

Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer

Nathalie Pettorelli, Jean-Michel Gaillard, Atle Mysterud, Patrick Duncan, Nils Chr. Stenseth, Daniel Delorme, Guy Van Laere, Carole Toïgo and Francois Klein

Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Stenseth, N. C., Delorme, D., Van Laere, G., Toïgo, C. and Klein, F. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. – *Oikos* 112: 565–572.

Animals in seasonal environments are affected by climate in very different ways depending on season and part of the climatic effects operates indirectly through the plants. Vegetation conditions in spring and summer are regarded as decisive for the reproductive success and the offspring's condition of large herbivores, but objective ways to determine key periods during the growing season have not been done often due to limitations in plant data. Using satellite data (NDVI), we determined how plant productivity from birth to fall influences the following winter body mass of roe deer fawns. We do this in two populations, the first inhabiting the low productive Chizé reserve in south western France with an oceanic climate and the second from Trois Fontaines, a highly productive forest with continental climate in east France. The effect of plant productivity was similar for male and female fawn mass, as expected from the weak intensity of sexual selection in roe deer life history traits. We found contrasting results between sites, with a strong effect of plant productivity in spring (April-May) in the Chizé population, but no effect in the Trois Fontaines population. The relatively low variability in winter fawn body mass could account for the absence of NDVI effects at Trois Fontaines. However, such results might also point to a limitation in the use of the NDVI, since the relationship between the canopy and the plant productivity at the ground level might be weak in the highly productive forest of Trois Fontaines.

N. Pettorelli, A. Mysterud and N. C. Stenseth, Centre for Ecological and Evolutionary Synthesis (CEES), Dept of Biology, Univ. of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway. – J.-M. Gaillard, Unité Mixte de Recherche No. 5558 « Biométrie et Biologie Evolutive », Bâtiment 711, Univ. Claude Bernard Lyon 1, 43 Boulevard du 11 novembre 1918, FR-69622 Villeurbanne Cedex, France (gaillard@biomserv.univ-lyon1.fr). – P. Duncan, Centre d'Etudes Biologiques de Chizé, Unité Propre de Recherche No. 1934, Villiers-en-Bois, FR-79360 Beauvoir-sur-Niort, France. – D. Delorme, G. Van Laere, C. Toïgo and F. Klein, Office National de la Chasse de la Faune Sauvage, Centre National d'Etudes et de Recherches Appliquées Cervidés-Sangliers, 85bis Avenue de Wagram, FR-75017 Paris, France.

The role of annual variation in climate for breeding phenology and performance of plants, amphibians and birds in specific populations has recently received much attention (reviewed by Walther et al. 2002, Stenseth et al. 2002). Clearly, the onset of breeding and the reproductive success in seasonal environments for organisms that

are either dormant (such as plants and amphibians, Beebe 1995) or migratory over broad scales (for birds, Slagsvold 1976) is coupled with temperature in early summer. Large herbivores are active over the entire year and a better understanding of how animal performance (i.e. survival, reproduction or growth) are linked to plant

performance and climatic conditions throughout the year is needed if we aim to anticipate the effect of climate change on ungulates.

Most studied ungulate populations around the North Atlantic respond to global climatic variations related to the winter index of the North Atlantic Oscillations (NAO, Hurrell 1995) (red deer *Cervus elaphus*: Mysterud et al. 2001a; reindeer *Rangifer tarandus*: Solberg et al. 2001; moose *Alces alces* and white tailed deer *Odocoileus virginianus*: Post and Stenseth 1998; Soay and domestic sheep *Ovis aries*: Mysterud et al. 2001b; caribou and muskox *Ovibos moschatus*: Forchhammer et al. 2002). However, as the growth of domestic sheep in Norway, that are kept indoor during the entire winter, is also connected to variation in the winter index of the NAO, it is likely that the effect of the NAO is at least partly indirect and thus operates through plants (Mysterud et al. 2001b). Indeed, an ongoing discussion among ecologists working on northern ungulates focuses on the relative importance of winter versus summer conditions in determining deer performances (Sæther 1997, Weladji et al. 2002). Klein (1965) proposed that the summer conditions are the main determinant of growth, as high energy requirement coincides with high energy intake in early July (Brotton and Wall 1997). The importance of summer conditions on deer growth rates (often referred to as the “range quality hypothesis”, Sæther and Heim 1993) has later been highlighted for different northern ungulates (moose: Sæther and Heim 1993; red deer: Mysterud et al. 2001a; reindeer and caribou: Weladji et al. 2003; roe deer *Capreolus capreolus*: Gaillard et al. 1996).

However, up to now, linking climate effects and plant productivity has not been an easy task. First, a detailed knowledge of the distribution and phenology of the different food items during the studied period has only been accumulated in few study sites. Traditional field ecological data on plant species are generally collected at a small spatial scale and vary in their type and reliability (Kerr and Ostrovsky 2003). Furthermore, since such data often come from a single time period during the year, it is difficult to identify the most important period of plant growth to the herbivore. Remote sensing data and the normalised difference vegetation index (NDVI) have recently changed this situation, and have offered to ecologists a promising way to couple vegetation and herbivore dynamics (Kerr and Ostrovsky 2003). The NDVI has shown consistent correlation with vegetation biomass and dynamics in various ecosystems worldwide (Running 1990, Myneni et al. 1995, 1997, see Birky 2001 in the particular context of temperate deciduous forests). However there are still limitations and causes of error associated with satellite data one should be aware of when using the NDVI (reviewed by Pettorelli et al. 2005b), such as the saturation of the relationship

between NDVI and vegetation productivity in highly productive areas.

Body mass of reindeer in mid-Norway (around 62°N) correlated positively with the NDVI on a fixed date in late spring (May), i.e. an earlier phenology led to higher body mass in autumn (Pettorelli et al. 2005a). However, as several aspects of breeding phenology of ungulates differ depending on latitude (Loe et al. 2005), studies in more temperate regions are needed to assess the generality of the effect of the NDVI. Populations living in temperate lowlands seem to be limited by climatic conditions during the spring-summer (roe deer: Gaillard et al. 1997, mouflon *Ovis gmelini*: Garel et al. 2004). However, as the onset of vegetation is earlier in France than in Norway, it is likely that the NDVI on an earlier date would predict autumn body weight better in France than in Norway.

Our aim in this study was to test how roe deer performance in two populations in France is related to vegetation dynamics as assessed by the NDVI. Roe deer are small (20–30 kg) deer widespread in Europe (Andersen et al. 1998). The summer survival of fawns (Pettorelli et al. 2005c), the winter survival of fawns (Pettorelli et al. 2003a), and the winter body mass of fawns (Pettorelli et al. 2003b) have been demonstrated to be very sensitive to variations in the availability of resources. In temperate environments, ungulate population dynamics has been generally described to be highly sensitive to recruitment and early performance, adult performance being generally described as high and more stable (Gaillard et al. 2000). Determining factors influencing early performance is thus of prime importance for ecologists. We accordingly studied cohort variation in winter fawn body mass as a measure of roe deer performance. Cohort-specific body mass of fawns can be considered as a reliable proxy for population condition (Hanks 1981). Moreover, it is closely related to subsequent adult body mass (Pettorelli et al. 2002), fawn winter survival (Gaillard et al. 1993a) and age at maturity (Gaillard et al. 1992).

As roe deer are income breeder (Andersen et al. 2000, sensu Jönsson 1997) and roe deer growth pattern follows a monomolecular model (Portier et al. 2000) with a growth rate decreasing from birth onwards, we expect (H1) a significant effect of spring/summer conditions in determining winter body mass of roe deer fawns (Pettorelli et al. 2003b).

Young males generally suffer more than young females under harsh conditions (Glucksmann 1974). However, contrary to most other ungulates (Clutton-Brock et al. 1982), roe deer of both sexes have similar birth mass, post-natal growth rate (Gaillard et al. 1993b) and juvenile survival (Gaillard et al. 1997). Because there is no difference in growth patterns between male and female fawns, we expect (H2) no between-sex

differences in the effect of spring/summer conditions on winter body mass.

Methods

Study areas

The study areas are two fenced forests managed by the Office National de la Chasse et de la Faune Sauvage, the 1360 ha Territoire d'Etude et d'Expérimentation of Trois Fontaines (48°43'N, 54°10'W) in eastern France and the 2614 ha Reserve of Chizé (46°05'N, 0°25'W) in western France, both being located inside 5000 ha large forests mainly composed of oak and beech. Those two sites differ with respect to climatic conditions: Trois Fontaines has a continental climate with relatively severe winters, whereas Chizé has an oceanic climate with mild winters and hot dry summers. Both sites have been described in detail elsewhere (Gaillard et al. 2003).

On a coarse scale, the Chizé reserve presents different habitats, according to the timber stand and the nature of the coppices (Pettorelli et al. 2003a). The dominant tree of the northern part of the reserve (1397 ha) is oak (*Quercus* sp.). Oak stands can be further distinguished according to the shrub-layer: the eastern part is dominated by hornbeam, the western part by maple. The southern plots (1143 ha) are dominated by beech (*Fagus sylvatica*).

On the other hand, the Trois Fontaines forest does not present different habitat types at the stand scale so that the forest appears homogeneous. The Trois Fontaines forest lies on rich soils and is highly productive. Based on the wood production, this forest is a more productive habitat than Chizé (long-term average of 5.92 m³ of wood produced ha⁻¹ year⁻¹ vs 3.77 m³ at Chizé, data from Inventaire National Forestier) so that Trois Fontaines can be considered as a more suitable habitat than Chizé for roe deer.

Vegetation (NDVI) data

Data collected by the National Oceanic and Atmospheric Administration satellites and processed by the GIMMS group (C. J. Tucker, J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote and N. Saleous, unpubl.) have been made available to ecologists. 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 the visible light reflected by the vegetation). The negative NDVI values correspond to an absence of vegetation (Justice et al. 1985). The spatial scale of resolution (pixel size) is 64-km² and a NDVI value is available on a bi-monthly basis, from July 1981 to nowadays. The NDVI

has been successfully applied to research such as vegetation monitoring (Rasmussen 1998), primary production estimation (Ricotta and Avena 1998) and environmental change detection (Franca and Setzer 1998). Some imprecision in the exact spatial location of the pixel have been reported before (Pettorelli et al. 2005b), especially at the 1 km scale. In our case, using one pixel or multiple pixels do not change the presented results. Considering that we work here with 8 × 8 km pixels and the fact that France is a rather urbanised country, we decided to present the analysis only for one pixel per study site (both forests being smaller than 8 × 8 km), to prevent contamination from using a too large scale that could encompass pixels disturbed by human activities. We used one pixel at Chizé (46.09°N, -0.72°E; in degree decimal) and one pixel at Trois Fontaines (48.72°N, 4.91°E).

Roe deer data

The roe deer populations have been intensively monitored using capture-mark-recapture methods since 1976 in Trois Fontaines and 1978 in Chizé. About ten days of capture in January and February lead 100–300 roe deer to be caught each year in both sites. Most animals are released with individual collars and the other roe deer caught are exported. In a particular capture session, >100 people drive animals into two to five kms of nets, which enclose chosen forestry plots. About one half to two third of the area at Chizé and the whole area at Trois Fontaines are sampled each year. Because more than 70% of roe deer older than 1 year are individually marked using numbered collars (Strandgaard 1967) and ear tags, reliable estimates of population sizes are available using generalization of the Cormack–Jolly–Seber model (Gaillard et al. 2003).

Marked differences in population dynamics occurred between Trois Fontaines and Chizé: the population size in Trois Fontaines is roughly constant and no evidence of density dependent responses have been reported throughout the study period (Gaillard et al. 2003). The roe deer population at Chizé fluctuated markedly during the study period, increasing from 350 deer older than 1-year of age in 1979 to >550 in 1983 and decreasing to <200 in 1993. Since 1993, the population size has been maintained around 200 roe deer >1 year of age (Gaillard et al. 2003).

Because of the hurricane “Lothar” that hit France in December 1999, we did not consider the cohorts born in 1999 and 2000 in both reserves (too low number of roe deer captured due to difficulty of forest access for the cohort 1999 (Gaillard et al. 2003), and marked short-term changes in habitat use by roe deer the year following the hurricane (Widmer et al. 2004)). We thus used a subset of the roe deer data, including 1126 fawns

in Chizé and 1114 in Trois Fontaines captured at eight/nine months of age between January-February 1983 and January-February 2004 (N = 20 years). For each individual, sex, year and month when animals were caught, habitat quality at the forest stand scale (only at Chizé) and body mass were recorded.

Statistical analyses

We used linear models (LM) to analyse variations in fawn body mass. A logarithmic transformation of body mass [$\ln(\text{body mass})$] was used in order to ensure residuals with constant variance. Individual body mass was also adjusted for the month the animal has been caught (this effect being of $+0.02 [\pm 0.008]$ (ln scale) from January to February in Trois Fontaines and $+0.02 [\pm 0.009]$ in Chizé, we used the same correction of $+0.02$ for both populations) and the habitat the animal was caught in (for Chizé only, with a yearly difference of $+0.05 [\pm 0.009]$ between the richer oak stand with hornbeam coppices and the rest of the reserve; Pettorelli et al. 2003b). Because vegetation productivity is expected to influence cohort-specific body mass of fawns, we performed the analysis on sex-specific yearly means of $\ln(\text{body mass})$.

The effect of vegetation productivity variation on roe deer performance can be explored at different temporal scales. First, it is possible to investigate if and how the inter-annual variation in the NDVI values at a fixed date correlates with cohort-specific body mass of fawns, repeating the analysis for different dates. This allowed us to define precisely the date when the best correlations between vegetation productivity and body mass of fawns in winter occur. Then, it is also possible to estimate the integrated NDVI value (INDVI), which corresponds to the sum of the NDVI values over a defined period (e.g. one month, two months, a semester, a year), and has also been described as a good index of vegetation productivity over the period considered (Justice et al. 1985, Myneni et al. 1997, Boelman et al. 2003).

We therefore chose to apply both approaches, by (1) simply exploring the temporal variation (from February to October) in the strength of the correlation between cohort-specific body mass of roe deer fawns in winter and vegetation productivity in order to define precisely which period was affecting roe deer body mass and (2) estimating from 1982 to 2003 the vegetation production during spring and fall, and then correlating those yearly indices to yearly body mass averages. Indeed, the spring and summer seasons are the critical period for roe deer (Gaillard et al. 1996, 1997). We thus investigated the relationship between the INDVI in April-May (hereafter INDVI in spring) and the body mass of roe deer fawns in winter to assess the influence of plant productivity during the last stages of gestation and early lactation

when fawns are mostly dependent of mother's milk. We also investigated the relationship between the INDVI from August to October (hereafter INDVI in fall) and body mass to assess the influence of plant productivity during the weaning and early post-weaning periods when fawns feed by themselves.

As density was reported to influence significantly body mass at Chizé (Gaillard et al. 1996), we considered the ratio between INDVI in spring and fall and density ($[\ln(\text{number of individuals})]$) to get a measure of per capita resource intake.

Model selection was performed using Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 1998). All continuous variables were standardized when checking for interactions between them. All statistical analyses were performed in the statistical package S-Plus (Venables and Ripley 1997).

Results

The average between-site NDVI patterns reflected the between-site difference in long-term average wood production: the yearly INDVI (the sum of NDVI values throughout a year) from 1982 to 2003 was indeed much higher in Trois Fontaines than in Chizé (Fig. 1). Likewise, the average temporal variation within a year reflected the between-site difference in seasonality expected from site locations, the onset of plant growth being later in Trois Fontaines than in Chizé (Fig. 1). However, such a good correspondence between NDVI measurements and between-site differences in wood production and seasonality cannot allow us to validate NDVI as a reliable measure of vegetation productivity in our study sites. The INDVI in spring and the INDVI in fall were positively correlated in Chizé ($R^2 = 0.34$, $n = 20$ years) but not in Trois Fontaines ($R^2 < 0.001$, $n = 20$ years). We thus removed the correlation at Chizé by considering the residuals in the following analyses.

At Chizé, there was a strong correlation between plant productivity in April-May and the following winter body mass of roe deer fawns (Fig. 2). The best correlation was found for the composite NDVI on 1st to 15th of May. Plant productivity from August to October was also reported to correlate with the body mass of fawns. On the other hand, at Trois Fontaines, the only significant correlations we reported between vegetation productivity at a fixed date and the body mass of fawns were negative (Fig. 2).

The INDVI in spring positively influenced the body mass of fawns at Chizé (Table 1, 2, Fig. 3). Sex, density and vegetation production in spring and fall accounted for 70% of the observed variation in cohort-specific winter fawn body mass, as compared with only 60% when excluding the vegetation (Table 1).

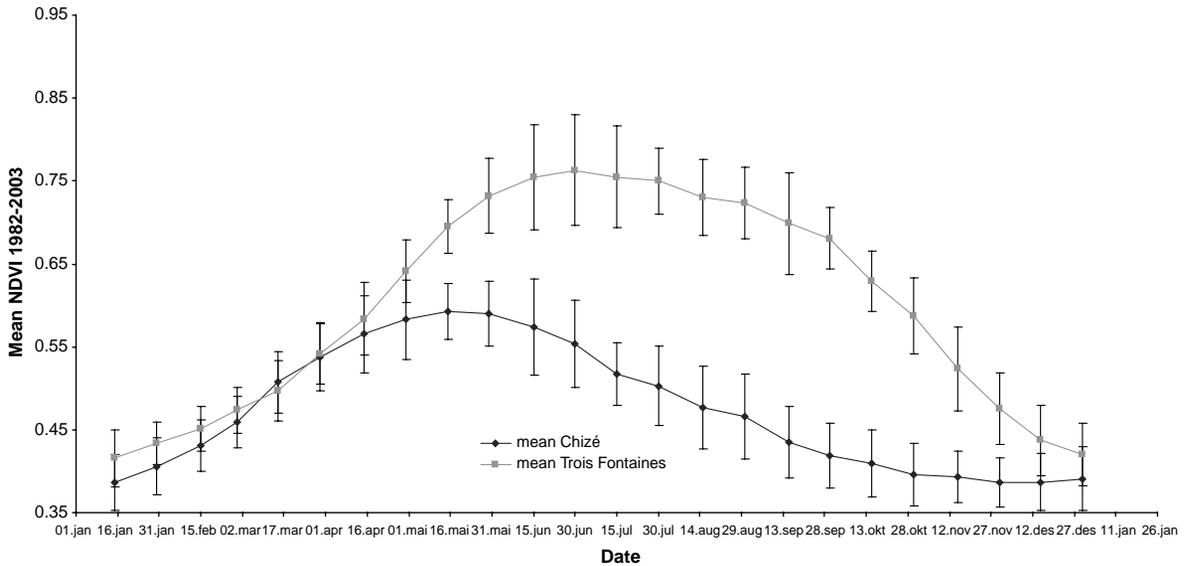


Fig. 1. Average NDVI (1982–2003) with SE in relation to date at Chizé and Trois Fontaines.

In Trois Fontaines, neither the INDVI in spring ($P=0.56$) nor the INDVI in fall ($P=0.16$) significantly influenced the cohort-specific winter body mass of fawns (Table 1, 2, Fig. 3). The best model accounted for 32% of the observed variation in body mass. At Trois Fontaines, the model including the additive effects of sex and year

accounted for 87% of the observed variation in cohort-specific winter fawn body mass. The seasonal INDVIs at Trois Fontaines thus poorly represented the among-year variation in winter fawn body mass.

In both populations, male and female body mass responded similarly to changes in NDVI (i.e. no interaction between sex and the INDVI; Chizé: $t = -0.34$, $P=0.52$ for spring and $t = -0.19$, $P=0.80$ for fall; Trois Fontaines: $t = -0.37$, $P=0.71$ for spring and $t=0.78$, $P=0.44$ for fall).

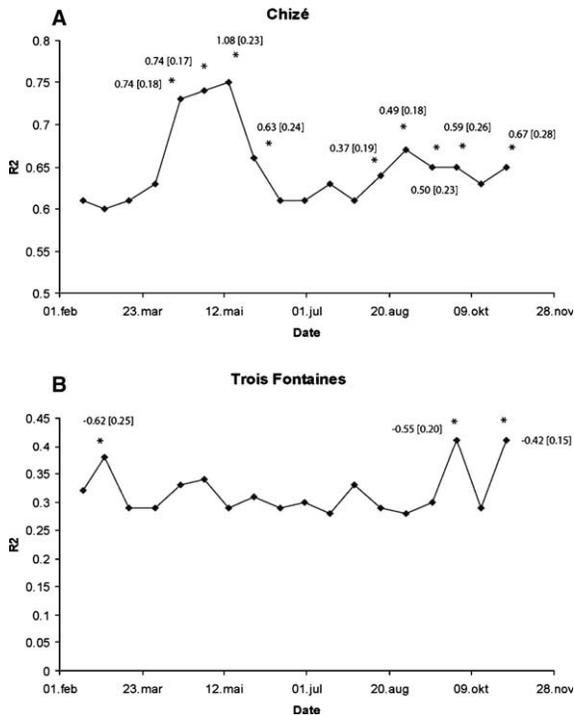


Fig. 2. Correlation between the bimonthly composite NDVI and the following winter body mass of fawns between February to October. Slopes [SE] are given when the correlation is significant ($<5\%$, marked with a star).

Discussion

Plant productivity in spring (April–May) had a marked effect on the winter body mass of fawns at Chizé. Roe deer are generalist feeders but are highly selective (Duncan et al. 1998): the spring and summer seasons are regarded as critical for the nutrition of this income breeder (Pettorelli et al. 2003b). This is similar to what is reported for reindeer (Pettorelli et al. 2005a), which is a capital breeder. In this period of high energy requirements for females (end of gestation, lactation), animals select food items which are highly digestible and rich in soluble carbohydrates (Maizeret et al. 1991). It is therefore likely that the difference in plant productivity in spring from one year to another affected the food supply of the breeding females which in turn led to higher body mass of fawns in winter.

Several aspects of breeding phenology of ungulates have been shown to be linked to latitude (Loe et al. 2005). A similar study conducted on reindeer in mid-Norway showed that the vegetation production in May positively influences calf body mass the following fall

Table 1. Model selection for Chizé (a) and Trois Fontaines (b). For each model, the number of parameters (p), the percentage of variance explained (R^2) and the AIC_c are provided. The selected model occurs in bold.

Model	p	R^2	AIC_c
(a)			
Year	19	0.86	-68.35
Sex	1	0.08	-71.54
Sex + year	20	0.95	-98.84
ln(density)	1	0.52	-97.04
Sex + ln(density)	2	0.60	-102.38
Sex + (NDVIs _{spg} /ln(density))	2	0.69	-111.94
Sex + (NDVIs _{spg} /ln(density)) + (NDVIf _{all} /ln(density))	3	0.70	-111.00
(b)			
Year	19	0.58	-66.56
Sex	1	0.29	-124.86
Sex + year	20	0.87	-104.19
Sex + NDVIs _{spg}	2	0.29	-122.88
Sex + NDVIf _{all}	2	0.32	-124.67
Sex + NDVIs _{spg} + NDVIf _{all}	3	0.33	-122.60

(Pettorelli et al. 2005a). Here we report an effect of vegetation production in April-May. For both species, the mean birth date is around the 15th of May (roe deer: Gaillard et al. 1993b, Reindeer: Reimers 2002), but the vegetation onset is earlier in France (around mid March – beginning of April) than in Norway (May). Here we thus reported that the NDVI around the onset of vegetation might be a good predictor of the body mass of calves for both species and in both countries.

Surprisingly, plant productivity did not influence winter fawn body mass at Trois Fontaines. A possibility is that we missed an important factor shaping winter body mass of fawns in Trois Fontaines, so that the effect of plant productivity in spring is shadowed (Sokal and Rohlf 1995). We can illustrate such a possibility by using the Chizé case study: when removing population density from the model, plant productivity in spring had no more detectable influence on fawn body mass. The much lower explanatory power of the final model at Trois Fontaines (32%) than at Chizé (70%) could support such an interpretation. Winter body mass of fawns varied twice more at Chizé (CV = 3.67% for males and 3.27% for females) than at Trois Fontaines (CV = 1.93% for males and 1.44% for females) whereas temporal variation in NDVI in spring (April/May) was similar in both sites (CV = 6.34% at Chizé and 4.59% at Trois Fontaines). Thus, a relatively low between-year variation in

fawn body mass could have prevented us to detect an effect of the NDVI at Trois Fontaines. Another possible explanation to the lack of influence of plant productivity on fawn body mass at Trois Fontaines is methodological and linked to how the NDVI is calculated. In Trois Fontaines, the forest is highly productive as to compare with the low productivity of the Chizé forest. NDVI is determined by the composition of species within the plant community, the vegetation form, vigour and structure, the vegetation density in vertical and horizontal directions, the reflection, absorption and transmission within and on the surface of the vegetation or ground, and the reflection, absorption and transmission by the atmosphere, clouds and atmospheric contaminants (Markon et al. 1995). The relationship between the NDVI and ANPP (aboveground net primary production) is not linear over the entire range of ANPP: indeed, the relationship shows saturation with high LAI (leaf area index (LAI) which is a common measure of canopy foliage content (Asner et al. 2003), and thus high ANPP (Asrar et al. 1984, Sellers 1985, Paruelo et al. 1997). Considering the difference in productivity between the two forests, it might be hypothesised that the correlation between NDVI and vegetation dynamics and resource availability are indeed higher at Chizé than at Trois Fontaines.

Table 2. Parameter estimates for body mass obtained from the linear model including the effects of sex, NDVI in spring and NDVI in fall at Chizé and Trois Fontaines.

Parameters	Estimates	SE estimates	T value	P value
Trois Fontaines				
Intercept	3.00	0.24	12.28	<0.001
Sex (female-male)	-0.06	0.01	-3.93	0.0003
INDVI spring	0.04	0.06	0.60	0.55
INDVI fall	-0.06	0.04	-1.42	0.16
Chizé				
Intercept	1.85	0.11	16.59	<0.001
Sex (female-male)	-0.05	0.017	-3.17	0.003
(NDVIs _{spg} /Ln(cohort density))	2.24	0.26	8.54	<0.001
(Residuals (INDVI fall))/Ln(cohort density)	0.46	0.38	1.19	0.24

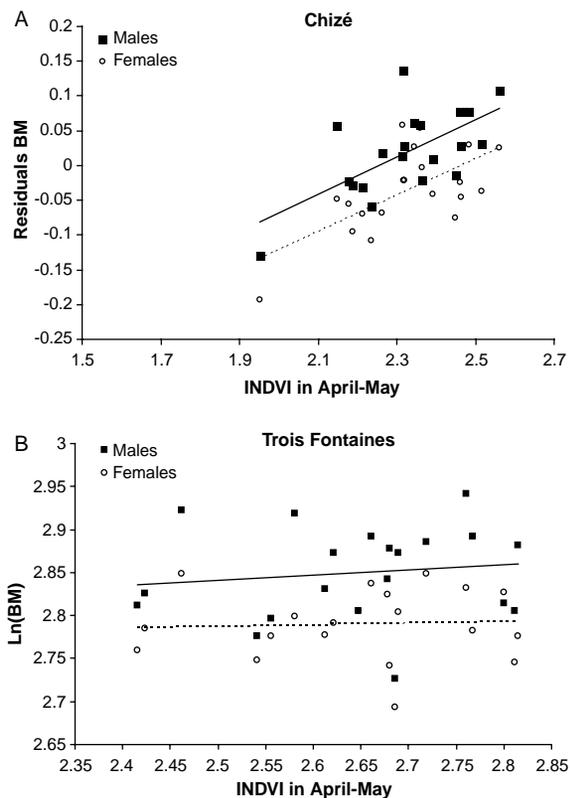


Fig. 3. Yearly variation in body mass of males and females in relation to the per capita INDVI in spring (April-May) in both study sites. At Chizé, the effects of the per capita INDVI in fall (August to October) were accounted for by considering the residuals between the yearly average body mass of both sexes and the expected body mass for a given per capita INDVI in fall. Regression lines for males (full line) and females (dotted line) are also provided.

In polygynous and dimorphic ungulates young males suffer more under harsh conditions than young females (Glucksmann 1974). On the contrary, we reported here similar responses of both sexes to changes in environmental conditions. Our results are thus consistent with the view that roe deer differ from most other ungulates studied so far by showing little sexual selection for most life history traits (Andersen et al. 1998).

Our study thus highlights the potential for remote sensing data to give valuable information on plant productivity in medium to low productive temperate areas, allowing managers and scientists to explore further the relationships between plant productivity and performance of ungulates in temperate forests. Caution should be made while working in highly productive forests because of either too little temporal variability in performance measures or a decreased relevance of remote sensing based indices.

Acknowledgements – We thank the Office National de la Chasse et de la Faune Sauvage for organizing all the captures of roe deer at the reserves. We are grateful to all the students, field

assistants and volunteers that spent time catching and monitoring the roe deer fawns on the study sites. Special thanks to Daniel Maillard and Bernard Boisaubert for ideas, comments and suggestions on previous drafts of this work. This study benefited from a grant from the European Union (Marie Curie Fellowship) to NP, from the Research Council of Norway to AM (YFF project), and from the ECOFOR and the ACI CLIM-POP to JMG and PD.

References

- Andersen, R., Duncan, P. and Linnell, J. D. C. 1998. The European roe deer: the biology of success. – Scandinavian Univ. Press.
- Andersen, R., Gaillard, J. M., Linnell, J. D. C. et al. 2000. Factors affecting maternal care in an income breeder, the European Roe deer. – *J. Anim. Ecol.* 69: 672–682.
- Asner, G. P., Scurlock, J. M. O. and Hicke, J. A. 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. – *Glob. Ecol. Biogeog.* 12: 191–205.
- Asrar, G., Fuchs, M., Kanemasu, E. T. et al. 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. – *Agr. J.* 76: 300–306.
- Beebee, T. J. C. 1995. Amphibian breeding and climate. – *Nature* 374: 219–220.
- Birky, A. K. 2001. NDVI and a simple model of deciduous forest seasonal dynamics. – *Ecol. Mod.* 143: 43–58.
- Boelman, N., Stieglitz, M., Rueth, H. et al. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. – *Oecologia* 135: 414–421.
- Brotton, J. and Wall, G. 1997. Climate change and the Bathurst caribou herd in the Northwest territories, Canada. – *Climate Change* 35: 35–52.
- Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. – Springer Verlag.
- Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. 1982. Red deer: behaviour and ecology of two sexes. – Univ. Chicago Press.
- Duncan, P., Tixier, H., Hofman, R. R. et al. 1998. Feeding strategies and the physiology of digestion in roe deer. – In: Andersen, R., Duncan, P. and Linnell, J. D. C. (eds), The European roe deer: the biology of success. Scandinavian Univ. Press, pp. 91–116.
- Forchhammer, M. C., Post, E., Stenseth, N. C. et al. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. – *Popul. Ecol.* 44: 113–120.
- Franca, H. and Setzer, A. W. 1998. AVHRR temporal analysis of a savannah site in Brazil. – *Int. J. Remote Sensing* 19: 3127–3140.
- Gaillard, J. M., Sempéré, A. J., Van Laere, G. et al. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer. – *Can. J. Zool.* 70: 1541–1545.
- Gaillard, J. M., Delorme, D., Boutin, J. M. et al. 1993a. Roe deer survival patterns: a comparative analysis of contrasting populations. – *J. Anim. Ecol.* 62: 778–791.
- Gaillard, J. M., Delorme, D. and Jullien, J. M. 1993b. Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. – *Oecologia* 94: 57–61.
- Gaillard, J. M., Delorme, D., Boutin, J. M. et al. 1996. Body mass of roe deer fawns during winter in 2 contrasting populations. – *J. Wildlife Manage.* 60: 29–36.
- Gaillard, J. M., Delorme, D., Van Laere, G. et al. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. – *Oecologia* 112: 502–513.

- Gaillard, J. M., Festa Bianchet, M., Yoccoz, N. G. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annu. Rev. Ecol. Syst.* 31: 367–393.
- Gaillard, J. M., Duncan, P., Delorme, D. et al. 2003. Effects of hurricane Lothar on the population dynamics of European roe deer. – *J. Wildlife Manage.* 67: 767–773.
- Garel, M., Loison, A., Gaillard, J. M. et al. 2004. The effects of a severe drought on mouflon lamb survival. – *Biol. Lett.* 271: S471–S473.
- Glucksmann, A. 1974. Sexual dimorphism in mammals. – *Biol. Rev.* 49: 423–475.
- Hanks, J. 1981. Characterization of population condition. – In: Fowler, C. W. and Smith, T. D. (eds), *Dynamics of large mammal populations*. Wiley, pp. 47–73.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. – *Science* 269: 676–679.
- Justice, C. O., Townshend, J. R. G., Holben, B. N. et al. 1985. Analysis of the phenology of global vegetation using meteorological satellite data. – *Int. J. Remote Sensing* 6: 1271–1318.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. – *Oikos* 78: 57–66.
- Kerr, J. T. and Ostrovsky, M. 2003. From space to species: ecological applications for remote sensing. – *Trends Ecol. Evol.* 18: 299–305.
- Klein, D. R. 1965. Ecology of deer range in Alaska. – *Ecol. Monogr.* 35: 259–284.
- Loe, L., Bonenfant, C., Mysterud, A. et al. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. – *J. Anim. Ecol.* 74: 579–588.
- Maizeret, C., Bidet, F., Boutin, J. M. et al. 1991. Influence de la composition chimique des végétaux sur les choix alimentaires des chevreuils. – *Rev. Ecol. Terre Vie* 46: 39–52.
- Markon, C. J., Fleming, M. D. and Binnian, E. F. 1995. Characteristics of vegetation phenology over the Alaskan landscape using AVHRR time-series data. – *Pol. Rec.* 31: 179–190.
- Myneni, R. B., Hall, F. G., Sellers, P. J. et al. 1995. The interpretation of spectral vegetation indexes. – *IEEE Trans. Geosci. Remote Sensing* 33: 481–486.
- Myneni, R. B., Keeling, C. D., Tucker, C. J. et al. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. – *Nature* 386: 698–702.
- Mysterud, A., Langvatn, R., Yoccoz, N. G. et al. 2001a. Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. – *J. Anim. Ecol.* 70: 915–923.
- Mysterud, A., Stenseth, N. C., Yoccoz, N. G. et al. 2001b. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. – *Nature* 410: 1096–1099.
- Paruelo, J. M., Epstein, H. E., Lauenroth, W. K. et al. 1997. ANPP estimates from NDVI for the central grassland region of the United States. – *Ecology* 78: 953–958.
- Pettorelli, N., Gaillard, J. M., Duncan, P. et al. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. – *Proc. R. Soc. B* 269: 747–754.
- Pettorelli, N., Gaillard, J. M., Duncan, P. et al. 2003a. Age and density modify the effects of habitat quality on survival and movements of roe deer. – *Ecology* 84: 3307–3316.
- Pettorelli, N., Dray, S., Gaillard, J. M. et al. 2003b. The distribution of preferred plant species in spring determines spatial variation in the body mass of roe deer fawns in winter. – *Oecologia* 137: 363–369.
- Pettorelli, N., Weladji, R., Holand, Ø. et al. 2005a. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. – *Biol. Lett.* 1: 24–26.
- Pettorelli, N., Vik, J. O., Mysterud, A. et al. 2005b. Using the satellite-derived normalized difference vegetation index (NDVI) to assess ecological effects of environmental change. – *Trends Ecol. Evol.* 20: 503–510.
- Pettorelli, N., Gaillard, J. M., Yoccoz, N. G. et al. 2005c. The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. – *J. Anim. Ecol.* 74: 972–981.
- Portier, C., Duncan, P., Gaillard, J. M. et al. 2000. Growth of European roe deer: patterns and rates. – *Acta Theriol.* 45: 87–94.
- Post, E. and Stenseth, N. C. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. – *J. Anim. Ecol.* 67: 537–543.
- Rasmussen, M. S. 1998. Developing simple, operational, consistent NDVI-vegetation models by applying environmental and climatic information: Part I. Assessment of net primary productivity. – *Int. J. Remote Sensing* 19: 97–139.
- Reimers, E. 2002. Calving time and foetus growth among wild reindeer in Norway. – *Rangifer* 22: 61–66.
- Ricotta, C. and Avena, G. C. 1998. Fractal modelling of the remotely sensed two-dimensional net primary production pattern with annual cumulative AVHRR NDVI data. – *Int. J. Remote Sensing* 19: 2413–2418.
- Running, S. W. 1990. Estimating primary productivity by combining remote sensing with ecosystem simulation. – In: Hobbs, R. J. and Mooney, H. A. (eds), *Remote sensing of biosphere functioning*. Springer-Verlag, pp. 65–86.
- Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanism. – *Trends Ecol. Evol.* 12: 143–149.
- Sæther, B.-E. and Heim, M. 1993. Ecological correlates of individual variation in age at maturity in female moose: the effects of environmental variability. – *J. Anim. Ecol.* 62: 482–489.
- Sellers, P. J. 1985. Canopy reflectance, photosynthesis and transpiration. – *Int. J. Remote Sensing* 6: 1335–1372.
- Slagsvold, T. 1976. Annual and geographical variation in the time of breeding of the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. – *Ornis Scand.* 7: 127–145.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*, 3rd ed. – W.H. Freeman & company.
- Solberg, E. J., Jordhøy, P., Strand, O. et al. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. – *Ecography* 24: 441–451.
- Stenseth, N. C., Mysterud, A., Ottersen, G. et al. 2002. Ecological effects of climate fluctuations. – *Science* 297: 1292–1296.
- Strandgaard, H. 1967. Reliability of the Petersen method tested on a roe deer population. – *J. Wildlife Manage.* 31: 643–651.
- Venables, W. N. and Ripley, B. D. 1997. *Modern applied statistics with S-plus*, 2nd ed. – Springer Verlag.
- Walther, G. R., Post, E., Convey, P. et al. 2002. Ecological responses to recent climate change. – *Nature* 416: 389–395.
- Weladji, R., Klein, D. R., Holand, Ø. et al. 2002. Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. – *Rangifer* 22: 33–50.
- Weladji, R., Steinheim, G., Holand, Ø. et al. 2003. Temporal patterns of juvenile body weight variability in sympatric reindeer and sheep. – *Ann. Zool. Fenn.* 40: 17–26.
- Widmer, O., Said, S., Miroir, J. et al. 2004. The effects of hurricane Lothar on habitat use of roe deer. – *For. Ecol. Manage.* 195: 237–242.

Subject Editor: Esa Ranta