Demographic consequences of harvesting: a case study from a small and isolated moose population

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ABSTRACT: Harvesting can have a substantial impact on population dynamics and individual performance in wild populations. While the direct consequences of harvest on individual survival and population growth rate are often apparent, harvesting can also have indirect and more subtle demographic consequences. Disentangling these consequences, however, requires in-depth knowledge of individual life histories of both females and males in the population. Here, we summarise demographic research on a population where such data exist: the Vega moose population in northern Norway. In this population, vital rates vary considerably among both females and males, and harvesting increases this variation by generating positive covariation between reproductive performance and survival. The skewed age and sex structure, which is typical of many harvested populations, also has demographic consequences: it reduces the ratio of effective to total population size and influences variation in vital rates in males and females. The moose harvest at Vega is structured by age- and sex-specific quotas, but it is not intentionally selective regarding size or other phenotypic characteristics. Still, harvest selection for earlier birth rates and larger calves was apparent, likely due to habitat–performance relationships and habitat-specific harvest mortality. Together, the bulk of research on this population shows that harvesting impacts population demography through many different pathways, with some being more subtle than others. These complex pathways influence the demographic variance and affect stochastic processes such as population growth, genetic drift, and rates of evolutionary change, and they must therefore be acknowledged in management plans to achieve sustainable harvesting.

KEY WORDS: Hunting · Harvest selection · Individual heterogeneity · Vital rates · Sustainable harvest · Inbreeding · *Alces alces* · Demographic rates

1. INTRODUCTION

Sustainable management of natural resources requires an understanding of how climate change and harvesting affect populations and ecosystems. To reach such an understanding, however, we first need knowledge about the fundamental consequences of harvesting on population processes, irrespective of environmental change. Although there is a consensus that harvest should be targeted towards sustainability (e.g. UN General Assembly 2015), strong economic pressures for maximising short-term harvest

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yield may compromise this goal (Sæther et al. 2001). In contrast to fisheries, where individual variation in harvest mortality is mainly related to body size, harvesting of many wildlife species such as most ungulates is allowed to be targeted towards specific age, sex, or even reproductive classes. Harvesting quotas are therefore often quite specific in many of these species (Apollonio et al. 2010). For instance, if the aim is to maximise population productivity and number of individuals that can be shot, quotas are often aimed at males and juveniles/subadults that have not yet started to reproduce (Beddington 1974, Caughley 1977, Sæther et al. 2001, Lavsund et al. 2003). This generates large variation in harvest mortality among individuals according to their age, sex, or reproductive status. Harvesting can also have other, more subtle consequences, such as generating artificial selection on phenotypes and thereby influencing the magnitude of genetic drift (Ericsson et al. 2001, Sæther et al. 2009, Sæther & Engen 2019) and the capacity to adapt to environmental fluctuations, or behavioural responses that affect individual fitness (Edeline et al. 2007, Coltman 2008). In turn, these consequences of harvest may affect long-term sustainable yield during periods with large environmental changes, such as an altered climate (Morrongiello et al. 2019). Although harder to detect, their impact on dynamics and evolutionary processes should not be ignored when developing management strategies to ensure the long-term sustainability of harvest (Coltman 2008).

Recent research has clearly demonstrated the strong influences that individual variation in vital rates can have on population dynamics, demography, and evolutionary processes (Engen et al. 2003, Hamel et al. 2018). This variation can be caused by differences in the underlying probability of survival and reproduction among individuals or groups (Cam et al. 2016) or simply by the stochastic realizations of survival and reproduction based on these probabilities (Engen et al. 1998, 2003). When individual differences are persistent through time, they are often termed individual heterogeneity (although the exact definition of this term varies; see Cam et al. 2016). Individual heterogeneity can be fixed (permanent differences in probability of survival or reproduction fixed at, or soon after, birth) or dynamic (persistent differences among individuals caused by realisation of stochastic processes, while the underlying probabilities are the same) (Cam et al. 2016). These different types of heterogeneity are difficult to separate in practice. Here, we use the term individual heterogeneity to mean persistent individual differences, whether they are fixed or dynamic.

Stochastic theory of population growth differentiates between environmental stochasticity, which tends to influence the survival and/or reproduction of all individuals simultaneously, and demographic stochasticity, which is random variation in realised survival and reproduction among individuals (Engen et al. 1998). Demographic variance, σ_d^2, is a commonly used metric of demographic stochasticity. Demographic stochasticity has a negative impact on the growth rate of small populations (Lande et al. 2003), increasing their risk of extinction (Engen et al. 2005b). In addition, demographic stochasticity may reduce the effective population size (N_e) (Engen et al. 2005a), increasing the loss of alleles and genetic drift. These properties make demographic stochasticity a fundamental concept in population ecology and evolutionary biology. Its influence on extinction rate, allele frequency variation, and phenotypic evolution makes it a crucial parameter for understanding the short- and long-term persistence of populations (Engen et al. 1998, 2003, Sæther & Engen 2019), particularly when they are small and isolated (Lande 1998).

There are several challenges involved in estimating the demographic variance of harvested populations and studying its causes and consequences. First, we need information about survival and reproduction at the individual level for a large proportion of the population, which, for many species, requires a great deal of time and resources to obtain. Second, estimation of age- or stage-specific vital rates often involves sophisticated statistical analyses, for instance, to separate harvest mortality from other sources of mortality. Moreover, to disentangle the different drivers of individual variation in demographic contributions, we need knowledge about other factors such as population density and structure and environmental conditions. Only with such information available can we start to fully understand the causes and consequences of individual variation in vital rates (Hamel et al. 2018, Festa-Bianchet et al. 2019). Still, it is a challenge to estimate demographic variance in fluctuating age-structured populations, because age dependences in life histories generate time lags in population dynamics (Engen et al. 2009). Using the concept of individual reproductive values can help resolve this issue, because it describes the expected contribution that an individual of a certain age and sex will make towards population growth or evolutionary processes relative to other individuals (Grafen 2006). Accordingly, by using individual reproductive values, it is also possible to estimate total and sex-specific demographic variance for age-structured populations with

overlapping generations (Engen et al. 2007a,b, Sæther et al. 2007), as is common for harvested species.

Here, we synthesise results from almost 30 yr of research focussing on how harvesting can influence the demographic processes of a moose population on the island of Vega, off the coast of northern Norway (see Fig. 1). Because of the small impact of environmental variation on individual performance and population dynamics (Sæther et al. 2007, Solberg et al. 2007), the Vega moose population is well suited for generating knowledge on the fundamental consequences of harvesting on population processes. In addition, it represents one of few harvested systems where detailed individual data make it possible to investigate the complexity of demographic effects of harvesting.

2. THE VEGA MOOSE STUDY SYSTEM

2.1. The island of Vega

Vega (65° 40′ N, 11° 55′ E) is an island with an area of 119 km², located off the coast of Helgeland in northern Norway (Fig. 1), approximately 100 km south of the Arctic Circle. The island is covered by a mixture of agricultural areas, marshes, and heather *Calluna vulgaris*-dominated moorland, interspersed with stands of deciduous forests and short-grown pine *Pinus sylvestris* forests (Angeloff et al. 2004). The deciduous forests are mainly found along rivers and creeks. The southwestern part of the island is more mountainous, with Trollvasstinden (800 m above sea level) as the highest point. The mountain area is steep and not utilised by moose, leaving approximately 80 km² of the island as moose habitat. The climate is oceanic, with relatively mild winters (November–April temperature: mean = 1.9°C, range 0.6–3.1°C) and shallow snow cover (November–April snow depth: mean = 4.9 cm, range 0–23.7 cm) given the high latitude. The summers are cool and wet (June–August: temperature, mean = 12.5°C, range 10.8–15.4°C, precipitation, mean = 73.2 mm, range 33.0–104.4 mm).

2.2. The Vega moose population

The moose population on Vega was founded by 1 male and 2 females that swam to the island, about 13 km off the mainland, in 1985. The population increased by reproduction and subsequent immigrations, and restricted hunting started in 1989. In 1991,

hunters killed 2 moose, and 24 individuals were recorded during a helicopter survey in the following winter. Since then, annual harvesting has kept the breeding population between 27 and 40 individuals (see Fig. 2). The population density is well below carrying capacity and it scores high on all performance parameters (Solberg et al. 2011). Calves weigh on average about 160 kg in autumn (80 kg carcass mass, which is body mass minus head, skin, metapodials, bleedable blood and viscera; Sæther et al. 1996), males weigh about 500 kg at prime age (5–10 yr old), and about 60% of reproducing females give birth to twins (Markussen et al. 2018). Moreover, as there are no large carnivores on the island, natural mortality rates are low and mainly due to traffic accidents. In the period 1991–2005, the number of moose harvested constituted about 91% of all calves recruited to the pre-harvest population in the same period of time, indicating that most moose are eventually killed during the hunting season (Solberg et al. 2010). The high fecundity and natural survival combined with a mostly female-dominated sex ratio (Herfindal et al. 2014a) allowed for an annual harvest of 24 moose on average in the period 1991–2018 (Solberg et al. 2010, Statistics Norway: www.ssb.no). Hunting permits are usually issued for a fixed number of calves, adult males, and adult females, but adults can also be split into young (mainly yearlings) and old adults (≥2.5 yr old) by the hunting right holders. Hunting can occur from 25 September to 23 December, but in most years the start of the hunting season was postponed to the first weekend of October and finished before the end of the same month. The peak rut occurs at the end of September on Vega, indicating that most females have conceived before the start of the hunting season.

2.3. Studies on the Vega moose population

The study of the moose population at Vega was initiated in 1992 (see Fig. 2), when 20 of 24 moose present on the island were captured, weighed, and marked with VHF radio-collars (Sæther et al. 2003). In the following years, new calves and immigrants to the island were radio-collared each year, with GPS collars gradually replacing VHF collars after 2004 (Herfindal et al. 2009, Solberg et al. 2011). Almost all captures were conducted with the use of helicopters in January–March, during periods with snow on the ground. The frequent captures ensured that a large proportion (>90%) of the breeding population were wearing radio collars during the study period.
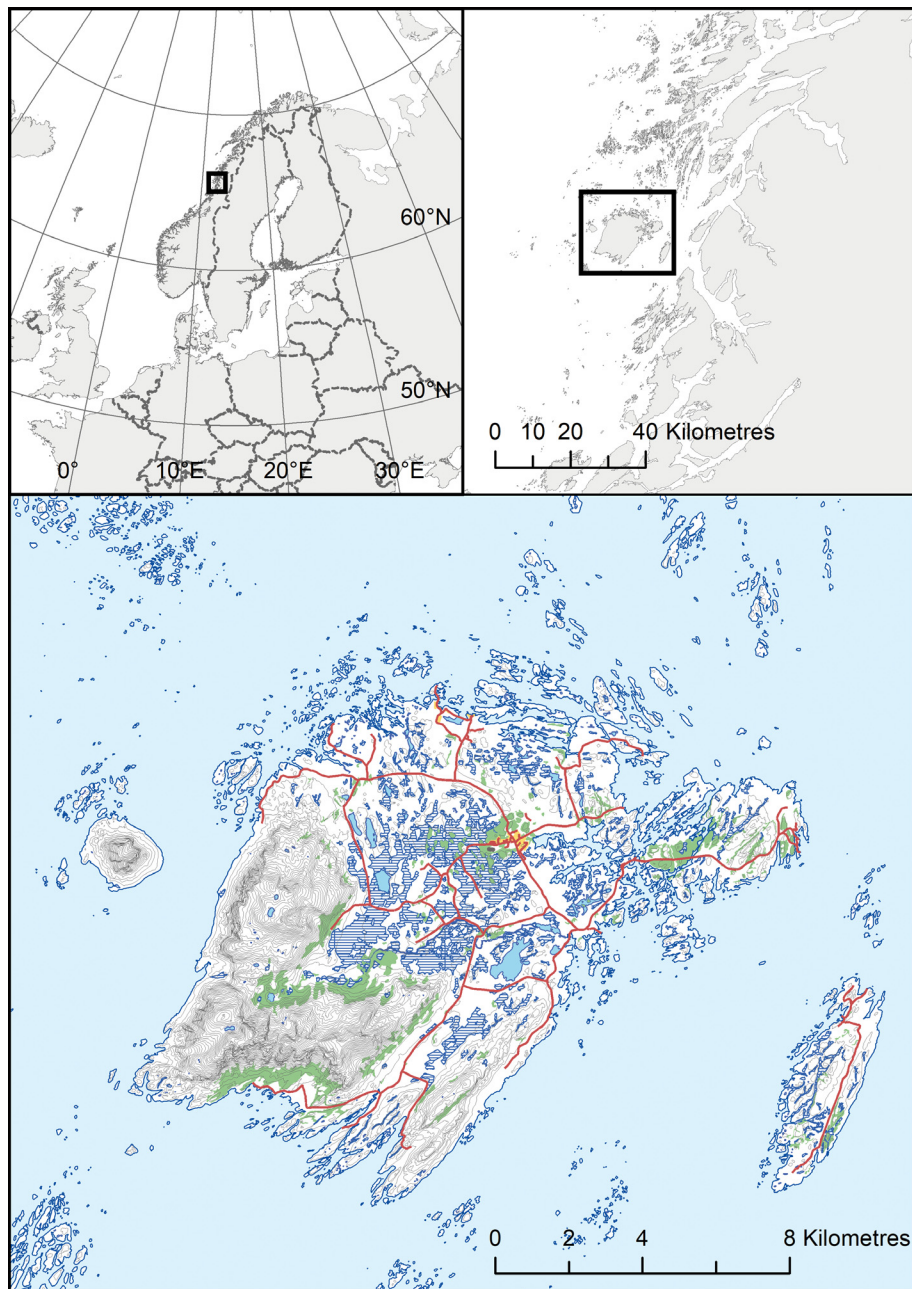
Fig. 1. The island of Vega, Norway, where research on the demographic consequences of harvesting on a moose population has been carried out since 1992. In the lower map, green areas: forests; blue-lined areas: bogs/wetlands; filled blue areas: open water; white areas: open areas (heather, bare mountain); red lines: public roads

The study at Vega was initiated mainly to examine the effect of skewed adult sex ratios on fecundity and calving dates (Sæther et al. 2003, 2004). To achieve this goal, the sex and age structures were manipulated by selective harvesting during the period 1994–1999. In 1994, all adult (≥1.5 yr) males in the population were killed after the rutting season (Fig. 2), leaving only young (≤2.5 yr) males as poten-

tial breeders in 1995 and 1996. The sex ratio was kept quite even (ca. 40% males) by shooting some cows. Thereafter, the adult sex ratio in the population was reduced to about 25% males from 1997–1999, while keeping some older males in the population (Sæther et al. 2003, 2004). The population grew rapidly the first 8 yr after colonisation (Sæther et al. 2007) and also experienced similar growth at
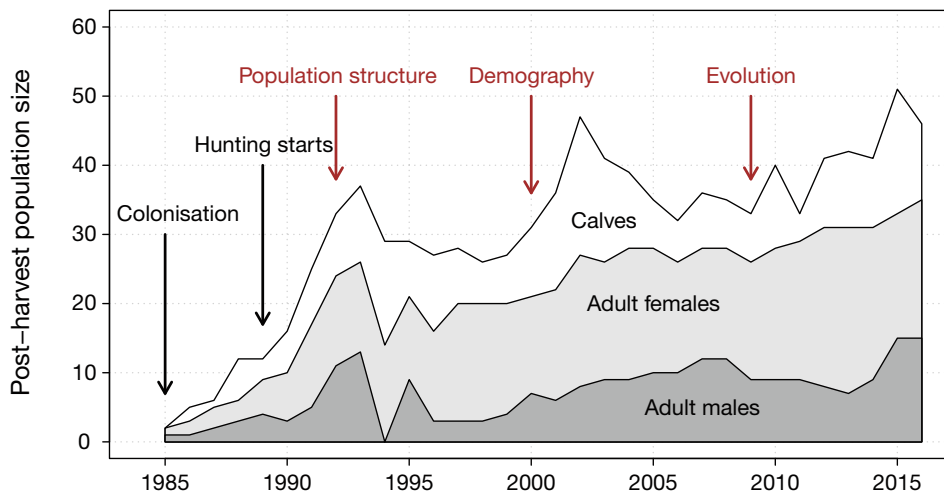
Fig. 2. Dynamics of the post-harvest moose population at Vega, with important events highlighted with arrows. Red arrows indicate when research projects started and the thematic focus of the research

the end of the 'population structure' research period (Fig. 2) before being stabilized through regular harvest (Fig. 2). Later studies at Vega have focussed on establishing a pedigree to investigate the evolutionary consequences of harvesting (Kvalnes et al. 2016).

3. WHAT HAS THE VEGA MOOSE POPULATION TAUGHT US ABOUT HARVESTING IMPACT ON DEMOGRAPHY?

3.1. Demographic effects of population properties

The age- and sex-specific harvesting that ungulate populations experience strongly affects their social structure (i.e. age and sex distribution). Structured harvesting quotas are often used to increase yield in terms of biomass or numbers of harvested individuals. This strategy is based on deterministic harvesting models showing that the annual yield can be enhanced by increasing the share of adult males and juveniles of both sexes in the harvest (Beddington 1974). However, stochastic processes affecting the population may alter the optimal harvesting strategy to be more conservative due to a higher variation in the annual yield (Sæther et al. 2001). Such strategies could be achieved by introducing harvest thresholds to relax harvest pressure at critically low population sizes (Lande et al. 1995, 1997). This demonstrates the importance of acknowledging stochasticity in demographic rates and in the environment for achieving sustainable harvest of populations (Lande et al. 1995, 1997, Engen et al. 1997, Sæther et al. 2001). Moreover, as variation in

age- and sex-structure strongly affects the effective size of a population (Engen et al. 2005a), the long-term ability of such sex- and age-selective harvesting strategies to maximise the annual yield can be questioned (Ericsson et al. 2001). In the Vega moose population, increasing the share of adult bulls in the harvest, and thus decreasing the share of calves, led to a decrease in N_e (Sæther et al. 2009) because these structural changes affected the demographic variance. This illustrates how a harvest strategy aimed at particular age groups and sexes can alter the genetic composition of a population by affecting the number of breeding males (Sæther et al. 2009, Sæther & Engen 2019) and indicates that harvest strategies for optimising short-term yield may have unfavourable long-term genetic consequences.

For polygynous species, most harvesting models assume that only a few males are needed to fertilise all fecund females (e.g. Mysterud et al. 2002). However, the consequences of a skewed sex ratio or changes in the age structure on individual performance have rarely been examined in natural populations. At Vega, we investigated the demographic consequences of sex-skewed harvesting by manipulating the population's sex and age structure into an overdominance of adult females and young males, respectively. Such a population structure occurs in several heavily managed moose populations in Fennoscandia (Lavsund et al. 2003, Solberg et al. 2006). The results showed that the number of calves produced remained mostly unchanged even when only a few or mainly young males were present in the population (Sæther et al. 2003, Markussen et al. 2018) but that calves were born substantially later

than in years with more balanced sex- and age-structure (Sæther et al. 2003). As late-born calves are smaller on average as adults (Solberg et al. 2007, 2008) and size seems to be a fundamental determinant of reproductive success in moose (Sæther & Heim 1993, Sæther et al. 1996), a sex-biased population structure can have unintended long-term consequences for the population growth rate. In addition, the male age structure seems to affect the secondary sex ratio, as significantly more male than female calves were sired by older than younger fathers (Sæther et al. 2003), a pattern that is supported when examining moose populations across Norway (Bjørneraas et al. 2009). Hence, although population structure had only minor immediate effects on the females' probability of reproduction, smaller calves and changes in sex ratios at birth generated long-lasting cohort effects on offspring characteristics that can affect population growth (Solberg et al. 2007, Markussen et al. 2018).

3.2. Individual heterogeneity in the Vega moose population

Despite the favourable environmental conditions for moose on Vega (Sæther et al. 2007, Solberg et al. 2011), there is substantial individual variation in female reproductive performance in terms of age at first reproduction, annual probability of reproduction, and lifetime twinning rate. Longevity is a fundamental component of lifetime reproductive success in long-lived species (Clutton-Brock 1988, Ericsson et al. 2001, Neumann et al. 2020), and on Vega, longevity is almost entirely determined by harvesting, with the exception of some natural mortality in the first year of life (Kvalnes et al. 2016, Stubsjøen et al. 2000). Moose cows can start mating in their second autumn and give birth the following spring, but age at first reproduction depends on female body mass (Sæther et al. 1996). Accordingly, larger female calves at Vega have a higher probability of giving birth at age 2 than smaller calves (Markussen et al. 2018), and females that reproduced at 2 yr of age are more likely to reproduce and to produce twins in subsequent years than are females that delay their start of reproduction (Markussen et al. 2018). This contradicts the usual trade-offs expected between early- and late-life investment in reproduction (Stearns 1992). Indeed, it has been demonstrated that individual variation in resource acquisition and allocation can mask the trade-offs expected by life-history theory (Stearns 1992), leading to positive rather than negative correlations among life-history traits at the individual level (van Noordwijk & de Jong 1986). The positive correlation between current and future reproductive success on Vega is probably caused by persistent individual differences in female quality, which in turn may be caused by maternal habitat use and early body growth (Markussen et al. 2018, Ofstad et al. 2020). Initially, we expected low variation in habitat use on an island the size of Vega, where moose can easily gain information about the distribution of resources. However, we actually found the variation in habitat use to be considerable, and that the mothers' habitat use also affected the body mass of their calves (Ofstad et al. 2020). This suggests that individual variation in behaviour and movement patterns can provide important contributions to the distribution of fitness-related life-history traits within a population (McLoughlin et al. 2007, Allen et al. 2017, Rolandsen et al. 2017).

Because harvesting is the main cause of mortality of adult females at Vega (Kvalnes et al. 2016, Stubsjøen et al. 2000), we did not expect to observe survival costs of reproduction. Compared to reproductive costs, survival costs of reproduction are more unlikely and have been less frequently reported in such long-lived species (Hamel et al. 2010) because survival is strongly canalized (Gaillard et al. 2000, Gaillard & Yoccoz 2003). Still, the probability of being shot is not random among females at Vega. Harvest mortality is lower among productive females because hunters, for ethical reasons, are unlikely to shoot a female accompanied by a calf (Markussen et al. 2018), and consequently, the frequency of orphaning is estimated to be low in Norway (1.7–1.9% of moose calves; Veiberg et al. 2016). For this reason, the most productive females are also winners with respect to survival, as a female with twins must lose both her calves before she becomes a real target (Markussen et al. 2018). This suggests that selective hunting based on reproductive status can impose strong artificial selection pressure in harvested populations.

Assessing the reproductive performance of males is challenging in species without paternal care. Individual heterogeneity in males' vital rates and life-history traits have therefore mainly been investigated for mortality, at least in mammals (Hamel et al. 2010, Bleu et al. 2016). However, molecular genetic tools have now made it more feasible to assess the reproductive success of males. At Vega, we have a near complete pedigree for all individuals present between 1985 and 2016 (Haanes et al. 2013), providing an ideal opportunity to assess heterogeneity in both

reproduction and survival among males. As expected for polygynous species, reproductive performance among males in a given year is highly variable, measured both as the number of successful matings and number of calves sired (Ofstad 2019). This difference persists over entire lifespans (Markussen et al. 2019), resulting in a considerably higher individual variation in lifetime reproductive success among males than females (Markussen et al. 2018, 2019). Interestingly, a positive temporal covariation in reproductive performance also exists in males, as most males that started reproducing at a young age had higher annual mating success during their life than males that delayed first reproduction (Markussen et al. 2019). Juvenile body mass was an important determinant of reproductive performance, emphasising the limited possibilities for males to compensate for a bad start in life (Solberg et al. 2008). The presence of such a positive covariation could also depend on the mating system. In sequentially polygynous species such as the European moose, where males do not frequently engage in energetically demanding fights, the cost of reproduction may be lower than in harem-holding species where males spend a large amount of energy in fights to obtain and protect a harem (Clutton-Brock et al. 1982).

When the management goal is to maximise production, harvesting is often targeted at males (Beddington 1974, Sæther et al. 2001, 2004). Thus, at Vega the harvest mortality of males is considerably higher than that of females (Kvalnes et al. 2016, Markussen et al. 2019) but lower among older (>2.5 yr) than younger males. The latter may appear odd in light of the often observed high focus on trophy animals among hunters, but can be explained by the wish of the local management to keep some prime-aged males in the population (Sæther et al. 2004). To avoid excessive hunting of trophy bulls, permits are often split between young (mainly yearlings) and older males based on body size and antler size, which can also explain why the harvest mortality was lower for the most successful males (Markussen et al. 2019). In fact, even among older males (>3.5 yr old), the harvest mortality was more than 4 times higher for unsuccessful than successful males, which we believe is caused by unsuccessful males being smaller and thus more likely to be judged as younger by the hunters (Markussen et al. 2019). Accordingly, selective hunting is adding to the positive covariation among life-history traits in males, and individual differences in early growth is the main determinant of the persistent individual heterogeneity in life-history traits of both male and female moose at Vega.

3.3. Consequences of individual heterogeneity for demography

Theoretical models have demonstrated that individual heterogeneity may influence both population dynamics (Vindenes et al. 2008) and evolutionary processes such as genetic drift (Engen et al. 2007b, Lee et al. 2011). In polygynous species, fluctuations in population size are generally driven by variation in the reproductive success and survival of females. However, the persistent differences in reproductive performance seen among female moose on Vega had only a very small effect on the demographic variance in this population (Lee et al. 2017). The effect was somewhat larger when the observed covariation between reproduction and survival was also included, because this covariation amplifies the individual differences. Females that had twins were not only more likely to produce twins again in the future if they survived, they were also more likely to survive, causing a synergistic effect between these 2 mechanisms. Nonetheless, the combined effect on the expected time to extinction was negligible (Lee et al. 2017). Thus, female individual heterogeneity seems to have minor effects on population dynamics in this population. This is likely in part because most female moose do eventually start producing twins, causing the differences between individuals to decrease over their lifetimes (Markussen et al. 2018). In fact, theoretical analyses indicate that individual differences in reproduction would have to be quite extreme to have a substantial effect on the expected time to extinction (Lee et al. 2017).

While mammalian population dynamics are assumed to be driven mainly by females, the genetic composition can be highly influenced by males, due to the high variance in male reproductive success in polygynous species (Clutton-Brock 1988, Markussen et al. 2019, Ofstad 2019). This also holds true for the moose population at Vega. The ratio of N_e to total population size ($N_e:N$) was especially sensitive to the demographic variance of older males in this population (Lee et al. 2020). Persistent differences in reproductive output and covariation between reproduction and survival in females had little impact on this ratio. In males, however, the resulting individual heterogeneity had a greater effect, increasing the demographic variance by almost 13%. Overall, persistent individual differences decreased $N_e:N$ from 0.34 to 0.28, which represents a change in the asymptotic N_e from 17 to 14, using the harmonic mean of the population size between 1992 and 2011 ($N = 50$) as N (Lee et al. 2020). This represents a substantial change in

such a small population, showing that individual heterogeneity does in fact play an important role in genetic processes in this population.

3.4. Harvest selection on phenotypes and life histories

The extent to which harvest acts as a selective force that results in evolutionary change of phenotypes in wildlife populations has recently been the subject of scientific debate (e.g. Coulson et al. 2018, Festa-Bianchet & Mysterud 2018). In the moose population at Vega, we can explore the effects of harvesting on phenotypic evolution because individual contributions to population growth are related to differences in a heritable trait — body mass — in both sexes (Markussen et al. 2018, 2019). Such size-dependent demography operating through earlier onset of reproduction in large individuals is a general pattern in Scandinavian moose populations (Sæther & Haagenrud 1983, 1985, Sæther & Heim 1993, Sand 1996, Ericsson et al. 2001) and seems to be related to the quality or quantity of available food in late spring or early summer (Sæther 1985, Bø & Hjeljord 1991, Sand 1996, Herfindal et al. 2006a,b, 2014b). This implies that the timing of birth relative to plant phenology can have important consequences for lifetime reproductive success in moose (Sæther et al. 2003, Markussen et al. 2018, Neumann et al. 2020) as in other cervids (Klein 1965, Plard et al. 2015). On Vega, there was harvest-induced directional selection for smaller calves (Kvalnes et al. 2016), which was caused by large-sized females being more likely to lose their calves during the hunt. Calves constitute a large part of the harvest on Vega, and large females produce more and larger calves. These females also use open areas more frequently, exposing themselves and their calves to a higher risk of being shot (Ofstad et al. 2020). Conversely, late-born calves were more often produced by smaller cows that use open areas less frequently. This introduces age-dependent selection, as young females give birth later than prime-aged females (Kvalnes et al. 2016). Because additive genetic variance was present for both body mass and birth date (Kvalnes et al. 2016), we would also expect selection for earlier calving as a response to earlier green-up in the area (Park et al. 2016). However, because of the harvest-induced selection for later birth, we may rather observe increasing maladaptation to the prevailing environmental conditions in the moose population at Vega.

3.5. Subtle pathways to harvest selection: the importance of animal behaviour

Studies of harvest selection have often focussed on direct selection for specific phenotypes such as horn or antler size or body mass (Proaktor et al. 2007, Pigeon et al. 2016). Nonetheless, it has recently become evident that harvest selection may also operate through more subtle pathways, such as selection for specific behavioural strategies (Leclerc et al. 2017, 2019). In this context, the use of habitat types with varying degrees of cover may be relevant, in particular since hunting for moose and other ungulates often requires open areas with good visibility for the hunters to spot and safely kill the animal. Accordingly, we found that the harvest mortality of yearlings and adult bulls was higher among those that more often used open areas, and the same was true for calves of mothers that frequently used open areas (Ofstad et al. 2020). The result was a clear fitness cost with respect to survival and recruitment for individuals using open habitats. Such habitats, however, are frequently used by moose at Vega (Herfindal et al. 2009, Ofstad et al. 2019) and elsewhere (Nikula et al. 2004, Bjørneraas et al. 2011, Allen et al. 2017), probably because they offer excellent foraging opportunities with abundant forage of high quality (Sviland 2001, but see Allen et al. 2017). In fact, cows that more often used open areas had higher twinning rates and heavier calves than those exhibiting low use of such areas (Sviland 2001, Klaussen 2012, Ofstad et al. 2020). At Vega, these open areas are often agricultural fields for grass production, but elsewhere similar benefits can be gained by using clear-cuts with rejuvenating forest (Wam et al. 2010, 2016, Bjørneraas et al. 2012) or other types of deciduous forests that offer high-quality forage for moose (Allen et al. 2017). The propensity to use human-made habitats thus induces a fitness benefit with respect to reproduction, but at the cost of reduced survival because of a higher risk of being shot (Ofstad et al. 2020). This results in a weak and non-significant cost among both males and females of using open areas, but the net gain or cost of using these areas depends on the harvest pressure (Ofstad et al. 2020).

3.6. Harvesting effects on inbreeding

In small and/or isolated populations, such as the Vega moose population, breeding among closely related individuals is common. Inbreeding is typi-

cally associated with reduced heterozygosity and can have severe fitness consequences (Charlesworth & Charlesworth 1987, Hedrick & Kalinowski 2000, Keller & Waller 2002). The level of inbreeding varies among individuals at Vega and fluctuates over time, partly due to immigration events (Herfindal et al. 2014a). Based on the pedigree of the Vega moose, the inbreeding coefficient (F), was on average 0.12 (SD = 0.11), with an annual value close to 0.20 in some years (Haanes et al. 2013). As a result, the level of genetic variation in the Vega moose population was substantially lower than in the mainland moose population (Haanes et al. 2011, 2013). This level of inbreeding is similar to what is observed in other small and isolated animal populations (Crnokrak & Roff 1999, Marr et al. 2006, Bozzuto et al. 2019).

A number of strategies to avoid inbreeding exist among animals, such as sex-specific juvenile dispersal or short-term migration during the rut (Blouin & Blouin 1988). However, as such strategies may not always be possible to adopt, individuals may have to choose between mating with a relative or simply not reproducing. The high relatedness among moose on Vega (Haanes et al. 2013, Herfindal et al. 2014a) and the limited possibilities to disperse suggest that moose on Vega face such a trade-off. The highest recorded inbreeding level in a single year was 0.47, and several cases of father–daughter breeding were recorded (Haanes et al. 2013, Herfindal et al. 2014a). In these cases, inbreeding avoidance was clearly traded off for the chance to reproduce. When the population structure allowed for it, however, as in years with a high number of males available for mating, more even sex ratios, and high population sizes, there was clear evidence of inbreeding avoidance (Herfindal et al. 2014a). Mating with close relatives was found to have fitness consequences, as offspring from closely related parents were born later and were generally smaller, and inbred adult females had lower twinning rates than outbred females (Haanes et al. 2013). Such fitness consequences of inbreeding may in turn lead to increased individual heterogeneity in reproduction and survival, and reduced mean individual fitness (Bozzuto et al. 2019), with likely effects on population dynamics and genetic drift in the Vega moose population.

4. CONCLUSIONS AND FUTURE PROSPECTS

Studies of the moose population on the island of Vega have shown how harvesting can have direct and indirect consequences for individual perfor-

mance and population dynamics, and demonstrate the complexity of human impacts on wild populations. These results are based on a combination of theoretical modelling and long-term empirical studies of individual life histories, and provide us with a deeper understanding of how harvesting and other anthropogenic factors shape ecological and evolutionary processes in natural populations. One clear take-home message from these results is that long-term sustainability is reached by more conservative age- and sex-distributions than what is indicated in deterministic models of maximum sustainable yield. Applying traditional harvesting models that do not acknowledge demographic consequences of skewed age- and sex-ratios can lead to restrictions in mechanisms that reduce genetic drift, such as inbreeding avoidance and mate choice (Sæther & Engen 2019). For harvesting to be sustainable, such processes must be accounted for. Moreover, managers must realise that harvesting is selective on phenotypes and that this selectivity has demographic consequences that affect long-term sustainability.

An important question is how the effects of harvesting interact with ongoing climate change (Gamelon et al. 2019), for instance through age- or sex-specific sensitivities to climate variation (Herfindal et al. 2015, Lee et al. 2022 in this Special). However, because range shifts or changes in large-scale movement patterns such as seasonal migrations are central mechanisms in animals' responses to climate change (Morrison et al. 2021), the study at Vega may be less ideal for generating general results about harvesting under climate change. Similarly, the lack of predation by large carnivores may constrain the generality of the results from the Vega moose population. Still, many ungulate populations worldwide are small and isolated, with few natural predators, and living in highly human-modified landscapes (Chapron et al. 2014, Ripple et al. 2014, Tucker et al. 2018). The results from the Vega moose may be highly relevant for understanding the dynamics in such populations.

The value of long-term, individual-based time-series in ecological and evolutionary research cannot be overemphasised (Clutton-Brock & Sheldon 2010, Festa-Bianchet et al. 2019). The importance of individual-based data becomes particularly evident when we observe the role that behaviours such as movement and mate choice play in demographic processes. Indeed, because animal behaviour is greatly affected by any type of human activity (Tucker et al. 2018), understanding human impact on animal populations requires behavioural observations. Studying how behaviour contributes to demo-

graphic processes often requires a different set of individual-based data, including metrics other than reproduction and survival. There is thus an urgent need to obtain data sets similar to the one available for the moose population at Vega to get more insights into behavioural processes and how they interact with harvesting and other human activities to affect the dynamics and long-term persistence of populations.

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