

1 Effects of climate and plant phenology on recruitment of moose at the
2 southern extent of their range

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14 Climate is increasingly viewed as playing a fundamental role in determining range limits for
15 individual species and is an important factor in the dynamics of large herbivores. Climate is
16 thought to be involved in the declines of moose populations across much of their southern extent,
17 yet reasons for apparent stability versus declines in performance among populations is unknown.
18 We examined effects of climate and plant phenology on temporal variation in recruitment rates
19 of Shiras moose (*Alces alces shirasi*) collected over 3 decades across a large geographic area in
20 the Rocky Mountains, USA. Of the 18 herd units with available data, calf-cow ratios declined in
21 8 during 1980-2009, while others failed to exhibit a temporal trend. Rates of calf recruitment
22 were affected negatively by warm temperatures and dry spring-summers 1 year prior to a cohort
23 of calves being raised, and were lower during years with a rapid rate of spring green-up. These
24 patterns indicate both direct (year_t) and delayed effects (year_{t-1}) of weather and plant phenology
25 on calf recruitment, which likely was mediated through effects on nutritional condition.
26 Suppressed nutrition could have been induced by (1) increased thermoregulatory costs associated
27 with warming temperatures and (2) increased rate of spring green-up caused by warmer, drier
28 springs shortening the duration when high-quality forage was available. Both pathways would
29 reduce net energetic gain leading to reduced fecundity, nutritional carryover, and ability to
30 provision offspring. Nevertheless, a temperature effect was not evident in populations with stable
31 calf-cow ratios, many of which were recently introduced or expanding populations that may have
32 been buffered against environmental perturbation because they had yet to reach carrying
33 capacity. Consequently, the role of climate in limiting the viability of populations at their
34 southern extent may be better understood from a nutritional perspective.

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36 Exposure of species to altered climatic regimes has resulted in modified behavior,
37 adjusted phenology, loss of geographic range, numeric decline, and in some instances, extinction
38 (Walther et al. 2002, Parmesan 2006, Beever et al. 2011, Monteith et al. 2011). Climate is
39 increasingly viewed as playing a fundamental role in determining range limits for individual
40 species (Parmesan and Yohe 2003); nonetheless, the diversity in species-specific responses
41 complicates expectations about climate change (Parmesan 2006, Dawson et al. 2011). Even
42 within species, effects of climate change are not consistent, with range expansion and population
43 growth occurring in some regions while range constriction and population decline occur in others
44 (Laliberte and Ripple 2004, Grøtan et al. 2009, Post et al. 2009, Doak and Morris 2010, Murray
45 et al. 2012). Populations occurring at the southern periphery of their geographic range are often
46 most sensitive to environmental change (Thompson et al. 1998, Channell and Lomolino 2000,
47 Laliberte and Ripple 2004, Doak and Morris 2010, Rodhouse et al. 2010, Beever et al. 2011).

48 Along with interactive effects of population density, variation in climate determines
49 environmental conditions that shape life-history variation and thus, population dynamics of large
50 herbivores (Sæther 1997). In particular, juveniles are the age class most sensitive to factors that
51 affect resource availability (Gaillard et al. 2000), which can have delayed and life-lasting effects
52 on their survival, growth, and reproduction (Monteith et al. 2009). With warming temperatures
53 observed with global warming (Shuman 2011), energy expended for thermoregulation by large-
54 bodied herbivores adapted to cold climates may affect performance of populations at the
55 southern extent of their range (Murray et al. 2006). Heat stress can be highly constraining for
56 domestic ruminants by reducing foraging time and suppressing appetite (Kadokawa et al. 2012).
57 Although, free-ranging herbivores seek thermal refugia and alter activity patterns to reduce
58 stressful climatic conditions (Bourgoin et al. 2011), whether such behavioral responses fully

59 compensate for thermoregulatory costs remains unanswered. Indeed, even slight reductions in
60 net energy gain through time could impair resource acquisition and thus, individual performance
61 over the long term (White 1983).

62 Large herbivores typically give birth in late spring and early summer to coincide with
63 vegetation green-up permitting intake of quality forage to support the energetic demands of late
64 gestation and lactation (Rutberg 1987). Nevertheless, global climate change is altering patterns
65 of vegetation phenology (Schwartz and Reiter 2000, Walther et al. 2002), which affect
66 nutritional resources available for reproduction. In temperate environments, food quantity
67 increases with a long season of photosynthetic activity (Ericsson et al. 2002), but cold and wet
68 spring and summers increase forage quality and nutrient gain by slowing phenological
69 advancement and increasing heterogeneity in onset of green-up (Walsh et al. 1997, Mysterud et
70 al. 2001); crude protein and digestibility peak early in the growing season, then decline rapidly
71 as vegetation matures (Crawley 1983, Mcart et al. 2009). Consequently, climatological
72 shortening of the period when forage quality is highest, reduces net energetic gain and lowers
73 performance of large herbivores (Albon and Langvatn 1992, Langvatn et al. 1996, Sæther et al.
74 1996, Walsh et al. 1997, Pettorelli et al. 2007).

75 Across much of the southern distribution of their range, which includes the northern
76 conterminous United States and southern Canada, populations of moose (*Alces alces*) have
77 experienced population decline and range loss. In particular, moose populations have declined
78 precipitously in northern Minnesota and northwestern Wyoming (Murray et al. 2006, Becker et
79 al. 2010). Such region-wide and somewhat synchronous declines in abundance suggest a
80 broad-scale explanatory factor such as climate (Stenseth et al. 2003). Research in northern
81 Minnesota, USA has consistently associated changing climate with nutritional stress, reduced

82 survival and productivity, and high parasite loads in moose (Murray et al. 2006, Lenarz et al.
83 2010, DelGiudice et al. 2011). Meanwhile, other populations within their southern distribution
84 appear resilient to similar changes in climate and have exhibited range expansion and population
85 growth (Brimeyer and Thomas 2004, Murray et al. 2012), which challenges the uniformity of a
86 northward recession of viable moose range (Thompson et al. 1998, Murray et al. 2006) and
87 supports the notion that vulnerability to climate change differs among populations (Post et al.
88 2009, Dawson et al. 2011).

89 The effect of climate on demographics and population performance of large herbivore
90 populations is difficult to disentangle from other confounding factors, especially when data are
91 collected over short temporal windows when climate variation may be minimal. Therefore,
92 long-term data that comprise a range in demographics as well as climate are necessary because
93 climatic relationships are complex and may involve lagged or cumulative effects (Murray et al.
94 2006). We used a long-term dataset on calf recruitment of Shiras moose (*Alces alces shirasi*)
95 across the southernmost distribution of their range to distinguish between hypotheses proposed to
96 explain declines in moose populations including: climate warming and its effects on heat stress
97 and nutrition, and altered plant phenology. Although our data occur at a coarse scale and may be
98 affected by sampling variation, incorporating long-term data from multiple populations should
99 enhance our ability to detect broad-scale processes that may be responsible for disparate trends in
100 trajectory of moose populations in the Rocky Mountains, USA.

101 Moose are uniquely adapted to a northern climate, but are consequently more susceptible
102 to thermoregulatory constraints than other northern ungulates because they have the lowest upper
103 critical temperature and are unable to sweat extensively (Telfer 1984, Schwartz and Renecker
104 2007). Heat stress thresholds among both adult and young moose occur at temperatures as low as

105 -5°C and 14°C during winter and summer, respectively with open mouth panting occurring at 0°
106 and 20°C during the same seasons (Renecker and Hudson 1986). Rising ambient temperatures
107 may negatively affect female moose via increasing heat loads, and warmer temperatures and
108 drier springs can negatively affect nutritional quality of forage in temperate regions (Langvatn et
109 al. 1996, Pettorelli et al. 2007), all of which could result in nutritional suppression and reduced
110 reproductive performance (Testa and Adams 1998). We therefore expected recruitment of young
111 to be associated negatively with ambient temperature and positively with spring and summer
112 precipitation (H₁, hypothesis 1). In addition, patterns of plant phenology affect productivity of
113 herbivore populations by modifying the timing and duration of access to quality forage
114 (Herfindal et al. 2006b, Pettorelli et al. 2007, Grøtan et al. 2009). We expected that early
115 vegetation onset, slow spring green-up, and a longer spring would be related positively to
116 recruitment of young by increasing the duration, and overall quality of forage available (H₂;
117 hypothesis 2). Finally, because moose are capital breeders and rely partially on somatic reserves
118 to support reproduction (Testa and Adams 1998), we expected conditions from preceding years
119 to potentially carry-over to influence calf recruitment in subsequent years through effects on
120 fecundity and nutritional condition (H₃, hypothesis 3).

121 **Methods**

122 **Study area and calf recruitment data**

123 The absence of fossil evidence suggests that the presence of moose in the central and southern
124 Rocky Mountains is the result of an historical southward expansion of the Shiras subspecies by
125 natural dispersal and translocation efforts. Moose are believed to have entered northwest
126 Wyoming from Idaho and Montana within the past 150 years, and have expanded southward into
127 viable moose habitat resulting in established moose populations from northwest Wyoming

128 through northeastern Utah. Subsequently, moose have been transplanted into the Bighorn
129 Mountains, Wyoming in the 1950s (Brimeyer and Thomas 2004), to North Park, Colorado in the
130 late 1970s (Kufeld and Bowden 1996), and into multiple herd units in Utah since 1973 (Wolfe et
131 al. 2010).

132 Although some populations contained non-migratory individuals, moose in our study area
133 were mostly migratory, and occupied high-elevation ranges during summer and low-elevation
134 riparian areas during winter (Kufeld and Bowden 1996, Becker et al. 2010). Terrain within herd
135 units was mountainous, with mean elevation ranging from 2000 to 3050 m. In most regions,
136 moose were associated closely with riparian communities, especially those dominated by willow,
137 mostly Drummond's (*Salix drummondiana*) and Geyer's willow (*Salix geyeriana*). Winter
138 ranges were generally characterized by large riparian complexes; however, mixed-mountain
139 shrub communities including sage brush (*Artemisia tridentata*) and bitterbrush (*Purshia*
140 *tridentata*) were sometimes used when available (Brimeyer and Thomas 2004, Wolfe et al.
141 2010). At higher-elevation summer ranges, riparian areas dominated by *Salix* species were
142 commonly bordered by extensive forests of lodgepole pine (*Pinus contorta*), aspen (*Populus*
143 *tremuloides*), cottonwood (*Populus augustifolia*), Englemann spruce (*Picea enelmannii*),
144 Douglas fir (*Psuedotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*). Most herds
145 experienced some predation from black bears (*Ursus americana*) and mountain lions (*Puma*
146 *concolor*), however, moose in the northwest corner of Wyoming in Targhee and Jackson herd
147 units also were exposed to growing and expanding populations of wolves (*Canis lupus*) and
148 grizzly bears (*Ursus arctos*) since the mid-1990s (Brimeyer and Thomas 2004, Smith et al. 2010,
149 Wolfe et al. 2010).

150 We obtained data on calf recruitment from observation data collected as part of routine
151 moose monitoring by state management agencies for 18 herd units (Fig. 1) in Wyoming ($n = 9$),
152 Utah ($n = 8$), and Colorado ($n = 1$). Herd units were delineated by agencies based on hydrologic
153 divides, major rivers, and other natural and man-made barriers to movement (Brimeyer and
154 Thomas 2004). Since 1980, postseason classifications were conducted on an annual basis for
155 most herd units; however, data were sparse for some. In Utah, surveys were often conducted
156 every third year (Wolfe et al. 2010). Helicopter surveys to classify herds by sex and age were
157 flown by agency personnel between December and February when moose were congregated on
158 winter ranges. Surveys were conducted when good snow cover was present, and encompassed
159 areas of riparian, deciduous, and conifer habitat that were frequented by moose during winter
160 (Brimeyer and Thomas 2004). Occasionally, supplemental surveys were conducted from the
161 ground to augment data collected during helicopter survey or cover areas not surveyed from
162 helicopter. Each moose encountered during aerial surveys was classified to: bulls, yearling bulls,
163 cows, calves, or unclassified adults. Calves were distinguished from yearlings and adults based
164 on body size, and features of the head including relatively small ears and short, pointed noses
165 (Timmermann and Buss 2007). For sexing adult moose, criteria included: antler or pedicel scars,
166 vulva patch, behavior, bell conformation and size, group composition, and body conformation
167 (Timmermann and Buss 2007).

168 Our study included data on calf recruitment rates representing 304 herd-years from 18
169 herd units during 1980-2009. Data during this period were available for 21 herd units; however,
170 we included only those herd units ($n = 18$) where surveys had occurred for a minimum of 10
171 years with an average number of observations larger than 50 individuals. Although reliable
172 estimates of population size were not available, moose populations in this region were variable in

173 size ranging from herd units with as few as 60 animals and up to 4500 animals. Average number
174 of individuals classified to estimate an annual recruitment rate, across all herds and years, was
175 346.3 (SE = 20.7). We used the number of calves per 100 adult female (calf-cow ratio) as our
176 estimate of recruitment rate (Raithel et al. 2007, Harris et al. 2008) at the population (i.e., herd
177 unit) level. The relative number of calves per female provides a robust representation of annual
178 patterns of reproductive success because adult survival is generally high and invariable (Gaillard
179 et al. 2000), the number of calves per female reflects pregnancy, twinning rate, and survival of
180 calves to weaning age (Franzmann and Schwartz 1985, Raithel et al. 2007, Grøtan et al. 2009),
181 and juvenile moose are easily distinguished from adult and yearling moose (Timmermann and
182 Buss 2007).

183 **Weather and plant phenology data**

184 We obtained spatially-explicit data on monthly precipitation and monthly averages of daily
185 minimum and maximum temperature for seasonal ranges occupied by each herd unit using
186 modeled values from the parameter-elevation on independent slopes model (PRISM) at a 4-km
187 resolution (Daly et al. 1994). The PRISM is a climate modeling system that generates gridded
188 estimates of monthly climate using point data, a digital elevation model, and other spatial data
189 (Daly et al. 1994). We extracted mean monthly weather data for pixels that occurred within
190 summer and winter ranges, which were delineated by agency personnel based on representative
191 habitat types and observed seasonal distributions of moose. We used a climograph to delineate
192 seasons based on months that grouped within similar ranges of temperature and precipitation
193 (Fig. 2). Subsequently, we calculated cumulative precipitation and average daily minimum and
194 maximum temperature within those seasons.

195 We used principal components analysis (PCA) of seasonal weather data, based on the
196 correlation matrix (McGarigal et al. 2000), to reduce the dimensionality of those data and derive
197 independent composite variables that described seasonal weather patterns(Grosbois et al. 2008).
198 We retained principal components (PCs) with eigenvalues >1.0 (McGarigal et al. 2000).
199 Seasonal weather patterns were adequately described by 3 PCs (eigenvalues [% variance
200 explained]: PC1: 6.11 [45.1%], PC2: 1.89 [18.2%], PC3: 1.08 [12.3%]). PC1 represented annual
201 temperature patterns contrasting relatively cool years with relatively warm years. PC2
202 corresponded to a measure of spring-summer precipitation opposing dry spring and summers
203 with wet spring and summers. PC3 corresponded to autumn-winter precipitation opposing dry
204 autumn and winters with wet autumn and winters.

205 The normalized difference vegetation index (NDVI) is derived from satellite imagery that
206 measures the greenness of vegetation based on the ratio of ground reflectance of red and near-
207 infrared radiation. NDVI is sensitive to environmental change (Pettorelli et al. 2005), is
208 associated with net primary production (Reed et al. 1994) and fluctuations in diet quality (Hamel
209 et al. 2009, Garel et al. 2011), and thus, is related to numerous aspects of the ecology of large
210 herbivores (Herfindal et al. 2006a, Pettorelli et al. 2007, Garel et al. 2011). From the Earth
211 Resources and Observation Science Center of the U.S. Geological Survey, we obtained a time
212 series of 7-day composite NDVI with 1-km² spatial resolution recorded by the Advanced Very
213 High Resolution Radiometer aboard the polar-orbiting weather satellites of the National Oceanic
214 and Atmospheric Administration. Data were further processed to remove effects of atmospheric
215 contamination with the method of Swets et al. (1999). We extracted mean NDVI values for each
216 1-week interval from 1989–2009 (with the exception of 1990 and 1994 when data were
217 unavailable) for pixels that occurred within the summer ranges of moose.

218 We expected the shape of the NDVI curve to vary among areas depending upon snow
219 accumulation, temperature, and summer precipitation, which we expected would influence
220 forage quality and availability and subsequently, calf recruitment of moose. From the NDVI
221 time-series data, we computed 3 NDVI metrics during spring-summer (Pettorelli et al. 2005b,
222 Pettorelli et al. 2007) using program TIMESAT (Jönsson and Eklundh 2004). We calculated date
223 of onset of spring to represent when quality forage became available in spring, and the length of
224 spring which represented the number of days between the onset of spring and peak NDVI
225 indicating how long growing vegetation was available (Pettorelli et al. 2005b). We also
226 calculated rate of spring green-up based on the rate of increase in NDVI between onset of spring
227 and the plateau in NDVI (Pettorelli et al. 2005b). Rate of spring green-up was highly correlated
228 ($r = 0.91$) with maximal increase in NDVI in any 2-week period during spring, a similar metric
229 used to represent rate of spring green-up (Pettorelli et al. 2007).

230 **Statistical analysis**

231 We used simple linear regression to evaluate correlations among PCs that reflected weather
232 patterns and spring plant phenology. We identified temporal trends in average temperature and
233 cumulative precipitation within seasons, and for annual plant phenology metrics using separate
234 linear mixed models (PROC MIXED; SAS Institute, Cary, NC), with a random intercept for herd
235 unit, year as a fixed effect, and each environmental variable as the response variable. We also
236 calculated the proportion of months when average maximum daily temperature on seasonal
237 ranges exceeded heat stress thresholds of 0 °C during winter and 20 °C during summer
238 (Renecker and Hudson 1986).

239 We assumed that survey data collected during the past 3 decades were representative of
240 variation in demographics of moose populations and that the apparent trends were biological,

241 rather than a result of measurement error. We believe the consistent methods of data collection
242 employed by each state agency upholds these assumptions; but, we also recognize that long-term
243 datasets collected under basic monitoring protocols rather than designed for statistical hypothesis
244 testing are subject to variation and errors (White 2000, Yoccoz et al. 2001). Because population
245 size and survey efforts were variable among herd units, we weighted calf-cow ratios in all
246 analyses based on the inverse of the variance in each calf-cow ratio estimate (Czaplewski et al.
247 1983). In this way, estimates with greater confidence (lower variance) were allocated more
248 weight in our analysis than those with less confidence (higher variance). We used simple linear
249 regression (Neter et al. 1996), weighted by the inverse of the variance in each estimate, to
250 identify temporal trends in calf-cow ratios separately for each herd unit. We considered herd
251 units to have declining calf-cow ratios if the coefficient for time was negative, and if $P < 0.10$; we
252 considered all others as stable.

253 Our approach was to model calf-cow ratios as a function of seasonal weather patterns or
254 plant phenology during both the year that a specific cohort of calves were raised and the same
255 weather and plant phenology covariates during the preceding year. We included environmental
256 covariates from the preceding year because patterns of calf recruitment observed during a single
257 year were likely not an isolated event, but could be affected either by nutritional carryover from
258 the previous year (Harrison et al. 2011) or environmental effects of the previous year on
259 fecundity (Testa and Adams 1998). We used linear mixed models (PROC MIXED; SAS
260 Institute, Cary, NC) weighted by the inverse of the variance in each calf-cow ratio estimate, to
261 model annual calf-cow ratios as a function of weather or plant phenology in 2 separate modeling
262 efforts because metrics of plant phenology were correlated with weather patterns, and weather
263 and plant phenology have the potential to cause different nutritional and physiological

264 constraints on calf recruitment. We included herd unit as a random effect allowing for a random
265 intercept to help account for unbalanced sample sizes among herd units, and because we
266 expected some level of unobserved heterogeneity and lack of independence within each herd unit
267 (Gillies et al. 2006). We included PCs representing weather and metrics of plant phenology as
268 fixed effects because we were interested in the marginal population-level response to those
269 covariates.

270 We used an information-theoretic approach to evaluate the importance of predictor
271 variables. In both analyses (i.e., weather and plant phenology), we evaluated all possible
272 combinations of predictor variables that we hypothesized would influence calf-cow ratios
273 (Arnold 2010). Variables that were correlated ($r > 0.50$) were not allowed to enter the same
274 model (Neter et al. 1996). For each model, we calculated Akaike's information criterion
275 (Burnham and Anderson 2002) adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike
276 weight (w_i). We then calculated model-averaged parameter estimates and the associated 90% CI,
277 based on unconditional SEs. Model averaging minimized effects of uninformative parameters,
278 and thereby provided a conservative assessment of variable importance (Arnold 2010). We
279 determined if model-averaged parameter estimates differed from zero based on whether their
280 90% CI overlapped zero, and used importance weights to evaluate their relative importance
281 (Arnold 2010, Monteith et al. 2011). We calculated importance weights as the sum of w_i across
282 all models that contained that particular variable (Arnold 2010). We standardized all variables so
283 that estimates of coefficients could be interpreted as the relative contribution of each variable to
284 the model sets (Neter et al. 1996).

285 We evaluated expected interactions among predictor variables using the global model
286 prior to modeling all possible combinations of predictor variables. Interactions were small, not

287 significant, and failed to improve model fit ($<2 \Delta AIC_c$), and thus, were excluded from further
288 modeling because their inclusion can alter model-averaged estimates of the independent
289 counterparts of those terms (Arnold 2010). We also predicted that sensitivity among herd units to
290 changes in climate and plant phenology may differ between those with declining trends in calf-
291 cow ratios and those that are stable. Using the best model ($\Delta AIC_c = 0$) identified in previous
292 analyses, we also evaluated an interaction between predictor variables and status (declining
293 versus stable) using the same aforementioned criteria.

294 In some instances, relationships between a biological factor, such as calf recruitment, and
295 a climate covariate may be an artifact of a co-occurrence of similar linear trends through time
296 (Grosbois et al. 2008). Consequently, calf recruitment could be a function of some other
297 overlooked causal factor, rather than climate. To account for the potential of this spurious result,
298 we evaluated the relationship between climate or plant phenology variables within our best
299 models ($\Delta AIC_c = 0$) identified in previous analyses and the residuals from a regression between
300 year and calf-cow ratios. The residual analysis allowed us to determine whether variation in de-
301 trended calf-cow ratios was still accounted for by climate or plant phenology covariates
302 (Grosbois et al. 2008).

303 **Results**

304 Calf-cow ratios during 1980-2009 across 18 herd units in the Rocky Mountains averaged 46.7
305 (SE = 0.81) and ranged between 15 and 100 calves per 100 adult females. We identified 8 herd
306 units that displayed evidence of declining calf-cow ratios (Table 1; Fig. 3a); those units occurred
307 in northwestern Wyoming, northeast Utah, and the sole herd unit in Colorado (Fig. 1). The other
308 10 herd units all had negative coefficients for the time trend, however, their slopes were not
309 different from zero (Table 1; Fig. 3b).

310 Significant changes in seasonal weather patterns and plant phenology were evident across
311 Shiras moose range in our study. During 1980-2009, average daily temperature during winter,
312 spring, summer, and autumn increased similarly at a region-wide average of 0.5-0.6 °C per
313 decade (Table 2). Daily maximum temperature during the same time period exceeded the upper
314 thermoregulatory threshold for moose 89.3% (SE = 0.009) during summer and 63.9% (SE =
315 0.017) during winter. Characteristics of spring green-up changed since 1989; start of spring and
316 length of spring decreased by ~3 days per decade, while spring green-up became more rapid
317 (Table 3).

318 Our evaluation of the effects of seasonal weather patterns indicated that calf-cow ratios
319 were associated mostly with PCs metrics that reflected annual temperature ($PC1_{t-1}$) and spring-
320 summer precipitation ($PC2_{t-1}$) from the year preceding when a cohort of calves was raised (Table
321 4). Standardized parameter estimates indicated a larger effect size of temperature ($\beta = -5.0$)
322 compared with spring-summer precipitation ($\beta = 3.2$). There was a significant interaction
323 between $PC1_{t-1}$ and herd unit status ($F_{2,280} = 17.3$, $p < 0.001$), indicating a difference in
324 sensitivity between herd units with declining and stable calf-cow ratios. Calf-cow ratios
325 decreased as $PC1_{t-1}$ increased in herd units with declining calf-cow ratios ($\beta = -9.86$, SE = 1.68,
326 $t_{280} = -5.87$, $p < 0.001$), but $PC1_{t-1}$ did not influence calf-cow ratios in herd units with stable calf-
327 cow ratios ($\beta = -0.95$, SE = 1.66, $t_{280} = -0.57$, $p = 0.57$; Fig. 4). In contrast, calf recruitment
328 increased similarly among herd units with declining and stable calf-cow ratios with rises in
329 spring-summer precipitation the preceding year (Fig. 5).

330 Metrics of seasonal plant phenology were often correlated with climatic variables PC1
331 (onset of spring: $r = -0.46$, $p < 0.001$; days of spring: $r = -0.13$, $p = 0.013$; rate of green-up: $r =$
332 0.38 , $p < 0.001$), and PC2 (onset of spring: $r = 0.52$, $p < 0.001$; days of spring: $r = 0.02$, $p = 0.66$;

333 rate of green-up: $r = -0.14$, $p = 0.006$). We assessed the relationship between calf-cow ratios and
334 plant phenology separately from climate because they were correlated and NDVI data were not
335 available prior to 1989. Rate of green-up during both the current and preceding year had
336 importance weights >0.90 , and displayed a similar negative relationship with calf-cow ratios
337 (Table 5). Only the parameter estimate for rate of green-up during the current year that a cohort
338 of calves was raised differed from zero. The effect of rate of green-up on calf recruitment was
339 similar between herd units with declining and stable calf-cow ratios indicating a more rapid rate
340 of spring green-up reduced calf-cow ratios the following winter (Fig. 6).

341 After accounting for a linear trend in calf-cow ratios through time, the outcomes from
342 previous analyses held, with slight decreases in effect size. Annual temperature during the
343 preceding year for herds with declining calf-cow ratios remained negative ($\beta = -4.75$, $SE = 1.57$,
344 $t_{280} = -5.87$, $p = 0.003$), and the effect of spring-summer precipitation during the preceding year
345 remained positive ($\beta = 2.22$, $SE = 0.70$, $t_{280} = 3.16$, $p = 0.002$). Likewise, the negative effect of
346 rate of spring green-up persisted with de-trended calf-cow ratios ($\beta = -2.70$, $SE = 1.07$, $t_{178} = -$
347 2.52 , $p = 0.013$).

348 **Discussion**

349 Recruitment reflects fecundity and survival of young, and because it is the most variable
350 demographic of large ungulate populations, determines interannual variation in population
351 growth (Raithel et al. 2007, Harris et al. 2008, DeCesare et al. 2012). Juveniles also are the age
352 class expected to be most sensitive to factors that affect forage quality and availability (Eberhardt
353 2002), because allocation of resources by their mother is secondary to maintenance and juveniles
354 lack the nutritional reserves to buffer against such variation. Therefore, understanding factors
355 that limit production and recruitment of young for moose at the southern periphery of its range

356 provides an indicator of how changing climatic conditions may affect viability of Shiras moose
357 populations. As expected, calf recruitment was affected by ambient temperatures and spring-
358 summer precipitation (H_1), but those effects occurred from the preceding year indicating
359 potential climate effects on fecundity and nutritional carryover (H_3). Although date of spring
360 green-up or length of spring had no apparent effect on calf recruitment, a more rapid rate of
361 green-up during the year a calf was raised had a negative effect on calf recruitment (H_2).

362 Extreme climate events, particularly during winter, are well-recognized events that can
363 reduce overwinter survival and subsequent recruitment of young for temperate herbivores (Hegel
364 et al. 2010a, Hegel et al. 2010b). Nevertheless, moose are uniquely adapted to a northern
365 environment, have the lowest thermal neutral zone and greatest chest height of any North
366 American ungulate, and are capable of feeding on willows above deep snow (Telfer and Kelsall
367 1984, Renecker and Hudson 1986). Although moose in some regions are sensitive to snow
368 conditions during winter (Crête and Courtois 1997, Sæther 1997), foraging conditions during
369 spring and summer frequently are more influential than winter snow for this northern herbivore
370 (Crête and Courtois 1997, Solberg et al. 1999, 2004, Herfindal et al. 2006a, Grøtan et al. 2009).
371 Also, given their often stochastic and yet, less frequent occurrence in recent decades (Shuman
372 2011), severe winters would not be expected to result in the near linear decline in calf
373 recruitment (Fig. 3) and abundance of moose populations at the southern periphery of their range
374 (Murray et al. 2006). Indeed, autumn-winter precipitation failed to enter our calf-recruitment
375 models as a variable of importance, and temperature had the opposite effect expected from a
376 context of severe winter weather (Table 4).

377 Owing to their almost obligatory use of *Salix* spp. throughout much of their range,
378 nutritional ecology of moose has been well studied. Studies have repeatedly shown that moose

379 effectively balance quality and quantity of forage acquisition to maximize digestible energy
380 within the constraints of consumption and digestion (Shipley 2010). Depending upon nutrient
381 intake, reproductive female can encounter a trade-off between the accumulation of body reserves
382 and investment in reproduction (Bårdsen et al. 2011). In accordance with life-history theory,
383 females of long-lived herbivores invest in reproduction according to their nutritional state (Testa
384 and Adams 1998), because somatic losses during lactation hold consequences for subsequent
385 survival and reproduction (Bårdsen and Tveraa 2012). Diet quality and the duration of its
386 availability during spring and summer is an important determinant of animal productivity (Cook
387 et al. 2004, Mcart et al. 2009), mainly because it occurs when fat accretion and energetic
388 demands for reproduction are greatest during that season (Bårdsen and Tveraa 2012). Although
389 early onset of vegetation green-up can be important following a long winter of nutritional deficits
390 (Pettorelli et al. 2005a, Herfindal et al. 2006b, Hegel et al. 2010a), our results suggest that
391 characteristics of the rate of green-up during spring were more important for calf recruitment in
392 Shiras moose. Warm springs may lead to rapid green-up and greater plant productivity, but a
393 slow and prolonged green-up increases the availability of high-quality forage by lengthening the
394 temporal window and spatial heterogeneity in green-up (Pettorelli et al. 2005a, 2007). Cool and
395 wet weather during the growing period improves forage quality by increasing nitrogen content,
396 whereas warm and dry spring conditions reduce nitrogen and increase fiber content and thus,
397 reduce digestibility (Lenart et al. 2002). Indeed, a longer window of access to growing and
398 highly digestible forage can increase growth and recruitment of juvenile ungulates (Ericsson et
399 al. 2002, Herfindal et al. 2006b, Pettoelli et al. 2007, Hegel et al. 2010a).

400 In addition to the immediate forage resources available to reproductive females,
401 carryover of previous winter and summer conditions can have profound effects on reproductive

402 success for capital breeders(Jönsson 1997), such as moose, that rely partially on nutrient reserves
403 to support reproduction (Testa and Adams 1998, Keech et al. 2000). We documented higher calf
404 recruitment 1 year after a year of cool temperatures with wet spring and summers. Direct weather
405 patterns had little detectable effect on calf recruitment of the current year, but presumably had a
406 cumulative effect on somatic reserves of females which could have reduced fecundity and
407 nutritional carryover (Testa and Adams 1998), and thereby, calf recruitment the following year.
408 Similarly, productivity of other moose populations is more strongly related to weather of the
409 preceding year than the current one (Crête and Courtois 1997, Solberg et al. 1999, Grøtan et al.
410 2009).

411 Moose are likely vulnerable to heat stress because they lack extensive abilities to sweat
412 and have the lowest upper critical temperature than any other northern ungulate (Schwartz and
413 Renecker 2007). Chronic heat stress may impair reproductive performance indirectly via
414 nutritional suppression as a result of increased metabolic costs, reduced appetite, and reduced
415 foraging time (Renecker and Hudson 1986, De Rensis and Scaramuzzi 2003). Over time, the
416 cumulative effects of only slight suppression in resource acquisition by increased heat loads
417 likely holds fitness consequences (White 1983), especially for females experiencing the burdens
418 of lactation. Although moose alter circadian activity patterns (Dussault et al. 2004) and seek
419 thermal refugia in response to warm temperatures (Schwab and Pitt 1991), whether such
420 behavioral responses compensate fully for warming thermal regimes remains unclear (Lowe et
421 al. 2010), especially when upper critical temperatures are surpassed consistently through summer
422 like they were in the Rocky Mountains. Female mouflon (*Ovis gmelini*) adjusted their daily time
423 budget to reduce thermal stress, but were unable to maintain daily activity rate during hot, calm
424 days (Bourgoin et al. 2011). When combined with deteriorating range conditions as a

425 consequence of climate warming or density dependence, thermoregulatory costs could be
426 contributing to reduced performance of moose populations at the southern periphery of their
427 range (Murray et al. 2006, Lenarz et al. 2010).

428 Density dependence plays an important role in shaping life-history traits of large
429 herbivores and in particular, growth and survival of young (Solberg et al. 1999, Stewart et al.
430 2005, Herfindal et al. 2006b, Gaidet and Gaillard 2008). The degree of food limitation is
431 determined by density-dependent feedback relative to the proximity of a population to carrying
432 capacity (K); thus, directional or stochastic changes in K caused by variation in the environment
433 complicate relationships between population density and performance (Sæther 1997, Pierce et al.
434 2012). We were unable to directly account for density within our recruitment models because
435 reliable population estimates were not available for most herd units. Nevertheless, density by
436 itself may only be meaningful when considered relative to resource availability unless K can be
437 assumed to be constant (Pierce et al. 2012), which was likely an invalid assumption given
438 warming climate with reduced precipitation and advancing plant phenology in our study area.
439 Furthermore, data from trend counts from herd units with declining calf cow ratios are
440 suggestive of declining populations (Brimeyer and Thomas 2004), which would have yielded a
441 positive relationship between population density and calf recruitment—a misleading result given
442 that K likely has declined through time.

443 Geographical variation in population dynamics of vertebrates is common, and in the
444 absence of predation, is underpinned by the interaction between stochastic and density-dependent
445 factors (Sæther 1997). Temporal variation in climate can synchronize population fluctuations at a
446 broad spatial scale (Grøtan et al. 2005), and likely was a primary reason for widespread declines
447 in calf recruitment in the Rocky Mountains. Despite similar changes in climate and plant

448 phenology across our study region, however, 10 of 18 herd units did not exhibit a temporal trend
449 through time and the effect of annual temperature regimes were not evident in herd units with
450 stable calf-cow ratios (Fig. 4), indicating that other local factors may be modulating the effects of
451 climate change. Following introduction or expansion into a previously unoccupied range,
452 herbivore populations often increase to peak abundance, crash, and subsequently, increase to a
453 new lower abundance (Forsyth and Caley 2006). This phenomenon, termed the irruptive
454 paradigm, occurs as herbivore populations benefit from previously unexploited resources that
455 become depleted by density-dependent herbivory (Forsyth and Caley 2006). Moose are
456 considered keystone species, and can function as engineers in ecosystems by modifying
457 vegetation structure, composition, and nutrient cycling (Molvar et al. 1993, Post et al. 1999,
458 Stolter 2008, Shipley 2010, Seaton et al. 2011); that when considered in tandem with variation in
459 life-history characteristics in response to density dependence, results in oscillatory populations
460 with overshoots of K (Sæther et al. 1996, Solberg et al. 1999). Herd units with declines in calf
461 recruitment during the past 3 decades, in general, emanated from herd units that have been
462 established for the longest duration (Fig. 1). In particular, moose have been present in northwest
463 Wyoming since the early 1900s (Brimeyer and Thomas 2004), and likely served as a source for
464 natural dispersal and expansion southward through western Wyoming and into northeastern Utah
465 to form established populations by the 1950s (Wolfe et al. 2010). Although calf recruitment in
466 North Park, Colorado also has declined and was recently established via introductions in the late-
467 1970s, most populations displaying stable trends in calf-cows were present since only the 1970s,
468 compared with most of those that were well established by the late-21st century.

469 We hypothesize that the disparity in calf-cow ratios across our study area was a result of
470 populations that were established recently having not yet reached the K of their habitat following

471 introduction or expansion into new range (Forsyth and Caley 2006). Reduced density and
472 browsing intensity in those ranges would improve food resources and enhance nutritional
473 condition (Mcart et al. 2009, Seaton et al. 2011), thereby providing a buffer against depletion in
474 critical body stores with changing climate and plant phenology (Tveraa et al. 2007). Indeed,
475 effects of environmental stochasticity are often stronger in populations already suppressed by
476 density dependence or other factors (Herfindal et al. 2006a, Wilmers et al. 2006, Tveraa et al.
477 2007). Management actions aimed at improving forage quality and reducing intraspecific
478 competition in populations with declining calf-cow ratios are liable to reduce the sensitivity to
479 and negative effects of current changes in climate, by enhancing their nutritional buffer against
480 such changes. We also suspect, however, as other populations continue to grow toward K , and
481 advancing plant phenology reduces K , that sensitivity to climate will increase as their nutritional
482 buffer is reduced. Evaluating nutritional status in conjunction with demographics will provide
483 fruitful avenues of research to disentangle the strength and direction of the effects of changing
484 climate, especially when evaluating expected viability of populations at their southern extent.
485 Accounting for nutritional status is critical for long-lived, iteroparous mammals because nutrition
486 underpins their conservative life-history strategy, and doing so likely will expose some of the
487 unexplained variation in population responses to climate across species range.

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705 Table 1. Temporal trends of calf-cow ratios for 18 herd units in Rocky Mountains, USA, 1980-
 706 2009.

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HerdUnit	Slope	r^2	P -value	n	Status
Bighorn	-0.07	0.00	0.83	27	Stable
Cache	-0.50	0.11	0.30	12	Stable
Chalk Creek	-0.50	0.33	0.051	12	Declining
Dubois	-0.02	0.00	0.94	23	Stable
Jackson	-1.04	0.64	<0.001	29	Declining
Kamas	-0.58	0.08	0.41	11	Stable
Lander	-0.33	0.07	0.15	30	Stable
Lincoln	-0.11	0.02	0.51	27	Stable
Morgan Rich	-0.59	0.31	0.074	11	Declining
North Park	-0.46	0.14	0.091	21	Declining
North Slope Daggett	-1.53	0.28	0.10	10	Declining
North Slope Summit	-0.74	0.22	0.11	13	Stable
Ogden	-0.49	0.10	0.34	11	Stable
Snowy Range	-2.42	0.24	0.18	10	Stable
South Slope	-0.36	0.14	0.28	10	Stable
Sublette	-0.56	0.45	<0.001	30	Declining
Targhee	-0.77	0.37	0.006	19	Declining
Uinta	-0.54	0.20	0.10	15	Declining

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711 Table 2. Parameter estimate, standard error, and test statistics describing temporal trend in
 712 seasonal patterns in average daily temperature (°C) and cumulative precipitation (cm) for Shiras
 713 moose range in 18 herd units in the Rocky Mountains, USA, 1980-2009. Temporal trends were
 714 modeled as a fixed effect of year with a random intercept for herd unit.

Climate	Season	β	SE	F-value	p-value
Temperature	Winter	0.064	0.0062	103.88	<0.001
	Spring	0.051	0.0071	51.62	<0.001
	Summer	0.061	0.0054	125.20	<0.001
	Autumn	0.052	0.0057	82.70	<0.001
Precipitation	Winter	-0.048	0.039	1.53	0.22
	Spring	-0.10	0.0022	22.20	<0.001
	Summer	-0.064	0.24	7.18	0.0076
	Autumn	-0.043	0.23	3.59	0.059

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718 Table 3. Parameter estimate, standard error, and test statistics describing temporal trend in spring
719 plant phenology based on the normalized difference vegetation index (NDVI) for Shiras moose
720 range in 18 herd units in the Rocky Mountains, 1989-2009. Temporal trends were modeled as a
721 fixed effect of year with a random intercept for herd unit.

Phenology metric	β	SE	F-value	p-value
Start of spring	-0.29	0.12	5.38	0.021
Length of spring	-0.30	0.12	6.15	0.014
Rate of spring green-up	0.0002	0.00004	15.46	<0.001

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725 Table 4. Model averaged parameter estimates, confidence interval, and Akaike importance
 726 weights from models of the effect of principal components (PCs) variables during the current and
 727 preceding year on calf recruitment of Shiras moose ($n = 304$) for 18 herd units in the Rocky
 728 Mountains, USA, 1980-2009. Principal components corresponded to annual temperature (PC1),
 729 spring-summer precipitation (PC2), and autumn precipitation (PC3). Covariates were
 730 standardized ($\bar{x} = 0$, $SD = 1$) and asterisks adjacent to parameter estimates indicate 90% CI do
 731 not overlap zero.

Parameter	Estimate	90% CI		Importance weight
		Lower	Upper	
PC1	-0.040	-0.11	0.029	0.01
PC2	0.087	-0.70	0.88	0.65
PC3	0.44	-0.44	1.33	0.72
PC1 _{t-1} *	-5.00	-6.93	-3.07	0.99
PC2 _{t-1} *	3.18	1.98	4.37	1.00
PC3 _{t-1}	0.22	-0.70	1.14	0.69

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735 Table 5. Model averaged parameter estimates, confidence interval, and Akaike importance
 736 weights from models of the effect of plant phenology metrics during the current and preceding
 737 year on calf recruitment of Shiras moose ($n = 199$) for 18 herd units in the Rocky Mountains,
 738 1980-2009. Covariates were standardized ($\bar{x} = 0$, $SD = 1$) and asterisks adjacent to parameter
 739 estimates indicate 90% CI do not overlap zero.

Parameter	Estimate	90% CI		Importance weight
		Lower	Upper	
Onset of spring	-0.049	-0.43	0.33	0.18
Rate green-up*	-2.70	-4.88	-0.53	0.97
Days spring	-0.13	-0.55	0.29	0.18
Onset of spring _{t-1}	1.04	-0.29	2.36	0.43
Rate green-up _{t-1}	-1.91	-4.52	0.71	0.90
Days spring _{t-1}	-0.015	-0.43	0.40	0.19

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743 List of Figures

744 Figure 1. Locations of 18 herd units of Shiras moose populations in the Rocky Mountains of
745 Wyoming, Utah, and Colorado, USA, in which effects of climate and plant phenology on calf
746 recruitment were evaluated. Herd units in red indicate populations with declining calf-cow ratios
747 ($P \leq 0.10$), 1980-2009. Herd units included Bighorn (A), Targhee (B), Jackson (C), Dubois (D),
748 Sublette (E), Lander (F), Lincoln (G), Uinta (H), Snowy Range (I), Cache (J), Ogden (K),
749 Morgan Rich (L), Chalk Creek (M), Kamas (N), North Slope Summit (O), North Slope Daggett
750 (P), South Slope (Q), Central Mountains (R), and North Park (S).

751 Figure 2. Climograph of mean monthly temperature and precipitation that define seasons for
752 Shiras moose range in Colorado, Utah, and Wyoming, USA, 1980-2009. Solid lines indicate
753 months within a particular season and dashed line separate seasons.

754 Figure 3. Annual recruitment rates (calf-cow ratio) for Shiras moose in 18 herd units in Rocky
755 Mountains, USA for stable ($p > 0.10$) and declining ($p < 0.10$) trends in calf-cow ratios, 1980-
756 2009.

757 Figure 4. Predicted relationship ($\pm 95\%$ CI) between annual recruitment rates (mid-winter calf-
758 cow ratios) of Shiras moose and a metric representing annual temperature during the preceding
759 year for populations with declining (solid line) and stable (dashed line) trends in calf recruitment,
760 for 18 herd units in Rocky Mountains, USA, 1980-2009. Size of each point represents the inverse
761 of the variance in each calf-cow ratio estimate, which was used as a weighting term in predictive
762 models.

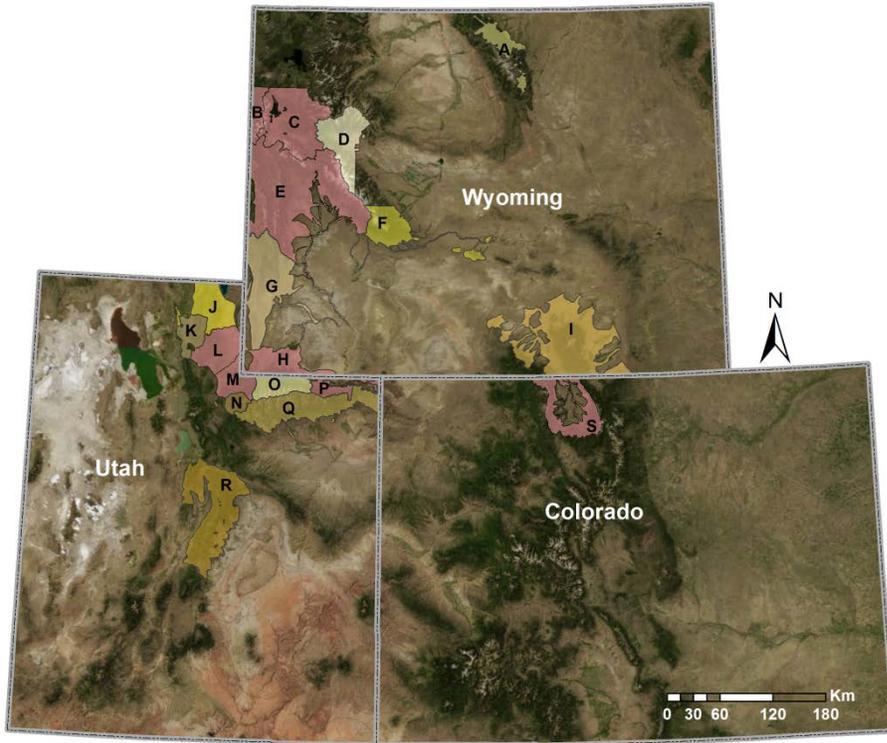
763 Figure 5. Predicted relationship ($\pm 95\%$ CI) between annual recruitment rates (mid-winter calf-
764 cow ratios) of Shiras moose and a metric representing spring-summer precipitation during the
765 preceding for year populations with declining and stable trends in calf recruitment for 18 herd

766 units in Rocky Mountains, USA, 1980-2009. Size of each point represents the inverse of the
767 variance in each calf-cow ratio estimate, which was used as a weighting term in predictive
768 models.

769 Figure 6. Predicted relationship ($\pm 95\%$ CI) between annual recruitment rates (mid-winter calf-
770 cow ratios) of Shiras moose and rate of spring green-up for populations with declining and stable
771 trends in calf recruitment for 18 herd units in Rocky Mountains, USA, 1980-2009. Size of each
772 point represents the inverse of the variance in each calf-cow ratio estimate, which was used as a
773 weighting term in predictive models.

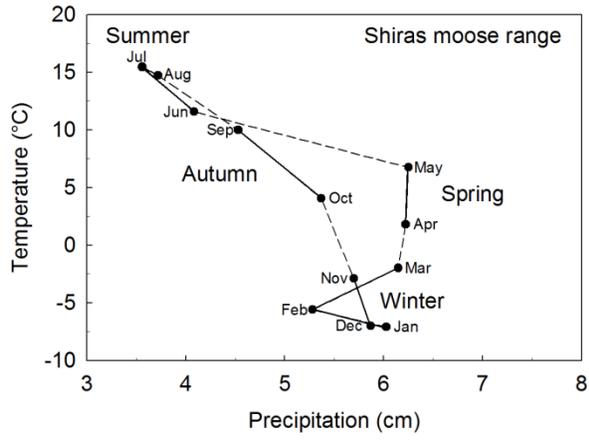
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775 Fig. 1.



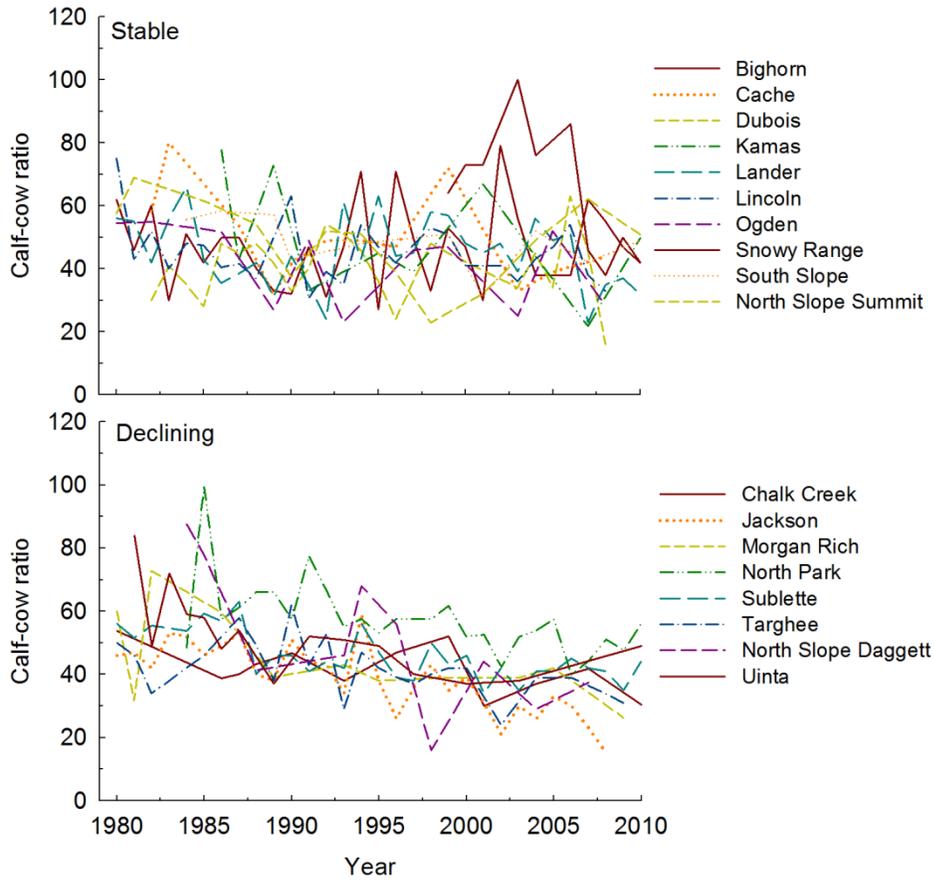
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779 Fig. 2.
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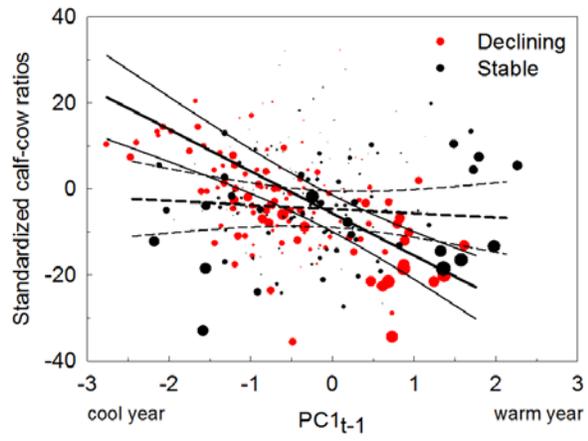
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782 Figure 3.
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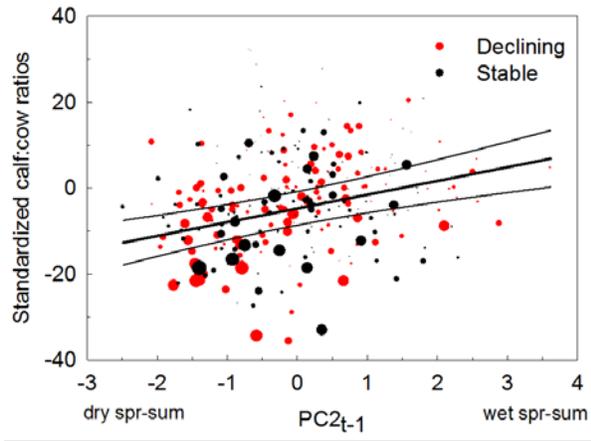
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787 Fig. 4.
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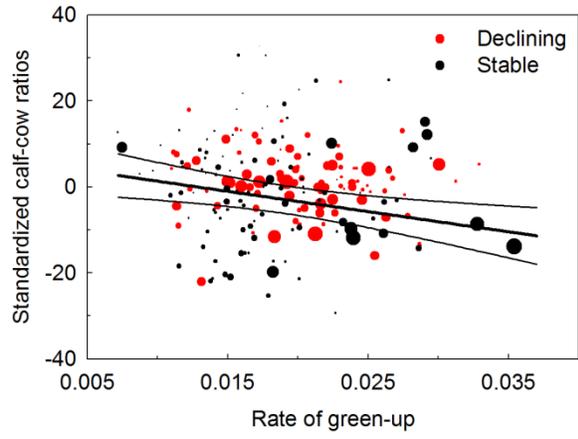
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793 Fig. 5.
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