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Title: Simultaneous age-dependent and age-independent sexual selection in the lekking black grouse (*Lyrurus tetrix*)

Year: 2016

Version:

Please cite the original version:

Kervinen, M., Lebigre, C., & Soulsbury, C. D. (2016). Simultaneous age-dependent and age-independent sexual selection in the lekking black grouse (*Lyrurus tetrix*). *Journal of Animal Ecology*, 85(3), 715-725. <https://doi.org/10.1111/1365-2656.12496>

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Simultaneous age-dependent and age-independent sexual selection in the lekking black grouse (*Lyrurus tetrix*)

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Summary

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

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

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

4. Therefore, sexual selection in black grouse operates primarily on male behaviour and morphological traits may act as additional cues to supplement female choice. These results demonstrate the multifaceted influence of age on both fitness and sexual traits and highlight the importance of accounting for such effects when quantifying sexual selection.

Key-words: annual reproductive success, fitness, lek, long-term data, mating success, selection differential, selection gradient, senescence, *Tetrao tetrix*

Introduction

Sexual selection underpins the evolution of extravagant male ornaments either through female preference for

higher expression of these traits (e.g. colourful feathers) or through the competitive advantage they offer during male–male competition (e.g. male weaponry, Andersson 1994). Therefore, direct relationships between male traits and mating success are generally interpreted as evidence for sexual selection on male traits. However, mating success in a particular year of a male's life may not accurately reflect the association between the trait and fitness, as individual mating success typically increases in early

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life and decreases at later ages (Jones *et al.* 2008; Nussey *et al.* 2013).

Age-dependent mating and reproductive success are typically explained by the inability to simultaneously maximize competing life-history traits (e.g. growth, reproductive investment, survival), due to the limited amount of resources available to the organisms (Stearns 1992). Such trade-offs are responsible for the constraints on reproductive effort in early ages, when resources are allocated to growth, leading to shorter (reproductive) life span (Curio 1983; Forslund & Pärt 1995; Descamps *et al.* 2006; Reed *et al.* 2008). Therefore, individuals might delay the onset of breeding until their condition allows them to display intensively and compete for mates and thus reduce the fitness costs associated with an earlier onset of breeding (Curio 1983; Beauchamp & Kacelnik 1990; Forslund & Pärt 1995). Apparent age-dependent reproductive success may also arise due to selection acting against individuals in poor condition leading to an increase in the proportion of 'high-quality' individuals within a cohort (selective appearance of good reproducers/selective disappearance of bad reproducers; van de Pol & Verhulst 2006), or due to the negative effects of ageing on individuals' physiological condition, which leads to a reduction in reproductive success, that is senescence (Stearns 1992; Williams *et al.* 2006; Bouwhuis *et al.* 2010; Nussey *et al.* 2013). All these mechanisms can explain the association between male age and their ability to mate and hence produce offspring. Thus, to better understand the overall variation in individuals' fitness, we need to measure the temporal dynamics in reproductive success resulting from life-history trade-offs.

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

Studies quantifying sexual selection on male traits while also accounting for age are still relatively scarce (Coltman *et al.* 2002; Kruuk *et al.* 2002; Freeman-Gallant *et al.* 2010), with the majority examining single traits (however see Freeman-Gallant *et al.* 2010). One reason for the paucity of such studies is that accurate measures of male mating success are difficult to collect in natural populations, because copulations can be difficult to observe and animals move in and out from the study area (Coltman *et al.* 1999; Kruuk *et al.* 2002). Molecular markers can be used to deduce female mating behaviour and male mating suc-

cess, but the accuracy of such methods will strongly depend on our ability to quantify accurately male reproductive success, to identify multiple matings, and whether post-copulatory sexual selection is occurring (Eberhard 1996; Birkhead 1998; Birkhead & Møller 1998). Therefore, accurate measures of the magnitude of sexual selection acting on male traits in the wild can only be done using study systems in which male mating success can reliably be measured and related to the expression of the multiple traits across their entire life span (Clutton-Brock & Sheldon 2010).

In the lekking black grouse (*Lyrurus tetrix*, formerly *Tetrao tetrix*), male mating success can easily be recorded as copulations are very conspicuous and most copulations take place on leks (Lebigre *et al.* 2007). Females usually mate only once with one male, and the parentage analyses demonstrated a very high concordance between observed mating success and genetic reproductive success (we sampled 34 broods of females observed mating on lek, 32 broods were sired by the male observed mounting the female; Lebigre *et al.* 2007). Males are very faithful to the leks where they initially established their territories and rarely switch lek sites (Rintamäki *et al.* 1995; Höglund *et al.* 1999; Lebigre *et al.* 2008). Hence, we can monitor the mating success of the same individuals over their whole life span, as all males holding central territories and >90% of all territorial males were ringed. Male mating skew is substantial due to the intense male–male competition and clear female choice (Alatalo, Höglund & Lundberg 1991; Alatalo *et al.* 1992). In theory, males with no mating success could gain indirect fitness benefits by increasing the mating opportunities of their close relatives, but such kin selected benefits amount only to *ca.* 3% of a copulation in this study system (Lebigre *et al.* 2014). Male black grouse express multiple morphological and behavioural traits that are related to their mating success (these traits are partially correlated; see Table S1, Supporting information). Lyre length and quality (Höglund *et al.* 1994; Rintamäki *et al.* 2001), the size of testosterone-dependent red eye combs (Rintamäki *et al.* 2000), body mass (Rintamäki *et al.* 2001; Lebigre, Alatalo & Siitari 2013) and blue chroma coloration of breast feathers (Siitari *et al.* 2007) are all positively correlated with male mating success. Moreover, females prefer mating with males that have high lek attendance (Alatalo *et al.* 1992), fight frequently and successfully against other males (Hämäläinen *et al.* 2012), and occupy central territories on leks (Hovi *et al.* 1994).

As, a substantial amount of the variation in all these traits is explained by male age (Kervinen *et al.* 2015; unconditional R^2 range in this study: 0.18–0.78). The aim of this study was to use longitudinal data describing both male mating success and the expression of these traits to quantify the multivariate age-specific sexual selection gradients.

We first tested the hypothesis that the variation in male mating success is age-dependent by quantifying the effects of age, age of first lek attendance (AFL), life span and terminal investment on males' annual mating success

(AMS). This enabled us to separate the effects of within-individual improvement and senescence on AMS from selective appearance and disappearance of certain phenotypes in the population. We then quantified the effect of each morphological and behavioural trait on male AMS using univariate sexual selection differentials and multivariate sexual selection gradients and accounted for other age-related effects (due to other traits not included in the models and/or unmeasured traits) by entering male age as a covariate. We tested whether these sexual selection gradients were age-specific by including an interaction term between male age and trait expression. Finally, we requantified the univariate sexual selection differentials and multivariate sexual selection gradients without male age as a covariate to determine whether accounting for age effects (and hence the expression of other age-related traits not directly used as covariates in the models) changes the strength of sexual selection acting on the measured traits.

Materials and methods

STUDY POPULATION AND FIELD METHODS

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

Data on morphological traits were collected from the study sites annually in January–March by catching birds from the winter flocks with oat-baited walk-in traps (for methods, see Kervinen *et al.* 2012; Lebigre *et al.* 2012). Each captured individual was aged as yearling or older according to plumage characteristics and individually ringed for future identification with an aluminium tarsus ring with a unique serial number and three coloured tarsus rings. All captured birds were blood sampled (for a parallel study) and measured for body mass, lyre (*i.e.* tail) length, eye comb size and blue chroma coloration of breast feathers (Siitari *et al.* 2007; Lebigre *et al.* 2012).

Male mating success and lekking behaviour were recorded on the study sites (leks) annually during the peak mating season (the period in late April–early May when virtually all copulations take place, Ludwig *et al.* 2006). During this period, typically lasting 1–2 weeks depending on the weather conditions, leks were monitored daily from *ca.* 3:00 to 8:00 a.m. by observers located in hides near the lek arenas (for detailed methods, see Kervinen *et al.* 2012; Lebigre *et al.* 2012). Male behaviour was scan sampled at regular intervals and categorized as rookooing, hissing (the two main vocal displays), fighting or inactive (methods and behaviours are described in detail in Höglund, Johansson & Pelabon 1997). Lek attendance (proportional to the most commonly present male on the same lek), the relative proportion of each behaviour and males' territory distances from the lek centre (hereafter 'territory centrality'; see Hovi *et al.* 1994) were calcu-

lated for all ringed males (see Rintamäki *et al.* 1995; Alatalo *et al.* 1996). Finally, we documented the occurrence of copulations, which are easy to observe, as males flap their wings conspicuously when mounting females, their location and the individuals involved.

DATA VALIDATION

In these analyses, we only included the males that were first caught as yearlings and could therefore be precisely aged. The data consisted of records of AMS, lekking behaviour (lek attendance, fighting rate, territory centrality) and morphological traits (body mass, lyre length, blue chroma, eye comb size) for 164 male black grouse with known year of hatching (2001–2008), known AFL (at age 1: $N = 89$, at age 2: $N = 66$, at age 3: $N = 9$) and known life span of 1–6 years (412 records in total); no males with detailed life history survived >6 years old. Due to male philopatry for their initial lekking site (Rintamäki *et al.* 1995; Höglund *et al.* 1999; Lebigre *et al.* 2008), life span was defined as the age at which the male was last time seen on the lek. Complete cohorts (*i.e.* no ringed males of the cohort alive in spring 2014) were available for males hatched in 2001–2008. Cohorts hatched 2009 onwards were excluded because of large proportions (>10%) of individuals being still alive in spring 2014.

STATISTICAL ANALYSES

All analyses were run in R 3.0.3 (R Development Core Team 2014). We used generalized linear mixed-effects models (GLMM) to test the effects of age, AFL, life span and terminal investment on AMS following the procedure detailed in van de Pol & Verhulst (2006). We used varIdent variance error structure from Poisson distribution ('*gls*' function from the R package 'nlme'; Pinheiro *et al.* 2015) to account for the overdispersion in the data. Age and age² represented the linear and quadratic within-individual change in AMS with age. Conversely, a significant positive effect of AFL on AMS can be interpreted as evidence for selective appearance of good reproducers. A significant negative effect of life span (*i.e.* age at last lek) on AMS, in turn, can be interpreted as evidence for selective disappearance of poor reproducers. The interactions of AFL and life span with age were also introduced as fixed effects to account for potential life-history differences (*e.g.* reproduction at early ages and short life span vs. long life span and reproduction at older ages). A binary fixed effect 'terminal event' (TE, indicates whether it was the male's last year alive or not) and its interaction with age was included to account for potential terminal investment in reproduction, as this can affect the magnitude of senescence (Rattiste 2004; Hammers *et al.* 2012). Individual identity nested within study site was fitted as a random effect in all models to account for multiple measures from the same individuals and locations.

Model selection was carried out for the pre-selected set of biologically relevant candidate models following the AIC-IT procedure (Table 1), and models within 95% cumulative model weight (*ca.* $\Delta AIC_c < 6$) were averaged (Burnham, Anderson & Huyvaert 2011; Grueber *et al.* 2011). Then, the relative importance and model-averaged coefficient estimates with unconditional SE and unconditional 95% CI were calculated for each parameter in the averaged models (R package 'AICCMODAVG' v. 2.0-1, Mazerolle 2014). As random slopes cannot be fitted in *gls* models, we repeated the same analysis using '*lme*' function from the R pack-

age 'NLME' with individual identity nested within study site fitted as the random intercept and its interaction with age fitted as the random slope to reduce the risk of potential type I and type II errors (Schielzeth & Forstmeier 2009). However, as including random slopes did not significantly change the interpretation of the results (Tables S2–S5) and as the *gls* models better accounted for the overdispersion in the data (based on the model residuals), we present the results of the initial *gls* approach.

Measures of senescence that do not account for within-individual age effects (random slopes) may mask within-individual patterns of ageing and mix together individuals with differing life-history strategies (Bouwhuis *et al.* 2009). As including random slopes did not significantly alter the interpretation of our results, we could ignore variation in within-individual patterns of ageing. Thus, we carried out a Poisson GLMM on AMS data after the age at which AMS showed its statistical peak with age and AFL fitted as linear effects only and individual identity nested within study site fitted as a random effect. In this additional analysis, a significant negative effect of age can be considered as evidence of senescence (Bouwhuis *et al.* 2009).

To quantify age-specific sexual selection, we first standardized male AMS by dividing each male's AMS by the annual mean AMS of all males on the same lek; the total number of copulations on the lek varied between sites and years (mean \pm SD = 30.84 \pm 20.18, $N = 49$), but it was not correlated with individual AMS (Spearman's $r = 0.05$, $P = 0.323$, $N = 412$). We then standardized (i.e. zero-centred: mean = 0, SD = 1) each morphological and behavioural trait using the yearly population mean as the reference and related each standardized trait and their quadratic terms to male standardized AMS using age and

age² as covariates to obtain linear and nonlinear sexual selection differentials (s_i and s_j). In addition, the models included the interaction of male age and trait expression to determine whether the magnitude and direction of sexual selection on a specific trait changes with age. When the interaction term or s_j was non-significant, s_i was quantified in the absence of these terms. Univariate selection differentials measure both direct selection acting on each trait and indirect selection resulting from selection acting on other traits with which the focal trait is correlated. Therefore, we also carried out multivariate selection analyses where multiple correlated (see Table S1) traits and their quadratic terms were used simultaneously to quantify linear (β) and nonlinear (γ) sexual selection gradients. In the multivariate analysis, the parameter estimate for each trait accounts for the selection acting on the other correlated traits, and hence allows direct comparison of the relative contribution of each trait to the variance in male mating success. The interactions of male age and trait expressions were included in the model, and when the interaction term or γ was non-significant, β was quantified in the absence of these terms. Due to our relatively limited sample size and the large number of parameters (two parameters for age, seven parameters for directional selection, seven parameters for nonlinear selection, seven interaction terms and the random effect term), the multivariate analysis was conducted separately for male morphological and behavioural traits (these traits are partly independent; Rintamäki *et al.* 2001; Lebigre *et al.* 2012; Kervinen *et al.* 2015). Therefore, using age as a covariate in the models relating, for instance, male mating success to the expression of the morphological ornaments enables us to account partially for the expression of the age-related behavioural traits and other potentially unmeasured traits.

Table 1. A suite of pre-selected biologically relevant candidate models predicting the effects of age, age², age of first lek attendance (AFL), life span (LS) and terminal event (TE; binary, indicates if it was the male's last year alive or not) on annual mating success in male black grouse, with the number of estimated parameters for each model (k), Log-likelihood and AIC_c values, model weights (w_i), cumulative model weights and evidence ratios (ER). Individual identity nested within study site was fitted as a random factor in all the models. Candidate models within 95% cumulative model weight were averaged (see Table 2)

| Rank | Model | k | LogLik | AIC _c | Δ AIC _c | w_i | Cum. w_i | ER |
|------|--|-----|---------|------------------|---------------------------|-------|---------------|--------------------|
| 1 | Age + Age ² + AFL | 11 | -858.52 | 1739.71 | 0.00 | 0.27 | 0.27 | |
| 2 | Age + LS + TE + AFL + Age*LS + Age*TE | 14 | -855.56 | 1740.19 | 0.48 | 0.21 | 0.48 | 1.27 |
| 3 | Age + Age ² + AFL + Age*AFL | 12 | -858.03 | 1740.85 | 1.14 | 0.15 | 0.63 | 1.77 |
| 4 | Age + Age ² + AFL + LS + TE + Age*LS + Age*TE | 15 | -855.28 | 1741.77 | 2.06 | 0.10 | 0.72 | 2.81 |
| 5 | Age + AFL + LS + TE + Age*AFL + Age*LS + Age*TE | 15 | -855.34 | 1741.90 | 2.20 | 0.09 | 0.81 | 3.00 |
| 6 | Age + Age ² + AFL + LS + TE | 13 | -858.01 | 1742.94 | 3.23 | 0.05 | 0.87 | 5.03 |
| 7 | Age + Age ² + AFL + LS + TE + Age*AFL + Age*LS + Age*TE | 16 | -855.08 | 1743.53 | 3.83 | 0.04 | 0.91 | 6.77 |
| 8 | Age + Age ² + AFL + LS + TE + Age*AFL | 14 | -857.54 | 1744.15 | 4.44 | 0.03 | 0.93 | 9.21 |
| 9 | Age + Age ² | 10 | -862.01 | 1744.56 | 4.86 | 0.02 | 0.96 | 11.34 |
| 10 | Age + Age ² + TE + Age*TE | 12 | -860.60 | 1745.98 | 6.27 | 0.01 | 0.97 | 23.05 |
| 11 | Age + Age ² + TE | 11 | -861.98 | 1746.61 | 6.91 | 0.01 | 0.98 | 31.63 |
| 12 | Age + LS + TE + Age*LS + Age*TE | 13 | -860.30 | 1747.52 | 7.82 | 0.01 | 0.98 | 49.82 |
| 13 | Age + AFL | 10 | -863.69 | 1747.93 | 8.22 | 0.00 | 0.99 | 60.99 |
| 14 | Age + AFL + Age*AFL | 11 | -862.82 | 1748.30 | 8.60 | 0.00 | 0.99 | 73.65 |
| 15 | Age + Age ² + LS + TE | 12 | -861.81 | 1748.41 | 8.70 | 0.00 | 1.00 | 77.52 |
| 16 | Age + Age ² + LS + TE + Age*LS + Age*TE | 14 | -860.00 | 1749.05 | 9.35 | 0.00 | 1.00 | 107.08 |
| 17 | Age + AFL + LS + TE | 12 | -863.38 | 1751.55 | 11.85 | 0.00 | 1.00 | 373.39 |
| 18 | Age + AFL + LS + TE + Age*AFL | 13 | -862.54 | 1752.00 | 12.29 | 0.00 | 1.00 | 467.29 |
| 19 | Age | 9 | -866.88 | 1752.20 | 12.50 | 0.00 | 1.00 | 517.40 |
| 20 | Age + TE | 10 | -866.80 | 1754.15 | 14.44 | 0.00 | 1.00 | 1366.80 |
| 21 | Age + TE + Age*TE | 11 | -866.73 | 1756.13 | 16.42 | 0.00 | 1.00 | 3685.64 |
| 22 | Age + LS + TE | 11 | -866.74 | 1756.13 | 16.43 | 0.00 | 1.00 | 3687.43 |
| 23 | Null | 8 | -880.90 | 1778.15 | 38.45 | 0.00 | 1.00 | 2.23 $\times 10^8$ |

Coefficients of the quadratic terms (s_j and γ) were doubled to measure balancing and disruptive selections respectively (Stinchcombe *et al.* 2008). Finally, for comparison and to estimate the age (in)dependency of sexual selection acting on male traits, we quantified s_i , s_j , β and γ as described above but without accounting for individual age.

Results

AGE EFFECTS ON MATING SUCCESS

There was substantial variation in lifetime mating success (LMS) as 52% (85/164) of the males did not mate, while the top 12 males accounted for 50% of all observed copulations ($N = 480$; maximum LMS = 32, Fig. 1). Most males reproduced only in a single year (68%; 54/79), and of these, 74% (40/54) died after this reproductive event. Of those 25 males that reproduced in multiple years, 16 males survived after the year of their maximum AMS and 20 males received >50% of their LMS in a single year (Fig. S1).

Nine of the pre-selected candidate models of AMS were within 95% cumulative model weight which led to multi-model inference (Table 1). Age was included in all and AFL in all but one of the averaged models, and thus, they had the highest relative importance (Table 2). Moreover, age and AFL were the only variables for which the 95% CI of the averaged coefficient estimate did not overlap 0. AMS increased with age until the statistical maximum at

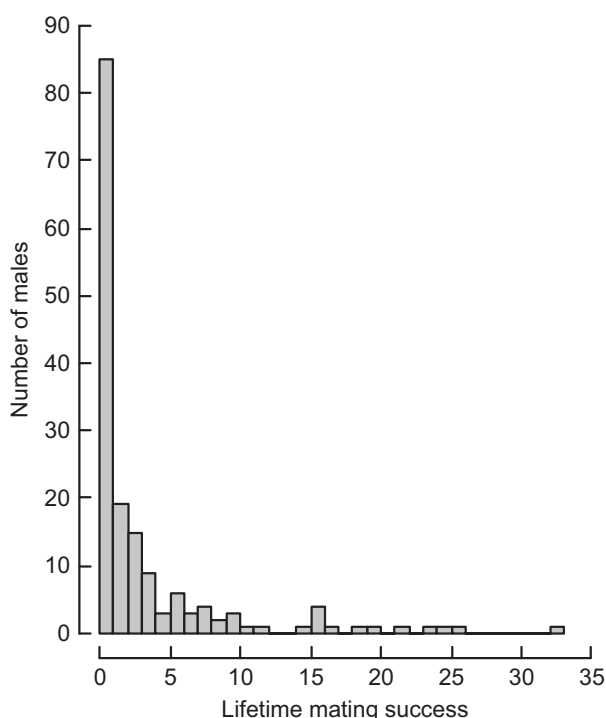


Fig. 1. The distribution of lifetime mating success (LMS) in male black grouse ($N = 164$). Mating skew was substantial: most males never mated at all, whereas the top 12 males accounted for roughly the half (238/480) of all copulations.

age of 3.7 years after which it levelled off but did not decrease significantly towards the end of life (GLMM: -0.709 ± 0.878 , $t = -0.807$, $P = 0.423$; Fig. 2a). In addition to these direct age effects, males' AFL was important; males lekking at age 1 tended to have higher AMS at age 2 than males that began lekking at age 2, and males that began lekking at age 1 or 2 tended to have higher AMS at age 3 than males that began lekking at age 3 (Fig. 2b). Among males known to be territorial in our study leks, these differences were absent at older ages and all strategies led to similar LMS (mean \pm SE: 2.71 ± 0.60 , 3.20 ± 0.69 and 3.11 ± 1.62 for males with AFL = 1 ($N = 89$), AFL = 2 ($N = 66$) and AFL = 3 ($N = 9$), respectively; ANOVA: $F_{1,162} = 0.242$, $P = 0.623$, $N = 164$). Life span was not correlated with AMS, and there was no clear evidence of terminal investment in reproduction (Table 2). Lastly, there was a significant positive relationship between AFL and life span ($r_s = 0.40$, $N = 164$, $P < 0.001$), indicating that males starting to lek older had longer life spans.

SEXUAL SELECTION ON MALE TRAITS

Sexual selection operated on all behavioural traits but not on all morphological traits when accounting for males' age. The significant interactions of lek attendance and lyre length with age indicated that the magnitude of sexual selection operating on these traits increased with age (Table 3a, Fig. 3a,b). Males' AMS increased nonlinearly (s_j) with lek attendance and territory centrality (Fig. 4a,b) and linearly (s_i) with fighting rate (Table 3a). Conversely, males' AMS increased linearly with body mass but for other morphological traits s_i and s_j were non-significant. When accounting for age and the expression of other morphological or behavioural traits (multivariate sexual selection gradients), we found a significant interaction of age with body mass on AMS, indicating stronger sexual selection on body mass in older males (Table 3a; Fig. 3c). Moreover, males' AMS increased nonlinearly (γ) with lek attendance and linearly (β) with body mass (Table 3a).

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

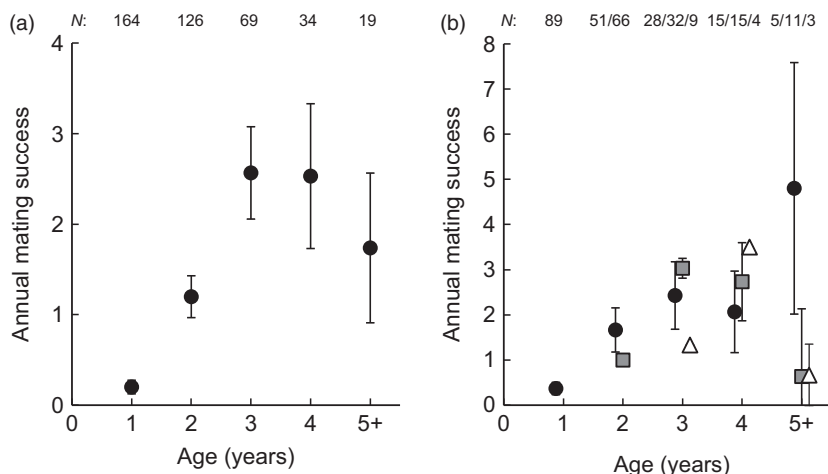


Fig. 2. Variation in mean annual mating success (AMS, mean \pm SE) with age for (a) all males ($N = 164$) and (b) separately for males that started lekking at age 1 (black circles, $N = 89$), at age 2 (grey squares, $N = 66$) or at age 3 (white triangles, $N = 9$). N denotes the age-specific sample sizes.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

Table 2. The relative importance and averaged coefficient estimates with unconditional standard errors and 95% unconditional confidence intervals of age, age², age of first lek attendance (AFL), life span (LS) and terminal event (TE; binary, indicates if it was the male's last year alive or not) and their relevant interactions on annual mating success in male black grouse

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

Discussion

AGE EFFECTS ON MATING SUCCESS

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

black grouse. Therefore, either these two processes are disconnected and females discriminate against old and very active males in a similar way as they discriminate against very active yearling males (Siitari *et al.* 2007; Kervinen *et al.* 2012) or, the previously documented terminal investment in reproductive effort (Kervinen *et al.* 2015) dampens a potential decline in mating success in male black grouse. The alternative to an increase in reproductive effort is a decline in fitness, that is senescence. However, we did not detect significant reproductive senescence in male black grouse in contrast to previous long-term studies (e.g. Bouwhuis *et al.* 2009; reviewed in Nussey *et al.* 2013). This is because most males that had any mating success reproduced only once and tended to die directly soon after reproducing. This means that their highest AMS was in their last year of life. Such high mortality possibly stems from the high energetic or physiological costs of reproductive effort (Lebigre, Alatalo & Siitari 2013). However, not all males had their highest AMS in their last year of life, but for those males that bred more than once, most copulations still occurred in a single year and there were sharp declines in AMS after this. Hence, across the population, terminal effects went in both directions depending on the number of reproductive episodes (death or strong decline in mating success after males' peak mating success), contributing to a lack of either ter-

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

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

^aTerritory centrality was analysed as the male's territory's distance from the lek centre.

minimal investment or reproductive senescence being detected.

Male life span had low relative importance and its averaged coefficient estimate was positive, but non-significant, indicating that short- and long-lived males did not differ in their age-specific AMS. Previously, we found significant positive effects of life span on male morphological and behavioural traits (Kervinen *et al.* 2015). Our results suggest that the trajectories of expression of male traits are partially independent from male mating success and that the outcome of sexual selection cannot be directly linked to the expression of each trait separately. This is perhaps not unexpected as age-specific trajectories typically vary across multiple traits (e.g. Hayward *et al.* 2015), meaning that phenotypic, reproductive and survival traits may be decoupled (Evans, Gustafsson & Sheldon 2011; Bouwhuis *et al.* 2012). However, relatively little is known about age-specific trade-offs between sexually selected traits and reproductive traits (Cornwallis, Dean & Pizzari 2014). The fact that there are differences in trait trajectories strongly suggests that no single process underlies these patterns, but there is critical need to quantify the physiological basis for such potential trade-offs (Cornwallis, Dean & Pizzari 2014).

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

SEXUAL SELECTION ON MALE TRAITS

Given that both male mating success (this study) and the expression of a multitude of male morphological and behavioural traits (Kervinen *et al.* 2015) depend on age, our aim was to quantify whether accounting for such age effects (and hence indirectly for the effect of age-related traits not used in the selection gradients) affected our estimates of sexual selection operating on the morphological and behavioural traits. We found that sexual selection operated strongly on most morphological and behavioural traits when not accounting for male age but these effects strongly declined when accounting for age. A similar effect has been found in common terns (*Sterna hirundo*) in

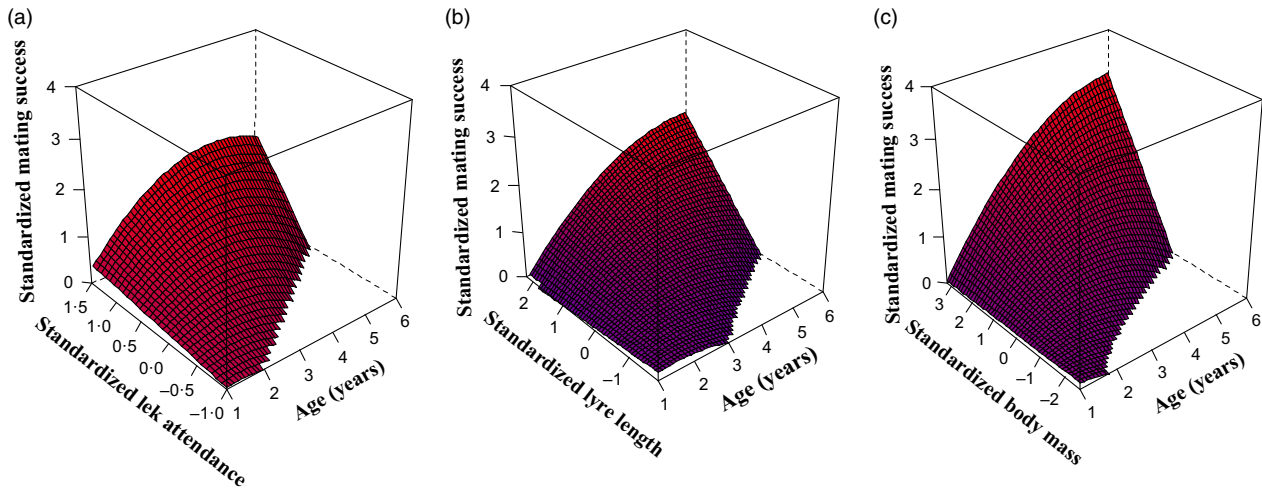


Fig. 3. The interactions of age with (a) lek attendance, (b) lyre length and (c) body mass on annual mating success (AMS), indicating that the strength of sexual selection on these traits increased with age. All parameters were standardized to account for the variation lek size and the total number of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

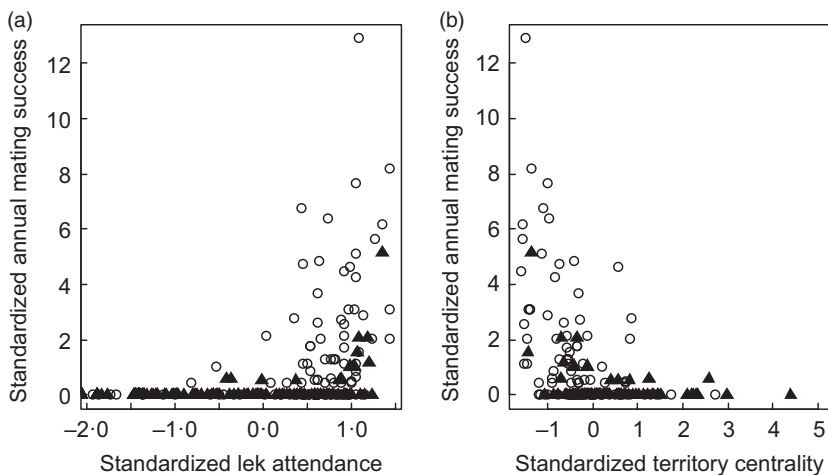


Fig. 4. Annual mating success (AMS) of yearling (filled triangles) and older (ages 2–6 years; open circles) male black grouse in relation to (a) lek attendance and (b) territory centrality (analysed as the male's territory distance from the lek centre). Significant s_j and γ values on these traits suggested thresholds after which AMS sharply increases. All parameters were standardized to account for the variation lek size and the total number of copulations on the lek (see Materials and methods).

which accounting for age decreased the magnitude of viability selection associated with individuals' trait expression (Zhang *et al.* 2015). Univariate sexual selection differentials indicated sexual selection acting more generally on male lekking behaviour than on male morphological traits when accounting for males' age. This might primarily be due to age-specific sexual selection acting on body mass, lyre length and lek attendance. Indeed, young males have low mating success regardless of their body mass, lyre length, as they lack lekking experience and central territories. In contrast, in prime age males and very old males that have the experience, high body mass is selected for as it enables successful lekking performance (Lebigre, Alatalo & Siitari 2013). To our knowledge, only two studies have quantified age-specific sexual selection gradients; one showed that sexual selection in horn length of big horn sheep increased with age (Coltman *et al.* 2002), and the other reported strong selection for antler size in red deer during peak reproductive age (Kruuk *et al.* 2002). In gen-

eral, such age effects are not due to age *per se* but are most likely due to the expression of other age-related traits that are not accounted for when quantifying the selection gradient.

Multiple sexual signals can convey different messages about male quality over a range of time periods (Doucet & Montgomerie 2003) leading to variation in female choice or mate choice errors which may dampen or even mask sexual selection (Chaine & Lyon 2008). This is very likely to apply to black grouse males' morphological traits as lyre length and blue chroma reflect male condition during moult which occurs shortly after the previous mating season (Siitari *et al.* 2007) while body mass and eye comb size are more plastic and reflect shorter term male condition (Pérez-Rodríguez & Viñuela 2008; Hämäläinen *et al.* 2012; Lebigre, Alatalo & Siitari 2013). The stronger sexual selection differentials found on male behaviour (such as lek attendance, fighting rate and territory centrality) might be explained by their extreme variation and strong

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

We found evidence of nonlinear sexual selection gradients (γ) for several traits which are commonly interpreted as evidence of balancing (negative γ) or disruptive (positive γ) selection (Stinchcombe *et al.* 2008; Hunt *et al.* 2009). However, the significant positive γ and s_j values found in this study more likely suggest 'threshold' values for male lek attendance and territory centrality as male mating success sharply increases when males have a lek attendance ≥ 0.8 , and defend territories within *ca.* 20 m from the lek centre. Other species show similar nonlinear 'threshold' relationships between mating success and both physical (e.g. bighorn rams *Ovis canadensis* and horn length: Coltman *et al.* 2002) and behavioural traits (e.g. topi bulls *Damaliscus korrigum* and territory centrality: Bro-Jørgensen & Durant 2003). In black grouse, territory centrality and lek attendance are strongly related and the threshold values found in this study may reflect the difference between the dominant males displaying very actively on central territories and the other, less successful males that hold territories further away from the lek centre. It is important to note that the relationship between lek attendance and mating success is not due to missed mating opportunities of the males attending less to the lek, because copulations take place on the leks when all territorial males are present (Kokko *et al.* 1999; Lebigre *et al.* 2007).

CONCLUSIONS

This study shows that the overall variation in male black grouse mating success is strongly related to male age with

substantial nonlinear increase over individuals' life span without a significant decrease at the end of life. Age of first lek attendance was negatively related to age-specific mating success, but unrelated to males' LMS. Young AFL was also associated with shorter life span, indicating that different male life-history strategies coexist in this population. Sexual selection seemed to operate on both morphological and behavioural traits when male age was not used to measure the sexual selection gradients. However, when accounting for the effect of other age-related traits, males' mating success was directly related only to behavioural traits, but was related to male body mass, lyre length and lek attendance in an age-specific manner (i.e. selection acted on these traits in old males only). Hence, sexual selection in this species primarily operates on male behaviour and morphological traits are used as additional cues to supplement female choice. This study shows that the complex dynamics of the expression of males' sexual traits with age needs to be accounted for and failing to do so might lead to an overestimation of the magnitude of sexual selection acting on these traits and of their potential microevolutionary changes.

Acknowledgements

We are grateful to the Associate Editor and the anonymous reviewers for their very helpful comments and suggestions on the previous drafts of this manuscript. We are grateful to Professor Rauno V. Alatalo for establishing the black grouse project and to Dr Heli Siitari for continuing the project after Rauno's retirement and passing. This study was funded by the Center of Excellence in Evolutionary Research in University of Jyväskylä (project no. 7211271 to R.V.A.), the Academy of Finland (project no. 7119165 to H.S.) and the Emil Aaltonen Foundation (personal grant to M.K.). Birds were captured under the permissions of the Central Finland Environmental Centre (permissions KSU-2003-L-25/254 and KSU-2002-L-4/254).

Data accessibility

Data associated with this manuscript are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2jj6q> (Kervinen, Lebigre & Soulsbury 2016).

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Received 20 November 2014; accepted 11 December 2015
 Handling Editor: Simon Verhulst

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Spearman's rank correlation coefficients for morphological and behavioural traits of male black grouse quantified for (a) all males, (b) yearling males and (c) older males (age ≥ 2 years).

Table S2. A suite of pre-selected biologically relevant alternative lme candidate models for comparison with Table 1 (in the main document).

Table S3. The relative importance and averaged coefficient estimates with unconditional standard errors and 95% unconditional confidential intervals of Age, Age², age of first lek attendance (AFL), lifespan (LS) and terminal event (TE; binary, indicates if it was the male's last year alive or not) and their relevant interactions on annual mating success in male black grouse in the model averaged lme models shown in Table S2.

Table S4. A suite of pre-selected biologically relevant lme candidate models for comparison with Table 1 in the main document.

Table S5. The relative importance and averaged coefficient estimates with unconditional standard errors and 95% unconditional confidential intervals of Age, Age², age of first lek attendance (AFL), lifespan (LS) and terminal event (TE; binary, indicates if it was the male's last year alive or not) and their relevant interactions on annual mating success in male black grouse in the model averaged lme models shown in Table S4.

Fig. S1. Proportion of the AMS of individual LMS in males that had at least one copulation in 2 or more years ($N = 25$).