Ecology of Moose on the Gustavus Forelands: Population Irruption, Nutritional Limitation, and Conservation Implications

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Abstract. Moose populations in southeastern Alaska have a relatively short history as a result of recent de-glaciation of regional landscapes. The colonization trajectories of such populations have typically been characterized by irruptive fluctuations. That is, following a period of initial establishment, populations generally have increased rapidly (possibly exceeding habitat carrying capacity) and subsequently declined precipitously. We describe preliminary findings from an ongoing study focused on population-level responses to food-limitation in an irruptive, high-density (ca. 3.9 moose/km^2) moose population inhabiting the Gustavus forelands. We document high levels of woody browse consumption and sub-optimal diet shifts by moose over a period in which the population roughly doubled. In addition, we compare measures of body condition (adult female rump fat thickness) and population productivity (pregnancy and twinning rates) to other populations in coastal Alaska. The management and conservation challenges associated with irruptive, high-density moose populations are discussed.

Introduction

Moose play an important role in the cultural and ecological landscape of southeastern Alaska. Moose are valued not only as a charismatic and watchable wildlife species, but also as a critical subsistence resource for many rural communities. Perhaps more significantly, moose also function as "ecosystem engineers". For example, at high moose population densities, selective browsing of key deciduous plant species can alter soil nutrient cycling processes and the successional trajectory of plant communities (Pastor and others, 1988). These processes can, in turn, catalyze trophic cascades that result in profound changes to avian (Berger and others, 2001) and invertebrate communities (Suominen and others, 1999). Consequently, advancing our understanding of regional, high-density moose populations has important conservation implications for moose and the landscapes they inhabit.

In this paper, we describe ongoing research efforts focused on detailing the ecology of the Gustavus moose population. This population has only recently colonized (ca. 1966) the Gustavus forelands yet, in the last five years, has exhibited extremely rapid growth and currently is at very high density (ca. 3.9 moose/km^2; fig. 1). Consequently, much interest has focused on whether this population is sustainable and the extent to which current high density is affecting moose nutritional ecology and reproduction as well as ecosystem processes. Here, we summarize findings focused on assessing the extent to which the Gustavus moose population is regulated by "bottom-up", or food-based, factors. As such, we highlight our results in a broad context by contrasting ecological field data (i.e. diet, body condition and reproduction) collected on the Gustavus forelands with two lower density coastal Alaskan moose populations.

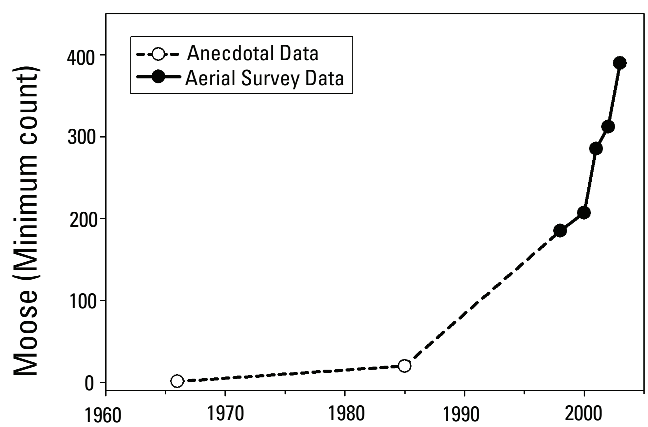

Figure 1. Gustavus moose population trajectory, 1966–2003. Both anecdotal (G. Streveler, Alaska Department of Fish and Game, pers. written commun.) and aerial survey data (N. Barten, Alaska Department of Fish and Game, unpub. data) are used to describe population trends. Population abundance data reflect the number of moose observed during winter surveys, these data represent a minimum estimate of the actual population size.

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Methods

Fieldwork was conducted on the winter range of the Gustavus moose population (ca. 100 km^2; fig. 2) between March 2000 and June 2004, although most data were collected between November 2003 and June 2004. Specifically, we collected data to determine moose diet selection, browse utilization, body condition, and reproductive success. Diet selection was determined by analyzing samples of fresh fecal pellets and enumerating plant species occurrence using microhistological techniques (Washington State University Nutrition Lab, Pullman, WA). We estimated willow browse utilization (proportion of current annual growth twigs browsed and actual proportions of willow biomass consumed) along six 500 m fixed transects in March–April 2000–2004. We determined moose body condition by measuring rump fat thickness (cm) on both live-captured and harvested adult female moose. Percent total body fat was estimated via rump fat measures using equations from Stephenson and others (1998). We measured moose body condition during the early- and late-winter periods (November/December and March/April, respectively). In-utero pregnancy and twinning rates were determined by examination of reproductive organs (collected from harvested adult female moose) and by using the pregnancy-specific protein B blood serum assay (Biotracking, Moscow, ID) for live captured animals. Additional confirmation of pregnancy status was determined during walk-in surveys of radio-marked animals during the calving period. Data used to compare measures of diet selection, body condition, and reproductive success for other moose populations (MacCracken and others ,1997; Crowley, 2002) were collected using identical protocols (except that samples for harvested animals were not used in other populations).

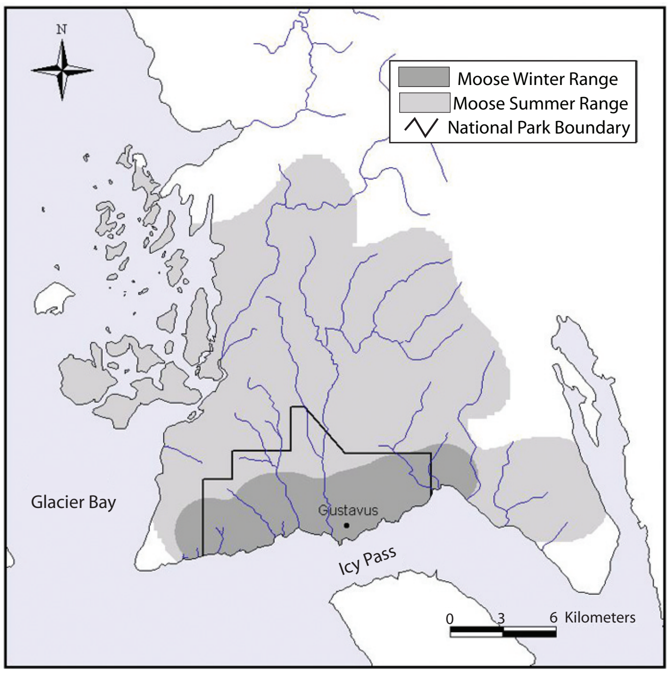

Figure 2. Gustavus moose research study area. Winter and summer range distributions are based on VHF telemetry relocation data acquired from 8 and 20 radio-collared moose, respectively. Data collection for this study occurred between 2003 and 2004, and took place primarily on winter range.

Results

We documented consistently high rates of willow browse utilization along transects during all years of sampling on the Gustavus forelands (table 1). On average, 88 percent (±3 percent) of current annual growth willow twigs were browsed and 37 percent (±2 percent) of the total current annual willow growth twig biomass was consumed. In contrast, only 41 percent (± 9 percent) of willow twigs were browsed and 7 percent (±0.6 see table 1 percent of the total twig biomass was consumed on the moose winter range in Cordova; comparable data are not available for Yakutat.

Woody browse (predominantly willow) and *Equisetum* sp. comprised the majority (76–90 percent) of food items consumed by moose during winter in 2001–04. However, during the period of rapid population increase between 2001

Table 1. Comparison of winter population density, woody browse consumption, body condition, and reproductive rates for coastal Alaska moose populations.

[Data sources: K. White, unpub. (Gustavus, 2003-04,), Crouse, unpub. (Yakutat, 2002–03), Crowley 2002 (Cordova, 2000–01; rump fat only), MacCracken and others, 1997 (Cordova, 1987–89; diet and browse only); Alaska Department of Fish and Game]

Population parameter	Gustavus			Yakutat			Cordova		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
Winter population density (moose/km^2)	3.9	--	--	0.9	--	--	0.4	--	--
Percentage of willow twigs browsed	88	3	6	--	--	--	41	9	11
Percentage willow biomass consumed	37	2	6	--	--	--	7	6	4
Fall body fat (percent)	10.5	0.9	26	17.0	1.5	22	17.5	6.0	15
Spring body fat (percent)	7.7	0.8	15	10.9	1.7	19	10.1	3.7	12
Pregnancy rate	79	8	28	100	0	19	--	--	--
Twinning rate	22	8	28	--	--	--	--	--	--

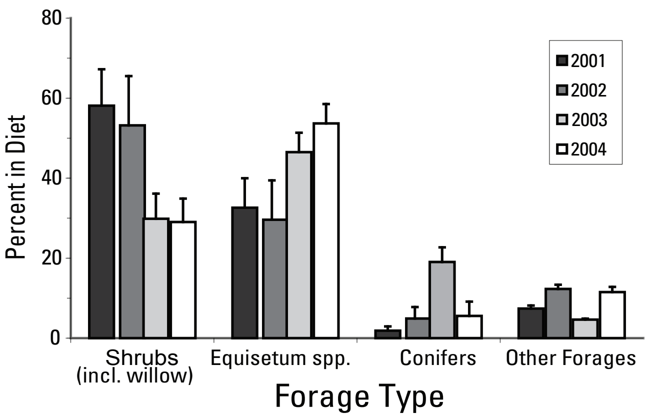

Figure 3. Annual variation in winter diet composition by moose on the Gustavus forelands as determined by microhistological analyses, 2001–04. "Other forages" included those constituting less than 5 percent of the diet.

and 2004, the proportion of woody browse in winter diets appears to have decreased (t=2.69, df=17, *P*=0.01) although the proportion of *Equisetum* sp. has increased (t=-2.35, df=17, *P*=0.03; fig. 3). Presumably, this resulted from increased competition for the limited supply of generally preferred woody browse species on the Gustavus winter range. More generally, the proportion of woody browse in Gustavus moose winter diets is low (35±4 percent, 2001–04) compared to coastal populations in Cordova (92 ±2 percent) and Yakutat (100 percent); *Equisetum* sp. constituted less than 1 percent of Cordova moose diets. Other forages, such as conifers (particularly western hemlock, *Tsuga heterophylla*) also comprise notable proportions of Gustavus winter diets (fig. 3).

Measures of percent total body fat for moose on the Gustavus forelands were low in both autumn and spring as compared to the lower density coastal moose populations in Yakutat and Cordova (table 1). Notably, the amount of fat reserves moose in Gustavus had at the beginning of winter was roughly equivalent to the amount moose in Cordova and Yakutat had at the end of winter. The body condition of Gustavus moose is among the lowest recorded for moose populations in Alaska.

In-utero pregnancy and twinning rates were low for moose on the Gustavus forelands as compared to the Yakutat population (table 1); reproductive data were not available for Cordova. The pregnancy rates recorded for moose on the Gustavus forelands are substantially below average for the species in North America (ca. 85 percent; Boer, 1992; Gasaway, 1992) and comparable to other populations near or greater than habitat carrying capacity.

Discussion and Conclusions

The Gustvaus moose population has increased rapidly over the last 5 years and appears to have entered an irruptive population growth phase (Caughley, 1970). In such cases, populations tend to be strongly regulated by nutritional constraints imposed by increased intra-specific competition and associated per capita decreases in availability of high quality forages. These conditions ultimately lead to reductions in individual body condition and reproductive rates. The findings reported here for the Gustavus moose population closely match those predicted for food-limited ungulate populations. Specifically, we documented high, range-wide rates of depletion of preferred woody browse biomass, evidence of diet shifts to alternative forages during a period of rapid population increase, poor body condition and low reproductive rates relative to other, presumably, "top-down" regulated coastal Alaska moose populations.

When populations reach a high density and closely approach or exceed habitat carrying capacity, long-term effects can include increased vulnerability to severe winters and overall declines in habitat carrying capacity. Winter snow accumulation can not only affect moose populations by increasing physiological costs associated with locomotion but also through burial of important forages. Winter diet composition of Gustavus moose includes high proportions of low-growing *Equisetum* sp. that, although widely available during snow-free winters, are especially prone to burial under only modest amounts of snow. Thus, for the Gustavus moose population, snow accumulation is likely to result in non-linear, or greatly accelerated, decreases in functional habitat carrying capacity that are triggered at much lower snow depth thresholds than would occur for populations, such as Cordova and Yakutat, that feed predominantly on taller, woody browse species. Habitat carrying capacity also can be reduced when high rates of herbivory negatively affect forage biomass productivity or plant persistence. One mechanism through which this can occur involves negative feedbacks between browsing pressure and soil nutrient cycling (see Hood and others, 2005). On the Gustavus forelands, we documented high rates of willow twig biomass consumption that are equivalent to those reported to cause productivity declines for willow species elsewhere (Singer and others, 2003). Thus, if parallel herbivory-induced declines in willow productivity are occurring on the Gustavus forelands, as suggested by Streveler and others (2003), then moose habitat carrying capacity is likely to be reduced as a result.

In food-limited populations, changes in the availability of important winter forages alter individual body condition and reproduction following predictable density-dependent pathways. From the standpoint of moose population dynamics, these density-dependent mechanisms are capable of independently initiating a change in the population trajectory of the Gustavus moose population. However, other extrinsic factors (namely predation) can greatly affect expected outcomes. Currently, little evidence of moose predation exists on the Gustavus forelands and rates of calf recruitment in fall continue to be high (ca. 55 calves/100 cows, 2003) despite low reproduction rates (described above). Nevertheless, wolves (*Canis lupus*) and bears (*Ursus arctos* and *U. americanus*) are highly adaptable predators and should predator-induced mortality rates increase, the trajectory of the Gustavus moose population could be altered significantly. Thus, it seems clear that the future of Gustavus moose population is dependent upon a dynamic array of both intrinsic and extrinsic interactions whose outcomes are complex and difficult to predict but represent surmountable challenges for future scientific investigations.

Management Implications

The Gustavus moose population plays an important local role not only as a key resource for human wildlife viewing and subsistence activities, but also through “ecosystem engineering” functions that span multiple trophic levels. In this context, the Gustavus moose population presents an interesting case study for resource scientists and managers. The Gustavus moose population is largely migratory and moves seasonally between distinct, but somewhat overlapping, summer and winter ranges. Specifically, about 75 percent of the radio-collared moose in this study (n=21) made “trans-boundary” movements between a small winter range on the Gustavus forelands to summer range areas in the Beardslee Islands and tributary drainages associated with Excursion Ridge. More importantly, the moose winter range occurs predominantly on non-park lands where moose are harvested by local and regional subsistence and sport hunters, whereas the summer range is mostly encompassed within protected National Park Service lands. Consequently, State-implemented management activities, focused on reducing population density well below habitat carrying capacity are likely to alter moose population density and associated ecosystem-level processes and wildlife-viewing opportunities inside Glacier Bay National Park. As a result, resource managers are faced with important challenges that involve balancing management policies that emphasize sustaining hunting opportunity, and natural regulation of wildlife populations and associated ecosystem processes.

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