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Population abundance and early spring conditions determine variation in body mass of juvenile chamois

Mathieu Garel,* Jean-Michel Gaillard, Jean-Michel Jullien, Dominique Dubray, Daniel Maillard, and Anne Loison

Office National de la Chasse et de la Faune Sauvage, Centre National d'Études et de Recherche Appliquée Faune de Montagne, 147 route de Lodève, Les Portes du Soleil, F-34990 Juvignac, France (MG, J-MG, DD. DM)
Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France (J-MG)
Laboratoire d'Ecologie Alpine (LECA), CNRS, UMR 5553, Université de Savoie, F-73376 Le Bourget du Lac, France (AL)

** Correspondent: mathieu.garel@oncfs.gouv.fr*

For species living in seasonal environments the understanding of demographic processes requires identifying the environmental factors during spring and summer that shape phenotypic variation. We assessed the effects of plant phenology and population abundance during spring–summer on variation in autumn body mass among cohorts (1995–2006) of juvenile alpine chamois (*Rupicapra rupicapra*). We computed several metrics based on the normalized difference vegetation index (NDVI) to assess interannual variation in plant phenology and productivity. Body mass of both sexes decreased similarly during years with late springs (−20%) and with increasing population abundance (−15%), with no interactive effect. Our results also suggested that forage quality more than forage quantity influenced body mass of juveniles. Variation in body mass of juveniles thus can be used as an indicator of the relationship between chamois populations and their environment. This study also demonstrates the utility of satellite-based data in increasing our understanding of the consequences of spring–summer conditions on life-history traits.

Key words: body mass, chamois, density dependence, French Alps, normalized difference vegetation index (NDVI), plant phenology, *Rupicapra rupicapra*

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In many species body mass is a pivotal life-history trait (Fairbairn 1997). In large mammals body mass generally is correlated positively with reproduction and survival within species, such that larger individuals tend to have higher lifetime reproductive success than smaller ones (Beauplet and Guinet 2007; Gaillard et al. 2000; Richard et al. 2000). Therefore, identification of factors shaping body mass is required to understand variation in fitness among individuals within and among populations.

Variation in body mass of ungulates is closely related to environmental conditions (Loison et al. 1999c; Weladji et al. 2002). Similarly, changes in population density generate variation in per capita resources that influence body mass (Bonenfant et al. 2009). These density-dependent and density-independent processes both strongly influence early development (Gaillard et al. 2000) when individuals are still growing and lack energy reserves that buffer adverse conditions.

In seasonal environments spring and summer more than winter might shape variation in phenotypic quality (Klein 1965). Energetic demands of reproduction require relatively high availability of food (Clutton-Brock et al. 1989), and even small variation in spring–summer conditions can have multiplier effects on body mass (White 1983). In addition, Mysterud et al. (2001) demonstrated that winter conditions influenced body mass of ungulates mainly through their effects on summer foraging conditions. Although most previous studies of herbivores have relied on climatic variables as surrogates for resources (Weladji et al. 2002), remotely sensed data such as the normalized difference vegetation index (NDVI) might perform better (Garel et al. 2006; Pettorelli et al. 2005a; Rasmussen et al. 2006) and provide information about a wide range of vegetation attributes at large spatial and temporal scales (Hamel et al. 2009; Pettorelli et al. 2005b).

We aimed to assess the influence of population abundance and plant phenology (indexed via NDVI) during spring–summer on

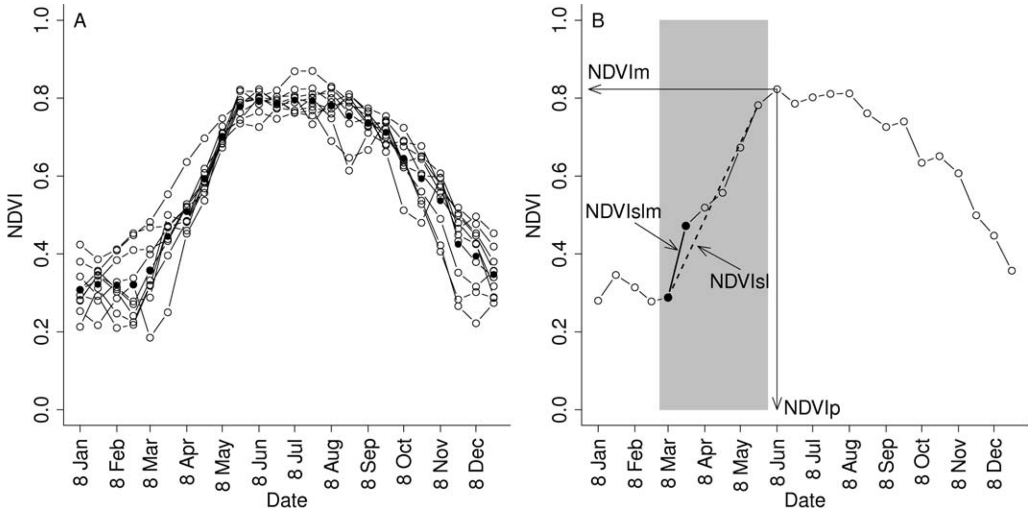

Fig. 1.—Annual variation in the normalized difference vegetation index (NDVI) in Massif des Bauges, French Alps, during 1995–2003 and 2006. A) Each curve represents changes of NDVI within a year. Black dots correspond to average NDVI values. B) NDVI curve in 2001, showing how NDVI metrics were computed (Table 1). The shaded area corresponds to the range (spring) over which the average (NDVIsl) and maximum increase (NDVIslm) of NDVI was obtained. Black dots correspond to the 2 NDVI values used for computing integrated NDVI in March (INDVIs).

variation in sex-specific body mass among cohorts of juvenile alpine chamois (*Rupicapra rupicapra*). We focused on the spring–summer period because a previous long-term study on marked individuals demonstrated that this period was more critical than winter for chamois survival (Loison et al. 1999a). We included several NDVI metrics to assess the relative contribution of vegetation productivity and plant phenology (Garel et al. 2006). We expected body mass to be influenced by early onset of spring (Pettorelli et al. 2005c; Post et al. 1999) or rapid changes during green-up (Pettorelli et al. 2007), or both, because timing of spring influences access to high-quality vegetation. Due to multiplier effects (White 1983) we also expected body mass to be influenced by spring–summer forage quality more than by forage quantity (Herfindal et al. 2006). As for many other ungulate species (Bonenfant et al. 2009), we expected density dependence in body mass to occur. Although juvenile chamois display low sexual size dimorphism (Garel et al. 2009), we expected males to be more sensitive than females to harsh environmental conditions (e.g., delayed spring) or to intraspecific competition for food. Even relatively small sexual size dimorphism involves greater absolute energy requirements for males than for females due to allometric constraints (Fairbairn 1997) and higher basal metabolic rates (Demment and Van Soest 1985). Finally, we expected changes in population abundance to influence body mass to a larger extent under harsh environmental conditions than under favorable conditions (Bonenfant et al. 2009; Portier et al. 1998).

Materials and Methods

Study area.—The study was conducted in the eastern part of Massif des Bauges (45°40′N, 06°13′E; elevation = 350–2,217 m) in the northern French Alps. Monitoring of chamois abundance was initiated in 1995 within 3 zones located in the national game and wildlife reserve of Massif des Bauges, which includes an area of 5,205 ha (Loison et al. 1999b). The 3 zones contain high-elevation meadows and forested areas, with virtually no exchanges of chamois among the zones.

Body mass and covariates.—We used data from chamois shot within the 3 zones during the hunting seasons from early September to late February in 1995–2007. Hunters recorded date, age, sex, and carcass mass (Garel et al. 2009). Shooting date was transformed to Julian date with day 1 beginning on 1 September, except in leap years (years with 366 days) when 1 September was actually day 2 to account for the difference of 1 day regarding the last hunting season.

Measurements of carcass mass (± 100–500 g) were made in 1 of 3 ways, either as full carcass mass (including rumen content; $n = 6$), eviscerated carcass mass minus bleedable blood ($n = 52$), or partially eviscerated carcass mass (heart, liver, and lungs present; $n = 27$). We used strong positive relationships previously established in our population among the different measures of mass (Garel et al. 2009) to transform all measures into eviscerated carcass mass (most frequently measured).

We used NDVI data (processed by the Global Inventory Modeling and Mapping Studies group and available since 1982—Tucker et al. 2005) to assess variation in vegetation phenology and productivity among years (Hamel et al. 2009; Pettorelli et al. 2005b; Fig. 1A). Pixel size was approximately 8 × 8 km, and daily NDVI images were computed into a 15-day maximum value composite image to reduce problems of cloud contamination (Holben 1986). We did not include surrounding pixels because the habitat there contained agricultural vegetation, low elevations, and urban areas. From the NDVI time series we computed 5 NDVI metrics during

TABLE 1.—Variables associated with phenology used to evaluate variation in body mass of chamois kids in Massif des Bauges, French Alps (see also Fig. 1). NDVI = normalized difference vegetation index.

Phenology variable (abbreviation)	Description
Spring NDVI slope (NDVIsl)	Overall increase between NDVI values from early March to end of May
Spring NDVI slope maximum (NDVIslm)	Maximal increase between any 2 consecutive bimonthly NDVI values from early March to end of May
Annual maximum NDVI (NDVIm)	Maximum value of the NDVI over a year
NDVI peak (NDVIp)	Julian date when NDVIm occurs within a year
Early spring INDVI (INDVIs)	Sum of NDVI values in March

spring–summer (Pettorelli et al. 2005b, 2007; Table 1; Fig. 1B). We used the integrated NDVI of March as a measure of the timing of the onset of vegetation growth (Hamel et al. 2009). We used overall increase and maximum increases of NDVI as measures of the period during which chamois should have access to high-quality forage (Pettorelli et al. 2007). We used annual maximum NDVI value (NDVIm) to index biomass production, and the date when NDVIm occurred was evaluated as another measure of timing of vegetation growth.

The NDVI is assumed to reflect variation in plant phenology and productivity among years. Although we could not test this assumption with vegetation data collected in the field, we assessed the correlations (Pearson r) between local climatic conditions and those NDVI metrics that were selected as the best explanatory variables of variation in body mass to detect expected patterns (Pettorelli et al. 2005c, 2007). Climate data were provided by 2 Météo France weather stations (http://france.meteofrance.com/) situated at Lescheraines (45°42′N, 06°06′E, elevation = 590 m; used for temperature parameters) and at Aillon-le-jeune (45°37′N, 06°04′E, elevation = 900 m; used for precipitation parameters). We retrieved 4 climatic variables from these stations (period 1982–2006): precipitation, amount of fresh snow, snow depth, and average temperature. In addition, we computed the number of days with an average temperature $>5°C$ as a proxy of length of growing season for vegetation (Frich et al. 2002).

We estimated chamois abundance within each zone during spring-summer using capture–mark–recapture methods (Loison et al. 2006); however, no surveys took place in 2004 and 2005. In addition, we did not get estimates for each zone in each year because of failures in meeting statistical requirements. Data sampling was in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Statistical analyses.—We adjusted body mass according to date of harvest because body mass of chamois is expected to change throughout the hunting season (Schröder 1971). We used additive models (Wood 2006) to account for potential nonlinear relationships between carcass mass and date of harvest and adjusted the mass to 15 October, which corresponded to the median date of harvest.

We used both partial least-squares regressions and ordinary least-squares regressions to analyze variation in body mass within the 3 zones (Graham 2003; Tenenhaus 1998) because we had a large number of predictor variables relative to our sample size and because collinearities occurred among predictor variables (e.g., $r = 0.72$, $n = 10$, $P = 0.02$ between NDVI slope [NDVIsl] and NDVI slope maximum [NDVIslm]). We considered the zones as replicates providing abundance variation within and among years. The full model included the effects of sex, the 5 phenology variables, chamois abundance, and all 2-way interactions among these variables (sex × phenology, sex × abundance, and phenology × abundance). We also accounted for potential nonlinearity by including quadratic terms (Pettorelli et al. 2007). We fitted the global model and used the root mean squared error of prediction, estimated from leave-one-out cross-validation and adjusted for bias (Mevik and Cederkvist 2004), for choosing the optimal number of components. We selected the global minimum root mean squared error of prediction as the basis for identifying the corresponding number of dimensions for the optimal model (Martens and Martens 2000; Mevik and Wehrens 2007). We then refit the model with the selected number of components and assessed the relative importance of each independent variable by using a modified jackknife estimation of parameter uncertainty (Martens and Martens 2000). The least significant variable with $P > 0.05$ was excluded in a backward-stepwise selection by starting with highest order terms. The procedure (component selection and then selection by jackknife) was repeated until only statistically significant variables were included in the model (Martens and Martens 2000). When model selection ended with simple models including few (typically fewer than $n/10$ covariates, with n being sample size—Burnham and Anderson 2002) uncorrelated covariates ($r < 0.30$—Graham 2003), we relied on ordinary least-squares regressions to perform variable selection. All variables were standardized ($\overline{X} = 0$, $SD = 1$) so that coefficient estimates could be interpreted as the relative contribution of each variable to the model (Tenenhaus 1998).

In some situations a relationship between body mass and a climatic covariate can be detected only because both variables exhibit similar linear trends over time. In such a situation we cannot rule out the possibility that the trend in body mass resulted from a relationship with some overlooked causal factors that also would exhibit a trend, rather than from a causal relationship with the focal covariate (Grosbois et al. 2008). In such a situation we regressed body mass and selected covariates against cohort to assess whether body mass variation still was accounted for by residual variation chamois kids in Massif Les Bauges in the explanatory variables once

TABLE 2.—Parameters for the model selected to explain variation in body mass of juvenile alpine chamois (n = 85, 42 males and 43 females) harvested in Massif des Bauges, French Alps. The estimate for sex is associated with the factor level ''males.'' Covariates were standardized ($\bar{X}$ = 0, SD = 1). INDVIs = sum of normalized difference vegetation index (NDVI) values in March.

Variable	β	*SE*	*t*	*d.f.*	*P*	Partial R^2
Sex	0.762	0.296	2.57	81	0.01	0.076
Chamois abundance	−0.526	0.153	−3.45	81	<0.001	0.127
INDVIs	0.541	0.152	3.56	81	<0.001	0.135

cohort effects were accounted for in the model (e.g., model: body mass = intercept + cohort + residuals(covariate 1 regressed on cohort)—Grosbois et al. 2008). We performed all statistical analyses using R 2.11.1 (R Development Core Team 2007) and pls library (Mevik and Wehrens 2007).

RESULTS

Our model selection process identified a relatively simple model to explain variation in body mass of juvenile alpine chamois (n = 85). The final model included uncorrelated variables that fit the data satisfactorily using ordinary least-squares regression (R^2 = 0.333; Table 2). Male juveniles (n = 42) were 6.9% heavier than juvenile females (n = 43). Among the 5 NDVI metrics that we evaluated (Table 1), integrated NDVI in March (INDVIs) explained most variation in body mass of juveniles (Table 2), supporting the importance of both timing of vegetation growth and forage quality. We found INDVIs to be correlated with most climatic variables in March (precipitation: $r = -0.31$, $n = 25$, $P = 0.13$; fresh snow: $r = -0.53$, $n = 21$, $P = 0.01$; snow depth: $r = -0.46$, $n = 21$, $P = 0.04$; temperature: $r = 0.59$, $n = 25$, $P = 0.002$; and growing season length: $r = 0.48$, $n = 25$, $P = 0.02$). Accordingly, early springs are related to lower snow cover and higher temperatures.

We also documented density-dependent responses of body mass. Standardized coefficients and partial R^2 values indicated that INDVIs and chamois abundance had similar influences on body mass of juveniles. Decreasing INDVIs and increasing chamois abundance in the year of birth resulted in lower body mass (−20% and −15% from the heaviest to the lightest mass, respectively; Figs. 2A and 2B), without any interactive effect ($\beta = 0.007$, $SE = 0.134$; $t_{81} = 0.051$, $P = 0.96$).

Although in the expected biological direction, none of the sex-specific interactions were retained in the final model (sex × INDVIs: $\beta = -0.347$, $SE = 0.295$; $t_{80} = -1.18$, $P = 0.24$, and sex × abundance: $\beta = -0.297$, $SE = 0.298$; $t_{80} = -1.00$, $P = 0.32$; Table 2). Even after correcting for observed temporal trends in mass of juveniles ($\beta = -0.178$, $SE = 0.060$; $t_{83} = -2.96$, $P = 0.004$), chamois abundance ($\beta = 4.29$, $SE = 1.94$; $t_{83} = 2.21$, $P = 0.03$), and INDVIs ($\beta = -0.032$, $SE = 0.004$; $t_{83} = -8.31$, $P < 0.001$), the effects previously reported held (additive effects of INDVIs and chamois abundance: $P < 0.02$; interactions: $P > 0.23$).

DISCUSSION

As expected from studies of other ungulates (Bonenfant et al. 2009) and suggested for Pyrenean chamois (*Rupicapra pyrenaica*) by Pépin et al. (1996), increasing chamois abundance negatively affected the autumn mass of juveniles. Likewise, an early onset of green-up as indexed by high NDVI values in March (INDVIs) led to heavier juveniles in autumn than did later springs, as previously reported for other species (Herfindal et al. 2006; Pettorelli et al. 2005c). Pettorelli et al. (2007) reported that 3 other mountain ungulates responded negatively to rapid changes in vegetation green-up (NDVIslm) more than to delayed onset of spring. However, these 2 metrics are probably often closely related (e.g., in our study: $r = -0.71$, $n = 10$, $P = 0.02$, between NDVIslm and INDVIs), and rapid changes in NDVI would be expected in late rather than in early springs, because vegetation should grow faster

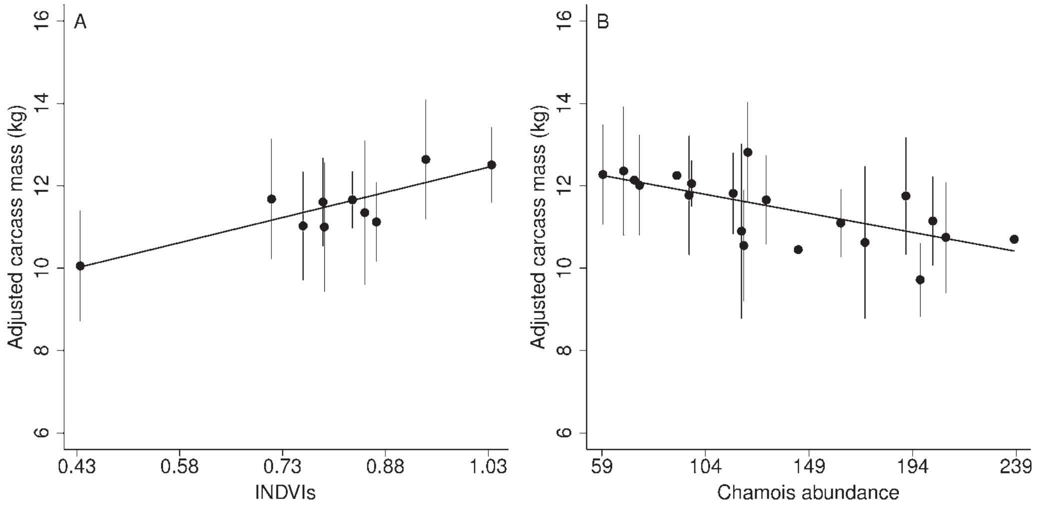

FIG. 2.—A) Effect of the sum of normalized difference vegetation index (NDVI) values in March (INDVIs) on body mass of chamois juveniles (adjusted for abundance and sex; Table 2). B) Effect of chamois abundance on body mass of kids (adjusted for INDVIs and sex; Table 2). Filled circles correspond to average body mass (± *SD*), and lines represent linear regressions fitted to individual data.

when springs are delayed (Hamel et al. 2009). Our results also suggested that variation in forage quality during spring and summer was more important than biomass production in explaining variation in body mass of juveniles.

These results reinforce the key role of plant phenology as a driving force in population dynamics of herbivorous mammals and the idea that early and long access to high-quality vegetation is a strong determinant of growth for species living in seasonal environments (Herfindal et al. 2006; Klein 1965; Pettorelli et al. 2007). Plant phenology, as indexed by INDVIs (Hamel et al. 2009), is a good proxy of plant quality because young plants are generally of high nutritional value, high digestibility, and have lower levels of secondary compounds (Van Soest 1994). During this period females incur high energy requirements because of the energetic cost of late gestation and early lactation (Clutton-Brock et al. 1989). Thus, small variation in spring forage conditions can have a considerable impact on body mass and development of females (White 1983). Moreover, condition of maternal females affects the size of their offspring (Solberg et al. 2007), which would benefit from greater maternal care provided by females with early access to high-quality forage compared to females on a lower nutritional level. Ultimately, variation in body mass generated by forage conditions is expected to influence several fitness components such as juvenile survival, which is known to be a critical component of population dynamics of large herbivores (Gaillard et al. 2000).

Other factors such as interspecific relationships, changes in habitat quality, or climatic variation outside of spring–summer also likely contribute to observed variation among cohorts in body mass of chamois. However, the high level of variance explained by our selected model (33.3% compared to <7% in most ecological studies—Møller and Jennions 2002) provides support for the importance of spring–summer conditions in shaping life-history traits of chamois (Loison et al. 1999a).

Increasing chamois abundance, high body mass, and early age of primiparity compared to other chamois populations (Garel et al. 2009) indicated that our study population was highly productive. Thus, we did not detect any evidence of interactions between chamois abundance and phenology variables (Pettorelli et al. 2007). Similarly, these overall good conditions were associated with a low degree of sexual size dimorphism in juveniles (Garel et al. 2009), which might explain the absence of sex-specific responses of body mass of juveniles to changes in either environmental conditions or abundance.

Our study provides additional support for the use of satellite-based information when studying the coupling between vegetation and herbivore performance (Garel et al. 2006; Pettorelli et al. 2007). Although INDVIs in our study was correlated in the expected way with climate in March, indirect and complex interactions often occur between climatic variables and vegetation. Thus, NDVI could be preferred to traditional climatic parameters when assessing resource availability for large herbivores (Garel et al. 2006; Rasmussen et al. 2006). Moreover, remotely sensed data are most often free and available at large spatial and temporal scales at increasing resolution (Pettorelli et al. 2005b).

In a context where global changes affect plant phenology (Theurillat and Guisan 2001), studying how plant phenology influences body mass is of prime importance for ecologists because body mass shapes most life-history traits in ungulates, and because ungulate population dynamics generally have been described as sensitive to early performance (Gaillard et al. 2000). Our results have additional implications for management. Body mass of juveniles could serve as an early warning sign of density dependence (see Fig. 2B). Monitoring annually this indicator of ecological change (Morellet et al. 2007) provides a quantitative basis for setting hunting quotas to achieve specific management objectives.

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