Factors limiting productivity of the Central Arctic Caribou Herd of Alaska

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Abstract: Many biotic and abiotic factors can limit productivity and growth of caribou (*Rangifer tarandus*) herds, but limiting factors typically vary by region. Identifying limiting factors may help to indicate which seasons are of relative importance to a caribou herd and possibly to suggest general life history strategies. Using regression techniques, we found that despite previous suggestions, net productivity of Alaska's Central Arctic Caribou Herd (CAH) did not respond to early summer forage biomass or summer insect severity from the previous year. Abiotic factors that did have apparent effects on CAH productivity included early fall snow deposition, winter snow condition, and spring snow ablation. To achieve a suitable weight for conception, caribou of the CAH may exhibit a seasonal time-minimizing foraging strategy by moderating weight gain during the warm summer insect season and feeding more intensively during the insect-free weeks before the autumn rut. A long-term trend of the Northern Hemisphere annular mode (NAM) may be linked to anthropogenic climate change and may have negative implications for the future success of the CAH.

Key words: climate change, foraging strategy, insect harassment, NAM, *Rangifer*, snow.

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Introduction

Many biotic and abiotic factors can limit caribou populations, but limiting factors generally vary by region and herd (Klein, 1991). However, some generalizations have been made. Northern caribou are often thought to be limited by densities and winter weather, as they affect forage availability (Bergerud, 1983; Ferguson, 1996; Valkenburg *et al.*, 1996). This may not be true at lower latitudes (*e.g.*, lat 57°N; Bergerud & Page, 1987). Severe winter weather in western and interior Alaska can reduce calf fitness and early survival (Adams *et al.*, 1995; Finstad & Prichard, 2000; Adams, 2003). Persistent spring snow delays plant emergence, which can negatively affect maternal condition at the end of gestation and concomitant neonate survival (Verme, 1977; Roffe, 1993; Post & Klein, 1999).

In considering population dynamics of the Alaskan Central Arctic Caribou Herd (CAH), researchers have primarily focused on summertime effects on net productivity (*i.e.*, the product of calf production and early survival). Wolfe (2000) suggested that early-summer forage biomass, determined by satellite imagery (see Tucker & Sellars 1986) and estimated at a landscape-level by the Normalized Difference Vegetation Index on 21 June (NDVI_621), could affect reproductive success of CAH cow caribou. Typically from late-June through mid-August when environmental conditions are suitable, insect harassment dominates movements of the CAH, potentially

Table 1. Estimates of Central Arctic Herd (CAH) net productivity ~1 week after the peak of calving (# calves:100 cows), summer insect severity (# harassment days from 15 June–15 August), NDVI_621 from the entire CAH calving grounds, NAM winter index, early fall snow from 15 August–30 September (cm), the first day of zero snow depth in the spring (FDZSD), and the number of days from the first one inch of lasting snow from the previous fall through FDZSD, 1977–2002.

Year	CAH Prod.[1]	Insect Index[2]	NDVI_621[3]	NAM Winter Index[4]	Early Fall Snow[5]	FDZSD	Snow Duration
1977					16.95		
1978	81			-0.577	4.50	11-Jun	246
1979	85			-0.569	6.53	10-May	226
1980	70			-0.514	17.45	10-Jun	254
1981	83		0.24	-0.514	16.69	1-Jun	252
1982	69			0.203	5.01	12-Jun	272
1983	91			-0.021	6.35	31-May	252
1984	89			-0.428	0.00	27-May	233
1985	88		0.15	-0.594	23.37	21-May	221
1986	56		0.09	-0.767	3.56	14-Jun	279
1987	74	12	0.13	-0.499	4.32	8-Jun	254
1988	66	17	0.21	-0.438	30.48	18-Jun	245
1989	48	36	0.20	1.552	0.00	17-Jun	270
1990	75	26	0.27	1.444	7.62	24-May	219
1991		12	0.18	0.275	7.11	3-Jun	255
1992	73	17	0.09	0.672	33.27	30-May	235
1993	49	28	0.13	1.059	9.14	7-Jun	265
1994	65	45	0.23	0.309	19.56	17-Jun	263
1995	56	17	0.23	0.563	0.25	8-Jun	253
1996	87	18		-1.149	18.29	27-May	228
1997	72	16		0.210	9.65	15-Jun	276
1998	80	21		-0.548	0.51	28-May	239
1999	78	20		-0.119	20.07	17-Jun	255
2000	77	18		0.545	3.30	15-Jun	264
2001	79	11		-1.050	4.83	10-Jun	253
2002	76			0.639		18-May	231

[1] 1978-1990: Fancy *et al.* (1992); 1992, 1994, and 1997: Lenart (1999); 1993, 1995, 1996, 1998-2002: Lawhead & Prichard (2003). No comparable data available for 1991 (Lenart, 1999).

[2] Index based on criteria from Walsh *et al.* (1992). Data from Kane & Hinzman (2003).

[3] Data from Wolfe (2000).

[4] Data from the NOAA National Weather Service Climate Prediction Center (Camp Springs, Maryland, USA).

[5] Snow parameters from 1983-2002 recorded at the NOAA weather station at Kuparuk, Alaska and made available by the National Climatic Data Center (Asheville, North Carolina, USA). Snow parameters from 1978-1982 recorded at Umiat, Alaska and made available by the Western Regional Climate Center (Reno, Nevada, USA); to standardize the dataset, these data were adjusted by mean differences with Kuparuk data from overlapping years (n = 18).

causing negative daily energy balances in lactating females (White *et al.*, 1975; Fancy, 1986). Thus, it has been largely assumed that summer stress can hinder female weight gain and consequently, successful conception during the fall rut (Cameron *et al.*, 1993; Cameron, 1994; Cameron *et al.*, 2002; National Research Council [NRC], 2003). NRC (2003) used 3-yr moving averages of the response and predictor variables to suggest that CAH net productivity was negatively affected by increasing number of days of high insect activity during July of the previous year.

There are advantages and disadvantages to using

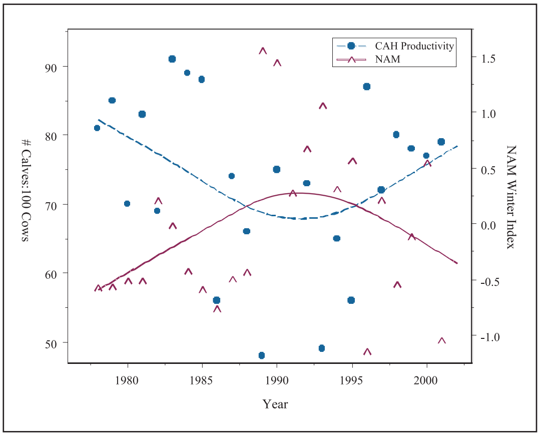

Fig. 1. Spline-smoothed trends of net productivity of the Central Arctic Herd estimated ~1 week after the peak of calving (Fancy *et al.*, 1992; Lenart, 1999; Lawhead & Prichard, 2003) and the Northern Hemisphere annular mode (NAM) averaged winter monthly means from November through April obtained from the NOAA National Weather Service Climate Prediction Center (Camp Springs, Maryland, USA), 1978–2001.

climate indices for ecological studies (reviews by Weladji *et al.*, 2002; Stenseth *et al.*, 2003), but modes of atmospheric variability have previously been shown to affect ungulate population dynamics in the Arctic (Post & Stenseth, 1999; Aanes *et al.*, 2002; Forchhammer *et al.*, 2002). Trends in net calf production of the CAH from, 1978–2001 appeared negatively correlated with a recent bi-decadal oscillation of the wintertime Northern Hemisphere annular mode (NAM) of sea-level atmospheric pressure deviations (Fig. 1). During its positive, high-index phase, the NAM may bring low atmospheric pressure and relatively warm and wet weather to northern Alaska from the Aleutian Low pressure system (Stone *et al.*, 2002; Wallace & Thompson, 2002); winter rain or snowmelt can effectively reduce forage availability to northern ungulates (Miller *et al.*, 1982).

To assess suggestions that early summer forage abundance and summer insect harassment affected CAH net productivity, we directly compared annual estimates of NDVI_621 and a summer insect severity index to CAH net productivity in the following year. Using best available data, we also assessed abiotic factors potentially limiting CAH net productivity. We believe that the NAM winter index may reflect snow condition on the winter range of the CAH. Identifying limiting factors may give some indication of the relative importance of seasonal determinants of herd productivity.

Material and methods

To assess limiting factors of CAH net productivity, we used the following resources. Productivity data were taken from Fancy *et al.* (1992), Lenart (1999), and Lawhead & Prichard (2003; see Table 1). These sources provided the largest sample sizes available based on aerial composition surveys about 1 week after the peak of calving, yielding some measure of early calf survival; most calf mortality can be expected to occur within 2 days of birth (Whitten *et al.*, 1992). We used the estimates of green forage biomass from the entire calving area on 21 June, NDVI_621, presented by Wolfe (2000); of the 3 sets of values that Wolfe (2000) presented for various regions of the CAH calving grounds, these corresponded best to productivity data presented by Fancy *et al.* (1992). For snow, spring rain, and winter temperature parameters, we used data from weather stations located at Kuparuk (1983–2002) and Umiat (1978–1982), Alaska, obtained from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (Asheville, North Carolina, USA) and the Western Regional Climate Center (Reno, Nevada, USA), respectively. Data from Umiat were standardized to those of Kuparuk by offsetting mean differences from overlapping years (n = 18). Data used to generate a NAM winter index from monthly means (Nov. –April) were obtained from the NOAA National Weather Service Climate Prediction Center (Camp Springs, Maryland, USA). To generate a summer insect severity index (1987–2001), we applied criteria from Walsh *et al.* (1992) to temperature and wind speed data collected in the Sagavanirktok River floodplain at Franklin Bluffs and made available by Kane & Hinzman (2003). We examined statistical relationships with regression techniques based on normal theory (Zar, 1999; Neter *et al.*, 1996) using S-PLUS 6 for Windows® (Insightful Corporation, Seattle, Washington, USA).

Results and discussion

Summer insect activity and NDVI_621 had no apparent effect on CAH net productivity the following year (Fig. 2). Other factors that we considered resulting in undetected effects included rain during the calving period and winter temperatures. Snow parameters were all statistically significant and inversely related to CAH productivity (Fig. 2). We entered significant parameters into a full stepwise regression. The selected model with interaction terms produced spurious partial coefficients, so we tested main effects only. Multicollinearity precluded snow duration from the selected model (Table 2).

The model residuals summed to 1.34 and were near normal with a slight negative bias and right-skew. The model tended to predict away from the extremes (*i.e.*, high during years of low observed productivity and low during years of high productivity; Fig. 3). However, examination of residuals against predictive variables indicated that no single variable caused undue influence to the selected model, suggesting that the linear model was appropriate although it was conceivable that any single variable may have exerted influence in a nonlinear fashion. Also, examination of factors yielding undetected effects during initial simple linear regressions (Fig. 2) and omitted from the final stepwise model to maximize sample size indicated no consistent explanation of variance in the final model.

Of the biotic and abiotic parameters we tested, abiotic fall, winter, and spring related stressors were the primary limiting factors of net productivity in the CAH over the past 25 years (Table 2). However, summer insect harassment may affect weight gain of early survivors and subsequent winter recruitment (Helle & Tarvainen, 1984), although forage availability in autumn may play a significant role as well (Gaillard *et al.*, 1993). Variability in juvenile survival is an important factor influencing population dynamics of large ungulates (reviews by Gaillard *et al.*, 1998, 2000). Data for winter recruitment were not available for examination as a response variable in this study, but this facet of juvenile survival could play a role in the population dynamics of north Alaskan caribou. Also, future summer stressors could have greater influence on caribou productivity if parasitic insect seasons become longer in duration along with the vegetative growing season (see Myneni *et al.*, 1997, Keyser *et al.*, 2000) and intraspecific competition increases along with abundance of the CAH (*i.e.*,

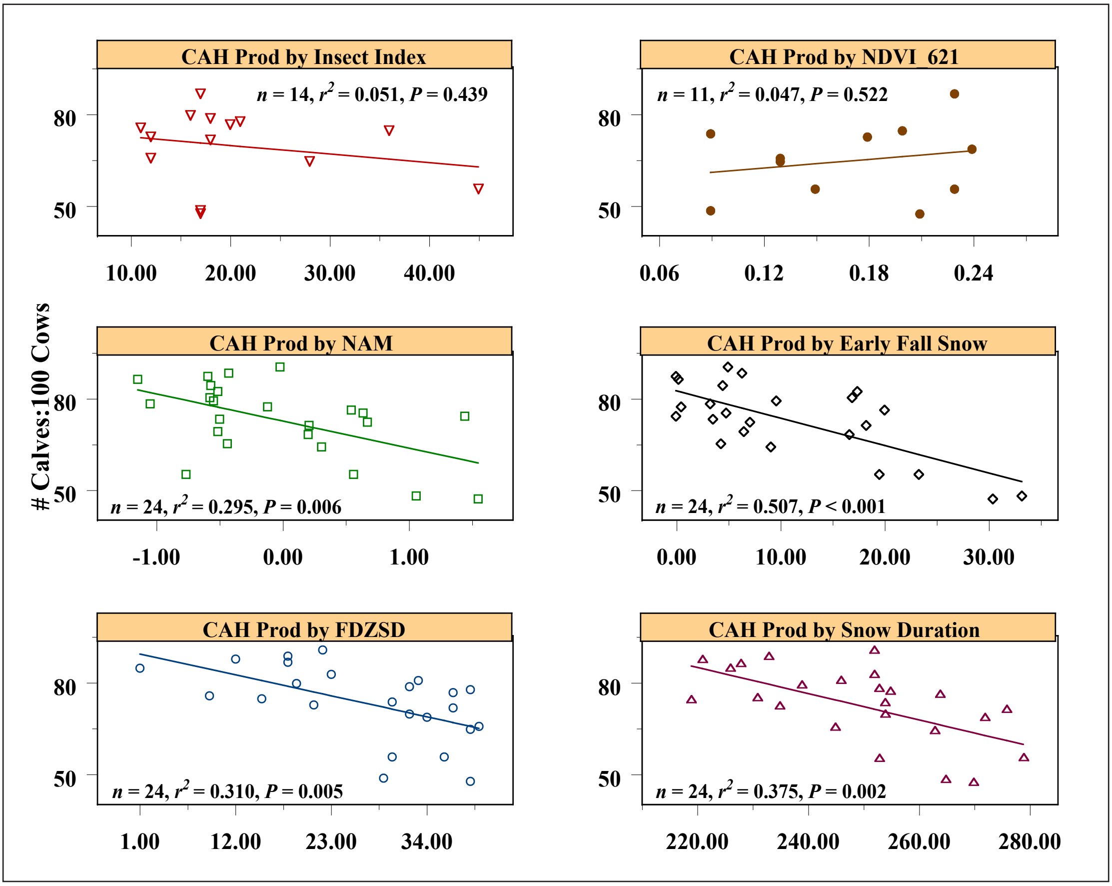

Fig. 2. Potential limiting factors of net productivity in the Central Arctic Herd as estimated ~1 week after the peak of calving, including a summer insect severity index from the previous year (# harassment days from 15 June–15 August), NDVI_621 from the previous year, NAM winter (Nov.–April) index, early fall (15 Aug.–30 Sept.) snow deposition (cm) from the previous year, first day of zero snow depth in the spring (FDZSD; 10 May = 1), and snow duration from the previous fall to spring (no. days), 1977–2002.

Table 2. Full stepwise regression results predicting Central Arctic Herd net productivity estimated ~1 week after the peak of calving based on the NAM winter index prior to calving, snowfall (cm) from 15 August–30 September of the previous year, and the first day of zero snow depth in the spring (FDZSD; 10 May = 1), 1977–2002.

Variable	Coefficient	Std. Error	t	*P*	Partial r^2
Intercept	89.15	4.21	21.20	<0.0001	
NAM Winter Index	-5.31	2.34	-2.27	0.035	0.070
Early Fall Snow	-0.53	0.20	-2.63	0.016	0.507
FDZSD	-0.37	0.16	-2.26	0.035	0.086

Selected model: F = 13.14 w/ 3 and 20 df, $R^2 = 0.6633$, $P < 0.0001$

~5000 caribou in, 1975 to ~32 000 in, 2002; Cameron & Whitten, 1979; Lenart, 2002).

Russell *et al.* (2000) found that non-lactating female summer weight gain in the CAH was inversely related to July body weight, suggesting that cows "targeted" a specific fall weight. The relationship was less significant for lactating cows, which was understandable given maternal demands. Similarly, Kojola (1993) reported that weight gain from post-calving through November in reindeer of Finland was greatest for those females experiencing heavy weight loss during the previous winter. Colman *et al.* (2003) found that Norwegian reindeer did not feed more at night to compensate for reduced feeding during diurnal periods of insect harassment. Our results along with those above suggest an emerging picture of cow caribou response to summer stresses. Currently, the summer period may not be critical for successful reproduction in the CAH. Instead, adult female caribou may exhibit a seasonal time-minimizing foraging strategy (Schoener, 1971; review by Kie, 1999) by moderating weight gain during the warm summer insect season, relying on the freedom to forage *ad libitum* between the insect season and rut (~6 weeks) to achieve a suitable weight for successful conception. Roby (1978:36) reported a seasonal increase in feeding activity by CAH caribou during the August–October pre-rut period. Forage quality is generally reduced as the growing season progresses (Whitten & Cameron, 1980), but delayed phenology of plants in wet areas near roads, lakes, and other impoundments may provide ample forage of suitable quality for caribou late in the season. Our results suggest that if snow limits availability of forage during this time period then productivity the following spring suffers (Fig. 2). Also, a recent study of domestic sheep found that modest undernutrition near the time of conception caused accelerated maturation of the fetal adrenal gland resulting in preterm births and sickly neonates (Bloomfield *et al.*, 2003; Miller, 2003). Our results concurred with previous studies (*see Introduction*) that found snow conditions in winter during gestation and the timing of spring snowmelt during early lactation affected caribou productivity, probably via neonate survival.

Colman *et al.* (2003) reported that carcass weights of females ≥2 yrs-old taken during the hunting season (20 Aug–14 Sep) were about 1.2 kg (4%) heavier following a summer of little insect harassment compared to weights sampled after a summer of greater harassment. However, reindeer sampled in that study were harvested 2–14 weeks prior to breeding (mid-rut around 10–12 Oct.; Jonathan Colman, University of Oslo, 2004, pers. comm.), thereby precluding further potential weight gain after the insect season and prior to general date of conception.

Ecosystem effects due to a rapidly changing arctic climate are not easily predicted but are becoming more prevalent (Chapin *et al.*, 1992; IPCC, 2001; Comiso, 2002; Overland *et al.*, 2002). Over the past 35 years, the NAM has had an overall trend toward its high-index polarity (Wallace & Thompson, 2002; John Wallace, University of Washington, 2003, pers. comm.), partially the result of anthropogenic greenhouse-gas forcing and polar ozone depletion (Shindell *et al.*, 1999, 2001). This trend may continue

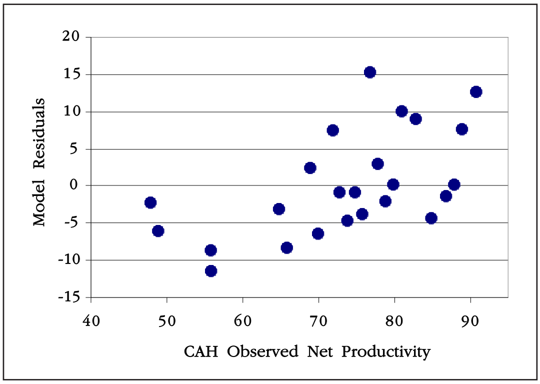

Fig. 3. Residuals (observed minus predicted values) of the final model selected by full stepwise procedures using a NAM Winter Index, Early Fall Snow from the previous year, and first day of zero snow depth in spring to predict net productivity (# calves:100 cows) observed during aerial surveys ~1 week after the peak of calving within the calving grounds of the Central Arctic Herd of Alaska, 1977–2002.

(Pitari *et al.*, 2002), having implications for northern ecosystems and associated flora and fauna, such as caribou and their habitats. If the observed negative correlation between the NAM and CAH net productivity continues, then future productivity of the CAH may become relatively depressed. Similar to other studies (Aanes *et al.*, 2003; Garrott *et al.*, 2003), our results suggested that the population declines observed in the CAH and adjacent Teshekpuk Lake Caribou Herd during the early–mid 1990s (Lenart, 1999) may have been due to local stochastic abiotic influences on net productivity, and perhaps winter recruitment, rather than summer insect harassment or early-summer forage availability.

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