

EARLY ONSET OF VEGETATION GROWTH VS. RAPID GREEN-UP: IMPACTS ON JUVENILE MOUNTAIN UNGULATES

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Abstract. Seasonal patterns of climate and vegetation growth are expected to be altered by global warming. In alpine environments, the reproduction of birds and mammals is tightly linked to seasonality; therefore such alterations may have strong repercussions on recruitment. We used the normalized difference vegetation index (NDVI), a satellite-based measurement that correlates strongly with aboveground net primary productivity, to explore how annual variations in the timing of vegetation onset and in the rate of change in primary production during green-up affected juvenile growth and survival of bighorn sheep (*Ovis canadensis*), Alpine ibex (*Capra ibex*), and mountain goats (*Oreamnos americanus*) in four different populations in two continents. We indexed timing of onset of vegetation growth by the integrated NDVI (INDVI) in May. The rate of change in primary production during green-up (early May to early July) was estimated as (1) the maximal slope between any two successive bimonthly NDVI values during this period and (2) the slope in NDVI between early May and early July. The maximal slope in NDVI was negatively correlated with lamb growth and survival in both populations of bighorn sheep, growth of mountain goat kids, and survival of Alpine ibex kids, but not with survival of mountain goat kids. There was no effect of INDVI in May and of the slope in NDVI between early May and early July on juvenile growth and survival for any species. Although rapid changes in NDVI during the green-up period could translate into higher plant productivity, they may also lead to a shorter period of availability of high-quality forage over a large spatial scale, decreasing the opportunity for mountain ungulates to exploit high-quality forage. Our results suggest that attempts to forecast how warmer winters and springs will affect animal population dynamics and life histories in alpine environments should consider factors influencing the rate of changes in primary production during green-up and the timing of vegetation onset.

Key words: body mass; green-up; NDVI; plant phenology; population dynamics; resource–animal interactions; survival.

INTRODUCTION

Predicting the effects of global warming on organisms of different ecosystems is a major challenge for ecologists (Walther et al. 2002). In recent decades, climate change has affected many biological systems (Crick and Sparks 1999, Post and Stenseth 1999, Inouye et al. 2000), and much effort is devoted to understand the consequences of such changes (Hughes 2000, Hulme 2005). Global climate change is altering seasonal patterns: for example, the average start of the growing season shifted by eight days from 1989 to 1998 in Europe (Chmielewski and Rötzer 2002) and by 5–6 days from 1959 to 1993 in North America (Schwartz and Reiter 2000). The life history strategies of species experiencing seasonal environments have been selected

to match the best environmental conditions. With seasonal patterns altered, however, the reproduction of these species may become out of phase with the period of highest environmental productivity (Thomas et al. 2001, Berteaux et al. 2004). The ultimate consequences of the timing of birth are expected to depend to a large extent on the phenology of organisms at other trophic levels (Visser et al. 2004). In seasonal environments, large herbivores typically give birth in late spring or early summer to match the vegetation green-up period and allow offspring to benefit from the entire vegetation growing season (Rutberg 1987). By shifting plant phenology toward an earlier vegetation onset, global warming could affect juvenile growth and survival of many species (Inouye et al. 2000, Visser et al. 2004, Pettorelli et al. 2005a, c). Highly seasonal environments such as those in arctic or alpine areas are expected to be strongly affected by climate change (Oechel et al. 1997).

There is much interest in the influence of global warming in mountainous regions (Diaz and Bradley

Manuscript received 25 May 2006; revised 3 August 2006; accepted 24 August 2006. Corresponding Editor: C. M. Herrera.

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1997), where warmer winters are expected to change the rain/snow ratio. In northern mountains, climate change may lead to more winter precipitation, resulting in deeper snowpack at high elevations (Inouye et al. 2000, Mysterud et al. 2001, Pettorelli et al. 2005a). Increasingly warm winters, however, may augment winter rain and run-off at the expense of snowpack, as the rain/snow boundary moves higher in elevation (Beniston and Fox 1996, Lapp et al. 2005).

The timing of snowmelt should determine the timing of spring vegetation onset and thereby affect life histories of alpine ungulates (Rutberg 1987, Kudo 1991). Because plant phenology is the major factor affecting forage quality (Laycock and Price 1970), it is frequently described as the driving force in habitat use by vertebrate herbivores (Fryxell 1991, Albon and Langvatn 1992). Both plant crude protein content and digestibility peak early in the growing season, and then rapidly decline as the vegetation matures: higher forage quality is thus associated with early phenological stages where new green leaves dominate biomass (Crawley 1983). Feeding patch choice and forage selection by ungulates are positively associated with plant quality (White 1983, Wilmshurst et al. 1995). A shorter period when high-quality forage is available should thus lower herbivore performance (Albon and Langvatn 1992, Langvatn et al. 1996). Because forage quality peaks during early phenological stages, slow vegetation growth should prolong access to high-quality forage. Moreover, spatial heterogeneity in snowmelt may lead to spatial heterogeneity in the timing of vegetation green-up onset, which may lengthen the period when high-quality forage is accessible to herbivores (Mysterud et al. 2001, Pettorelli et al. 2005a). Rapid temporal changes in plant productivity might thus correlate both with fast vegetation growth and reduced spatial heterogeneity in timing of vegetation onset in alpine areas, shortening the period of access to high-quality forage for herbivores.

Many studies have focused on the impact of an early start of vegetation growth on herbivore performance (e.g., Portier et al. 1998, Côté and Festa-Bianchet 2001a, Griffith et al. 2002). Few, however, have attempted to partition the effect of an early start of vegetation growth from that of a rapid rate of changes in vegetation phenology, possibly leading to a shorter period of access to high-quality forage. Here we assess the effects of annual variations in the timing of vegetation green-up onset and the rate of change in plant productivity during green-up on the growth and survival of juvenile mountain ungulates in North America and Europe. We indexed vegetation dynamics by the normalized difference vegetation index (NDVI), a satellite-based measurement that correlates strongly with aboveground net primary productivity (Pettorelli et al. 2005b). Previous studies generally considered climatic variables as proxies for plant phenology (Portier et al. 1998, Toïgo et al. 1999). The links between weather and vegetation

phenology, however, are complex, involving a number of climatic variables and depending on location, while the link between primary productivity and NDVI is direct and has been shown to be linear, robust, consistent, and strong in temperate areas (Pettorelli et al. 2005b). We considered three species of mountain ungulates: bighorn sheep *Ovis canadensis*, Alpine ibex *Capra ibex*, and mountain goat *Oreamnos americanus* in four populations. These species have broadly similar habitat use, social organization, foraging behavior, sexual size dimorphism, fertility, and body mass (Festa-Bianchet 1988a, Festa-Bianchet et al. 1997, Toïgo et al. 1999, Côté and Festa-Bianchet 2003). Because juveniles are the age class most likely to be affected by both extrinsic and density-dependent processes in ungulates (Gaillard et al. 2000), we focused on the relationships between vegetation phenology and juvenile growth and survival.

Early vegetation onsets positively affect the performance of ungulates inhabiting highly seasonal environments (Giacometti et al. 2002, Pettorelli et al. 2005c). We consequently expected (H_1 , hypothesis 1) a positive effect of early vegetation onsets on juvenile growth and survival. Rapid changes in plant productivity during green-up should be associated with a reduced period of access to high-quality forage, either through rapid vegetation growth or reduced spatial heterogeneity in the timing of the vegetation onset. We therefore expected that (H_2 , hypothesis 2) rapid changes in NDVI during green-up would be negatively related to juvenile survival and growth. Finally, we expected that late vegetation onsets or rapid changes in plant productivity would have stronger effects under harsh environmental conditions such as at high population density (H_3 , hypothesis 3).

MATERIALS AND METHODS

Study areas and sample collection

Ram Mountain (52° N, 115° W; elevation, 1700–2200 m), Alberta, Canada, is an isolated mountain ~30 km east of the main Canadian Rockies. The area used by sheep (~38 km²) is characterized by alpine and subalpine habitat. Each year, sheep are trapped from the end of May to late September and weighed to within 125 g with a spring scale. All ewes have been marked since 1976, and >80% of the lambs were caught in most years. Here we considered the body mass of 332 lambs weighed between 1982 (when NDVI measurements first became available) and 2004. We also calculated the proportion of marked lambs in September ($n = 634$) that were reobserved as yearlings the following spring (end of May) to estimate first-year overwinter survival (see Festa-Bianchet et al. 1997 for more details on field methods).

The Sheep River bighorn sheep population (50° N, 114° W) is also in Alberta, 160 km south of Ram Mountain. In winter, the population uses a low-elevation range (1450–1700 m) in the eastern slopes of

the Rocky Mountains. In spring, ewes migrate to higher elevation (1800–2250 m) ~12–15 km west of the winter range (Festa-Bianchet 1988a). The winter range (14 km²) is characterized by grassy meadows interspersed with aspen (*Populus tremuloides*) copses, while the summer range (~50 km²) consists of alpine and subalpine habitat. Since 1981, >95% of the sheep have been marked (Festa-Bianchet 1988a, b). Each autumn, lambs aged 4–6 months are immobilized with a dart gun and their chest girth is measured. Chest girth is highly correlated with lamb mass ($r = 0.90$, Pelletier et al. 2005). We considered the mean chest girth adjusted for capture date, per year and per sex, of 428 lambs born between 1982 and 2004. To estimate lamb overwinter survival, we considered the proportion of lambs marked in September–November ($n = 464$) that were reobserved as yearlings the following spring (end of April–May).

Caw Ridge is located in the Rocky Mountains of west-central Alberta (54° N, 119° W). Mountain goats use ~28 km² of alpine tundra and open subalpine forests from 1750 to 2185 m (Côté and Festa-Bianchet 2001a). Since 1989, the population has fluctuated from 76 to 147 individuals. We considered the sex-specific average mass of 137 kids weighed between late May and early October in 1989–2004. No kids were weighed in 1998–2000. We used the proportion of kids in September ($n = 349$) that were reobserved as yearlings the following spring (end of May–June) to estimate kid overwinter survival, from 1989 to 2004.

The Gran Paradiso National Park (GPNP hereafter) in northwestern Italy (45° N, 7° E) is composed entirely of mountainous terrain. Alpine pastures, moraines, cliffs, glaciers, and rock account for 59% of its 720 km². Ibex use elevations ranging from ~800 m to beyond the upper limit of vegetation at ~3200 m. Yearly autumn counts are conducted in the entire park by ~30 park wardens over two consecutive days in September, when the number of kids, yearlings, and adult males and females are determined (Jacobson et al. 2004). We used the proportion of kids that were seen as yearlings the following autumn to estimate first-year overwinter survival in 1982–2004 (number of yearlings in year t /number of kids in year $t - 1$). Because censuses are done in September, juvenile survival in the GPNP was from 4 to 16 months of age. Estimates of survival based on population counts are subject to biases, and their quality is far lower than estimates based on marked individuals (Gaillard et al. 2000). However, those biases should not vary from year to year, making the comparison of vegetation phenology and survival estimates possible in GPNP.

Weather data

Alberta.—Data on snowfall (in centimeters), precipitation in water equivalent (in millimeters) and average temperature (in degrees Celsius) in April and May were obtained from the Environment Canada meteorological stations near the study sites (Grande Cache [1255 m] for

Caw Ridge, Nordegg [1326 m] for Ram Mountain, High River [1219 m] for Sheep River). Those data were available from 1988 to 2004 for Caw Ridge, and from 1982 to 2004 for Sheep River and Ram Mountain.

GPNP.—Data on snow depth (in centimeters), rain (in millimeters), and average temperature (in degrees Celsius) in April and May were obtained from the Serrù meteorological Station (Azienda Elettrica Municipalizzata Torino) located inside the GPNP at an elevation of 2240 m (1982–2004). The average temperature was defined as (average maximal temperature + average minimal temperature)/2.

NDVI data

Data collected by the National Oceanic and Atmospheric Administration satellites and processed by the GIMMS group (Tucker et al. 2005) are available. From these, NDVI values have been produced from visible and near-infrared reflectance measurements ($NDVI = [NIR - VIS]/[NIR + VIS]$, where NIR is the near infrared light reflected by the vegetation, and VIS is the visible light reflected by the vegetation). We used the best available corrected NDVI time series for the number of years considered. The spatial scale of resolution (pixel size) for that series is 64 km² and an NDVI value is available on a bimonthly basis, from July 1981 to now (Pettorelli et al. 2005b). Bimonthly NDVI values are based on 15-d temporal composites (maximum value compositing) to reduce cloud contamination problems (Pettorelli et al. 2005b). We used NDVI averages from one pixel for Ram Mountain, eight pixels for Sheep River, five pixels for Caw Ridge, and 11 pixels for the GPNP. For Ram Mountain, we thus used the minimum possible scale, i.e., 64 km². For the other study areas, we used the total spatial range of the populations, covering areas likely much larger than those actually used by the study populations. We used the minimum number of pixels possible considering the shape of the study areas and their overlap with NDVI pixels. We thus traded spatial resolution for data quality, assuming that the annual phenological signal captured at the scale of the GIMMS data would be correlated with vegetation productivity in the different study sites. We could not, however, test this assumption, because there are no data on the phenology of forage available for our study sites.

We used NDVI measurements around the mean date of green-up to distinguish early from late annual onsets of vegetation growth. The timing of the onset of vegetation growth was thus indexed using the sum of the two bimonthly NDVI values in May (vegetation growth typically starts in May in all study sites; see Fig. 1a), an index that correlates with vegetation biomass (integrated NDVI [INDVI], Pettoelli et al. 2005b). The rate of change in plant productivity during green-up, when indexed using NDVI, is defined as the rate of increase between two fixed dates (generally between the estimated date when vegetation starts growing and the

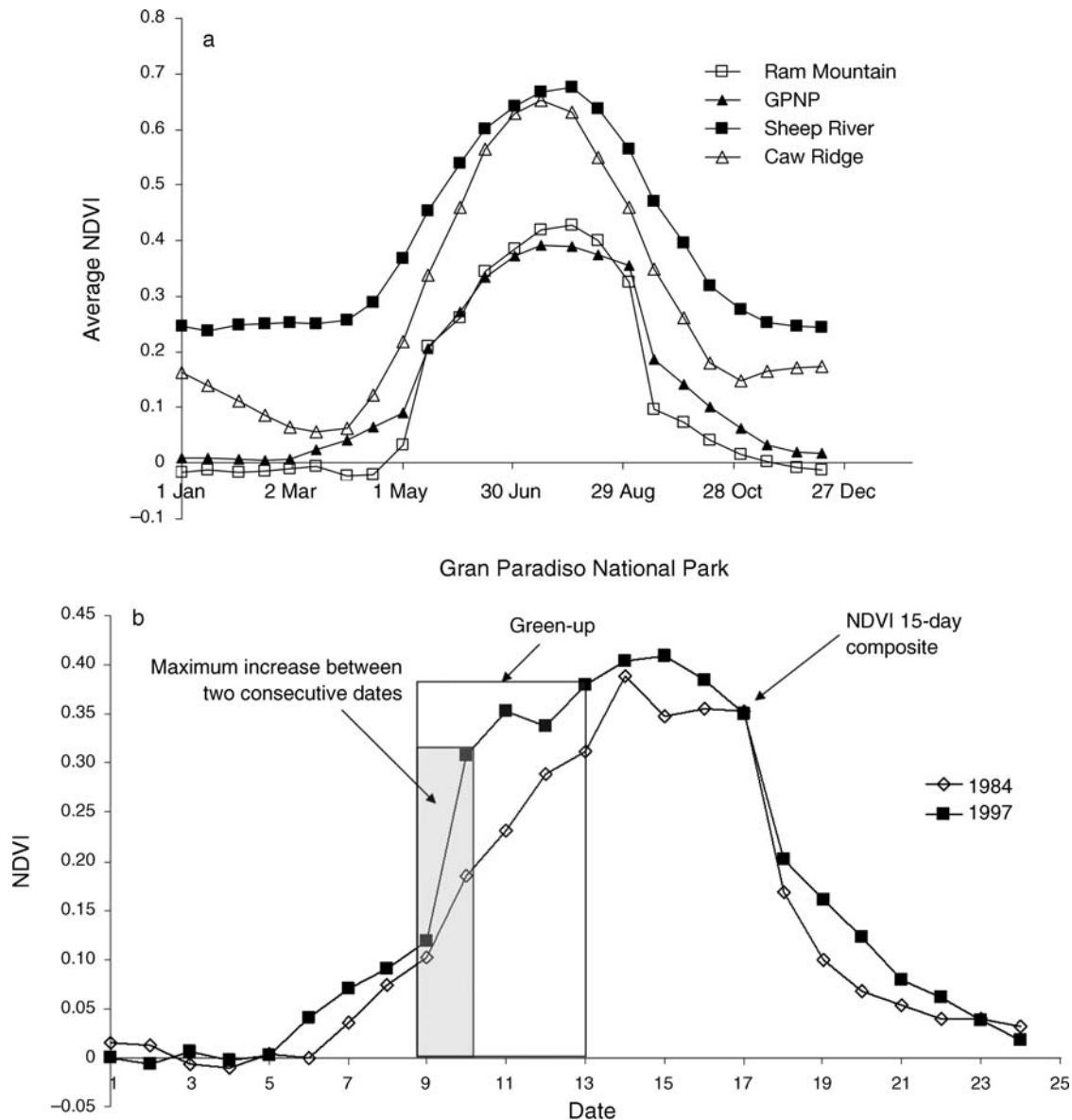


FIG. 1. (a) Average normalized difference vegetation index (NDVI) values (1982–2004) in four study areas: Ram Mountain (Alberta), Sheep River (Alberta), Caw Ridge (Alberta), and Gran Paradiso National Park (GPNP, Italy). (b) Illustration of the concept of the maximal increase in NDVI. We present two years (1984 and 1997) in the Gran Paradiso National Park exhibiting contrasted vegetation dynamics. The x -axis represents each NDVI picture available (two per month, for a total of 24 pictures per year), ranging from 1 to 24 and starting on 1 January. The period considered in the analyses extended from early May to early July. In both years (1984 and 1997), the maximal increase in NDVI occurred between 1–15 May and 15–30 May; however the rate of increase between these two periods in 1997 was double that in 1984.

estimated date when vegetation biomass reaches a plateau; Pettorelli et al. 2005b). Because for all sites vegetation growth reaches a plateau in July (Fig. 1a), we considered the slope between early May and early July as an index of the rate of vegetation changes during green-up. This last index, however, does not capture any deviation from a linear increase in NDVI between those two dates and smooths the rate of change during green-up. For example, a linear and a logarithmic

increase between the two dates would provide the same slope. We therefore also indexed the rate of vegetation changes during green-up as the maximal slope between any two consecutive bimonthly NDVI values from early May to early July (Reed et al. 1994, Kaduk and Heinmann 1996, Fig. 1b). Higher maximal increases indicate faster changes in vegetation growth and higher deviations from a linear increase in NDVI during green-up.

Analyses

We expected climatic conditions in April/May to determine the average and maximal rate of changes in primary productivity during green-up. Precipitation was transformed as “ $\log(\text{precipitation} + 4)$ ” to stabilize the variance (Pettorelli et al. 2005a). Because there were no a priori reasons to believe that different relationships between climate and phenology should be expected between Ram Mountain, Sheep River, and Caw Ridge, climatic data for Alberta were pooled and study site was considered as a factor. Because temperature and snowfall in April were correlated in Alberta ($R^2 = 0.11$, slope = -0.05 ± 0.02 , mean \pm SE, $P = 0.01$), we considered the residuals of this regression as an index of snowfall in April when analyzing the relationships between phenological measures and weather data.

As lamb chest girth and body mass increased during the period of capture, both parameters were adjusted (girth at Sheep River to 20 November; body mass at Ram Mountain to 15 September; Festa-Bianchet et al. 1997, Pelletier et al. 2005) before determining the yearly sex-specific means. At Caw Ridge, kid body mass was adjusted to 30 July (the mean date of capture for the 137 kids considered) using the slope of the linear regression between mass and date without distinction for sex (Côté and Festa-Bianchet 2001a), before determining the yearly sex-specific means. Mass and chest girth were ln-transformed to stabilize the variance (Sokal and Rohlf 1995). Using linear models weighted for yearly sample size, we explored the linear and quadratic relationships between NDVI measures and the chest girth or body mass of juveniles.

The annual proportion of juveniles that survived the winter was arcsine square-root transformed (Sokal and Rohlf 1995). First-year winter survival is not sex-biased (Festa-Bianchet et al. 1997, Côté and Festa-Bianchet 2001a). Lamb survival at Sheep River and Ram Mountain was affected by cougar (*Puma concolor*) predation episodes (Sheep River: one from 1993 to 1995, and one from 1999 to 2004; Ram Mountain: one from 1997 to 2003; Festa-Bianchet et al. 2006) and a pneumonia epizootic in Sheep River (1985–1986; Festa-Bianchet 1988a). To account for such effects, we used a dummy variable (0/1, with 1 coding for cougar predation or the occurrence of the epizootic). Using linear models on arcsine square-root transformed proportions, we then explored the linear and quadratic relationships between NDVI measures and survival.

Because density-dependent responses were expected at Ram Mountain and the GPNP (Portier et al. 1998, Jacobson et al. 2004), we took into account population density while modeling the effect of NDVI on body mass and first-year survival. Density at Ram Mountain was indexed as the ln-transformed average body mass of yearling females in June, an index of resource availability (Coltman et al. 2003, Festa-Bianchet et al. 2004). Because the yearly maximal increase in NDVI at time t correlated with this index of density at time t ($R^2 = 0.21$,

slope = -0.63 ± 0.27 , $P = 0.03$), we used the residuals of this regression to account for changes in density. Density in the GPNP was indexed using yearly total population counts (Jacobson et al. 2004). There was no correlation between this index of density and the yearly maximum increase in NDVI at the GPNP.

In three out of the four populations, several factors have been described to influence juvenile survival and growth such as birth date and age or condition of the mother (Festa-Bianchet 1988b, Festa-Bianchet et al. 2000, Côté and Festa-Bianchet 2001a, b, Gendreau et al. 2005). Here we used yearly averages because we were interested in the impact of annual variations in phenology on annual average performance. We also wanted to explore whether similar patterns could be observed in Canada and in Europe, in the GPNP, where individual data are not available.

Model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 1998). All continuous variables were standardized when checking for interactions between them. Temporal autocorrelation among residuals was checked, and was not significant for all comparisons. All statistical analyses were performed in the statistical package R (*available online*).⁶

RESULTS

Phenology and local climate

Indicators of warm and wet springs influenced vegetation phenology as assessed by NDVI in our study sites. In Alberta (Appendix: Table A1), warmer springs tended to be associated with rapid changes in plant productivity: temperatures in April (slope = 0.006 ± 0.003 , $P = 0.08$) and precipitation in May (slope = 0.03 ± 0.02 , $P = 0.06$) tended to affect positively maximal increases in NDVI. On the other hand, low snowfall in April (slope = -0.11 ± 0.06 , $P = 0.05$) and high precipitation in May (slope = 0.14 ± 0.04 , $P = 0.002$) favored high INDVI values in May. Neither temperature in April nor snowfall in April or precipitation in May was significantly related to the average slope of NDVI from early May to early July (all $P > 0.13$; Appendix: Table A1). In the GPNP (Appendix: Table A2), both high temperatures in May and low snow depth in April appeared to favor both the INDVI in May (suggesting early onset of vegetation growth) and the maximum increase in NDVI (suggesting rapid changes in plant productivity), but these relationships were nonsignificant (all $P > 0.09$).

Vegetation dynamics and early performance

Contrary to our first hypothesis (H_1), high INDVI in May did not influence the growth of bighorn lambs at Sheep River or mountain goat kids at Caw Ridge (Table 1; Appendix: Table A3; all $P > 0.77$). At Ram

⁶ (www.r-project.org)

TABLE 1. Parameter estimates from linear models weighted for sample sizes for the mean chest girth of bighorn lambs at Sheep River and the body mass of bighorn lambs at Ram Mountain and mountain goat kids at Caw Ridge.

Parameter	LSM	SE	T	P
A) Sheep River				
Intercept	4.43	0.02	317.76	<0.001
(Females – males)	-0.04	0.007	-5.41	<0.001
Max. inc.	-0.37	0.10	-3.50	0.001
B) Ram Mountain				
Intercept	3.41	0.04	82.43	<0.001
(Females – males)	-0.09	0.02	-3.85	<0.001
Res(BMY)	0.79	0.16	4.81	<0.001
Max. inc.	-0.48	0.17	-2.86	0.006
C) Caw Ridge				
Intercept	3.03	0.13	23.76	<0.001
(Females – males)	-0.07	0.04	-1.67	0.11
Max. inc.	-1.70	0.82	-2.08	0.05

Notes: Model selection procedures are presented in the Appendix (Table A3). “Res(BMY)” is the residual from the linear relationship between the maximum increase in NDVI and the average body mass of yearling females, indexing resource availability; “Max. inc.” is the maximum increase in NDVI during green-up.

Mountain, however, INDVI in May tended to negatively affect lamb mass in mid-September (slope = -0.19 ± 0.11, P = 0.08, Table 1; Appendix: Table A3). We found no effect in any study area of INDVI in May on first-year overwinter survival (Table 2; Appendix: Table A4; all P > 0.17).

As expected (H₂), rapid changes in plant productivity during green-up negatively influenced the growth of lambs and kids of both sexes at Ram Mountain, Sheep River, and Caw Ridge (Table 1, Fig. 2a–c; Appendix:

TABLE 2. Parameter estimates for overwinter survival of juvenile ungulates at (a) Ram Mountain, (b) Sheep River, (c) Caw Ridge, and (d) the GPNP, Italy.

Parameter	LSM	SE	T	P
A) Ram Mountain				
Intercept	1.22	0.14	8.45	<0.001
Res(BMY)	1.56	0.53	2.94	0.008
Max. inc.	-1.64	0.65	-2.51	0.02
B) Sheep River				
Intercept	1.31	0.17	7.67	<0.001
Predation	-0.27	0.08	-3.29	0.004
Max. inc.	-2.62	1.36	-1.92	0.07
C) Caw Ridge				
Intercept	1.07	0.04	26.95	<0.001
D) Gran Paradiso National Park				
Intercept	1.07	0.10	10.63	<0.001
Max. inc.	-2.34	0.73	-3.19	0.004

Notes: Model selection procedures are presented in the Appendix (Table A4). “Predation” is a dummy variable (0, absence of heavy predation or pneumonia epizootic; 1, heavy predation or pneumonia); “Res(BMY)” is the residual from the linear relationship linking the maximum increase in NDVI and the average body mass of yearling females, indexing resource availability; “Max. inc.” is the maximum increase in NDVI during green-up.

Table A3). At Sheep River, the yearly average chest girth differed by up to 2.9 cm for males (3.6% of average male chest girth) between years with low and high maximal increases in NDVI, while the yearly average mass of lambs at Ram Mountain varied by as much as 3.06 kg for males (~11.2% of the average). At Caw Ridge, yearly average kid mass differed by up to 2.5 kg for males (15.5% of the average) between years with low and high maximal increases in NDVI. Similar results were obtained for female lambs and kids.

The negative effect of the maximal increase in NDVI on lamb growth was followed by a similar negative effect on first-year overwinter survival at Ram Mountain and

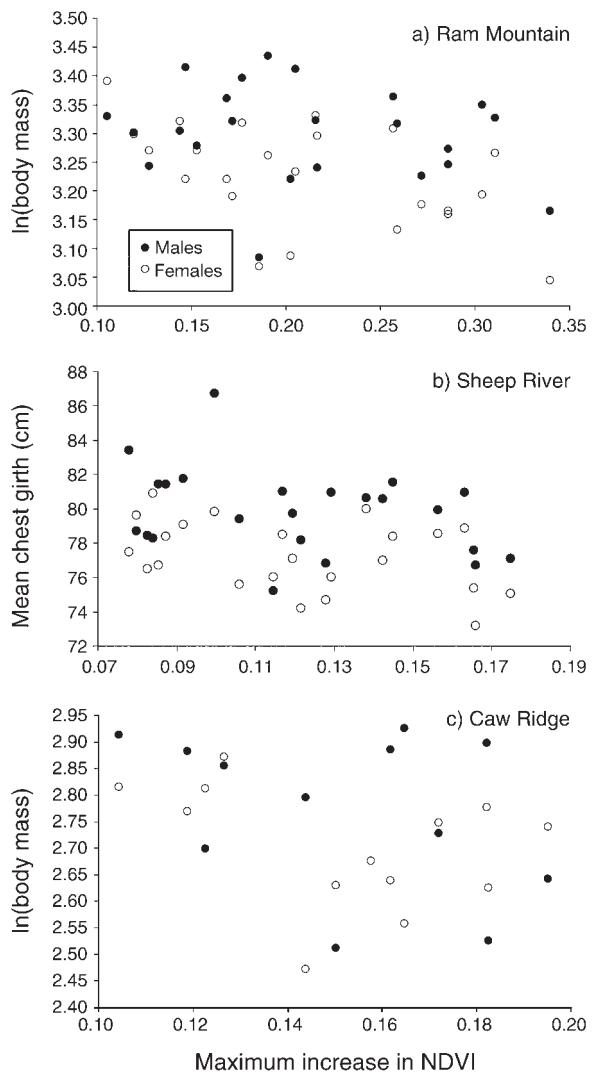


FIG. 2. (a) Log-transformed mean body mass (measured in kg) adjusted for density of male and female bighorn lambs at Ram Mountain (Alberta) according to the maximal increase in NDVI. (b) Mean chest girth for male and female bighorn lambs according to the maximal increase in NDVI at Sheep River (Alberta). (c) Log-transformed mean body mass (measured in kg) of male and female mountain goat kids at Caw Ridge (Alberta) according to the maximal increase in NDVI.

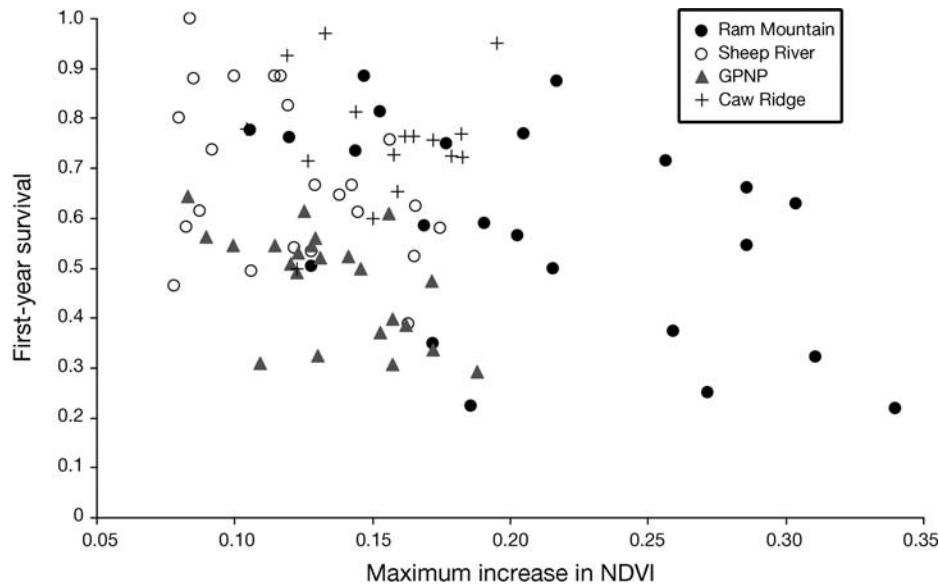


FIG. 3. Winter survival of juveniles according to the maximal increase in NDVI at Ram Mountain (bighorn sheep, Alberta), Sheep River (bighorn sheep, Alberta), Caw Ridge (mountain goats, Alberta), and the GPNP (ibex, Italy). Survival was adjusted for density at Ram Mountain and for predation or pneumonia epizootic at Sheep River.

the GPNP (Table 2, Fig. 3; Appendix: Table A4). The annual maximal increase in NDVI explained 18% of the variability in the average first-year overwinter survival of lambs at Ram Mountain and 33% for kids in the GPNP. At Sheep River, the effect was in the same direction and approached significance (slope = -2.62 ± 1.36 , $P = 0.07$). At Caw Ridge, however, the maximal increase in NDVI was not related to kid survival (Table 2; Appendix, Table A4). The slope in NDVI between early May and early July did not affect juvenile growth or survival in any populations (all $P > 0.10$).

Although population density negatively affected growth and survival of lambs at Ram Mountain (Tables 1 and 2), contrary to (H_3), density did not interact significantly with INDVI in May, the NDVI slope between early May and early July, or the maximal increase in NDVI in affecting body mass or survival of juveniles at Ram Mountain or in the GPNP (Appendix: Tables A3 and A4).

DISCUSSION

As expected, we found a negative effect of rapid changes in plant productivity during green-up on juvenile growth in three alpine ungulate populations. Reduced growth presumably led to a negative effect of rapid changes in plant productivity on juvenile survival (Gaillard et al. 1997). However, we found no positive effect on juvenile growth and survival of either early vegetation onset as indexed by INDVI in May or negative effect of steep vegetation onset as indexed by the slope between NDVI in early May and early July. In populations where density dependence was previously reported (Portier et al. 1998, Jacobson et al. 2004), we did not find any interaction between INDVI in May or

high maximal increase in NDVI and population density in determining growth or overwinter juvenile survival. The reported patterns were coherent among the four populations, three species, and two continents considered.

The duration of the vegetation growing period when herbivores can access high-quality forage appears mainly constrained by spring weather (Pettorelli et al. 2005a). Topographic variability in alpine habitats, on both meso- and micro-scales, and associated differences in snowmelt, can result in swards of different phenological stages in close proximity, generating spatially heterogeneous vegetation (Kudo 1991). Warm temperatures in spring may reduce this spatial heterogeneity if they generate rapid snowmelt over the landscape, reducing the period during which herbivores can access high-quality forage. Warm temperatures and high moisture favor rapid plant growth (Defila 1991), which also shortens the period of high forage quality (Hay and Heide 1984). In Alberta, we found a positive association between warm springs and high values of the maximal increase in NDVI, which allowed us to establish a link between warm springs and rapid changes in plant productivity during green-up. Snowfall in April was positively correlated with the maximum increase in NDVI but had negative effects on INDVI in May. Because the timing of snowmelt is the main determinant of vegetation onset in mountainous environments (Kudo 1991), the negative relationship between INDVI in May and April snowfall was expected. Water from abundant snowfall in April and heavy precipitation in May, associated with warm temperatures in April/May, may lead to a vegetation bloom and fast changes in plant productivity.

Nutritional requirements of animals vary with their physiological state. For ungulate females, nutritional demand peaks in late gestation and during lactation (Clutton-Brock et al. 1989). The daily energetic requirement may increase by 150% during peak lactation compared to maintenance (Loudon 1985). In highly seasonal environments such as alpine habitats, spring forage conditions can thus have profound effects on the energy balance during late gestation and lactation. Much emphasis has been placed on the importance for herbivores inhabiting seasonal environments to match vegetation green-up and birth period to access the longest possible vegetation growing period (Bunnell 1982, Rutberg 1987). Females with access to high-quality forage during lactation could provide greater maternal care than females on a low nutritional plane and reach sufficient body condition in autumn to conceive again. Offspring should benefit from greater maternal care by maximizing growth and overwinter survival. Indeed, late-born offspring are more likely to die during winter since they are smaller in autumn (Festa-Bianchet 1988b). Early vegetation onset measured by INDVI in May, however, did not affect juvenile growth or survival in our study.

Contrary to the timing of vegetation onset, little attention has been paid to the role of the rate of change in plant productivity during green-up and the possible variation in the duration of the period of access to high-quality forage in determining performance of herbivores (but see Langvatn et al. 1996, Mysterud et al. 2001, Pettorelli et al. 2005a). Here, we underlined the relevance of indexing the rate of changes in plant productivity during green-up using the maximum rate of change in NDVI, and highlighted the sensitivity of alpine ungulates to the shape of the vegetation phenology curve. The only exception was in mountain goats, where overwinter survival was not related to vegetation dynamics indexed by NDVI. A previous study at Caw Ridge reported that fecal crude protein content in June, an index of forage quality, affected positively kid mass, but not kid survival (Côté and Festa-Bianchet 2001a). The absence of an effect of fecal crude protein on survival could be due to an effect on growth that was not sufficient to lead to a higher juvenile mortality (Gaillard et al. 1997), consistent with the results presented here.

The slope between NDVI values in early May and early July, which describes the steepness of the entire green-up period, did not correlate with spring weather or juvenile performance. The rate of changes in plant productivity during green-up in a particular year would always be smoothed when considering the slope between two fixed dates. Therefore, the slope between NDVI values in early May and early July was less likely than the maximal increase in NDVI to measure rapid changes in vegetation productivity influencing the period of access to high-quality forage by herbivores.

Surprisingly, we did not find any interaction between density and the maximal increase in NDVI in determining early growth or survival of alpine ungulates in sites where density dependence was previously reported. The interaction of density dependence and climate affects the early performance of ungulates (e.g., Gaillard et al. 1997, Portier et al. 1998). The absence of interaction in our study could result from density variations that were insufficient to exacerbate the effects of rapid changes in plant productivity during the green-up on early performance.

In all study sites, NDVI was assessed at a scale that was generally higher than the areas used by animals. We believe that the phenological signal captured at such large scale is likely to be coherent with vegetation phenology in the study sites, but it is possible that NDVI data at a smaller spatial resolution could enhance the signal we already captured.

Rapid changes in plant productivity during green-up decreased juvenile performance in all study sites. We suggest that rapid changes in NDVI during green-up reduce the period of access to high-quality forage. This could occur through a faster growth rate of plants, a reduction in the spatial heterogeneity of snowmelt, or a change in the plant community accessible to animals. To test such hypotheses will require independent data on the spatiotemporal availability and phenology of forage over many years in the four study sites, data that are not currently available. However, data on feeding sites of female mountain goats during two years indicate that vegetation quality, as measured by protein content of plants in June, is high when the maximum increase in NDVI is low (2003, proteins = 20.1 ± 0.5 , maximum NDVI increase = 0.118) and low when the maximum increase in NDVI is high (2002, proteins = 17.3 ± 0.6 , maximum NDVI increase = 0.172; comparison of protein content between years, $F_{1,140} = 5.1$, $P = 0.02$). Further work is required to explain the interannual variability in the maximal increase in NDVI and to understand the mechanisms by which rapid changes in plant productivity (as reflected by NDVI) during the green-up affect early performance. Considering its importance in determining growth and survival in all four populations measured, those studies are critically needed.

Since we were unable to highlight any consistent effect of INDVI in May, our results point toward the greater influence of a measure of the average duration of the period of access to high-quality forage such as maximal increase in NDVI, than a measure of the average timing of vegetation onset (INDVI in May), in determining growth and survival of juvenile alpine ungulates. Previous work had shown that in Norway warmer winters could lead to higher snowfalls and delayed vegetation onsets at high altitudes, affecting negatively reindeer performance (Pettorelli et al. 2005c). Our results highlight another mechanism that could become more frequent with global climate change (Lapp et al.

2005): warmer springs could negatively affect alpine ungulates through a shorter period of access to high-quality forage. In two of our study areas, the annual maximal increase in NDVI appeared to increase over time (Appendix: Fig. A2), possibly reflecting a warming trend. Finally, our study illustrates how satellite-based information on vegetation can be useful in investigating the coupling between vegetation and herbivore performance, particularly in highly seasonal environments where phenological signals are strong.

ACKNOWLEDGMENTS

We are grateful to the many people who helped with field work. We thank J. Hogg, K. Smith, and J. Jorgenson for their pivotal contribution to field research in the Alberta sites, and S. Hamel for data on plant protein content from Caw Ridge. Special thanks to J.-M. Gaillard, A. Mysterud, T. Coulson, A. Provenzale, and J. Huot for ideas, comments, and suggestions on previous drafts of this work. Research at Caw Ridge, Ram Mountain, and Sheep River was financed by the Alberta Fish and Wildlife Division, the Natural Sciences and Engineering Research Council of Canada, the Rocky Mountain Goat Foundation, the Alberta Conservation Association, the Alberta Sport, Recreation, Parks and Wildlife Foundation, the Fonds Québécois pour la formation de Chercheurs et l'Aide à la Recherche, the Université de Sherbrooke, and Université Laval. We are thankful to A. E. M. Torino for providing the weather data from the Serrù Meteorological Station.

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APPENDIX

Tables showing climatic factors influencing the INDVI in May, the maximum NDVI increase, and the average slope of NDVI between early May and early July in three study sites in Alberta; climatic factors influencing the INDVI in May, the maximum NDVI increase, and the average slope in NDVI between early May and early July, and correlation coefficients between climatic variables for the GPNP (Italy); and model selection procedures. Also included are figures showing interannual variations in NDVI during the study periods and maximum increase in NDVI from 1982 to 2004 in four study sites in Alberta and Italy (*Ecological Archives* E088-023-A1).