



Lying in wait: Limiting factors on a low-density ungulate population and the latent traits that can facilitate escape from them



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ABSTRACT

Predation, habitat, hunting, and environmental conditions have all been implicated as regulatory mechanisms in ungulate populations. The low-density equilibrium hypothesis predicts that in low-density populations, predators regulate their prey and that the population will not escape unless predation pressure is eased. We evaluated survival of adult and juvenile moose (*Alces alces*) in north-central Alaska to determine whether or not the population supported the hypothesis. We instrumented adult male and female moose with radiocollars and used aerial observations to track parturition and subsequent survival of juvenile moose. Generalized linear mixed-effects models were used to assess survival. Adult annual survival rates were high (~89%), but may be negatively influenced by winter conditions. Migratory status did not affect moose survivorship or productivity. Approximately 60% of the calf crop died before 5 months of age. Productivity was significantly lower in the northern section of the study area where there is less high-quality habitat, suggesting that, even in this low-density population, nutrition could be a limiting factor. It appears that predation on young calves, winter weather, and nutritional constraints may be interacting to limit this population. Latent traits, such as overproduction of calves and migratory behavior, which do not currently enhance fitness, may persist within this population so that individuals with these traits can reap benefits when environmental conditions change.

1. Introduction

Debate over the relative importance of top-down versus bottom-up influences on prey populations has a long and rich history (e.g., Hairston et al., 1960; Burk, 1973; Boutin, 1992; Hunter and Price, 1992; Power, 1992). All influences that affect mortality, whether density-dependent or density-independent, are potentially limiting; however, only those that are density-dependent can be regulating (Sinclair, 1989; Messier, 1991). Historical studies have focused on top-down influences, where predators regulate prey populations (Gasaway et al., 1983; Bergerud et al., 1983; Van Ballenberghe, 1987; Skogland, 1991), or alternately highlighted bottom-up influences, where habitat regulates consumer populations (Caughley, 1976; Sinclair, 1977; Houston, 1982). Further research advocated a more nuanced conclusion that top-down influences are thought to have greater impact on low-density populations, whereas bottom-up influences are thought to be critical at high densities (Boertje et al., 1988; Messier, 1991; Jedrzejewska and Jedrzejewski, 1998; Haskell and Ballard, 2007).

In a review of a diverse set of circumstances, including in low-

density prey populations, White (2013) contended that predators do not regulate their prey; rather, both predator and prey are ultimately limited by food. During population irruptions, predators are obviously not regulating prey populations. Eventually, habitat becomes limiting as carrying capacity is reached or exceeded. As nutrition, body condition, and fecundity drop, decreases in abundance follow (Messier and Crete, 1984; Gasaway et al., 1992; Caughley and Sinclair, 1994; White, 2013). In a lagged response, predator abundance declines as the prey population returns to a low density. At this point, predators appear to be regulating their prey (White, 2013). When there are increases in the limiting resource (i.e., forage), White (2013) posits that the prey population will respond positively and not be limited by predation. In other words, predator abundance, like prey abundance, is ultimately regulated by its forage base (Vucetich et al., 2005).

One scenario not explored by White (2013) is the low-density equilibria (LDE) hypothesis (Van Ballenberghe, 1987; Boutin, 1992; Van Ballenberghe and Ballard, 1994; Ballard and Van Ballenberghe, 1997), which is also known as the low-density dynamic equilibrium (LDDE; Gasaway et al., 1992). This hypothesis states that prey can be

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kept at low densities for long periods of time (e.g., decades) by predation. In this scenario, the body condition, productivity, and survival of adults is relatively high and sufficient to allow for population growth. However, the population does not expand because predation restrains recruitment and the population remains static at low levels for long periods (Gasaway et al., 1992; Van Ballenberghe and Ballard, 1994; Ballard and Van Ballenberghe, 1997). Further, the LDE hypothesis suggests that populations will not increase until predation pressure is alleviated (Ballard and Van Ballenberghe, 1997). Thus, there is inherent conflict between the idea that habitat, not predation, is the driver of prey populations (e.g., White, 2013) and the LDE hypothesis. Assessing fitness could help elucidate whether one, or some combination of these theories, applies in the northern boreal forests.

Fitness is the relative, life-time genetic contribution an individual makes to the population. Individuals must manage trade-offs between the production of off-spring and their own survival to maximize their fitness. These trade-offs include balancing predation risk and forage intake, as well as allocating nutrients between themselves and their offspring. Among other functions, migration is thought to be a strategy to reduced risk of predation on neonates (Estes, 1976; Bergerud, 1988; Fryxell and Sinclair, 1988; Middleton et al., 2013; White et al., 2014). Prey species exhibit a wide range of movement patterns (from non-migratory to fully migratory) that often exist within a single population (Mauer, 1998; White et al., 2014; Joly et al., 2015a). However, migration does not always lead to higher adult survival rates or production of young (Middleton et al., 2013).

Most taxa often produce more offspring than can survive; this is sometimes referred to as overproduction (Darwin, 1859). Overproduction can be influenced by resource limitation and/or extrinsic factors such as predation. Predation on neonates can be heavy, leading to losses of over 80% in the first 5 months of life (e.g., Van Ballenberghe and Ballard, 1997; Bertram and Vivion, 2002b). If predation is acting as the ultimate cause of mortality, it is removing otherwise healthy individuals from the population and, therefore, is a regulating factor if it is density-dependent. In contrast, if predation is a proximate cause of mortality, the individual would have died from other causes (e.g., starvation, illness) even if it had not been depredated. Predators consuming malnourished individuals are not regulating their prey population (Caughley and Sinclair, 1994). This can be true even in cases where there is overproduction. Thus, not all behavioral (e.g., migratory characteristics) and physiological (e.g., overproduction) traits that exist within a population necessarily confer increased fitness.

Conditions allowing for a LDE appear to persist for moose (*Alces alces*) over wide swaths of the boreal forest (e.g., Gasaway et al., 1992; Crete and Courtois, 1997). In north-central Alaska, moose persist at low densities (0.06–0.12 moose/km²) over long time periods (i.e., decades) without apparent large oscillations in population size (Lawler et al., 2006; Lake et al., 2013; Sorum et al., 2015). Body condition, productivity, and survival of adults are high enough to allow for population growth. Habitat does not appear to be limiting as browse utilization rates in the region are among the lowest in Alaska (Paragi et al., 2008; Julianus, 2016). Therefore, the moose population appears to exist at a low-density equilibrium. Our objectives were to: 1) quantify the productivity and survivorship of moose in north-central Alaska; 2) determine if the population fits the characteristics ascribed by the LDE hypothesis; and 3) assess if top-down and/or bottom-up influences contribute to population regulation.

2. Materials and methods

2.1. Study area

Our study area was located in the upper Koyukuk River drainage in north-central Alaska (Fig. 1). A full complement of native species inhabits the area. Predators of moose, such as wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and black bears (*U. americanus*) occur at relatively

low densities. Contemporary, quantitative density estimates of these predators are lacking for this region (but see Bertram and Vivion, 2002a; Adams et al., 2008; Lake et al., 2013). Caribou (*Rangifer tarandus*) can be found in the region at low densities during the winter months (Wilson et al., 2014) and Dall's sheep (*Ovis dalli*) at low densities throughout the year in the mountainous regions (Schmidt and Rattenbury, 2013). Hunting and trapping pressure from humans is relatively low, yet uneven, due to its relative inaccessibility and statutory hunting restrictions.

We divided the study area into northern and southern sections based on differences in physiography. The rugged Brooks Range, with mountains that reach up to 2000 m, dominates the northern section of the study area. There, willow (*Salix* spp.) thickets and riparian forests of white spruce (*Picea glauca*) and poplar (*Populus balsamifera*) line the banks of narrowly-confined river valleys. Black spruce (*Picea mariana*) forests dominate the low-lying areas, while birch (*Betula papyrifera*) stands occur on some southern exposures. Trees quickly give way to alder (*Alnus* spp.) thickets and alpine communities as elevation increases. Deciduous and mixed forest cover 6% of the northern section, 13% by spruce forest, 20% by dwarf shrubs, 10% by barrens, and 50% by shrubs. Parts of the Gates of the Arctic National Park and Preserve (GAAR) and Dalton Highway Corridor Management Area (DHCMA) are included within the northern section of the study area. The DHCMA is thought to have lower predator densities than the rest of the study area due to increased human activity associated with towns, the Dalton Highway and associated access roads, and multiple aircraft runways, which provide access for hunters, trappers, and recreationists.

The southern section of study area is a much different environment. The terrain is gentler and is characterized by flatlands and rolling hills; elevations are mostly < 500 m. There are expanses of tussock (*Eriophorum* spp.) tundra, dwarf birch (*Betula glandulosa*), and muskegs within a matrix of boreal forest, broad rivers, and associated riparian zones. Due, in part, to the physiography, there is more available moose habitat in the southern section of the study area than in the northern section. This section is 14% deciduous and mixed forest cover, 27% spruce forest, 6% dwarf shrubs, 1% barrens, and 48% shrubs. All of Kanuti National Wildlife Refuge (KNWR) is contained within the southern section of the study area.

The climate throughout the study area is quintessentially continental, with cold winters and warm summers. Winters last 6 months and temperatures can reach −45° C. Snow depths > 90 cm are not uncommon, with at least 60 cm occurring in most winters. Snow accumulates during the season, with the greatest depth of snow pack occurring in April. Summers are short (~2 months), with high temperatures often around 20° C but occasionally reaching 30° C. Wildfires are common during the summer months, especially in the southern section of the study area (Joly et al., 2016).

2.2. Moose observational data

We captured 120 adult moose between March 2008 and April 2011 (93 females and 27 males) using helicopter darting techniques (Keech et al., 2000). One female was censored from analyses due to presumed capture myopathy. Of the remaining moose, 67 (45 F, 22 M) were captured in the northern section of the study area ('northern' moose) and 52 (47 F, 5 M) in the southern section ('southern' moose). All captured moose received a collar that had a VHF beacon and 37 of those also contained GPS units. We were not able to determine ages of moose. We attempted to radiotrack all collared moose monthly in small fixed-wing aircraft (e.g., Piper PA-18 Super Cub, Bellanca Scout, or Cessna 182) during the study (March 2008–May 2013) but our efforts were not always successful due to inclement weather, logistics and funding. Radiotracking efforts were more consistent in the southern section of the study area but more northern moose had GPS units. GPS units collected 1–3 locations per day. The number of calves present with a female was recorded during 3 seasons: post-calving (i.e., late May/early

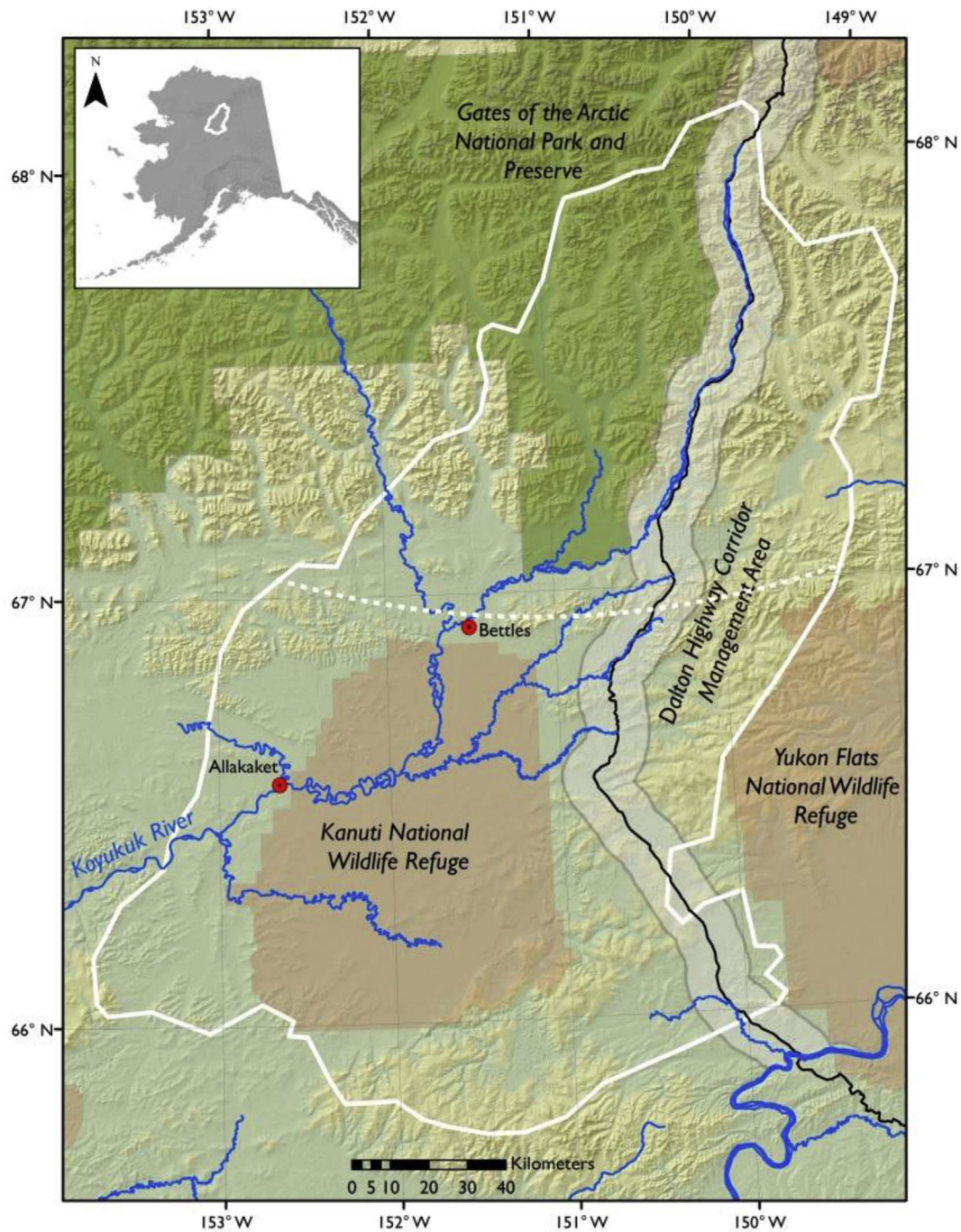


Fig. 1. Upper Koyukuk River drainage study area, delineated by the white boundary, north-central Alaska, 2008–2013. Dashed white line represents the boundary between the northern and southern sections of the study area. Pale yellow areas are more mountainous, while light green indicates lower elevations.

June), fall (i.e., September or October) and spring (i.e., March or April) when the calves were approximately 1 week, 4 months, and 10 months old, respectively.

2.3. Productivity and survival analyses

For productivity, we were interested in factors contributing to both the probability of a parturition event and probability of twinning given a parturient female. We examined whether parturition and twinning were influenced by physiography, migration strategies, environmental factors, or costs associated with parturition and calf rearing the previous year using a candidate set of binomial generalized linear mixed-effects models (GLMM) with a logit link function. We used parturition

events (whether the female had any calves, regardless of number) as the response in the parturition analysis and twinning events of parturient females (whether the female had 2 or more calves) for the twinning analysis. Individual was included as a random effect. As covariates, we used section of the study area (northern versus southern), migratory behavior (migratory, non-migratory, other strategy as determined by Joly et al. (2015a)), year, number of freezing (below 0° C) days the prior winter, and number of days with snow depth > 75 cm the prior winter, as measured in Bettles, Alaska (National Oceanic and Atmospheric Administration data; accessed from <http://xmacis.rcc-acis.org/>). We also tested for effects from reproductive events the year prior by including a dummy-variable for each of the following scenarios: a parturition event the previous year, parturition followed by a calf

Table 1

Top 10 model selection results for factors affecting probability of parturition for moose in north-central Alaska, 2008–2013. Probability of parturition was used as the response in binomial generalized linear mixed-effects models with individual as a random effect. Predictors considered included section of study area (“Section”; northern or southern), migration behavior (“Migrant”; migratory, non-migratory, or other), year (“Year”), parturition success the previous year (“PrevPart”), whether the female had a calf at the end of the previous summer (“SummerCalf”), whether the female raised a calf through winter the previous year (“PrevYearling”), number of days below 0° C (“Temp”), number of days with snowfall > 75 cm (“SnowDays”), and the number of years the animal had been collared (“CollarAge”).

Model	K	AICc	Δ AICc	w _i
Section	3	267.50	0.00	0.22
Section + PrevPart	4	268.51	1.01	0.13
Section + PrevPart + SnowDays	5	269.41	1.91	0.09
Section + SummerCalf	4	269.44	1.94	0.08
Section + PrevYearling	4	269.58	2.08	0.08
Section + PrevPart + CollarAge	5	269.91	2.42	0.07
Section + SummerCalf + SnowDays	5	270.47	2.97	0.05
Section + PrevYearling + SnowDays	5	270.58	3.08	0.05
Section + PrevPart + Temp	5	270.59	3.09	0.05
Section + SummerCalf + Temp	5	271.48	3.98	0.03

surviving to the end of summer, and parturition with the calf surviving the first year. We did not measure age of adults at capture, but as a proxy to test for age effects, we included a running count for collared animals for each year we termed ‘collar age’ (Prichard et al., 2012). We

only included reproductive years for which the individual could be classified for their prior reproductive year, ensuring all models being compared used the same data set (parturition: $n = 204$; twinning: $n = 128$). Number of freezing days per winter was scaled (i.e., number of days minus the mean divided by the standard deviation) to ameliorate convergence issues. We built a candidate set of models (Table 1) and performed model selection based on Akaike’s information criteria adjusted for small sample size (AICc; Burnham and Anderson, 2002). Analyses were performed in R version 3.3.3 (R Core Team, 2017), models fit with the package ‘lme4’ (Bates et al., 2015), and confidence intervals estimated with the package ‘AICcmodavg’ (Mazerolle, 2017).

To investigate calf survival in its first year of life, we used calf counts for collared cows collected at 3 occasions in the year – post-calving, fall, and spring – to indicate calving, summer survival, and overwinter survival, respectively. Apparent survival rates were estimated using the Young Survival from Marked Adults model developed by Lukacs et al. (2004) in Program Mark (White and Burnham, 1999; <http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>). To meet the assumption of known ‘family group size’, only encounter histories in which the collared female was observed post-calving were used. We considered a candidate set of models to test for differences between sections of the study area, among migratory behaviors, among years, and for effects of the severity of the winter experienced by the female before parturition as well as the winter experienced by the calf. We used the same weather data from Bettles, Alaska, as described above,

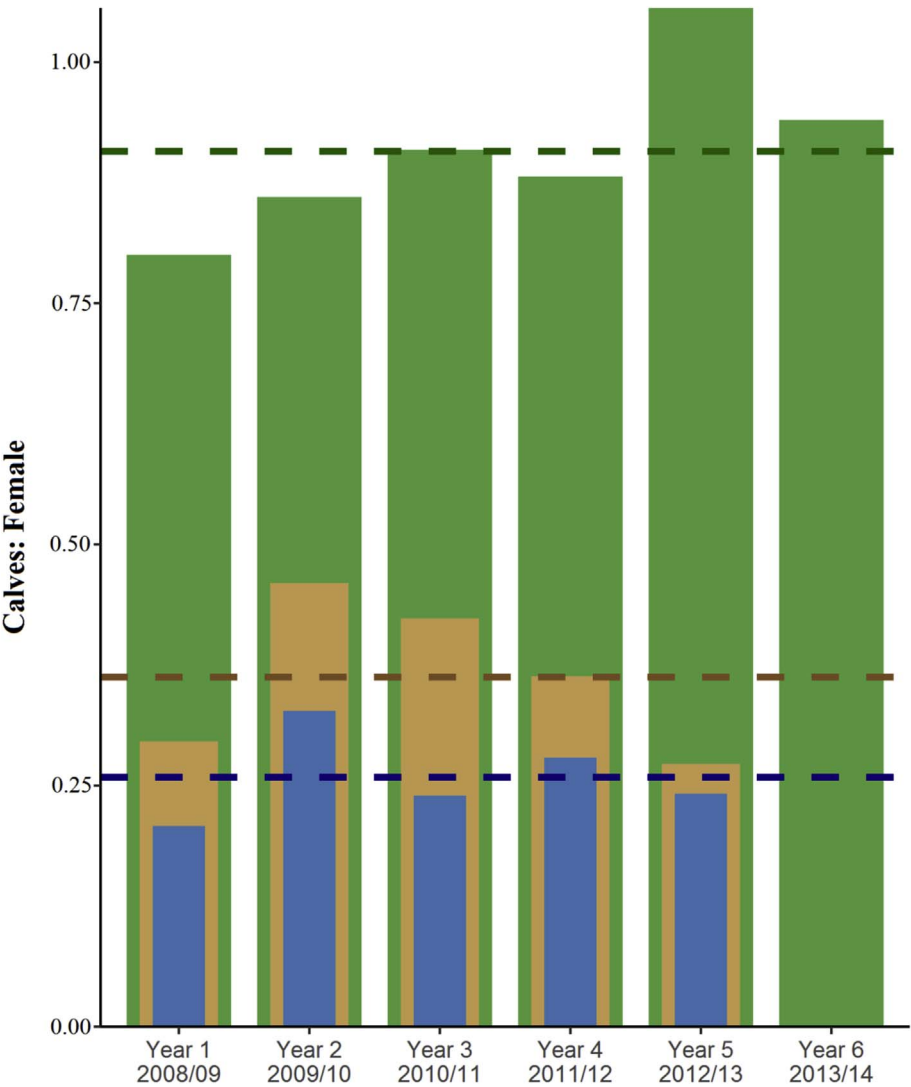


Fig. 2. Productivity of moose in north-central Alaska, 2008–2013. Bars depict the ratios of calves observed per female during calving (late May/early June; in green), fall (tan), and the following spring (blue). Dotted lines depict seasonal averages over the course of the study.

and scaled both counts of freezing days and days of snow depth > 75 cm. We set the apparent survival (ϕ) to vary between the summer interval (ϕ_1 : post-calving to fall) and the winter interval (ϕ_2 : fall to spring) for all models. We assumed constant detection probability (p), which is based on detection of VHF transmitters from aerial surveys that have a high success rate, for both observation occasions so we could estimate ϕ across both intervals. A logit link function was used to estimate parameters and we judged fit by AICc.

We used both radiotracking efforts and GPS data to determine adult moose survival on a monthly basis for the duration of the study. Survival rates were estimated from known-fate models in Program Mark. We tested for differences between sexes, sections of the study area, and among migratory classes, seasons (summer, fall, winter, spring), and level of winter severity as determined by Joly et al. (2015a), which was based on temperature and snow depth. We defined a year as July 1 – June 30 and seasons as summer (June, July, August), fall (September, October, November), winter (December, January, February, March), and spring (April, May). Study-period estimates were not produced for winter severity as moose did not experience winter for 12 months of the year nor have 5 consecutive years experiencing the same winter severity. We used a logit link function for parameter estimation, AICc and the change in AICc (Δ AICc) to determine the most parsimonious models. We further evaluated the support for effects of interest by examining the parameter estimates and confidence intervals for covariates in competing models (i.e., those within 2 AICc of the best supported model).

3. Results

3.1. Female productivity and survivorship of calves

Female moose produced an average of 0.91 calves/female (range 0.80–1.06) across the study area from 2008 to 2013 (Fig. 2). The ratio dropped to 0.36 calves/female (range 0.27–0.46) by fall. This represents a 60% decline in the number of calves from parturition to fall. By the following spring, the ratio for the entire study area dropped to 0.26 calves/female (range 0.21–0.33); representing a total loss of 71% of the cohort. Thus, 85% of the annual loss of the calf cohort, on average, occurred during the summer months.

The most influential factor for probability of parturition was the section of the study area a moose resided in: the top model included only this covariate and all 4 models with < 2 Δ AICc also contained it (Table 1). Southern moose exhibited a greater probability of parturition (0.72, 95% CI = 0.63–0.81) than northern moose (0.53, 95% CI: 0.43–0.63; Fig. 3A). Southern moose (1.00 calves/female) were more fecund than northern moose (0.66 calves/female). Of the 4 top models, 2 included parturition status the previous year, suggesting that having a calf the prior year increased the probability of parturition (8% for northern moose and 7% for southern moose). We found no evidence for an effect of migration strategies, number of freezing days, or our index of collar age on the probability of parturition.

Winter severity, as indexed by the number of freezing days the prior winter, appeared to have the greatest influence on the probability of twinning given a parturition event: the top model was comprised only of this covariate and all 3 models with < 2 Δ AICc included it (Table 2). In all 3 models, the effect of number of freezing days was similar; a reduction in the probability for female moose to twin as the number of freezing days the prior winter increased (Fig. 3B). Study area section appeared to have a similar effect on twinning in the second and third top models as it did with parturition, but the effect was approximately half the magnitude as from the parturition analysis results. Similar to the parturition results, prior parturition also appeared to have a positive effect on twinning. The number of days with snow depth above 75 cm appeared to have a weak positive effect. We found no significant effects of migration strategy, prior calf rearing to yearling, or collar age on the probability of twinning.

For the calf survival analysis, we had 166 observation-years in which at least 1 calf was detected. Six models were all within 2 AICc (Table 3). The top model for calf survival included only the number of snow days the winter prior to parturition for summer survival (ϕ_1) and only the number of freezing days that winter for winter survival (ϕ_2 , Table 3). Apparent survival estimates from this model for the summer interval (ϕ_1) was estimated as 0.44 (95% CI: 0.37–0.51) and for the winter interval (ϕ_2) as 0.74 (95% CI: 0.58–0.86). The overall probability of a calf surviving the first year was estimated as 0.32 (95% CI = 0.25–0.41) and the detection probability as 0.91 (95% CI = 0.80–0.96). In this model, as well as others which included different combinations of these 2 abiotic indices, the effect of the number of snow days during the previous winter on summer survival was negative. The effect of number of freezing days on winter survival was positive. The second top model essentially fit the data equally well (Δ AICc = 0.03) and included an effect of study area on calf survival across both ϕ_1 and ϕ_2 , in which calves in the southern section of the study area were more likely to survive than calves in the north. The null model, which modeled ϕ_1 and ϕ_2 separately and without any covariates, was in the top candidate set. Our results indicate that calf survival is significantly lower during summer than winter, and suggest that abiotic factors from both the winter before a calf is born and the winter experienced in the first year of life have an effect on survival. We found no significant effect of migration strategy on calf survival.

Twinning rates have been previously reported in 2 ways: the proportion of all adult females that had twins (or triplets), and/or the proportion of females with calves that had twins (e.g., Schwartz, 1997). The latter is used more commonly (e.g., Boertje et al., 2007; Seaton et al., 2011), but does not directly address lower pregnancy rates associated with resource limitation. We report both here for clarity. The twinning rate for all cows averaged 30% (range 20–37%). The proportion of twins for females with calves averaged 50% (range 33–57%). The proportion of twins for females with calves averaged 36% for northern moose and 59% for southern moose. Of the 252 calving observations, the only female that had twins in 5 consecutive years was a southern moose. One southern moose was observed with triplets once. The proportion of all adult females with twins dropped to 4% by the following spring, with 98% of the decline occurring during the summer months. Survival of single neonates (24%) to the following spring was similar to that of twins (21%). Females that had a single calf in May had an average of 0.24 calves the following spring, whereas females that had twin calves averaged 0.73 calves. We did not detect evidence of reproductive pauses in this population of moose.

3.2. Survivorship of adults

Of the 119 adult moose we captured, 38 (29 females and 9 males) died during our 5-year study. The cause of mortality for 2 of the 38 (5.3%) mortalities was hunting (both males). Due to the remote setting, costs, and logistics, the ultimate cause of mortality was not ascertained for the remaining mortalities. The proximate cause of mortality was unknown for 68.4% of the mortalities. Based on visual observations, wolves and either grizzly or black bears were suspected to be the proximate cause for 18.4% and 7.9% of the mortalities, respectively. An adult male moose with only 1 eye at the time of its capture survived another 14 months before it died. Mortalities occurred in all months of the year except December. The 3-month period with the largest proportion (36.1%) of non-hunting mortalities was March–May.

Adult survival was high, ranging from 98.5–99.2% monthly and 41.1–63.0% for the entire 5-year study (Fig. 4). Survival was higher for females, but lower for individuals that displayed a mixed migratory behavior pattern (i.e., those that were not clearly migratory or non-migratory); however, confidence intervals overlapped in all cases (Fig. 4). Annual survival rate was estimated to be 89.8% for females and 85.0% for males. Moose in both the northern and southern sections of the study area had annual survival rates of ~89%. Annual survival

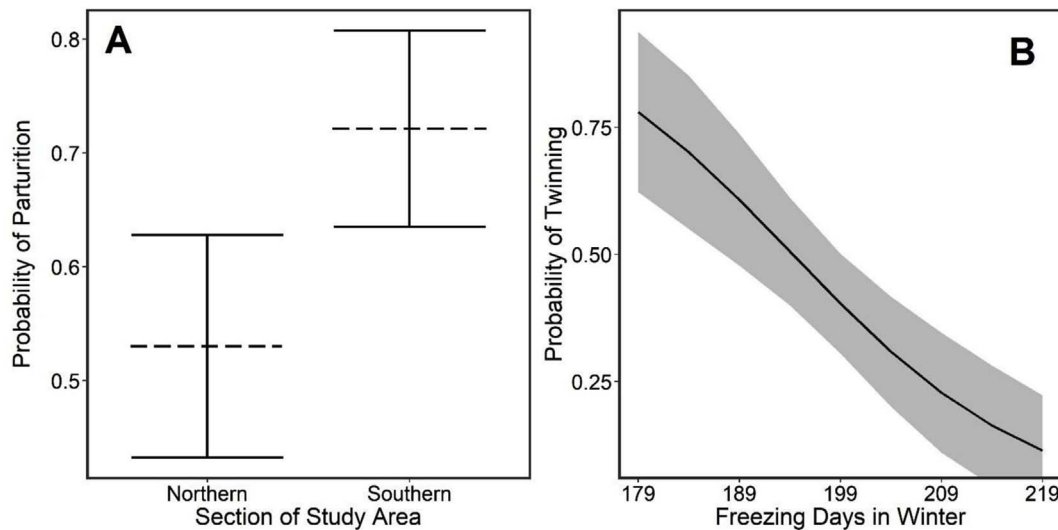


Fig. 3. Predicted probabilities of (A) parturition and (B) twinning given a parturition event for moose in north-central Alaska, 2008–2013, based on the top-performing binomial generalized linear mixed-effects models ((A) section of study area and (B) number of freezing days) with individual as a random effect. Bars (A) and shaded interval (B) indicate the 95% confidence intervals. Horizontal dashed lines (A) indicate the average for each section of the study area.

Table 2

Top 10 model selection results for factors affecting probability of twinning for parturient moose in north-central Alaska, 2008–2013. Probability of twinning was used as the response in binomial generalized linear mixed-effects models with individual as a random effect. Predictors considered included section of study area (“Section”; northern or southern), migration behavior (“Migrant”; migratory, non-migratory, or other), year (“Year”), parturition success the previous year (“PrevPart”), whether the female had a calf at the end of the previous summer (“SummerCalf”), whether the female raised a calf through winter the previous year (“PrevYearling”), number of days below 0° C (“Temp”), number of days with snowfall > 75 cm (“SnowDays”), and the number of years the animal had been collared (“CollarAge”). The null model did not include any covariates.

Model	K	AICc	Δ AICc	w_i
Temp	3	164.04	–	0.40
Section + PrevPart + SnowDays + Temp	6	165.35	1.31	0.21
Section + PrevPart + Temp	5	165.97	1.93	0.15
Section + SummerCalf + Temp	5	166.49	2.45	0.12
Section + PrevYearling + Temp	5	166.89	2.85	0.10
Collar Age	3	171.47	7.43	0.01
Section + PrevPart + CollarAge	5	174.54	10.50	0.00
SnowDays	3	176.74	12.70	0.00
Null	2	177.99	13.95	0.00
Migrant	4	178.08	14.04	0.00

rates were estimated to be 91.7%, 89.5%, and 82.5%, for non-migratory, migratory, and mixed-migratory moose, respectively.

The most parsimonious model assessing factors that influenced adult moose survival included only winter severity (Table 4). Monthly survival was highest during moderate winters (99.6%; CI 98.9–99.8%) compared to severe (98.5%; CI 96.4–99.4%) or mild (98.6%; CI 97.3–99.3%) winters. Monthly survival during moderate winters also was higher than survival rates during summer (98.9%; CI 98.3–99.4%). However, the null model predicting constant adult survival was the next best performing model and had similar weight as the top model (Table 4). This suggests that none of the factors we investigated were particularly influential predictors, as supported by a 2% proportional reduction in deviance by the top model (Guisan and Zimmerman, 2000). The models suggesting that female moose had higher survival rates than males had a Δ AICc score < 2, suggesting that there may be differences between those groups. Differences in adult survivorship between the northern and southern moose were not well supported (Table 4).

The addition of a model which included migratory behavior (migratory, non-migratory or mixed), which excluded 10 individuals without classified migratory behavior, had little effect. Winter severity

Table 3

Top 10 models from Lukacs Young Survival from Marked Adults analysis for factors affecting apparent survival probabilities of moose calves in north-central Alaska, 2008–2013. Apparent survival (ϕ) was modeled in 2 intervals: from calving to fall (ϕ_1) and from fall to spring (ϕ_2). Factors tested in the models were section of the study area (“Section”; northern versus southern), number of days with snow depth > 75 cm in the winter before parturition (“PrevSnow”) and during the winter experienced by the calf (“ThisSnow”), number of freezing days in the winter before parturition (“PrevTemp”) and during the winter experienced by the calf (“ThisTemp”), migration behavior (non-migratory, migratory, and other), and year (5 years total). Migration and year were not in the top 10 performing models. Detection probability (p) was modeled as equal across the 2 intervals for all models.

Model	Deviance	# Parameters	AICc	Δ AICc	w_i
ϕ_1 (PrevSnow), ϕ_2 (ThisTemp)	397.15	5	407.45	0.00	0.15
Section + ϕ_1 (PrevSnow), ϕ_2 (ThisTemp)	395.07	6	407.48	0.03	0.15
ϕ_1 (PrevSnow), ϕ_2	399.81	4	408.00	0.55	0.12
ϕ_1, ϕ_2 (ThisTemp)	400.15	4	408.35	0.90	0.10
ϕ_1, ϕ_2	402.50	3	408.62	1.17	0.09
Section + ϕ_1, ϕ_2	400.53	4	408.72	1.27	0.08
ϕ_1 (PrevSnow), ϕ_2 (ThisSnow)	399.77	5	410.07	2.62	0.04
Section + ϕ_1 (PrevSnow), ϕ_2 (ThisSnow)	397.66	6	410.08	2.63	0.04
ϕ_1 (PrevTemp), ϕ_2 (ThisTemp)	399.92	5	410.21	2.76	0.04
ϕ_1 (PrevTemp), ϕ_2	402.17	4	410.36	2.91	0.04

remained the top model, followed by the constant models. Migratory behavior was the third-ranked model with a Δ AICc = 1.20 and w_i = 0.105.

4. Discussion

Moose in north-central Alaska appear to fit the characteristics of a low-density equilibrium because the population has persisted at a low density over a long period of time (Lawler et al., 2006; Lake et al., 2013; Sorum et al., 2015). However, it is not clear what role predation plays in either limiting or regulating the population. Adult annual survival (~89%) in our study area was relatively high (Crete and Courtois, 1997; Van Ballenberghe and Ballard, 1997) and very similar to other locations in Interior Alaska and the Yukon (e.g., Bangs et al., 1989 [92%]; Larsen et al., 1989 [91%]; Ballard et al., 1991 [95%]; Bertram and Vivion, 2002b [89%]). Slightly lower survival rates for adult males

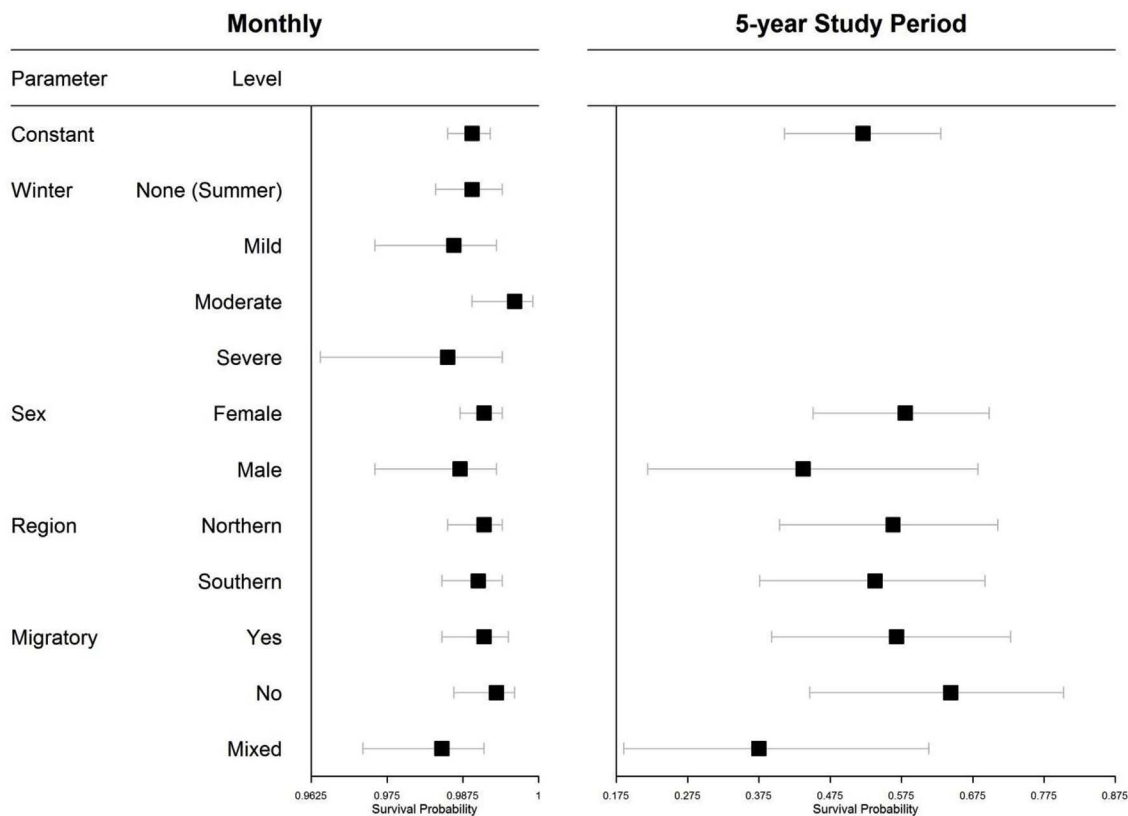


Fig. 4. Survival estimates for moose in north-central Alaska, 2008–2013. Study-period estimates were not produced for winter severity as moose did not experience winter for 12 months of the year nor have 5 consecutive years experiencing the same winter severity.

Table 4

Model selection results for factors affecting monthly survival probabilities of moose in north-central Alaska, 2008–2013. Factors in the models were each month interval (time), month of year (month), season, year (1 July–30 June), sex (male or female), region (northern or southern section of the study area), winter severity (mild, moderate or severe), and constant.

Model	Deviance	# Parameters	AICc	Δ AICc	w_i
Winter severity	353.89	4	361.91	0.00	0.19
Constant	360.17	1	362.18	0.27	0.17
Sex	359.20	2	363.20	1.30	0.10
Region	360.13	2	364.13	2.23	0.06
Year	354.59	5	364.60	2.70	0.05
Sex(female) + Region(south)	359.06	3	365.07	3.17	0.04
Sex + Year	353.87	6	365.89	3.99	0.03
Season	358.06	4	366.08	4.17	0.02
Sex(female) + Season	357.06	5	367.08	5.17	0.01
Month	349.20	11	371.28	9.37	0.00

versus females may be due to the rigors of the rut (Ballard et al., 1991; Miquelle et al., 1992; Crete and Courtois, 1997; Modafferi and Becker, 1997) and/or more hunting seasons open for males (Modafferi and Becker, 1997) in our study area. Migration did not appear to affect vulnerability of adults to predation. Adult survivorship was nearly identical for the northern and southern sections of our study area. The impact of hunting was limited; however poaching can impact isolated places in this region (Bertram and Vivion, 2002b). The high survival rates of adult moose make it difficult to identify factors that impact adult mortality because, in general, moose surviving to adulthood are fairly resilient. Nonetheless, we did not find evidence that predation on adult moose was regulating or limiting this moose population.

Predation on moose calves can be quite high, with annual survival rates as low as 0.1 (Van Ballenberghe, 1987; Ballard et al., 1991; Larsen et al., 1989; Bertram and Vivion, 2002b). Much of this mortality comes

in the first 8 weeks of life. For example, Gasaway et al. (1992) reported that 83% of neonates died during this time period. Our analyses reveal that annual survival of calves was higher in our study area (0.29) than elsewhere in Alaska and the Yukon. Similar to other studies, the majority (60%) of neonates in our study area died during their first 5 months of life (i.e., during the summer and early fall). However, these losses were not as dramatic as seen elsewhere (e.g., Van Ballenberghe, 1987; Ballard et al., 1991; Larsen et al., 1989; Bertram and Vivion, 2002b). Assuming that predation is the proximate cause of much of this mortality (Ballard, 1992; Bertram and Vivion, 2002b), bear and wolf predation during the summer months appears to have a greater impact on the moose population than overwinter predation, which is predominately attributed to wolves (Lake et al., 2013). This assumption must be viewed with some caution as substantial over-summer calf losses can occur with negligible predation (Milner et al., 2013). Indeed, both calf and yearling moose mortality were low in areas adjacent to our study area, regardless of whether or not wolf control (i.e., culling) took place (ADFG, 2016). In fact, changes in the moose population were not detected after wolf control efforts occurred (ADFG, 2016). Gasaway et al. (1992) also found that wolf reduction alone did not statistically increase moose calf survival. Further, moose residing in the DHCM, an area where predator density is likely lower, recruited calves into the population at the same rate as moose residing elsewhere in our study area (NPS, unpublished data). Calf survival was lower in the northern section of our study area where there is less high-quality moose habitat. To the east of our study area, moose have been increasing without predator control efforts (Lake, 2015); which may be related to improvements in habitat quality induced by disturbances (e.g., wildfires and river ice scouring) that increase the amount of early seral habitats (Sorum and Joly, 2016) or other factors. Migratory behavior did not reduce predation pressure on calves. Studies that estimate predator densities, kill rates and/or diets should be initiated to help elucidate the role of predators in the survival of juvenile moose in this region.

Female moose in the southern section of our study area, where there is more extensive high-quality moose habitat, produced 50% more calves (1.00 calves/female) than females in the northern section (0.66 calves/female). Fecundity was very low for northern moose, even compared to other unproductive boreal forest areas (e.g., 0.78 calves/females; Crete and Courtois, 1997). While fecundity was higher for southern moose, it was still lower than in some other parts of Alaska (e.g., 1.27 calves/female; Schwartz and Hundertmark, 1993). Twinning rates are strongly correlated with maternal condition and habitat quality, and are used as an index of nutrition status of moose populations (Gasaway et al., 1992; Keech et al., 2000; Boertje et al., 2007). Populations with twinning rates exceeding 40–50% are not thought to be strongly limited by nutrition (Van Ballenberghe and Ballard, 1997). Unfortunately, this hypothesis did not define whether twinning rate was for all females or just females that had calves. We found that 30% of all female moose in our study area produced twins and that 50% of females that had calves produced twins. Like calf production, our overall twinning rates (i.e., twins/parturient females) were middling (Schwartz, 1997; Boertje et al., 2007; Seaton et al., 2011). Twinning rates were higher in the southern section of our study area (59%), and in other regions (> 60%; Schwartz, 1997; Boertje et al., 2007; Seaton et al., 2011), where there is more high-quality moose habitat, than in the northern section of our study area (36%). Even in the southern section of our study areas, available browse is low relative to areas at lower latitudes (Julianus, 2016). Migration did not improve fecundity. From these results we infer that bottom-up influences (e.g., habitat quantity, habitat quality, nutrition) may be limiting moose productivity; particularly in the more mountainous north. Female moose are nonetheless overproducing calves throughout the study area.

Overwinter conditions have the potential to affect movements, habitat selection, body condition, productivity, and survival in moose populations (Thompson, 1980; Mech et al., 1987; Modafferi and Becker, 1997; Van Ballenberghe and Ballard, 1997; Joly et al., 2015b; Joly et al., 2016, this study). Winter severity was the top model for adult survival but it did not receive much more support than the model of constant survival (Table 4). Survival was highest during moderate winters, providing some support for the hypothesis that moose may have an advantage when snow is deep enough to impede the movement of wolves, but not deep enough to impede their own movements. The causal mechanism for the positive correlation between the number of freezing days and winter survival in our study is unknown, however warmer winter temperatures are known to be correlated with lower survival rates of moose at the southern edge of their range (Lenarz et al., 2009). The end of winter (March–May), when snow was deepest, and body condition is thought to be at its lowest, had the highest proportion of mortalities. Similarly, over-summer calf survival and twinning rates were lower following a more severe winter.

We found that females that were productive, stayed productive year after year (i.e., females that successfully reared more calves produced more calves the following season). The Alaska/Yukon moose (*A. alces gigas*) is the largest of the North American moose subspecies and well-adapted to snow (Bubenik, 1997). We posit that in this low-density population, there are many large, healthy females that are able to survive and produce offspring under most winter conditions that they encounter in this region. Despite harsh winter conditions that affect some individuals, there are enough robust females to mask the impacts of severe winter weather on the population as a whole regardless of the less robust individuals. The lack of effect of snow on moose calf production and twinning rates has been documented elsewhere in the boreal forest (e.g., Messier, 1991). Thus, while overwinter conditions may limit the survivorship and productivity of moose in this region, those effects are likely more pronounced on the more vulnerable individuals.

The LDE hypothesis asserts that predation regulates the population and also assumes that there is enough high-quality habitat to support higher densities of moose if the population is released from the

constraints of predation. It is not clear that either of these conditions are met in our study area of north-central Alaska. Survival of adults is high and so predation upon adults is likely not limiting the population. Predation on young (< 5 months old) moose has the potential to limit the population – although overproduction does not always connote regulation by predation. Calf mortality was moderate in our study area compared to other boreal forest regions. Implementation of wolf control did not lead to greater moose densities in an area bordering the southern section of our study area (ADFG, 2016). However, other predators, such as bears, were not controlled in the experiment and have the potential to limit moose populations (Ballard, 1992; Bertram and Vivion, 2002b).

Ungulate density can be a misleading indicator of habitat quality (Van Horne, 1983); low densities of ungulates can inhabit either high- or low-quality habitats. Thus, while moose density (Lawler et al., 2006; Sorum et al., 2015) and browse utilization (Paragi et al., 2008; Julianus, 2016) are low in our study area, habitat still could be a factor contributing to limiting this population. We detected some indications of nutrient limitation; most notable were the very low fecundity of adult female moose and lower survival of calves in the northern section of the study area. While robust individuals are resilient to the range of winter conditions experienced during our study, harsh winter conditions may impact vulnerable adults and calves in this population. Further, harsh winter conditions can also act in concert with predation pressure to affect ungulate populations (Hegel et al., 2009, 2010). Thus, we agree with other research that a suite of factors often interact to limit ungulate populations (e.g., Crete and Courtois, 1997; Thompson and Peterson, 1988; Bertram and Vivion, 2002b; Brown et al., 2007; Hegel et al., 2010; Joly et al., 2011). In our study, these factors include extent of high-quality habitat, predation on young calves, and winter conditions.

We documented behavioral and physiological traits existing within a moose population near the northern limits of the range of the species that did not appear to confer fitness benefits. Specifically, moose we studied that displayed migratory behavior did not have greater survivorship or productivity than non-migratory moose and females produced substantially more calves than survived. Variability in migratory behavior (i.e., partial migration) is common among individuals where habitats support resident populations but fitness varies spatially (Fryxell and Holt, 2013). Similarly, overproduction is common across a wide range of taxa. What is the purpose of these traits? We suggest that a diversity of traits exist within a population so that if conditions change, individuals will be poised to take advantage of those changes and reap the fitness benefits. A diversity of traits within the population contributes to the population's ability to adapt and be resilient to changes in land use and climate change (Chapman et al., 2011; Middleton et al., 2013; Gilroy et al., 2016). If individuals with fitness-enhancing traits thrive, the traits could eventually dominate the population. These traits are, in essence, lying in wait to escape the constraints that limit them.

Analyses of the effects of top-down and bottom-up influences need to assess a suite of factors and their interactions, including density-dependent and density-independent factors. If management actions, such as predator control, are to be implemented, they can be more effective if the ecological relationships of a system have been investigated robustly (Treves et al., 2016). In north-central Alaska, further research into the ultimate and proximate causes of mortality of moose calves during the first few months of life is warranted. Given the high survivorship of adult moose in this region, hunting should be considered primarily as an additive source of mortality rather than compensatory. In addition, when reporting and using twinning rates as an index of nutritional status, researchers need to explicitly note whether it reflects the rate for all females or just parturient ones because the twinning rate using all adult females was approximately 40% lower than the rate determined considering only females with calves. Lastly, our use of the Young Survival from Marked Adults model (Lukacs et al., 2004) to

analyze moose calf survival appears to be a novel application of the technique (outside the field of ornithology) that may have wide-ranging and important uses for studies of other taxa where detection is < 100% or there are missing observations and there may be > 1 offspring per female.

Statement of authorship

KJ and TC designed and performed the research; KJ, TC and MSS handled data management; MDC, AEG and KJ performed statistical analyses; all authors contributed to data interpretation and manuscript development.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2017.11.004>.

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