On fitness and partial migration in a large herbivore – migratory moose have higher reproductive performance than residents

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Partially migratory populations comprise both resident and migratory individuals. These tactics may coexist if their demographic contribution to future generations (i.e. fitness) are equal or vary temporally with environmental conditions, or if individuals switch between being migrant and resident. Alternatively, the choice of movement tactic can be based on individual attributes such as age, competitive ability or personality. In the latter cases, the two tactics are not expected to have similar average fitness. In this study, we examined the effect of movement tactic on reproductive performance and survival of 82 GPS-marked female moose and their offspring in a partial migratory population in central Norway. The results indicated higher growth in the migrating part of the population because migrating females produced more twins than resident females. We found no differences in pregnancy rates or survival of adults or their offspring, indicating a net fitness benefit of being migrant. We found the average shoulder height of residents to be slightly lower than of migrants, but doubt that this affected their migration ability. A more likely explanation is that migratory females are both more fecund and grow bigger because of better conditions in their summer ranges. This may be a temporal phenomenon if the fitness differences between migratory and resident moose vary according to environmental fluctuations.

The distribution of individuals in the landscape is a central issue in ecology (Morris 2003). One interesting phenomenon is the widespread migrations between seasonal distinct home ranges. Such a movement tactic is documented for numerous taxa and is typically assumed to be an adaption to seasonal environments (Dingle 1996, Milner-Gulland et al. 2011). Birds and mammalian herbivores, for instance, benefit from increased food availability or food quality by following variation in plant phenology (McNaughton 1984, 1986, Fryxell and Sinclair 1988, Albon and Langvatn 1992, Levey and Stiles 1992, van der Graaf et al. 2006, Holdo et al. 2009). In turn, this may translate into higher body weight and more offspring produced in migrants than in residents. Migration can also lead to relaxed density dependence (Nelson 1995, Geremia et al. 2011, Griswold et al. 2011, Mysterud et al. 2011) and reduced predation risk (Bergerud et al. 1983, Fryxell et al. 1988, Hebblewhite and Merrill 2007, McKinnon et al. 2010). However, migration can also increase mortality risk during the migration period, e.g. due to drowning (Miller and Gunn 1986) and increased physiological costs (Morrison et al. 2007), and may lead to delayed breeding (O'Connor 1985, Gillis et al. 2008).

While many populations seem to be exclusively migratory, other populations are only partially migratory, and consist of a mixture of migrants and residents (Cresswell et al. 2011). A common explanation for partial migration is that the two movement tactics have equal long-term demographic contributions to future generations (i.e. a measure of fitness, Lande et al. 2003) when at equilibrium frequencies (Lundberg 1987, Chapman et al. 2011a, Griswold et al. 2011, Holt and Fryxell 2011). In such situations, partial migration may persist if there are no systematic long-term differences in fitness components (survival and recruitment) between tactics, or because differences in fitness components are balanced within tactic. For instance, in the latter case it has been suggested that migrants could be exposed to higher mortality, which is balanced by a lower reproductive success of residents (Swingland and Lessells 1979, Hebblewhite and Merrill 2011).

As an alternative explanation, variation in movement tactic may be associated with individual characteristics such as age, sex, body size, physical condition, competitive ability and personality (Lundberg 1988, Chapman et al. 2011a, b). In species that compete for breeding- or overwintering sites, residents have been found to gain access to better breeding

sites (Lundberg 1987, Adriaensen and Dhondt 1990, Gillis et al. 2008) or overwintering sites (Adriaensen and Dhondt 1990, Grayson et al. 2011) than migrants. This suggests that the migrant tactic in these situations has lower relative fitness and is adopted by less competitive individuals, i.e. they make 'the best of a bad situation'. As these individual attributes may change over time, individuals can switch between movement tactic during their life (Gillis et al. 2008, Grayson et al. 2011), but the reported switching frequency was low (e.g. 4 out of 169 American dippers followed for more than one year changed movement tactic; Gillis et al. 2008). Also several studies of large herbivores report that individuals may opportunistically choose between being migrant and resident among years (Nicholson et al. 1997, Fieberg et al. 2008, Hansen et al. 2010, Cagnacci et al. 2011), and as an example Eggeman et al. (2016) recently estimated a switching rate of 15% per year. Hence, the frequency of migrants and residents in the population may be due to persistent differences in movement tactics between individuals or because individuals switch movement tactic among years.

Regardless of which factors that maintain partial migration, the relative fitness of the two movement tactics can be differentially affected by changes in environmental conditions such as climate (Griswold et al. 2011), predation risk (Hebblewhite and Merrill 2011) or spatial variation in resource availability (Nilsson et al. 2006, Hobbs and Gordon 2010). Therefore, we may expect fluctuating frequencies of the two tactics over time, or more permanent changes in frequencies following trends in environmental change (Nilsson et al. 2006, Griswold et al. 2011, Hebblewhite and Merrill 2011).

Partial migratory populations of large herbivores have been recognized for a long time (Maddock 1979), and has been documented for many species across the northern hemisphere (e.g. white-tailed deer *Odocoileus virginianus* (Nelson 1995), roe deer *Capreolus capreolus*, (Mysterud 1999, Cagnacci et al. 2011), red deer *Cervus elaphus* (Albon and Langvatn 1992, Mysterud et al. 2011), elk *Cervus canadensis* (Hebblewhite et al. 2008, Robinson et al. 2010), pronghorn *Antilocapra Americana* (White et al. 2007), bison *Bison bison* (White et al. 2011), reindeer *Rangifer tarandus platyrhunchus* (Hansen et al. 2010), and moose *Alces alces* (Ball et al. 2001, Hjeljord 2001, Bunnefeld et al. 2011)). Typically, migrants and residents congregate on sympatric winter ranges at relatively low altitudes before migrants move to alternative summer ranges, often at higher altitudes, in spring and early summer (but see Andersen 1991 for an opposite pattern). The general assumption is that summer ranges are less available during winter because deep snow limits access to food and increases movement cost (Ball et al. 2001). However, few studies have simultaneously examined relative differences in reproduction and survival related to migratory behaviour in large herbivores (but see Hebblewhite and Merrill 2011).

We examined the demographic consequences of a migratory versus resident movement tactic of female moose in a partially migratory population in central Norway. Based on movement data from 82 GPS marked individuals we first classified female moose as migratory or resident and characterized their altitudinal movement patterns. We also examined to what extent the tactic was consistent within females among years to assess the level of individual switching. We then examined whether survival, reproductive performance (i.e. pregnancy rate and twining rate), and offspring survival differed between resident and migratory females. We hypothesized that there are no differences in these fitness components between females with resident and migratory behaviour, and consequently both tactics should on average lead to the same individual fitness in the sense of demographic contribution to future generations. Alternatively, resident and migratory moose may show systematic differences in fitness components due to 1) demographic balancing, or 2) individual attributes. According to the demographic balancing hypothesis, we may expect residents and migrants to show different tradeoffs between recruitment and survival, but no overall differences in fitness and thus no individual switching of movement tactics between years. This is in accordance with predictions from the ideal free distribution (IFD) and density dependent habitat selection (Fretwell and Lucas 1969, Morris 2003). Conversely, the individual attributes hypothesis predicts that one movement tactic has higher relative fitness than the other and that only individuals with specific characteristics (e.g. body condition or age) are suited to follow this tactic (i.e. other individuals are 'doing the best of a bad situation'). This also implies that we could expect individual switching of movement tactic over time, for instance following changes in age or body condition. The 'active' choice of migration can either be taken by the smallest individuals because they cannot compete for home ranges in the same areas as residents, or by the largest individuals because small individuals lack the necessary resources for migration. In both cases, we would expect the larger individuals to show the on average highest fitness. The fitness of individuals following either of the two movement tactics may also depend on environmental conditions that vary temporally, such as the relative food quality or quantity available for residents and migrants in the non-shared habitats (Hebblewhite et al. 2008, Griswold et al. 2011).

Methods

Study area

The study area covers parts of central Norway and of central Sweden (Fig. 1), and ranges from boreonemoral vegetation zones at the coast to alpine vegetation zones in the inland (Moen 1999, Karlsen et al. 2006). The forested part is mainly found within the boreal vegetation zones and is dominated by Norway spruce *Picea abies*, followed by birch *Betula pubescens* and Scots pine *Pinus sylvestris* (Moen 1999). Cultivated land is most common at lower altitudes (Moen 1999). The vegetation growing season lasts from approximately May to September, decreasing in length from coast to inland and with increasing altitude (Karlsen et al. 2006).

Moose capture, reproductive performance and migratory behaviour

In the period 2006–2008, we captured 106 adult (≥ 18 months) female moose and marked them with GPS-collars.
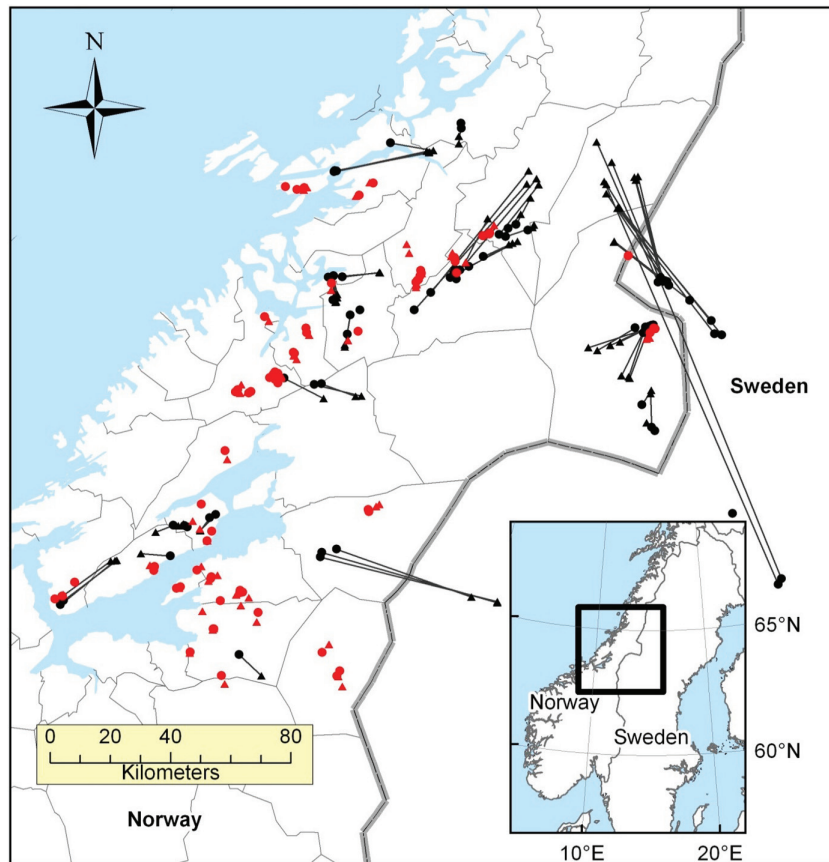
Figure 1. The study area with municipality borders (in Norway only). The mean winter (circle) and summer (triangle) position of 82 GPS-marked female moose in one or several years are indicated. Winter and summer positions within year for migratory females (black) are connected with lines. Summer and winter positions for resident females are in red.

We fitted 101 female moose with GPS PLUS/GPS PRO Light collars and five female moose with Tellus GPS collars. All collars were equipped with very high frequency (VHF) transmitters. All procedures were approved by the Norwegian Animal Research Authorities. Moose were marked on their winter ranges in 21 municipalities (hereafter called winter municipalities) during February and March, except for five females that were marked in November 2006 in their summer range just before the onset of migration. Four of these five females turned out to have their winter range in Sweden (Fig. 1). For 85 females we were able to determine their migratory or resident movement pattern, as well as their reproductive status (singletons or twins) in one or several years. Regarding the other 21 females we either were not able to determine their reproductive status, collars stopped working, or they died before the next calving season. Three females were living on islands and were therefore excluded because of their restricted migration opportunities (exclusion of these females did not affect the conclusions). The remaining 82 females were included in the analysis.

To classify female moose as migrants and resident, we used a combination of several methods. Following the recommendations by Cagnacci et al. (2015), we examined the patterns of net squared displacement (NSD) (Bunnefeld et al. 2011), and the overlap between individual home ranges (90% kernel UD) in March and July the same year. To be a migrant, moose had to be classified as a migrant or

a disperser by the NSD method and at the same time have non-overlapping seasonal home ranges, i.e. in March and July. We included dispersers in the migrant category as the NSD method classifies individuals as dispersers when only data from spring migration is available. Moreover, as our aim was to compare long-distance migrants with more resident individuals, we decided that distances between seasonal ranges, as estimated by the NSD method, should be at least 10 km. The latter allowed us to discriminate between 'true' seasonal migrants and females that are conducting only small seasonal habitat shifts within their home range (see Cagnacci et al. 2015, Eggeman et al. 2016 for a similar assessment).

We estimated the reproductive status of the females by the use of two methods: first, we examined a subset of females for pregnancy (pregnant or not) by rectal palpation during the marking procedure in February or March. Second, we approached females on foot aided by the VHF–beacon, and then visually determined their number of calves during the calving season from mid-may until late June. For a subsample we also repeated this procedure in late August and September before the start of the autumn hunting season (25 September–31 October). In addition, we obtained information about reproductive status from hunters when the marked females and their calves were shot, or observed during hunting, or when observed and reported by field personnel or the public during winter and spring in the subsequent year. One migratory female gave birth to triplets,

but in the analysis she was classified as a twin producer. In 18 cases we included calving events in years after the GPS-unit had stopped working. For these females and years we tracked them using the VHF-beacon to record their calving position and number of calves born. Their movement tactic did not differ from their tactic in previous years.

We measured the shoulder height as a measure of body size for 72 females during marking, of which we had reproductive status for 56 individuals the same year. Shoulder height correlates quite closely with body weight (Franzmann et al. 1978), although it shows less temporal fluctuations for instance in relation to varying living conditions.

GPS positions were taken with two-hour interval and screened for location errors (Bjørneraas et al. 2010). We used a 10×10 m digital elevation model (DEM) to assess the altitude of the locations in order to characterise seasonal variation in the use of altitudes.

The probability of producing twins as a fitness component

As a measure of reproductive performance we recorded the probability of producing twins (i.e. the twinning rate). Like several other deer species, moose is polytocuous, and regularly produce twins and in a few cases even triplets when experiencing good nutritional conditions (Schwartz 1998, Nygrén 2003). Females of higher body mass for a given age are more likely to produce twins than are smaller females (Sæther and Haagenrud 1983, 1985, Sand 1996), and high population twining-rates are typically found in areas with earlier age at maturity, higher parturition rates, lower moose browsing pressure, and higher yearling and calf body mass (Boertje et al. 2007, Tiilikainen et al. 2012). Because the probability of twin production varies with age (Ericsson et al. 2001), we partly controlled for female age in the analyses. We used relative age, i.e. age in years since marking, as most females are still alive and thus could not be accurately aged by tooth sectioning.

Statistical analysis

We first determined the proportion of migrants, and characterized the horizontal (net displacement) and vertical (altitude) movement pattern of residents and migrants. For the analysis of vertical movement pattern we used a linear mixed effect model (lmer-procedure; Bates and Maechler 2010), where winter municipality and individual moose were included as random factors to account for differences in the proportion of migrants in different parts of the study area and interdependence within individual moose. If migrants and residents used different altitudes during the year, we expected a significant interaction between movement tactic and time entered as the combination of year and month (as factor).

Next, we tested if reproductive performance (pregnancy rate and twinning rate) was related to spatial movement tactic. For the analysis of pregnancy rate we used logistic regression, as pregnancy rate was measured only during marking (i.e. once per female). For the analysis of twinning rate we used a generalized mixed effect model (GLMM) with a binomial link function (glmer-procedure; Bates and

Maechler 2010), where moose identity and winter municipality were included as random factors. Winter municipality was entered to account for differences in environmental conditions and moose densities in the winter range. To control for a potential increase in the probability of producing twins with age, we also included female relative age (i.e. age relative to the year of marking), but acknowledge that differences in absolute age between movement tactics may still have affected the results.

The models were ranked by the use of the Akaike's information criteria (AIC) corrected for small sample size (AICc; Burnham and Anderson 2002). We considered candidate models that differed by two or less in absolute value (ΔAICc ≤ 2) to be the set of models best supported by the data (Burnham and Anderson 2002). Credible intervals (CI) from the mixed model were based on 10 000 resamplings from the posterior distribution of the parameters using the 'sim'-function in the library 'arm' (Gelman et al. 2012). Parameter estimates where considered significant if the 95% CI, computed as the interval between the 2.5% quantile and the 97.5% quantile, did not include zero.

We tested if adult female mortality differed between residents and migrants with Cox proportional hazards regression ('coxph'-function, time-to-event analysis), with the library 'survival' (Therneau and original Splus-> R port by Thomas Lumley 2011). We did one analysis including mortalities caused by other factors than hunting (natural mortality) and another based on natural and hunting mortalities combined. Both analyses were based on encounter histories for each GPS-marked female. Females entered the study population the week they were marked (week 0), and was given a fate at the time of last detection (where $0 =$ survived and $1 =$ died). Individuals were censored (i.e. exited the study population) at the time when the GPS-collars stopped working or at the time they were shot by hunters (natural mortality).

Summer survival (neonate survival) was estimated from a sample of calves ($n = 73$) that were observed with their mother shortly after birth. Calves were considered to have died during summer if they were not re-sighted together with their mother before the start of the autumn hunting season (i.e. before 25 September). For this analysis we used a GLMM with binomial link function (glmer-procedure; Bates and Maechler 2010), and mother identity as a random effect. We also controlled for potential confounding effects of year (as a factor) and whether the calf was a singleton or twin (litter size).

Because females were not systematically checked for calf losses at later stages, we had no similar data available for analyses of hunting mortality and winter mortality rates. However, based on the summer losses, calves reported to be shot by hunters, and the calves reported to be missing when collared females were observed during winter, we estimated a minimum mortality rate of calves during their first year of life for the two movement tactics. Assuming that the likelihood of being reported was unaffected by the movement tactic of the mother, this analysis provides a test of whether the first year survival of calves differed between resident and migratory female moose. As for summer mortality, we tested for differences in mortality by using a GLMM with

mother identity as random effect and mother's movement tactic, year and litter size, as fixed effects.

To test for differences in body size, we compared shoulder heights of resident and migratory females using a standard two-sample *t*-test. We report differences in shoulder height based on 56 females with known reproductive status the same year as the marking year (i.e. the year we measured shoulder height). We used the same sample in a GLMM to examine the effect of shoulder height on twinning-rate. As for the other GLMMs, we included winter municipality as a random factor.

All analysis were performed using R ver. 3.2.0 (<www.r-project.org>). Parameter estimates regarding twinning rate and survival are given at the logit scale.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j0r00> (Rolandsen et al. 2016).

Results

Variation in spatial movement behaviour

Twenty-four females (29%) were categorized as migratory, 53 (65%) as residents, and 5 (6%) switched tactic between years. One female switched from resident to migratory, three females switched from migrant to resident, while one female first switched from resident to migrant, and then back to being resident the third year. The six switching events made by 5 of 48 (10%) females followed for two or more years, corresponds to 9% of potential switching events (n = 68).

Based on NSD, the average distance between winter and summer range was 35.7 km (SE = 4.8, n = 50) for migrants and 3.9 km (SE = 0.2, n = 89) for residents. In addition, we found a consistent significant interaction-effect of tactic and year-month (as factor) on altitude, after controlling for winter municipality and individual moose as random factors. The interaction suggested that migrants used ranges at 100–150 m higher altitude during summer and autumn while no altitudinal differences between migratory and resident females was observed in winter (Fig. 2). This also provides support for the assumptions that the two tactics are sympatric and can effectively be compared for e.g. sharing the same environmental conditions during winter (the sympatric season).

The effect of movement tactic on pregnancy rate

During capture, 30 of 33 females examined for pregnancy were pregnant. The pregnancy rate was similar for resident (90%, n = 21) and migrant (92%, n = 12) females ($\beta = 0.147$, SE = 1.282, $\chi^2 = 0.013$, DF = 1, p = 0.909).

The effect of movement tactic on twinning rate

Whether females gave birth to singletons or twins was recorded in 3 consecutive years for 20 females (24%), 2 years for 28 females (34%) and 1 year for 34 females (41%), providing 150 reproductive events (i.e. on average 1.8 events per female).
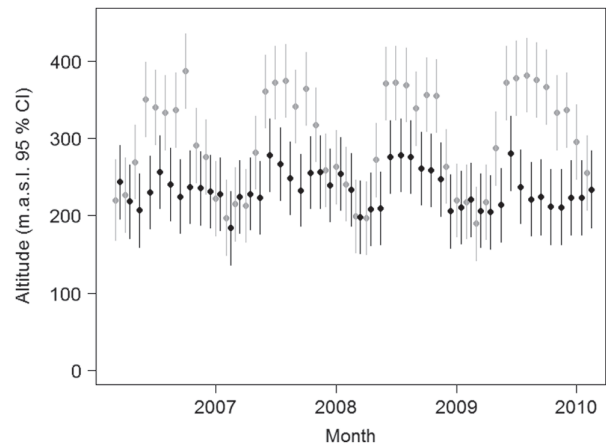

Figure 2. The mean monthly altitude (meter above sea level ± 95% CI) of positions of resident (black) and migratory (grey) female moose. The study period was form March 2006–February 2010.

The highest ranked model according to AICc suggested that migratory females produced twins with a higher probability than resident females ($\beta_{migratory-resident} = 0.99$, 95% CI: 0.020–1.945, Fig. 3), after controlling for individual moose and winter municipality as random factors. In addition, relative age was included in the highest ranked model, indicating that twinning rate increased with age ($\beta_{relative\ age\ 2-relative\ age\ 1} = 0.153$, 95% CI: –0.719–1.044, $\beta_{relative\ age\ 3-relative\ age\ 1} = 1.365$, 95% CI: 0.189–2.520). This model (AICc = 193.94, AICc-weights = 0.38) was better supported by the data than alternative models only including movement tactic (ΔAICc = 0.54, AICc-weights = 0.29) or only relative age (ΔAICc = 1.44, AICc-weights = 0.19). The intercept-only model performed less good (ΔAICc > 2). Based on AICc-weights for these models, the relative support for a model including movement tactic is twice as high as a model only including age. The parameter estimates from
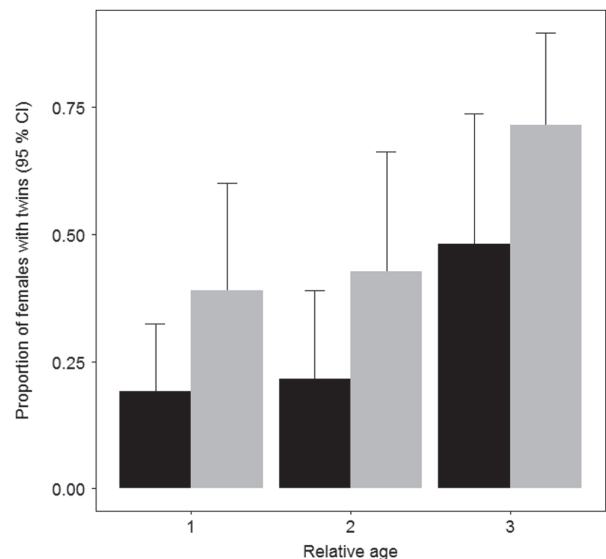

Figure 3. Predicted twinning-rates ± 95% CI for resident (black bars) and migratory (grey bars) female moose in relation to relative age of females, i.e. age relative to the year of marking (year of marking = relative age 1).

the highest ranked model suggest that migratory females had 2.03, 1.97 and 1.48 times higher probability of producing twins compared to a resident female at a relative age of 1, 2 and 3 years, respectively (Fig. 3).

The effect of movement tactic on adult female survival

Only 10 mortality events occurred during 177.2 female-years. Two were shot by hunters, three killed in traffic accidents, two killed by bears, one drowned and two died of unknown causes. The Cox proportional hazard regression did not indicate significant differences in survival between resident and migratory females (hazard ratio [HR] = 0.46, 95% CI = 0.09–2.35, z = –0.93, p = 0.35), and the same relationship appeared if we included hunting mortality (HR = 0.36, 95% CI = 0.07–1.72, z = –1.287, p = 0.20).

The effect of the mothers' movement tactic on calf survival

For the subsample of calves (n = 73) examined for summer survival in the years 2006–2008, 14% (5 of 35) of calves born by resident and 13% (5 of 38) of calves born by migratory mothers were lost during summer – indicating no effect of movement tactic on summer survival of calves ($\beta_{migratory-resident}$ = 0.248, 95% CI: –1.543–2.060). Moreover, there was no significant effect of litter size ($\beta_{twins-singletons}$ = –0.442, 95% CI: –2.354–1.444) or year ($\beta_{2007-2006}$ = –0.023, 95% CI: –2.974–0.934, $\beta_{2008-2006}$ = –0.025, 95% CI: –2.244–2.171).

In total, 82 females gave birth to 206 calves during the years 2006–2009, of which at least 43 calves were lost during their first year of life. This included 23% of calves (30/128) born by resident mothers and 17% of calves (13/78) born by migratory mothers. Losses occurred mainly during summer (n = 10) and hunting (n = 32). The estimated survival from birth to yearling was not significantly related to the mother's movement tactic ($\beta_{migratory-resident}$ = –0.424, 95% CI: –1.209–0.367), and there was no significant difference between calves belonging to a twin-set or not ($\beta_{twin-singleton}$ = 0.421, 95% CI: –0.366–1.200). However, the estimated total calf mortality varied significantly among years ($\beta_{2007-2006}$ = –2.158, 95% CI: –3.183– –1.134, $\beta_{2008-2006}$ = –1.150, 95% CI: –2.086– –0.204, $\beta_{2009-2006}$ = –3.501, 95% CI: –5.662– –1.368).

Body size of resident and migrant adult female moose

The shoulder height of migrant females (181.8 cm ± 1.7 SE, n = 18) were higher than for resident females (175.7 cm ± 1.4 SE, n = 38, t = –2.68, DF = 40, p = 0.011). However, twining-rate in the year of capture was not significantly related to shoulder height the same year (β = 0.042, 95% CI: –0.029–0.111).

Discussion

We studied how resident and migratory movement tactics were related to reproductive performance and survival of adult female moose and their offspring in central Norway. Migratory moose – characterised by using higher altitudes during summer while sharing the winter ranges with residents at lower altitudes in winter – had higher relative fitness than resident females. This was caused by higher twinning rates in migrants (Fig. 3) while we found no differences in pregnancy rate, adult female survival, or survival of their offspring. Our results confirms the general pattern among large herbivores, with high adult survival and variable calf survival (Gaillard et al. 1998). The lack of differences in survival among migrants and residents is therefore most likely not related to sample size. Consequently, we found no support for the hypothesis that resident and migratory females have equal demographic contributions to future generations. In contrast, as we found the average shoulder height of migrants to be slightly higher than of residents, we cannot reject the attributes hypothesis. This could mean that resident females 'do the best of a bad situation', or alternatively, that migratory females both grow bigger and have higher fecundity due to better conditions in their summer ranges.

The attribute hypothesis has found support in several partially migratory species. Studies of birds (Gillis et al. 2008) and amphibians (Grayson et al. 2011), for instance, have suggested that migrants are making "the best of a bad situation", as they are often found to have smaller body size compared to residents (Chapman et al. 2011a) and lose in the competition for good breeding or overwintering sites. The moose, however, is not territorial, and unlike the above examples we found migrants to be slightly bigger and perform better. We also doubt that the slightly smaller resident females are lacking the necessary resources for migration as the migration distances were on average 36 km. This is a distance resident moose should have the necessary energetic resources to migrate if they chose to do so (Teitelbaum et al. 2015).

We therefore suggest that the larger size and higher twinning rates of migrants are consequences of migration. If the feeding conditions is better in the exclusive summer ranges of migratory females, we could expect them to have higher rate of both body growth and fecundity compared to residents. However, the differences in size (shoulder height) of females does not seem to be very important for fecundity as we found no relationship between twinning rate and size. Probably other body size metrics such as body mass is a better index of fecundity. This explanation is in line with several recent studies of large herbivores indicating a benefit of migration. In red deer and elk, migratory individuals have access to higher quality food and have larger body mass (Albon and Langvatn 1992, Mysterud et al. 2001, 2002, Hebblewhite et al. 2008), and migratory female elk have higher pregnancy rates (Hebblewhite 2006). Similarly, Hansen et al. (2010) showed that calving success of Svalbard reindeer was higher for seasonally migrating females than for residents. However, as the yearly movement tactic of the female reindeer was highly variable (none migrated every year), the propensity to migrate may itself may have been affected by the pregnancy status (Hansen et al. 2010).

If there is a net fitness benefit of migration in moose, why does not a higher proportion of the females migrate? According to our results, migratory females produce twins with an approximately 1.8 times higher probability than resident

females, indicating that residents could perform substantially better by migrating. One possibility is that our observations is just a transient phenomenon, e.g. caused by a recent change in environmental conditions. Indeed, as females following the different tactics spend their summers at different altitudes, recent changes in climate may have modified the relative conditions for body growth and calf production in the different summer ranges. For instance, following the warmer climate and recent increase in the length of vegetation growing season (Førland et al. 2004, Karlsen et al. 2009), food quality and quantity may have increased relatively more in the higher altitude areas than at lower altitudes. Indeed, during the last 30-year, the onset of spring has become earlier in all of Fennoscandia, varying from no change to more than fifteen days among areas (Høgda et al. 2013). This affects moose fitness (Herfindal et al. 2006) and may now make it more beneficial to be a migratory moose in our study area (Hebblewhite et al. 2008).

Whether the fitness benefit of migration will also be present in the long term depends on the ability of adult moose to switch to the migratory movement tactic, as well as the propensity of the calves to follow their mother's tactic. If a larger proportion of moose adopt the migratory tactic we would expect a stronger density dependent effect of food limitation or harvest mortality in the exclusive summer ranges and in turn a better balance in the fitness outcome between residents and migrants. In several species, individuals alternate by being resident or migrants depending on different environmental clues such as snow conditions (Nelson 1995) or population density (Mysterud et al. 2011), which could lead to a balance if the switching rate is high. In our population, we found the switching rate to be about 9 % for female moose, which is slightly less than what has recently been found for elk (15%, Eggeman et al. 2016) and wildebeest *Connochaetes taurinus* (18%, Morrison and Bolger 2012). In cases of switching, however, females did not systematically go from resident to migratory, as we would expect, but rather the opposite – if anything. Hence, based on our results it is not likely that the migratory tactic will increase in frequency due to switching.

The other mechanism that could lead to changes in the rate of migration – that calves are following their mothers' tactic – can increase the proportion of migratory moose as long as their recruitment of calves is higher than among residents. However, the changes in frequency distribution of migrants and residents may nevertheless be slow if the association in movement tactic between a mother and her calves is weak. For a calf to choose the same movement tactic as its mother it has to be either genetically controlled, culturally transmitted, or the same environmental cues initiating migration (e.g. snow depth) in the mother may be experienced by the calf after independence. Few studies have examined if the migratory propensity of calves is related to the behaviour of their parents in moose, and the results are not consistent. In our study population, we examined the movement tactic of 26 radio-collared calf–mother pairs and found calves to not systematically follow their mothers tactic, although we were only able to follow the calves for 1 to 2 years after independence (Rolandsen unpubl.). In contrast, Sweanor and Sandegren (1988) found offspring to adopt the same movement tactic as their mothers, and also found

migratory and resident moose to stick to their movement tactic among years. They therefore concluded that the proportions of migrants and residents were mainly determined by the survival and reproductive success of moose of each tactic.

If the latter will show to be a general phenomenon in moose, we may expect the frequency of migratory moose to increase in our study population in the near future, unless the higher fecundity of migrants is balanced by a decrease in other fitness components. We found no support for such a demographic balancing in our study, but this may change. Moose is exploited by harvesting all over Norway and hunting quotas are often adjusted to local densities of moose. Hence, if moose density increase at higher altitude because of the higher recruitment of migratory moose, we may also expect an increase in harvest rate as most migrations start after the hunting season. During the study period, we observed no higher hunting mortality of migratory females or their calves, but the hunting mortalities were generally low. This was probably related to the fact that hunters were requested to not shoot GPS-marked females during the study period, and to some extent this may also have affected the survival of their calves. Although we have no reason to believe that this affected migratory more than resident moose, we cannot reject that harvesting differently affected survival of migratory and resident moose.

We found that the choice of movement tactic can affect the fitness in moose, but have yet to understand the mechanisms and to what extent the pattern persists over time and across generations. The study period was relatively short, and although the number of collared moose were rather large, we acknowledge that the sample size is relatively small for a demographic analysis. To improve our understanding of partial migration in ungulates, we therefore see a need for more long-term studies of individual migratory/resident behaviour (Gaillard 2013), as well as studies of the movement tactic development in young individuals. If, for instance, a large proportion of offspring disperse, as is reported for moose (Labonté et al. 1998), the environmental association between mothers and calves may be weak, and calves may be better of choosing a different tactic. Accordingly, the role of learning and spatial memory (Van Moorter et al. 2009, Oliveira-Santos et al. 2015) may also be important. The potential genetic component of migratory behaviour should also be subject for future research (Liedvogel et al. 2011). However, recent results regarding the strength of genetic control of migration in ungulates seems to suggest that this is of less importance (Barnowe-Meyer et al. 2013, Northrup et al. 2014).

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