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Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore

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Summary

1. Climate is an important factor influencing the population dynamics of large herbivores operating directly on individuals or through its effect on forage characteristics. However, the seasonal effect of climate may differ between forage- and predator-limited populations because of a climatic influence on predation rates. The influence of climate on predator-limited large herbivores is less well known than on forage-limited populations. Further, the effect of Pacific-based climate on large herbivore populations has been rarely assessed.

2. We investigated the effect of the Pacific Decadal Oscillation (PDO), across different seasons, on recruitment in 10 populations (herds) of mountain-dwelling caribou *Rangifer tarandus caribou* L. in the Yukon Territory, Canada. These low-density populations occur in highly seasonal environments and are considered predator-limited with high neonatal calf mortality. Hence, in most years females do not spend resources through lactational support during the summer and resource intake is devoted to self-maintenance. We predicted that climate affecting environmental conditions at calving would have a strong effect on recruitment via its influence on predation rates. We also predicted that climatic conditions prior to conception could have an effect on recruitment through its influence on female fecundity. We modelled recruitment ($n = 165$) by seasonal PDO values using generalized linear mixed-effects models with herd-varying coefficients.

3. We found that recruitment variability was best explained by variation in winter climate ($\beta = 0{\cdot}110$, SE $= 0{\cdot}007$) prior to birth (*in utero*) and May climate ($\beta = 0{\cdot}013$, SE $= 0{\cdot}006$) at calving. There was little support for a pre-conception climate effect influencing female body condition and hence fecundity. These results confirm that recruitment in these populations is limited by predation and that forage-limitation is not a significant factor in their population dynamics. There was considerable variability in herd-specific relationships between the PDO and recruitment. Incorporating herd-specific characteristics, such as variable predator densities or terrain characteristics within a herd range, may shed greater light on the complex relationship between climate and ungulate population dynamics.

Key-words: calving, PDO, *Rangifer tarandus caribou*, snow, Yukon Territory

Introduction

The influence of climate on ungulate population dynamics and life-history traits is well documented in western Europe (e.g. Post & Stenseth 1999; Coulson *et al.* 2001; Mysterud *et al.* 2001) and eastern North America (e.g. Post & Stenseth 1998, 1999; Patterson & Power 2002; Vucetich & Peterson 2004) where the ecological effects of the North Atlantic Oscillation (NAO) are strong (Stenseth *et al.* 2002, 2003; Mysterud *et al.* 2003). Research on the influence of climate on ungulates in western North America is sparse (Griffith *et al.* 2002), and few studies have explicitly examined the role of Pacific-based climate (Hebblewhite 2005). Further, much of the research relating large-scale climate to large herbivore populations has been assessed on forage-limited populations with few or no natural predators. Climate influences herbivore population dynamics through its effect on forage characteristics (Forchhammer *et al.* 1998; Vucetich & Peterson

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2004); however, in predator-limited populations climate may also affect population dynamics through its effect on predation rates (Hebblewhite 2005). Here, we investigated the seasonal influence of climate on population recruitment patterns of northern mountain-dwelling caribou in the Yukon Territory (Yukon), Canada, using the Pacific Decadal Oscillation (PDO; Mantua *et al.* 1997) as a climate index.

Mountain-dwelling caribou populations in northwest North America are considered predator-limited (Gauthier & Theberge 1986; Hayes *et al.* 2003) and typically occur at low density. They are generally characterized by high pregnancy rates (Wittmer, Sinclair & McLellan 2005; Gustine *et al.* 2006), variable parturition rates (Adams & Dale 1998; Gustine *et al.* 2006), and low juvenile survival (Seip 1992; Hayes *et al.* 2003) in which predation on neonates is often the primary mortality source (Adams, Dale & Mech 1995a; Adams, Singer & Dale 1995b; Gustine *et al.* 2006). Density plays a weak role in the dynamics of these populations as predators keep numbers sufficiently low to limit density-dependent forces (Crête 1999; Wang *et al.* 2009). Recruitment (i.e. the joint contribution of fecundity and calf survival), indexed here by the fall calf : cow ratio, is highly variable and often $< 0·3$ (Hayes *et al.* 2003). Age ratios such as this are effective at tracking population growth rates and trajectories (Harris, Kauffman & Mills 2008), yet the role of climate on recruitment in these populations is currently not well understood.

Mechanistically, climate may be related to recruitment through its influence on fecundity and/or calf survival (Table 1). We hypothesized (H1) that because of high neonatal calf losses from predation, seasonal climate during winter preceding birth (*in utero*) and in springtime should have a strong influence on recruitment through its effect on snow depth during the neonatal period.

Due to high neonate losses, the majority of females are unburdened of providing energetic resources to offspring, thus allowing them to allocate all acquired resources to self-maintenance. However, given the highly seasonal conditions in the Yukon, female fecundity may be influenced by pre-conception climate (Table 1) as a result of an insufficient time window to restore body reserves prior to breeding, resulting in a stronger influence of these climate conditions (H2). H1 and H2 are not mutually exclusive.

Materials and methods

STUDY POPULATIONS

Recruitment data are from 10 northern mountain caribou herds (i.e. populations; Fig. 1), representing nearly half of the 22 herds residing

Table 1. Potential mechanisms relating seasonal climate to fall recruitment in northern mountain-dwelling caribou through effects on fecundity (a) and calf survival (b)

Season[a]	Mechanism	Reference
(a) Fecundity		
Winter_{t-1}	Harsh conditions in the winter prior to conception may result in females being in sufficiently poor condition that they may be unable to regain adequate body mass to reproduce the subsequent year.	Adams & Dale (1998)
Summer_{t-1} Fall_{t-1}	Fecundity is strongly related to female body condition at breeding. Poor forage conditions prior to breeding may limit successful reproduction by females unable to obtain sufficient resources during summer and fall.	Cameron *et al.* (1993), Crête & Huot (1993), Cook *et al.* (2001, 2004)
(b) Calf survival		
Spring April May	Increased snow depth due to either cool temperatures and/or spring snowfall may prevent parturient females from moving up in elevation (i.e. dispersing) to calving sites away from predators.	Bergerud & Elliot (1986), Bergerud & Page (1987), Adams *et al.* (1995a,b)
June	Climatic conditions leading to poorer forage quality and/or quantity can result in reduced calf development and survival. Nutritional requirements at this time are high as it is the period of peak lactation.	Albon, Guinness & Clutton-Brock (1983), Griffith *et al.* (2002), Pettorelli *et al.* (2005, 2007)
Summer	Temperature may influence insect harassment levels thus affecting energetic demands, through avoidance behaviour, and subsequently calf growth and survival.	Helle & Tarvainen (1984)
	Climatic effects on summer forage conditions may influence calf growth and development.	Reimers *et al.* (1983), Crête & Huot (1993), Lenart *et al.* (2002)
Winter	Calf birth mass and development are negatively related to winter severity during gestation.	Adams *et al.* (1995a), Adams (2003, 2005)
	Increased snowfall that persists late into the spring may prevent parturient females from moving up in elevation away from predators.	Bergerud & Elliot (1986), Bergerud & Page (1987), Adams *et al.* (1995a,b)
Winter_{t-1} Fall_{t-1} Summer_{t-1}	Calf birth mass is positively correlated to maternal mass at breeding, which is subsequently influenced by climatic conditions prior to conception (see above).	Reimers *et al.* (1983), Adams (2005)

The subscript $t-1$ indicates a pre-conception season. Variables without a subscript represent seasons post-conception. We treated fall climate during breeding as occurring prior to conception. Based on PDO – local weather relationships (see Tables S1–S3) we expect the relationship between each season and recruitment to be non-negative.

[a] Seasons defined in the text (see Methods).

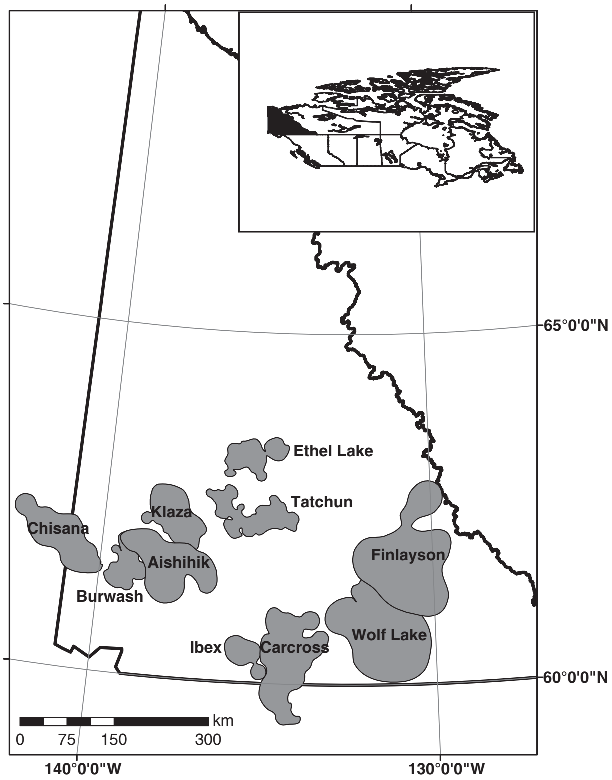

Fig. 1. Locations of ten mountain-dwelling woodland caribou herds in the Yukon Territory, Canada, in which seasonal effects of the PDO on calf recruitment were assessed.

at least partially in the Yukon (Farnell *et al.* 1998). They represent the northern mountain ecotype of woodland caribou in Canada (Thomas & Gray 2002) and are federally designated as a species of special concern under Canada's Species at Risk Act (COSEWIC 2002). Densities ranged from *c.* 0·03–0·20 individuals km^{-2} (Thomas & Gray 2002) and are much lower than those reported for forest-dwelling reindeer in, for instance, the mountainous regions of Norway with much fewer natural predators (e.g. 1·03–1·41 individuals km^{-2}: Reimers, Klein & Sørumgård 1983). All herds reside within relatively intact multi-predator (e.g. black bear *Ursus americanus* Pallus, grizzly bear *U. arctos* L., wolf *Canis lupus* L.), multi-prey (e.g. Dall sheep *Ovis dalli* Nelson, moose *Alces alces* L.) systems (Hayes *et al.* 2003). Mountain caribou are seasonal migrants moving relatively short distances between seasonal ranges. Terrain within herd ranges was mountainous with substantial topographic relief. Mean elevation varied from *c.* 1000 to 1500 m a.s.l. Herds were distributed in the southern portion of the Yukon (*c.* 60–63° N, 129–141° W) in the boreal cordillera ecozone (Marshall & Schut 1999) with highly seasonal sub-arctic climate characterized by long, cold winters and relatively short, mild summers.

CARIBOU RECRUITMENT DATA

Herds were aerially surveyed from a rotary aircraft to estimate recruitment from 1980 to 2007 as part of monitoring activities in the Yukon (Farnell *et al.* 1998). Following a standardized protocol, surveys occurred during the fall breeding season from the last week of September through mid-October. Groups of animals were classified and the ratio of total numbers of calves to cows used as an index of recruitment at the population (i.e. herd) level. Calves were identified by their small size and females distinguished from immature males by the presence of a black vulva patch. During breeding, animals aggregate on high alpine plateaus devoid of trees, thus making sightability of animals, particularly calves, much greater than in forested habitats. A comparison of calf : cow ratios based on aerial survey data, as used here, with temporally concurrent calf : cow ratios based on sampled adult females, captured for radiocollaring, indicated no significant difference (T. Hegel, unpublished data). Data on recruitment rates represented 165 herd-years from 10 herds during the period 1980–2007 (Fig. 2). The total number of annual recruitment rates estimated per herd ranged from 9 to 26. The average number of animals classified to estimate an annual recruitment rate, across all herds and years, was 516·9 (SE = 42·5).

POPULATION RECOVERY ACTIVITIES

A number of management programmes aimed at increasing low population sizes have occurred in the Yukon (Farnell *et al.* 1998). During 1983–1989, wolves were annually removed from the Finlayson herd range (Fig. 1) to < 20% of pre-removal numbers (Farnell &

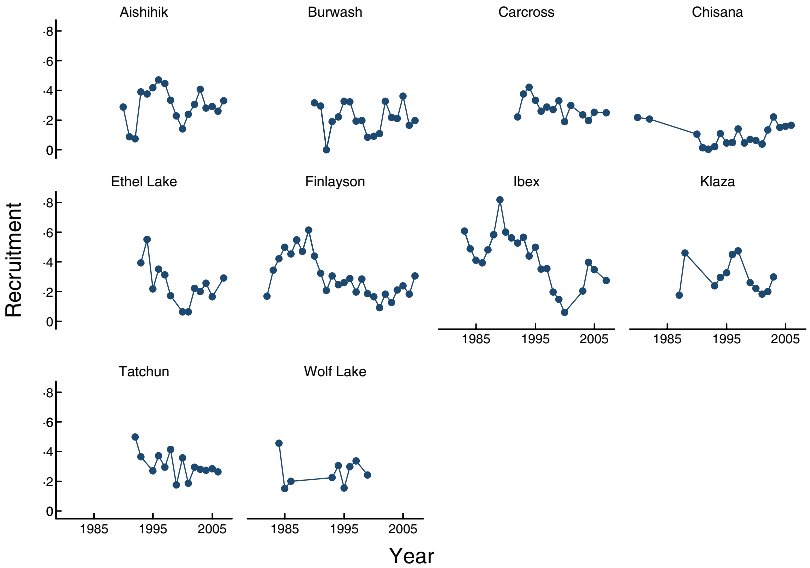

Fig. 2. Annual recruitment rates (calf : cow ratio) for ten mountain-dwelling caribou herds in the Yukon Territory, Canada (1980–2007).

McDonald 1987; Hayes & Harestad 2000). During 1993–1997, a wolf removal and sterilization programme occurred in the Aishihik herd range, with some actions overlapping onto the ranges of the adjacent Burwash and Klaza herds (Fig. 1; Hayes *et al.* 2003). During 2003–2006, a captive-rearing programme was undertaken for the Chisana herd (Fig. 1) to enhance low recruitment. During late winter, parturient females were captured and transferred to a predator-free facility where they calved and were subsequently released in early June. To avoid potential bias associated with increased survival and recruitment due to the Chisana recovery programme, we censored captured females and their surviving captive-born calves (Yukon Fish and Wildlife Branch, unpublished data) from the data.

CLIMATE DATA

The PDO is a measure of climatic variability in the north Pacific region characterized by shifts between warm and cool phases on an interdecadal time-scale (Mantua *et al.* 1997; Mantua & Hare 2002). It is measured as the leading principal component of monthly sea surface temperatures (SST) in the north Pacific from 20° N poleward. Positive (warm phase) PDO values are characterized by cool SST in the central Pacific and warm SST along coastal areas. The PDO is related to sea level pressure (SLP) such that warm phase PDO values (i.e. cool SST) generally coincide with below average north Pacific SLP (Stenseth *et al.* 2003). The PDO is also related to terrestrial weather patterns (Mantua *et al.* 1997; Papineau 2001) and ecological processes such as forest fires (Duffy *et al.* 2005) in western North America. The PDO likely also influences population dynamics in other vertebrate taxa in the Yukon (Hik & Carey 2000; Morrison & Hik 2007).

We used summarized PDO values (data available at http://jisao.washington.edu/pdo) in seasons with biological significance for caribou recruitment: winter (November–April), summer (June–August), fall (September–November), and spring (March–May) or calving (April, May and June). We used four time windows from March to June, representing the springtime/calving seasons, as each could have a different mechanistic effect on caribou. March–May (early spring) PDO values represent conditions of the 3 months immediately preceding calving when most foetal mass is deposited *in utero* (Barboza & Parker 2006). April represents conditions immediately prior to calving. May climate summarizes conditions during peak calving season (mid to late May; Yukon Fish and Wildlife Branch, unpublished data) and June represents conditions for lactation when the need for highly nutritious forage is strong.

In the Yukon, the PDO is positively correlated with mean air temperature across all seasons (Table S1, Supporting information). Winter-PDO is negatively correlated with total precipitation (Table S1, Supporting information), and there is a negative relationship between both springtime and winter-PDO and the Julian date of the first snow-free day of the year (Morrison & Hik 2007; Table S2, Supporting information) and snow depth (Table S3, Supporting information). The relationship between summer- and fall-PDO and precipitation is generally weak (Table S1, Supporting information).

STATISTICAL ANALYSIS

We used generalized linear mixed-effects models [(GLMM) Skrondal & Rabe-Hesketh 2004; Gelman & Hill 2007] with a binomial distribution and logit link function to model recruitment (calf : cow ratio) as a function of seasonal PDO, and other covariates. Since female caribou typically do not produce twins, limiting the response to the unit scale (0, 1) was deemed appropriate. We included 'herd' and 'year' as crossed (i.e. non-hierarchical) random effects. We treated them as random effects because we assumed they contained unobserved heterogeneity we could not model and to account for pseudo-replication. Further, one of our aims was to estimate a global (i.e. population-averaged or marginal) model of the effect of PDO on recruitment which could be used to generalize beyond these years and herds (Skrondal & Rabe-Hesketh 2004), and our data were unbalanced across herds and years which could bias parameter estimates (Gillies *et al.* 2006). We included a 'trend' variable to account for possible long-term trend in recruitment which could potentially mask a climate effect. The effects of seasonal PDO and trend were modelled as random coefficients varying among herds because we could not assume a constant effect across all herds. As binomial count data, such as used here, often contain extra-binomial variation (i.e. are overdispersed) which may bias precision estimates (Gelman & Hill 2007), we fitted models using a quasi-GLMM approach whereby this extra variation (ø), or dispersion parameter, was also modelled. We used the package 'lme4' (Bates & Maechler 2009) in the statistical programme R 2·9·1 (R Development Core Team 2009).

We compared models using a quasi-Akaike information criterion (QAIC) adjusted for small sample sizes (QAIC*c*; Burnham & Anderson 2002). Within the candidate set, the model with the lowest QAIC*c* was selected as best, with models having ΔQAIC*c* < 2 compared to the best model interpreted as having strong support (Burnham & Anderson 2002). A current challenge for model selection among competing random effects models is the calculation of degrees of freedom (d.f.). For any random effect (e.g. year), the number of effective parameters may range between 1 and $N-1$, where N is the number of levels within the random effect (Bolker *et al.* 2009). As our level of inference was not focused on the specific herds or years, *per se*, we counted one d.f. for each fixed-effect, one for each random coefficient and intercept, and one for ø (Vaida & Blanchard 2005).

While our objective was not to estimate the effect of wolf control on recruitment *per se*, accounting for its effect was necessary to adequately separate climatic effects from recruitment changes due to reduced wolf numbers. A description of how this effect was modelled is provided in Appendix S1, Supporting information. Following the identification of models to account for wolf control, we specified models including single- and multi-season PDO variables (seasons identified in Table 1). Correlated seasons (r > 0·6; Table S6, Supporting information) were not specified in the same model. For models including PDO values from >1 season, springtime (calving season) was represented by the season/month (spring, April, May or June) having the lowest QAIC*c* among these four single-season models.

Results

The effect of wolf removal was represented by a constant effect during the years of active removal for the treatment herds (Aishihik and Finlayson) followed by a five-year declining effect (Table S4, Supporting information). For the adjacent herds (Burwash and Klaza), a two-year lag followed by a constant effect during the remaining years of active removal (Table S5, Supporting information) best represented the wolf removal effect on recruitment. In years of active wolf removal the average increase in recruitment rate for the treatment and adjacent herds was 0·20 and 0·11, respectively.

Table 2. Models of the effect of seasonal PDO on calf recruitment ($n = 165$). Models include the seasonal PDO values modelled as random coefficients, trend, two variables representing the effects of wolf removal (see Table S5), and random intercepts for both herd and year. A null model with no PDO variables is included for comparative purposes

Number	Model	Log-likelihood	K^a	AICc	ΔAICc
1	Winter + May	−487·6	11	998·93	0·00
2	Summer + Winter	−506·3	11	1036·33	37·40
3	May + Winter$_{t-1}$	−520	11	1063·73	64·80
4	Summer + Winter$_{t-1}$	−522·1	11	1067·93	69·00
5	Winter + Winter$_{t-1}$	−524·6	11	1072·93	74·00
6	Fall$_{t-1}$ + May	−528	11	1079·73	80·80
7	Summer$_{t-1}$ + May	−530·1	11	1083·93	85·00
8	Summer$_{t-1}$ + Summer	−531·3	11	1086·33	87·40
9	Summer + Fall$_{t-1}$	−531·5	11	1086·73	87·80
10	Summer	−538·6	9	1096·36	97·44
11	May	−539	9	1097·16	98·24
12	Winter	−546·4	9	1111·96	113·04
13	June	−547·8	9	1114·76	115·84
14	Fall$_{t-1}$ + Winter$_{t-1}$	−546·5	11	1116·73	117·80
15	Summer$_{t-1}$ + Winter$_{t-1}$	−549	11	1121·73	122·80
16	April	−554·5	9	1128·16	129·24
17	Spring	−556·4	9	1131·96	133·04
18	Winter$_{t-1}$	−556·9	9	1132·96	134·04
19	Fall$_{t-1}$	−565·4	9	1149·96	151·04
20	Summer$_{t-1}$	−566·2	9	1151·56	152·64
21	Null	−574·1	7	1162·91	163·99

[a] Number of estimated parameters.

Table 3. Parameter estimates (logit scale) and standard errors for the top-ranked model (Table 2) relating seasonal PDO and wolf control effects on recruitment

Variable	Parameter	SE
Winter-PDO	0·110	0·007
May-PDO	0·013	0·006
Trend	−0·023	0·001
Treatment Wolf Control	0·824	0·003
Adjacent Wolf Control	0·489	0·006
Constant	−0·742	0·019
σ^a (winter-PDO random coefficient)	0·273	
σ (May-PDO random coefficient)	0·239	
σ (trend random coefficient)	0·054	
σ (year random intercept)	0·422	
σ (herd random intercept)	1·168	
$ø^b$	0·045	

[a] Standard deviation; [b] dispersion parameter.

Of the candidate models, the most supported model included winter- and May-PDO (Table 2), supporting H1. Coefficients for both climate variables were significant, with the effect size of winter-PDO ($\beta = 0{\cdot}110$, SE $= 0{\cdot}007$) being substantially greater than that for May-PDO ($\beta = 0{\cdot}013$, SE $= 0{\cdot}006$) (Table 3). Standardized estimates were calculated, on the scale of two standard deviation units (Gelman 2008), to allow for easier comparison between them and were 0·171 and 0·024 for winter- and May-PDO respectively. Recruitment rose with increasing winter- and May-PDO, corresponding to increasing temperature and decreasing precipitation during these periods (Tables S1–S3, Supporting information). The most supported model also indicated a declining trend in recruitment ($\beta = -0{\cdot}023$, SE $= 0{\cdot}001$).

The estimated dispersion parameter (ø) was 0·045 for the top model in Table 2, indicating underdispersion. This underdispersion may be due to increased variability in the data being modelled through the random components of the model. For example, ø estimated from the data in the absence of any random effects, but with the same fixed effects as the top model, was 17·011. This indicates that in the absence of these random effects accounting for unobserved heterogeneity, substantial overdispersion was present. There is a lack of consensus on whether or not QAICc should be used in the presence of underdispersion (Cooch & White 2009). Model rankings were insensitive to the use of either AICc or QAICc and thus we report only AICc (Table 2). For comparison, results for the top model fitted without adjusting for underdispersion are provided in Table S7, Supporting information. Coefficients were unchanged; however, standard errors fixed effects were increased by a factor of $ø^{-1}$.

There was considerable variability in the herd-specific responses to both winter- and May-PDO (Fig. 3, Table S8, Supporting information) and trend (Table S8, Supporting information). In all cases, a random coefficient model was more supported than a random intercept model. For comparison, ΔAICc of the winter- and May-PDO model without random coefficients was 384, and the most supported model with no random coefficients included winter$_{t-1}$- and fall$_{t-1}$-PDO and had ΔAICc = 379. Residuals were assessed using a Shapiro-Wilk test and were normally distributed when pooled across herd and year ($W = 0{\cdot}99$, $P = 0{\cdot}50$). When assessed by herd and year individually, residuals were

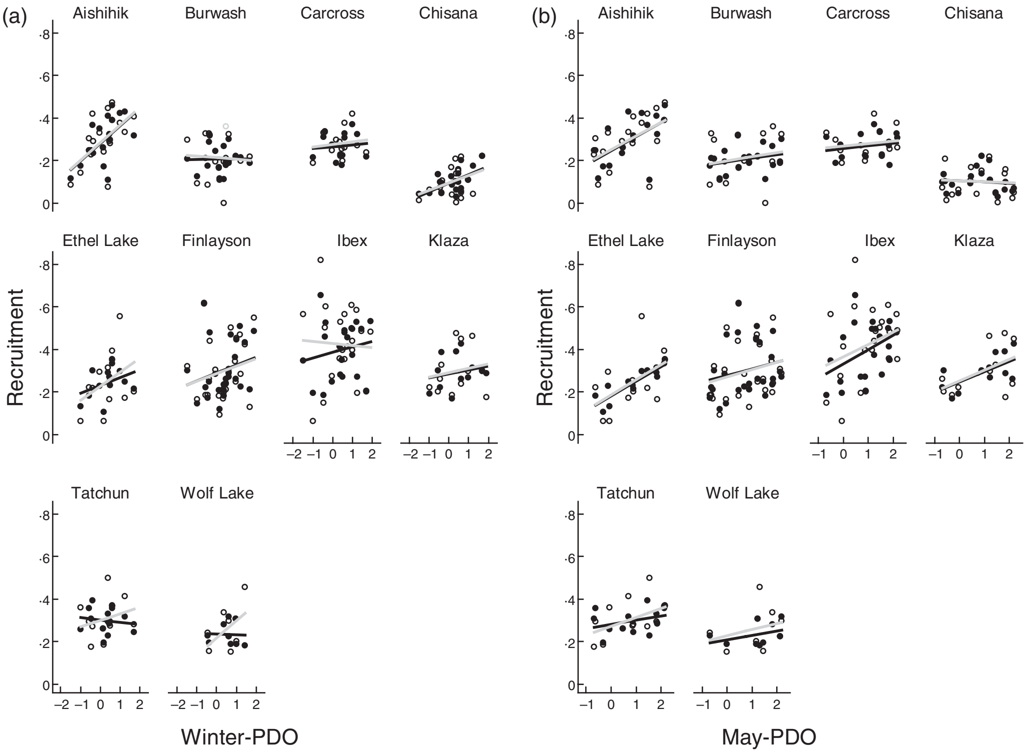

Fig. 3. Relationship between recruitment (calf : cow ratio) and winter-PDO (a) and May-PDO (b). Black circles represent observed recruitment rates while open circles indicate model predictions. Black and grey lines represent lines of best fit for observed and predicted recruitment respectively.

normally distributed for all levels with the exception of 1993 ($W = 0{\cdot}78$, $P = 0{\cdot}01$). We also assessed residuals, by herd, for any remaining autocorrelation not accounted for in the model structure. There was indication of remaining autocorrelation for the Tatchun herd [AR(1) = −0·51, $P = 0{\cdot}024$].

The model fit the pooled data well (Fig. 4), with predicted and observed recruitment rates highly correlated ($r = 0{\cdot}86$, $P < 0{\cdot}001$). The degree of model fit varied by herd (Fig. 5) and the correlation between predicted and observed recruitment ranged from $r = 0{\cdot}97$ to $r = 0{\cdot}07$. Generally, model fit was adequate for all herds except Tatchun and Wolf Lake.

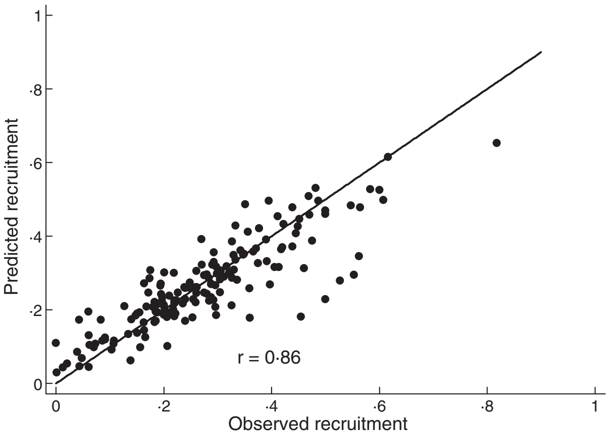

Fig. 4. Relationship between observed and predicted recruitment rates pooled across all herds and years ($r = 0{\cdot}86$, $P < 0{\cdot}001$). The diagonal line represents perfect correlation ($r = 1{\cdot}0$).

From the most supported model (Table 3), we compared predicted to observed recruitment from an external data set of 13 recruitment rates estimated on eight herds (two of which were not included in the training data set) over 6 years (one of which was not included in the training data set). The mean per cent error of predicted recruitment values was 15·7% (Fig. 6). The two herds not included in the training data set, Nahanni and Coal River (Weaver 2008), are both distributed along the eastern Yukon border with the Northwest Territories and are located directly east and southeast of the Finlayson herd (Fig. 1) respectively.

Discussion

Recruitment is a valuable indicator of population productivity as it represents the joint contribution of fecundity and calf survival. It is the most variable parameter in ungulate populations and thus a key factor influencing observed variation in population growth rates (Gaillard, Festa-Bianchet & Yoccoz 1998). We have provided a comprehensive analysis, in terms of numbers of populations and years, on the influence of large-scale climate on recruitment in a predator-limited large herbivore. Our work also adds to the sparse body of literature on the effects of Pacific-based climate on large herbivore population dynamics.

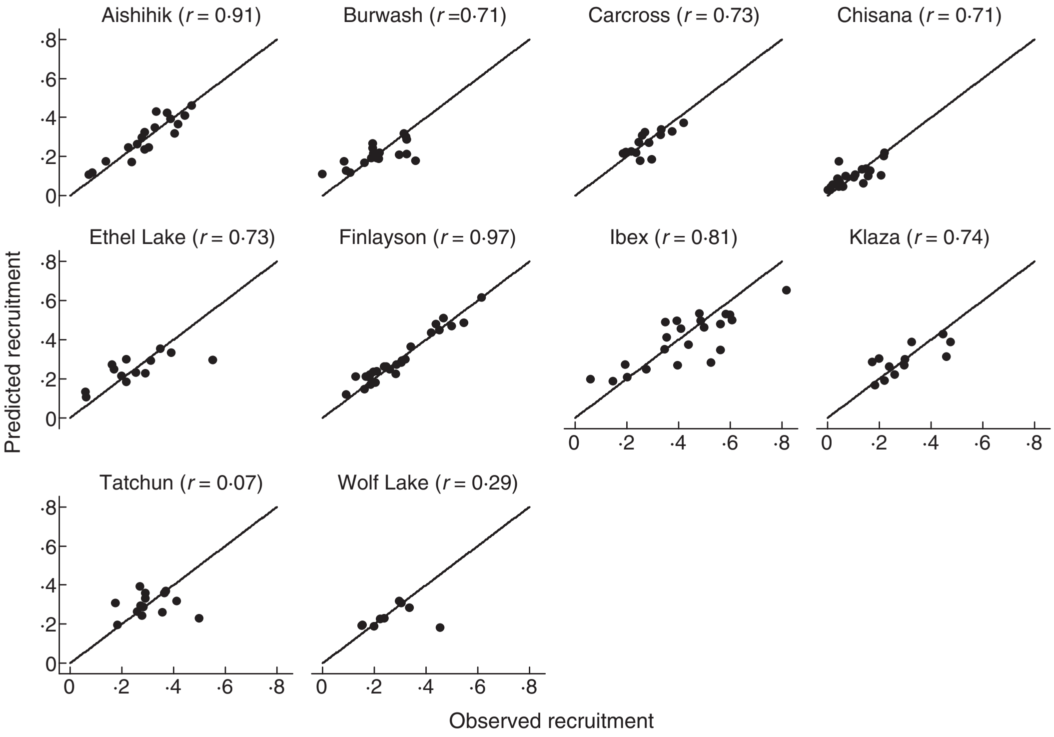

Fig. 5. Relationship between observed and predicted recruitment rates by herd. All reported correlations are significant ($P < 0{\cdot}05$) except for Tatchun ($P = 0{\cdot}82$) and Wolf Lake ($P = 0{\cdot}45$). The diagonal lines represent perfect correlation ($r = 1{\cdot}0$).

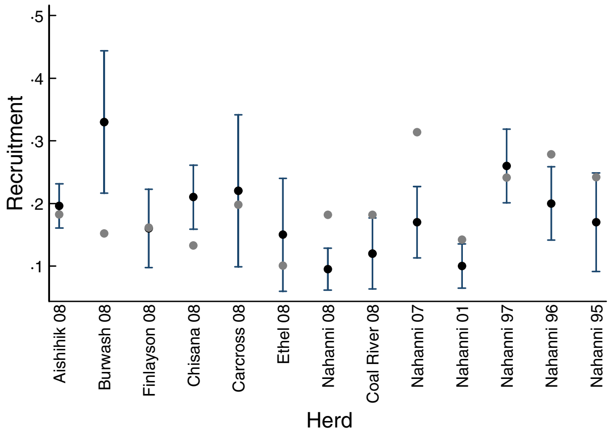

Fig. 6. Predicted (grey circles) and observed (black circles values) for 13 out of sample recruitment rates of mountain-dwelling caribou in the Yukon Territory. Error bars represent 95% confidence intervals of the observed rates. Herd names are noted on the *x*-axis and are followed by the year of the recruitment estimate.

Seasonal climate affecting environmental conditions at calving (see Table 1) were much more supported than those affecting fecundity (i.e. pre-conception) in mountain-dwelling caribou in the Yukon (Table 2), supporting H1. Recruitment was positively related to both winter- and May-PDO. There was weak support for H2, that seasonal climate affected fecundity in these populations. Higher winter- and May-PDO represents decreased precipitation and increased temperature through winter and May respectively, a reduced snowpack at calving, and an earlier onset of the first snowfree day of the year.

Consistent with the view that wolf predation plays a major role on recruitment in these populations there was a marked effect (Table 3) of the wolf removal programmes as earlier reported (Hayes *et al.* 2003). There was a strong, and spatially variable, relationship between the PDO and local environmental conditions (e.g. snow depth; Table S3). Wang *et al.* (2009) reported that density dependence was weak for northern ungulates coexisting with large carnivores. Our results confirm that in these relatively small populations with intact predator communities, top-down forces play a greater role on recruitment than bottom-up factors. Prevailing weather conditions such as snow depth are known to influence predation rates on neonatal ungulates (Bergerud & Page 1987; Adams *et al.* 1995b). Winter-PDO was negatively related to both the amount of snowfall in the spring (Table S3, Supporting information) and the first snow-free day of the year (Table S2, Supporting information). Both of these environmental factors could influence the degree of predation on newborn caribou calves by limiting the ability of parturient caribou to move away from predators and other calving females (Bergerud & Page 1987), and possibly on the ability of post-parturient caribou and their calves to move away from calving locations (Gustine *et al.* 2006). Skogland (1991) commented that the spatial relationship between predator and prey may be a large factor affecting predator–prey dynamics. The inability of parturient caribou to move away from predators due to environmental conditions at calving, following a low winter-PDO, supports this assertion. Given this strong mechanistic link between snow depth at calving and neonatal calf survival, the strong effect of winter-PDO was expected.

The effect of climate at calving (May-PDO), while smaller than for winter (Table 3), was nevertheless sufficiently influential to be present in the most highly supported model (Table 2). One would anticipate climate at calving to influence calf survival given the high degree of mortality shortly after birth. Indeed, an extremely warm spring (high PDO) could negate the effect of a high winter snowfall, or a very poor spring (e.g. heavy spring snowfall) could result in higher calf mortality regardless of *in utero* winter conditions. Thus, extreme springtime climate (above or below average) may be influencing recruitment in these herds where extremely warm and dry springs result in a reduced snowpack and earlier snowmelt, thus reducing predation rates on neonates. Conversely, a strongly below average spring characterized by lower temperatures and/or increased precipitation in the form of snow, may limit parturient female's movements to safe calving sites. Extremely poor weather at calving (e.g. cold and wet) may also have a direct influence on neonate survival (Gauthier & Theberge 1986). Extreme climate events are influential in the population dynamics of numerous species (Parmesan, Root & Willig 2000). For example, an extreme icing event in winter coated forage with thick layer of ice and resulted in the 80% decline of a reindeer population on Svalbard (Chan *et al.* 2005).

The positive effect of the PDO on caribou recruitment in the Yukon is consistent with Hebblewhite's (2005) finding of a negative effect of the North Pacific Oscillation (NP) on elk (*Cervus elaphus* L.) population growth rates in Alberta, Canada, given the negative relationship between the PDO and NP (Yang *et al.* 2005). Hebblewhite (2005) also reported variability across populations in their growth rate response to the NP. Elk density and the NP were more influential when wolves were rare, while predation and its interaction with the NP became more influential when wolf numbers were greater. We regarded our index of a wolf removal effect on recruitment as too coarse, and the absence of wolf population data across herds insufficient to warrant inclusion of wolf abundance as an interaction with the PDO.

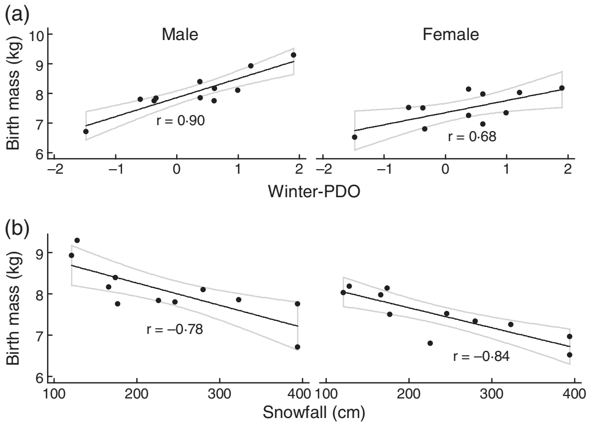

Fig. 7. Relationship between average caribou calf birth mass, by sex, (1987–1997) from Denali National Park, Alaska (data from Adams 2005) and (a) winter-PDO and (b) winter snowfall. Lines of best fit with 95% confidence intervals are shown. $P < 0{\cdot}05$ for all reported correlations.

Calf body mass in ungulates is related to climate (Weladji & Holand 2003; Adams 2005), maternal condition during gestation (Thorne, Dean & Hepworth 1978; Keech *et al.* 2000), and maternal body mass at breeding (Kojola 1993; Adams 2005). Subsequent calf development is also related to pre-parturition conditions (Kojola 1993; Adams 2003). Lighter-born calves and those with reduced growth and developmental capabilities early in life may be subject to increased mortality from birth throughout the summer (Guinness, Clutton-Brock & Albon 1978; Mech, Nelson & McRoberts1991). Winter-PDO and winter snowfall were positively and negatively correlated, respectively, with average annual birth mass of Denali calves (from Adams 2005; Fig. 7). Thus, winter climate may affect calf survival throughout the first summer of life, in addition to early mortality due to predation. Our index of recruitment measured during the fall could not separate mortality occurring during different periods after birth.

As our results were only suggestive of an effect on calf survival, we related seasonal PDO to calf mortality over different time periods shortly after birth using mortality hazard rates from radiocollared neonates in Denali (from Adams *et al.* 1995a,b). For comparative purposes, we included seasonal climate both pre- and post-conception. As expected (Table 1), climate affecting environmental conditions at calving (i.e. winter-PDO, May-PDO) was negatively correlated with early calf mortality, while the relationship with mortality later through summer became weaker (Table 4). Conversely, seasonal climate affecting female condition at breeding (i.e. winter-PDO$_{t-1}$, summer-PDO$_{t-1}$ and fall-PDO$_{t-1}$) was more strongly related to later calf mortality. While the correlation between pre-conception climate and

Table 4. Correlation between seasonal PDO and mortality hazard rate[a] over various ages and time periods for caribou calves in Denali National Park, Alaska (1984–1991)

	Mortality time period			
Season	Birth to 15 days[b]	Birth to 30 days[b]	Birth to 120 days[c]	30–120 Days[c]
Winter-PDO	**−0·90**[d]	**−0·80**	−0·81	−0·78
Winter-PDO$_{t-1}$	−0·58	**−0·86**	**−0·92**	**−0·91**
Summer-PDO$_{t-1}$	−0·65	−0·56	−0·69	−0·69
Fall-PDO$_{t-1}$	**−0·71**	−0·68	−0·80	−0·79
May-PDO	**−0·91**	**−0·77**	−0·86	−0·84
Years of data	8	7	5	5

[a] Mortality hazard rates were calculated as $-\log_e(S)$, where S is the percentage of calves alive at the beginning of the time period surviving to its end. Hazard rates were used instead of S as they make the correlations invariant of the time units; [b] source – Adams *et al.* (1995a,b); [c] source – Adams *et al.* (1995a); [d] significant correlations ($P < 0{\cdot}05$) are bolded.

later calf mortality was strong and significant for the Denali herd, these relationships, if present, were not influential enough to result in pre-conception climate being supported in our candidate models of Yukon caribou recruitment.

For both of the climate predictors there was considerable variability in their herd-specific effects on recruitment (Fig. 3, Table S8 Supporting information). This variability is consistent with Martínez-Jauregui *et al.* (2009) who found a lack of a general climatic effect on red deer weights across Europe. While the average effects of winter- and May-PDO were positive and significant in our model, local characteristics of individual herds and their ranges (e.g. terrain features, latitude) may result in the downscaled effect of the PDO resulting in different localized weather conditions (Mysterud *et al.* 2000; Pettorelli *et al.* 2005). The spatial variability in the correlation between local weather and large-scale climate (Tables S1, S3, Supporting information), such as the PDO, may also lead to variability in its effect on herd population parameters (Ginnett & Young 2000). Additionally, intrinsic characteristics of these herds may also affect the role of climate on recruitment. For example, the effect of climate may be more pronounced at higher population density (Wilmers *et al.* 2006), and may affect age classes differentially (Coulson *et al.* 2001). Information on age-structure for the herds considered here was unavailable. However, herds with greater proportions of young and/or older females may be expected to respond to winter climate more strongly as smaller (e.g. younger) females or those with reduced body conditions (e.g. senescent animals) may not be able to fully carry a calf to term under more severe winter weather.

Given the strong effect of predation on recruitment in these herds, predator and alternate prey density may also play an important role in influencing the effect of climate. Wolf numbers may also be influenced by climate indirectly through the direct influence on their prey base (Post & Forchhammer 2001). This may result in a lag effect as wolves numerically respond to changes in prey density (Fuller, Mech & Cochrane 2003). In systems where moose and caribou coexist with wolves, and other predators, caribou are often a secondary prey species with wolf density being most strongly affected by moose density (Seip 1992). Thus, climate effects on moose may also play a large part in predation rates on caribou, heightening the complexity by which climate affects wolf populations and hence caribou numbers. Further, climate may affect wolves behaviourally by altering characteristics such as pack size which in turn may increase predation rates (Post *et al.* 1999). Incorporating annual variability in predator and/or alternate prey density across herds could strengthen our understanding of climate's effect on recruitment. The influence of calving season climate may also best be understood in terms of its interaction with predator density, as it is environmental conditions at calving that can have a strong influence on predation rates. Hence, a multiplicative rather than additive effect of calving season climate may be warranted. Predator data were unavailable for the majority of years and herds considered here, precluding the incorporation of such an interactive effect in this study.

Overall, our model fit the pooled and herd-specific data well (Figs 4 and 5). However, two herds, Tatchun and Wolf Lake, were poorly fitted. These herds had the fewest data points among all the herds considered (Fig. 2) which could have affected their modelled relationship with the PDO. The external data used to evaluate the model also indicated relatively good predictive ability (Fig. 6). As should be expected, since our model did not incorporate herd-specific characteristics, it generally predicted recruitment better for those herds included in model training (e.g. Finlayson, Aishihik). The incorporation of herd-specific variables may enhance our understanding of the environment-climate mechanisms (e.g. Pettorelli *et al.* 2005) shaping recruitment patterns.

Our goal was not to compare the PDO with local weather variables in their ability to explain recruitment patterns. Indeed, given the remoteness of some of the herds used in this analysis, weather stations at relevant locations were not available. This fact demonstrates the utility of using large-scale climate indices. Additionally, weather variables measured at one location may not be relevant for a highly mobile species such as caribou (Stenseth & Mysterud 2005). Elsewhere in a direct comparison of local weather and the PDO, the PDO proved to be a more highly supported predictor of caribou population parameters than local weather (T.M. Hegel, A. Mysterud, F. Huettmann & N.C. Stenseth, unpublished data). Rather, our goal was to compare the effect of different seasons on recruitment in these herds using the PDO to facilitate that comparison. We acknowledge that there are limitations in using a large-scale climate index across seasons. For example, the relationship between the PDO and local weather may not be consistent across seasons. In the Yukon, the PDO-local weather relationship appears strongest during winter and spring, with a weaker relationship in summer, thus reducing our power to detect a relationship between the PDO and recruitment at this time. However, this would not have affected our ability to detect a difference between *in utero* winter climate (winter-PDO) and pre-conception winter climate (winter$_{t-1}$-PDO). The PDO may also not be related to a specific local weather variable important to recruitment. However, this issue is present in any observational study in that the proper variable(s) must be selected for analysis. Finally, the PDO-local weather relationship may also vary spatially. Such a spatially varying relationship could confound a general relationship between the PDO and recruitment; however, the inclusion of random coefficients across herds would aid in accounting for this spatial variability.

This is one of the first studies to explicitly examine the influence of the PDO on large herbivore populations. Hik & Carey (2000) reported an oscillatory pattern of horn growth in Dall sheep rams with a suggested relationship to the PDO. In northern Yukon and Alaska, phase-shifts in the PDO were suggested as a factor influencing changing trends in population growth of the Porcupine caribou herd (Griffith *et al.* 2002). A phase-shift of the winter-PDO from −1·5 to +1·5, for example, would result in an average increase in recruitment of *c.* 25% in Yukon mountain caribou. The PDO has previously been shown to be a factor in the population dynamics of, for example, Pacific salmon (*Oncorhynchus* spp.; Mantua *et al.* 1997), songbirds (Ballard *et al.* 2003), and small herbivores (*Ochotona collaris* Nelson; Morrison & Hik 2007). At broader scales the PDO influences freshwater (Winder & Schindler 2004), marine (Field, Francis & Aydin 2006), and terrestrial (Loik *et al.* 2004) ecosystem dynamics.

Recent future climate scenarios indicate that while temperatures are expected to increase over the next century across the Yukon, precipitation will also rise, as will the frequency of extreme climatic events (Carter *et al.* 2007) such as rain-on-snow icing events, which can have a substantial negative effect on ungulate populations (Chan *et al.* 2005; Helle & Kojola 2008). Climate projection models suggest increases in winter precipitation in the Yukon ranging from *c.* 5 to +30% (Canadian Climate Change Scenarios Network: http://www.cccsn.ca). Increases in snowfall of this magnitude could have significant impacts on recruitment; however, given an increase in temperature both in spring and fall it is uncertain how this would affect the length of the summer growing season. Further, in multi-predator multi-prey systems such as the Yukon, the interactions across trophic levels (Post & Forchhammer 2001) coupled with individual species' responses to changes in climatic conditions are complex and difficult to predict (Stenseth *et al.* 2002; Walther *et al.* 2002).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of the approach for modelling wolf removal effects on recruitment.

Table S1. Local weather–PDO relationships.

Table S2. Snowmelt–PDO relationship.

Table S3. Snowpack–PDO relationships.

Table S4. Models representing wolf removal effects on recruitment in the ‘treatment’ herds.

Table S5. Models representing wolf removal effects on recruitment in the ‘adjacent’ herds.

Table S6. Correlation among seasonal PDO values.

Table S7. Parameter estimates of the top model without adjustment for underdispersion.

Table S8. Herd-specific relationships between caribou recruitment and the PDO.

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