Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates

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Summary

1. In recent years, the Normalized Difference Vegetation Index (NDVI) has been used to assess the relationships between habitat quality and animal life-history traits. Since numerous ecological studies now use NDVI rather than perform direct vegetation assessments, field validations are essential to provide confidence in the biological significance of NDVI estimates. While some studies have compared NDVI with plant biomass, very few have examined the relationship between NDVI and changes in vegetation quality.

2. Using data from two long-term studies of alpine ungulates, we assessed the relationship between two NDVI indices and the date of peak in faecal crude protein (FCP), which represents temporal variability in the availability of high-quality vegetation. We also evaluated if NDVI data could predict annual variation in the timing of spring green-up.

3. In both populations, integrated NDVI in June was negatively correlated with the date of the peak in FCP, indicating that high integrated NDVI values corresponded to early springs in alpine habitats. Maximum NDVI increase during spring green-up was positively correlated with the timing of peak FCP, illustrating that rapid increases in NDVI represented delayed springs.

4. Predicted values of date of peak FCP estimated each year from NDVI data satisfactorily fitted observed values, and prediction intervals included all observed values. These results suggest that NDVI can reliably predict variation over years in the timing of spring.

5. *Synthesis and applications.* Our long-term studies demonstrate that a multi-year time series of Normalized Difference Vegetation Index (NDVI) can reliably measure yearly changes in the timing of the availability of high-quality vegetation for temperate herbivores. This finding therefore supports the use of NDVI as a proxy for vegetation attributes in population ecology and wildlife management studies.

Key-words: NDVI, faecal crude protein, alpine tundra, bighorn sheep, mountain goat, habitat quality, timing of spring

Introduction

The Normalized Difference Vegetation Index (NDVI) is a satellite-derived global vegetation indicator obtained from the red near-infrared (NIR) ratio of vegetation reflectance in the electromagnetic spectrum (NDVI = (NIR – RED)/(NIR + RED); Reed *et al*. 1994; Myneni *et al*. 1995). NDVI provides information on vegetation productivity and phenology over large temporal and spatial scales and has been widely used in recent ecological studies as a proxy for vegetation productivity and phenology (for reviews see Kerr & Ostrovsky 2003; Pettorelli *et al*. 2005). Rather than perform direct habitat assessments, numerous studies now use NDVI to link habitat quality and herbivore life-history

traits (e.g. Pettorelli *et al.* 2007; Ryan, Knechtel & Getz 2007; Wiegand *et al.* 2008). These studies are important because they provide knowledge on population dynamics and guide management practices. Many commonly used NDVI measures, however, have not been validated with ground vegetation or habitat traits to assess their biological significance, mainly because validation requires vegetation data that are difficult to obtain.

Although NDVI is an attractive tool to monitor herbivore habitat quality, its interpretation requires caution (Pettorelli *et al.* 2005). For example, NDVI values may inaccurately represent productivity due to the difference in reflectance in heterogeneous habitats, such as those with interspersed woody and herbaceous vegetation or sparse vegetation and abundant bare ground (Elvidge & Lyon 1985; Huete, Jackson & Post 1985; Huete & Tucker 1991). Furthermore, several indices (e.g. maximum NDVI, integrated NDVI, maximum NDVI increase; see Lloyd 1990; Reed *et al.* 1994; Pettorelli *et al.* 2005 for definitions of the different NDVI indices) can be derived from NDVI data, each thought to measure a distinct phenological trait. Because the significance of each NDVI index may vary according to habitat type, however, not all NDVI indices may be valid estimates of specific vegetation attributes in every habitat (Box, Holben & Kalb 1989). Hence, the biological significance of NDVI indices should be assessed in various habitat types before they can be widely used in ecological studies. Finally, different NDVI time series are available at various temporal and spatial scales, the most recent data sets generally providing estimates at finer resolutions than longer time series (Kerr & Ostrovsky 2003). Hence, although researchers should favour the use of NDVI data at finer resolution than the size of their study area, use of NDVI in long-term ecological studies typically requires a tradeoff between spatial precision and temporal scale. Because low-resolution NDVI data are often used in ecology, it is essential to determine if the biological signal of large-scale NDVI time series is representative of the relative variations observed at smaller scales.

Previous studies related different NDVI indices to plant biomass (Tucker *et al.* 1985; Box *et al.* 1989; Diallo *et al.* 1991; Persson *et al.* 1993; Hobbs 1995; Laidler, Treitz & Atkinson 2008), net primary productivity (Tucker *et al.* 1981, 1983; Box *et al.* 1989; Paruelo *et al.* 1997; Seaquist, Olsson & Ardö 2003), and leaf area index (Gilabert, Gandia & Melia 1996; Steltzer & Welker 2006). Very few studies compared NDVI with the timing of the availability of high-quality vegetation for herbivores (see Ryan 2006 for an example in African buffalo *Syncerus caffer* Sparrman). Recently, Levin *et al.* (2007) linked NDVI values with mountain plant richness and rarity patterns. This is one of the rare studies that have conducted assessments of field measurements with NDVI data in mountainous habitat (see also Schino *et al.* 2003).

We assessed the reliability of both large-scale (64 km^2) and small-scale (1 km^2) NDVI measures for providing valid indices of the timing in the availability of high-quality vegetation. We used annual data on summer faecal crude protein (an indicator of vegetation quality, see below) from long-term studies of two alpine ungulate populations. In the highly seasonal alpine environment, the timing of spring vegetation growth can greatly affect the seasonal availability of high-quality vegetation, which can considerably influence individual life-history traits and population dynamics of large herbivores (Albon & Langvatn 1992; Van der Wal *et al.* 2000; Mysterud *et al.* 2001; Garel *et al.* 2006; McLoughlin *et al.* 2007). Therefore, we focused on two NDVI indices that could reflect timing of spring green-up, and thus, the seasonal availability of high-quality vegetation. We used the integrated NDVI in June (the sum of NDVI values for June, Fig. 1C; Lloyd 1990; Reed *et al.* 1994), assuming that high NDVI values would represent early springs. June is when vegetation usually starts to grow in our study areas. We also used the maximum increase in NDVI between two consecutive bimonthly records between late May and early August (i.e. the overall temporal range over which NDVI can increase in alpine habitats, Fig. 1C; Pettorelli *et al.* 2007). Since vegetation should grow faster when spring is late (Bliss 1971; Pettorelli *et al.* 2007), we expected higher maximum increases in late than in early springs. Therefore, high maximum increases should represent reduced temporal access to high-quality vegetation, and may negatively affect life-history traits such as juvenile mass and survival, as reported in moose *Alces alces* L. (Herfindal *et al.* 2006) and in four populations of alpine ungulates, including the two considered here (Pettorelli *et al.* 2007).

We compared integrated June NDVI and the maximum NDVI increase with the date of peak faecal crude protein (FCP). FCP is the percentage of protein in faecal samples and is a reliable indicator of the quality of the vegetation eaten by grazing and mixed-feeding herbivores (Cordova, Wallace & Pieper 1978; Leslie & Starkey 1985; Brown *et al.* 1995; Hodgman, Davitt & Nelson 1996). It has been widely used as a proxy for plant phenology in studies of wild herbivores (O'Donovan *et al.* 1967; Cordova *et al.* 1978; Festa-Bianchet 1988) and is correlated with several life-history traits such as birth mass, offspring survival, individual condition, and mass gain in our study populations (Côté & Festa-Bianchet 2001; Blanchard *et al.* 2003; Gendreau, Côté & Festa-Bianchet 2005). We used the date of peak FCP to represent temporal variability in the availability of high-quality vegetation. An early peak indicates earlier access to high-quality vegetation and should correlate with high integrated NDVI for June. Because vegetation grows rapidly when spring starts late (Bliss 1971), we also predicted that a late peak in FCP would correlate with a high maximum increase in NDVI during the period of vegetation growth. We present a long-term assessment of the relationship between NDVI and the timing of availability of high-quality vegetation for temperate herbivores. We first determined the relationship between NDVI and date of peak FCP, and then evaluated the accuracy of NDVI data to predict variation over years in the timing of spring. The use of NDVI to replace direct habitat assessments in population ecology and wildlife management studies that explore interactions between animals and their habitat is increasing. Therefore, it is essential to assess the biological significance of NDVI indices.
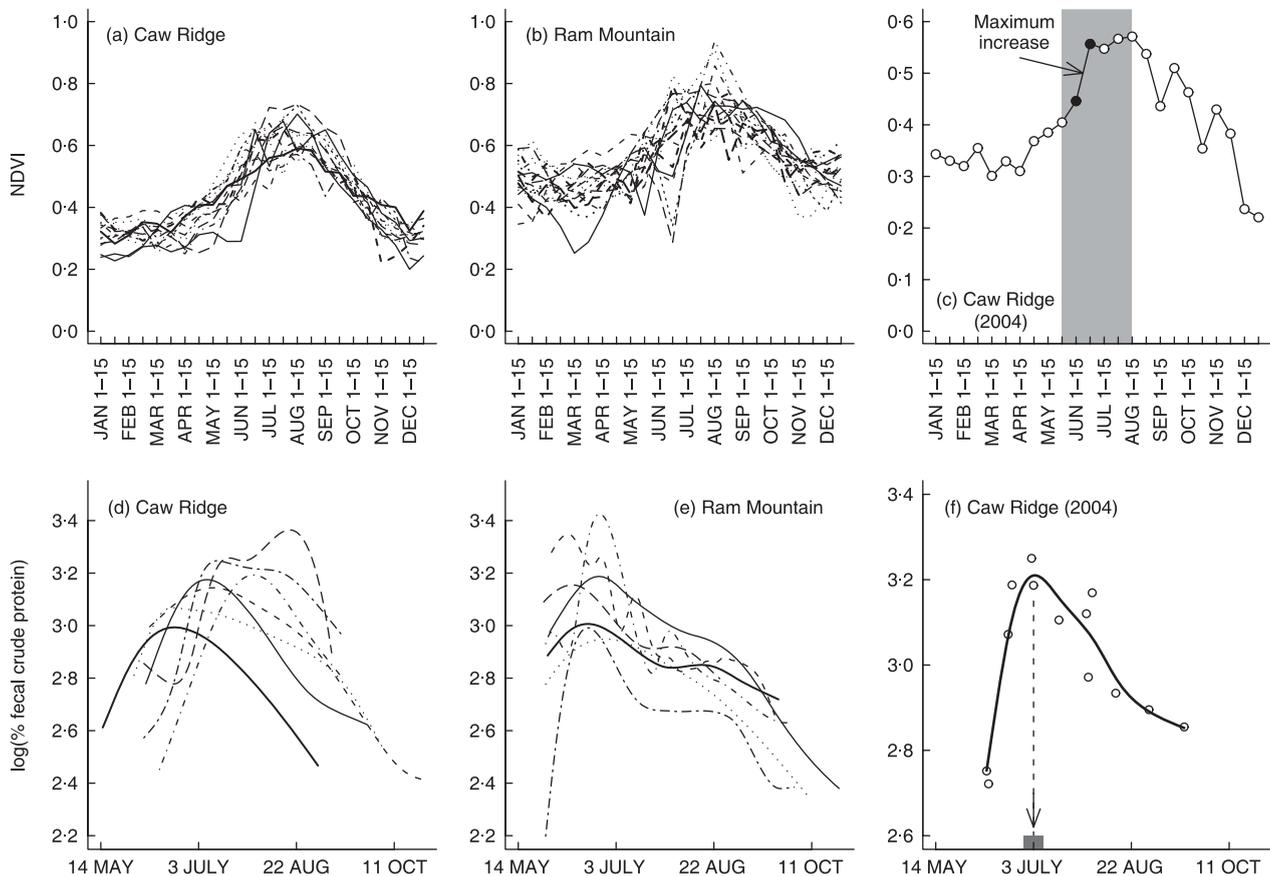
Fig. 1. Annual variations in NDVI and faecal crude protein (FCP) for mountain goats at Caw Ridge (1992–2006, $n = 14$) and bighorn sheep at Ram Mountain (1982–2006, $n = 17$), Alberta, Canada. A and B: each curve represents changes in NDVI over 1 year, for all years included in the analyses. C: NDVI curve for Caw Ridge in 2004, showing the range over which the maximum increase in NDVI was obtained (shaded area), and the two NDVI values (black dots) used for computing integrated NDVI in June. NDVI estimates were computed from data collected by the National Oceanic and Atmospheric Administration satellites and processed by the GIMMS group (Tucker *et al.* 2005). D and E: each curve represents the predicted variations in FCP over one summer estimated from a cubic spline smoother model (see text). For clarity, we only present 7 years for each site. Years were selected to represent the range of curves observed. F: FCP curve estimated for Caw Ridge in 2004, where each dot represents observed % FCP averaged from samples collected from 5 to 12 individuals on the same day. The arrow represents the estimated date of peak FCP and the shaded area the standard deviation estimated from simulations (see text). For this example, date of peak FCP is 3 July ± 5 days.

Materials and methods

STUDY AREA

We compared NDVI data with peak FCP in two alpine populations in west-central Alberta, Canada: mountain goats *Oreamnos americanus* De Blainville at Caw Ridge (54°03′N, 119°23′W), and bighorn sheep *Ovis canadensis* Shaw at Ram Mountain (52°20′N, 115°45′W). Caw Ridge is in the eastern foothills of the Rocky Mountains, whereas Ram Mountain is located about 30 km east of these mountains. Goats and sheep respectively use 28 and 38 km² of alpine tundra and subalpine open forest of Engelmann spruce *Picea engelmanii* Parry ex Engelm. and subalpine fir *Abies lasiocarpa* Hook at about 1750–2200 m elevation. Both species are generalist herbivores and their summer diet is principally composed of alpine forbs, grasses and sedges (Laundré 1994). In both study areas, landscape includes gently rolling hills and steep grassy slopes, as well as rockslides and cliff faces that are crucial escape terrains for both species. Ram Mountain includes vast areas of exposed rock and

scree slope, which are much more limited on Caw Ridge. The climate is characterized by long, cold winters and short, cool summers, with snowfall possible during any month of the year. These populations have been intensively studied since 1988 (Caw Ridge) and 1975 (Ram Mountain). Details of study areas and populations have been published elsewhere (Festa-Bianchet, Jorgenson & Réale 2000; Festa-Bianchet & Côté 2008).

VEGETATION QUALITY

In both populations, we collected fresh faecal samples from 5 to 12 individuals (≥ 1 year old), every 2 or 3 weeks from mid- or late May to late September. We air-dried samples in paper bags. Percentage protein content in faecal samples was assessed using the macro-Kjedahl acid digestion procedure (AOAC 1984). We analysed samples collected between 1992 and 2006 at Caw Ridge ($n = 1172$, annual range = 59–150), and between 1982 and 2006 at Ram Mountain ($n = 1965$, annual range = 53–228). For each summer, we determined the date of the peak in faecal crude protein (FCP) from the relationship

between date and the natural logarithm of FCP using a cubic spline smoother (see Fig. 1F and Blanchard *et al.* 2003). Figure 1 (panels D and E) displays examples of curves obtained for each study area. We did not evaluate the peak in FCP in years when we did not collect faecal samples for the entire summer or before the first week of June, or when the peak occurred prior to the collection of the first sample (*n* = 1 year for Caw Ridge and *n* = 8 for Ram Mountain).

Although NDVI and FCP data were both available on a monthly basis, we used the date of peak FCP rather than monthly FCP values because we were interested in quantifying yearly variability in the timing of spring green-up (see Rasmussen *et al.* 2006 for a similar approach on conception rates), a fundamental parameter affecting the ecology of herbivores (Garel *et al.* 2006; Herfindal *et al.* 2006; Pettorelli *et al.* 2007). Furthermore, FCP values can be confounded by other variables (Brown *et al.* 1995; Blanchard *et al.* 2003; Ryan 2006), and thus using the peak of a smoothed curve reduced potential noise in the data set. The precision of the estimated date of peak FCP can also be influenced by the number and distribution of faecal samples and by the shape of the cubic spline (obvious peaks compared with flatter curves; see Fig. 1). To assess the uncertainty around the estimated peak date of FCP, we simulated new data from the fitted cubic spline smoother for each site and year, by assuming that an observation *i* was the random realization of a normal distribution of mean $\hat{y}_i$ and standard deviation σ (square root of the estimated variance of the random error). We then re-fitted the cubic spline smoother to obtain a new estimate of peak date in FCP. This procedure was replicated 1000 times for each site and year. The average standard deviation of the distribution of simulated peak dates was 4·8 days and 4·2 days for Caw Ridge and Ram Mountain, respectively. We used the inverse of the variance of simulated peak dates to weight estimates of peak dates in all analyses (as recommended by Burnham *et al.* 1987), therefore accounting for the uncertainty on estimated dates of peak in FCP obtained from the cubic spline smoother.

We first performed weighted correlations to assess the relationships between date of peak FCP and the two NDVI indices for each study area. Secondly, to assess whether NDVI could predict variations in FCP peaks over years, we performed linear regressions (again weighted by the error on date of peak in FCP) using NDVI as the explanatory variable. Although NDVI probably included some sampling error, the error term in the model should be on FCP rather than on NDVI. That is because peaks in FCP cannot be considered as true values since they were estimated from raw data with some uncertainty, while NDVI was not estimated but measured and thus by definition it was 'correct'. Therefore, we used these linear regressions to obtain the predicted value of peak date in FCP each year. We assessed how well NDVI could predict annual variations in date of peak FCP by looking at the relationship between predicted and observed peak in FCP date among years, and by determining whether observed values fell within the 95% prediction interval.

NDVI DATA

We used NDVI data available from the Advanced Very High Resolution Radiometer (AVHRR) sensor onboard the afternoon-viewing NOAA satellite series and processed by the GIMMS group (Tucker *et al.* 2005). The resolution, or pixel size, for this series is approximately 8 × 8 km, and daily NDVI images are computed into 15-day maximum value composite images to account for cloud cover (Holben 1986). For further details on the GIMMS data set and processing, especially regarding treatment of noise caused by atmospheric conditions, see Tucker *et al.* (2005). We wrote a program (available upon request)

using the software R to extract the pixels we required from the primary Geotiff files (ftp://ftp.glcf.umiacs.umd.edu/glcf/GIMMS/Geographic). For Caw Ridge, we averaged bimonthly NDVI values of the three pixels overlapping with the study area. A single pixel encompassed most of Ram Mountain. We avoided pixels on the edges of the study areas that contained mostly conifers, because evergreen reflectance resulted in higher NDVI values compared with habitats composed principally of alpine tundra (see also Reed *et al.* 1994). Annual variations in NDVI values are displayed in Fig. 1 (panels A and B) for each study area. From these values, we computed two NDVI indices: the sum of the bimonthly values for June (integrated NDVI; Fig. 1C), and the maximum increase between successive bimonthly values between late May and early August (Fig. 1C; see Reed *et al.* 1994 and Pettorelli *et al.* 2005 for more details).

The GIMMS data set was the best corrected NDVI time series available for the years for which we had FCP data. Other NDVI time series were available at finer spatial scales but shorter temporal scales, and hence provided limited sample sizes to assess the correlation with FCP. Nevertheless, because large-scale pixels of the GIMMS data set included areas not used by goats or sheep, we assessed if estimates of NDVI for these pixels corresponded to estimates for smaller pixels composed only of utilized habitat. We thus evaluated the correlation between large-scale GIMMS and small-scale SPOT-VGT time series (Tucker *et al.* 2005). SPOT-VGT has a resolution of approximately 1 × 1 km and NDVI values are available every 10 days from April 1998 (Saint 1996). For both study areas, we averaged monthly NDVI values for GIMMS (2 values) and SPOT-VGT (3 values). We used the same pixels as described above for GIMMS. For SPOT-VGT, we only used pixels including habitat used by the study animals (*n* = 58 for Ram Mountain, and *n* = 60 for Caw Ridge). We determined habitat used from daily observations of goats and sheep in each study area during summer. We used topographic maps to estimate UTM locations (±100 m) for each observation. We considered all pixels that encompassed locations recorded during the study as habitat used by each species. Because daily observations were not recorded systematically, we assigned equivalent weights to all pixels in the computation of mean NDVI values. We evaluated the correlation between these two time series between April 1998 and December 2006. Although sample size was only six for Ram Mountain and eight for Caw Ridge, we also computed the integrated NDVI in June and the maximum increase between successive NDVI values between late May and early August for the SPOT-VGT time series, to assess their correlation with the date of the peak in FCP, again using correlations weighted by the inverse of the variance in date of peak FCP estimated from simulations. We performed all statistical analyses in SAS 9·1 software (Littell, Stroup & Freund 2002) and present results as means ± SE.

Results

The date of the peak in FCP was negatively correlated with integrated June NDVI in both populations [Caw Ridge: *r* = −0·81 (CI: −0·93, −0·47), *P* < 0·001, *n* = 14 years; Ram Mountain: *r* = −0·84 (CI: −0·93, −0·58), *P* < 0·001, *n* = 17], indicating that high integrated NDVI values corresponded to early springs. The date of peak FCP was also positively correlated with the maximum increase in NDVI between late May and early August [Caw Ridge: *r* = 0·83 (CI: 0·51, 0·94), *P* < 0·001, *n* = 14; Ram Mountain: *r* = 0·90 (CI: 0·73, 0·97), *P* < 0·001, *n* = 17], illustrating that rapid NDVI increases
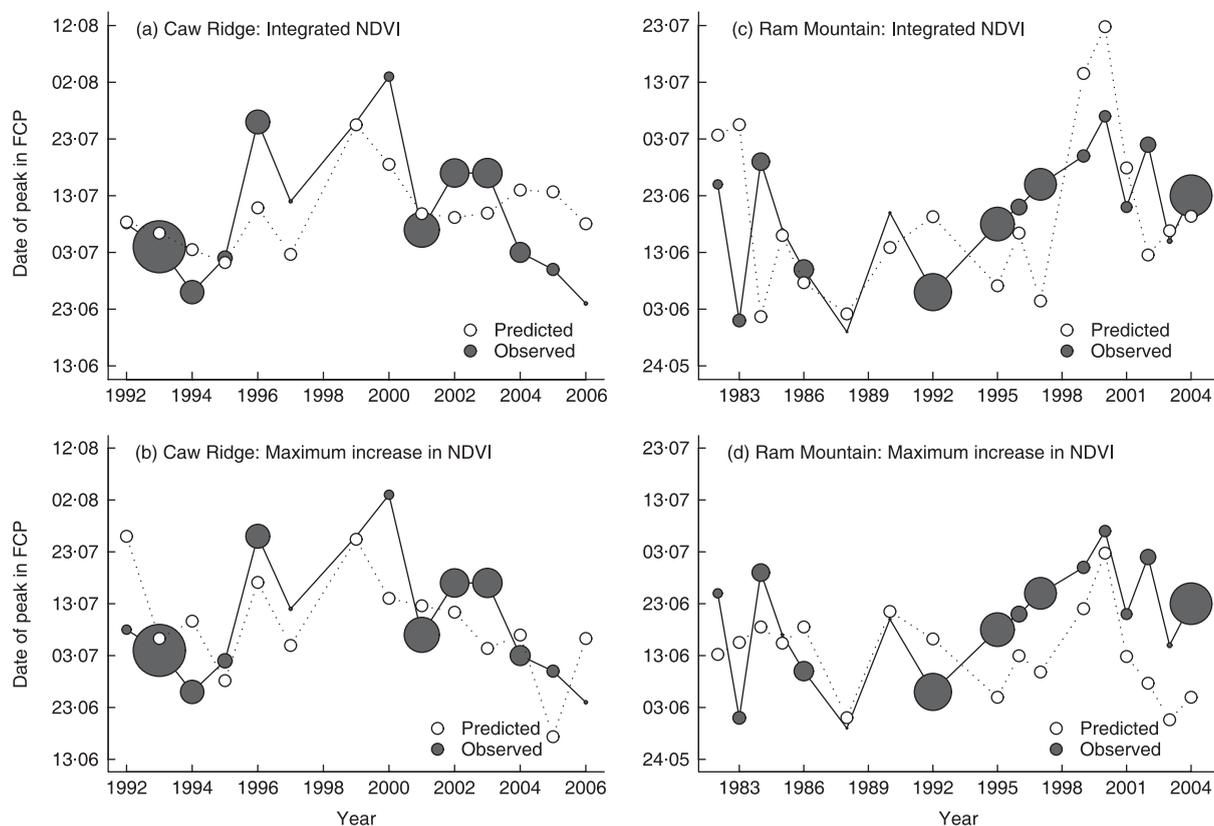
Fig. 2. Predicted and observed values of the date of peak FCP for each year according to integrated NDVI (top panels) and maximum increase in NDVI (bottom panels), for Caw Ridge (left panels) and Ram Mountain (right panels). For observed values, the size of circles illustrates the error of the date of peak in FCP estimated from simulations (see text); the smallest circle represents a standard deviation of 0 day and the largest of 13 days. Predicted values were obtained from weighted linear regression models (see text and Table 1). For clarity, prediction intervals (95%) for each year are not shown in the figure. Intervals varied between 14 and 355 days for Caw Ridge and between 10 and 260 days for Ram Mountain. The lowest intervals (10–14 days) were associated with more precise estimates of date of peak FCP (i.e. greater weights in the relation, represented here by smaller circles).

Table 1. Linear regression equations used to obtain predicted values for date of peak FCP, using NDVI as the explanatory variable (integrated NDVI in June and maximum increase in NDVI) and weighting regressions by the error on date of peak in FCP, for mountain goats at Caw Ridge (1992–2006, $n = 14$) and bighorn sheep at Ram Mountain (1982–2006, $n = 17$), Alberta, Canada

	Linear regression equation	d.f.	F	P
Caw Ridge:				
Integrated NDVI	FCP = 242·7 ± 8·9 + (−46·6 ± 9·7 * NDVI)	1,12	23·0	< 0·001
Maximum increase	FCP = 157·2 ± 8·7 + (286·8 ± 55·9 * NDVI)	1,12	26·4	< 0·001
Ram Mountain:				
Integrated NDVI	FCP = 255·6 ± 15·8 + (−68·8 ± 11·5 * NDVI)	1,15	35·6	< 0·001
Maximum increase	FCP = 144·4 ± 2·5 + (135·5 ± 16·9 * NDVI)	1,15	64·4	< 0·001

represented delayed springs. Comparing this analysis with correlations not accounting for uncertainty in the estimation of date of peak FCP, coefficients were higher when including than when excluding weights for both integrated NDVI (Caw Ridge: $r = -0.81$ vs. -0.71, Ram Mountain: $r = -0.84$ vs. -0.53) and maximum increase in NDVI (Caw Ridge: $r = 0.83$ vs. 0.45, Ram Mountain: $r = 0.90$ vs. 0.36). The relationships with maximum increase in NDVI were highly significant when including weights, whereas only trends were found when weights were excluded (Caw Ridge: $P = 0.10$, Ram Mountain: $P = 0.15$).

Predicted values of date of peak FCP obtained from both NDVI indices satisfactorily fitted observed variations in peak date over years at each study site (Fig. 2). Predicted values were obtained from coefficients of linear regressions using NDVI as the explanatory variable (Table 1). Prediction intervals (95%) from regressions included all observed values. With weighted regressions, the prediction interval for each value does not depend on the variance from multiple observations but is inversely related to the uncertainty of the individual measurement. Therefore, prediction intervals varied between 14 and 355 days for Caw Ridge and between

10 and 260 days for Ram Mountain, with the lowest intervals being associated with more precise estimates of date of peak FCP, which had greater weights in the relation (smaller circles in Fig. 2).

Monthly NDVI values of the large-scale GIMMS series were strongly correlated with those of the fine-scale SPOT-VGT series for both study areas [Caw Ridge: $r = 0.94$ (CI: 0.91, 0.96), $P < 0.001$, $n = 105$; Ram Mountain: $r = 0.82$ (CI: 0.74, 0.87), $P < 0.001$, $n = 105$]. Using SPOT-VGT pixels, the date of the peak in FCP was negatively correlated with integrated NDVI in June at Caw Ridge [$r = -0.99$ (CI: −1.00, −0.93), $P < 0.001$, $n = 8$], and the confidence interval was smaller than with GIMMS data for the same years [$r = -0.96$ (CI: −0.99, −0.77), $P < 0.001$, $n = 8$]. We found similar results at Ram Mountain [SPOT-VGT: $r = -0.84$ (CI: −0.98, −0.02), $P = 0.03$, $n = 6$; GIMMS for the same years: $r = -0.82$ (CI: −0.98, 0.04), $P = 0.04$, $n = 6$], but the confidence intervals for both NDVI time series were very large, likely because of low sample size. The date of peak FCP was positively correlated with maximum increase in NDVI computed from SPOT-VGT data, similarly to the results found for the GIMMS series, but the relationships were not significant [Caw Ridge: $r = 0.50$ (CI: −0.35, 0.88), $P = 0.2$, $n = 8$; Ram Mountain: $r = 0.45$ (CI: −0.60, 0.92), $P = 0.4$, $n = 6$]. The maximum increase in NDVI computed from the GIMMS time series using only years for which NDVI data were available for the SPOT-VGT series revealed significant correlations for both sites [Caw Ridge: $r = 0.91$ (CI: 0.52, 0.98), $P = 0.002$, $n = 8$; Ram Mountain: $r = 0.92$ (CI: 0.38, 0.99), $P = 0.008$, $n = 6$].

Discussion

Recently, Pettorelli *et al*. (2007) reported that rapid changes in NDVI during spring green-up, assumed to represent shorter temporal access to high-quality vegetation, were correlated with reduced juvenile survival in our study populations, as well as in another population of bighorn sheep and one of Alpine ibex *Capra ibex* L. In African buffalo, Ryan *et al*. (2007) showed that monthly NDVI values, a surrogate measure of habitat quality (Ryan 2006), were correlated with the timing of birth. Other studies also related NDVI estimates with breeding phenology (Wittemyer, Rasmussen & Douglas-Hamilton 2007), phenotypic traits (Garel *et al*. 2006; Herfindal *et al*. 2006; Pettorelli *et al*. 2006), habitat use and herbivore distribution (Gustine *et al*. 2006; Marshal *et al*. 2006; Wiegand *et al*. 2008). These studies illustrate how NDVI can help in understanding the effects of habitat quality on population parameters, individual life-history traits, and habitat use. Furthermore, understanding the relationships between satellite data and habitat attributes is becoming a central issue with the increasing use of GPS collars, because it is often impossible to directly measure data at the appropriate temporal and spatial scales (see Bro-Jørgensen *et al*. 2008 for an example emphasizing the importance of scales using NDVI data). In this context, assessments of the reliability of NDVI indices are necessary to provide confidence in their biological significance before they become widely used in population ecology and wildlife management. Unfortunately, these assessments are lacking in most studies.

Using both large- and fine-scale NDVI time series, we showed that integrated NDVI in June strongly correlated with the date of peak FCP in two alpine ungulates. Annual NDVI indices therefore reflect the timing of spring green-up, which is important for early access to high-quality vegetation (Bliss 1971). We also showed that the maximum increase in NDVI during green-up strongly correlated with the date of peak FCP, but only using large-scale NDVI time series. The weaker correlations for this NDVI index using fine-scale data might result from the difference in temporal scale over which NDVI data are computed for each time series. Maximum increase in NDVI is assessed over 10 days for the SPOT-VGT and 15 days for the GIMMS time series. Maximum increases in NDVI computed over a shorter time-scale may not capture the same habitat variations, and hence may be less representative than estimates computed over a longer time-scale. Therefore, although they are often correlated, different NDVI indices may not always be equivalent for representing habitat attributes, reinforcing the importance of carefully selecting specific NDVI indices to properly describe the habitat under study. Furthermore, our results indicate that NDVI can reliably predict variations in the annual timing of spring in alpine habitats. Generally, longitudinal studies focus on assessing relative variations among years rather than on determining absolute measurements for a given year. Consequently, our findings justify the use of NDVI as a proxy for vegetation attributes to examine trophic interactions between animals and their habitat in ecological and management studies.

Although we used FCP as a reference, FCP is not a gold standard measure as it can be confounded by other variables (Brown *et al*. 1995; Blanchard *et al*. 2003; Ryan 2006) leading to uncertainties in estimates of date of peak FCP. Including this uncertainty in the analyses greatly improved the relationships between FCP and NDVI. Prediction intervals were very small in years when uncertainty on estimates of date of peak FCP was small compared with years with high uncertainty, illustrating that, when dates of peak FCP were estimated accurately, they strongly correlated with NDVI. Although years with a gradual onset of spring could have higher variance in the estimates of date of peak FCP and hence affect the predictive power of NDVI, years with greater uncertainty (larger circles in Fig. 2) were evenly distributed among early and late springs, and late springs have a more rapid onset of vegetation growth than early springs. These findings support NDVI as a powerful predictor of temporal variations in the timing of spring. Because of uncertainties in estimates of date of peak FCP, our results also suggest that NDVI could even be a better indicator of the timing of spring than FCP.

Brown *et al*. (2006) demonstrated that NDVI time series derived from different sensors were consistent with one another. A strong correlation between large-scale GIMMS data and small-scale SPOT-VGT data has also been reported (Tucker *et al*. 2005; Fensholt, Nielsen & Stisen 2006). From an ecological perspective, an interesting finding of our study

is that this correlation persisted between large-scale NDVI data that included coniferous habitat outside the study area and fine-scale NDVI estimates that included only areas used by the study animals (mainly alpine habitats). Because we compared relative temporal variations in NDVI and not absolute NDVI values, this result provides confidence in the decision to trade spatial precision for longer time series, as is often required in long-term studies (Brown *et al.* 2006). Nevertheless, further studies should evaluate this result in different habitat types. Not surprisingly, however, we found a stronger relationship between the date of peak in FCP and small-scale NDVI estimates compared to large-scale data. Using NDVI data at a smaller resolution than the size of the study area should thus provide better estimates of vegetation productivity, and hence should be favoured when possible.

Because of the scarcity of long-term data on habitat productivity and quality, few studies performed NDVI assessments in relation to vegetation attributes, especially over large temporal and spatial scales in remote habitats. To our knowledge, our study is the first to relate NDVI indices with the timing in the availability of high-quality vegetation in temperate herbivores. In a contrasting ecosystem, Ryan (2006) reported a positive correlation between monthly average NDVI and faecal nitrogen for African buffalo. Since our results and those of other studies suggest that the relationships between different NDVI indices and vegetation attributes can vary, ecological and management studies should validate the ecological significance of NDVI indices whenever possible. This will allow selecting the best index for a particular habitat in specific studies, but will also expand our understanding of suitable NDVI indices in circumstances where it may be impossible to assess the reliability of NDVI (Kerr & Ostrovsky 2003).

Acknowledgements

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