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

Kyle Joly[a,*], Tim Craig[b,1], Matthew D. Cameron[a], Adrian E. Gall[c], Mathew S. Sorum[a]

[a] Gates of the Arctic National Park and Preserve, National Park Service, 4175 Geist Road, Fairbanks, AK 99709, United States
[b] Kanuti National Wildlife Refuge, US Fish and Wildlife Service, 101 12th Avenue, Fairbanks, AK 99701, United States
[c] ABR, Inc., 2842 Goldstream Road, Fairbanks, AK 99709, United States

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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 over-production 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

* Corresponding author.
E-mail address: kyle_joly@nps.gov (K. Joly).
[1] Retired.

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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/km^2) 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 in 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

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