | (Intercept) | ... | 222.55 | .88 | ... |
| id : site variance = 35.95 | **Age** | **1.00** | **35.16** | **2.93** | **.55 (.47, .62)** |
| residual variance = 54.05 | **Age$^2$** | **1.00** | **−67.95** | **8.35** | **−.41 (−.49, −.31)** |
| | LS | 1.00 | −6.57 | 3.40 | −.10 (−.21, .00) |
| | TE | 1.00 | .38 | 3.13 | .01 (−.10, .11) |
| | Age : LS | .64 | 13.57 | 8.13 | .09 (−.02, .20) |
| | Age : TE | .71 | 11.10 | 5.97 | .10 (−.01, .20) |
| | **Age$^2$ : LS** | **1.00** | **38.65** | **5.76** | **.34 (.24, .43)** |
| | **Age$^2$ : TE** | **.70** | **10.96** | **5.39** | **.11 (.00, .21)** |
| c. Blue chroma, $n = 161$ | (Intercept) | ... | 26.81 | .42 | ... |
| id : site variance = .37 | **Age** | **.90** | **1.14** | **.54** | **.14 (.01, .27)** |
| residual variance = 4.55 | **Age$^2$** | **.83** | **−1.90** | **.95** | **−.14 (−.26, −.00)** |
| | LS | .76 | −.88 | .65 | −.09 (−.22, .04) |
| | TE | .61 | .33 | .54 | .04 (−.09, .17) |
| | Cohort | 1.00 | ... | ... | ... |
| | **Age : LS** | **.59** | **−2.42** | **1.06** | **−.15 (−.28, −.02)** |
| | Age : TE | .21 | −.10 | 1.05 | −.01 (−.14, .13) |
| | Age$^2$ : LS | .15 | .43 | 1.29 | .02 (−.11, .15) |
| | Age$^2$ : TE | .12 | −.31 | 1.06 | −.02 (−.15, .11) |
| d. Eye comb size, $n = 162$ | (Intercept) | ... | 3.78 | .10 | ... |
| id : site variance = .25 | **Age** | **1.00** | **2.56** | **.18** | **.66 (.59, .72)** |
| residual variance = .79 | **Age$^2$** | **1.00** | **−2.13** | **.49** | **−.26 (−.36, −.14)** |
| | LS | .74 | −.29 | .22 | −.08 (−.20, .04) |
| | TE | .44 | .01 | .18 | .00 (−.12, .12) |
| | Age : LS | .20 | .11 | .57 | .01 (−.11, .13) |
| | Age : TE | .15 | .34 | .40 | .05 (−.07, .17) |
| | **Age$^2$ : LS** | **.59** | **1.18** | **.55** | **.13 (.01, .25)** |
| | Age$^2$ : TE | .12 | .09 | .48 | .01 (−.11, .13) |
| e. Tarsus length, $n = 164$ | (Intercept) | ... | 59.39 | .17 | ... |
| id : site variance = .66 | Age | .33 | .11 | .17 | .04 (−.07, .14) |
| residual variance = 1.04 | Age$^2$ | .20 | −.04 | .20 | −.01 (−.12, .10) |
| | LS | .25 | .15 | .20 | .04 (−.06, .15) |
| | **TE** | **.93** | **.29** | **.13** | **.12 (.01, .22)** |
| | Cohort | .23 | −1.76 | 1.12 | −.08 (−.19, .02) |
| | Age$^2$ : TE | .04 | −.07 | .25 | −.01 (−.09, .12) |
| f. Lek attendance, $n = 164$ | (Intercept) | ... | 1.85 | .13 | ... |
| id : site variance = 1.97 | **Age** | **1.00** | **1.86** | **.17** | **.37 (.30, .44)** |
| residual variance = 1.00 | **Age$^2$** | **1.00** | **−7.60** | **.43** | **−.55 (−.61, −.49)** |
| | LS | 1.00 | −.56 | .34 | −.06 (−.14, .01) |
| | **TE** | **1.00** | **1.01** | **.13** | **.28 (.20, .35)** |
| | **Age : LS** | **1.00** | **3.25** | **.38** | **.31 (.24, .38)** |
| | Age : TE | .47 | .57 | .45 | .05 (−.03, .12) |
| | **Age$^2$ : LS** | **1.00** | **5.58** | **.39** | **.48 (.41, .54)** |
| | **Age$^2$ : TE** | **.76** | **.70** | **.28** | **.09 (.02, .17)** |

**Table 1** (*Continued*)

| Model | Parameter | Relative importance | Estimate | SE | Effect size, *r* (95% CI) |
|---|---|---|---|---|---|
| g. Fighting rate, *n* = 164 | (Intercept) | ... | −1.15 | .07 | ... |
| id : site variance = .44 | **Age** | **1.00** | **1.00** | **.20** | **.33 (.20, .44)** |
| residual variance = 1.00 | Age² | 1.00 | −.18 | .31 | −.04 (−.17, .10) |
| | LS | .90 | −.44 | .24 | −.12 (−.25, .01) |
| | **TE** | **1.00** | **−.49** | **.15** | **−.22 (−.34, −.08)** |
| | **Age : LS** | **.86** | **−.99** | **.38** | **−.18 (−.30, −.04)** |
| | Age : TE | .34 | −.21 | .32 | −.05 (−.18, .09) |
| | Age² : LS | .23 | .04 | .28 | .01 (−.12, .14) |
| | **Age² : TE** | **1.00** | **.68** | **.22** | **.21 (.08, .33)** |
| h. Distance,[a] *n* = 164 | (Intercept) | ... | 4.33 | .11 | ... |
| id : site variance = .67 | **Age** | **1.00** | −1.25 | **.30** | **−.26 (−.37, −.14)** |
| residual variance = .99 | Age² | .62 | .38 | .40 | .06 (−.06, .19) |
| | LS | .56 | .25 | .37 | .04 (−.08, .17) |
| | TE | .45 | .17 | .25 | .04 (−.08, .17) |
| | Age : LS | .38 | .83 | .48 | .11 (−.02, .23) |
| | Age : TE | .11 | −.03 | .41 | −.01 (−.13, .12) |
| | Age² : LS | .06 | −.02 | .65 | −.00 (−.13, .12) |
| | Age² : TE | .06 | .23 | .52 | .03 (−.10, .15) |

Note: The relative importance, coefficient estimates, SEs, and effect sizes (Pearson's *r* with 95% confidence intervals [CIs]) of the fixed effects of age, age², life span (LS), terminal event (TE), cohort, and the relevant interactions (denoted by colons) on morphological (pts. a–e) and behavioral (pts. f–h) traits after model averaging are shown. Statistically significant effects (95% CI does not overlap with 0) are in boldface type. Individual identity nested within study site (id : site) was fitted as a random effect in all models. Parameter values of blue chroma were rescaled by multiplying the original values by 100 to obtain more informative coefficient estimates and SEs. Random effects are represented as id : site and residual variances in the full model.

[a] Territory distance from the lek center (square root transformed).

ward were excluded because of large proportions (>10%) of individuals still alive in the spring of 2013.

### Statistical Analyses

Linear mixed-effects models (R package lme4, ver. 0.999999-2; Bates et al. 2013) with Gaussian distributions (for all morphological traits and square-root-transformed territory distance from the lek center) or binomial error distributions with logit link function (for lek attendance and fighting rate, coded as binomial denominators) were used to analyze the data. Parameters were estimated using maximum likelihood, which is recommended instead of restricted maximum likelihood in model averaging (Bartón 2013). As our data consisted of several measurements from the same individuals at different ages, individual identity (nested within the study site, as each male was observed only at a single study site) was included as a random effect in all models (van de Pol and Verhulst 2006).

First, the general effects of age (years) and life span (years) on the expressions of morphological traits (body mass, lyre length, blue chroma, eye comb size) and behavioral attributes (lek attendance, fighting rate, territory distance from the lek center) were quantified. Tarsus length was also analyzed as an invariant trait since it should not

change after males' first year of life. The fixed effects of male age and life span as well as their interaction were introduced to the model to determine whether the effect of age on trait expression differs across males with different life spans. Potential senescence (Jones et al. 2008; Nussey et al. 2013) was accounted for by including quadratic age as a fixed effect. The interaction between quadratic age and life span was also introduced as a fixed effect to investigate possible life-history differences between individuals. A binary fixed-effect "terminal event" (1 = last observation, 0 = not the last observation) and its interaction with age and quadratic age were also included to account for potential terminal investment, as this can affect the evidence of senescence (Rattiste 2004; Hammers et al. 2012). Finally, the year of hatching was used as a fixed effect to account for potential cohort effects (i.e., the long-term effect of natal environmental conditions on individual performance; e.g., Millon et al. 2011). Although male fighting rate and territory distance from the lek center can be related to lek size, we did not include lek size as a fixed effect in any of the models due to issues with model convergence. To directly compare the rate of age-specific change across different morphological and behavioral traits, the same analyses were carried out using dimensionless rates of change (estimated as the difference in trait

values at subsequent ages divided by the trait value at the youngest age) as dependent variables.

Significant quadratic age effect may provide limited evidence of senescence, since it might solely result from a steep increase in trait expression in early life (Bouwhuis et al. 2009). Therefore, the maximum trait values were identified for each individual, and the previous analysis was implemented again without quadratic age effects using these pruned post-peak trait data sets, where a significant negative relationship between age and trait expression would provide evidence of senescence.

Finally, to investigate how male black grouse express morphological and behavioral traits in relation to the timing of their reproductive effort, a peak-centering approach was applied by rescaling age according to male peak lekking effort (hereafter, peak-centered age). This novel method was modified from a recent model aimed at separating within- and between-individual effects of age on individual performance (see van de Pol and Wright 2009, eq. [2]). Peak-centered age was calculated by subtracting the age at which a male's lek attendance was highest (relative to other males on the same lek in the same year) and was subsequently used as a fixed effect. Individual age at peak lekking effort (hereafter, age at peak) and the quadratic term of peak-centered age were introduced as fixed effects to express selective (dis)appearance of lekking males and to account for potential nonlinear age effects, respectively. These models applied to each trait were then slightly modified by replacing the peak-centered age by the original age (see van de Pol and Wright 2009, eq. [3]). In these modified models, the effect of age at peak expressed the difference between selective (dis)appearance and individual scheduling in trait expression, thereby enabling the estimation of the relative importance of these two processes (van de Pol and Wright 2009). Peak-centered age was calculated only for males that had ≥75% lek attendance in their peak-lekking-effort year, to exclude males that were not territorial on the studied leks. As lek attendance was used to scale the peak-centered age, the peak-centering analysis was not conducted on lek attendance.

Data used in the statistical analyses are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad .rg8d4 (Kervinen et al. 2014). All analyses were performed with R software (ver. 2.15.2; R Development Core Team 2012). Model selection followed the information theoretic Akaike information criterion (AIC) approach (Burnham and Anderson 2002). Due to model uncertainty, model averaging was used to combine the effects of the best candidate models within a corrected AIC difference (ΔAICc) of ≤7 (Burnham et al. 2011; Grueber et al. 2011) with the R package age MuMIn (ver. 1.9.13; Bartón 2013). Variable significance could then be compared by the averaged coefficient estimates (and SEs) and the relative importance of each variable

(the sum of Akaike weights of the models in which the variable appeared). As *P* values for linear mixed-effects models are not provided in the R package lme4 (Bates et al. 2013), the effect sizes (Pearson's *r*) with 95% confidence intervals were calculated for all fixed effects to enable comparison of the biological importance of the effects (Nakagawa and Cuthill 2007). Effect sizes described using Pearson's *r* values can be interpreted as small, medium, and large when ≥0.1, ≥0.3, and ≥0.5, respectively (Cohen 1988).

## Results

### Age-Dependent Expression of Male Traits

For all traits, several candidate models had ΔAICc of ≤7, and multimodel inference was required (table S2). Overall, age contributed substantially to all models, with body mass, lyre length, blue chroma, and eye comb size increasing with male age but in a nonlinear fashion, as indicated by the significant quadratic age effects (table 1, pts. a–d; fig. 1*a*–1*d*).

The high relative importance and the positive interactions between age and life span and between quadratic age and life span on body mass, lyre length, and to some extent eye comb size indicated that long-lived males (i.e., life span of ≥4 years) had lower age-dependent trait expressions and delayed maximum trait values (table 1, pts. a–d; fig. 1*a*–1*d*). Moreover, life span had a major contribution to the best candidate models, as it had high relative importance for all morphological traits (range: 0.74–1.00).

Terminal investment explained a substantial amount of the variation in body mass and lyre length, as indicated by the positive interactions between age and terminal event on body mass and between quadratic age and terminal event on lyre length, as well as their high relative importance (table 1, pts. a, b). These interactions were primarily due to a greater increase in traits from age 1 to 2 years in males that died at 2 years old (fig. 2*a*, 2*b*). There was no evidence of terminal investment for blue chroma and eye comb size (table 1, pts. c, d). As expected and in contrast to all other morphological traits, tarsus length was unrelated to male age, life span, and their interactions (table 1, pt. e; fig. 1*e*).

Consistent with the morphological traits, age was the key determinant of the expressions of all behavioral traits (table 1, pts. f–h). Specifically, lek attendance and fighting rate increased significantly with age, males defended their territories closer to the lek center as they got older (fig. 1*f*–1*h*), and there was a negative quadratic effect of age on lek attendance. Long-lived males had lower age-specific lekking effort and delayed peak lekking effort, as indicated by the substantial amount of variation in lek attendance and fighting rate explained by the interaction between age
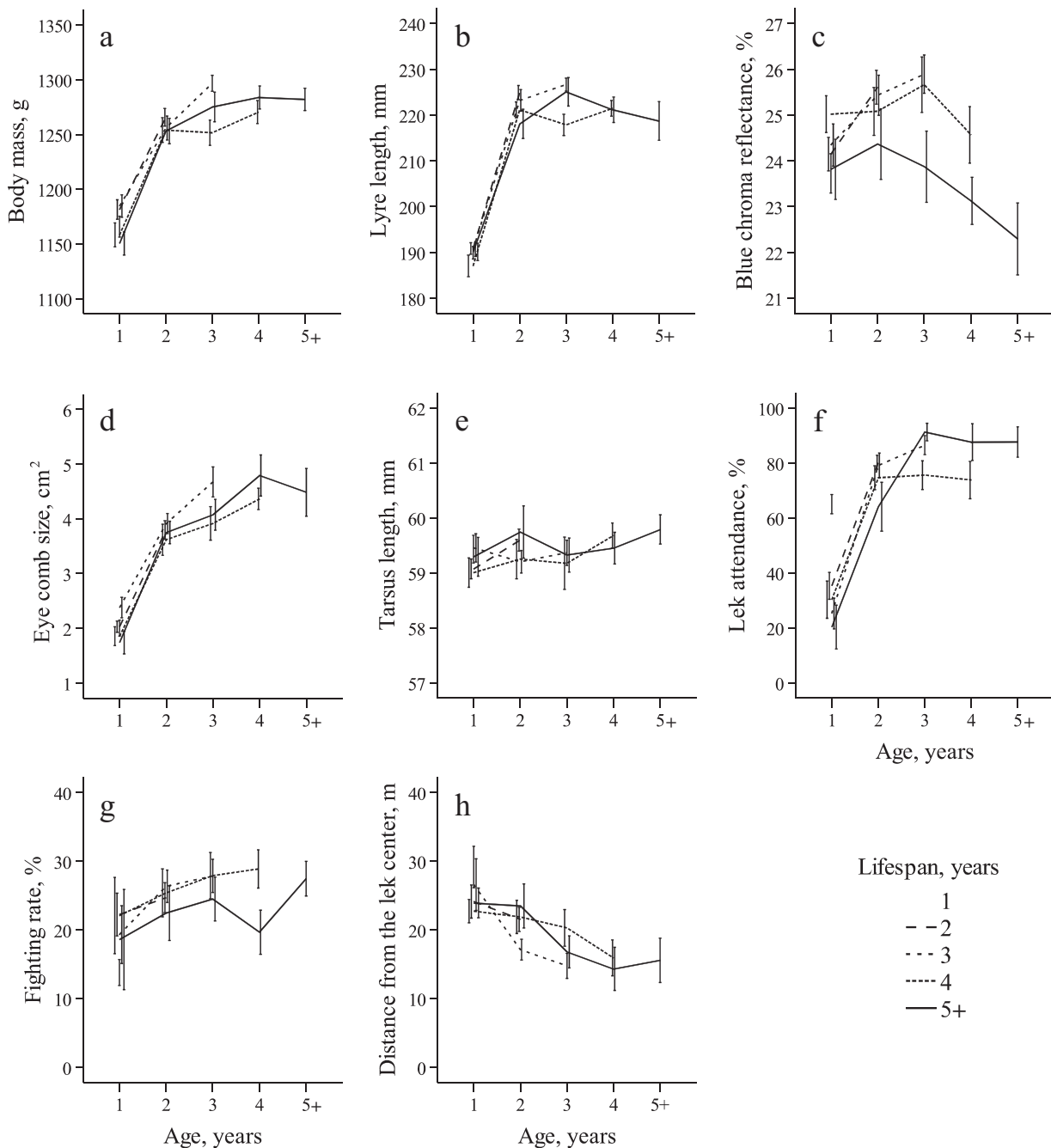
**Figure 1:** Cross-sectional patterns of the observed age-specific expressions (mean ± SE) of morphological traits (*a–e*) and behavioral attributes (*f–h*) for male black grouse of known age and life span (1–6 years; 5 and 6 years old are pooled into age class 5). Lines connecting the observed values have been added to aid visualization.

and life span and between quadratic age and life span (fig. 1*f*, 1*g*). Positive interactions between quadratic age and terminal event on lyre length, lek attendance, and fighting rate and between age and terminal event on body mass indicated higher trait expression on the last observation, especially in short-lived males (see also fig. 3*a*, 3*b*, 3*e*, 3*f*). In addition, there was a positive main effect of terminal event on lek attendance and a negative effect on fighting rate.

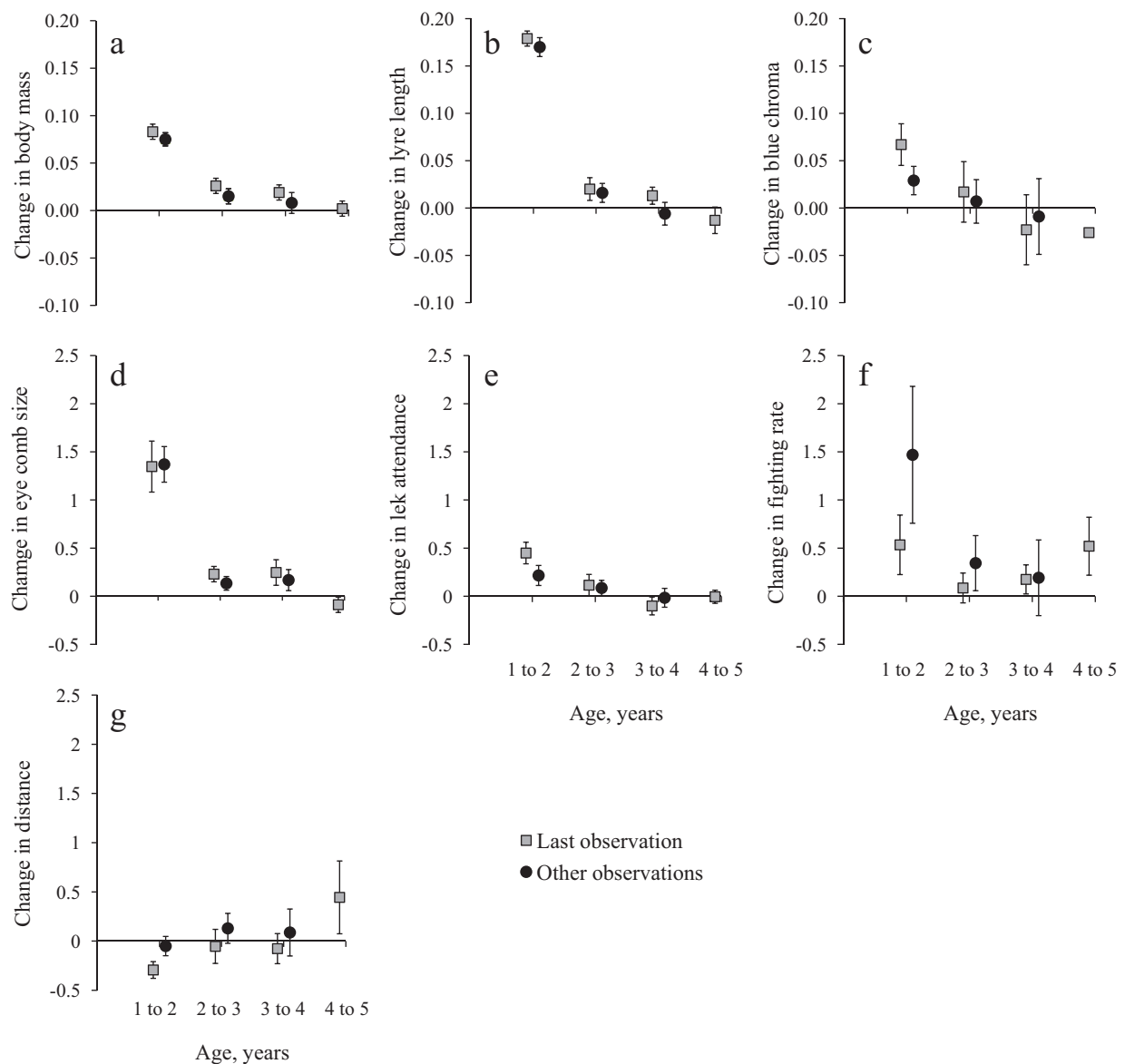The analysis of dimensionless rates of change in trait

**Figure 2:** Relative rate of change in trait expressions between subsequent years. The change was most rapid between ages 1 and 2 years, but there were no major differences in the magnitude of change between different traits.

values revealed that there was no overall major difference in the effects of male age and life span on the expressions of males' morphological and behavioral traits (tables S3, S4; fig. 2). More specifically, the rates of change were most rapid between ages 1 and 2 years for all traits, after which the change was slow. Eye comb size had the greatest relative age-specific change (fig. 2d).

### Senescence

Across all traits, there was a strong negative age effect following the maximum trait expression (tables S5, S6; fig.

3), with very little variation in their relative importance (range: 0.98–1.00; table S6). Overall, the effect sizes of morphological and behavioral traits were similar. Male life span explained substantially less variation in trait values than in the previous analysis; the effects of the interactions between age and life span were limited overall, and the relative importance of life span ranged from 0.31 (eye comb size) to 1.00 (lek attendance). Age-dependent decrease in trait expression was further shaped by terminal investment; specifically, the interactions between age and terminal event indicated that the increase in body mass,
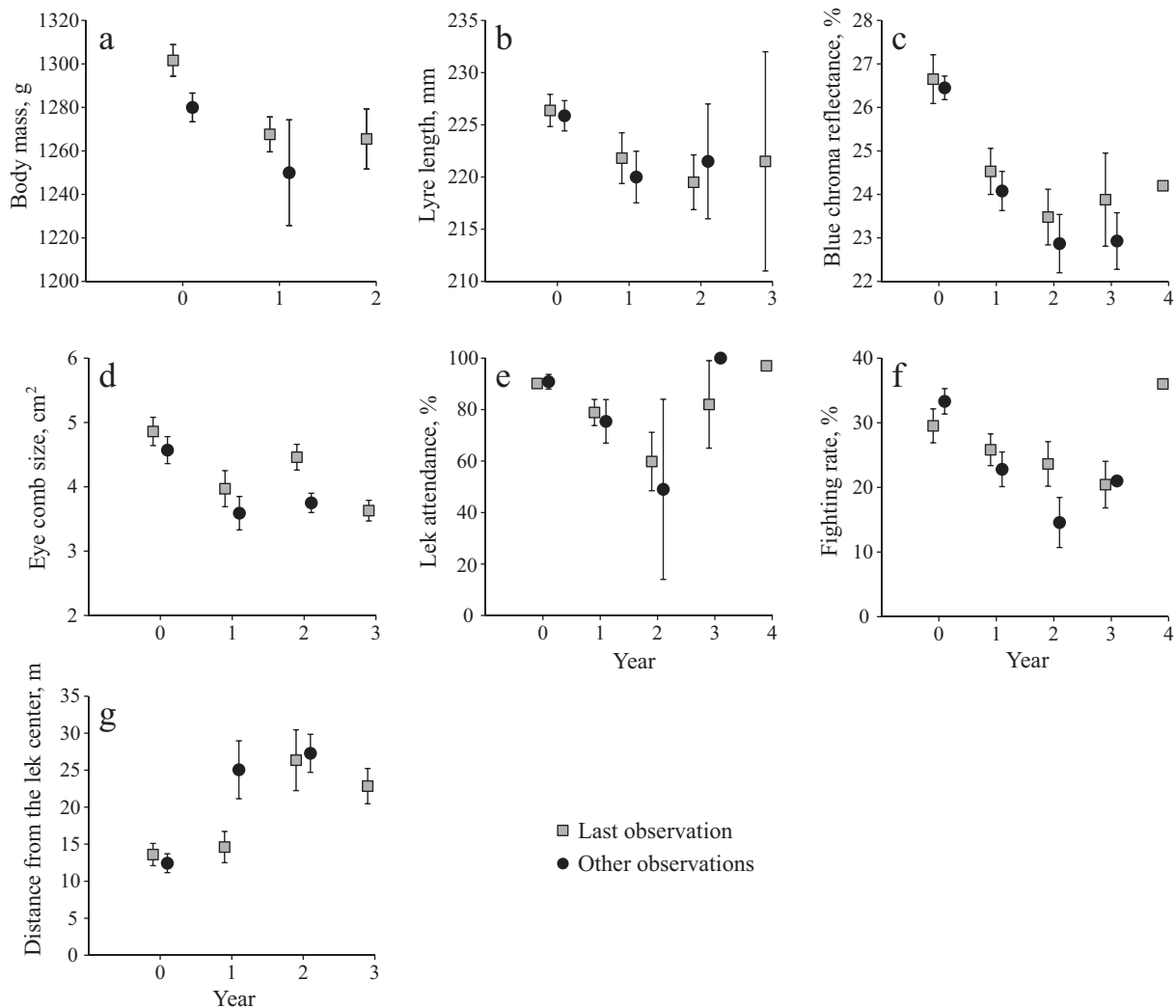
**Figure 3:** Trait expressions (mean ± SE) after the individual trait maxima. Year 0 represents the observation of the maximum trait expression of the given trait of a given individual. Gray squares represent observations of terminal events, and black circles represent observations from other years.

lek attendance, and fighting rate and the decrease in territory distance from the lek center in the last observation were greatest in males that died young (table S6, pts. a, e–g; fig. 3a, 3e–3g). Across all ages, body mass increased during the males' last breeding season.

### Trait Expression in Relation to Peak Lekking Effort

There was substantial variation in the age at peak lekking effort among male black grouse (median: 2 years; range: 1–5). Body mass, lyre length, and eye comb size increased toward the year of individual peak lekking effort and was higher in males that had their peak lekking effort at older

age (table 2, pts. a, b, d; fig. 4a, 4b, 4d). In addition, the negative quadratic effect of peak-centered age on lyre length had high relative importance, suggesting that males had shorter lyres after the year of peak lekking effort. Blue chroma and tarsus length were unrelated to peak-centered age or age at peak (table 2, pts. c, e; fig. 4c, 4e).

Males fought more and defended their territories closer to the lek center with increasing peak-centered age but fought less and defended territories further from the lek center after the year of peak lekking effort, as indicated by the quadratic peak-centered age effects (table 2, pts. f, g; fig. 4f, 4g). Overall, fighting rate was higher and distance from the lek center was lower in males that had their peak effort at older ages.

**Table 2:** Expressions of morphological (pts. a–e) and behavioral (pts. f, g) traits in relation to individual scheduling of male reproductive effort

| Model | Parameter | Estimate | SE | Effect size, r (95% CI) |
|---|---|---|---|---|
| a. Body mass, $n = 124$ | Intercept | 1,179.42 | 10.72 | ... |
|   id : site variance = 1,090.98 | **Peak-centered age** | **40.95** | **2.67** | **.67 (.60, .73)** |
|   residual variance = 2,146.47 | Peak-centered age$^2$ | −2.43 | 1.31 | −.10 (−.22, .01) |
| | **Age at peak** | **28.64** | **4.12** | **.38 (.27, .47)** |
| | **Age at peak vs. peak-centered age** | **−12.31** | **3.95** | **−.18 (−.29, −.06)** |
| b. Lyre length, $n = 123$ | Intercept | 191.30 | 2.33 | ... |
|   id : site variance = 6.44 | **Peak-centered age** | **10.84** | **.91** | **.66 (.57, .72)** |
|   residual variance = 192.35 | **Peak-centered age$^2$** | **−.88** | **.37** | **−.17 (−.30, −.03)** |
| | **Age at peak** | **9.87** | **.92** | **.62 (.52, .69)** |
| | Age at peak vs. peak-centered age | −.97 | 1.05 | −.07 (−.21, .08) |
| c. Blue chroma, $n = 121$ | Intercept | 25.15 | .48 | ... |
|   id : site variance = 1.58 | Peak-centered age | −.00 | .13 | −.00 (−.13, .12) |
|   residual variance = 2.82 | Peak-centered age$^2$ | .02 | .06 | .02 (−.10, .15) |
| | Age at peak | −.15 | .18 | −.05 (−.18, .08) |
| | Age at peak vs. peak-centered age | −.15 | .17 | −.05 (−.18, .07) |
| d. Eye comb size, $n = 123$ | Intercept | 1.93 | .20 | ... |
|   id : site variance = .18 | **Peak-centered age** | **.89** | **.06** | **.72 (.64, .77)** |
|   residual variance = 1.10 | Peak-centered age$^2$ | −.01 | .03 | −.03 (−.17, .10) |
| | **Age at peak** | **.72** | **.08** | **.54 (.44, .63)** |
| | **Age at peak vs. peak-centered age** | **−.17** | **.07** | **−.16 (−.29, −.03)** |
| e. Tarsus length, $n = 124$ | Intercept | 59.28 | .25 | ... |
|   id : site variance = .64 | Peak-centered age | .10 | .06 | .09 (−.02, .20) |
|   residual variance = 1.13 | Peak-centered age$^2$ | −.01 | .03 | −.02 (−.13, .10) |
| | Age at peak | .04 | .10 | .02 (−.09, .14) |
| | Age at peak vs. peak-centered age | −.06 | .09 | −.04 (−.15, .08) |
| f. Fighting rate, $n = 124$ | Intercept | −1.46 | .15 | ... |
|   id : site variance = .36 | Peak-centered age | .06 | .03 | .14 (−.01, .27) |
|   residual variance = 1.00 | **Peak-centered age$^2$** | **−.09** | **.02** | **−.41 (−.51, −.28)** |
| | **Age at peak** | **.14** | **.06** | **.18 (.04, .31)** |
| | Age at peak vs. peak-centered age | .08 | .06 | .19 (−.05, .24) |
| g. Distance,[a] $n = 124$ | Intercept | 4.81 | .25 | ... |
|   id : site variance = .52 | **Peak-centered age** | **−.33** | **.09** | **−.25 (−.37, −.12)** |
|   residual variance = 1.01 | **Peak-centered age$^2$** | **.10** | **.04** | **.18 (.04, .30)** |
| | **Age at peak** | **−.34** | **.09** | **−.24 (−.37, −.11)** |
| | Age at peak vs. peak-centered age | −.01 | .11 | −.01 (−.14, .13) |

Note: Statistically significant effects (95% confidence interval [CI] does not overlap with 0) are in boldface type. Age at peak versus peak-centered age difference expresses the relative importance of these effects (see "Material and Methods"). Nonsignificant quadratic terms of peak-centered age were excluded from the final models, and values of the excluded variables refer to the step before their exclusion. Individual identity nested within study site (id : site) was fitted as a random effect in all models. Parameter values of blue chroma were rescaled by multiplying the original values by 100 to obtain more informative coefficient estimates and SEs. Random effects are presented as id : site and residual variances in the final model.

[a] Territory distance from the lek center (square root transformed).

## Discussion

Our study shows that the overall variation in trait expression on which sexual selection is acting results from very different allocation strategies that can be revealed only by using comprehensive longitudinal data. Indeed, we found that two strategies of trait expression co-occur in this black grouse population, with short-lived males generally having higher age-specific morphological and behavioral trait expression than long-lived males. Trait expression dynamics were also partly explained by terminal investment, suggesting fine tuning of male investment in trait expression according to their perceived current and future condition. Even with terminal investment, there were clear consistent declines in trait values following the age of maximum expression, indi-
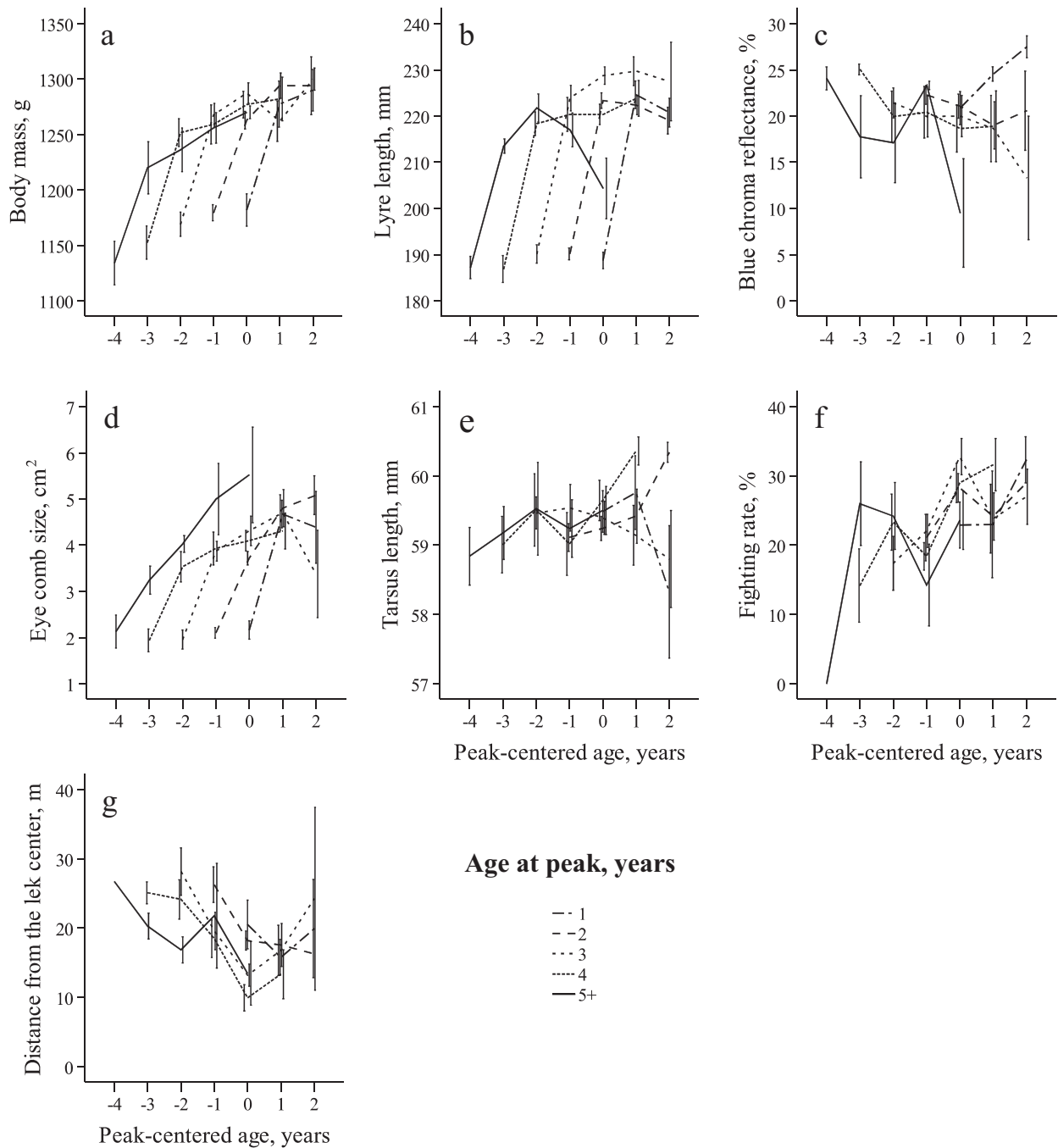
**Figure 4:** Cross-sectional patterns of the observed expressions (mean $\pm$ SE) of morphological (*a–e*) and behavioral (*f, g*) traits in relation to year of male peak lekking effort for male black grouse with known age at peak (1–6 years; 5 and 6 years old are pooled into age class 5). Peak-centered age of 0 is the year when a male's lek attendance was highest during its life span. Lines connecting the observed values have been added to aid visualization.

cating that senescence occurred in both morphological and behavioral traits. Furthermore, a novel peak-centering analysis indicated that the individual timing of lekking effort is a major driver of the age- and life span–related patterns in trait expression in male black grouse. Accounting for such effects is fundamental to better understanding sexual selection and the maintenance of genetic variation if the fitness payoffs of the two alternative

allocation strategies differ and if such strategies are partly genetically determined.

### Effects of Age on Trait Expression

Consistent with the expectation that the expression of morphological and behavioral traits is constrained in young individuals (Curio 1983), we found that the greatest change in trait values occurred from yearlings to 2-year-old males. During the first 6 months of their life, male black grouse grow rapidly, increasing their body mass approximately 50-fold. Therefore, yearling males may need to allocate most of their limited resources to the growth of vital traits, leaving limited resources for the expression of their ornaments. Such a pattern has been reported in species with conspicuous secondary sexual traits (Nussey et al. 2009; Evans et al. 2011) and might play a role in mate choice through discrimination against young but active males that have not undergone viability selection (Manning 1985; Alatalo et al. 1991). These age-dependent patterns differed from male tarsus length, which reached its final length during the first year of life. Therefore, the age-dependent expression of other morphological traits and behaviors were not artifacts arising from increased overall body size with age.

All male behavioral traits were also age dependent, with the greatest change in the expression of these traits occurring during the transition from yearlings to 2-year-old males. Lekking is energetically costly (Vehrencamp et al. 1989; Siitari et al. 2007; Lebigre et al. 2013), and heavy individuals are more capable of handling these costs (McElligott et al. 2002; Hämäläinen et al. 2012; Lebigre et al. 2013). Thus, yearling male black grouse, being on average some 100 g (~10%) lighter than older males, may not be able to sustain as high a lek attendance as older males (Kervinen et al. 2012). Males defended their territories closer to the lek center as they aged, supporting the hypothesis that territory centrality is an honest cue of male quality and viability in lekking species (e.g., Höglund and Lundberg 1987; Kokko et al. 1998, 1999).

There was no major difference in rates of change in trait expression between different traits, and only the change in the size of red eye combs was substantially more age dependent than that of all the other traits. It is well established that eye combs and other fleshy structures, such as wattles, are testosterone dependent in birds (black grouse: Rintamäki et al. 2000; Siitari et al. 2007; see also Zuk et al. 1995; Mougeot et al. 2004). Therefore, such a substantially greater rate of increase in male eye combs might be explained by the very large increase in male gonads and testosterone levels with age, especially from yearlings to 2-year-old males (Rintamäki 2000).

### Life-History Differences in Trait Expression

There were major differences in life histories among male black grouse, as the magnitude of the change in morphological and behavioral traits was strongly related to the interaction between age and life span, indicating that long-lived males had consistently lower trait values at ages 1 to 3 years than males with a shorter life span. Therefore, two strategies of trait expression co-occur in this population, and major survival costs on the timing of expression might occur. This is a commonly predicted (Stearns 1992) but less frequently empirically shown life-history pattern (see, e.g., Candolin 2000), suggesting that high trait expression at an early stage of life has survival costs (Kotiaho 2001). Specifically, long-lived males were lighter, had shorter lyres, and had lower lek attendance as yearlings than short-lived males. Although these results should be interpreted cautiously, given the unknown fate of many yearling males (Kervinen et al. 2012), they are consistent with previous studies investigating the age dependence of life-history traits (Bouwhuis et al. 2010) and secondary sexual traits (Balbontín et al. 2011). Moreover, a number of studies have shown that elevated reproductive rate is associated with reduced life span and, in some cases, accelerated aging (Kotiaho 2001; Hunt et al 2004). These results are even more remarkable because random mortality due to predation may reduce the power to detect the relationship between trait expression and life span. However, mortality in male black grouse is highest during the initial weeks following the lekking season, when their body condition is at its lowest (Lebigre et al. 2013). Therefore, predation may drive the effect of life span on male trait expression if individuals' predation risks are related to their lek performance and their ability to sustain the costs of the lek display.

It is unclear whether such differences in reproductive scheduling are genetically and/or environmentally driven. Our analysis found cohort effects in male body mass and blue chroma coloration but not in other traits. Therefore, the natal environment had little effect on ornament expression in black grouse, although it can have long-lasting effects on individual life histories and the variation in trait expression (Lindström 1999; Metcalfe and Monaghan 2001). However, further analyses are needed to disentangle the causes as well as the consequences of life-history differences in trait expression.

### Terminal Investment and Senescence

Male reproductive strategies driven by sexual selection may lead to reduced life span because of the costs associated with the expression of sexually selected morphological and behavioral traits (Bonduriansky et al. 2008). Such a reduction in life span is expected to reduce the magnitude of natural

selection acting on late-acting genes and, hence, increase the rate of aging in males (Carranza and Pérez-Barbería 2007; Preston et al. 2011). However, the relationship between senescence and sexual selection may not be found in species where sexually selected traits are condition dependent, because sexual selection may favor individuals that are better able to sustain the costs of reproduction early in life and reach maximum trait values later in life (Clutton-Brock 1988; Bonduriansky et al. 2008). As a result, senescence in secondary sexual traits and behavior is less frequently recorded in nature than senescence in life-history traits (e.g., Hoikkala et al. 2008; Nussey et al. 2009; Lecomte et al. 2010; Balbontín et al. 2011). In black grouse, all morphological and behavioral traits reached a maximum expression and subsequently declined with age; therefore, senescence does occur in black grouse.

Declines in traits did not continue linearly, as body mass, lek attendance, and fighting rate increased and territory distance from the lek center decreased during males' last lekking season. As reproductive effort is expected to increase when residual reproductive value decreases, this increased reproductive effort prior to disappearance suggests terminal investment (Williams 1966; Clutton-Brock 1984; Sadd et al. 1996; Velando et al. 2006). Effect sizes for the interaction between age and terminal event were stronger for behavioral traits, suggesting that male black grouse were able to increase their reproductive effort but could not resist the physical decline as they aged (Williams 1957; Hamilton 1966; Kokko 1997). This might be because the size and quality of structural ornaments are strongly related to male physiological condition during molt, which occurs shortly after the lekking season. Behavioral traits are in this sense more flexible; males can adjust their lekking behavior according to their condition just prior to the mating season. Therefore, the costs of lekking are more likely to be seen in terms of reduced overwinter survival and reduced ornament expression the following spring than in male lekking effort.

### Trait Expression in Relation to Peak Lekking Effort

Our last analysis, where the data were reanalyzed with peak-centered age, indicated strong congruence between maximum trait expression and peak lekking effort. Males expressed higher trait values with increasing peak-centered age, but the year of peak lekking effort tended to occur in the last year the male was alive, especially in short-lived males. This suggests that although males may be able to modulate their reproductive effort according to their current condition (see above), lekking might induce substantial fitness costs in terms of reduced survival with stronger fitness costs in short-lived males, which in turn suggest

that long-lived males are of high genetic quality, as they not only have proven their viability but are also more likely to survive to the next autumn and to the next breeding season (Alatalo et al. 1991). Therefore, the costs of reproductive effort (i.e., lekking) may underpin not only the expressions of ornaments (e.g., tail plume in Jackson's widowbirds [*Euplectes jacksoni*]; Andersson 1994) but ultimately the temporal scheduling of reproductive effort, that is, life-history strategies.

### Conclusions

Overall, this study shows that the expressions of morphological and behavioral traits in black grouse are strongly age dependent but that these effects are not consistent across all sexually selected traits. Furthermore, there are major differences in trait expression trajectories between short- and long-lived males. There was also evidence of both senescence (in all traits) and terminal investment (particularly in behavioral traits). These complex interactions could explain the substantial variation observed in the sexually selected traits in male black grouse as well as in many other species with weaker sexual selection. This study shows that accurate quantification of the magnitude of sexual selection acting on male morphological and/or behavioral traits in this and other species requires accounting for the simultaneous effects of individual age, life span, and fine-tuned investment in reproduction.

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