



RESEARCH ARTICLE

Opposing fitness consequences of habitat use in a harvested moose population

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Abstract

1. Landscape changes are happening at an unprecedented pace, and together with high levels of wildlife harvesting humans have a large effect on wildlife populations. A thorough knowledge of their combined influence on individual fitness is important to understand factors affecting population dynamics.
2. The goal of the study was to assess the individual consistency in the use of risky habitat types, and how habitat use was related to fitness components and life-history strategies.
3. Using data from a closely monitored and harvested population of moose *Alces alces*, we examined how individual variation in offspring size, reproduction and survival was related to the use of open grasslands; a habitat type that offers high-quality forage during summer, but at the cost of being more exposed to hunters in autumn. The use of this habitat type may therefore involve a trade-off between high mortality risk and forage maximization.
4. There was a high repeatability in habitat use, which suggests consistent behaviour within individuals. Offspring number and weight were positively related to the mothers' use of open grasslands, whereas the probability of surviving the subsequent harvest season was negatively related to the use of the same habitat type. As a consequence, we found a nonsignificant relationship between habitat use and lifetime fitness.
5. The study suggests that harvesting, even if intended to be nonselective with regard to phenotypes, may be selective towards animals with specific behaviour and life-history strategies. As a consequence, harvesting can alter the life-history composition of the population and target life-history strategies that would be beneficial for individual fitness and population growth in the absence of hunting.

KEYWORDS

demographic heterogeneity, habitat use, harvest-induced selection, herbivore, individual differences, life-history trade-off, lifetime reproductive success, resource acquisition

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1 | INTRODUCTION

In many populations, harvesting is the main cause of mortality (Allendorf, England, Luikart, Ritchie, & Ryman, 2008) and may act as a powerful selective force that can influence individual life histories (Darimont et al., 2009; Kvalnes et al., 2016), population dynamics (Biro & Post, 2008) and have evolutionary consequences (Engen, Lande, & Sæther, 2014; Mysterud, 2011). Besides apparent evolutionary consequences, such as changes in horn morphology due to trophy hunting (Darimont et al., 2009), harvesting can also induce evolutionary effects through more subtle pathways, for example, if the harvest is higher in areas that are used mainly by individuals with specific behavioural phenotypes (Mysterud, 2011). Understanding such harvest-induced variation in fitness becomes increasingly more important as levels of habitat alterations increase, and behavioural diversity can be important for how a population responds to such changes (Dammhahn, Dingemanse, Niemelä, & Réale, 2018). However, as harvesting and habitat alterations can affect several fitness-related traits simultaneously, it is not straightforward to assess the population dynamical and evolutionary consequences of such human-induced factors.

Optimal habitat utilization involves using habitats that maximize energetic uptake and minimize mortality (Gaillard et al., 2010; Lima & Dill, 1990). Accordingly, individual variation in fitness, which is a combination of reproduction and survival (Sæther & Engen, 2015), will normally be the result of the foraging conditions affecting reproductive performance (Allen et al., 2016; McLoughlin, Boyce, Coulson, & Clutton-Brock, 2006; McLoughlin et al., 2007), as well as the access to cover or escape opportunities that reduce predation or other mortality risks (Johnson, Parker, & Heard, 2001; McLoughlin, Dunford, & Boutin, 2005; Sigaud et al., 2017). However, since habitats rarely offer the possibilities to simultaneously maximize forage intake and minimize predation, animals will have to make trade-offs between fitness-traits when choosing habitats (Morris & Davidson, 2000). For instance, agricultural grasslands are often important for ungulates as they provide abundant high-quality forage (Bjørneraas et al., 2012; Brinkman, Jenks, DePerno, Haroldson, & Osborn, 2004), but such habitats may also be associated with higher mortality rates due to the lack of cover (Godvik et al., 2009; Sigaud et al., 2017).

The risk allocation hypothesis predicts that the time animals spend in habitats with favourable foraging conditions should be affected by the mortality risk in that habitat relative to alternative habitats (Lima & Bednekoff, 1999). These spatial differences in risk (i.e. 'landscape of fear'; Laundre, Hernandez, & Altendorf, 2001) are often generated by the spatial distribution of predators in the landscape, or by multiple predator species that differ in their hunting tactics (Norum et al., 2015; Proffitt, Grigg, Hamlin, & Garrott, 2009). Moreover, increasing human impact through activities such as harvesting or infrastructure also shapes the spatial differences in risk (Ciuti et al., 2012; Rolandsen, Solberg, Herfindal, Van Moorter, & Sæther, 2011). However, individuals may also vary with respect to how they perceive risk and correspondingly to what extent they

utilize risky habitats (Hebblewhite & Merrill, 2008). Moreover, when different habitats have different fitness gains, individual variation in the trade-off between foraging and predator avoidance will result in individual differences in the trade-off between vital rates, such as reproduction and survival (Engen & Stenseth, 1989; McNamara & Houston, 1986; Stearns, 1989), and may also be linked to life-history traits such as current and future fitness (Stearns, 1989).

A given behaviour is usually much less variable within than between individuals, resulting in behavioural differences among individuals that are consistent across contexts, such as between seasons or predator regimes (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). This diversity in behaviour can be important for population viability in a stochastic and changing environment (Dammhahn et al., 2018). However, behavioural diversity among individuals does not imply that individuals are not plastic and may change habitat use according to changes in, for example, density, but that individuals that are more risk-prone in one setting will also be more risk-prone in other settings (Bell, Hankison, & Laskowski, 2009; Dingemanse, Kazem, Réale, & Wright, 2010). Consistent individual behaviour has been shown in several taxa, such as rodents (Koolhaas et al., 1999), fish (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011) and birds (Dingemanse, Both, Drent, & Tinbergen, 2004). Studies suggest that such behaviours are heritable and thus subject to selection (de Villemereuil, Schielzeth, Nakagawa, & Morrissey, 2016; Réale et al., 2007), although behavioural traits also can be culturally transmitted, for instance, by offspring following their parents during migration (Jesmer et al., 2018). However, although behavioural variation among individuals can influence population dynamics (Bolnick et al., 2011) and recent studies have shown how behavioural traits can be related to life-history traits (Bonnot et al., 2018; Vetter et al., 2016), few studies have documented the fitness consequences of behavioural differences (Biro & Stamps, 2008).

Here, we used individual data on reproductive performance and survival in a harvested moose *Alces alces* population to investigate whether habitat use is related to fitness components and lifetime reproductive success (LRS). We focussed specifically on the use of agricultural grasslands which are highly available in the study area and of high nutritional value for the moose (Bjørneraas et al., 2012). A vegetation survey showed that forage is particularly abundant in this habitat type (>500 g biomass per m²), compared to coniferous (251 g/m²) and deciduous (189 g/m²) forests (Sviland, 2001). Moreover, as agricultural grasslands are harvested several times over the summer, they regularly provide plants at early phenological states, which are high-quality forage for herbivores (Albon & Langvatn, 1992; Deinum, 1984; Mårell, Hofgaard, & Danell, 2006). The moose is a capital breeder, where body growth also outside of breeding season is important for reproductive performance (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000; Van Ballenberghe & Miquelle, 1993). Contrary to forests, however, open grasslands provide no protective cover, and the use of this habitat type may be associated with a higher predation risk, for example, because moose in open habitats are more easily spotted by hunters, and hunters may rely on open habitat to shoot moose.

In accordance with the risk allocation hypothesis (Lima & Bednekoff, 1999), we expected a higher reproductive performance by moose that frequently use open grasslands, but at the cost of higher harvest mortality rates. More specifically, we predicted the number and body mass of calves (an important fitness-related life-history trait in moose; Solberg, Heim, Grøtan, Sæther, & Garel, 2007) to be positively related to the mother's use of open grasslands, and the number of calves sired to be positively related to the father's use of open grassland. In addition, we predicted that frequent use of open grasslands will increase the exposure and reduce the survival of moose during the hunting season (Ciuti et al., 2012). For such fitness consequences of habitat use to occur, an individual's propensity to use open areas must be consistent over time, that is, that there is high repeatability in the level of use of open areas, and that moose inclined to use open habitats are also more often killed by hunters.

It is less clear if this behaviour will also affect the LRS. In a recent study in the same population, Kvalnes et al. (2016) found a harvest-induced selection towards smaller calf body masses, presumably because females that were larger as calf lost a higher proportion of calves to hunters as adults. This indicates that the costs of using open grassland with respect to survival may be higher than the gains with respect to reproductive performance. Hence, we predicted a negative relationship between LRS and the use of open grassland.

2 | MATERIALS AND METHODS

2.1 | Study system and data collection

Vega (119 km², 65°39'N, 11°54'E) is an island off the coast of northern Norway that was colonized by three moose in 1985. Harvesting is the main source of mortality (natural mortality <2%, Kvalnes et al., 2016), and have, since it started in 1989, been used to regulate the population at about 20–50 moose during winter. As harvesting keeps the density fairly low (0.35 moose/km² moose terrain, excluding lakes, human settlements and unproductive areas, year-to-year CV = 0.10), and combined with a benign climate, there is no detectable density-dependent effects on condition (Sæther, Engen, Solberg, & Heim, 2007; Solberg et al., 2007). Likely for the same reason, the commonly observed trade-off between offspring number and size (Stearns, 1989) is not apparent in moose on Vega (Sæther, Heim, et al., 2001). Based on annually collected tissue samples, an almost complete genetic pedigree of the population was constructed for the period 1985–2015 (Haanes et al., 2013). The pedigree has confirmed several immigration events (Haanes et al., 2013).

Moose hunting on the island lasted from 25 September to 31 October during the study period, but in most years, hunting started in the first weekend of October, that is, after the moose rutting peak. Harvesting quotas are set by the local wildlife management and are specified to calves, adult females and adult males. The climate is oceanic, with mild and wet winters and cool summers (Angeloff, Bjørklund, Bryn, & Hofsten, 2004). The landscape on the island is

quite open (84% of the total area), including farmland used for grazing and grass production (35%), and otherwise characterized by deciduous forest (8%) and conifer stands (7%) (Angeloff et al., 2004). The open habitat types used by moose on Vega are dominated by heath, short herbs or grasslands, where open grasslands by far offers the highest quality and quantity of forage as they are regularly harvested and fertilized.

GPS locations were collected at 1-hr intervals and screened for errors following the procedure of Bjørneraas, Moorter, Rolandsen, and Herfindal (2010). Using piecewise linear regression, we found that home range sizes at Vega increased with number of locations to about 430 locations, and then levelled off. We assumed that estimation of space use in general follows the same relationship with number of locations. To ensure unbiased and precise estimates of individual habitat use, we therefore only included days with minimum eight locations, and individuals with a total of minimum 430 locations per summer (15 May to 2 September; starts with calving and vegetation greening, and ends with the onset of male rutting, Franzmann & Schwartz, 2007). Average number of locations per individual per day was 21.47 (*SD* = 5.74, range = 8–24), and average number of locations during the summer was 2,112 (*SD* = 734, range = 484–2,645). We measured habitat use as the mean daily proportion of GPS locations of an individual within open grasslands during summer. Moose are able to cross distances larger than the study area during the summer (Bjørneraas et al., 2010), making the entire island available. Consequently, habitat use is similar to habitat selection at the landscape scale, where habitat use is found to be proportional to availability, that is, no habitat selection (Ofstad et al., 2019). However, the high availability of open grassland implies that moose can frequently use this resource without necessarily showing a selection for it (Herfindal et al., 2009).

We used data from 102 GPS-collared moose ($N_{\text{moose-years}} = 222$, $N_{\text{males}} = 42$, $N_{\text{females}} = 60$) monitored during 2004–2017 to examine how calf weight, reproductive success and survival were related to habitat use. Calves ($N_{\text{calves}} = 79$, $N_{\text{mothers}} = 25$, $N_{\text{years}} = 10$) were weighed in mid-February (live weight at approximately 8-month old) or after being killed during harvest (carcass weight at approximately 4-month old; Haanes et al., 2013). We fitted a linear regression with calf weight as response and sex, weighing date relative to mean marking date (15 February) and birth year as explanatory variables. The residuals from this regression were then used as adjusted weight estimates. The number of offspring fathered by males ($N_{\text{calves}} = 44$, $N_{\text{fathers}} = 31$, $N_{\text{years}} = 10$), as well as the female twinning rates ($N_{\text{female-years}} = 59$, $N_{\text{females}} = 22$, $N_{\text{years}} = 13$) were based on the genetic pedigree (Haanes et al., 2013) or from visual observations (twinning rate, year 2015–2017: $N_{\text{female-years}} = 18$, $N_{\text{females}} = 13$). This is a closely monitored system, and only 17 out of 412 resident individuals were not marked and monitored during parts of their life span. Survival of individuals with known status was analysed for males ($N_{\text{male-years}} = 68$, $N_{\text{males}} = 38$, $N_{\text{years}} = 12$), females without calves ($N_{\text{female-years}} = 143$, $N_{\text{females}} = 58$, $N_{\text{years}} = 14$) and calves ($N_{\text{calves}} = 123$, $N_{\text{mothers}} = 31$, $N_{\text{years}} = 13$, year 2017 is excluded for calf survival as calves shot this year have not been assigned any parents).

Twinning rate was analysed using calf-producing females (mean proportion reproducing females during 2004–2017 = 0.77, $SD = 0.34$, $N_{\text{female-years}} = 82$), excluding females of age 2 years because of their low twinning rate (Markussen et al., 2018). There is no evidence for cost of reproduction in females in this population; females with calves were more likely to reproduce the following year than females without calves (Markussen et al., 2018). Moreover, the high-performing individuals are typically larger as calves and also produce larger offspring irrespective of litter size (Markussen et al., 2018). This emphasizes that calf body mass is an important life-history trait, and explain why we predicted both litter size and calf body mass, two traits that are expected to be traded off according to life-history theory (Stearns, 1992), to be positively related to mothers use of grassland.

For analyses of LRS, we only included individuals that were monitored during their full life span and with a life span ≥ 2 years ($N_{\text{females}} = 42$, $N_{\text{males}} = 26$), as 2 years is the age at first potential reproduction in moose. On average, females and males were GPS-monitored for 3.00 ($SD = 1.68$) and 2.50 ($SD = 1.54$) years, respectively. The GPS-monitoring was not continuous for all individuals, that is, due to delayed replacement of malfunctioning GPS-collars, making the mean proportion of life span covered to be 0.59 ($SD = 0.28$, 24% were GPS-monitored their entire life span) and 0.53 ($SD = 0.26$, 26% were GPS-monitored their entire life span) in females and males, respectively. For females, LRS was measured as the number of calves they recruited to the yearling stage, whereas for males we used the number of offspring they sired during their life span as a measure of LRS.

We analysed variation in calf weight in relation to the summer habitat use of mothers in the birth year of the calf, whereas the variation in reproductive performance of males and females was analysed in relation to habitat use in the summer of the year of mating, that is, the year before the offspring was born. Individual age was then the age at mating. For analyses of survival during the autumn hunt, we used habitat use in the summer before the hunt. Assuming low within-individual variation in summer habitat use, we used mean habitat use during all summers with data as predictor of variation in LRS.

2.2 | Statistical analyses

To account for interdependencies between observations, all models with repeated observations (i.e. all models except LRS analyses) included year and moose identity (mother identity for analyses of calf body mass) as random intercepts in (generalized) linear mixed models, (g)lmm. We assessed whether calf weight and twinning rate were related to use of open grasslands with lmm and glmm (binomial distribution, logit link function), respectively, while accounting for mother/female age (age classes; 2-year olds, 3-year olds and >3 years). Number of offspring sired by males was related to males' use of open grasslands with glmm (poisson distribution, log link function), accounting for individual age class (1-year olds,

2-year olds, 3-year olds and >3 years). In addition, we accounted for population characteristics that are known to influence male mating and reproductive success in a given year (Herfindal et al., 2014). This included mean male age, adult sex ratio (ASR), population size (N) and the interaction between ASR and N. The probability to survive the harvest was analysed using a glmm (binomial distribution, clog-log link function) with the proportional use of open grasslands included as independent variables. Moreover, to account for differential mortality, we also included harvest quota and census size (both specified to calves, adult males, adult females), and the interaction between the two. Individual LRS was analysed in relation to individual mean use of open grassland using a negative binomial model. Statistical support was assessed with the likelihood-ratio test in R 3.3.2 (R Core Team, 2017) and the `lme4`-package (Bates, Maechler, & Bolker, 2011). Parameter estimates are given on link-scale with associated bootstrapped 95% confidence intervals in square brackets.

Repeatability, that is, within-individual consistency in habitat use, is a measure closely related to heritability (de Villemereuil et al., 2016). As a measure of consistency in habitat use among years, we estimated the repeatability among years in summer habitat use, R_{Summer} . This was found by fitting a linear mixed model with habitat use as response, and sex, N and ASR as fixed effects, and individual identity and year as random intercepts. These fixed effects would then also account for variation in parameters that might affect both within- and between-individual variation in habitat use (Dingemanse & Dochtermann, 2013), while the test statistic is a likelihood-ratio test with one degree of freedom (Stoffel, Nakagawa, Schielzeth, & Goslee, 2017). As a measure of behavioural consistency across contexts within years, we used the relationship between habitat use during summer and during harvest, $R_{\text{Summer-Harvest}}$. This was estimated as the relationship between the logit-transformed habitat use in summer and harvest, while accounting for sex, N and ASR as fixed effects, and year and individual identity as random intercepts ($N_{\text{moose-years}} = 164$, $N_{\text{moose}} = 81$, fewer than the total of 102 due to individuals being shot on the first day of the hunt and malfunctioning GPS collars after the summer). A positive slope, $R_{\text{Summer-Harvest}} > 0$, implies consistent habitat use across contexts, and was assessed using a likelihood-ratio test comparing a model with the summer habitat use against a model without. R_{Summer} and $R_{\text{Summer-Harvest}}$ were estimated for both sexes combined, as the analyses suggested small sex differences in behavioural consistency.

3 | RESULTS

Males and females showed similar use of open grasslands during summer (males: 0.42, $SD = 0.09$; females: 0.36, $SD = 0.09$) and hunting season (males: 0.39, $SD = 0.10$; females: 0.41, $SD = 0.13$). Repeatability in habitat use across summers, R_{Summer} , was 0.64 (0.52; 0.75, $\chi^2 = 275.5$, $df = 1$, $p < 0.001$) while the repeatability across contexts within years ($R_{\text{Summer-Harvest}}$) was 0.59 (0.37; 0.81, $\chi^2 = 24.6$, $df = 1$, $p < 0.001$). Hence, individuals were quite

consistent in their habitat use both within and among years (Figure 1).

Mean calf body mass was 75 kg ($SD = 4.9$, $N = 40$) and 181 kg ($SD = 9.9$, $N = 39$) measured as autumn carcass mass and winter live mass, respectively. Mean individual twinning rate was 0.61 ($SD = 0.34$, $N = 27$). Mean male reproductive success was 1.90 calves ($SD = 1.63$, $N = 31$). Mean census sizes of calves, adult females and adult males, prior to harvest, were 24.23 (year-to-year $CV = 0.18$),

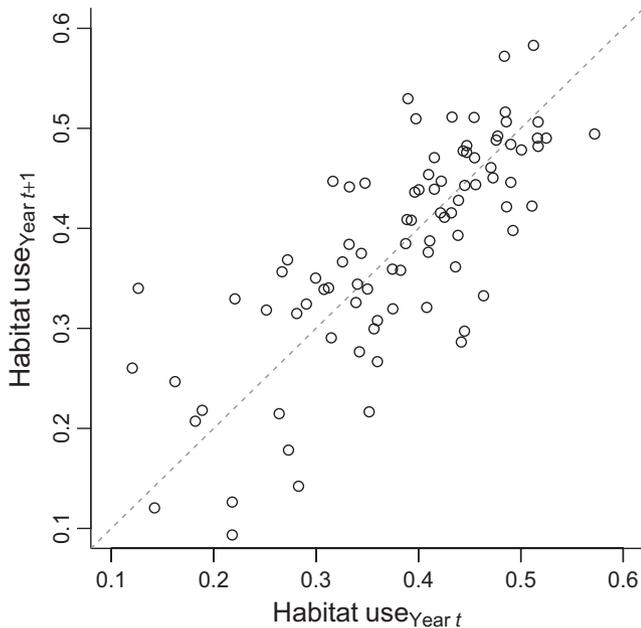


FIGURE 1 Scatter plot of individuals' use of open grassland during summer in year t and in year $t + 1$. Use of open grassland in summer is measured as the proportion of observations that are found in the habitat type. The dashed line shows the 1:1 relationship

24.78 ($CV = 0.17$) and 16.00 ($CV = 0.15$), respectively, while the observed harvest survival was 0.50 ($CV = 1.01$), 0.77 ($CV = 0.55$) and 0.67 ($CV = 0.70$), for calves, adult females and adult males, respectively. Harvest size was not a constant proportion of the population, but increased with population size among adults (log-log: $\beta = 1.61$, $SE = 0.42$, $df = 12$, t value = 3.77, $p = 0.002$) and tended to decrease among calves (log-log: $\beta = 0.81$, $SE = 0.61$, $df = 12$, t value = 1.33, $p = 0.209$).

Females' use of open grasslands during summer was positively related to calf body mass ($\beta = 51.44$ [24.64; 78.24]; $\chi^2 = 10.26$, $df = 1$, $p = 0.001$; Figure 2a; Table S1) and twinning rate ($\beta = 5.35$ [0.57; 10.12]; $\chi^2 = 5.19$, $df = 1$, $p = 0.022$; Figure 2b; Table S1), whereas reproductive success of males was positively, but nonsignificantly related to their use of open grasslands ($\beta = 1.39$ [-3.86; 6.64]; $\chi^2 = 0.22$, $df = 1$, $p = 0.640$; Table S1). The probability to survive the harvest decreased with the use of open grasslands during summer in all demographic groups ($\beta = -2.41$ [-4.76; -0.06]; $\chi^2 = 6.83$, $df = 1$, $p = 0.039$; Figure 2c; Table S1) and did not differ among age-sex groups ($\chi^2 = 0.78$, $df = 2$, $p = 0.676$).

The results imply that two reproducing females that spend 29.7% and 41.5% (i.e. the 25th and 75th percentiles) of their time in open grasslands will on average recruit 3.50 [2.74; 4.14] and 4.33 [3.44; 4.95] twin sets (i.e. the sum of twinning probabilities for a female living 6 years) in their lifetime in absence of harvest mortality. By multiplying annual calf loss probabilities with twinning probabilities, these values were reduced to 1.57 [1.02; 2.32] and 1.57 [0.98; 2.40], respectively. This suggests that the benefit of a higher use of grassland to produce twins over singletons disappears after harvesting. Similarly, if one assumes reproduction every year, females with low use of open grassland were 1.53 times more likely to reach age 6 than females with high use of open grassland. This appeared even though females experienced low harvest rate and are usually not

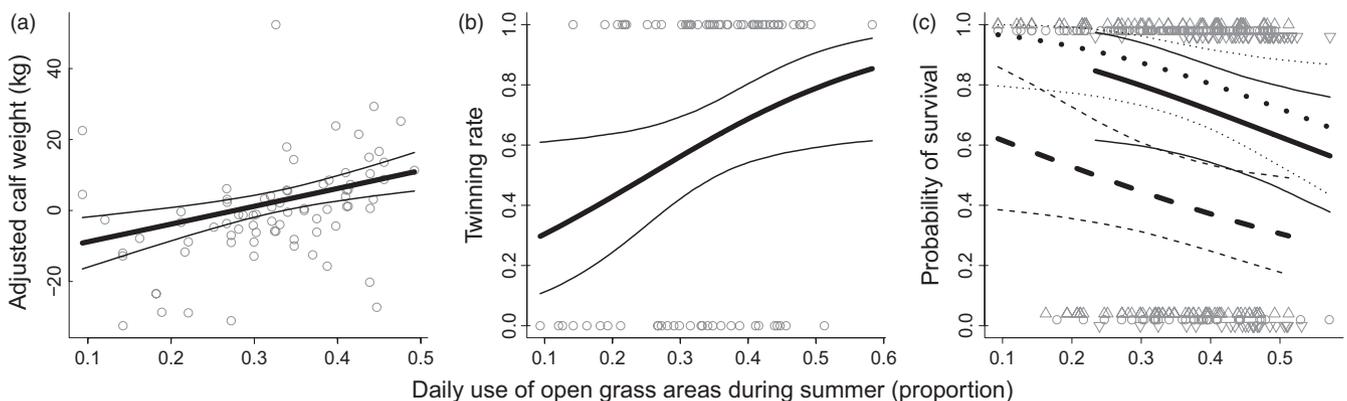


FIGURE 2 Predicted relationships between the use of open grassland habitat during summer by moose at Vega, and (a) adjusted calf weight, (b) twinning rate among reproducing females and (c) probability of survival in adult males (solid line/downward triangles), adult females without offspring (dotted/circles) and calves (dashed line/upward triangles) during autumn hunt. Thin lines show 95% confidence intervals based on parametric bootstrapping ($n = 20,000$). In panels (a) and (b), the predicted relationships are for age class >3 years old, and in panel (c) the other covariates in the model that describes population properties are set to mean values for the study period ($N_{calves,shot} = 12.31$, $N_{calves} = 24.23$, $N_{males,shot} = 5.42$, $N_{males} = 16.00$, $N_{females,shot} = 5.86$, $N_{females} = 24.79$) and the points are vertically shifted by group to improve readability. Note that female hunting quota is typically low compared to other age-sex classes, resulting in an overall high survival. See Table S1 for parameter estimates

hunnable before all accompanying calves are shot. Hence, risk-prone reproducing females with high use of open grasslands will show similar lifetime recruitment of calves, but lose due to shorter longevity compared to risk-averse reproducing females with low use of open grassland.

Mean LRS of females (number of recruits >1 year) was 5.52 ($SD = 4.30$) and mean life span was 6.02 ($SD = 3.78$) years, whereas in males, the mean LRS (number of offspring sired) was 7.65 ($SD = 10.82$) and their life span 4.69 ($SD = 2.60$) years. LRS was not significantly related to the use of open grassland in both sexes (females: $\beta = -0.26$ [-3.37; 2.80]; $\chi^2 = 0.03$, $df = 1$, $p = 0.864$; males: $\beta = -0.71$ [-22.45; 19.88]; $\chi^2 = 0.004$, $df = 1$, $p = 0.950$).

Accounting for the experienced hunting pressure (i.e. the product of harvest rates across years alive), we found that use of open grassland became significantly less beneficial with increasing harvest rates of adult females ($\beta_{\text{scaled harvest rate}} = -0.76$ [-1.04; -0.51], $\beta_{\text{scaled habitat use}} = -0.16$ [-0.32; 0.003], $\beta_{\text{scaled harvest rate} \times \text{scaled habitat use}} = -0.27$ [-0.51; -0.02], compared to model accounting for only harvest rates, females: $\chi^2 = 4.93$; $p = 0.085$, $df = 2$; males: $\chi^2 = 1.69$; $p = 0.430$, $df = 2$). This implies that risk-averse and risk-prone individuals who experience low harvest pressure (i.e. 25th percentile) will exhibit LRS of 9.33 ($SE = 0.83$) and 9.65 ($SE = 0.98$), respectively, while under high harvest pressure (i.e. 75th percentile) the risk-averse individuals will have a LRS of 6.26 ($SE = 0.55$), while risk-prone individuals 4.84 ($SE = 0.66$).

4 | DISCUSSION

We hypothesized that moose that use open, food-rich habitats must make a trade-off between reproductive success and survival because such individuals are also more exposed to hunting risks. In our study area, open grasslands have abundant, high-quality forage during summer, which generates a positive relationship between the use of this habitat type and reproductive success of females (Figure 2a,b). In addition, females that frequently used open grasslands produced calves with higher body mass than calves from females that used open grasslands to a small extent. Also, the reproductive success of males increased with the use of open grasslands, but the relationship was not significant. However, moose that used open grasslands during summer were also more likely to be harvested during the autumn hunt (Figure 2c), indicating a fitness-cost of such a behaviour. This appears to occur because the propensity to use open habitats was consistent within individuals (Figure 1) and because individuals that use open habitats during the hunting season were more likely to be killed. Overall, the contrasting habitat use resulted in no significant effects on LRS, which underlines the importance of considering habitat-performance relationships for several fitness-related traits to elucidate the evolutionary consequences.

In a previous study of the same moose population at Vega, Kvalnes et al. (2016) demonstrated a harvest-induced selection towards smaller body mass which opposes the fitness benefits of

large body mass (Keech et al., 2000). If habitat use is the mechanism behind this selection pressure, individuals in this population should exhibit a high repeatability in habitat use. Conversely, a link between behaviour and phenotypic traits, such as body mass, is found to be crucial for the evolution of consistent among-individual differences in behaviour (Luttbeg & Sih, 2010; Wolf & Weissing, 2010). Repeatability (and therefore heritability; Bell et al., 2009) in behavioural traits has been found in several species (e.g. Bell et al., 2009; Réale et al., 2007). Also, behavioural traits are often related to vital rates (Biro & Stamps, 2008; Dingemanse et al., 2004). Our results show that moose at Vega exhibit a particularly high repeatability in their habitat use ($R = 0.64$), compared to what has been reported for other animals (e.g. in a meta-study: $R = 0.57$, Bell et al. (2009); red deer *Cervus elaphus*: $R = 0.32$, Dupke (2016); golden-mantled ground squirrels *Callospermophilus lateralis*: $R = 0.50$, Hefty and Stewart (2018); and brown bears *Ursus arctos*: $R = 0.42$, Leclerc et al. (2016)). Hence, even if the overall use of open grasslands changes between seasons, individuals that have higher than average use of open habitats during the summer will also have so during the hunt. As a consequence, these individuals become more exposed to hunters, and may also choose more risk-prone behaviours when chased during the hunt (Ciuti et al., 2012).

Individual variation in behaviour must covary with individual fitness to cause selection (Biro & Stamps, 2008; Price, 1972). However, predicting the direction of selection can be difficult when a behavioural trait shows opposing relationships with different fitness components (Mysterud, 2011). Kvalnes et al. (2016) found that survival and fecundity showed opposite selection pressures on calf body mass and birth dates, which could follow from opposite effects of habitat use on fecundity and survival. A negative relationship between LRS and use of open grassland would confirm a habitat-related selection for smaller body mass, but we did not find evidence for such a relationship. Possibly this is so because there is a balance in the cost-benefits of habitat use, that is, that the benefits of habitat use are offset by the increased mortality. A similar mechanism has been suggested to explain partial migration in ungulates, that is, where migratory individuals may benefit from reduced predation at the expense of reduced fecundity (Hebblewhite & Merrill, 2011; Rolandsen et al., 2017). However, we cannot rule out that there are also other important mechanisms behind the selection for smaller body mass on moose on Vega, or that we have not been able to account for confounding variables that also influence LRS (McLoughlin et al., 2006). For instance, LRS can, in some cases, be a less informative measure for fitness (e.g. Brommer, Gustafsson, Pietiäinen, & Merilä, 2004). This can occur in populations with strong age structure that fluctuates over time (Engen, Sæther, Kvalnes, & Jensen, 2012; Grafen, 1988), overlapping cohorts (Coulson et al., 2006) or large annual variation in juvenile mortality (Brommer et al., 2004). This is partly the case for the Vega moose population where most of the offtake stems from harvesting calves and yearlings (Sæther, Engen, & Solberg, 2001; Solberg, Saether, Strand, & Loison, 1999). Still, the high repeatability in habitat use suggests a harvest selection against individuals exposing themselves in open grasslands. This

results in individuals that trade off high reproduction for higher survival, thereby changing the frequency and diversity of behavioural types within a population.

The specific cost–benefit ratio of using open grasslands, and thus the direction of selection of such behaviour, will vary among years according to population size and harvest quotas. As the harvesting pressure declines, the benefits of using open habitats will increase. Consequently, variation in harvesting pressure can generate frequency-dependent selection against certain behaviours (Wilson, Clark, Coleman, & Dearstyne, 1994). This means that a specific behavioural strategy that is more advantageous in some years may not give the same fitness benefits in other years. Since survival of moose at Vega shows large year-to-year variation compared to many other ungulate populations (Gaillard et al., 2000), the propensity to use open habitats will most likely continue to vary much among individuals. Possibly, such among-year variation in behaviour-specific costs and benefits can lead to the maintenance of a high diversity of behavioural types with associated life-history strategies within the population (Réale et al., 2010; Wolf, Doorn, Leimar, & Weissing, 2007).

Natural landscapes are increasingly being converted to human-dominated landscapes, such as farmlands (Hooftman & Bullock, 2012). Although many of these landscapes can provide good access to forage for wild ungulates (Hooftman & Bullock, 2012; Wam, Hjeljord, & Solberg, 2010), the actual and perceived mortality risk from natural predators and humans are different from many natural habitats (Fahrig, 2007). Predicting the outcome of habitat change is further complicated if natural mortality differs from harvest mortality (Hebblewhite & Merrill, 2011; Lone et al., 2014). Such changes in the spatial configuration of costs and benefits can have a large impact on the evolution of behaviour (Dochtermann, Jenkins, Swartz, & Hargett, 2012). Although harvest selection sometimes operate in the same direction as natural selection (Edeline et al., 2007), harvest selection may often occur at a faster pace than natural selection (Darimont et al., 2009). Consequently, it can deplete genetic variation at a faster rate and thus the populations' ability to adapt to novel environments, such as human-made open habitats (Biro & Post, 2008).

Our results demonstrate that individual differences in behaviour and associated habitat use is one mechanism by which harvest-induced selection can occur. Since individuals that frequently use open areas can acquire more high-quality food, targeting these individuals during the hunt will select against high body mass and reproductive performance. Although we did not detect significant relationships between habitat use and LRS, harvesting affects the cost–benefit ratio of habitat use and thus potentially both population dynamics and evolutionary processes. This may occur through the link between behaviour and individual fitness. If harvesting alters the frequency of different behavioural types, it affects individual heterogeneity in vital rates in the population which can have demographic consequences for instance affecting effective population size, N_e (Lee et al., 2020).

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AUTHORS' CONTRIBUTIONS

E.G.O., S.S.M. and I.H. developed the concept for the study; H.H. constructed the pedigree in collaboration with K.H.R.; analyses were performed by E.G.O. with input from I.H., S.S.M., E.J.S. and B.E.S.; M.H. oversaw the fieldwork; E.G.O. and S.S.M. wrote the article with input from all co-authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.31zcrjdh5> (Ofstad et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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