

Determinants of age at first reproduction and lifetime breeding success
revealed by full paternity assignment in a male ungulate.

S. S. Markussen^{*1}, I. Herfindal¹, A. Loison², E. J. Solberg³, H. Haanes⁴, K. H. Røed⁵,
M. Heim³ and B.-E. Sæther¹

- ¹ Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of
Science and Technology, Trondheim, Norway.
- ² CNRS, UMR 5553 Laboratoire d'Écologie Alpine, Université de Savoie, Le Bourget
du Lac, France
- ³ Norwegian Institute for Nature Research (NINA), Trondheim, Norway
- ⁴ The Norwegian Radiation Protection Authority (NRPA), Oslo, Norway
- ⁵ Department of Basic Sciences and Aquatic Medicine, Norwegian University of Life
Sciences, Oslo, Norway

*Corresponding author: stine.markussen@ntnu.no

ORCID ID: <https://orcid.org/0000-0002-5351-8976>

Abstract

Age at first reproduction is an important determinant of individual variation in reproductive success in ungulates, but few studies have examined its relationship with later fitness-related traits in males. We used a long-term individual based study of a harvested moose population to quantify the individual reproductive performance and survival of males, as well as to examine the determinants of age at first reproduction and consequences of age at first reproduction on lifetime breeding success. The probability that a male successfully reproduced at the age of two was negatively related to the mean age of adult males in the population, but the relationship weakened with increasing population size. Large antlers and large body mass relative to other males in the population increased the number of calves sired at their first successful mating season. In addition, those that successfully reproduced as two year-olds were more likely to sire calves the next year, making them more productive at a given age compared to those that first reproduced at the age of three or older. We emphasize the importance for males to start reproducing as soon as possible in a harvested population to gain lifetime fitness benefits, as surviving the hunt is a major determinant of reproductive success in this population. We found no costs of early reproduction in males, hence leading to high individual heterogeneity in male reproductive performance. The apparent lack of reproductive costs could partly be explained by the age distribution in the population, individual variation in early-life body mass and antler size, and differences in probabilities of being hunted of successful and unsuccessful males.

Key-words: Age at maturity, age structure, Alces alces, hunting, individual heterogeneity, male mating success, life history, sex ratio

Introduction

Individual reproductive effort at a particular time is expected to be a function of a trade-off between the costs of current reproduction and subsequent reproductive potential (Stearns 1992). Individuals with an early age at first reproduction (AFR) may experience higher lifetime reproductive success as they have a higher number of lifetime reproductive attempts (Oli and Dobson 1999, Herfindal et al. 2015). On the other hand, they may also experience reduced future reproduction and/or survival if they cannot sustain the associated energetic demands of reproduction (Williams 1966, Reiter and Le Boeuf 1991). A young AFR is typically favoured by natural selection because it reduces the period during which animals risk dying before reproducing (Stearns 1976).

The causes and consequences of variation in female AFR on individual fitness and population demography have been studied in a wide variety of species (e.g. Reiter and Le Boeuf 1991 in elephant seals, *Mirounga angustirostris*; Festa-Bianchet et al. 1995 in bighorn sheep, *Ovis canadensis*; Lambin and Yoccoz 2001 in voles, *Microtus townsendii*; Descamps et al. 2006 in squirrels, *Tamiasciurus hudsonicus*; Robbins et al. 2006 in gorillas, *Gorilla gorilla beringei*; Aubry et al. 2009 in black-legged kittiwakes, *Rissa tridactyla*), but few have studied the variation in AFR in mammalian males. Estimating the number of offspring sired by males is challenging, especially in species where males do not take part in parental care (Clutton-Brock 1991), and because observation do not allow accounting for the possibility of extra-pair copulation (in case of monogamous species). Hence, studies of AFR in males and the possible costs on growth, survival and reproduction, have in most cases been based on male participation during mating (Clinton and Le Boeuf 1993, Komers et al. 1997, Kruuk et al. 1999) and not on breeding success.

This may be about to change as the advent of genetic methods of parentage assignment allows for determining fathers (Haanes et al. 2013). However, the number of studies where genetic material from a sufficient number of offspring have been collected and can be combined with a long-term monitoring of males is still limited (Festa-Bianchet 2012 for a review; and e.g. Coltman et al. 2002, Martin et al. 2016 in bighorn sheep, *Ovis canadensis*; Vanpé et al. 2009 in roe deer, *Capreolus capreolus*; Nussey et al. 2009 in red deer, *Cervus elaphus*) and this has hampered our ability to identify the causes and extent of among-individual variation in male reproductive success.

In polygynous species, male reproductive success depends on their ability to outcompete rival males and on the number of females they can fertilize (Festa-Bianchet et al. 1990, Komers et al. 1994, Clutton-Brock and McAuliffe 2009, Clutton-Brock 2017). Thus, males usually compete intensely for mates, which may create large variation in male mating success (Emlen and Oring 1977, Clutton-Brock 1988) and, in turn, strong selection on sexual traits (such as horns, antlers, tusks; Geist 1966; Andersson 1994). In ungulates, body mass dimorphism increases with degree of polygyny (Loison et al. 1999), and at the intra-specific level, positive relationships between male reproductive success, age, body size and horn or antler size have been reported for several species (e.g. Coltman et al. 2002, Kruuk et al. 2002, Mainguy et al. 2009, Festa-Bianchet 2012). Moreover, since reproductive success depends strongly on phenotypic condition, males may be sensitive to a bad start in life (Solberg et al. 2004). As a consequence, factors that affect early development, including maternal effects and environmental conditions (Lindström 1999, Monteith et al. 2009, Thalmann et al. 2015), can have large impact on AFR.

Because male mating success depends on body size relative to other males in the population, the costs and benefits of mating at a given age is likely to also depend on the population sex and age structure (Mysterud et al. 2003, Sæther et al. 2003, 2004, Clutton-Brock 2017). Fluctuating age and sex structure are common in unmanaged (Coulson et al. 2001) and managed ungulate populations (Langvatn and Loison 1999, Mysterud et al. 2002, Festa-Bianchet 2017) and offer different competitive environment for males about to mate. Hence, young males, which have not yet reached full body size, may account for a higher proportion of conceptions when adult sex ratio is strongly female-biased (Stevenson and Bancroft 1995), and young males can also be more likely to mate when the proportion of older males in the population is small (Newbolt et al. 2017). This may be particularly so in harvested populations that often have very biased sex ratios and young male age structure (Solberg et al. 2002). In turn, this can affect demography (e.g. Ginsberg and Milner-Gulland 1994, Milner et al. 2007) and genetic variability in the population by affecting the amount of genetic drift (the effective population size, e.g. Ryman et al. 1981, Sæther et al. 2009) and selection processes through female mate choice (Bowyer et al. 2007).

In this study, we used 28 years of detailed life history data and genetic parentage assignment (Haanes et al. 2013, Kvalnes et al. 2016) from a harvested, insular population of moose (*Alces alces*) to investigate the causes and consequences of AFR in males. In almost all individuals, life histories have been monitored since birth (e.g. Sæther et al. 2003, 2004, 2007, Solberg et al. 2007), and during the study period the population has undergone large fluctuations in age and sex structure. This gives us a unique opportunity to quantify the reproductive performance of almost all males on the island and to study

the variation in AFR relative to several individual and population characteristics. Specifically, we examined the separate effects of the population sex and age structure and individual variation in early body mass on the probability of males to reproduce as two year-olds (successfully mate as yearlings). Controlling for population size, we expected a larger proportion of young males to successfully breed in years with a more female-biased sex ratio and lower mean age of males, and that large body mass and antler size increased the chances of siring calves. We next quantified the variation in age-specific survival and reproductive success of males in relation to previous reproductive success and assessed if there were any apparent direct costs of siring calves on future reproduction and survival.

Materials and methods

STUDY SITE AND DATA COLLECTION

In 1985, three moose colonized the island of Vega (119 km², 65°40'N, 11°55'E) off the coast of northern Norway. The population increased and since 1991 harvesting has kept the annual breeding population between 20 and 40 individuals (Haanes et al. 2013).

Moose hunting occurs annually in October, usually after the peak of the rut. Hunting permits are usually issued as a fixed number of calves, adult males and adult females (or unspecified animals). Due to varying age- and sex-specific harvesting, the proportion and age of males in the population has been fluctuating (Herfindal et al. 2014; Fig. 1a-c).

Environmental conditions have little effect on the dynamics of this population (Sæther et al. 2007), and were therefore ignored in this study. More information about the moose population at Vega can be found in Sæther et al. (2003) and Solberg et al. (2008).

Using genetic parentage assignment, we developed a 28-year long pedigree (1984-2012) for the population (Haanes et al. 2013). The pedigree includes individual data on reproduction and survival of 254 males, of which 135 survived the first year (and could potentially have been sexually mature during the mating season). Of these, 23 became fathers for the first time as two-year olds, 13 as three-year olds, nine as four-year olds and two as five-year olds. Of all calves sampled, 92 % was assigned to a father. The annual mean AFR of males in the population varied between 2 and 4 years (Fig. 1d). Since 1992, all new calves that survived the annual hunt, has been radio collared and measured annually in January-March (except in 2003 and 2008). Also, female moose are observed around potential parturition dates and recorded with/without calves. During our study period, 16 calves have been recorded right after birth that died during summer. However, none of these calves were sired by male first-time breeders and hence did not influence our analysis of AFR. Body mass in early life was measured as carcass mass for males shot during the autumn hunt or live body mass (about twice the carcass mass) as measured when captured for radio collaring in winter, adjusted for date of weighing (Herfindal et al. 2006; Kvalnes et al. 2016). To be able to compare body mass from individuals with different weight type (live or carcass, Fig. A1) and age, we used the standardized residuals from a separate linear model for carcass mass and a linear mixed model for live body mass with age class (age: 0-1, 1-2, 2-3, 3 and older; c.f. Herfindal et al. 2006, Solberg et al. 2008) and year as fixed variables, and individual identity as random variable. However, for further analyses, we only used live body mass for calves (approx. 8 months of age), and carcass mass from yearlings (16-18 months), since these age groups are not affected by reproductive costs to the same degree older individuals

(Solberg et al. 2008). In the case of repeated sampling of individuals (mass measured at 8 months and 16-18 months of age), we used the mass measured at 16-18 months as this is the measurement closest in time to age of potential mating. Antler size was measured as the mean number of antler points (> 2 cm) of right and left antler from observations of live animals and from shot individuals (Fig. A2).

Because female moose can produce up to two calves per reproduction, we quantified the mating success of males as number of females successfully mated and the reproductive success as number of calves sired. These measures were closely related ($r = 0.97$, $df = 265$, $p < 0.001$) and gave qualitatively the same results in the models used in this study. Male age at mating is expressed as their age during the rutting season while male AFR is expressed as their age when their calves are born. Hence, a male can at best mate as yearling (1-year old) and reproduce as 2-year old. It is important to note that a male may be dead (hunted) by the time the calves are born (e.g. killed by hunters immediately after rutting season).

STATISTICAL ANALYSES

Using ordinary logistic regression (binomial family, logit link function), we first examined the probability to successfully reproduce as a two year-old in relation to demographic parameters. Demographic parameters included Adult sex ratio (number of adult males/number of adult females), the mean male age in the population and total population size of adults ($N = \text{adults} > 1.5 \text{ years old}$). We included the interaction between and mean male age and N and adult sex ratio. . Thereafter, we examined if residual body mass or antler size affected the probability to reproduce at the age of two.

For this we used smaller data sets, as we did not have body mass ($N = 86$) or antler size ($N = 62$) for each individual. Moreover, using generalized linear models (GLMs) with Poisson family and log link function, we analysed the relationship between the number of calves sired by first-time breeders and their residual body mass or antler size, their relative age (age of individual male - mean adult male age in the population), population size and adult sex ratio. Due to challenges with regard to modelling reproductive output (Kendall and Wittmann 2010), the number of calves sired by first-time breeders were also analysed with a Poisson error structure with square root function, a generalized Poisson distribution and a linear model with Gaussian error structure. These models gave the same qualitatively results.

We used multistate models (E-SURGE, version 1.9.0, Choquet et al. 2009a) to assess the influence of age, previous reproductive status, AFR and possible interactions on hunting mortality η , natural mortality ϕ and reproduction ψ probabilities. Initially we assessed that the Jolly-Move (JMV) model (Brownie et al. 1993) satisfactorily fitted the data in U-CARE (version 2.3.2, Choquet et al. 2009b; $\chi^2 = 0.273$, $P < 0.999$). Males, who potentially can father many litters, were divided into three states: no reproduction (ψ^{NR}), sired one or two calves (ψ^{1-2}) and sired three or more calves (ψ^{3+}). The capture probability was fixed to 1 as we assumed no error in determination of survival and reproductive status. Males were divided into four age classes, partly based on their AFR and low sample size at the older ages: 1: calves, 2: yearlings, 3: 2.5 years old, and 4-11: 3.5 – 10.5 years old (no males were older than 11 years). First, we estimated the hunting η , natural mortality ϕ and reproduction ψ probabilities for all males, including the effect of age class and previous reproductive event. Thereafter, we assessed the additional effect

of AFR on the probabilities to reproduce (ψ^{NR} , ψ^{1-2} or ψ^{3+}) the following year. AFR as 3-5 years old was pooled together for sample size reasons, resulting in two AFR groups: AFR 2: AFR as two years old and AFR 3+: AFR as 3 years old and older. In this case, we excluded the non-breeders, as these do not affect reproduction probabilities for the breeders. For more details about the models, see Supplementary material (Appendix A2).

The relationship between AFR and lifetime breeding success was examined using a negative binomial model of number of calves sired in relation to AFR, accounting for life span (ln-transformed). Males still alive at the end of the study were excluded from this analysis (N = 5). Model selection was based on the principle of parsimony assessed by AICc (Burnham and Anderson 2002).

Results

The highest ranked model explaining probability to reproduce as a two year-old included the interaction between the population mean male age and total population size ($\beta \pm \text{SE}$ (95 % CI) logit scale interaction = 0.13 ± 0.06 (0.03; 0.23)) Hence, given a low population size, there was a higher probability to successfully mate as a yearling (reproduce at the age of two) when there were few older males in the population (Fig. 2a). However, for high population sizes, the relationship between probability to successfully mate as a yearling and mean male age in the population was weak. Neither antler size nor the age-specific body mass were included in the best models (Table 1). However, the number of calves sired by successful first-time breeders increased with increasing antler size (Fig. 2c, $\beta = 0.12 \pm 0.06$ (0.00; 0.24)) and increasing residual body mass (Fig. 2d; $\beta = 0.27 \pm 0.11$ (0.06; 0.50)). The average antler size of successful yearlings was 2.83 antler

points (SD = 0.62, N = 12) compared to 2.58 antler points (SD = 0.62, N = 50) for yearlings that did not mate successfully. The averaged calf body mass (live weight; approx. 8 months of age) was 204 kg (SD = 15.34, N = 16) for those who successfully mated later that year, compared to 200 kg (SD = 23.73, N = 72) for the unsuccessful males.

Among males ≥ 1 -year old (N = 135), lifetime calf production ranged from 0 to 44 calves, with an average of 3.20. The associated variance was 59.39 and the standardized variance (σ^2/\bar{x}^2) was 5.80. Some males mated with up to eight females each year, but a large proportion of males never sired calves (65 % of males' ≥ 1.5 year old; 26 % of males' ≥ 3.5 year old) during their lifetime. The annual mean age of fathers varied between 1.5 and 6.5 years. According to the AICc, age class and previous reproductive success best explained the male reproductive success in the current year (Fig. 3a-b; Appendix A2; Table A1, A2). Those that reproduced as two year-olds were more likely to sire three or more calves at the age of 3 years (not reproduced the year before: $\psi^{NR \rightarrow 3+} = 0.10 \pm 0.04$; sired one or two calves: $\psi^{1-2 \rightarrow 3+} = 0.38 \pm 0.09$; sired three or more calves: $\psi^{3+ \rightarrow 3+} = 0.57 \pm 0.07$). Similarly, older males (3.5-10.5 years old) were more likely to successfully sire calves the next year if they had sired calves in the previous year (not reproduced the year before: $\psi^{NR \rightarrow 3+} = 0.17 \pm 0.05$; sired one or two calves: $\psi^{1-2 \rightarrow 3+} = 0.47 \pm 0.08$; sired three or more calves: $\psi^{3+ \rightarrow 3+} = 0.61 \pm 0.07$; Fig. 3b).

Including AFR in the multi-state models, the most parsimonious model according to AICc retained the effect of age class and AFR on the probabilities to mate (Appendix A1; Table A1, A2). Not including AFR in the models had a much lower support (model including age class and previous reproductive status: $\Delta AICc = 65.86$). Males with AFR

as two year-olds had a higher reproductive success at successive ages (Age 3.5-10.5: AFR2: $\psi^{3+} = 0.66 \pm 0.09$, AFR3+: $\psi^{3+} = 0.46 \pm 0.06$; Fig. 3c-d), which resulted in, on average, a higher cumulative calf production (Fig. 4a) and lifetime breeding success in terms of sired calves (Fig. 4b). For a life span of five years, males with AFR at age two would have sired on average 11.81 calves, while the corresponding number for those starting to reproduce later was 6.39 calves. Hence, starting to mate early is beneficial with regard to lifetime breeding success.

When we looked closer at the 2.5 % most successful males in terms of age-specific number of calves sired (> 3 calves per year); five out of seven started to reproduce as two year-olds. With one exception, their live body mass at eight months and their carcass mass when hunted were above average (positive standardized residuals).

The probability to die from hunting were in general high, especially for calves and yearlings (calves: $\eta = 0.45 \pm 0.03$; yearlings: $\eta = 0.47 \pm 0.05$; 2.5-years olds: $\eta = 0.44 \pm 0.06$; Age 3.5-10.5: $\eta = 0.26 \pm 0.04$). Hunting probability also depended on their reproductive status in the mating season of the same year as they were hunted. Those that had successfully mated had a much lower probability to be killed than unsuccessful males (Age 3.5-10.5: $\eta^{NR} = 0.57 \pm 0.13$; $\eta^{I-2C} = 0.24 \pm 0.07$; $\eta^{3+C} = 0.13 \pm 0.07$).

Discussion

In this long-term study, we show how AFR and reproductive success of males in a large herbivore — the moose — are related to individual characteristics and demographic parameters in a hunted population. Males were more likely to reproduce for the first time as two year-olds when the proportion of older males in the population was low and with a

low population density (Fig. 2a). The successful first-time breeders sired more calves when their antler size and body mass were larger (Fig. 2b-c). Those that successfully reproduced as two year-olds also had a higher probability to sire calves at later ages (Fig. 3) and ended up with more calves for a given life span (Fig. 4). The high harvest rate in the population combined with the lower hunting mortality for males that successfully mated the same year, makes surviving the hunt a main determinant of reproductive success in this population. The fitness benefits of surviving the hunt has also been emphasised in other studies of hunted populations (e.g. Zedrosser et al. 2013).

The relationships found in this study support the expectations that reproductive success of males in polygynous species depends on their ability to prevail against competing males (Festa-Bianchet 2012), e.g. by having larger antlers, body size and more experience than other males in the population (Komers et al. 1997). Younger males are also found to rut more in synchrony with older males when the intra-male competition for mates decreases (Myserud et al. 2008), which suggests that a young male age structure leads to relaxed sexual selection (Myserud et al. 2005).

Body size has been identified as a reliable predictor of male reproductive effort in numerous herbivores (e.g. McElligott et al. 2001, Myserud et al. 2004), but contrary to other studies of male mating effort (Pelletier et al. 2006, Newbolt et al. 2017), our results suggest that the population structure is a better predictor of variation in AFR than individual body condition. Young males may invest less in antlers, as they incur a cost for further body growth (Stewart et al. 2000), and may depend less on these when competing for mates. However, few individuals with data on antler and body size at AFR made it challenging to determine the relative importance of these two traits on the

probability to reproduce for the first time. Since rutting is energetically expensive due to higher activity and reduced feeding (Solberg and Sæther 1994, Clutton-Brock 1988), early breeding effort may limit body growth (Stevenson and Bancroft 1995, Garel et al. 2006) and potentially confound the relationship between body mass and age at first reproduction. However, our results suggest no trade-off between body growth and reproduction, since the majority (seven of the eight) of the most successful males in terms of age-specific calf production had a higher live weight as calf and higher age-specific carcass weight than the population mean. Previous studies at Vega also concluded that smaller individuals show little compensatory growth later in life (Solberg et al. 2008).

In contrast to the scarcity of studies of male reproductive trade-offs, life history relations have been well documented in female vertebrates (reviewed in Hamel et al. 2010), for which many studies indicate a positive covariation between current and future reproduction (e.g. Weladji et al. 2008, Hamel et al. 2009, Fay et al. 2016). This suggests that there is persistent among-individual differences in fitness due to differences in resource acquisition and allocation (van Noordwijk and de Jong 1986) or differences in early-life environmental conditions resulting in cohort effects (Herfindal et al. 2015). Studies of costs of reproduction in males are often rooted in the theory of sexual selection, and refer to the cost of producing or maintaining sexual traits on future survival (Kotiaho 2001, Bleu et al. 2016). In polygynous males, costs of reproduction often arise from energy expenditure and injuries while attempting to mate, weakening the correlation between individual costs and fitness returns, as those losing the mate competition do not sire offspring (Festa-Bianchet 2012). Our study showed that those who established themselves as successful breeders in early life had a higher probability to successfully

mate with several females again, i.e. a positive covariation between early and late reproductive success. This leads to individual heterogeneity in mating success and ultimately a higher lifetime calf production for early-reproducing males. Such quality difference in terms of reproductive success in males has also been shown for other mammals (Arnould and Duck 1997, McElligot and Hayden 2000). This highlights that conditions experienced early in life for males are important (e.g. by affecting the phenotypic quality such as the size of a sexual ornament), and might have lifelong consequences (Lindström 1999, Jensen et al. 2006, Douhard et al. 2014, Lemaître et al. 2014). Young age structure in combination with low population density also makes it more probable that yearlings successfully mate, as there are few older competitors in the population. Such a “silver spoon” effect (e.g. Lindström 1999, Monaghan 2008) will follow yearlings throughout their lives because there is low immigration to the island (20 immigrants over 28 years) and few older competitors. However, to be successful males must also survive the high hunting pressure. We show here that starting early paid off in terms of lifetime breeding success for male, but lifetime breeding success can be used as a fitness proxy only in stable populations. In our case, the population was increasing, especially during the first years, and in this case, offspring produced early in life contribute more to fitness than do offspring produced late in life (Kaar and Jokela 1998). This means that, in terms of fitness, the benefit for males to start reproducing at age two early in our study period, may be even greater than measured here.

Early reproduction may also carry a survival cost in males, as e.g. indicated by the higher survival of Soay rams (*Ovis aries*) prevented from reproducing by castration (Stevenson and Bancroft 1995). However, several studies of wild ungulates have shown

that highly successful males do not suffer survival costs of reproduction (McElligott et al. 2002, Pelletier et al. 2006, Bergeron et al. 2008, Bonenfant et al. 2009). Indeed, we rather found a positive covariation between reproduction and survival as the probability to be killed during hunting was lower for those males that mated successfully the same autumn. The specific mechanism behind this is unknown, but could arise because hunters choose not to shoot the largest males (Kvalnes et al. 2016), which in turn may produce a positive covariation between male reproductive success and survival. Another explanation could be that successful males are also more successful in hiding (e.g. a more shy behaviour) during the hunting season (Ciuti et al. 2012).

The moose has a fast life cycle and therefore lower AFR and higher reproductive effort in young males, than in other similar-sized ungulates (Gaillard 2007, Festa-Bianchet 2012). The high reproductive success of older males, irrespective of their AFR, might be a combination of high body mass compared to other males, higher probability to survive the hunt, and a female preference for older males. Female mate choice has been shown to be an important determinant of male reproductive success also in mammals (Clutton-Brock and McAuliffe 2009). Indeed, female moose are inclined to delay conception when the mean age of males in the population is low (Sæther et al. 2003, 2004, Herfindal et al. 2014), indicating a strong mating preference for older males.

Most population models are female-based and neglect the presence of males. However, males are important for population processes and dynamics (e.g. Mysterud 2002, Sæther et al. 2003, 2004, Rankin and Kokko 2007, Herfindal et al. 2014), and knowledge of the variation in male reproductive success is imperative for the understanding of evolutionary processes such as sexual selection and effective population size (e.g. Engen et al. 2005,

Sæther et al. 2009). To develop more realistic population models, we therefore need to include both sexes. Although challenging in the wild for species where males do not contribute to parental care, cheaper and better genetic analyses makes it increasingly more possible to study male life histories by combining marked individuals with genetic parental assignments (Festa-Bianchet et al. 2017).

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- Supplementary material: Appendix A1, Appendix A2

TABLES AND FIGURES

Table 1. AICc-based ranking of models explaining **(a)** the probability to reproduce as a two year old among male breeders (P(reproduce at age 2)) and **(b)** the number of calves sired at age at first reproduction (AFR) using 1. data on population properties, 2. data on individual body mass or 3. data on antler size. Shown are the three highest ranked models considering the following individual and demographic parameters as explanatory variables: The population mean male age (Male Age), population density (N), adult sex ratio, relative age (Age of individual - population mean male age), antler size and residual body mass. Δ AICc is the difference in AICc of each model relative to the highest ranked model. AICc weights (AICc-w) were calculated separately for each model selection. * indicates interaction between parameters. For details regarding the model structures, see Methods.

Model specification	AICc	ΔAICc	AICc-w
(a) P(reproduce at age 2)			
<i>1. Population properties</i>			
Male Age*N	112.1	0.00	0.352
Male Age*N + Adult sex ratio*N		0.31	0.302
Male age*N + Adult sex ratio		2.00	0.129
<i>2. Body mass</i>			
N	83.2	0.00	0.405
Male Age		1.71	0.172
Male Age*N		2.01	0.149
<i>3. Antler size:</i>			
N	47.9	0.00	0.164
Male Age		0.62	0.120
Male Age + N		0.79	0.110
(b) Number of calves sired at AFR:			
<i>3. Antler size:</i>			
Antler size	43.3	0.00	0.332
Intercept		0.95	0.206
Antler size + N		3.52	0.057
<i>2. Body mass</i>			
Residual body mass	119.5	0.00	0.360
Residual body mass + Relative Age		1.74	0.151
Residual body mass + Male Age		2.36	0.111

FIGURE LEGENDS

FIGURE 1. Annual variation in demographic parameters of the moose population at Vega from 1985-2012. **(a)** Number of adult males (≥ 1 years old; black circles), adult females (grey circles), and total population size (N, dashed line) **(b)** Adult sex ratio (number of adult males/number of adult females), **(c)** mean adult male age in the population, and **(d)** mean age at first reproduction (AFR) including number of individuals per year reproducing for the first time.

FIGURE 2. (a) Predicted relationships \pm SE between the probability to reproduce as a two year-old, $P(\text{reproduce at age } 2)$, and the population mean age for the 25 % quantile (dashed lines) and 75% quantile (solid lines) of population size (N). Grey and black points are below and above mean population size during the study period. **(b)** Relationship between the numbers of calves sired at age at first reproduction (AFR) \pm SE and antler size, and **(c)** residual body mass \pm SE (relative to measuring method, age and year).

FIGURE 3. Probability to reproduce \pm SE for male moose according to age class and first reproduction (AFR) **(a)** Probability to reproduce one or two calves (ψ^{1-2}) for all males, **(b)** Probability to reproduce three or more calves (ψ^{3+}) for all males. ■ = No reproduction (NR), ● = Sired one or two calves, and ▲ = Sired three or more calves at previous state **(c)** Probability to reproduce one or two calves (ψ^{1-2}) for males that reproduced at least once, **(d)** Probability to reproduce three or more calves (ψ^{3+}) for males that reproduced at least once. ■ = AFR 2 years old, and ● = AFR 3 years old and older. Transition probabilities are from Appendix A1, Table A2.

FIGURE 4. (a) Mean cumulative calf production \pm SE by male moose according to their age and age at first reproduction. ■ = AFR 2 years old, and ● = AFR 3 years old, ▲ = AFR 4 years old, ▼ = AFR 5 years old. **(b)** Mean total calves sired \pm SE by male moose according to their age at death. ■ = AFR 2 years old, and ● = AFR 3 years old and older.

FIGURE 1.

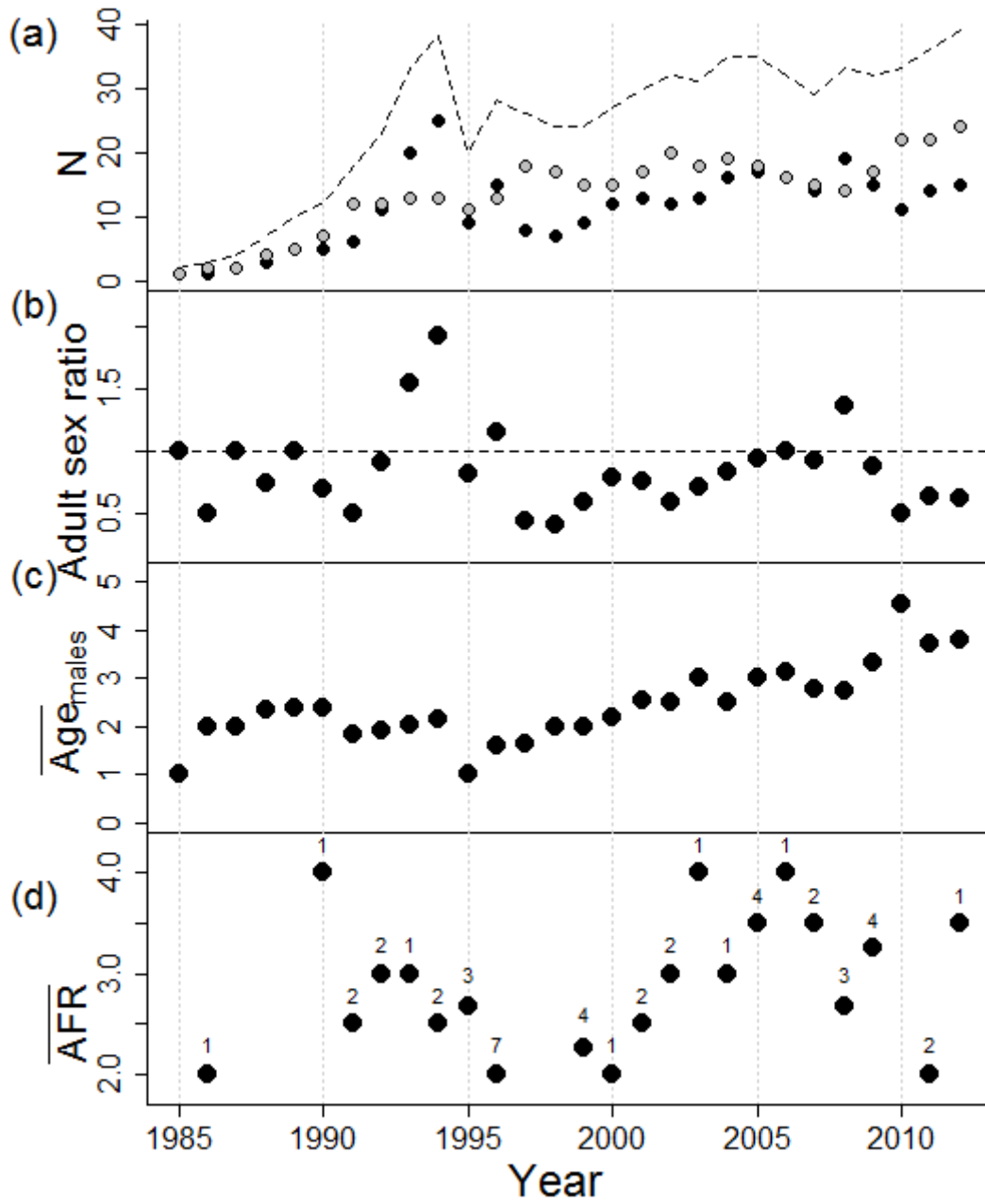


FIGURE 2.

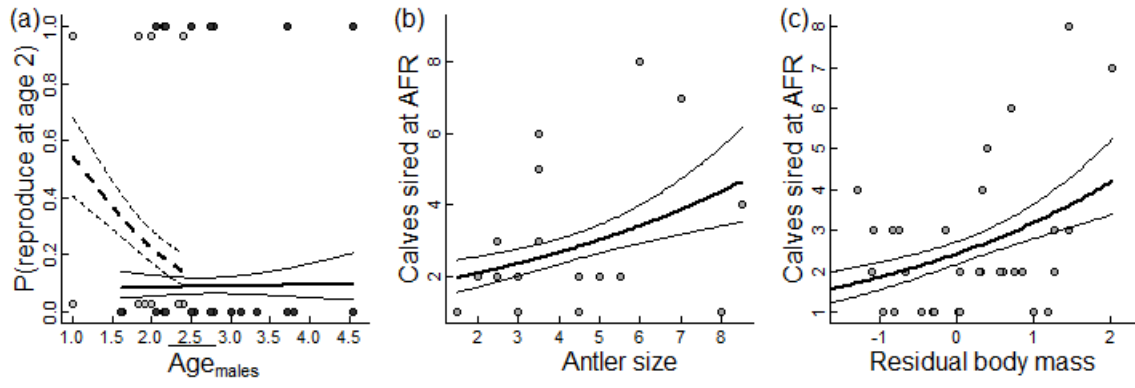


FIGURE 3

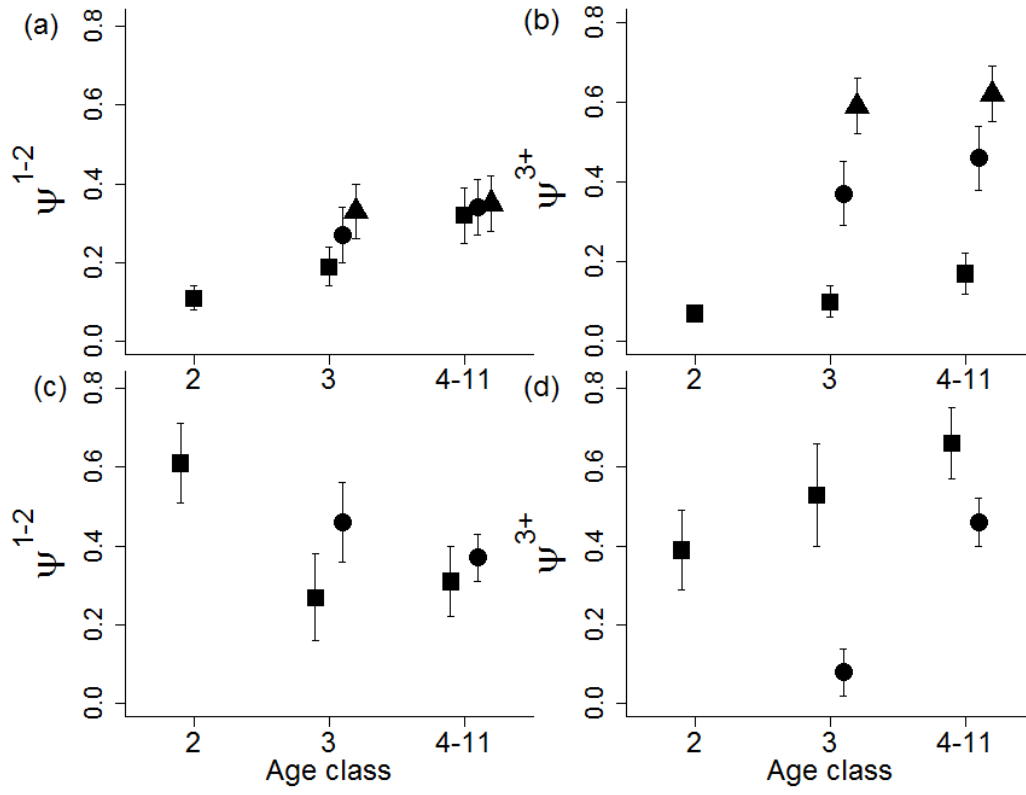


FIGURE 4.

