



Fitness correlates of age at primiparity in a hunted moose population

Stine S. Markussen¹ · Anne Loison² · Ivar Herfindal¹ · Erling J. Solberg³ · Hallvard Haanes⁴ · Knut H. Røed⁵ · Morten Heim³ · Bernt-Erik Sæther¹

Received: 30 January 2017 / Accepted: 22 November 2017 / Published online: 2 December 2017
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Abstract

Trade-offs between fitness-related traits are predicted from the principle of resource allocation, where increased fecundity or parental investment leads to reduced future reproduction or survival. However, fitness traits can also be positively correlated due to individual differences (e.g. body mass). Age at primiparity could potentially explain variation in individual fitness either because early primiparity is costly, or it may lead to higher lifetime reproductive success. Based on long-term monitoring and genetic parentage assignment of an island population of moose, we quantified reproductive performance and survival, and examined whether early maturing females have higher total calf production than late maturing females. We explored if harvesting of calves affected the subsequent reproductive success of their mothers, i.e. also due to a post-weaning cost of reproduction, and whether there are any intergenerational effects of female reproductive success. There was a positive relationship between current and future reproduction. The probability to reproduce was lower for females that were unsuccessful the year before, indicating a strong quality effect on productivity. Females that started to reproduce as 2-year olds had a slightly higher total calf production compared to those starting at age three or four. High-performing mothers were also correlated with daughters that performed well in terms of reproductive success. Our results suggest that the observed individual heterogeneity in fitness could be associated with differences in age at primiparity. This heterogeneity was not affected by reproductive costs associated with tending for a calf post-weaning.

Keywords Age of maturity · Cost of reproduction · Individual heterogeneity · Life history · Ungulates

Communicated by Jean-Michel Gaillard.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-017-4021-2>) contains supplementary material, which is available to authorized users.

✉ Stine S. Markussen
stine.markussen@ntnu.no

- ¹ Department of Biology, Centre for Biodiversity Dynamics, 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

Introduction

Life history theory predicts that iteroparous species should allocate resources to maximize individual fitness, resulting in trade-offs between fitness-related traits (Stearns 1992). Trade-offs in life history evolution are often based on the principle of resource allocation (Williams 1966), where resources allocated to one fitness component will lead to a decrease in resources allocated to other fitness components. One example is the cost of reproduction, in which increased fecundity or parental investment causes reduced longevity of the parent or a reduced capacity for future reproduction (Reznick 1985). Such a negative covariation between competing traits is an element of most early models of life history evolution (e.g. Williams 1966; Schaffer 1974; Michod 1979). However, the amount of resources available and the acquisition and handling abilities of individuals are rarely constant (van Noordwijk and de Jong 1986). Accordingly, fitness-related traits can also positively covary because the costs may be higher in some individuals than others

(Partridge 1987) or due to individual variation in resource acquisition and/or utilization (e.g. Bell and Koufopanou 1986; Cam et al. 2002; Hamel et al. 2009a, b; Chambert et al. 2013). This individual variation could lead to differences in individual quality where quality is defined as “an axis of among-individual heterogeneity that is positively correlated with fitness” (Wilson and Nussey 2010), such as differences in body condition (Bérubé et al. 1999), experience or age (McNamara and Houston 1996).

The age at first reproduction (hereafter age at primiparity) is an important trait with substantial potential for influencing lifetime reproductive success (Bell 1980) and population dynamics (Reiter and LeBoeuf 1991). Within species, early-maturing individuals can have higher lifetime reproductive success than late-maturing individuals as they may obtain a higher number of successful reproductive events (Stearns 1992; Oli and Dobson 1999; Herfindal et al. 2015). However, early start of reproduction may also involve a fitness cost such as reductions in growth, survival and future reproduction (Pyle et al. 1997; Proaktor et al. 2008).

If age at primiparity is related to individual quality, its trade-off with future fitness may be less apparent (Sæther and Heim 1993; Festa-Bianchet et al. 1995; Neuhaus et al. 2004). In capital breeders (Gaillard et al. 2000a), reproduction and age at primiparity are often related to body condition (Jorgenson et al. 1993; Gaillard et al. 2000b), and large, high-quality females reproduce more successfully and with lower future fitness costs than small females—particularly in species with low or no variability in litter size (Green and Rothstein 1991; Festa-Bianchet et al. 1998; Weladji et al. 2008). Moreover, variation in quality among females may generate size and quality differences in their offspring (Solberg et al. 2007; Hamel et al. 2012) and in turn their fitness (Hamel et al. 2010), leading to possible intergenerational effects of varying age at primiparity. Such intergenerational effects have, however, rarely been investigated in long-lived species (but see Moore et al. 2016).

Measuring the costs of reproduction is challenging for at least two reasons. First, reproduction involves several phases during which energy expenditure varies. In mammals, different expenditures during gestation, lactation and post-weaning care may lead to different costs (Clutton-Brock et al. 1983). The pre-weaning care is related mainly to foetus growth and milk production, as opposed to post-weaning care, which is associated with fending for the calf from weaning to independence (Clutton-Brock 1991). The latter may involve reduced food consumption of the mother due to direct feeding competition, or because mothers trade off good feeding opportunities for better anti-predator conditions for the calf (Green et al. 1989; White and Berger 2001). Substantially fewer studies have examined maternal costs associated with the post-weaning than the pre-weaning stage in ungulates (L’Heureux et al. 1995; Andersen et al. 2000;

Froy et al. 2016). However, each of these stages may vary differently with age or environmental factors, which means that teasing apart which stage is more likely to lead to future fitness consequences is essential for a better understanding of life history strategies. Still, this is difficult in the wild because of the need for detailed data on success or failure during the different steps of the reproductive period. The second challenge for evaluating the costs of reproduction is methodological. Methods used usually rely on phenotypic or genetic correlations, and experimental manipulations (Lande 1982; Reznick 1985; Bell and Koufopanou 1986). Experimental manipulations have been performed in the wild mostly in birds and lizards, e.g. by manipulating litter size or phenotypes (Lindèn and Møller 1989; Nilsson and Svensson 1996; Cox and Calsbeek 2010), but have turned out to be difficult to perform in mammals (but see Tavecchia et al. 2005; Gélin et al. 2015). Hence, in most studies of wild populations of large mammals, the cost of reproduction is determined by phenotypic correlations (e.g. Clutton-Brock et al. 1982; Bérubé et al. 1999). This is considered a rather weak method, due to individual heterogeneity in available resources, and should if possible also include some kind of manipulation of fitness traits. Such a manipulation can be induced when an offspring dies from non-natural causes, such as harvesting. While such an “experimental” setting has led to some studies of the effect of post-weaning care on offspring performances when a mother was harvested (e.g. Festa-Bianchet et al. 1994; Holand et al. 2012), it has seldom been used in the context of measuring reproductive costs in females.

Here, we analysed the age-specific costs of reproduction in a moose population that is harvested by recreational hunting. Based on long-term monitoring (28 years) and genetic parentage assignment of individually marked moose (Haanes et al. 2013), we focused on the consequences of age at primiparity and post-weaning costs on the reproductive performance and survival of females. We first examined if early maturing females have higher total calf production than late maturing females, or alternatively, if late maturing females may be able to compensate by increasing reproductive output later in life. All else being constant, early maturing females are expected to produce more calves throughout their lifetime simply because they will gain additional breeding attempts. Then, we tested if mothers experience a post-weaning cost of reproduction by analysing their reproductive success in relation to their loss of calves during the previous hunting season. If there is a post-weaning cost of reproduction, we expected a lower reproductive output in females that successfully retained a calf after the hunting season than those that did not. Finally, we assessed whether there were any intergenerational correlations in reproductive performance, i.e. if high performing females are correlated with high performing offspring.

Materials and methods

Study system and data collection

Vega (65°40'N, 11°55'E) is an island of approximately 119 km², 13 km off the coast of northern Norway. The moose population on the island was founded by two yearling females and one yearling male that swam to the island in 1985. Harvesting started in 1989 and has since 1992 been used to keep the breeding population at 20–40 moose, resulting in 15–26 calves born per year (Haanes et al. 2013). Calves are generally weaned in mid-September (Bubenik 1998).

Moose hunting on the island can occur from the 25th of September to the 31st of October, but in most years started in early October, i.e. after the start of the rut. Hunting permits are typically issued as a fixed number of calves, adult females and adult males (or unspecified animals), but given that hunters have a harvesting plan approved by the local wildlife authorities, they are granted some flexibility with regard to how many of each category they can harvest within a year. Hunters can among themselves decide to focus their harvest on young or old adult males or females. In general, harvested females are either without calves that year, or the calves are shot together with the female at the same occasion.

During 1992 and 1993, all individuals on the island were radiocollared for the first time. In January–March every year (except 2003 and 2008), this procedure was repeated to mark and measure all new calves (born in May–June) which survived the annual hunt. In addition, we collected sex, age, carcass mass, and tissue samples from almost all moose harvested on Vega. This included 4- to 5-month-old calves that were not yet collared. For more information about the moose population and study site, see Sæther et al. (2003, 2004, 2007), Solberg et al. (2007, 2008) and Kvalnes et al. 2016.

By the use of genetic parentage assignment based on 22 microsatellite loci, we developed a 28-year-long pedigree for all > 4-month-old moose recorded alive (Haanes et al. 2013) from 1984 to 2012. This includes individual histories of 222 females, of which 59 reproduced successfully at least once. 36 females started to reproduce at the age of 2 years while the remaining 23 started at the age of 3 or 4. The natural mortality rate, φ , is in general low (0.05 ± 0.02 for calves and 0.02 ± 0.01 for females aged 3–9 years old), making hunting the main mortality factor on the island. 19 of the 59 reproducing females were still alive at the end of the study. To increase our sample size, we included the 19 females still alive in our life span variable (age at last observation) used in our analysis of total calf production and intergenerational correlations.

However, excluding those still alive did not change the best model and direction of the results. Based on previous studies (Sæther and Haagenrud 1983; Garel et al. 2009), we divided females into five age classes: calves, yearlings, 2-year-olds, 3- to 9-year-olds (prime-aged females) and ≥ 10 -year-olds (potentially senescent females; Sæther et al. 2007). Calf body mass was measured as live body mass during winter (approximately 8 months old) and adjusted relative to the date of weighing (Herfindal et al. 2006; Kvalnes et al. 2016). We had calf body mass for 37 of 59 females recorded to reproduce. Total calf production was defined as the total number of calves produced per female at age of death or age at last observation (year 2012) if alive.

Statistical analysis

Initially, we addressed whether total calf production was related to age at primiparity, accounting for life span (natural log transformed age at death/last observation) with a generalized linear model with Poisson error structure. As modeling of reproductive output can be challenging (Kendall and Wittmann 2010), the total calf production was also analysed with a Poisson error structure with square root link, a generalized Poisson distribution and linear model with Gaussian error structure. However, the choice of statistical model did not affect our results qualitatively. To assess how survival and reproduction were related to age, previous reproductive state, age at primiparity and their interactions, we used multistate capture-mark-recapture models (Lebreton et al. 2009) in E-SURGE (version 1.9.0, Choquet et al. 2009a). This method allows for simultaneous estimation of survival probabilities (from hunting or natural causes) and probabilities of transitioning between reproductive states. Due to the thorough pedigree (Haanes et al. 2013), we assumed that the fate of all individuals was known (no error in determination of reproductive or survival state). As we also know which individuals were hunted or died naturally, the capture probability was fixed to 1. Before starting our analysis, we conducted a goodness-of-fit (GOF) assessment of the Jolly-Move (JM) model (Brownie et al. 1993) in U-CARE (version 2.3.2, Choquet et al. 2009b). It satisfactorily fitted the data ($\chi^2 = 53.882$, d.f. = 83, $p = 0.995$).

We divided the analysis into four steps: first, we focused on estimating hunting mortality and reproduction probabilities for all individuals. The models included three types of parameters:

η_a^r , the probability that an individual in state r at age a was not hunted until $a + 1$.

φ_a^r , the probability that an individual in state r at age a survived until $a + 1$.

ψ_a^{rs} , the probability that an individual in state r at age a was in state s at $a + 1$, given that the individual survived from age a to age $a + 1$.

The possible states were as follows: not reproduced (ψ^{NR}), produced one calf (ψ^1), and produced twins (ψ^2). The general model included the effect of previous reproductive state (PR) and age class a on hunting mortality η and natural mortality φ . For reproduction ψ probabilities also the transition to current reproductive state (CR) was included:

$$\eta_{a \times \text{PR}}, \varphi_{a \times \text{PR}}, \psi_{a \times \text{PR} \times \text{CR}}$$

Second, we assessed the effects of age, age at primiparity (AP) and previous reproductive success on the probabilities to reproduce (NR, 1C or 2C) the following year for those that reproduced, given the general model:

$$\eta_{a \times \text{PR}}, \varphi_a, \psi_{a \times \text{PR} \times \text{AP} \times \text{CR}}$$

Because few mature individuals died of natural causes, φ included only an effect of age. Age at primiparity as 3- and 4-year-olds were pooled for sample size reasons.

Third, we included the body mass of each female as calf as a covariate to the best model in step two. This was to investigate if body mass in early life could explain any variation in reproductive success that was not already accounted for by other covariates (e.g. age at primiparity). The general model included the same variables as in the second step.

In the last step, we investigated the post-weaning cost of reproduction by examining to what extent hunting of calves affected the subsequent reproductive success of mothers. For this, we introduced two potential states in the model: females had calf/calves that survived, and females had calves that were hunter-killed during the following hunting season. Due to small sample size, we also divided the females into two age classes: 2- and ≥ 3 -year-olds. All models were run with random initial values repeated five times to protect against local minima. Including individual identity as random effect in the reproductive transitions in our best models led to models with equal or higher deviance and higher AIC_c -values and were left out (including individual identity: all individuals $\Delta\text{AIC}_c = 1.99$, reproducing individuals $\Delta\text{AIC}_c = 10.74$).

For more information about the models, see supplementary materials.

To search for intergenerational relationships, we examined whether age at primiparity of daughters was correlated with the age at primiparity of their mother with a χ^2 test. Fifty-four unique mother–daughter pairs included daughters that reproduced at least once ($N_{\text{mothers}} = 27$). We used generalized linear mixed models with a Poisson error structure and maternal identity as random factor, to analyse the variation in total calf production of daughters (≥ 2 years of age). Explanatory variables included natural log transformed age at death or age at last observation of the daughters, the

mother total calf production divided by her age at death or age at last observation (mean age-specific calf production), maternal age and her age at primiparity and their interactions as covariates. Finally, we analyzed the variation in daughter body mass in relation to mothers' age, age at primiparity, and total calf production, as well as birth date, twin status and their interactions as covariates. We used generalized linear mixed models with a Gaussian error structure with year and maternal identity as random factors.

Akaike's Information Criterion corrected for sample size (AIC_c , Burnham and Anderson 2002) was used for model selection; the best models being the most parsimonious (lowest AIC_c value). We also computed Akaike weights (AIC_{c-w}) to compare the relative performance of different models (Burnham and Anderson 2002).

Results

Age at primiparity and calf production

During the study period, 54% of all 2-year-old females ($N = 67$) reproduced successfully and 7% produced twins. At age 3, 82% of all females reproduced ($N = 57$, among which 35% were primiparous) and 37% had twins. 37% of mature females skipped reproduction in one or several years throughout their life, or they lost their calves too early to be detected. Total calf production was positively related to age at last observation in interaction with age at primiparity ($\text{AIC}_{c-w} = 0.407$, evidence ratio to the second best model = 1.109; $\beta \pm \text{SE} = 0.43 \pm 0.28$, 95% CI $-0.10; 0.99$). The accumulated calf production of females at the age at last observation or death was on average higher for those starting to reproduce at the age of two compared to those that reproduced successfully as 3- or 4-year-olds (Fig. 1). For a typical life span of 5 years old, a female that started to reproduce as a 2-year-old produced 4.95 calves, while a female that started at the age of three or four produced on average 3.29 calves.

Individual heterogeneity in life history traits

The best model explaining the probability to reproduce in females included interactive effects of age class and the previous and current reproductive state (Table 1A). Prime-aged females (3–9 years old; $N = 63$) had higher probability to reproduce than females aged 10 years and older ($N = 20$), independent of their reproductive success the previous year (for females that had not reproduced the year before: $\psi^{\text{NR} \rightarrow \text{R}} = 0.84 \pm 0.07$ vs $\psi^{\text{NR} \rightarrow \text{R}} = 0.70 \pm 0.08$; for females that had a singleton: $\psi^{1\text{C} \rightarrow \text{R}} = 0.86 \pm 0.04$ vs $\psi^{1\text{C} \rightarrow \text{R}} = 0.73 \pm 0.06$; for females that had twins: $\psi^{2\text{C} \rightarrow \text{R}} = 0.94 \pm 0.04$ vs $\psi^{2\text{C} \rightarrow \text{R}} = 0.88 \pm 0.05$; for 3–9 years

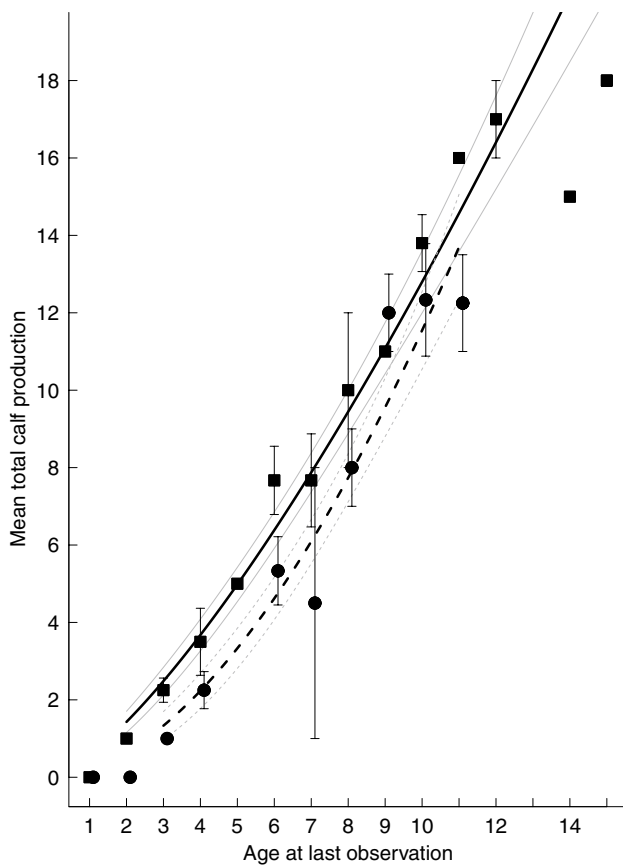


Fig. 1 Mean total calf production at age at last observation (age at death or at the end of study period if still alive) \pm SE for female moose according to their age at primiparity, with regression lines \pm SE. Black square, solid line Age at primiparity as 2-year-old ($n = 36$); Black circle, dashed line age at primiparity as 3- 4-year-old ($n = 23$). Age at primiparity 2: $\ln(\text{Total calf production}) = (1.36 \pm 0.13 \times \ln(\text{Age at last observation})) - 0.59 \pm 0.27$; Age at primiparity 3-4: $\ln(\text{Total calf production}) = (1.79 \pm 0.35 \times \ln(\text{Age at last observation})) - 1.69 \pm 0.61$

vs ≥ 10 years old, respectively; Fig. 2; Table 2A). Moreover, the probability to produce twins was lower for females that were unsuccessful the year before than for females that produced singletons or twins, indicating a strong quality effect on calf production (Fig. 2; Table 2A).

Age at primiparity also influenced reproductive success in a more complex way. For females with at least one previous reproductive event, the reproduction transitions were best explained by also accounting for the three-way interaction between age class, age at primiparity and current reproductive state (Table 1B). Early maturing females showed a slightly higher probability to reproduce (singletons and twins, age 3–9: $\psi^{\text{NR} \rightarrow \text{R}} = 0.88 \pm 0.08$, $\psi^{\text{1C} \rightarrow \text{R}} = 0.87 \pm 0.05$, $\psi^{\text{2C} \rightarrow \text{R}} = 0.94 \pm 0.05$) compared to those that started to reproduce at the age of 3 or 4 (age 3–9: $\psi^{\text{NR} \rightarrow \text{R}} = 0.83 \pm 0.08$, $\psi^{\text{1C} \rightarrow \text{R}} = 0.83 \pm 0.06$, $\psi^{\text{2C} \rightarrow \text{R}} = 0.92 \pm 0.06$; Fig. 3; Table 2B). This heterogeneity

was more pronounced when females were ≥ 10 years old (for early maturing females: $\psi^{\text{NR} \rightarrow \text{R}} = 0.76 \pm 0.08$, $\psi^{\text{1C} \rightarrow \text{R}} = 0.75 \pm 0.06$, $\psi^{\text{2C} \rightarrow \text{R}} = 0.88 \pm 0.04$; for late maturing females: $\psi^{\text{NR} \rightarrow \text{R}} = 0.69 \pm 0.08$, $\psi^{\text{1C} \rightarrow \text{R}} = 0.68 \pm 0.08$, $\psi^{\text{2C} \rightarrow \text{R}} = 0.84 \pm 0.06$).

For yearlings, the probability to be killed by hunting was 0.33 ± 0.04 (95% CI 0.25; 0.42), while for 2 years and older the hunting mortality depended on their reproductive status before the hunting season. Females that were accompanied by a calf had almost half the probability to be killed during hunting than females without calf, and the probability was lowest for those accompanied by twins [age 3–9: $\eta^{\text{NR}} = 0.18 \pm 0.06$ (95% CI 0.10; 0.33); $\eta^{\text{1C}} = 0.09 \pm 0.03$ (95% CI 0.05; 0.17); $\eta^{\text{2C}} = 0.05 \pm 0.02$ (95% CI 0.03; 0.10)].

Adding females body mass as calf did not improve the model fit ($\Delta\text{AIC}_c = 16.74$; Table 1C), possibly because of its close covariation with age at primiparity. Indeed, females that started to reproduce at the age of 2 had nearly significant higher mean body mass as calf ($\beta \pm \text{SE} = 186.09 \pm 4.22$ kg, 95% CI 177.53; 194.65, $N = 21$) than late-maturing females ($\beta \pm \text{SE} = 173.44 \pm 6.42$ kg, 95% CI 151.86; 195.03, $N = 16$). Hence, body mass in early life seems to have no other effects on reproductive performance than the indirect effects on age at primiparity and current reproductive status.

Fitness cost of recruitment

Caring for a calf/calves during winter did not seem to increase the cost of reproduction as the probability to reproduce next year was similar for females whose calves survived or were lost during hunting (for early maturing females aged ≥ 3 , $N = 33$: $\psi^{\text{Calves recruit} \rightarrow \text{R}} = 0.90 \pm 0.04$, $N_{\text{females}} = N_{\text{transitions}} = 78$; $\psi^{\text{Calves lost} \rightarrow \text{R}} = 0.91 \pm 0.06$, $N_{\text{transitions}} = 43$; for late maturing females aged ≥ 3 , $N = 23$: $\psi^{\text{Calves recruit} \rightarrow \text{R}} = 0.87 \pm 0.06$, $N_{\text{transitions}} = 49$; $\psi^{\text{Calves lost} \rightarrow \text{R}} = 0.85 \pm 0.06$, $N_{\text{transitions}} = 34$; Tables 1D, 2C). Females that successfully recruited calves to the adult population had a higher probability of giving birth to twins (for early maturing females aged ≥ 3 : $\psi^{\text{Calves recruit} \rightarrow \text{2C}} = 0.59 \pm 0.05$, $N_{\text{transitions}} = 53$; for late maturing females aged ≥ 3 : $\psi^{\text{Calves recruit} \rightarrow \text{2C}} = 0.61 \pm 0.06$, $N_{\text{transitions}} = 33$) than singletons (for early maturing females aged ≥ 3 : $\psi^{\text{Calves recruit} \rightarrow \text{1C}} = 0.31 \pm 0.04$, $N_{\text{transitions}} = 27$; for late maturing females aged ≥ 3 : $\psi^{\text{Calves recruit} \rightarrow \text{1C}} = 0.26 \pm 0.06$, $N_{\text{transitions}} = 17$; Fig. 4, Table 2C).

For females that started to reproduce as 2-year-olds and that gave birth to twins, the probability that both of the twin calves was hunter-killed was 0.36 ± 0.05 , while it was 0.28 ± 0.06 for those who started to reproduce later. If the mother had only a single calf, the probability that it was harvested was 0.25 ± 0.05 for early and 0.46 ± 0.08 for late maturing individuals.

Table 1 Results from model selection of multistate models for estimation of hunting mortality (η), natural mortality (φ) and future reproductive performance (ψ) for female moose on Vega, Norway, 1984–2012, for (A) all females, (B) females with at least one reproductive event, (C) including calf body mass and (D) reproductive females with hunting mortality of their calves

Model specification	<i>K</i>	ΔAIC_c	AIC_{c-w}
(A) All females			
1. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age+Age \times PR \times CR}$	16	0.000	0.491
2. $\eta_{Age+Age_{3-9} \times PR}, \varphi_{Age}, \psi_{Age+Age \times PR \times CR}$	16	2.221	0.162
3. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age \times CR+Age_{3-9} \times PR \times CR}$	17	2.316	0.154
(B) Including age at primiparity			
1. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age+Age \times AP \times CR+Age \times PR \times CR}$	18	0.000	0.452
2. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age \times AP \times CR+Age \times PR \times CR}$	20	0.664	0.324
3. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age+AP \times PR \times CR}$	20	2.197	0.151
(C) Including calf body mass			
1. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age+Age \times AP \times CR+Age \times PR \times CR}$	18	0.000	> 0.999
2. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age+Age \times AP \times CR \times BM+Age \times PR \times CR}$	26	16.744	< 0.001
3. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age+Age \times AP \times CR+Age \times PR \times CR+BM}$	27	18.776	< 0.001
(D) Calf/calves hunted			
1. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age_{2,3+} \times AP \times PR \times CR}$	20	0.000	0.564
2. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age_{2,3+} \times AP \times CR+Age_{2,3+} \times PR \times CR}$	17	0.555	0.427
3. $\eta_{Age+Age \times PR}, \varphi_{Age}, \psi_{Age \times AP \times CR+Age \times PR \times CR}$	23	8.426	0.008

Only the three highest ranked models according to AIC_c value are shown. The effects considered were variation between age classes (Age), previous reproductive state (PR), current reproductive state (CR), age at primiparity (AP), calf body mass (BM). The symbol “ \times ” was used to denote the statistical interaction between the effects, while the symbol “+” was used for additive effects. For further information about models, see “Materials and methods”. *K* number of parameters in the model. AIC_c weights (AIC_{c-w}), defined as the relative likelihood of a model given the data and set of models. The best model in (A) had an $AIC_c = 1076.208$, (B) $AIC_c = 830.632$, (C) $AIC_c = 490.345$ and (D) $AIC_c = 1167.493$

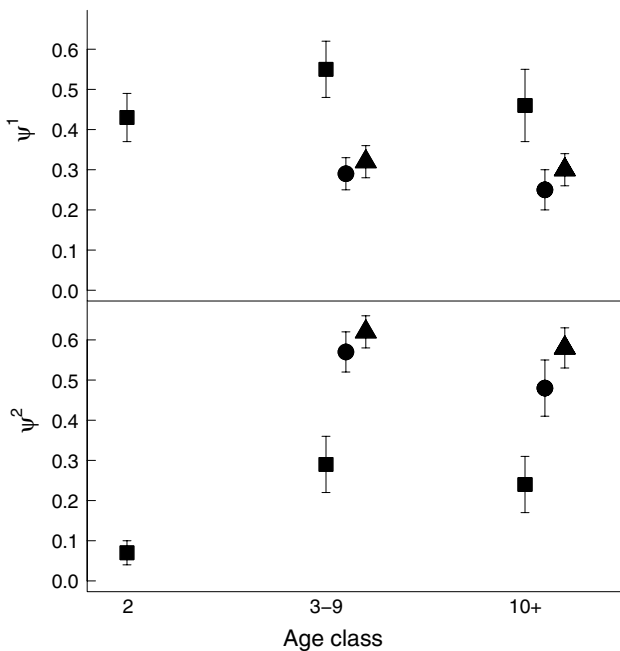


Fig. 2 Probability to reproduce one (ψ^1) or two (ψ^2) calves \pm SE for female moose according to age class and their previous reproductive state. Black square Not reproduced (NR), black circle reproduced 1 calf, and black triangle reproduced two calves at previous state. Probabilities are from the best model in Table 1A

Intergenerational correlations

There was no significant association between the age at primiparity of mothers and their offspring ($\chi^2 = 1.32$, $p = 0.251$). The variation in the daughter’s calf production was best explained by their age at last observation ($\beta = 1.53 \pm 0.13$, $AIC_{c-w} = 0.339$, evidence ratio to the second best model = 1.215) and the mother’s mean age-specific calf production ($\beta = 0.63 \pm 0.30$). Mothers with above average reproductive success were more likely to produce daughters that also performed well in terms of reproductive success. The variation in daughter’s body mass was best explained by the age of the mother ($AIC_{c-w} = 0.240$, evidence ratio to the second best model = 1.437). Older mothers gave birth to heavier calves irrespective of their age at primiparity ($\beta = 2.91 \pm 0.89$).

Discussion

Twenty-eight years of detailed reproductive histories of female moose revealed positive relationships between current and future reproduction. Early age at primiparity was associated with higher total calf production (Fig. 1), and successful breeders had a higher probability to reproduce at similar levels in subsequent years (Figs. 2, 3). Moreover, the probability to reproduce twins was higher for those

Table 2 Parameter estimates \pm SE (95% CI) for the transition probabilities (from state \rightarrow to state) of future reproductive performance (ψ) for female moose on Vega, Norway, 1984–2012, from the highest ranked models according to AIC_c model selection in Table 1

Model	Age	Group	From state	Parameter estimates SE (95% CI)			
				To state			
				1C	2C	Recruit	
(A)	2		NR	0.43 \pm 0.06 (0.32; 0.55)	0.07 \pm 0.01 (0.03; 0.16)		
			3–9	NR	0.55 \pm 0.07 (0.41; 0.69)	0.29 \pm 0.07 (0.18; 0.43)	
	10+		1C	0.29 \pm 0.04 (0.21; 0.39)	0.57 \pm 0.05 (0.47; 0.66)		
			2C	0.32 \pm 0.04 (0.25; 0.41)	0.62 \pm 0.04 (0.53; 0.70)		
			NR	0.46 \pm 0.09 (0.29; 0.64)	0.24 \pm 0.07 (0.13; 0.39)		
			1C	0.25 \pm 0.05 (0.17; 0.36)	0.48 \pm 0.07 (0.34; 0.62)		
(B)	2	AP2	NR	0.83 \pm 0.06 (0.68; 0.92)	0.14 \pm 0.06 (0.06; 0.29)		
			3–9	NR	0.55 \pm 0.09 (0.38; 0.71)	0.33 \pm 0.08 (0.19; 0.50)	
	10+		1C	0.31 \pm 0.05 (0.22; 0.41)	0.56 \pm 0.05 (0.46; 0.67)		
			2C	0.32 \pm 0.05 (0.24; 0.42)	0.62 \pm 0.05 (0.52; 0.71)		
			NR	0.48 \pm 0.09 (0.29; 0.67)	0.29 \pm 0.08 (0.16; 0.46)		
			1C	0.27 \pm 0.05 (0.32; 0.55)	0.49 \pm 0.07 (0.35; 0.63)		
	3–9	AP3+	2C	0.30 \pm 0.05 (0.22; 0.40)	0.58 \pm 0.05 (0.47; 0.68)		
			NR	0.51 \pm 0.08 (0.36; 0.65)	0.32 \pm 0.07 (0.20; 0.47)		
			1C	0.28 \pm 0.06 (0.18; 0.40)	0.55 \pm 0.07 (0.42; 0.67)		
			2C	0.30 \pm 0.05 (0.21; 0.42)	0.62 \pm 0.06 (0.50; 0.72)		
			NR	0.42 \pm 0.09 (0.29; 0.64)	0.27 \pm 0.07 (0.15; 0.43)		
			1C	0.23 \pm 0.06 (0.13; 0.37)	0.45 \pm 0.09 (0.29; 0.63)		
(C)	2	AP2	2C	0.28 \pm 0.05 (0.18; 0.42)	0.56 \pm 0.07 (0.48; 0.67)		
			3+	Not recruit	0.83 \pm 0.06 (0.68; 0.92)	0.14 \pm 0.06 (0.06; 0.29)	
	3+		AP3+	1C			0.75 \pm 0.05 (0.64; 0.83)
				2C			0.64 \pm 0.05 (0.54; 0.73)
				Recruit	0.31 \pm 0.04 (0.23; 0.40)	0.59 \pm 0.05 (0.50; 0.68)	
				Not recruit	0.39 \pm 0.07 (0.27; 0.53)	0.52 \pm 0.07 (0.39; 0.64)	
3+	AP3+	1C			0.54 \pm 0.08 (0.38; 0.69)		
		2C			0.72 \pm 0.06 (0.59; 0.83)		
		Recruit	0.26 \pm 0.06 (0.17; 0.39)	0.61 \pm 0.06 (0.48; 0.73)			
		Not recruit	0.45 \pm 0.06 (0.33; 0.58)	0.40 \pm 0.06 (0.29; 0.53)			

(A) All females, (B) females with at least one reproductive event, and (C) reproductive females with hunting mortality of their calves. Age = age classes, Group: AP2 = age at primiparity as 2 year olds, AP3+ = age at primiparity as 3 years old and older. States: NR = not reproduced, 1C = reproduced one calf, 2C = reproduced two calves, not recruit = no calf/calves survived to year $t + 1$, recruit = one or two calves survived to year $t + 1$

females that already had successfully recruited calves into the population (Fig. 4). This suggests that the fitness contribution to the next generation from reproduction and survival is substantially higher in some females than in others and could potentially last over generations since high-performing females were correlated with high-performing calves in terms of total calf production.

The among-females differences in calf production were partly related to individual differences in age at primiparity; the most successful females matured at the age of 2 years. Such a positive relationship between age at maturity and other fitness components has also been found in other moose

populations (Sæther and Haagenrud 1983, 1985), as well as in other ungulates (Moyes et al. 2006; Weladji et al. 2008) and long-lived mammals (Pistorius et al. 2001; Moore et al. 2016). However, it is not found in some long-lived birds, where early maturing individuals tend to suffer higher mortality rates (e.g. Pyle et al. 1997; Barbraud and Weimerskirch 2005).

In many ungulate species, age at maturity is often inversely related to body mass: large females mature earlier than smaller ones (Jorgenson et al. 1993; Gaillard et al. 2000a). This also occurs at Vega where a favourable environment results in high body masses (Solberg et al. 2015) and

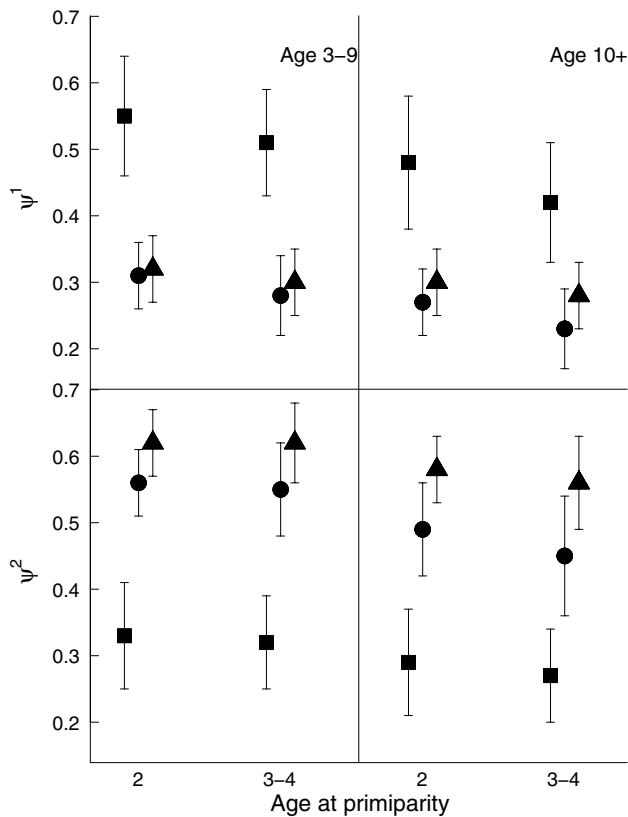


Fig. 3 Probability to reproduce one (ψ^1) or two (ψ^2) calves \pm SE for female moose according to age at primiparity, age class and their previous reproductive state. Black square Not reproduced (NR), black circle reproduced 1 calf, and black triangle reproduced 2 calves at previous state. Probabilities are from the best model in Table 1B

high population growth rates (Sæther et al. 2007). Still, there is large inter-individual variation in offspring production among females. This shows that individual heterogeneity does not only occur in populations facing stressful environmental conditions (Lomnicki 1978) and suggests that there are consistent individual differences among females in their ability to acquire resources (van Noordwijk and de Jong 1986). In moose, variation in body mass of young females may be related to availability of high-quality food plants during summer (Sæther 1985; Sæther and Heim 1993) or variation in snow conditions during late winter (Sæther and Gravem 1988). This indicates that individual differences in calf production may be related to spatial heterogeneity in quality of the females' home ranges (Pettorelli et al. 2001), a hypothesis that should be tested further as we currently lack studies showing how heterogeneity in habitat quality transfers to heterogeneity in individual demographic performances in large herbivores (Gaillard et al. 2010).

Individual differences in female reproductive success may be related to the timing of conception, which can be affected by the sex- and age-structure of the population. On Vega, the sex and age structure was manipulated by selective

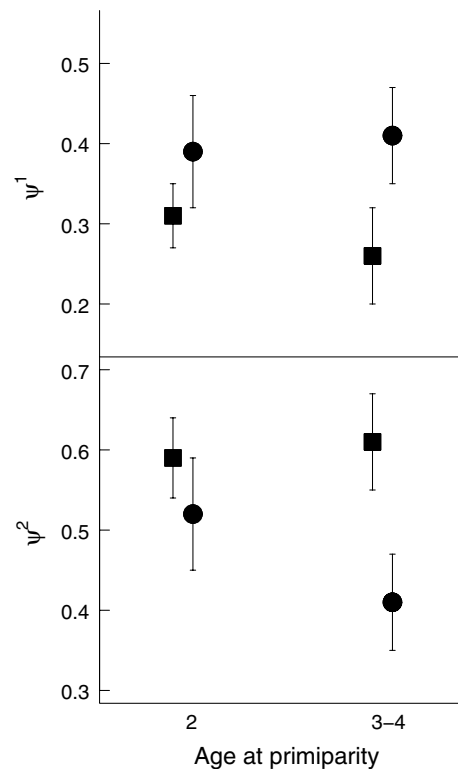


Fig. 4 Probability to reproduce one (ψ^1) or two (ψ^2) calves \pm SE for female moose dependent on whether her previous calf/calves survived the hunting season. Black square At least one calf survived the hunt, black circle calf/calves lost during the hunt. Probabilities are from the best model in Table 1D

harvesting during the period 1994–1999 (Sæther et al. 2003) leading to a female-biased sex ratio and low mean male age. A mating preference for older males seems to make females inclined to delay conception when the sex ratio is very biased (Sæther et al. 2003, 2004; Herfindal et al. 2014). This in turn results in relatively large variation in calving date, which can affect the demography. Such effects may provide a link between social organization, demography and population dynamics in moose.

The reproductive costs associated with postweaning maternal care have rarely been investigated in ungulates (Green et al. 1989; Andersen et al. 2000; Holand et al. 2012; Froy et al. 2016). L'Heureux et al. (1995) investigated post-weaning mother–daughter associations in bighorn sheep and concluded that post-weaning associations did not appear costly to mothers. Costs to mothers of protracted associations with offspring have, however, been found in red deer (*Cervus elaphus*; Clutton-Brock et al. 1982; Froy et al. 2016), red-necked wallaby (*Macropus rufogriseus*; Johnson 1986) and bison (*Bison bison*; Green et al. 1989). Loss of calves from hunting did not seem to increase the probability to reproduce for mothers, indicating that maternal post-weaning costs may be of minor importance in moose

and that calf harvest has no or little effect on female reproduction. Instead, females that recruited calves to the adult population had higher probability to give birth to twins the next year, reinforcing the individual quality hypothesis.

The cost of reproduction in ungulates is more pronounced in young and old individuals (Clutton-Brock et al. 1983; Tavecchia et al. 2005). There seems to be a threshold in body mass that females must reach to reproduce, and they may take reproductive pauses or adjust the effort later in the reproductive cycle (e.g. abortion; Hamel et al. 2009b; Milner et al. 2013) according to their current body reserves. As females reach prime-age, the cost of reproduction is likely lowered by the completion of body growth and increased maternal experience (Weladji et al. 2006), giving a higher probability to reproduce and recruit offspring into the population. At old age, senescence leads to reductions in survival and/or breeding success (e.g. Loison et al. 1999; Lemaître et al. 2015), which is observed as lower reproductive probability in the old females.

The cost of earlier age of first reproduction depends on the relative position of a species along the fast–slow continuum (Gaillard et al. 1989; Sæther and Bakke 2000). Moose have a rapid life cycle with short generation time and high reproductive output compared to other, similar-sized ungulates (Gaillard 2007; Gaillard et al. 2000a). To reach their high reproductive output, moose have to trade quality of offspring (small newborns compared to newborns of other, similar-sized ungulates) for a higher quantity, as female moose produce twins as soon as environmental conditions allow. Probability to produce twins is, therefore, an additional indication of individual quality which influence the extent of the inter-individual heterogeneity found in this study.

Being under high hunting pressure, female moose may try to reproduce as early as possible, and not be as conservative as, e.g. bighorn sheep (Bérubé et al. 1999) or red deer (Moyes et al. 2006). At Vega, this effect is enhanced by differential hunting mortality, as hunters kill non-reproducing females with a higher probability than females accompanied by one or two calves (see Ericsson 2001 for similar results). As females are observed with similar probability independent of calf status (Rolandsen et al. 2003; Solberg et al. 2010), we believe that the varying hunting mortality rate is because hunters avoid killing calf-rearing females and not because non-producing females are more easily detected. Females can, therefore, increase their survival probability by reproducing early and may gain a fitness benefit even if the capacity for future reproduction is reduced (Nilsen and Solberg 2006). However, so far we see no indications of such a trade-off between current and future reproductive performance in moose on Vega.

Contrary to the Vega population, several ungulate populations, throughout the world, has natural predation as an important source of mortality. Natural predators can affect ungulate demography both through predation-associated mortality (Krivan and Eisner 2003) and indirectly through the costs of anti-predator behavioural and physiological responses (Creel and Christianson 2008) leading to, e.g. changes in habitat use (Creel et al. 2005). Predation can change the distribution of life history traits over generations through prey selectivity (Reznick et al. 1990). Dependent on their selectivity and the preys individual variation in predation risk (due to, e.g. differences among the sexes, age, phenotypic attributes, habitat use), predation can lead to higher or lower between-individual variation in reproductive success of prey (Pettorelli et al. 2011).

Theoretical studies show that individual heterogeneity in demography may strongly affect the population dynamics by, e.g. affecting the demographic variance (e.g. Vindenes et al. 2008; Plard et al. 2016) and temporal variation in genetic composition (Lee et al. 2011), and should be accounted for in population models applied to moose. Recent studies have incorporated individual heterogeneity using mixed or mixture models (e.g. Cam et al. 2002; Péron et al. 2010; Chambert et al. 2013). In our case, we grouped the individuals a priori into groups according to their previous reproductive status and age at primiparity. The groupings of individuals may successfully account for the major axes of variation in the data, but could in theory bias the parameters.

To summarize, our study of individual variation in reproductive success among female moose showed individual heterogeneity in demography, associated with individual differences in age at maturity. These differences were not affected by variation in reproductive costs of tending for a calf after the end of lactation.

Acknowledgements We are grateful to the local moose hunters and managers for cooperation in collecting data. This study was supported by the European Research Council (ERC-2010-AdG 268562), the Research Council of Norway (SFF-III 223257/F50 and project number 244647) and the Norwegian Environment Agency.

Author contribution statement SSM, AL and BES developed the concept and idea. HH performed genetic analyses and constructed the pedigree in collaboration with KHR. Statistical analyses were performed by SSM with input from AL, IH, EJS and BES. MH was in charge of the fieldwork, tissue sampling and the life history databases. SSM wrote the article with input from all co-authors.

Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare.

Ethical statement All applicable national guidelines for the care and use of animals were followed.

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