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Fitness in Male Black Grouse
(*Tetrao tetrix*)

Effects of Life Histories and Sexual Selection on Male Lifetime Mating Success

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ABSTRACT

Fitness, which describes individuals' overall genetic contribution to the next generation(s), is a central concept in evolutionary ecology, as it results from individuals' ability to survive and reproduce and hence reflects individuals' life histories and the selection acting on them. As individual age is typically related to both male mating success and sexual traits determining mating success, it is crucial to use longitudinal individual-level data to account for age effects when quantifying the relationship between male traits and mating success to avoid overestimation of the role of sexual selection. We used such data describing male morphological traits, behavioural traits and mating success in the lekking black grouse (*Tetrao tetrix*) to quantify the relative contribution of life histories and sexual selection to the overall variation in male fitness. As predicted, the opportunity for sexual selection was high as male annual and lifetime mating success were highly skewed. Male annual mating success and the expression of male morphological and behavioural traits increased with age until declined towards the end of life. We found evidence of terminal investment in reproduction, indicating high viability costs of lekking especially in short-lived males, suggesting that long-lived males were high overall genetic quality, as they had proven their viability. Sexual selection acted directly mainly on male behaviours and indirectly on male morphological traits, suggesting that behaviours act as better cues to females of male overall genetic quality and that females use morphological traits as age cues, thereby promoting the maintenance of multiple ornaments in this species. Such indirect selection on male morphological traits associated with strong condition-dependence of both morphological and behavioural traits makes it unlikely that the consistent selection on these traits through female choice will lead to the depletion of the additive genetic variance in these traits and male fitness, meaning that females likely gain indirect fitness benefits through their preference for dominant males.

Keywords: Age effects; lek; long-term data; ornaments; senescence.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original articles, which will be referred to in the text by their Roman numerals I–IV. I am the first author in articles I–III and was primarily in charge of organising and analysing the data and writing the first versions of the manuscripts. My contribution to IV included literature search, data organisation and commenting and editing the later manuscript versions, while C.D.S. analysed the data and wrote the first draft. C.D.S. and C.L. contributed significantly to the analyses in I–III. Authors in each article jointly developed the original idea, collected the data and commented/wrote the manuscript drafts in every stage, except R.V.A. who did not contribute to the writing due to his serious illness.

I   Kervinen, M., Alatalo, R.V., Lebigre, C., Siitari, H. & Soulsbury, C.D. 2012. Determinants of yearling male lekking effort and mating success in black grouse (*Tetrao tetrix*). *Behavioral Ecology* 23: 1209–1217.

II   Kervinen, M., Lebigre, C., Alatalo, R.V., Siitari, H. & Soulsbury, C.D. Life history differences in age-dependent expression of multiple ornaments and behaviors in a lekking bird. Submitted manuscript.

III Kervinen, M., Lebigre, C. & Soulsbury, C.D. Age-dependent sexual selection in male black grouse (*Tetrao tetrix*). Manuscript.

IV   Soulsbury, C.D., Kervinen, M. & Lebigre, C. Sexual size dimorphism and the opportunity for sexual selection in birds and mammals. Submitted manuscript.

1 INTRODUCTION

1.1 Fitness

1.1.1 The many definitions of fitness

> *"Fitness: something everyone understands but no one can define precisely."*
> – S. C. Stearns (1976)

Defining and quantifying fitness has been – and will presumably always be – challenging (Stearns 1976, 1989, Metz et al. 1992, Benton & Grant 2000, Brommer 2000). Broadly speaking, the concept of fitness describes individuals' overall genetic contribution to the next generation(s), but there are multiple ways to quantify fitness, ranging from the use of proxies of individuals' short term reproductive success to the notion of invasibility of particular phenotypes (Metz et al. 1992, Brommer 2000). Such diversity in the definition of fitness in the literature highlights the complexity of fitness, and it is unlikely that there is a universal way to quantify fitness in all possible situations – or at least fitness would then be impossible to measure in practice (Benton & Grant 2000). Instead, fitness is context-dependent, and it is crucial to clearly define it each time it is used (Metz 1992, Stearns 1992).

1.1.2 How to measure fitness?

Fitness can be measured as absolute (e.g. number of mating events or offspring produced) or relative fitness (e.g. reproductive success in relation to other individuals of the same sex in the population; Hunt & Hodgson 2010). Because evolution is defined as the change in allele/phenotype frequencies in the population through time, selection (the key force that drives evolution) operates on relative fitness. Thus, it is not the absolute fitness *per se* that matters, but how well an individual performs in relation to other individuals in the population. Typically absolute and relative measures of fitness are positively correlated, but this relationship can be non-linear (Orr 2007). Thus, conclusions drawn from

comparisons of absolute fitness measures between individuals or populations should be carried out with caution, as they might not necessarily reflect the actual selection operating on the population.

The measures used to quantify fitness in evolutionary ecology range from simple short-term fitness proxies to inclusive fitness that also captures the effect of each individual's action on the fitness of their close relatives (Table 1). Some of the measures are rate-sensitive, such as the individual rate of increase (λ_{ind}, McGraw & Caswell 1996), meaning more weight is given to the offspring produced early in an individual's life as these offspring will have opportunities to reproduce while their parents are still able to reproduce themselves, thus efficiently capturing the importance of the onset of reproduction (Brommer et al. 2002). In contrast, other measures are rate-insensitive, such as lifetime reproductive success (LRS, e.g. Clutton-Brock 1988, Newton 1989), where fitness is independent from the timing of reproduction. All fitness measures have their own advantages and disadvantages: e.g. short-term fitness proxies are typically easy to measure, but they may not always be strongly correlated with individual LRS. Furthermore, some individuals may have high annual reproductive success (ARS) but short lifespan, meaning that their LRS may be substantially smaller than that of individuals producing few offspring in each breeding season but having longer lifespan (Stearns 1992, Hunt & Hodgson 2010). Therefore, interpreting a measure of only one short-term fitness proxy or fitness component (see below) as a surrogate of overall fitness can be too short-sighted (Brommer et al. 2002), and ideally empirical information on the entire life history of all individuals (or an unbiased sample) of the population using genetic markers to quantify individuals' real reproductive success is needed to reliably measure fitness (Clutton-Brock 1988, Shuster & Wade 2003, Shuster 2009). However, in practice it is often impossible to measure fitness in the optimal way, simply because data available are inadequate. In these cases it is of course reasonable to use practical measures, and discuss their limitations, instead of not measuring fitness at all. After all, knowledge is built piece by piece.

1.1.3 Why is fitness central to evolutionary ecology?

Fitness is at the core of all central phenomena of evolutionary ecology. Selection, as a major evolutionary force, describes the effects of individuals' phenotypic traits on their fitness. When traits are heritable, selection will lead to evolutionary changes that partly underpin short- and long-term temporal changes in populations' phenotypic characteristics (Darwin 1859, Andersson 1994). As selection acts to maximise individual fitness, variance in fitness determines the maximum opportunity for selection (I_{ss}) on any trait related to fitness (Crow 1958, Arnold & Wade 1984a, Shuster & Wade 2003). Age-specific variances and covariances in fitness thus define the components that contribute to this opportunity, and hence reflect the potential influence of population age structure on evolutionary dynamics (Lebigre et al. 2013). Therefore, fitness provides a quantitative way to measure the strength of selection, which is crucial e.g. to estimate the rates of evolutionary changes in the population.

TABLE 1 A list of the fitness measures commonly used in evolutionary ecology.

Measure	Definition	Assumption	References
Short-term fitness proxies			
Morphological traits	Measurement of traits reflecting individual reproductive success (RS).	Traits are related to individual total fitness.	1–2
Measures of age	Number of breeding seasons during which an individual was alive (and might have reproduced).	ARS is age-dependent, so individuals' ARS can be described using individuals' age.	3–4
Fitness components			
Annual mating success (AMS)	Total number of mating events of an individual within a breeding season.	Males: AMS is closely related to ARS. Females: successful insemination requires multiple mating.	5–6
Annual reproductive success (ARS)	Number of offspring produced within a breeding season.	As LRS is the sum of individuals' ARS, variation in ARS partly captures the variation in LRS.	7–8
De-lifing (P_{ti})	Changes in the annual population growth rate if an individual would not have been present.	Similar to ARS.	9–10
Lifespan	The period between birth and death of an individual.	If age at first breeding is similar for all individuals, lifespan equals individual reproductive lifespan which is related to LRS.	11–12
Lifetime fitness			
Lifetime reproductive success (LRS)	Total number of offspring produced over an individual's lifespan.	LRS reflects an individual's total genetic contribution to the next generation.	13–14
Lifetime de-lifing	Sum of the changes in the annual population growth rate if an individual would not have been present.	Similar to LRS.	9, 15
Lambda individual (λ_{ind})	Dominant eigenvalue of an individual projection matrix ("individual growth rate").	Similar to LRS.	16–17
Inclusive fitness			
	Sum of an individual's direct fitness and the weighed fitness consequences of his/her action on other individuals (fitness costs and benefits).	—	18–19

1) Boratynski & Koteja 2010, 2) Forsyth et al. 2005, 3) McComb et al. 2011, 4) Baker & Thompson 2007, 5) McElligott et al. 2001, 6) Bro-Jørgensen & Durant 2003, 7) Schulte-Hostedde et al. 2002, 8) Pörschmann et al. 2010, 9) Coulson et al. 2006, 10) Di Fonzo et al. 2011, 11) Weladji et al. 2006, 12) Silk et al. 2010, 13) Clutton-Brock 1988, 14) Newton 1989, 15) Foerster et al. 2007, 16) McGraw & Caswell 1996, 17) Brommer et al. 2002, 18) Hamilton 1964, 19) Sharp & Clutton-Brock 2011.

Individual fitness arises from several interdependent components; it is not only how many mates an individual manages to attract (mating success), or how many offspring it reproduces (reproductive success) that matters, but also how many reproductive events it has during its life (survival/lifespan). Furthermore, these fitness components are usually related to individual phenotypic traits (Andersson 1994), and the degree to which phenotypic traits covary with individuals' reproductive or mating success quantifies the magnitude of natural and sexual selection acting on these traits, respectively. Conversely, if there is no correlation between fitness and phenotypic traits, the overall variation in fitness across all population members measures the rate of genetic drift, which determines the potential for inbreeding and genetic divergence (Nunney 1993). These in turn are crucial to formation of kin groups, where some individuals produce more offspring than others (Waples 1998, Reid and Keller 2010), although kin selection (or kin competition) can also arise from sexual or natural selection under male philopatry (Petrie et al. 1999), as a male with a certain phenotypic trait attracts more females and produces more offspring which will interact with one another. In sum, understanding fitness therefore forms the basis of understanding life histories and sexual selection which are key to understand evolution, the basis of all biology (Stearns 1992).

1.2 Life histories

Each organism has its specific schedule of reproduction and survival known as a life history, which optimally leads to maximal lifetime reproductive output, the primary goal of any organism (Roff 1992, Stearns 1992). Traits that shape an organism's growth, reproduction, and survival are called life history traits, and include for instance growth patterns, age and size at maturity, number, size and sex ratio of offspring, age- and sex-specific reproductive investments, age- and sex-specific survival rates, and lifespan. Life histories vary substantially between taxa and even within a single species. In particular, male and female life histories typically differ, and it is common that within a sex, high lifetime reproductive success can be obtained by two or more different life history strategies (Oliveira et al. 2008). Individual age is a major factor driving the variation in life history traits and thus accounting for age effects is crucial when quantifying individual fitness.

Individuals living in natural populations have limited resources (e.g. time, energy) to be allocated to different functions. A central tenet to life history theory is that with these limited resources, all life history traits cannot be maximised simultaneously, because the resources allocated in one trait cannot be allocated to other traits (Stearns 1992, Roff 1992, Reznick 2000). These occasions where the increased expression of one trait is associated with the decreased expression of another trait are called trade-offs. As 'trade-off' is an ill-defined term indicating practically any negative relationship between two or more traits, trade-offs are often classified as physiological or evolutionary trade-offs to more precisely

emphasize the nature of the phenomenon. Physiological trade-offs are caused by allocation of limited resources in competing processes within an individual, whereas evolutionary trade-offs that typically include physiological trade-offs are defined as population-level responses to selection (Stearns 1992).

There are many potential life history trade-offs (Stearns 1992), but the best documented ones include e.g. investment in growth vs. reproduction (e.g. Green & Rothstein 1992), current vs. future reproduction (e.g. Candolin 1998, Verboven & Tinbergen 2002), current reproduction vs. survival (e.g. Hunt et al. 2004, Descamps et al. 2006), and number of offspring vs. offspring quality (e.g. Williams 2001, Wilson et al. 2009). Although trade-offs between life history traits might seem self-evident, they do not always exist where expected, and sometimes they can be found where not expected (Stearns 1992, Reznick et al. 2000). This might be because individuals typically vary in their resource acquisition and allocation, meaning the costs and benefits individuals experience due to their resource allocation on different traits vary (van Noordwijk & de Jong 1986). Therefore, the magnitudes of the trade-offs existing between life history traits are not identical to all individuals, but depend on individual condition. In addition, genotype by environment interactions (i.e. crossing reaction norms) can also mask the trade-offs, and if the linkage of two life history traits has been fixed as an invariant physiological mechanism, which lacks the genetic correlation, the trade-off cannot exist (Stearns 1989, 1992). In sum, understanding trade-offs between life history traits is important, as they set the limits for the possible life histories that can exist (Roff 1992, Stearns 1992).

1.3 Sexual selection

1.3.1 The definition and origin of sexual selection

Sexual selection arises from differences in reproductive success between individuals competing over mates (Darwin 1871, Andersson 1994). Sexual selection therefore targets the traits that enhance individuals' ability to attract mates, whereas natural selection operates on the traits that increase individuals' reproductive success through increased survival, feeding capability and other adaptations to the environment (Darwin 1859).

Sexual selection requires sexual reproduction, i.e. the (re)combination of genetic material of the two parents in progeny (Andersson 1994). Competition over mates differs between the sexes due to unequal investment in gametes: females produce large eggs with loads of energy, while males produce sperm with little energy stores. Therefore, female reproductive success is mainly limited by the number of produced eggs, whereas male reproductive success depends mainly on the number of their mates. Consequently, females are expected to show more parental care than males, and thus carefully choose their mates, whereas males are expected to compete for the access to females to maximise their reproductive success, leading to higher variance in mating and

reproductive success in males than in females (Bateman 1948, Trivers 1972, Andersson 1994).

Sexual selection operates on conspicuous male secondary sexual traits, *s.l.* ornaments (Darwin 1871, Andersson 1994; but see sexual selection on female ornaments in Clutton-Brock 2007, 2009). These traits include morphological (e.g. colouration and weapons), behavioural (e.g. fights, song and other display) and physiological (e.g. immunoglobulins, Major Histocompatibility Complex, cuticular hydrocarbons in insects) characters that increase male success in competition for mates, but decrease male survival. Ornaments are thought to have evolved primarily through male-male competition and female choice (Andersson 1994). The two main hypotheses to explain the evolution of female preference for conspicuous male secondary sexual traits are Fisherian runaway (Fisher 1930, a.k.a. 'Fisher process' and 'sexy sons') and 'good genes' models (a.k.a. 'indicator mechanism' and 'handicap theory': Zahavi 1975, 1977, Grafen 1990, Iwasa et al. 1991).

Fisherian runaway posits first that there is genetic variation in a male trait that enhances male survival, and in females' tendency to mate with males with different expression of that trait. Consequently, females that mate with males bearing the favourable trait expression produce sons with high survival, and the alleles coding the favourable trait expression, and female preference for it, will spread in the population (Lande 1981). Then, males with favoured trait expression enjoy not only higher survival but also higher mating success, which creates a feedback that increases the trait expression, and the female preference for it, until the decreased survival of males due to the conspicuous trait expression stops the process. Alternatively, good genes models suggest that elaboration of conspicuous ornaments and sexual display are energetically costly to produce, and thus only high quality males can express high quality ornaments or high rate of display (Zahavi 1975, 1977, Grafen 1990, Iwasa et al. 1991, Rowe & Houle 1996, Kotiaho 2001). Females choosing such males for mates benefit indirectly by producing offspring of better than average genotypic quality. Despite the juxtaposition in the past, Fisherian runaway and good genes models are currently seen as the ends of a continuum, and enhanced mating success and survival are seen as equally valid genetic benefits of mate choice, which relative importance depends on the costs of female choice (Kokko et al. 2002).

Both the Fisherian runaway process and the good genes hypothesis are expected to underpin the evolution of remarkable male ornaments through the increase in the fitness of the females' offspring (i.e. indirect fitness benefits of mate choice). However, in many species, both males and females are needed to rear the offspring and hence females may not only gain indirect fitness benefits from their mate choice, but also substantial direct fitness benefits (e.g. ability to produce a greater number of offspring, increased survival rate of the offspring). In this case, traits associated with male mating success signal their ability to provide parental care or the amount of food or other resources on their territories. Irrespective of the type of fitness benefits gained by females through their mate choice and the mechanisms underlying the indirect fitness benefits, sexual selection is widely acknowledged as an important factor contributing to

the evolution of the diversity of shape, colours and behaviours we observe across species (Andersson 1994).

1.3.2 Evolution and maintenance of multiple ornaments

Sexual displays are often highly complex, and mate choice can be based simultaneously on multiple cues (Candolin 2003). In particular, multiple cues are expected to be common in polygynous species with high opportunity for sexual selection and where females can evaluate several cues simultaneously with little effort, thus having large fitness benefits with low costs of mate choice (e.g. lekking and social species; Møller & Pomiankowski 1993). Several hypotheses have been raised to explain the evolution and use of multiple cues in mate choice (reviewed in Candolin 2003). First, different cues can provide different information on male quality depending on the context, thus enabling the estimation of male overall quality ('multiple messages'; Møller & Pomiankowski 1993, Johnstone 1997, van Doorn & Weissing 2004). Alternatively, multiple cues can provide information on the same aspect of male quality, thus enforcing the signal and reducing the risk of choice errors made by females ('back-up'/'redundant signal'; Møller & Pomiankowski 1993, Johnstone 1997). In addition, males and females can use different cues to estimate the quality of their conspecifics, meaning inter- and intrasexual selection can act on different male traits simultaneously ('multiple receivers'; Anderson et al. 2002, Guindre-Parker et al. 2013). However, multiple cues can also include traits that do not indicate male quality but take advantage of arbitrary female preference either by exploiting receivers' sensory biases or being remnants from the past selection ('unreliable' and 'Fisherian cues'; Møller & Pomiankowski 1993, Ryan & Rand 1993, Holland & Rice 1998). A signal that constitutes of multiple cues can also have greater impact on the receiver than any single cue, hence enforcing the detection, discrimination and evolution of the signal ('receiver psychology'; Rowe 1999). Moreover, different cues can provide different information in different environments or stage of the choice process (Candolin & Reynolds 2001), and may play a role in species recognition and promote sexual conflict and antagonistic coevolution (Andersson 1994, Holland & Rice 1998). In general, the use of multiple cues in mate choice may substantially influence the strength of sexual selection and hence the maintenance of the variation in the preferred traits (Brooks & Endler 2001, Candolin 2003). This can further promote the evolution of alternative signalling tactics (Johnstone 1996) and eventually lead to speciation (Pomiankowski & Iwasa 1998).

A central dilemma in understanding the evolution of female preference on male secondary sexual traits is how additive genetic variation is maintained in the target traits under consistent directional selection, which should drive these traits to fixation and eradicate the indirect genetic benefits of mate choice for females, meaning selection on these traits should no longer exist ('the lek paradox'; Borgia 1979, Taylor & Williams 1982, Kirkpatrick & Ryan 1991, Rowe & Houle 1996). As a resolution to the lek paradox, several alternative but mutually non-exclusive hypotheses have been suggested, including preference for

unrelated males (Hoffman et al. 2007, Reid 2007), evolving mutation rates (Petrie & Roberts 2007) and indirect genetic effects (Rowe & Houle 1996, Miller & Moore 2007), most supported ones being 'fluctuating selection' and 'genic capture' hypotheses. The use of multiple traits as cues in mate choice is included in the fluctuating selection hypotheses suggesting that the optimal phenotype varies either in time or space (Brooks & Endler 2001, Chaine & Lyon 2008), for instance due to parasite-host arms race (Hamilton & Zuk 1982). Alternatively, the genic capture hypothesis suggests that male sexual traits and display are costly to produce and depend on male overall condition which itself is regulated by multiple genes in many loci (Kotiaho et al. 2001, Tomkins et al. 2004). Thus, directional selection through female choice cannot deplete the genetic variance in fitness, providing the ultimate resolution on lek paradox (Kotiaho et al. 2008).

1.3.3 How to measure sexual selection?

Sexual selection and potentially sexually-selected traits can be easily observed in nature, but to accurately measure the strength of sexual selection is not simple (e.g. Klug et al. 2010a, 2010b, Krakauer et al. 2010, Kokko et al. 2012). Sexual selection operates on mating success, but copulations are often difficult to observe in the wild, and movements of marked individuals to and from the study area can restrict the measurement of reproductive success to a few individuals (Coltman et al. 1999a, Kruuk et al. 2002). Instead, if observed mating success and genetic paternities are strongly positively correlated, observed male reproductive success can be used to assess female mating behaviour and male mating success, enabling the strength of sexual selection to be estimated (Griffith et al. 2002). However, the goodness of genetic paternity as a proxy for mating success depends directly on the number of females sampled and the number of offspring produced per female, and is readily biased if all copulations do not result in offspring (Brommer et al. 2007), or if post-copulatory sexual selection occurs (i.e. sperm competition or cryptic female choice; Eberhard 1996, Birkhead 1998, Birkhead & Møller 1998). Undoubtedly, there is no universal measure for sexual selection that fits to all possible situations, but rather the goodness of each measure is context-dependent. Thus, the selection of the measure used in any study depends on the study questions and the data available. The most commonly used measures of sexual selection have been recently reviewed in Klug et al. (2010a), and are summarised in Table 2.

1.3.4 Why is sexual selection so important?

Sexual selection is universal and it is present virtually anywhere we take a look at. Sexual selection is an essential part of natural selection, and thus its contribution to evolution as one of the fastest and strongest evolutionary forces is undoubtedly substantial (Andersson 1994). Consequently, the huge variety of the phenotypic characteristics of all the living species that can be seen around us is largely due to sexual selection. In addition, sexual selection reduces the effective population size (i.e. the individuals in the population that actually reproduce at a

TABLE 2 Common measures used to quantify, predict and explain patterns of sexual selection. MS = mating success (i.e. number of observed copulations), RS = realised reproductive success (number of offspring produced, in males based on genetic paternity). Table adopted and re-edited from Klug et al. (2010a).

Measure	Brief description	References
The opportunity for sexual selection (I_{ss})	Variance in MS / (mean MS)^2 for a given sex.	1–3
Bateman gradient (β_{ss})	The slope of the least squares regression of RS on MS.	3–4
Sexual selection gradient (β)	Univariate: The slope of regression of relative MS on the phenotypic trait. Multivariate: The partial regression coefficient of the phenotypic trait.	1, 3–6
Sexual selection differential (s)	The difference between mean phenotypic trait value before and after an episode of sexual selection. Equivalent to the covariance between relative MS and a phenotypic trait value.	1, 5, 7
Morisita's index (I_δ)	The observed variance in MS corrected for by an estimate of the variance expected when all mate acquisition probabilities are equal.	8–9
Index of resource monopolization (Q)	The ratio of observed variance in MS and the maximum possible variance in MS, with both variances corrected for by an estimate of the variance expected when all mate acquisition probabilities are equal.	9–10
Operational sex ratio (OSR)	The average ratio of males to females who are ready to mate at any given time in a given place.	6, 11
Potential reproductive rate (PRR)	For a given sex, the number of independent, fledged offspring that parents can produce per unit time if the mate availability is unconstrained.	12–13

References: 1) Arnold & Wade 1984a, 2) Shuster & Wade 2003, 3) Jones 2009, 4) Arnold & Duvall 1994, 5) Lande & Arnold 1983, 6) Andersson 1994, 7) Arnold & Wade 1984b, 8) Morisita 1962, 9) Fairbairn & Wilby 2001, 10) Ruzzante et al. 1996, 11) Emlen & Oring 1977, 12) Clutton-Brock & Vincent 1991, 13) Clutton-Brock & Parker 1992.

given time), which can have major population level impacts, for instance by increasing inbreeding and kin competition. Finally, sexual selection and divergence of secondary sexual traits can produce isolation mechanisms that can eventually (with or without ecological divergence) lead to speciation.

1.4 Life histories and sexual selection, merge!

Life histories are traditionally expected to be shaped by natural selection (Stearns 1992), and although it is clear that sexual selection is incorporated into measures of natural selection (see above), its role in the evolution of life histories has often been neglected. Another reason to explain the lack of studies quantifying the impact of sexual selection on the evolution of life histories is that female life histories have been more intensively studied than male life histories. This bias

results mainly from the relative ease with which female reproductive success can be measured, whereas genetic data or reliable surrogate measures needed to estimate male reproductive success are difficult to obtain due to the mismatch of observed copulations and genetic paternity (Griffith et al. 2002). However, as sexual selection is typically stronger in males than in females, sexual selection can be an important factor shaping male life histories (Bonduriansky et al. 2008, Monaghan et al. 2008).

It has been suggested that sexual displays (e.g. ornaments, behaviour) should be regarded as life history traits, because sexual display, as an honest indicator of male overall genetic quality, depends on male condition, and condition is typically related to age (Andersson 1994, Kokko 1997, Höglund & Sheldon 1998). Therefore, males are expected to optimize their sexual display according to their condition, which can lead to physiological trade-offs between sexual display and life history traits (e.g. Gustafsson et al. 1995, Griffith 2000). Hence, it is crucial to understand the link between life histories and sexual selection, to understand the variation in individuals' ability to attract mates, the first component of fitness.

1.5   Aims

The overarching aim of this thesis was to investigate how the interplay between life histories and sexual selection shapes individual fitness using long-term data collected in male black grouse. As fitness constitutes of many interdependent components (see above), we first focussed on each of these components separately before combining them to achieve the ultimate goal. Since age at first reproduction can have a major influence on LRS (Stearns 1992), we first identified, in paper I, multiple factors determining reproductive effort, mating success and survival in yearlings male black grouse (i.e. individuals that are <1 year old, but physiologically mature, *cf.* juvenile). Age is a major factor that influences individuals' ability to express sexually selected traits. Therefore, in paper II, we quantified the age-dependent patterns and the role of lifespan in the expression of multiple morphological and behavioural traits that are related to mating success. Furthermore, we tested the hypothesis that the expression of male traits is highest in the year of peak lekking effort with expected patterns of early life improvement and declines in trait expression following males "best" reproductive season. In paper III, we quantified the relative contribution of age, age at first lek, lifespan and the expression of multiple sexually-selected morphological and behavioural traits on male AMS. In particular, we first quantified the overall variation in male mating success (the opportunity for sexual selection, I_{ss}), and tested the hypothesis that a substantial proportion of this variation is age-dependent and is influenced by individuals' lifespan and age at first lek. Finally, we quantified the effect of each morphological and behavioural trait on male AMS while accounting for male age using univariate sexual selection differentials and multivariate sexual selection gradients. In paper

IV, we adopted a broader view on sexual selection, and tested whether sexual size dimorphism (SSD) in body mass is related to the strength of sexual selection in birds and mammals, to link each original paper into a broader context of sexual selection.

2   MATERIALS AND METHODS

2.1   Study species and population

Black grouse (*Tetrao tetrix*) is a lekking galliform inhabiting Eurasian boreal forests. Lekking is a rare but taxonomically widespread mating system where males cluster on specific arenas to display and defend territories to attract females (Höglund & Alatalo 1995). In general, leks vary in the level of male aggregation from closely clumped males in classical leks (Bradbury 1981) to dispersed or exploded leks where males may not even see each other (Gilliard 1969, Emlen & Oring 1977), and in the availability of resources for females (Höglund & Alatalo 1995). Black grouse lek is one of the best examples of a classical lek: lek sites are virtually used only for display and mating and they provide no other resources for females than the males, males provide no parental care and females are free to choose with whom they mate (Bradbury 1981, Höglund & Alatalo 1995). Hence, black grouse leks provide an ideal study system to investigate sexual selection in a wild animal population.

Mating skew among male black grouse is substantial due to the intense male-male competition and clear female choice on the leks (Alatalo et al. 1991, 1992). Indeed, female black grouse prefer mating with older males that fight frequently and victoriously against other males (Hämäläinen et al. 2012), hold central territories on the lek (Hovi et al. 1994), and have high lek attendance in relation to the other males on the same lek (Alatalo et al. 1992). In addition, male black grouse have multiple morphological traits that are (directly or indirectly) related to male mating success (lyre, i.e. tail length and quality, Höglund et al. 1994, Rintamäki et al. 2001; red eye combs, Rintamäki et al. 2000; blue colouration of breast feathers, Siitari et al. 2007; body mass, Rintamäki et al. 2001, Lebigre et al. 2013). A substantial proportion of the variation in both morphological and behavioural traits is explained by male age (Siitari et al. 2007, II) and condition (Siitari et al. 2007, Hämäläinen et al. 2012, Lebigre et al. 2013), and it is likely that females use morphological traits as age cues to avoid mating with actively

lekking young males that have not gone through viability selection (Manning 1985, Alatalo et al. 1991).

Copulations in black grouse are conspicuous, as males flap their wings while mounted on females, which enables the direct observation of male mating success (I, III). Observed mating success and genetic paternities are strongly positively correlated, as female black grouse typically copulate only once with a single male, which is enough to fertilise all eggs (Alatalo et al. 1996a, Lebigre et al. 2007). Furthermore, male black grouse are faithful to the lek on which they initially establish a territory, and switching lek is rare among older males (Rintamäki et al. 1995, Höglund et al. 1999, Caizergues & Ellison 2002, Lebigre et al. 2008), which means that the same individuals can be monitored over their whole lifespan. Therefore, observed mating success provides a reliable proxy for male real reproductive success, assuming variation in female fertility and reproductive success is limited.

This study uses longitudinal data describing male mating success, lekking behaviour, and measures of multiple sexual traits collected in five study sites in Central Finland (ca. 62°15′N; 25°00′E) during 2001–2013. Each study site is a local main lek with 5–40 territorial males (Kervinen et al. 2012). During the study period, population density of black grouse in Central Finland varied from 6.2 to 19.4 individuals per km^2 of woodland (Fig. 1), which was consistent with the number of individuals on winter flocks and the number of males on the leks (I, II). As local hunting clubs have refrained from hunting on study leks and in their surroundings, the age structure of the study population can reasonably be assumed to be natural.
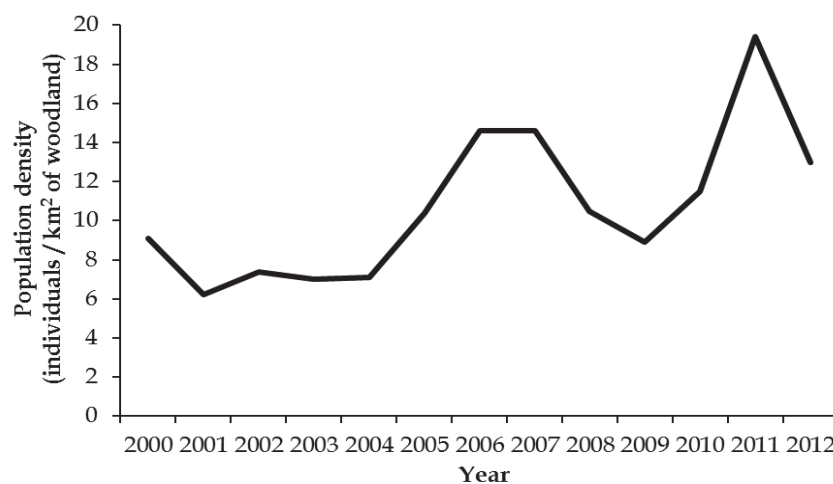

FIGURE 1   The variation in the black grouse population density (individuals / km^2 of woodland) in the central Finland game management district between 2000–2012, based on the autumnal (August–September) wildlife triangle censuses (Riista- ja kalatalouden tutkimuslaitos 2013).

2.2 Winter captures

Black grouse form relatively stable winter flocks from November onwards, which enables the efficient capture of a substantial proportion of the individuals of the local population, especially adult males who have established territories on the site the captures are carried out. During 2001–2013, birds were provided with oats on the five lekking sites from late November – early December onwards, and captured during January–March with oat-baited walk-in traps (see details in I, II, Lebigre et al. 2012). During the capture mornings, the feeders were covered with snow and oats were placed only under the traps. The simultaneous springing of all the traps enabled catching up to 20 individuals at one attempt. Each captured bird was aged as yearling or older according to plumage characteristics (Helminen 1963), and marked individually with an aluminium tarsus ring and three coloured plastic tarsus rings for future identification. All birds were blood sampled for various DNA analyses (for parallel studies), parasite counts and physiological measures, and measured for multiple morphological traits (I, II, Lebigre 2012). Eye combs were recorded against a scale with a digital video camera, and the total eye comb size was calculated afterwards from the video clips using Image Pro Plus™ or ImageJ softwares. Reflectance of the blue chroma colouration of breast feathers (hereafter blue chroma) was measured subsequently in laboratory with Avantes Spectrophotometer (GS 3100, EG & G Gamma Scientific, San Diego, CA; see details in Siitari et al. 2007) from a sample of breast feathers taken from each captured individual in the field.

Birds were handled with caution by trained field assistants to avoid injuries and deaths in all stages, and <1 % of all the captured individuals were observed visible injuries or died, virtually always due to collisions with the trap structures. Instead, handling *per se* was not observed to injure any bird. Captures were carried out under the permissions of the Central Finland Environmental Centre (permissions KSU-2003-L-25/254 and KSU-2002-L-4/254) and the Animal Care Committee of the University of Jyväskylä (ESLH-2009-05181/Ym-23).

2.3 Lek observations

Data on male lekking behaviour and mating success was collected annually during the peak mating season in late April – early May (exact timing depending on April temperature, Ludwig et al. 2006). Within this period, typically lasting less than two weeks, each study lek was monitored daily from *ca*. 0300 to 0800 hours from hides near the leks (I, II). Due to the unique combination of coloured tarsus rings that enables identification of individuals, males' behaviour (rookooing, hissing (the two most common vocal displays), fighting or inactive; described in Höglund et al. 1997) and location on the lek were recorded at regular intervals. In addition, each copulation was recorded with information of the time, location and the identities of the male and female that mated. Lek

attendance (proportional to the highest attending male on the same lek), the relative proportion of each behaviour, and territory distance from the lek centre (see I, II for descriptions) were then calculated from these records for all ringed males (see Rintamäki et al. 1995; Alatalo et al. 1996b).

2.4 Data sets and statistical analyses

The massive field work effort 2001–2013 led to a total of nearly 1700 captured, ringed and measured males (and nearly 1300 females). Most birds were caught only during a single winter (74 % of males, 89 % of females), but some individuals were caught in up to six consecutive winters. This sum to a total of more than 3700 sampled birds during the study period, of which I used a subset of 193 yearling males with complete morphological and behavioural data captured during the study period of 2001–2008 (I), and a subset of 164 (II, III) males with known year of hatching (2001–2008), known lifespan (1 to 6 years) and records of morphological traits, lekking behaviour and mating success over the individuals' lifespans (II, III). For paper IV, the data of I_{ss} and SSD were collected or recalculated from published studies.

All statistical methods used are described in detail in each original paper (I–IV). Data in paper I was analysed with binary logistic regression (territoriality, survival) and zero-inflated general linear models with negative binomial error distribution (ZINB-GLM, mating success). The datasets used in II and III constituted of one to six observations from the same individuals, and thus these observations were non-independent. Therefore, linear (LMM) and generalised linear mixed effects models (GLMM) were used, with individual identity as a random effect to control for the non-independence of the data points. In the last study (IV), a phylogenetic generalized least squares approach (PGLM) was adopted. All analyses were run in R (versions 2.12.2 (I) and 2.15.2 (II–IV), R Development Core Team 2010, 2012).

3   RESULTS AND DISCUSSION

3.1   Opportunity for sexual selection (III, IV)

The opportunity for sexual selection (I_{ss}, described as the variance in mating success divided by the square of the mean mating success of the individuals of one sex in the population; Arnold & Wade 1984a, 1984b, Shuster & Wade 2003, Jones 2009) is a dimensionless measure of the variation in mating success that reflects the maximum potential strength of sexual selection. In our broad comparative study investigating the relationship between I_{ss} and two measures of sexual size dimorphism (SSD) in birds and mammals, we found that in general, mammals had higher I_{ss} and SSD than birds (IV). Moreover, in birds SSD was not related to I_{ss}, but in mammals this relationship was significant. These results were in line with earlier studies in mammals (Mitani et al. 1996, Weckerly et al. 1998, Lindenfors et al. 2007, Vanpé et al. 2008), but differed from previous studies in birds that investigated the relationship of SSD and mating systems as a measure of sexual selection (Björklund 1990, Owens & Hartley 1998, Székely et al. 2007). This might be because mating systems are usually quite coarse measures of sexual selection and because birds typically express higher variety of sexual dimorphism in phenotypic and behavioural traits than mammals do (Owens & Hartley 1998). Furthermore, whilst direct physical male-male contest is common in mammals, avian mating systems are often more characterised by other sexually-selected behaviours, such as display agility that may select for reduced body mass in males (Székely et al. 2004, 2007).

The greatest opportunities for sexual selection were found in lekking bird species (e.g. white-bearded manakin *Manacus manacus*, Shorey 2002, lance-tailed manakin *Chiroxiphia lanceolata*, DuVal & Kempenaers 2008), highly sexually-dimorphic polygynous ungulates (e.g. red deer *Cervus elaphus*, Pemberton et al. 1992, Soay sheep *Ovies aries*, Coltman 1999a, 1999b), and pinnipeds (grey seal *Halichoerus grypus*, Twiss et al. 2007, southern elephant seal *Mirounga leonina*, Galimberti et al. 2002). However, lekking birds differed substantially in their type of SSD. Specifically, males are much larger than females when physical contest

plays a more important role in mate choice (e.g. black grouse *Tetrao tetrix*, Kruijt & de Vos 1988, Alatalo et al. 1992, III, IV; wild turkey *Meleagris gallopavo*, Krakauer 2008), while females are heavier than males in species where male display itself matters (e.g. lance-tailed manakin, DuVal & Kempenaers 2008). Therefore, lekking as a mating system with strong sexual selection does not promote SSD *per se* but the size and type of SSD depends on the type of male-male competition (Höglund 1989, Höglung & Sillén-Tullberg 1994, Lislevand et al. 2009).

3.2 Age-dependent trait expression and mating success (I, II, III)

3.2.1 Age at first lek – Does an early onset of lekking pay off? (I, III)

Age at first reproduction can have a strong influence on individual fitness, as it largely determines an individual's reproductive success at its first breeding attempt and the length of its reproductive lifespan (Roff 1992, Stearns 1992). The advantages of early start of reproduction include better survival to the first reproduction and shorter generation interval (Bell 1980, Stearns 1992). Conversely, delaying first reproduction to older ages often leads to longer lifespan and better reproductive success later in life, which can compensate the lost reproductive opportunities when young (Curio 1983, Stearns 1989, Forslund & Pärt 1995). As individuals have to allocate their limited resources to several competing life history traits, reproduction is expected to begin when the fitness benefits of reproduction outweigh the costs of reproduction on reduced somatic growth, survival or future reproduction opportunities (Pianka & Parker 1975, Stearns 1989, 1992). Thus, individuals are expected to optimize their reproductive effort according to their phenotypic quality (Pärt 1995).

In lekking species, the first step for a male towards any mating success is to establish a territory on a lek (Apollonio et al. 1989, Balmford et al. 1992, Höglund & Alatalo 1995). This is because females of many lekking species typically prefer mating with males occupying central territories on the lek (Höglund & Lundberg 1987, Balmford et al. 1992, Hovi et al. 1994, Partecke et al. 2002, Shorey 2002, Bro-Jørgensen & Durant 2003), and to achieve a central position on the lek typically requires years of active lekking (Kokko et al. 1999, DuVal 2012). In black grouse, we found that territorial yearling males were significantly heavier than non-territorial yearling males. This might primarily be due to the large energetic costs of display and fighting for territories on a lek (Vehrencamp et al. 1989, Höglund et al. 1992), meaning that heavy males can better cope with the energetic costs of lekking. Male body mass might also be linked to their success in male–male interactions (Balmford et al. 1992, McElligott et al. 2001, Alonso et al. 2010, Lebigre et al. 2013). Therefore, heavy yearling males might be better able to settle down on a lek territory. However, although body mass in male black grouse is not directly related to fighting success, it is positively related to fighting rate (Hämäläinen et al. 2012). Since there is hardly any overlap in body mass between

yearling and older males (older males being on average ca. 100 grams heavier than yearling males, II), greater body mass in territorial than in nonterritorial yearling males more likely indicated their better capability to afford the energetic costs of lekking, rather than the likelihood to succeed in contest with other males *per se* (Bachman & Widemo 1999, Hämäläinen et al. 2012, Lebigre et al. 2013).

When a yearling male black grouse establishes a territory on the lek, its mating success is still far from guaranteed. Nearly 60 % of the yearling black grouse males did not establish territories, and across territorial yearling males only 15 % managed to copulate (range 1–10 copulations, median was 1 across territorial yearling males that mated and 0 across all territorial yearling males). Yearling male mating success was mainly explained by male lekking behaviour: successful yearling males tended to attend more on the lek, fought more often with neighbouring males and had their territories closer to the lek centre than unsuccessful yearling males. High lek attendance is crucial for territorial males, because unoccupied territories are readily reoccupied by other males (Apollonio et al. 1989, Hill 1991, Fiske et al. 1998, Friedl et al. 2005), and fighting rate in turn largely explains male dominance (Alatalo et al. 1991, Komers et al. 1996, McElligott & Hayden 2000). Instead, morphological traits had no significant effects on yearling male mating success. In fact, similarly with body mass, there is only little overlap in ornament size or quality (lyre length, eye-comb size and redness, blue coloration; Siitari et al. 2007, II) between yearling and older male black grouse. Therefore, if mate choice acts on morphological traits, it is unlikely that yearling males expressing smaller (or lower quality) ornaments than older males will be selected for.

Variation in population density is expected to influence the onset of reproduction, and early reproduction is thought to be favoured in increasing population densities because of low cost and high reward of reproduction (Cole 1954, Lewontin 1965, Stevenson & Bancroft 1995). In particular, this means that when population density increases, intraspecific competition is mild and offspring are likely to survive. Instead, delayed onset of reproduction is expected in decreasing populations due to the low reproductive success and offspring survival of the young first-time breeders (Hamilton 1966, von Biela et al. 2009). Our data supported these hypotheses, as yearling males were more likely to be territorial when population density was increasing or high than when population density was decreasing or low. Consequently, all observed copulations of yearling males took place between 2005–2007, when the local population density was increasing (Riista- ja kalatalouden tutkimuslaitos 2013). Thus, this highlights that stochastic events such as environmental conditions that shape population dynamics can have significant effects on male fitness (Brommer et al. 1998, Krüger 2005, Descamps et al. 2008, Cooper et al. 2009).

We have shown that yearling male black grouse can have some limited mating success, which might seem trivial. However, taking into account that most male black grouse never manage to copulate (Alatalo et al. 1992, III), it seems that starting lekking as a yearling can pay off, if this early reproductive investment does not reduce their future opportunities to mate. In fact, we did not find significant difference in survival to the next breeding season between

territorial (58 % survived) and nonterritorial (48 % survived) male black grouse. Body mass was crucial for survival in both territorial and nonterritorial yearling males, and higher fighting rate and microfilaria (nematode blood parasites) load in surviving territorial yearling males compared to the ones that died, indicated that the surviving males were in better physiological condition and capable of handling the energetic costs of lekking (Vehrencamp et al. 1989, Höglund et al. 1992, Lebigre et al. 2013) and elevated parasite load caused by increased testosterone levels (Alatalo et al. 1996b, Siitari et al. 2007). This supports the hypothesis and earlier observations that individuals being able to start reproduction early in life are of high quality (Zahavi 1975, Grafen 1990, Hunt et al. 2004, Descamps et al. 2006), although fitness costs of early reproductive effort can appear as decreased reproductive success and/or survival later in life (Williams 1966, Bell 1980, Stearns 1989). However, our data also showed that males that started lekking as yearlings had even higher age-specific AMS later in life than males that started lekking as ≥2 year-olds (see 3.2.3). This pattern was probably influenced by the difference in AMS between these two groups at age two, when males that started lekking as yearlings – and survived to their second lek – already had some experience, which is crucial for obtaining central position on the lek (Kokko et al. 1999), whereas males that started lekking as two-year-olds had no experience yet.

3.2.2 Effects of age on the expression of male traits (II)

Individuals' age often determines their ability to express specific morphological and behavioural traits, because of the constraints imposed by the complex allocation to growth and maintenance of these traits. The expression of all studied morphological and behavioural traits in male black grouse increased with age until the oldest ages, and the largest change in trait expression took place between age one and two. These results are consistent with previous studies investigating age-dependence of life history traits (Bouwhuis et al. 2010), and secondary sexual traits (Balbontín et al. 2011), which was expected, as yearling males are still growing and thus the resources they can allocate on sexual display are limited (Curio 1983, Stearns 1992). In addition, we found that lifespan was significantly related to the expression most morphological and behavioural traits, and interactions between individual age and lifespan indicated that long-lived males (lifespan ≥4 years) had consistently lower trait values at ages 1 to 3 than males with shorter lifespan, suggesting that major survival costs on the timing of expression might occur. In fact, longer-lived males tended more often not to lek at all as yearlings than short-lived males. However, this result should be interpreted cautiously given the uncertain fate of many yearling males for whom it was not possible to determine whether they died before the lekking season or dispersed outside our study population (see I).

   We also found evidence of strong selection for trait expression over the peak lekking effort (i.e. the year when a male's lek attendance was highest), which tended to occur in the last year the male was alive, suggesting that lekking might induce substantial fitness costs in terms of reduced survival, especially in

short-lived males. Remarkably, mortality after the peak lekking effort year was lower in long-lived males suggesting larger fitness costs of lekking in short-lived males. Terminal investment could also explain the high trait values in the last year males were alive, whereby individuals increase their reproductive effort when their residual reproductive value decreases (Clutton-Brock 1984, Isaac & Johnson 2005). This supports the idea that long-lived males are also high quality as they not only have proven their viability but are also more likely to survive to the next breeding season (Alatalo et al. 1991). If male viability is partly heritable, females might gain good genes benefits by choosing long-lived males (Møller & Alatalo 1999). Overall, these results show how important it is to account for the complex interaction between individual age and investment in reproduction to better understand the variation in sexually-selected traits and fitness benefits associated with sexual selection.

3.2.3 Effects of age on male mating success (III)

Male AMS showed similar age-dependence as the morphological and behavioural traits and increased significantly with age and decreased towards the end of individuals' life. There was a huge skew in both male AMS and LMS, with 52 % of the males having LMS of zero, and 12 males accounting for nearly half of all observed copulations during the study period (Fig. 1 in III). Contrary to morphological and behavioural traits, AMS was not significantly related to male lifespan, which suggests 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 (see section 3.3). Instead of an effect of lifespan on AMS, we found a significant negative effect of males' age at first lekking on AMS, indicating that males that began lekking as yearlings had higher age-specific AMS than males that started lekking at age ≥2. This could be interpreted as selective appearance of poor reproducers (van de Pol & Verhulst 2006), but that is unlikely to be the case here because 38% (35/89) of the males that started lekking as yearlings died before age 2 (44% mortality in data used in I). Therefore, only the yearling males that survived from age 1 to age 2 did consistently better at subsequent ages than males starting lekking at age ≥2, but the overall LMS was similar due to the high mortality among territorial yearling males. Moreover, this unexpected pattern might be influenced by our inability to estimate the proportion of nonlekking versus dead males, if these males never establish territories in our study leks. As lekking experience is positively correlated with mating success (Kokko et al. 1998), males that were lekking at age 1, had better AMS at age 2 than males that started lekking at age 2 either because they defended more central territories, or were better able to fight with their neighbours due to their past experience in displaying with the other males. These results show that the choice of delaying the onset of sexual display might be beneficial in short term (increased survival likelihood) but detrimental in the long term due to a lag in display experience.

3.2.4 Senescence – Do male black grouse get old? (II, III)

Until recently, senescence was erroneously thought to be rare or absent in natural populations because of predation, diseases and other environmental challenges that would end individuals' lives before negative effects of ageing would occur (reviewed in Nussey et al. 2013). However, currently senescence is seen as a natural part of an individual's life also in the wild, and it has been reported in a wide range of vertebrates, but the mechanisms underlying the variation in ageing patterns and their link to sexual selection are not thoroughly known yet (Bonduriansky et al. 2008, Jones et al. 2008, Monaghan et al. 2008, Nussey et al. 2013).

We found weak evidence of senescence in male black grouse in both the expression of morphological and behavioural traits and mating success. The more evident senescence (or stronger non-linear age effects, meaning slower increase in trait expression towards the end of life) on morphological traits than on behaviours suggested that males 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 size and quality of structural ornaments are strongly related to male physiological condition during the moult, whereas lekking behaviour is more plastic and can be adjusted according to male condition and other males on the same lek just prior to the mating season. If males survive over summer and moult, they have several months to recover their physiological condition before next mating season. Thus, energetic costs of lekking are more likely to be seen as reduced survival and reduced expression morphological traits than as reduced male lekking effort in the following spring.

Decreased AMS towards the end of individuals' lives was in line with the observation that male black grouse cannot maintain their top position on the lek typically more than for one year (Kokko et al. 1998), and suggested that females might avoid mating with very old males that possibly have lower sperm quality (Møller et al. 2009, Dean et al. 2010, Preston et al. 2011). However, senescence in lekking behaviour and mating success was not as obvious as one could have expected. As reproductive effort is expected to increase when residual reproductive value decreases, the observed high reproductive effort at the end of males' lives suggested that terminal investment in reproduction might occur in male black grouse, which could partially explain the weak evidence of senescence in behavioural traits (Williams 1966, Pianka & Parker 1975, Clutton-Brock 1984, Sadd et al. 1996, Velando et al. 2006).

Senescence in wild populations has been thought to evolve because alleles with beneficial effects on survival or reproduction early in life can be favoured by natural selection despite negative effects on health and fitness later in life (antagonistic pleiotropy; Medawar 1952 cited in Nussey et al. 2013, Williams 1957), or because key resources such as energy are limited, so natural selection will adjust the allocation of these resources between somatic maintenance and reproduction (disposable soma; Kirkwood 1977, Kirkwood & Rose 1991). The observed ageing patterns in male black grouse supported at least the latter, but

more detailed analyses are needed to test these hypotheses and better understand the origin and mechanisms of senescence in this species.

3.3 Sexual selection on male traits when controlled for age (III)

As the expression of sexual traits and age are often related, and both can be related to male mating success, it is important to separate these effects to avoid the overestimation of the importance of sexual selection (Höglund & Sheldon 1998). The analyses using linear univariate sexual selection differentials and multivariate sexual selection gradients, when controlled for male age, indicated that sexual selection in black grouse operates primarily directly on male lekking behaviour and indirectly on male morphological traits. In particular this means that male AMS was highest in males that had high lek attendance and fighting rate and defended territories close to the lek centre irrespective of their age. The nonlinear univariate sexual selection differentials and multivariate sexual selection gradients further suggested no disruptive selection (Lande & Arnold 1983, Stinchcombe et al. 2008) but rather thresholds for lek attendance and territory distance from the lek centre, before which male mating success is virtually occasional, and after which male mating success increases sharply. For lek attendance this threshold seems to be *ca*. 0.8 (i.e. 80 % lek attendance in relation to the most attending male on the same lek) and for territory distance from the lek centre *ca*. 20 metres, meaning that males occupying territories >20 metres away from the lek centre have only very limited mating success (see Fig. 3 in III).

That male behaviour was directly and more strongly selected by females than male ornaments makes sense, as behaviour is plastic and reflects males' current physiological condition and its short-term changes (Hämäläinen et al. 2012, Lebigre et al. 2013). This also applies to eye combs, which size depends on male testosterone level that increases in spring towards the mating season (Alatalo et al. 1996b), and body mass that is linked to male behaviours (Hämäläinen et al. 2012). Lyre feathers and the blue breast feathers are formed during moult, which occurs in summer after the mating season. Thus the size and quality of these ornaments on the lek express males' condition in the previous summer but not their current condition. Moreover, as females usually prefer mating on the lek centre (Höglund & Lundberg 1987, Balmford et al. 1992, Hovi et al. 1994, Kokko et al. 1998, 1999b, Partecke et al. 2002), lekking behaviour can also indicate male long-term phenotypic quality (viability, long-term lekking effort), as a central position on a lek is usually the outcome of years of active lekking (Kokko et al. 1999, DuVal 2012). Thus, male lekking behaviour reflects both short- and long-term phenotypic quality of males, and hence can act as a more reliable cue of male overall genetic quality than morphological traits. However, male morphological traits might still be important in the process of sexual selection, although not necessarily directly selected for, as they can act as reliable cues of male age to females, and hence enable discrimination against

young but active males that have not undergone viability selection (Manning 1985, Alatalo et al. 1991). These results fit to the more general expectation that multiple sexual traits provide different cues conveying different information across the various stages of the mate choice process (Candolin & Reynolds 2001).

Finally, as these sexually-selected morphological and behavioural traits expressed in male black grouse are strongly condition-dependent (Siitari et al. 2007, Hämäläinen et al. 2012, Lebigre et al. 2013), consistent directional selection acting on these traits is unlikely to reduce additive genetic variation in these traits, because individual condition is regulated by many genes with small context-dependent effects (Rowe & Houle 1996, Kotiaho, et al. 2001, Tomkins et al. 2004). Furthermore, variation in multiple morphological and behavioural traits expressed in male black grouse can be maintained, because they provide females with information in different timescales about males' overall genetic quality. In general, these results highlight the importance of accounting for age in sexual selection studies, because age can simultaneously affect both the expression of sexual traits and mating success. Thus, neglecting the effects of age on the expression of sexually selected traits can lead to overestimation of the magnitude of sexual selection.

4 CONCLUSIONS

Individual age is undoubtedly a key determinant of the size and quality of morphological and behavioural traits that lead to individual mating success. The outstanding dataset collected in black grouse provided us with the opportunity to quantify these effects across multiple traits. As age affects both male mating success and traits under sexual selection, this study emphasises the importance of accounting for individual age to avoid overestimation of the role of sexual selection. Furthermore, the observed life history differences between short- and long-lived males in the expression of sexually-selected traits and mating success support the idea that sexual display should be seen as a life history trait that can be traded off with other life history traits, such as survival and future reproduction.

The finding that sexual selection in black grouse operates directly mainly on male behaviour and indirectly on male morphological traits indicates that behaviour acts as more reliable cue of male overall genetic quality to females. This is because behaviour reflects both short- and long-term condition of the males, whereas morphological traits mainly reflect males' condition in the previous summer. However, for instance body mass and eye comb size are strongly related to male fighting rate on the lek and might thus have substantial indirect effects on male fitness. Moreover, male morphological traits – although not directly sexually-selected for – provide females with reliable age cues that indicate male viability. As morphological and behavioural traits provide different information on male overall genetic quality, this study indicates that females benefit from the simultaneous evaluation of multiple traits on leks, because it decreases the risk of mate choice error, thus promoting the maintenance of multiple ornaments expressed in males. Finally, the condition-dependence of these sexually-selected traits provides a resolution to the lek paradox, because consistent directional selection is unlikely to fix all the genes that regulate individual condition, and hence the additive genetic variance in male traits under sexual selection is maintained.

Future work should test for the interactions between different sexually-selected male traits, and quantify the temporal variation in the direction and

strength of sexual selection operating in black grouse leks. Moreover, measures of the heritability of male sexual traits and female preference for these traits would largely improve our understanding of the evolution of multiple ornaments and leks as a mating system in general. This can only be done with detailed individual-level long-term data collected in wild populations.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Teerikoiraiden (*Tetrao tetrix*) kelpoisuus – Elinkiertopiirteiden ja seksuaali-valinnan vaikutukset koiraiden elinikäiseen parittelumenestykseen

Luonnonpopulaatioissa yksilöiden välillä on usein huomattavia eroja lisäänty-mismenestyksessä. Tämä tarkoittaa, että joidenkin yksilöiden vaikutus seuraa-viin sukupolviin on suurempi kuin toisten, mikä johtaa vähittäiseen muutok-seen lajin perimässä ja ilmiasussa – evoluutioon. Yksilön kelpoisuus, eli kyky siirtää perimäänsä seuraaviin sukupolviin riippuu etenkin yksilön kyvystä houkutella parittelukumppaneita, toteutuneesta lisääntymismenestyksestä ja lisääntymiskertojen lukumäärästä. Koska kaikilla eliöillä on rajallinen määrä resursseja, kuten energiaa ja aikaa, käytettävissä lisääntymiseen ja muihin vält-tämättömiin toimintoihin, kuten kasvuun ja perusaineenvaihduntaan, yksilö ei voi maksimoida kaikkia kelpoisuutta lisääviä toimintoja samanaikaisesti. Niin-pä esimerkiksi suuri panostus lisääntymiseen nykyhetkessä voi heikentää yksi-lön todennäköisyyttä selviytyä seuraavaan lisääntymiskertaan tai vähentää li-sääntymiseen käytettävissä olevia resursseja tulevaisuudessa. Koiraan lisään-tymismenestys riippuu yleensä voimakkaasti sen parittelukumppanien luku-määrästä, joka puolestaan on yhteydessä naaraiden suosimiin koiraiden ilmen-tämiin sukupuoliominaisuuksiin, ornamentteihin. Koska sekä koiraan paritte-lumenestys että siihen vaikuttavien ornamenttien koko ja laatu ovat usein yh-teydessä koiraan ikään, on iän huomioiminen tärkeää mitattaessa kelpoisuutta, jotta koiraidenvälisen kilpailun ja naaraan parinvalinnan vaikutuksia koiraan kelpoisuuteen ei tule yliarvioitua.

Seksuaalivalinnaksi kutsutaan valintaa, joka aiheutuu eroista parittelume-nestyksessä yksilöiden välillä koiraiden keskinäisen kilpailun ja naaraiden pa-rinvalinnan seurauksena. Ryhmäsoidin on melko harvinainen, mutta eläinkun-nassa useasti itsenäisesti kehittynyt lisääntymissysteemi, jossa seksuaalivalinta on erityisen voimakasta; koiraat esittelevät laatuaan erityisillä soidinareenoilla, ja naaraat ovat vapaita valitsemaan parittelukumppaninsa. Lisäksi koiras ei osallistu lainkaan jälkeläisten hoitoon, vaan naaras hyötyy parinvalinnastaan vain epäsuorasti saamalla koiraan perintötekijät jälkeläisilleen. Tutkimuslajim-me teeri (*Tetrao tetrix*) on malliesimerkki ryhmäsoidinlajista, jonka koiraat kil-pailevat naaraiden suosiosta puolustamalla reviirejä erityisillä soidinareenoilla, ja jonka naaraat valitsevat tarkkaan parittelukumppaninsa, minkä seurauksena muutama soidinta hallitseva koiras saa valtaosan paritteluista suurimman osan koiraista jäädessä kokonaan ilman paritteluita.

Tämän tutkimuksen tavoitteena oli selvittää millaista vaihtelua teeri-koiraiden vuotuisessa ja elinkaaren aikaisessa parittelumenestyksessä sekä koi-raiden ilmentämissä rakenteellisissa ominaisuuksissa ja käyttäytymispiirteissä on, ja kuinka nämä vaihtelut ovat yhteydessä toisiinsa. Tutkimuksessa kiinni-timme erityisesti huomiota elinkiertopiirteiden, kuten eliniän ja soidintamisen aloittamisiän sekä seksuaalivalinnan vaikutuksiin koiraiden parittelumenestyk-seen. Tutkimuksessa hyödynsimme vuosina 2002–2013 kerättyä aineistoa teeri-

koiraiden rakenteellisista ominaisuuksista, soidinkäyttäytymisestä ja parittelumenestyksestä yksilöllisesti rengastetuilta koirailta, joiden kuoriutumisvuosi ja elinkaaren pituus tunnetaan tarkasti. Tällainen pitkäaikaisaineisto mahdollistaa yksilötason muutosten havaitsemisen parittelumenestyksessä ja sitä selittävissä ominaisuuksissa, ja siten edesauttaa ymmärtämään kuinka koiraiden huomiota herättävät seksuaaliominaisuudet ja ryhmäsoidin lisääntymissysteeminä ovat voineet kehittyä.

Tutkimuksessamme havaitsimme, että sekä koiraiden parittelumenestys että siihen yhteydessä olevien ornamenttien (rakenteelliset ominaisuudet ja soidinkäyttäytyminen) koko ja laatu kasvoivat koiraiden vanhetessa. Erityisen selkeää kasvua tapahtui ensimmäisen ja toisen lisääntymiskauden välillä, mutta elämän loppuvaiheessa kasvu hidastui tai muuttui jopa negatiiviseksi. Lisäksi ornamenttien koko ja laatu kasvoivat pitkäikäisillä koirailla hitaammin kuin lyhytikäisillä koirailla, mikä viittaa siihen, että ornamenttien ylläpito ja reviirin puolustaminen soitimella ovat energeettisesti kalliita, ja suuri panostus ornamentteihin liian aikaisin lisää riskiä kuolla nuorena. Vuotuinen parittelumenestys ei kuitenkaan ollut suoraan yhteydessä koiraan elinikään, mutta koiraat, jotka aloittivat soidintamisen ensimmäisenä keväänään nauttivat paremmasta keskimääräisestä parittelumenestyksestä kaksivuotiaina kuin koiraat, jotka perustivat reviirinsä vasta kaksivuotiaina. Ensimmäisenä keväänään soitimen väliin jättäneen koiraat kuitenkin elivät keskimäärin pidempään kuin soitimella ensimmäisenä keväänään olleet koiraat ja siten saivat jopa enemmän paritteluita elämänsä aikana kuin ensimmäisenä keväänään soitimelle tulleet koiraat.

Aineistomme perusteella seksuaalivalinta kohdistuu teerellä suorasti koiraiden käyttäytymispiirteisiin ja epäsuorasti koiraiden rakenteellisiin ominaisuuksiin. Tämä johtuu siitä, että soidinkäyttäytyminen ilmentää sekä koiraan nykyistä että pitkän aikavälin kuntoa, kun taas rakenteelliset ominaisuudet riippuvat lähinnä koiraan kunnosta sulkasadon aikaan ja ilmentävät lisääntymiskauden aikaan lähinnä koiraan kuntoa edellisen lisääntymiskauden jälkeen. Näin ollen teerinaaras voi saada luotettavampaa tietoa koiraiden kunnosta arvioimalla niiden käyttäytymistä rakenteellisten ominaisuuksien sijaan. Rakenteelliset ominaisuudet voivat kuitenkin toimia tärkeinä vihjeinä naaraille koiraiden iästä ja auttaa niitä välttämään parittelemista nuorien, aktiivisesti soidintavien koiraiden kanssa, jotka eivät kuitenkaan ole vielä todistaneet elinkykyisyyttään. Teerinaaraat voivat saada moninkertaista tai täydentävää tietoa koiraiden kelpoisuudesta suhteellisen pienillä kustannuksilla arvioimalla samanaikaisesti useita koiraiden ominaisuuksia soitimella. Tämä puolestaan vähentää epäsuotuisan parinvalinnan riskiä naarailla, ja on siten voinut edesauttaa usean rakenteellisen ominaisuuden ja käyttäytymispiirteen samanaikaisen ilmentämisen kehittymistä ja säilymistä teerellä.

Koiraiden seksuaaliominaisuuksien vahva yhteys koiraan kuntoon selittää myös miksi perinnöllinen vaihtelu naaraan suosimissa koiraan ominaisuuksissa säilyy, vaikka jatkuvan yhdensuuntaisen naaraan valinnan pitäisi hävittää vaihtelu. Tämä johtuu siitä, että yksilön kuntoon vaikuttaa iso joukko perintötekijöitä, eli geenejä, jotka sijaitsevat eri puolilla yksilön perimää. Naaraan valitessa

tietyn koiraan parittelukumppanikseen sen jälkeläisille siirtyy koko koiraan perimä, eikä ainoastaan valinnan kohteena suorasti olevia ominaisuuksia säätelevät geenit. Näin ollen naaraan valinta ei riitä poistamaan vaihtelua koiraiden kuntoa säätelevissä geeneissä eikä siten koiraiden parittelumenestystä selittävissä ominaisuuksissa.

Tulevissa tutkimuksissa tulisi syventää tämän tutkimuksen tuottamaa tietoa tutkimalla seksuaalivalinnan kohteena olevien koiraan eri ominaisuuksien vuorovaikutussuhteita ja mitata mahdollisia ajallisia muutoksia valinnan suunnassa ja voimakkuudessa. Lisäksi tässä tutkimuksessa havaitun koiraan iästä ja kunnosta riippuvan kelpoisuusvaihtelun perinnöllisen taustan selvittäminen edesauttaisi paremmin ymmärtämään soitimen evoluutiota ja moninaisten koiraiden ornamenttien kehittymistä.

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ORIGINAL PAPERS

I

DETERMINANTS OF YEARLING MALE LEKKING EFFORT AND MATING SUCCESS IN BLACK GROUSE (*TETRAO TETRIX*)

by

Matti Kervinen, Rauno V. Alatalo, Christophe Lebigre, Heli Siitari, & Carl D. Soulsbury 2012

Original Article

Determinants of yearling male lekking effort and mating success in black grouse (*Tetrao tetrix*)

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Age at first reproduction is a crucial component of individual fitness as it often determines the length of reproductive lifespan. The reproductive success of males generally varies more than that of females, but it is challenging to study because the genetic data or proper surrogate measure needed to investigate reproductive success are usually not available. In black grouse (*Tetrao tetrix*), a lekking species with strong male mating skew and female preference for older males, there is a strong relationship between observed matings and genetic paternity. Using this relationship, we studied the effects of morphological, and behavioral traits on probability of being territorial, mating success, and survival of yearling males. Heavier yearling males were more likely to be territorial, and higher population density increased the frequency of yearling male territoriality. Mating success was positively related to population density, lek attendance, and fighting rate, but not to morphological traits. Overwinter survival did not differ between territorial and nonterritorial yearling males. Our results show that yearling male black grouse in good condition can establish territories and have some limited mating success, especially during increasing population density. In black grouse, the direct fitness benefits gained as yearlings undoubtedly contribute substantially to individual fitness, as the high reproductive skew means few males successfully copulate during their lifetime. For other species, early reproduction may relate to individual lifetime mating success but depends both on the direction and magnitude of the relationship between age-specific mating success and survival, and, as our results also demonstrate, on extrinsic factors such as population density. *Key words*: age at first reproduction, fitness, male–male competition, sexual selection, survival. *[Behav Ecol]*

INTRODUCTION

Individual fitness is often more sensitive to changes in age at first reproduction than to changes in any other life history trait (Cole 1954; Lewontin 1965; reviewed in Roff 1992; Stearns 1992) and has consequently been the subject of much theoretical and empirical investigation. Reproduction is expected to begin when the fitness benefits of reproduction outweigh the costs of reproduction on reduced somatic growth, survival, or future reproduction opportunities (Pianka and Parker 1975; Stearns 1989, 1992). Early reproduction enables shorter generation interval and better survival to first reproduction event (Bell 1980; Stearns 1992), but delaying first reproduction can lead to longer lifespan with better reproductive success, which can compensate for the loss of early reproductive opportunities (Curio 1983; Stearns 1989; Forslund and Pärt 1995). Consequently, individuals are expected to optimize their reproductive effort according to their phenotypic quality (Pärt 1995). Understanding the factors affecting the variation in age at first reproduction is therefore seen as pivotal for estimating the consequences this variation has on individual lifetime reproductive success (Forslund and Pärt 1995).

Previous work has shown that individuals starting reproduction early in life can be both high-quality individuals capable of handling the costs of early reproduction (Zahavi 1975; Grafen 1990; Hunt et al. 2004; Descamps et al. 2006) or low-quality individuals with low likelihood of surviving to the next reproductive season (Pärt 1995). This suggests that individual determinants of early reproduction can vary especially in response to extrinsic factors, which can include population density (Ferrer et al. 2004; Krüger 2005; Cooper et al. 2009), environmental conditions during early life (Brommer et al. 1998; Prevot-Julliard et al. 2001; Descamps et al. 2008; Millon et al. 2010, 2011), timing of birth (Prevot-Julliard et al. 1999; Descamps et al. 2006), and social systems (Wiley 1974; Hawn et al. 2007; Charpentier et al. 2008). In particular, changes in population density can strongly influence the selection pressure on the age at first reproduction, and early reproduction is thought to be favored during increasing population densities because of low cost and high reward of reproduction due to less intense intraspecific competition and better offspring survival (Cole 1954; Lewontin 1965; Stevenson and Bancroft 1995). In contrast, selection should favor delayed first reproduction in stable or decreasing populations because of the low levels of reproductive success and offspring survival of young first-time breeders (Hamilton 1966; von Biela et al. 2009). Therefore, fluctuating population size might have substantial effects on individual lifetime reproductive success.

The factors influencing the age at first reproduction in females have been studied widely in birds (e.g. Brommer

et al. 1998; Cooper et al. 2009; Millon et al. 2010, 2011) and mammals (e.g. Gaillard et al. 1998; Prevot-Julliard et al. 1999; Beauplet et al. 2006), but the factors underlying the age of first reproduction in males have received less attention (e.g. Komers et al 1996; Pyle 2001; Becker et al. 2008). This is because female reproductive success is easy to quantify, whereas the genetic data or reliable surrogate measures needed to accurately estimate male reproductive success are typically difficult to establish due to the mismatch of observed matings and genetic paternity (Griffith et al. 2002). However, if the field observation of male mating success is a reliable substitute for paternity data, such data can be used to estimate male reproductive success and enable the investigation of the factors underlying male life histories. Such studies are crucial, as males are generally more variable in their reproductive success than females; hence, studying solely variation in female reproductive success may lead to a biased view of the reproductive life histories of the sexes (Stearns 1992; Shuster and Wade 2003).

The black grouse (*Tetrao tetrix*) is a lekking species with strong sexual selection and extremely skewed mating success among males (Höglund et al. 1990; Alatalo et al. 1992). A few viable and active older males (≥2 years old; maximum observed lifespan in our study population is 7 years) obtain the vast majority of the matings at the lek, whereas yearling males are generally unsuccessful (Alatalo et al. 1992). Male mating success is related to multiple condition-dependent ornaments (e.g., eye comb size, Rintamäki et al. 2000; lyre length, Rintamäki et al. 2001; blue coloration of breast feathers, Siitari et al. 2007) and behavioral attributes (e.g., territory centrality, Hovi et al. 1994; fighting rate, and lek attendance, Höglund et al. 1997). Observed matings and genetic paternity are strongly correlated, because the act of mating and partners (if individually color ringed) are easily identifiable; most females (88%, $N = 109$, Lebigre et al. 2007) mate only once; and broods sired by multiple males are very rare (single-male paternity in 96.2% of the broods, $N = 130$, Lebigre et al. 2007). Therefore, observed mating success is an accurate measure of true male mating success and can be used as a reliable substitute for male reproductive success (assuming low variation in female reproductive success). These characteristics make black grouse an ideal species to study the variation in male reproductive success.

As female black grouse prefer older, vigorous males with multiple years of lek display for mates (Alatalo et al. 1992; Kokko et al. 1999) and experimentally increased lek display in yearling males led to substantial fitness costs (decreased survival to the next mating season, decreased future reproductive success, reduced sexual ornament size, Siitari et al. 2007), yearling males are generally assumed to delay their first breeding attempt to the following mating season. Nevertheless, some yearling male black grouse do join leks in their first year and some do successfully mate. However, it is not known what the key determinants of yearling male reproductive effort and mating success are and how these might relate to external factors such as population density, which naturally fluctuates in 6- to 7-year cycles due to the variation in annual breeding success and juvenile mortality (Ludwig et al. 2006; Helle and Wikman 2010).

In this study, we identified the factors underlying the variation in reproductive effort and mating success of yearling male black grouse using detailed behavioral observations and measures of key morphological traits. First, we identified which factors are related to yearling male territoriality, which is crucial to any mating success. Second, we investigated which morphological and behavioral traits are most significantly related to mating success of territorial yearling males. Third, we tested whether territorial and nonterritorial

yearling males differ in their survival to the following mating season and identified the key determinants of survival.

MATERIALS AND METHODS

Study population

We monitored 5 study sites in Central Finland (lat 62°15´N, long 25°00´E) during the period 2001–2008. Each study site consisted of a mixed-sex winter flock and a local main lek with 5–40 territorial males. Because local hunting societies have agreed not to hunt on these leks and in the direct vicinity of our study sites, the age structure of males in our study population can be considered natural. During the study period, the local black grouse population density was first low but then increased rapidly and remained at a high level until the end of the study period (estimates are based on the wildlife triangle censuses in the preceding autumn; Helle and Wikman 2010), which resulted in a highly variable number of observed yearling males in different years and sites in the data (Figure 1).

Winter captures, and morphological and physiological measures

Each January–March, we captured black grouse from winter flocks with oat-baited walk-in traps. We sprung the traps simultaneously, and up to 20 birds were captured in 1 attempt. We covered all the traps immediately after capture to calm down the birds and to reduce any risk of hypothermia. Birds were removed from traps and placed in soft cloth bags only immediately prior to handling. Males were ringed individually with an aluminum tarsus ring and 3 colored plastic tarsus rings and aged as yearlings or older (≥2 years old) according to plumage differences (Helminen 1963). We measured the body mass (to the nearest 10g) and the maximum lyre (tail), tarsus, and wing length (to the nearest 1.0mm, 0.1mm, and 1.0mm, respectively) of all captured individuals. As physiological parameters are likely to influence males' lekking performance, we sampled the blood (1–2ml taken from the brachial vein; Lebigre et al. 2012) from each bird to measure individual hematocrit level (the volume of red blood cells in the total blood volume) and microfilaria parasite counts (hereafter, microfilaria count).

Lek performance, mating success, and survival estimates

We monitored the lekking behavior and mating success of male black grouse from hides at the 5 study sites annually from late April to early May (i.e., during the mating season), daily from 0300 to 0900h. We drew activity maps at regular intervals and recorded the spatial location and current behavior (inactive, hissing, rookooing, or fighting; Höglund et al. 1997) of each male and the presence of females on the leks. All copulations were recorded and partners identified (if ringed). We estimated the relative proportion of behaviors carried out by each male during the entire lekking period, but due to the mutual dependence of the behaviors, we solely used male fighting rate in the analyses. Moreover, we estimated each male's lek attendance (proportional to the highest attending male on the same lek) and territory distance from the lek center from the activity maps according to Rintamäki et al. (1995).

Males that were recorded in ≥30% of the activity maps and in ≥50% of the observation days were classified as territorial. Males that visited the leks less frequently than described above were classified as nonterritorial. This was because a male visiting a lek only occasionally might have had a territory in a nearby lek or no territory at all, and thus its lekking performance (or the lack of it) on the main lek might
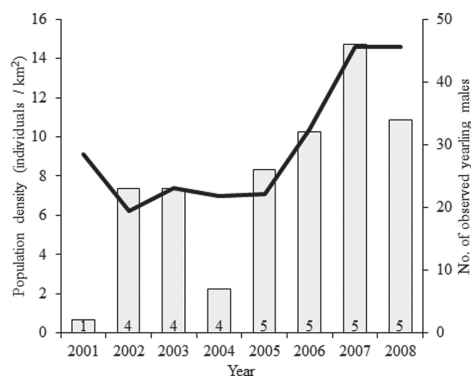
Figure 1
Population density (line) of black grouse in Central Finland (the autumn preceding the captures and observations, based on the national wildlife triangle censuses; Helle and Wikman 2010) and the number of observed yearling males (bars) in our data during the study period 2001–2008. Number of study sites monitored in each year is shown in the bar labels.

have been misleading. Thus, only yearling males classified as territorial were included in the male mating success analyses. We also monitored smaller leks surrounding the main leks, but yearling males classified as nonterritorial on the main lek were not observed elsewhere either. We excluded from the analyses the males ($N = 8$) that were captured in at least 3 consecutive years in the winter flock but had no territories at the main leks, as they may have joined the winter flocks only to forage but were not part of the lek.

We based the survival estimates on field observations. As male black grouse are strongly philopatric to the lek they first start displaying at (Höglund et al. 1999; Caizergues and Ellison 2002; Lebigre et al. 2008), we assumed that territorial males that were never seen again after the mating season had died (Alatalo et al. 1991; Siitari et al. 2007). False deaths (alive, but not seen) are more likely to occur among nonterritorial males, as they never had stable territories on the studied leks (Alatalo et al. 1992). However, as winter flocks formed of black grouse from a large area gather to feed at our study sites and the capturing rate of males is >95% of the number of individuals observed in the winter flock, the observation or capture of these males during winter is highly likely.

Statistical analyses

Our morphological, physiological, and behavioral variables were characterized by collinearity and some missing values, which are known to be problematic in model selection (Nakagawa and Freckleton 2008, 2011; Freckleton 2011). As we could not create relevant, satisfactorily loaded principal components, we selected a biologically relevant combination of individual variables without significant collinearity and missing values to form a suite of candidate models for each analysis (Supplementary Table S1). As the observed number of yearling males varied substantially between years and study sites, some year-sites had zero or very few observations. Thus, we disregarded systematic year and site effects, and combined the data from all sites and years for the analyses.

Table 1

The global models used in the analyses

Response variable	Explanatory variables
Territoriality	Mass + lyre + microfilaria + density
No. of copulations	Log(mass) + log(lyre) + microfilaria + fight + attend + density
Survival[a]	Mass + lyre + microfilaria + fight + attend + density
Survival[b]	Mass + lyre + microfilaria + density

Mass = body mass, lyre = maximum lyre length, microfilaria = microfilaria count, density = population density in the preceding autumn, fight = fighting rate, attend = lek attendance. See MATERIALS AND METHODS for further details on the variables.
[a]territorial males.
[b]nonterritorial males.

We tested which morphological traits and physiological parameters are crucial determinants of the territoriality (territorial/nonterritorial) of yearling male black grouse using binary logistic regression. To investigate the role of morphology and behavior on mating success of yearling males, we excluded the nonterritorial males from the analyses, because territoriality is a crucial step toward mating success in black grouse males, and copulations away from the lek are extremely rare (Alatalo et al. 1996a; Lebigre et al. 2007). We tested whether morphology or behavior had the strongest effects on the number of copulations of territorial yearling male black grouse with zero-inflated general linear model with Poisson error distribution. The coefficient estimates of the global submodels with standard errors are provided in the Supplementary material (Supplementary Table S2). To explore the role of morphological and physiological traits explaining the survival (survived/died) of territorial and nonterritorial yearling males to the following mating season, we used binary logistic regression. In the survival analyses of territorial males, we also included the behavioral variables in the models. The global models of each analysis are shown in Table 1.

All statistical analyses were performed in R version 2.12.2 (R Development Core Team 2011). We used the Information theoretic approach based on Akaike's information criterion (AIC-TH; Burnham and Anderson 2002) model selection procedure to select the variables that best explained our data. As the model selection indicated model uncertainty (Table 2), we used model averaging to combine the set of best models (Grueber et al. 2011). Currently, there is no consensus about the optimal cutoff point for model rejection (Burnham and Anderson 2002; Richards 2005, 2008; Bolker et al. 2009; Burnham et al. 2011; Richards et al. 2011). Therefore, we selected the models with $\Delta_i \leq 3$ (difference in the correct Akaike information criterion [AIC_c]) values between the best and the compared models) for model averaging, as this selection is expected to include the best model (Burnham and Anderson 2002) and was supported by large increases in AIC_c in the model selection after this point. Exceptionally, in the survival analysis of nonterritorial males, the null model had Δ_i of 2.12, but the likelihood ratio test indicated it fitted significantly worse to the data than the best candidate model ($\chi^2 = 4.189$, degrees of freedom [df] = 1, $P = 0.041$). Therefore, in this special case, we only averaged the candidate models with lower Δ_i value than the null model (Table 2).

RESULTS

Territoriality

Our sample comprised 193 yearling males with complete data captured during the period 2001–2008. In total, 80 males were

Table 2

A suite of best candidate models ($\Delta_i \leq 3$) predicting territoriality, mating success, and survival of yearling male black grouse and their AIC$_c$ values, model weights (wi), cumulative model weights (acc wi) and evidence ratios (ER). None of the analyses supported only one best model, but a suite of candidate models had considerable model weights and were averaged. Results of the model averaging are shown in Table 3. Variable names are explained in the footnote of Table 1 (and in more detail in MATERIALS AND METHODS)

Analysis/candidate model	k	AIC$_c$	Δ_i	w_i	acc w_i	ER
Territoriality						
Mass + density	3	254.79	0.00	0.33	0.33	—
Mass + microfilaria + density	4	254.86	0.07	0.32	0.65	1.04
Mass + lyre + density	4	256.71	1.92	0.13	0.78	2.61
Mass + lyre + microfilaria + density	5	256.80	2.01	0.12	0.90	2.73
Mating success						
Lyre + fight + attend + density	5	86.28	0.00	0.34	0.34	—
Lyre + microfilaria + fight + attend + density	6	87.13	0.85	0.22	0.56	1.53
Mass + lyre + fight + attend + density	6	88.27	1.99	0.12	0.68	2.70
Mass + lyre + microfilaria + fight + attend + density	7	88.83	2.55	0.09	0.77	3.58
Mass + fight + attend + density	5	89.17	2.89	0.08	0.85	4.24
Survival[a]						
Microfilaria + fight + density	4	100.14	0.00	0.20	0.20	—
Microfilaria + fight + attend + density	5	101.29	1.15	0.11	0.31	1.78
Lyre + microfilaria + fight + density	5	101.85	1.71	0.08	0.39	2.35
Microfilaria + density	3	102.00	1.86	0.08	0.47	2.53
Mass + microfilaria + fight + density	5	102.40	2.26	0.06	0.53	3.10
Microfilaria + fight	3	103.09	2.95	0.04	0.57	4.37
Survival[b]						
Mass	2	156.35	0.00	0.22	0.22	—
Mass + microfilaria	3	157.28	0.93	0.14	0.36	1.59
Mass + density	3	157.93	1.58	0.10	0.46	2.20
Mass + lyre	3	158.45	2.10	0.08	0.54	2.86

[a]territorial males.
[b]nonterritorial males.

classified as territorial, but the number of territorial yearling males and the proportion of territorial yearling males of all yearling males varied substantially between the years. Model selection indicated that 4 candidate logistic regression models had $\Delta_i \leq 3$ and could therefore be regarded as equally describing the data (Table 2). Population density (Figure 2) and body mass were both significantly positively related to yearling male territoriality, whereas maximum lyre length and microfilaria count both contributed to model fits but were of low overall importance and had no significant individual effects on territoriality (Table 3; Supplementary Table S3). Furthermore, body mass was negatively related to population density (Figure 3) in both the territorial ($r_s = -0.23$, $N = 80$, $P = 0.039$) and the nonterritorial yearling males ($r_s = -0.31$, $N = 113$, $P < 0.001$).

Mating success

Of the 80 territorial yearling males, only 12 successfully copulated (median 1, range 1–10 copulations). Furthermore, only 1 nonterritorial male copulated ($N = 1/113$). All observed matings of yearling males took place during the mating seasons 2005–2007 when the population density was increasing, but not when it was high and stable (i.e., 2008). Moreover, 5 candidate models fitted the data equally well ($\Delta_i \leq 3$; Table 2). Lek attendance, fighting rate, and population density were positively associated with individual mating success (Figure 4), whereas morphology played a minor role (Table 3). The effects of fighting rate and population density were significant in all the averaged models (Supplementary Table S4). The successful yearling males tended to attend the lek more frequently and spent nearly twice the proportion of their attendance time fighting compared to the unsuccessful yearling males. We did not include male territory distance from the lek center in the analysis due to its collinearity with male fighting rate ($r_s = -0.45$, $N = 80$, $P < 0.001$) and lek attendance ($r_s = -0.52$, $N = 80$, $P < 0.001$). Instead, we tested the relation
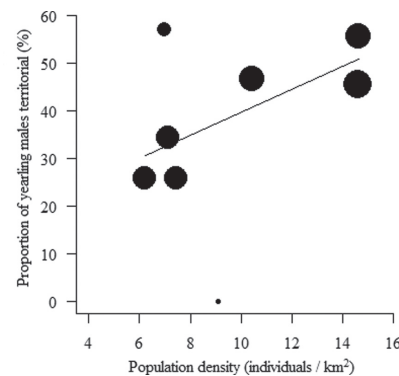

Figure 2
The relationship between population density and the proportion of territorial yearling males (of all yearling males). Symbol size is related to the total number (log transformed) of observed yearling males in each study year. In 2001, only 1 study site was monitored and both yearling males observed were nonterritorial (i.e., 0% territorial).

of the number of copulations to the male territory distance from the lek center separately: Yearling males who copulated had territories closer to the lek center than unsuccessful territorial yearling males ($r_s = -0.35$, $N = 80$, $P = 0.002$).

Survival

There was no significant difference in survival to the following mating season between the territorial (58%: 46 of 80 survived)

Table 3

The coefficient estimates, unconditional standard errors, and relative importance of the explanatory variables after model averaging in territoriality, mating success, and survival analyses. Variable estimates, standard errors, and significance for each averaged model are shown in the Supplementary material (Tables S3, S4, S5 and S6)

Analysis/variable	Coefficient	Unconditional standard error	Relative importance	Variable significance
Territoriality				
(intercept)	−0.373	0.153		
Body mass	0.870	0.328	1.00	a
Maximum lyre length	0.035	0.116	0.28	ns
Microfilaria count	0.216	0.299	0.49	ns
Population density	0.957	0.330	1.00	a
Mating success				
(intercept)	−56.584	32.015		
Body mass	−1.898	3.471	0.35	ns
Maximum lyre length	11.325	5.986	0.91	b
Microfilaria count	−0.090	0.453	0.37	ns
Fighting rate	6.596	1.707	1.00	a
Lek attendance	1.814	1.581	1.00	ns
Population density	0.361	0.073	1.00	a
Survival[a]				
(intercept)	0.437	0.270		
Body mass	0.007	0.063	0.11	ns
Maximum lyre length	0.056	0.138	0.14	ns
Microfilaria count	1.750	0.757	1.00	a
Fighting rate	0.970	0.654	0.87	b
Lek attendance	−0.107	0.221	0.19	ns
Population density	−0.956	0.647	0.92	a
Survival[b]				
(intercept)	−0.093	0.194		
Body mass	0.790	0.414	1.00	b
Maximum lyre length	−0.005	0.061	0.14	ns
Microfilaria count	0.111	0.215	0.26	ns
Population density	−0.056	0.136	0.19	ns

Variable significance in averaged candidate models is expressed as *a* (significant effect in all averaged models), *b* (significant effect in at least one of the averaged models), and ns (no significant effects in any of the averaged models).
[a]territorial males.
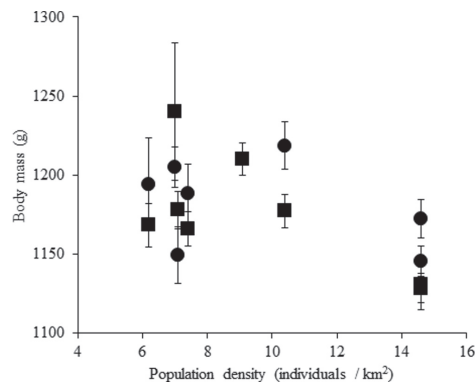[b]nonterritorial males.

Figure 3
The negative relationship between body mass ($\bar{x} \pm$ standard error, SE) of territorial (circles) and nonterritorial (squares) yearling male black grouse to population density. On average, territorial yearling males were heavier than nonterritorial ones. The reverse pattern in 2004 (population density: 7.0 individuals/km²) is due to the low sample size with bias toward very heavy nonterritorial males (indicated by a large SE). In 2001 (population density: 9.1 individuals/km²), only 2 yearling males were observed and both were nonterritorial.
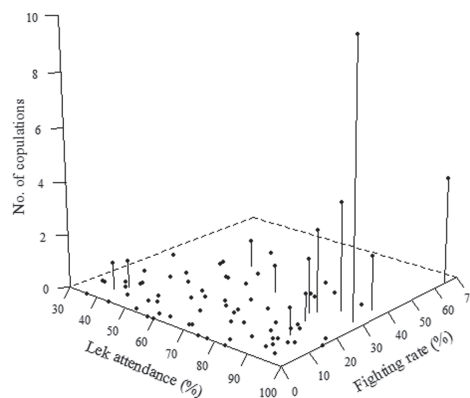

Figure 4
The relationship between the number of observed copulations, lek attendance (%), and fighting rate (%) among territorial yearling male black grouse. Territorial yearling males that were frequently present at the lek and had high fighting rate were most likely to gain mating success.

and nonterritorial (48%: 54 of 113 survived) yearling males (χ^2 = 0.336, df = 1, P = 0.562). Thus, 6 candidate models for territorial yearling male survival and 4 candidate models for nonterritorial yearling male survival fitted the data equally well ($\Delta_i \leq 3$; Table 2). Fighting rate and microfilaria count were positively related and population density negatively related to the survival of territorial yearling males, whereas morphology and lek attendance were less important (Table 3; Supplementary Table S5). In contrast, body mass was positively related to survival in nonterritorial males, with other factors being of minor importance (Table 3; Supplementary Table S6).

DISCUSSION

Early reproduction is a crucial component of lifetime fitness, so it is fundamental to understand the drivers both of early reproductive effort and reproductive success. Territoriality, mating success, and survival of yearling male black grouse were related to both individual body condition and lekking behavior but in different proportions. Although yearling male territorial status (territorial/nonterritorial) was mainly determined by body mass, mating success was most strongly related to male lekking behavior, more specifically fighting rate and lek attendance. Survival to the following mating season did not differ between territorial and nonterritorial yearling males but was related to different factors. Moreover, our results indicate that population dynamics might have substantial effects on reproductive effort, mating success, and survival in yearling male black grouse. Hence, male black grouse in good body condition may be capable of establishing territories and can gain mating success as yearlings without direct survival costs, which can have a significant effect on male lifetime fitness. However, as there can be trade-offs between early reproductive effort and future reproductive success and/or survival (Williams 1966; Bell 1980; Stearns 1989), a longitudinal individual-level approach is needed to comprehensively understand the effects of age at first reproduction on lifetime fitness.

Territoriality

Territorial yearling male black grouse were significantly heavier than nonterritorial yearling males. Body mass is a key feature explaining territoriality in many lekking species (e.g. Balmford et al. 1992; McElligott et al. 2001; Alonso et al. 2010). Moreover, lekking is energetically costly (Vehrencamp et al. 1989, Höglund et al. 1992), and heavy males are assumed to be better able at maintaining their muscle stores and dominance than light males (Bachman and Widemo 1999). In black grouse, dominance is largely determined by fighting success, and victorious males have the most central territories (Alatalo et al. 1991; Hämäläinen et al. unpublished data). However, body mass is not directly related to pairwise fighting success in yearling or older males, as other factors, including experience, may be more important in determining the outcome of fights (Kokko et al. 1998; Kokko et al. 1999; Hämäläinen et al. unpublished data). Instead, body mass is related to fighting rate (Hämäläinen et al. unpublished data) indicating that greater body mass in territorial yearling males is more likely linked to the ability to support the energetic costs of lekking, rather than the likelihood of succeeding in contests per se (see also Lebigre 2008).

Mating success

Territoriality is a crucial step toward mating success in many lekking species (e.g. Apollonio et al. 1989; Balmford et al. 1992; Höglund and Alatalo 1995). Even so, most yearling male black grouse (nearly 60% in this study) did not establish territories during their first mating season, and only 15% of the territorial yearling male black grouse managed to copulate. Moreover, as mating away from leks is rare (Lebigre et al. 2007), yearling male mating success in this species is certainly very low. Although body mass was an important determinant of yearling male territoriality, it did not directly relate to mating success, unlike in several other lekking species (e.g. Balmford et al. 1992; McElligott et al. 2001; Alonso et al. 2010). Although lyre length is related to mating success of older male black grouse (Rintamäki et al. 2001), it is unlikely to be an important determinant of yearling male mating success, despite its contribution to most of the best candidate models. As there is only minor overlap in the lyre length of yearling and older male black grouse (mean ± standard deviation [SD]: 190 ± 9 and 223 ± 12 mm for yearling (N = 92) and ≥2-year-old males (N = 103), respectively; Siitari et al. 2007), a relatively long lyre of a yearling male is nevertheless shorter compared to the lyres of older males on the same lek. This applies to other male sexual ornaments as well, and there is very little overlap in ornament size or quality (body mass, eye comb size and redness, and blue coloration; Siitari et al. 2007) between yearling and older males. Therefore, if mate choice is based purely on morphological traits, it is unlikely that yearling males would be selected and hence it is unsurprising that yearling male mating success in black grouse is unrelated to morphological traits.

Instead, yearling male reproductive success was directly related to lekking behavior and particularly to fighting rate. Fighting rate largely determines male dominance, with the most actively fighting, victorious males being the most dominant and reproductively successful (Alatalo et al. 1991; Komers et al. 1996; McElligott and Hayden 2000). Furthermore, high attendance at the lek is pivotal for mating success in many lekking species (e.g. Apollonio et al. 1989; Hill 1991; Fiske et al. 1998; Friedl and Klump 2005). In this study, lek attendance contributed to the best models explaining mating success of yearling male black grouse, but the effect of this variable was not significant in any of the best models. However, high lek attendance is important for male black grouse defending central territories, as unoccupied central territories are readily reoccupied by other males (Hovi et al. 1994, Rintamäki et al. 1999). Hence, in male black grouse, a combination of high fighting rate and high lek attendance are needed for high reproductive success.

In lekking species, the most successful males usually occupy central territories (e.g. Höglund and Lundberg 1987; Balmford et al. 1992; Hovi et al. 1994; Partecke et al. 2002; Shorey 2002, Bro-Jørgensen and Durant 2003). Male black grouse get closer to the lek center with increasing age and lekking experience, and territory centrality can be seen as an honest cue of male quality and viability (Kokko et al. 1998; Kokko et al. 1999). Leks are sometimes seen as queues where males move toward the lek center as they get older and more experienced (McDonald 1993; Bro-Jørgensen 2011). However, in black grouse, the queue discipline is not strict, and other male characteristics can strongly affect male mating success (Kokko et al. 1998). Our results indicate that yearling males that managed to copulate had territories closer to the lek center than their unsuccessful peers, supporting the idea that territory centrality is an honest cue of male quality irrespective of age.

All observed copulations of yearling males occurred in 2005–2007, when the local black grouse population started to increase after a few years of low population density (Helle and Wikman 2010). We showed that yearling male black grouse were more likely to be territorial when population density was increasing or high. Consequently, yearling males

were more likely to mate in increasing population density, as they presumably had better access to females due to the presence of fewer older males in relation to yearling males compared with the situation under declining or low population density (Stevenson and Bancroft 1995; Mysterud et al. 2003). These results support the theory suggesting that early reproduction effort is favored in increasing populations (Cole 1954; Lewontin 1965) and are similar to a previous study on male Soay sheep (*Ovis aries;* Stevenson and Bancroft 1995). Some studies report a delayed age at first reproduction during increasing or high population density, through competition for limiting resources such as nest sites (Ferrer et al. 2004; Krüger 2005; Cooper et al. 2009). However, such resources are not as important for male black grouse, and therefore unlikely to be limiting their opportunities to mate.

Survival

Survival to the following mating season did not differ between territorial and nonterritorial yearling male black grouse. However, early reproductive investments can have negative effects on future reproductive success and/or survival (Williams 1966; Bell 1980; Stearns 1989). The fitness costs of reproductive investments usually depend on individual phenotypic quality and age (e.g. McElligott et al. 2003; Tavecchia et al. 2005; Hadley et al. 2007; Hamel et al. 2009) and can be related to external factors such as population density (Clutton-Brock et al. 1996; Festa-Bianchet et al. 1998). Therefore, the possible fitness costs of early reproductive effort in male black grouse could be deferred to their future reproductive success, and hence, were not seen in their survival to the following mating season.

For territorial yearling males, survival was positively related to fighting rate and microfilaria count. Display activity is positively related to testosterone level (Alatalo et al. 1996b, Siitari et al. 2007), but as testosterone is immunosuppressive, territorial male black grouse trade off increased display activity with lower immunity (Alatalo et al 1996b). Combined with the energetic costs of display (Vehrencamp et al. 1989, Höglund et al. 1992), this leads to increased microfilaria count (Lebigre 2008). As surviving territorial yearling males had higher microfilaria counts and fighting rates, both of which are costly, this indicates that the surviving territorial yearling males were in good condition and capable of handling the energetic costs of display, a pattern similar to that in fallow deer (*Dama dama*, McElligott et al. 2002). Moreover, survival of territorial yearling males was also negatively related to population density, which might reflect the favorable natal environmental conditions during population increase that enabled individuals with low body mass to survive to yearlings (see Figure 3).

Among the nonterritorial yearling males, survival was positively related only to body mass. Because territorial yearling males were heavier than nonterritorial yearling males, this indicates that body mass is a crucial parameter for all yearling males' survival. Predation by goshawk (*Accipiter gentilis*) and red fox (*Vulpes vulpes*) is the main cause of mortality in male black grouse, with peaks during winter and especially in early summer, when males undergo a postnuptial molt (Angelstam 1984; Caizergues and Ellison 1997; Warren and Baines 2002). Molting is energetically costly (Murphy and King 1992), and the quality of the new feathers is related to body condition (Bortolotti et al. 2002). Poor-quality feathers can reduce survival by reducing flight capability and thermoregulation (Nilsson and Svensson 1996; Dawson et al. 2000). For black grouse, high predation pressure and thermoregulatory constraints during winter emphasize the importance of high body mass during molt and thus on survival.

CONCLUSIONS

We showed that territoriality, mating success, and survival of yearling male black grouse were related to both individual morphological and behavioral traits but that the determinants of each were different. Though yearling male mating success is generally low, most male black grouse do not achieve any copulation during their lifetime (Alatalo et al. 1992); hence any copulation as a yearling may be important.

Our results indicate that yearling males in good condition (heavier body mass) showed higher reproductive effort and that behavior primarily determined their mating success. Furthermore, population-level effects impacted yearling male reproductive effort, mating success, and survival. Our results support earlier conclusions that population-level effects are important determinants of age at first reproduction, and therefore also the length of reproductive lifespan. Understanding that these parameters are not only influenced by individual-level effects, but also by broader population processes such as changes in population density, is therefore fundamental to understanding the longitudinal differences in individual lifetime fitness.

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