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Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations

Kyle Joly, David R. Klein, David L. Verbyla, T. Scott Rupp and F. Stuart Chapin III

K. Joly (Kyle_Joly@nps.gov), National Park Service, Gates of the Arctic National Park and Preserve, and Arctic Network Inventory and Monitoring Program, Fairbanks, AK 99709, USA. – D. R. Klein and F. S. Chapin III, Univ. of Alaska Fairbanks, Inst. of Arctic Biology, Fairbanks, AK 99775, USA. – D. L. Verbyla and T. S. Rupp, Univ. of Alaska Fairbanks, School of Natural Resources and Agricultural Sciences, Fairbanks, AK 99775, USA.

Recent research has linked climate warming to global declines in caribou and reindeer (both *Rangifer tarandus*) populations. We hypothesize large-scale climate patterns are a contributing factor explaining why these declines are not universal. To test our hypothesis for such relationships among Alaska caribou herds, we calculated the population growth rate and percent change of four arctic herds using existing population estimates, and explored associations with indices of the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO). The AO, which more strongly affects eastern Alaska, was negatively associated with the population trends of the Porcupine Caribou Herd and Central Arctic Herd, the easternmost of the herds. We hypothesize that either increased snowfall or suboptimal growing conditions for summer forage plants could explain this negative relationship. Intensity of the PDO, which has greatest effects in western Alaska, was negatively associated with the growth rate of the Teshekpuk Caribou Herd in northwestern Alaska, but the Western Arctic Herd in western Alaska displayed the opposite trend. We suggest that the contrasting patterns of association relate to the spatial variability of the effects of the PDO on western and northwestern Alaska. Although predation and winter range quality have often been considered the primary causes of population variation, our results show that large-scale climate patterns may play an important role in caribou population dynamics in arctic Alaska. Our findings reveal that climate warming has not acted uniformly to reduce caribou populations globally. Further research should focus on the relative importance of mechanisms by which climate indices influence caribou population dynamics.

Climate warming has been implicated in declines of caribou and reindeer (both *Rangifer tarandus*) populations across the northern hemisphere (Post et al. 2009, Vors and Boyce 2009). However, these declines were not universal. The causes of population variation in arctic ungulate populations are complex. Population trajectories are thought to respond to summer range condition (Manseau et al. 1996), winter range condition (Klein 1968, 1970, Parker et al. 2005), predation rates (Bergerud 1980), snow conditions (Griffith et al. 2002, Dau 2005), disturbance/development (Johnson et al. 2005, Vors and Boyce 2009), disease, parasites, and insect harassment (Pederson et al. 2007, Hughes et al. 2009), stochastic events (Hummel and Ray 2008), density-dependent forage reduction (Messier et al. 1988, Couturier et al. 2009a), and climate change (Vors and Boyce 2009). Many of these factors are interrelated; for example, deep or ice-crusted snow can reduce availability of terricolous (ground-dwelling) lichens (Collins and Smith 1991), a staple winter food for large herds of barren-ground caribou (Russell et al. 1993, Joly et al. 2007b) and increase their vulnerability to predators (Telfer and Kelsall 1984). Climate, however, is a primary driver that could influence all of these factors.

We hypothesize that climate change will not impact *Rangifer* populations uniformly due to the complex dynamics and condition of the climate system. Long-lasting, large-scale climate patterns affect different geographic regions differently, often in an opposing manner. Several indices have been developed to quantify the intensity of large-scale climate patterns, including the North Atlantic Oscillation (NAO), Arctic Oscillation (AO), and the Pacific Decadal Oscillation (PDO). All of these indices in turn have been associated with the population dynamics of Arctic ungulates; changes in caribou and muskox *Ovibos moschatus* populations in Greenland (Post and Stenseth 1999, Post and Forchhammer 2002) and caribou calf body mass in northeastern Canada (Couturier et al. 2009b) have been tied to the NAO, while the AO has been linked to reindeer population dynamics in Svalbard (Aanes et al. 2002) and caribou population dynamics in the Northwest Territories, Canada (Zalatan 2008), and the PDO to elk population growth rates (Hebblewhite 2005) and caribou calf recruitment in the Yukon Territories, Canada, and interior Alaska (Hegel et al. 2010). The mechanisms by which these climate patterns might affect ungulate population trajectories include changes in forage availability, predation rates, calf recruitment, body condition, and/or reproductive performance due to deep snow conditions, rain-on-snow and icing events or altered forage quality due to delayed snow melt and phenology. Understanding how the different climate patterns affect summer and winter environment is critical to determining which to use in analyses (Forchhammer and Post 2004).

The NAO, AO, and PDO indices are fundamentally similar in that each gauges differences in oceanic temperatures and sea-level pressure (Hurrell 1995, Mantua et al. 1997, Thompson and Wallace 1998). Each index can be divided into two phases; "positive" or "negative", whose effects depend on geographical location. The effects of the NAO are most substantial in Europe and eastern North America (Hurrell 1995). The AO has stronger effects in the Arctic, especially northeastern Canada, and to a lesser degree in northwestern Canada and Alaska (Thompson and Wallace 1998, Rigor et al. 2000). The effects of the PDO are strong in the Pacific Northwest region of the continental US and British Columbia, but also affect the interior and western regions of Alaska (Hartmann and Wendler 2005). The PDO can have secondary effects in tropical regions, thus acting in a similar but opposite manner to its more widely known counterpart, the El Niño-Southern Oscillation (ENSO). Unlike the short-lived ENSO, the AO and PDO can remain in one phase for years to decades (Mantua et al. 1997, Hartmann and Wendler 2005).

The positive (also known as "high" or "warm") phase of the AO and PDO occurs with low sea-level pressure and is associated with warmer temperatures and wetter conditions in the north (Table 1; Thompson and Wallace 1998, Thompson et al. 2000, Hartmann and Wendler 2005). The negative ("low" or "cool") phase of the AO and PDO typically ushers in cooler, drier conditions. However, there is pronounced seasonal and regional variation (Post and Stenseth 1999, Hartmann and Wendler 2005). For example, the 1976 shift to the positive phase of the PDO ushered in warmer and wetter conditions in western and interior Alaska, but total precipitation and snowfall declined in arctic Alaska (Hartmann and Wendler 2005). Similarly, while the positive phase of the AO is associated with warmer, wetter conditions during winter, summer months tend to be cooler and cloudier (Thompson et al. 2000, Aanes et al. 2002). This is different from the PDO in which decreased summer cloudiness allowed for warmer summer temperatures. Increased cloudiness during winter, associated with positive phases, has led to warmer temperatures because solar radiation is weak but the clouds trap thermal radiation (Hartmann and Wendler 2005). It is unclear how climate change may affect the duration and intensity of these climate patterns.

Our objective is to determine whether large-scale climate indices could account statistically for the asynchronous caribou population trajectories in Alaska. We predict that the intensity of large-scale climate patterns will help explain why caribou populations are not universally declining due to climate warming. If we are correct, we would expect to see significant associations between the AO and PDO climate indices and the growth rates of caribou populations. The AO should show stronger associations with more easterly populations and the PDO with populations further west.

Study area

Arctic Alaska is home to the calving grounds of four caribou herds (Fig. 1); the Porcupine Caribou Herd (PCH), Central Arctic Herd (CAH), Teshekpuk Caribou Herd (TCH) and Western Arctic Herd (WAH). Size varies dramatically among herds and over time (Table 2); the WAH reached 490 000 individuals in 2003, whereas the CAH was thought to be just 5000 caribou in 1978 (Dau 2007, Lenart 2007b). The population trajectories of the herds also appear to be asynchronous: the CAH and TCH have increased over the past few years, in contrast to the global trend (Hummel and Ray 2008, Vors and Boyce 2009), whereas the WAH and PCH have declined.

The annual range of these herds covers all of western and northern Alaska and the northern portion of the Yukon Territories, Canada (Fig. 1). This vast area (ca 500 000 km^2, 63°–71°N, 134°–166°W) spans numerous ecoregions (Nowacki et al. 2001). North of the Brooks Range, where all of these herds calve (Carroll 2007, Dau 2007, Lenart 2007a, b, Person et al. 2007), is treeless tundra and sparsely vegetated foothills. The more southerly and interior portions of the range lie in a tundra-boreal forest ecotone where low-density white spruce *Picea glauca* and black spruce *P. mariana* stands are interspersed in patterns that depend on elevation, slope, exposure, and soil moisture (Chapin et al. 2006).

Table 1. Summary of the general effects of the positive (+) and negative (−) phases of two large-scale climate regimes, the Arctic Oscillation (AO) and Pacific Decadal Oscillation (PDO), on different regions of arctic Alaska. "+" symbolizes increases associated with this phase and "−" denotes decreases (Thompson and Wallace 1998, Hartmann and Wendler 2005).

Variable	Eastern Alaska		Western Alaska		Northwestern Alaska	
	+ AO	− AO	+ PDO	− PDO	+ PDO	− PDO
Sea-level pressure	−	+	−	+	−	+
Temperature (winter)	+	−	+	−	+	−
Temperature (summer)	−	+	+	−	+	−
Annual Precipitation	+	−	+	−	−	+
Snowfall	+	−	+	−	−	+
Cloudiness (winter)	+	−	+	−	+	−
Cloudiness (summer)	+	−	−	+	−	+

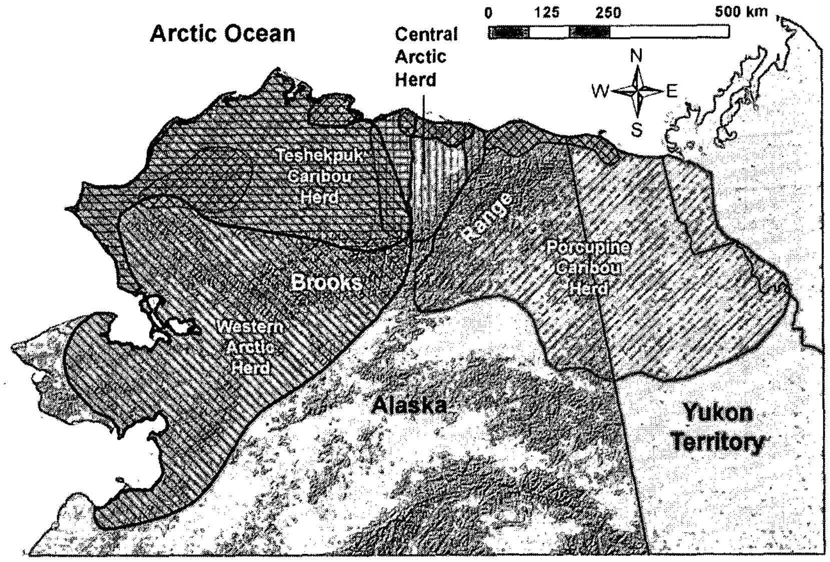

Figure 1. Annual (hatched) and calving areas (crosshatched) of Alaska's four arctic caribou populations. The Teshekpuk range is contained within the range of the Western Arctic Herd range. The calving area of the former is along the coast and the latter is inland and farthest west. Adapted from Griffith et al. 2002, Carroll 2007, Dau 2007, Lenart 2007a, 2007b, and Person et al. 2007.

The PCH, whose range straddles eastern Alaska and the Yukon Territory, is the easternmost herd that we analyzed. The herd grew from ca 100 000 caribou in 1972 to 178 000 in 1989 (Table 2; Lenart 2007a). Since that time, the herd gradually declined to 123 000 in 2001. The herd typically migrates around and through the Brooks Range to reach its winter range in the boreal forest of northern Yukon Territory and adjacent Alaska. The CAH, whose range lies just to the west and overlaps with the range of the PCH has grown from an estimated 5000 caribou in 1978 to ca 67 000 in 2008 (Table 2; Lenart 2007b, Alaska Dept of Fish and Game pers. comm.). The CAH overwinters primarily in the Brooks Range and its northern foothills. The TCH, which ranges further west, grew from ca 12 000 caribou in 1984 to ca 28 000 caribou in 1993 (Table 2; Carroll 2007). The herd then fluctuated around that number until 1999 after which it increased, reaching 64 000 caribou in 2008 (Alaska Dept of Fish and Game pers. comm.) despite a high subsistence harvest rate (Carroll 2007). The TCH, unlike the other three herds, often spends the entire year on the North Slope of Alaska, but its winter distribution is the least predictable. The WAH suffered a population crash in the early 1970s, bottoming out at 75 000 caribou in 1976 (Table 2; Dau 2007). The herd quickly rebounded and grew rapidly to 490 000 caribou in 2003 (Dau 2007). The most recent census revealed that the herd had declined to 377 000 in 2007. The herd typically migrates south to its winter ranges in the Nulato Hills and Seward Peninsula in western Alaska (Dau 2007, Joly et al. 2007a, 2007b).

Methods

We utilized the monthly values of the PDO index provided by the Univ. of Washington's Joint Inst. for the Study of the Atmosphere and Ocean (<http://jisao.washington.edu/pdo/>, accessed 6 October 2009) for 1970 through 2008. We also retrieved National Weather Service data for the AO (<www.cpc.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html>, accessed 6 October 2009), which had data from 1950 to 2008. We averaged the intensity values of each month to develop a single annual signal for both the PDO and AO for each year for which we had population estimates. Intensity values further from 0 indicate stronger pattern signals. We also analyzed winter seasonal averages (January–March).

The size of various Arctic caribou herds has been estimated periodically by the Alaska Dept of Fish and Game (ADFG), typically using a photocensus technique (Davis et al. 1979). This minimum count technique entails taking aerial photographs of the herds during peak insect harassment, when the herds are most tightly aggregated, and counting each and every individual caribou. Groups are located using radiotelemetry and visual observation. Corrections (adding caribou to the count) are made for radiocollars that were not detected during the census operations. For the WAH, estimates began in 1970 (Table 2; Dau 2007), but later for the PCH (1972; Lenart 2007a), CAH (1978; Lenart 2007b) and TCH (1984; Carroll 2007). The most recent census data for the WAH was from 2007, 2008 for the TCH and CAH, and 2001 for the PCH.

We calculated the population growth rate λ (also called the finite rate of change) in each of the herd's population trajectory using the following equation: $\lambda = \text{PE time}_2/\text{PE time}_1$, where PE is the photocensus population estimate. For this analysis we assumed that λ was constant in all of the intervening years between population estimates as census estimates were not available every year. This interpolation artificially inflates the power of these analyses. The 1999 census of the WAH was thought to be underestimated due to poor survey conditions (Dau 2007). Therefore, we analyzed the WAH data a second time excluding the 1999 census. We used linear regression to identify associations between climatic variables and the finite rate of change of the various caribou herds, utilizing a 1-yr time lag as identified by previous ungulate studies

Table 2. Population estimates based on Alaska Dept of Fish and Game aerial censuses of caribou in the Porcupine Caribou Herd (PCH), Central Arctic Herd (CAH), Teshekpuk Caribou Herd (TCH), and the Western Arctic Herd (WAH) from 1970 to 2008, Alaska (Carroll 2007, Dau 2007, Lenart 2007a, b). Values for the averaged annual intensities of the Arctic Oscillation (AO) and Pacific Decadal Oscillation (PDO) as well as their averaged winter (W; January–March) signatures are also presented (Joint Inst. for the Study of the Atmosphere and Ocean, National Weather Service; see Methods).

Year	WAH	TCH	CAH	PCH	AO	AO-W	PDO	PDO-W
1970	242000				−0.344	−1.940	−0.398	0.730
1971					0.006	−0.725	−1.291	−1.670
1972				99959	0.052	−0.057	−0.922	−1.857
1973					0.241	0.852	−0.804	−0.600
1974					−0.203	−0.334	−0.337	−1.023
1975					0.434	0.647	−1.102	−0.840
1976	75000				−0.031	0.759	0.008	−1.233
1977				105000	−0.432	−1.811	0.231	0.710
1978	107000		5000		−0.150	−0.953	0.236	1.360
1979				105683	−0.365	−1.248	0.335	−0.047
1980	138000				−0.643	−1.478	0.603	1.300
1981			8537		−0.435	−0.698	0.918	1.300
1982	172000			125174	0.298	0.388	0.114	0.067
1983			12905	135284	0.032	−0.338	1.648	1.707
1984		11822			−0.192	−0.595	0.838	1.500
1985		13406			−0.519	−1.232	0.449	0.567
1986	229000				0.085	−0.514	1.239	1.780
1987				165000	−0.544	−1.456	1.821	2.003
1988	343000				0.040	−0.333	0.532	1.200
1989		16649		178000	0.950	2.638	−0.179	−0.723
1990	416000				1.024	2.464	−0.356	−0.333
1991			19046		0.197	−0.227	−0.419	−0.980
1992			23444	160000	0.437	0.885	0.928	0.577
1993	450000	27686			0.079	1.481	1.417	0.720
1994				152000	0.532	0.244	−0.152	0.813
1995		26076	18100		−0.275	0.556	0.643	0.680
1996	463000				−0.456	−0.840	0.641	1.073
1997			19730		−0.040	0.841	1.461	0.660
1998				129000	−0.271	−0.839	0.246	1.613
1999		28627			0.113	−0.300	−1.063	−0.467
2000			27128		−0.046	0.632	−0.590	−0.063
2001				123000	−0.162	−1.089	−0.563	0.143
2002		45166	31857		0.072	1.196	0.221	−0.463
2003	490000				0.152	0.196	0.969	1.480
2004					−0.192	−0.965	0.345	0.553
2005					−0.375	−0.754	0.375	1.067
2006					0.138	−0.643	0.191	0.370
2007	377000				0.269	0.636	−0.196	−0.053
2008		64000	67000		0.177	0.781	−1.293	−1.000

(Aanes et al. 2002, Post and Forchhammer 2002). We used linear regression to identify an association between 30 yr of productivity (calves: 100 cows) data from the CAH (Lawhead and Prichard 2009) and the intensity of the AO. Similar data were not available for the other herds. Since we determined that the growth rate data were autocorrelated, we added an autoregressive term to the regression models and used Akaike's information criteria ($\mathrm{AIC_c}$) for small sample sizes to compare models with and without the autoregressive term (Burnham and Anderson 2002).

To obtain a dataset that did not artificially inflate the degrees of freedom through interpolation and was not autocorrelated, we also calculated the percent change (using the following equation: $100 \times [\mathrm{PE\ time_2} - \mathrm{PE\ time_1}]/\mathrm{PE\ time_1}$) in herd sizes between successive censuses and compared them to the average value of the oscillation index for the corresponding time period (i.e. Σ PDO time$_{1 \ldots 2}$/[time$_2$ − time$_1$]) and also using a 1-yr delayed time period. Density data are not available for any herd for the time periods we investigate here because it is difficult to estimate range use precisely in this vast and remote study area. We also gathered historical information about the population trends of the WAH dating back to the 1850s (Davis et al. 1980) to compare to historical trends in the PDO. We designated $p < 0.05$ as the critical significance level.

Results

Arctic Oscillation (AO)

For the PCH, the 1-yr lagged λ was significantly associated with the average annual value of the intensity of the AO (Table 3; $R^2 = 0.216$, $F = 7.42$, $DF = 28$, $p = 0.011$). Positive phase values of the AO (warm cloudy winters with high precipitation and cool cloudy summers) associated with herd decline ($\lambda < 1$). We identified this same trend for the CAH, but the relationship was not significant ($R^2 = 0.090$, $F = 2.77$, $DF = 23$, $p = 0.107$). The average annual intensity of the AO was not significantly associated with the population trajectories of either the TCH or the WAH (Table 3). The winter (January–March) seasonal signature of the AO had a significant negative association with λ for the PCH ($R^2 = 0.307$, $F = 11.98$, $DF = 28$,

Table 3. Linkages among the Arctic Oscillation (AO), Pacific Decadal Oscillation (PDO) and the population trends of Alaska's arctic caribou herds; Western Arctic Herd (WAH), Teshekpuk Caribou Herd (TCH), Central Arctic Herd (CAH) and Porcupine Caribou Herd (PCH). "Annual" intensities are averaged over the entire year while "winter" indices are averaged from January through March. "**" symbolize significant associations ($p < 0.05$) and "*" symbolize notable relationships ($p < 0.10$), while "+" and "−" denote positive and negative trends, respectively. Empty cells indicate non-significant ($p > 0.1$) regressions.

Methodology	Climate pattern	WAH	TCH	CAH	PCH
Population growth rate (λ)	AO (annual)				− **
Population growth rate (λ)	AO (winter)			− *	− **
Population growth rate (λ)	PDO (annual)	+ **	− **		
Population growth rate (λ)	PDO (winter)	+ **	− **		
Percent change	AO (annual)			− *	− *
Percent change	AO (winter)			− *	− **
Percent change	PDO (annual)	+ *	− *		
Percent change	PDO (winter)	+ **			

$p = 0.002$). This winter AO signal also showed a linkage with λ for the CAH ($R^2 = 0.124$, $F = 3.97$, $DF = 29$, $p = 0.056$), but not for the other 2 herds (Table 3). Models that included the autoregressive terms plus the AO were appropriate for both the PCH ($\Delta AIC_c = 0.00$) and CAH ($\Delta AIC_c = 0.67$).

The percent change in herd size between censuses (Table 3) showed linkages with the average AO intensity for the corresponding time period (delayed 1 yr) for both the PCH ($R^2 = 0.380$, $F = 4.90$, $DF = 9$, $p = 0.058$) and CAH ($R^2 = 0.370$, $F = 4.11$, $DF = 8$, $p = 0.082$). Similarly, percent change in herd size was also linked with the average AO winter intensity for CAH ($R^2 = 0.354$, $F = 3.83$, $DF = 8$, $p = 0.091$) and was significantly associated with the PCH ($R^2 = 0.477$, $F = 7.31$, $DF = 9$, $p = 0.027$). The average annual intensity of the AO was not significantly associated with the population trajectories of the TCH or the WAH (Table 3).

We found that the annual intensity of the AO had a significant (Fig. 2; $R^2 = 0.165$, $F = 5.73$, $DF = 30$, $p = 0.023$) negative relationship with CAH productivity (i.e. June calf:cow ratios). The winter seasonal signature also had a significant negative relationship with CAH productivity ($R^2 = 0.178$, $F = 6.26$, $DF = 30$, $p = 0.018$) and explained slightly more of the variance. CAH productivity had a significant positive association with λ ($R^2 = 0.264$, $F = 9.69$, $DF = 28$, $p = 0.004$). Similar productivity data were not available for the other herds. The negative relationship between the averaged annual intensities of the AO and PDO was not significant.

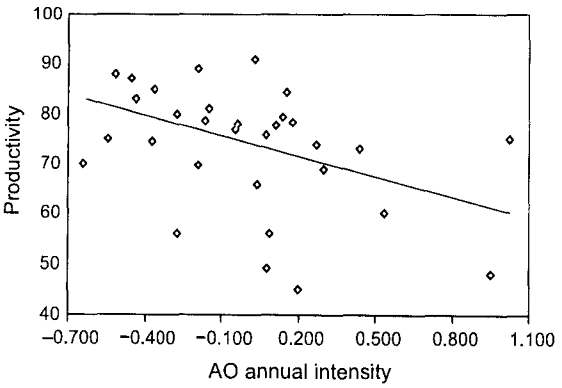

Figure 2. Significant ($R^2 = 0.165$, $F = 5.73$, $DF = 30$, $p = 0.023$) relationship between the productivity (number of calves per 100 cows in June) of the Central Arctic Herd (data from Lawhead and Prichard 2009) and the annual intensity of the Arctic Oscillation (AO), 1978–2008 (National Weather Service). The regression equation was $\text{Productivity} = 73.3 - 12.6 \times \text{AO}$.

In summary, AO intensity was negatively linked with measures of caribou population growth in eastern Alaska (the PCH and to a lesser degree the CAH), where the AO pattern was most pronounced, but was unrelated to herd dynamics in western and northwestern Alaska (WAH and TCH), where the AO pattern was weak.

Pacific Decadal Oscillation (PDO)

We determined that averaged values of the intensity of the PDO were significantly associated with 1-yr lagged λ for the TCH (Table 3; $R^2 = 0.306$, $F = 9.69$, $DF = 23$, $p = 0.005$) and WAH (Table 3; $R^2 = 0.325$, $F = 16.88$, $DF = 36$, $p = 0.002$). Positive annual phase values of the PDO associated with herd growth ($\lambda > 1$) for the WAH but with herd decline ($\lambda < 1$) in the TCH. The averaged annual intensity of the PDO was not significantly associated with population trajectories of the CAH or the PCH. The winter seasonal signature of the PDO was significantly but negatively associated with λ for the TCH ($R^2 = 0.223$, $F = 6.31$, $DF = 23$, $p = 0.020$) and positively with the WAH ($R^2 = 0.191$, $F = 8.27$, $DF = 36$, $p = 0.007$), but not for the other 2 herds. Models that excluded the 1999 WAH census results had greater explanatory power than those that used it, providing independent support for the suggestion that this census was biased low due to poor survey conditions. We found that models that included the autoregressive terms plus the PDO were appropriate for both the TCH ($\Delta AIC_c = 0.00$) and WAH ($\Delta AIC_c = 0.14$).

The percent change in herd size between censuses showed linkages with the annual average PDO intensity for the corresponding time period (delayed 1 yr) for both the TCH ($R^2 = 0.465$, $F = 4.34$, $DF = 6$, $p = 0.092$) and WAH (censuring the 1999 census; $R^2 = 0.296$, $F = 3.78$, $DF = 10$, $p = 0.084$). The trends were again negative for the TCH and positive for the WAH. Similarly, percent change in herd size was also significantly associated with the average PDO winter intensity for the WAH ($R^2 = 0.367$, $F = 5.23$, $DF = 10$, $p = 0.048$), but not the TCH. The best long-term historical records of any Arctic caribou herd in Alaska are found for the WAH. The cycles of the WAH roughly tracked those of the annual means of the PDO (Table 4).

Table 4. Trends of the population size of the Western Arctic Herd (WAH) and annual averages of the Pacific Decadal Oscillation (PDO) for different time period since 1850, western Alaska (Davis et al. 1980, Dau 2007, Joint Inst. for the Study of the Atmosphere and Ocean). The symbol "+" means either an increasing population trend or positive phase values of the PDO, while "−" signifies the opposite trends.

Time period	WAH trend	Time period	PDO trend
1850–1880	+	–1889	n/a
1880–1920	−	1890–1924	−
1920–1950	+	1925–1946	+
1950–1959	−	1947–1956	−
1960–1964	+	1957–1962	+
1964–1976	−	1963–1976	−
1977–2003	+	1977–2003	+

In summary, PDO intensity was significantly associated with measures of caribou population growth in western and northwestern Alaska (the WAH and TCH), where the PDO pattern was most pronounced but was unrelated to herd dynamics in eastern Alaska (PCH and CAH), where the PDO pattern was weak. Associations with annual and winter values of PDO were positive for WAH and negative for TCH.

Discussion

We documented consistent connections between large-scale climate regimes and the population trends of caribou populations in the Arctic. Our results add to the existing evidence of this nexus in other regions (Post and Stenseth 1999, Aanes et al. 2002, Forchhammer et al. 2002, Post and Forchhammer 2002, Hebblewhite 2005, Zalatan 2008). Our results represent, to our knowledge, the first time that these associations have been documented in Alaska. We believe that the linkages we identified represent authentic connections between caribou population dynamics and climate for six primary reasons. First, and most strikingly, the population growth rates for all four caribou herds we investigated were associated with either the AO or PDO. Second, we found the AO had significant associations only in eastern Alaska and the PDO only in western Alaska, consistent with the locations where these indices show the strongest correlation with local weather conditions (Rigor et al. 2000, Hartmann and Wendler 2005). Moreover, the AO showed a more pronounced influence on the PCH, which is the further east, than the CAH. Similarly, the PDO had stronger associations with the WAH, which is closer to the center of influence of the PDO, than the TCH. Weak correlation between some large-scale climate patterns and local weather has resulted in studies that did not identify linkages between *Rangifer* population dynamics and these patterns (i.e. Reimers et al. 2005). Third, the large, recent (2002–2008) increases in the CAH and TCH herds did not alter the significance or trend of the associations we detected. Fourth, both methodologies (i.e. utilizing λ and percent change) revealed statistically significant associations with identical trends. Fifth, CAH calf counts were associated with the AO (Fig. 2), which could provide a mechanism for the correlation between herd dynamics and climate (as productivity was associated with λ). This effect of large-scale pattern may have acted through reduced calf body condition (indexed by mass) as noted in other studies (Weladji and Holand 2003, Couturier et al. 2009b). Finally, WAH population trends have roughly mirrored the PDO for more than a century (Table 4).

The population trends for the PCH and the CAH were negatively associated with the intensity of the AO, consistent with the findings for *Rangifer* in Svalbard (Aanes et al. 2002) and the Northwest Territories (Zalatan 2008). The "active season" of the AO is January through March (Thompson et al. 2000), which we found to have the greater explanatory power than annual averages. Positive ("warm") phase values of the AO were associated with reduced population growth in these herds. Two plausible explanations for this association are readily apparent. First, the positive phase of the AO is associated with increased precipitation. Increased winter snowfall and snow depths could directly reduce forage availability (Collins and Smith 1991) or increase vulnerability to predation (Telfer and Kelsall 1984, Post and Stenseth 1998) and thus be detrimental to *Rangifer* populations (Aanes et al. 2000). Warmer winter temperatures would also increase the probability of icing events (Putkonen and Roe 2003) that could be detrimental to caribou populations (Griffith et al. 2002, Dau 2005) by making it difficult to access ground-dwelling forage. Other studies have shown that deep snow is related to decreased birth mass of caribou calves, postnatal development, and survival of caribou calves (Adams et al. 1995, Adams 2003, 2005, Couturier et al. 2009b). The second potential explanation is that in the positive AO phase (cloudy, cool, wet summer conditions) could retard vascular plant growth (Chapin et al. 1995, Post and Stenseth 1999, Aanes et al. 2002, Lenart et al. 2002). The indirect effects of sub-optimal plant growth on caribou include reduced reproductive performance (Adams and Dale 1998a) and delayed parturition (Adams and Dale 1998b). We found reduced productivity of the CAH associated with increasing AO intensity (Fig. 2; also see Griffith et al. 2002, Haskell and Ballard 2004). Cloudy summers, however, have also been associated with extending the early summer peak of high quality forage (Bø and Hjeljord 1991, Lenart et al. 2002). Increases in summer forage biomass, as measured by the Normalized Difference Vegetation Index (NDVI), have been linked to warmer summer temperatures associated with the positive phase of the AO (Griffith et al. 2002, Verbyla 2008) and increased caribou calf birth mass (Couturier et al. 2009b).

The negative association between population growth rates of the TCH with the positive ("warm") phase values of the PDO is the most nuanced association to interpret. Like the AO, the positive phase of the PDO is generally associated with warmer and wetter winter conditions (Hartmann and Wendler 2005). However, in northwestern Alaska, positive-phase values of the PDO are associated with reduced snowfall (unlike the rest of Alaska) and summer warming (unlike the AO; Table 1; Hartmann and Wendler 2005). These differences appear to contradict the arguments (i.e. increased snowfall and poor plant growth conditions) used above to explain the negative association in the PCH and CAH. Indeed, arctic tundra in Alaska has experienced significant greening during the most recent positive phase cycle of the PDO (Verbyla 2008). The increased prevalence of icing events due to associated warmer winters may explain the negative association (see above and Griffith et al. 2002).

The WAH winters primarily in western Alaska (Dau 2007, Joly et al. 2007a), where snowfall is positively correlated with positive phase values of the PDO, not northern Alaska where snowfall is negatively correlated (Hartmann and Wendler 2005). The population growth rates for the WAH, in contrast to the TCH, were positively associated with positive phase values of the PDO. The WAH summers at the confluence of the western and arctic regions of Alaska (Dau 2007). In both of these regions, positive phase values of the PDO are associated, during summer, with reduced cloudiness and increased temperatures while precipitation is not significantly affected. These conditions could lead to optimal growth conditions for vascular plants, of benefit to the herd in summer (Chapin et al. 1995, Lenart et al. 2002, Verbyla 2008), although similar conditions on the winter range can result in a decrease of lichens, an important component of the winter diet (Joly et al. 2009, Klein and Shulski 2009). Our results, however, suggest that the WAH could respond positively to optimal summer growth conditions despite winters with deeper snow and potentially more icing events. Doubtless, this is only true up to a certain point where winter conditions become so difficult that, no matter how good summer conditions are, the herd will not be able to rebound. The total length of the growing season does not appear to be increasing because of increased snowfall in autumn (Hartmann and Wendler 2005).

Large-scale climate oscillations have the potential to affect many important aspects of caribou ecology other than snow depth, icing, predation rates, and forage quantity and quality during both summer and winter. Climate oscillations affect the prevalence of wildfire (Duffy et al. 2005), and caribou tend to avoid recently burned sites in midwinter (Joly et al. 2007a). They affect the summer growing conditions of winter forage (e.g. lichens), which could influence population dynamics (Klein 1991, Cornelissen et al. 2001). Similarly, climate oscillations can affect the levels of insect harassment and infestations of parasitic flies and other potentially important influences on caribou ecology (Callaghan et al. 2004).

While we do not discount the importance of the negative influences exerted by directional changes in climate, such as changes in phenology, increased alternative prey availability, and extreme weather events on caribou and reindeer populations (Joly et al. 2009, Vors and Boyce 2009), large-scale climate oscillations may modulate these impacts. Our results suggest that large-scale, long-lasting climatic patterns, such as the AO and PDO, may have significant direct and indirect impacts on the population growth rates of arctic caribou herds in Alaska. We suggest that climatic variability should be taken into account when modeling caribou population dynamics. Additional, timely research will be critical because there are signs that the PDO may be shifting back to its negative phase (Hartmann and Wendler 2005), and numerous caribou populations are declining across the Arctic (Vors and Boyce 2009).

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