

Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer

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Abstract In arctic and alpine environments, warm summer temperatures may force a reduction in foraging time of large herbivores, whose tolerance for heat is lower than for species adapted to warmer weather. We constructed time budgets for marked ibex (*Capra ibex*) males over two summers to test whether warm temperatures constrained foraging behaviour and forced altitudinal migrations. As daily temperature and solar radiation increased, feeding activity was reduced at midday and evening, but increased in the early morning, probably to anticipate for an expected reduction in foraging later in the day. With increasing temperature and solar radiation, ibex moved to higher elevations where they spent very little time feeding. Changes in forage quality and availability could not explain altitudinal migration. Temperatures above 15–20°C apparently result

in heat discomfort in male Alpine ibex. As temperature and solar radiation increased, older and larger ibex spent less time feeding during daylight and showed a steeper decrease in feeding time than younger and smaller ibex. Larger males may be more sensitive to temperature and solar radiation, or may have more flexibility in allocating time to different activities, given their lower relative energetic requirements.

Keywords Foraging · Space use · Thermoregulation · Ungulates · Climate change

Introduction

Large herbivores spend much of their time feeding, and their foraging tactics have important fitness consequences (White 1983; McLoughlin et al. 2006). Optimal foraging theory predicts that animals will forage so as to maximise the net fitness benefit, taking into account all possible costs and benefits of foraging behaviour (Pyke 1984). In ungulates, much attention has been paid to the potential foraging costs and benefits of predation risk (Kie 1999) and of spatial differences in forage quality and quantity (Belovsky 1984). The physiological effects of high ambient temperature on foraging behaviour have also been examined in an optimality context. At high temperature, the cost of thermoregulation may mean that the best foraging tactic is to rest and wait for cooler temperatures (Dussault et al. 2004; Maloney et al. 2005; Owen-Smith 1998). Behaviours play an important role in the thermal balance of ungulates (Belovsky and Slade 1986; Dussault et al. 2004; Maloney et al. 2005) because autonomic thermoregulation can be much more energetically expensive than behavioural thermoregulation (Maloney et al. 2005).

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Herbivores inhabiting highly seasonal temperate environments are subject to drastic daily and seasonal changes in environmental quality (Post and Stenseth 1999). During summer, they must acquire sufficient resources for growth, reproduction, and to survive the following winter (Festa-Bianchet 1998; Festa-Bianchet et al. 1997; Parker et al. 1996). Foraging behaviour in summer is thus vitally important (Parker et al. 1996; White 1983). Here, we examine how changes in daily temperature and altitudinal changes in forage quality and quantity affect the feeding behaviours and daily altitudinal migration of male ibex in summer.

The space use and foraging patterns of ungulates are usually thought to be determined by spatial distribution and seasonal variation in food quality and availability (Festa-Bianchet 1988; Owen-Smith 1994). Many mountain ungulates exhibit seasonal migrations in altitude, tracking newly grown forage, which is highly nutritious and digestible (Van Soest 1994) [woodland caribou, *Rangifer tarandus* (Oosenberg and Theberge 1980); Stone's sheep, *Ovis dalli stonei* (Seip and Bunnell 1985); bighorn sheep, *O. canadensis* (Festa-Bianchet 1988); red deer, *Cervus elaphus* (Albon and Langvatn 1992; Mysterud et al. 2001); roe deer, *Capreolus capreolus* (Mysterud 1999)]. Later snow melt at higher altitude delays the onset of plant growth and prolongs access to high-quality vegetation (Albon and Langvatn 1992; Mysterud et al. 2001). Mountainous habitats also provide an array of vegetation phenological stages and biomass, through heterogeneity in aspect, slope, and altitude (Albon and Langvatn 1992). Thus, mountain ungulates can find vegetation that differs widely in quality, quantity and species composition just by moving a few hundred metres.

Ruminants generally alternate feeding bouts with ruminating and resting periods (Owen-Smith 1998). In summer, ruminants shift their peak activity from midday to mornings and evenings, possibly to avoid activities during the hottest periods of the day (Roberts and Dunbar 1991). Temperate ungulates experience heat discomfort or stress at lower temperatures than species adapted to warmer environments (Owen-Smith 1998; Schab and Pitt 1991). For examples in moose (*Alces alces*), respiration and metabolic rate increase rapidly above 14°C in summer and -5°C in winter (Renecker and Hudson 1986). In mule deer (*Odocoileus hemionus*), Parker and Robbins (1984) observed hyperthermia when temperature exceeded 20°C in summer and 5°C in winter. As temperature increases from 10 to 20°C, temperate ungulates reduce activity by nearly 50% (Belovsky and Slade 1986), whereas African savannah species only reduce activity when temperatures exceed 30–32°C (Owen-Smith 1998).

Alpine ibex (*Capra ibex*) may experience heat stress in summer (Grignolio et al. 2004). In June–July, Neuhaus and Ruckstuhl (2002) reported that adult male ibex spent less

than 9% of daylight feeding. That result is surprising, because with a body mass of 50–100 kg, ibex should feed for 52–55% of the time (Mysterud 1998). Therefore, warm temperature may constrain foraging during the day. Grignolio et al. (2004) reported that during summer 2001, which was hotter than summer 2002, female ibex had larger home ranges and moved to higher elevations.

Preliminary observations of Alpine ibex males in the Gran Paradiso National Park, Italy, suggested a regular daily altitudinal movement that appeared more evident in warm days. Based on a possible thermal constraint of feeding activity (Belovsky and Slade 1986; Dussault et al. 2004), we contrasted the effects of thermal environment and forage characteristics on daily altitudinal movements and feeding behaviour of male ibex in summer. We predicted that ibex should respond to warm temperatures by migrating to higher elevations and reducing activity. In addition, we expected that the foraging constraints caused by high temperatures would affect small males more than large ones. Ibex males accumulate mass over many years and range in weight from 45 to 110 kg. Small individuals have higher energetic requirement per unit of mass than large individuals, because while energy requirements vary allometrically with size ($W^{0.75}$), rumen volume varies isometrically with size (Demment and Van Soest 1985; Illius and Gordon 1987). Small individuals also have lower thermal inertia and higher conductance than large ones (Peters 1983). Consequently, small ibex should have less flexibility in foraging tactics than larger males. We expected small males to spend more time feeding and migrate to higher altitude than large ones.

Materials and methods

Study area and population

We studied adult male Alpine ibex in the Levionaz basin, Gran Paradiso National Park, Italy (GPNP; 45° 34' N, 07° 13' W). The winter range (used from December to May), between 1,600 and 2,000 m a.s.l., includes pastures, ravines and coniferous forests. The summer range, above the tree line, lies between 2,000 and 3,200 m a.s.l. and is characterised by alpine meadows (mainly *Festuca* spp., *Carex* spp., and *Poa* spp.), rocks, cliffs, ravines, moraines and glaciers. Large predators were extirpated over a century ago, and ibex hunting is prohibited in Italy and France, the country that borders the GPNP to the west.

We monitored 61 marked adult males from late May to early September 2003 and 2004. Ibex were captured with tranquillizing darts and marked with coloured plastic ear tags (Allflex®) (Bassano et al. 2004). Marked ibex were 3–16 years old and were aged at capture by counting annual

horn growth rings (Couturier 1962). About 220 ibex (100 males and 120 females) used the Levionaz basin during our study (GPNP, unpublished data).

Behavioural observations

Ibex were observed at distances of 50 to 300 m using binoculars (10×42) and spotting scopes ($15\text{--}45\times$). We recorded ibex behaviour during daylight ($\sim 06:00\text{--}21:00$ h) using focal sampling (Altmann 1974) for continuous periods of up to 14 h (mean $7.2 \text{ h} \pm \text{SD} = 2.5$ in 2003 and $6.4 \text{ h} \pm 2.6$ in 2004) for a total of 6,457 ibex-hours of observation (56 ibex, mean of $51.7 \text{ h} \pm 22.7$ per ibex in 2003 and 51 ibex, $78.9 \text{ h} \pm 24.3$ in 2004) on 57 days in 2003 and 60 in 2004. Observers chose up to ten marked individuals to monitor for at least 6 h consecutively. Focal animals were selected to distribute observations across marked individuals and daylight hours every 2 weeks. Up to 18 marked animals at a time were observed (mean $6.7 \pm \text{SD} = 3.3$ per day in 2003 and 10.5 ± 3.6 in 2004), by two observers in radio contact in 2003 and three in 2004.

We constructed activity budgets following Ruckstuhl (1998). We noted the times of transition between behaviours that lasted more than a minute, including grazing, moving, standing and resting. Other behaviours accounted for less than 4% of daily activity budgets. We noted the location of individual ibex on a map (1:10,000) of the study area.

We performed hourly scans of the behaviour of all non-focal marked males visible during focal observations. While travelling in the study area, we also noted the identity, date, location, time of sighting and behaviour of each marked animal seen, to supplement data on the daily maximum altitude reached by individual ibex (see below).

Mass measurements

We weighed individual ibex from June to September using an electronic platform scale baited with salt (Bassano et al. 2003). We adjusted individual body mass to 1 August each year (42 ibex in 2003 and 28 in 2004) as described in von Hardenberg (2005).

Weather data

We obtained air temperature (T_a , °C) and solar radiation (R_{Sol} , W/m^2) from the meteorological station at Pont, 6.2 km south of our study area (1,951 m a.s.l., Meteorological office of the Aosta Valley). T_a and R_{Sol} were hourly averages of readings taken every minute. In addition, we calculated daily mean (06:00–21:00 h, approximating daylight hours) T_a and R_{Sol} .

Forage availability

We monitored forage availability from mid-May to September by measuring plant biomass at biweekly intervals in four quadrats ($25 \text{ cm} \times 25 \text{ cm}$) (Higgins et al. 1996) along six permanent 150-m transects along an elevation gradient (1,600–2,800 m). In each quadrat, average vegetation height (cm) was estimated by measuring it in a ten-point grid using a ruler. The vegetation was then clipped at 1 cm aboveground, air dried, subsequently oven-dried and weighed to estimate aboveground biomass (g/m^2). Subsequent plots were clipped next to earlier ones to avoid the effects of previous sampling. We registered all transect and quadrat location and altitude using a GPS unit. Of 192 potential samples a year, we obtained 149 in 2003 and 133 in 2004. Snow at high altitude early in the season and livestock grazing in the lowest transect during summer prevented us from sampling vegetation.

Forage quality

We assessed forage quality by measuring percent crude protein ($N \times 6.25$) using the Kjeldahl method (Association of Official Analytical Chemists 1980), neutral detergent fibre (NDF) and lignin (ADL) (Van Soest 1963; Van Soest et al. 1991) of clipped vegetation samples. These vegetation constituents are good indicators of nutritional quality of forage for ruminants (Van Soest 1994). Nitrogen content is correlated with forage digestibility, while fibre and lignin tend to decrease digestibility. We obtained 282 crude protein, 281 NDF and 278 ADL measurements. Some vegetation samples were too small to measure all three variables.

Ibex maximum daily altitude

We determined the maximum altitude reached by individual ibex each day from focal and opportunistic observations collected between 11:00 and 16:00 h. Respectively, 76 and 99% of focal ibex reached their maximum daily altitude by 11:00 and 16:00 h. When they resumed grazing in the late afternoon, ibex typically moved to lower altitude. We obtained 1,206 individual maximum altitudes during 92 days of observation in 2003 and 1,321 during 73 days in 2004, for a mean of $13.1 \pm \text{SD} = 9.9$ ibex per day in 2003 and 18.1 ± 10.7 in 2004.

Statistical analyses

For each complete hour of focal observations, we calculated the proportion of time spent in different behaviours by each individual. We used the hourly proportion of time spent grazing as the dependent variable to explore the effects of T_a and R_{Sol} on grazing time. Because grazing

activity had a quadratic relationship with time of the day and T_a , R_{Sol} and time of the day presented multicollinearity problems (Glantz and Slinker 1990); we analysed hourly grazing proportions over three equal periods: morning (06:00–11:00 h), midday (11:00–16:00 h) and evening (16:00–21:00 h). This grouping approximated changes in ibex activity, with morning and evening peaks of grazing and a resting period at midday. We used linear mixed models (LMMs) and generalised linear mixed models (GLMMs). Random effects allowed us to analyse repeated observations of the same ibex and to use the same weather variables associated with daily or hourly individual observations (Pinheiro and Bates 2000).

The distribution of data on grazing activity was bimodal with very few intermediate proportions and was not normalised by any transformation (Sokal and Rohlf 1981). Therefore, values below 0.50 were converted to zero, while other values to one. Data were consequently modelled using GLMMs with binomial errors and a logit link function. In all cases, we included ibex identity and an additive hourly weather measurement term (HW) as random effects, because the same weather value was associated to each hourly individual ibex observation, and these values were not independent from each other from 1 h to the next. Daily maximum altitude and square-root transformed vegetation data were normally distributed and were modelled using LMMs. An additive daily weather measurement term (DW) was included as random effects in the analysis of maximum daily altitude. Given the nature of the vegetation sampling design, we included random effects of a sampling period term (eight periods) and an additive transect term (six transects). We tested the significance of random terms by comparing the log-likelihood values of models with and without random terms following Steele and Hogg (2003).

All grazing activity analyses included Year as factor, Julian date (JD) and its quadratic function (JD2), Age of ibex in years, T_a , R_{Sol} and time of observation (Hour) and the second-order interactions among Age, T_a , R_{Sol} and Hour as fixed terms. R_{Sol} was excluded from the morning and evening grazing activity analyses as it was highly correlated with Hour (morning $r = 0.71$, $P < 0.001$, and evening $r = -0.78$, $P < 0.001$). We chose Hour because R_{Sol} was absent or minimal early and late in the day, when most of the study area was shaded by high mountains. The same fixed terms included in the grazing activity analysis were tested in the analysis of ibex maximum daily altitude, except that Hour was omitted, and for T_a and R_{Sol} we used daily mean (06:00–21:00 h) rather than hourly values. We tested the effect of Year, JD, altitude (Alt, in m) and their interactions in all vegetation analyses. Finally, the effects of ibex body mass were assessed by replacing Age with Mass in all models in which it was included. This latter procedure was justified by the strong correlation between Mass and

age ($r = 0.71$, $P < 0.001$) and because we knew the Age, but not the mass of all marked ibex each year.

For all models, we used a backward model selection procedure to account for unbalanced sampling design. Higher order interactions and subsequent single variables of the fixed part of the model were tested and removed sequentially based on their approximate chi-square Wald statistic. Total variance explained by the selected final model was estimated by the difference in residual deviance between a null model and the final model (Schemper 1990). All analyses were conducted using GenStat 8.1 (VSN International Ltd.).

Results

Ibex activity budget and altitude use

On average, male ibex spent 50.9% of their daily activity budget grazing, 38.1% resting, 4.8% standing, 2.4% moving and 3.8% in other behaviours. Grazing predominantly occurred in the morning and evening, and resting at midday (Fig. 1). Daily altitudinal movements presented a consistent pattern of use of lower altitude in the morning, an upward movement in late morning and a downward movement in late afternoon or early evening (Fig. 1).

Ibex grazing activity

Morning grazing time more than doubled from early June to early September (Table 1). In the evening, ibex grazed for about 70% of the time in early June, 35% in mid-July and 85% in early September. No seasonal effect was found

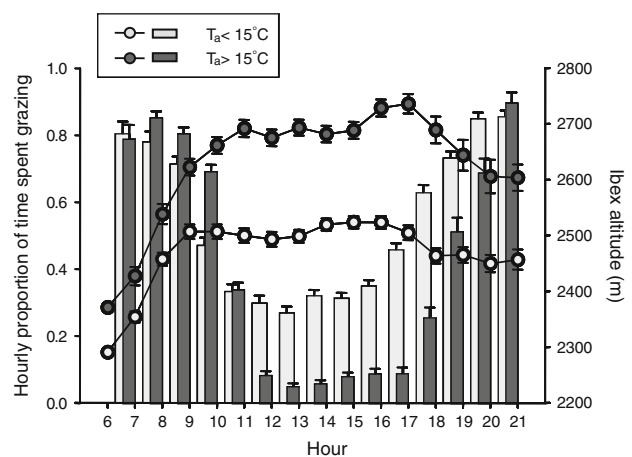


Fig. 1 Mean \pm SE hourly proportion of time spent grazing (histograms) and mean \pm SE hourly altitude (circles) of male Alpine ibex between 06:00 and 21:00 h for days when mean ambient temperature (T_a) was below (light grey) and above (dark grey) 15°C. Data from summers 2003–2004 at Levionaz, Italy

Table 1 Minimum adequate generalised linear mixed models with binomial error structure describing the grazing activity of male Alpine ibex in the morning, at midday and in the evening in Levionaz, Gran Paradiso National Park, Italy, in the summer of 2003 and 2004

Variables	Morning (06:00–11:00 h) ^a		Midday (11:00–16:00) ^b		Evening (16:00–21:00) ^c	
	Coeff (SE)	Wald χ^2 (P)	Coeff (SE)	Wald χ^2 (P)	Coeff (SE)	Wald χ^2 (P)
Year 2004	ns	ns	ns	ns	1.06 (0.37)	8.31 (0.004)
JD	0.17 (0.07)	6.28 (0.012)	ns	ns	−0.46 (0.08)	30.16 (<0.001)
JD2	−0.00035 (0.00018)	3.93 (0.047)	ns	ns	0.0012 (0.0002)	31.34 (<0.001)
Age	ns	ns	ns	ns	ns	ns
Hour	−1.46 (0.16)	83.56 (<0.001)	ns	ns	1.0060 (0.1148)	76.70 (<0.001)
T_a	ns	ns	−0.35 (0.03)	132.28 (<0.001)	−0.12 (0.05)	5.47 (0.019)
R_{Sol}	na	na	−0.0019 (0.0004)	20.31 (<0.001)	na	na
Hour \times T_a	−0.12 (0.03)	14.30 (<0.001)	ns	ns	ns	ns
Age \times T_a	ns	ns	0.011 (0.005)	4.58 (0.032)	ns	ns

All models included ibex identity (61 marked ibex) and hourly weather as random terms (all significant at $P < 0.001$)

JD, Julian date; JD2, quadratic of JD; T_a , air temperature in °C; R_{Sol} , solar radiation in W/m^2 ; ns, non significant; na, variable not tested in the model

^a Model based on 1,744 observations with 256 hourly weather measurements, explaining 38.2% of the total variance

^b Model based on 3,151 observations with 467 hourly weather measurements, explaining 25.8% of the total variance

^c Model based on 1,562 observations with 262 hourly weather measurements, explaining 44.3% of the total variance

for midday. T_a strongly reduced the time spent grazing at midday and in the evening (Table 1, Figs. 1 and S1). R_{Sol} also had a negative effect on time spent feeding at midday (Table 1, Fig. S1). The interaction between Hour and T_a in the morning suggested that, contrary to later in the day, early in the morning ibex fed more if it was warm (Table 1, Fig. 1). An interaction between ibex Age and T_a at midday, but not during other periods suggested that the decrease in feeding time with increasing temperature was steeper for older ibex. When it replaced Age, Mass had a negative effect on feeding time at midday ($r^2 = 0.018$, $\beta = -0.025 \pm SE = 0.007$, $n = 2080$, $\chi^2 = 11.50$, $P = 0.001$), but not in the morning and evening (Fig. 2). Mass also showed interactions with Hour for both midday ($\beta = -0.0088 \pm 0.0033$, $n = 2080$, $\chi^2 = 7.26$, $P = 0.007$) and evening ($\beta = -0.014 \pm 0.006$, $n = 1011$, $\chi^2 = 5.84$, $P = 0.016$) periods (Fig. 2). As the midday hours progressed, heavy males increased the time feeding at a faster rate than small ones. In contrast, in the evening small ibex increased their feeding time progressively faster compared to heavy males (Fig. 2).

Ibex daily maximum altitude

Accounting for seasonal effects, the maximum daily altitude increased with T_a and with R_{Sol} (Table 2, Figs. 3, S2). The interaction between T_a and R_{Sol} suggested that for a given T_a , ibex moved higher as solar radiation increased. At T_a of 15°C in cloudy days (R_{Sol} 200–250 W/m^2) ibex reached elevations averaging ~2,500 m, but in sunny days (R_{Sol} 450–500 W/m^2) they reached on average ~2,750 m. Older ibex used lower altitudes than younger ones. An

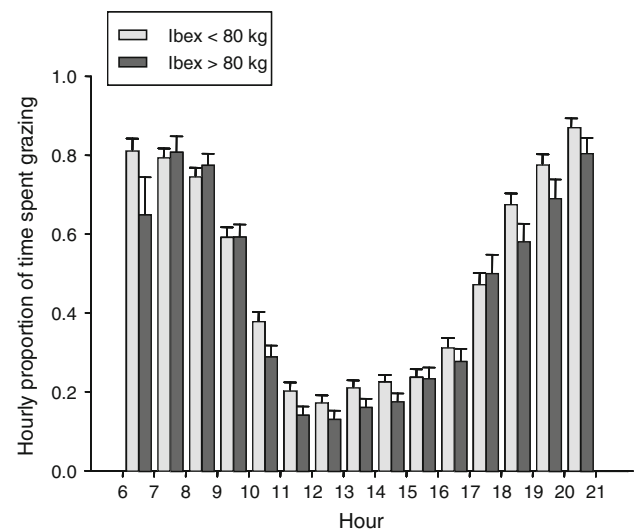


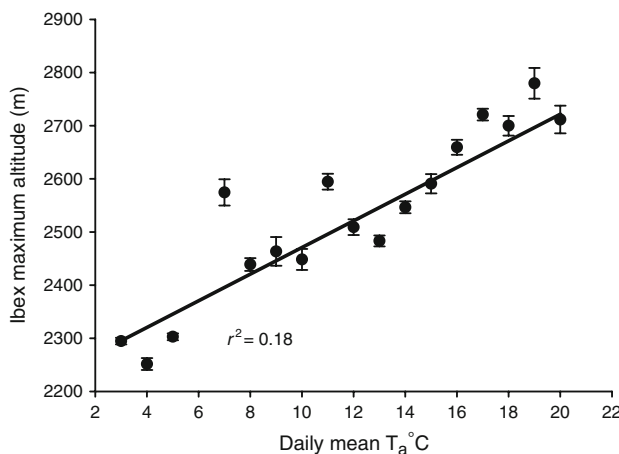
Fig. 2 Mean \pm SE hourly proportion of time spent grazing between 06:00 and 21:00 h by male Alpine ibex of body mass below 80 kg (light grey) and above 80 kg (dark grey) in summer of 2003 and 2004 at Levionaz, Italy

interaction between T_a and Age suggested that older males moved higher for a given increase in T_a compared to younger ones. Substituting Age with Mass, we found that heavy males used lower altitudes than light ones ($r^2 = 0.004$, $\beta = -0.73 \pm 0.26$, $n = 1746$, $\chi^2 = 8.15$, $P = 0.004$). The interaction of T_a and Mass ($\beta = 0.12 \pm 0.05$, $\chi^2 = 5.70$, $P = 0.017$) was concordant with the $T_a \times$ Age interaction. Heavier males moved higher in elevation for the same increase in T_a compared to smaller ones.

Table 2 Minimum adequate linear mixed model describing the daily maximum altitude (m) reached by male Alpine ibex in Levionaz, Gran Paradiso National Park, Italy, in the summer of 2003 and 2004

Variables	Coeff (SE)	Wald χ^2 (P)
JD	36.61 (6.96)	27.63 (<0.001)
JD2	-0.086 (0.018)	23.89 (<0.001)
Age	-6.92 (1.14)	37.09 (<0.001)
T_a	10.43 (4.73)	4.86 (0.027)
R_{Sol}	0.79 (0.16)	24.55 (<0.001)
$T_a \times R_{Sol}$	0.078 (0.037)	4.45 (0.035)
$T_a \times Age$	0.76 (0.19)	15.80 (<0.001)

Ibex identity and daily weather were included as random terms (both $P < 0.001$). The model is based on 2,527 observations of 61 ibex and 165 daily weather measurements, and explains 37.3% of the variance JD, Julian date; JD2, quadratic of JD; T_a , air temperature in °C; R_{Sol} , solar radiation in W/m^2

**Fig. 3** Mean daily maximum altitude (\pm SE) reached by male Alpine ibex under different ambient temperature (T_a) conditions in their summer range in 2003–2004, Levionaz, Italy. Although points show averages for each degree, the r^2 and the regression line are for all observations

Vegetation biomass and quality

Vegetation height and biomass first increased then levelled off as the summer progressed, and decreased with increasing altitude (Table 3, Figs. 4, 5). Crude protein content decreased by about 0.10% per day (Table 3, Fig. 4) and increased by about 0.14% per 100 m elevation (Table 3, Fig. 5), or 0.56% over the 400-m altitudinal migration undertaken by ibex in warm days (Fig. 1). The NDF content of vegetation increased over the summer by 0.077% a day and decreased with altitude by 0.54% per 100 m (Table 3, Figs. 4, 5). As the season progressed, vegetation increased significantly faster in NDF content at low than at high altitude. ADL content decreased with altitude by 0.056% per 100 m (Table 3).

Table 3 Minimum adequate linear mixed models of characteristics of Alpine vegetation samples collected within ibex summer range at Levionaz, Gran Paradiso National Park, Italy, 2003–2004

Variables	Height (cm) ^a		Biomass (g/m^2) ^b		Crude protein (%) ^c		NDF (%) ^d		ADL (%) ^e	
	Coeff (SE)	Wald χ^2 (P)	Coeff (SE)	Wald χ^2 (P)	Coeff (SE)	Wald χ^2 (P)	Coeff (SE)	Wald χ^2 (P)	Coeff (SE)	Wald χ^2 (P)
Year 2004	-0.80 (0.08)	97.84 (<0.001)	-2.77 (0.25)	126.69 (<0.001)	0.49 (0.03)	226.41 (<0.001)	-0.25 (0.04)	52.57 (<0.001)	-0.25 (0.05)	22.09 (<0.001)
JD	0.19 (0.02)	93.03 (<0.001)	0.78 (0.11)	49.92 (<0.001)	-0.015 (0.001)	153.78 (<0.001)	0.0050 (0.0006)	62.47 (<0.001)	ns	ns
JD2	-0.00044 (0.00005)	79.56 (<0.001)	-0.0018 (0.0003)	39.61 (<0.001)	ns	ns	ns	ns	ns	ns
Alt	-0.0032 (0.0003)	101.42 (<0.001)	-0.0084 (0.0014)	36.11 (<0.001)	0.00018 (0.00009)	4.29 (0.038)	-0.00044 (0.00019)	5.31 (0.020)	-0.00019 (0.00009)	4.41 (0.036)
JD \times Alt	ns	ns	ns	ns	ns	ns	-0.0000086 (0.0000024)	13.07 (0.001)	ns	ns

All models first included eight sampling periods and six additives transects as random terms. Only significant random terms were retained in the final models

JD, Julian date; JD2, quadratic of JD; Alt, altitude in metres; ns, non significant; NDF, neutral detergent fibre; ADL, acid detergent lignin

^a Model based on 264 samples, explaining 71.9% of total variance (period = ns; transect = $P < 0.001$)

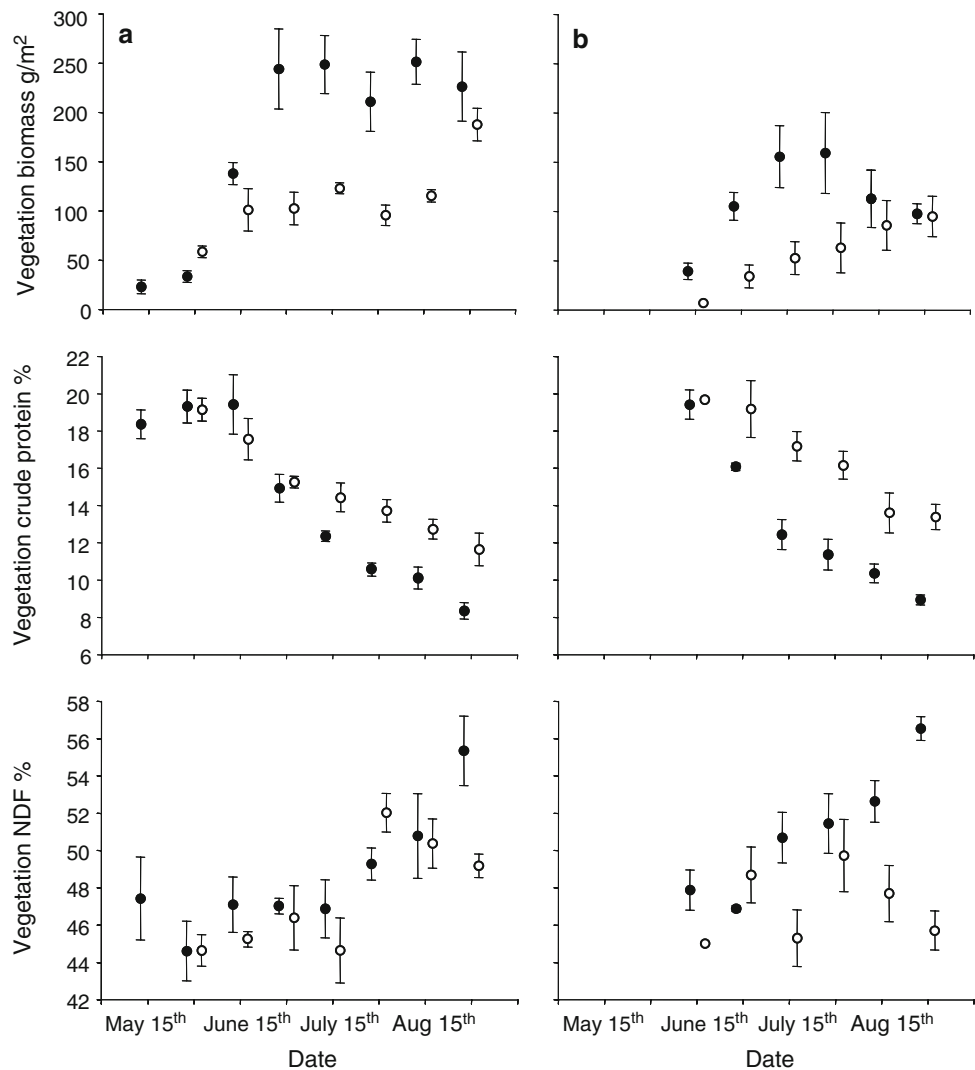
^b Model based on 282 samples, explaining 80.5% of total variance (both period and transect = $P < 0.001$)

^c Model based on 282 samples, explaining 78.4% of total variance (both period and transect = $P < 0.001$)

^d Model based on 281 samples, explaining 24.5% of total variance (periods = ns; transect = $P < 0.001$)

^e Model based on 278 samples, explaining 3.3% of total variance (period = $P < 0.001$; transect = ns)

Fig. 4 Summer seasonal time effect on vegetation biomass, % vegetation crude protein and vegetation neutral detergent fibre (NDF) (\pm SE) at altitudes of (a) 2,200 m, (b) 2,650 m in 2003 (solid circles) and 2004 (open circles) in Levionaz, Italy



Discussion

Our study produced three main results. First, it is the first report of weather-dependent daily altitudinal migration in a temperate ungulate. Second, male ibex behaviour suggested that warm temperatures prevented them from foraging. Third, we documented age and mass differences in daily altitudinal migration and feeding activity. The space-use behaviour of male ibex in summer appeared driven by thermoregulation rather than by spatial differences in forage characteristics.

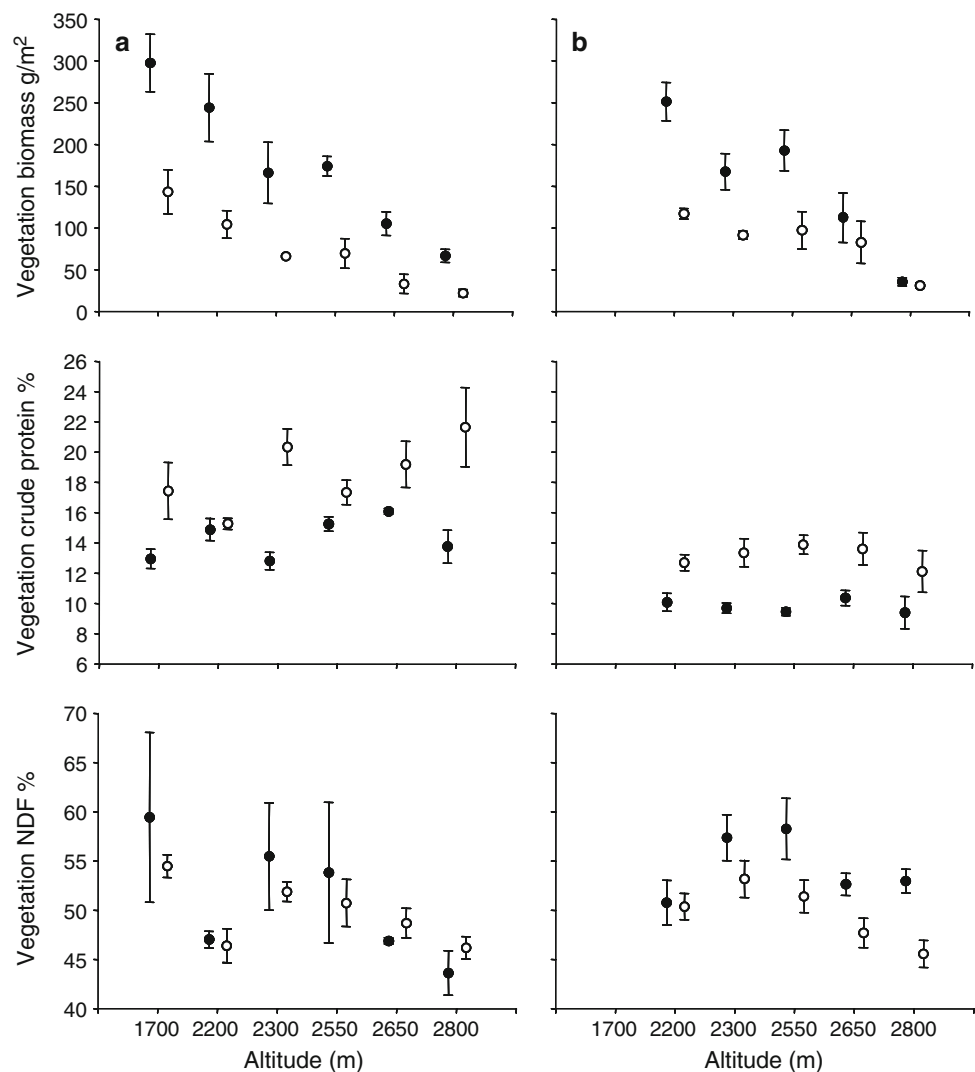
Daily altitudinal migration

Male Alpine ibex fed at low altitude at dawn, migrated to high altitude in late morning and returned to low elevations in late afternoon or early evening. The downward migration continued overnight, as ibex were about 200 m lower at 06:00 h than at 21:00 h the previous day. Very little feeding took place at midday when ibex were at their highest elevation

(Fig. 1). On hot and sunny days, ibex moved to high elevation and nearly stopped feeding, while on cooler and cloudy days they remained at low elevations and fed at all hours (Figs. 1, S1). Daily migrations of up to \sim 800 m in elevation involve substantial energy costs, and hence ibex must derive some benefits from these displacements. Although the crude protein to NDF or ADL ratios increased with elevation, suggesting increased forage digestibility (Van Soest 1994), the effect of altitude on vegetation quality was trivial compared to the results of other studies. Albon and Langvatn (1992) found crude protein differences as high as 8.0% per 100 m elevation in late May in Norway. Ibex usually fed while moving to high altitudes, but after resting and ruminating they quickly moved back to lower elevations in the evening, where they fed on the more abundant vegetation.

We suggest that the daily altitudinal migration of ibex is a behavioural thermoregulatory tactic. Generally, T_a decreases by about 0.5 to 1.0°C for every 100 m increase in elevation (Dodson and Marks 1997). Altitudinal migrations of 400 m

Fig. 5 Effect of altitude on biomass, % crude protein and neutral detergent fibre (NDF) (\pm SE) of vegetation samples collected on (a) 1 July and (b) 15 August in 2003 (solid circles) and 2004 (open circles) in Levionaz, Italy



could lower T_a by 2.0–4.0°C. The difference may seem small, but ibex rested at higher elevation for several hours. We cannot, however, explain the effect of R_{Sol} on migration, as radiation increases with altitude. Ibex could have found shade at any elevation as rocks, cliffs and steep slopes were abundant. Although we did not measure wind speed, it is possible that stronger wind at high altitude may have reduced operative temperature, despite increasing R_{Sol} .

Daily altitudinal migration behaviour has been observed in a tropical ungulate, Chanler's mountain reedbuck (*Redunca fulvorufula*), in Kenya (Roberts and Dunbar 1991) that was typically found at lower elevations at mid-day than in the morning or evening. That diurnal movement pattern opposite to that of ibex was also related to thermal considerations. Reedbuck fed in the upper slopes and rested and ruminated at lower elevation where there was more shade.

Sporadic movements to mountaintops or snow patches, correlated with T_a and R_{Sol} , have been reported in reindeer and attributed to avoidance of biting insects (Colman et al.

2001; Hagemoen and Reimers 2002). Although we did not quantify biting insects, they were not common, and it seems unlikely that ibex migrated to avoid insect harassment.

Grazing activity

In summer, male Alpine ibex spent on average 51% of daylight time feeding, as predicted by the allometric relationship in Mysterud (1998). That estimate, however, contrasts with the less than 9% daylight feeding time observed by Neuhaus and Ruckstuhl (2002), probably because most of their observations started in late morning (Ruckstuhl, pers. comm.) and might have been carried out mostly on sunny days. During midday hours in days with mean T_a above 15°C, ibex in our study area spent about 7.5% of their time feeding.

Male ibex showed the typical ruminant activity pattern, alternating grazing bouts with periods of rumination and resting. Ibex probably avoided activity during the hottest and sunniest part of the day, as reported for other ungulates

(Roberts and Dunbar 1991; Shi et al. 2003). In cattle, feeding and moving generate respectively five and three times as much endogenous heat as standing (Malechek and Smith 1976) in addition to increasing exposure to solar radiation. On hot days (mean T_a above 15°C), ibex avoided activity during midday, but on cooler days they spent four to five times more time feeding (Fig. 1).

The absence of effect of T_a on grazing time in the morning may be because in the morning potential exogenous heat gain is at its minimum for the daylight hours. The interaction between morning Hour and T_a (Table 1, Fig. 1) suggests that ibex adopt an anticipatory foraging tactic and spend more time feeding in warm mornings in the expectation of reduced foraging later in the day. Similarly, reed-buck fed more in the early morning during the hot dry season, apparently to compensate for more time resting under thermal cover later in the day (Roberts and Dunbar 1991). Shade-deprived cattle had higher feed intake in early morning than cattle provided with shade (Brown-Brandl et al. 2005). In the warm summer of 2003, ibex tended to feed more in the morning and fed significantly less in the evening than in the cooler summer of 2004 (Table 1). This result indicates that ungulate foraging behaviour is not simply a function of current temperature, but can be modified by the expectation of foraging conditions at a later time.

On warm evenings, ibex spent almost a third less time feeding than on cooler days. Many herbivores feed at night following hot days (Maloney et al. 2005; Winterbach and Bothma 1998). We could not systematically observe ibex at night due to logistical and safety reasons. Male ibex were seen foraging on many occasions at different hours of the night, regardless of the phase of the moon (Pers. obs.; Couturier 1962). Most mountain ungulates usually forage during the day, possibly because they rely on sight to detect predators (Festa-Bianchet 1991). Male ibex in summer may forage at night to compensate for lost feeding time during hot days. This behaviour may not be very costly at present in the GPNP as there are no large predators.

Age and mass effects

Similar to bighorn rams (Pelletier and Festa-Bianchet 2004), small ibex fed more than large ones, supporting the interspecific allometric relationship of temperate ruminants reported by Myserud (1998) and contrary to Owen-Smith's (1988, 1992) results for African ruminants. Despite having greater absolute energetic needs, larger individuals have lower relative metabolic rates and higher digestive capacities (Dement and Van Soest 1985; Illius and Gordon 1987), which allows them to feed efficiently on low-quality vegetation.

Because larger males forage less than small ones, they have more flexibility in allocating time. At midday, the decrease in feeding time with increasing temperature was

steeper for older ibex than for younger ones. Although this result may suggest that older and larger males were more sensitive to high T_a , we interpreted it as older ibex having the choice to feed or not at midday according to potential heat stress. Instead, younger ibex appear forced to feed under unfavourable thermal conditions to meet their energetic requirements.

Climate change

Alpine areas are expected to be strongly affected by climate change (Luterbacher et al. 2004; Oechel et al. 1997), which is already changing the distribution and phenology of animals and plants (McCarty 2001; Walther et al. 2002). Our research suggests that Alpine ibex foraging behaviour will be affected by climate change. Less feeding time on hot days will require increased feeding at night, or increased feeding intensity through higher bite rates (Neuhaus and Ruckstuhl 2002; Ruckstuhl et al. 2003), which may only be possible with abundant forage (Iason et al. 1999). Hot days constrained ibex behaviour, and in cool days, ibex spent much more time foraging and showed little or no altitudinal movements. Renecker and Hudson (1986) reported declining or static weight in moose at high ambient temperature in summer. Continued warming, therefore, may reduce ibex growth, particularly in populations with no high-altitude habitat.

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References

- Albon SD, Langvatn R (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502–513
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Association of Official Analytical Chemists (1980) Official methods of analysis, Washington DC
- Bassano B, Gauthier D, Joccolé L, Peracino V (2004) Capture d'ongulés de montagne par téléséquestration. Parc Nationale de la Vanoise/Parco Nazionale Gran Paradiso, Chambéry Cedex/Torino
- Bassano B, von Hardenberg A, Pelletier F, Gobbi G (2003) A method to weight free-ranging ungulates without handling. *Wildl Soc Bull* 31:1205–1209
- Belovsky GE (1984) Herbivore optimal foraging: a comparative test of three models. *Am Nat* 124:97–115

- Belovsky GE, Slade JD (1986) Time budgets of grassland herbivores: body size similarities. *Oecologia* 70:53–62
- Brown-Brandl TM, Eigenberg RA, Nienaber JA, Hahn GL (2005) Dynamic response indicators of heat stress in shaded and non-shaded feedlot cattle, part 1: analyses of indicators. *Biosyst Eng* 90:451–462. doi:10.1016/j.biosystemseng.2004.12.006
- Colman JE, Pedersen C, Hjermann DØ, Holand Ø, Moe SR, Reimers E (2001) Twenty-four-hour feeding and lying patterns of wild reindeer *Rangifer tarandus tarandus* in summer. *Can J Zool* 79:2168–2175
- Couturier MAJ (1962) *Le bouquetin des Alpes*. Imprimerie Allier, Grenoble
- Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am Nat* 125:641–672. doi:10.1086/284369
- Dodson R, Marks D (1997) Daily air temperature interpolated at high spatial resolution over a large mountainous region. *Clim Res* 8:1–20
- Dussault C, Ouellet JP, Courtois R, Huot J, Breton L, Larochelle J (2004) Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* 11:321–328
- Festa-Bianchet M (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580–586. doi:10.1007/BF00776423
- Festa-Bianchet M (1991) The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. *Anim Behav* 42:71–82. doi:10.1016/S0003-3472(05)80607-4
- Festa-Bianchet M (1998) Condition-dependent reproductive success in bighorn ewes. *Ecol Lett* 1:91–94. doi:10.1046/j.1461-0248.1998.00023.x
- Festa-Bianchet M, Jorgenson JT, Bérubé CH, Portier C, Wishart WD (1997) Body mass and survival of bighorn sheep. *Can J Zool* 75:1372–1379
- Glantz SA, Slinker BK (1990) *Primer of applied regression and analysis of variance*. McGraw-Hill, New York
- Grignolio S, Rossi I, Bassano B, Parrini F, Apollonio M (2004) Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. *Ethol Ecol Evol* 16:255–264
- Hagemoen RIM, Reimers E (2002) Reindeer summer activity pattern in relation to weather and insect harassment. *J Anim Ecol* 71:883–892. doi:10.1046/j.1365-2656.2002.00654.x
- Higgins KF, Oldemeyer JL, Jenkins KJ, Clambey GK, Harlow RF (1996) Vegetation sampling and measurement. In: Bookhout TA (ed) *Research and management techniques for wildlife and habitats*, 5th edn. The Wildlife Society, Bethesda, pp 567–591
- Iason GR et al (1999) Can grazing sheep compensate for a daily foraging time constraint? *J Anim Ecol* 68:87–93. doi:10.1046/j.1365-2656.1999.00264.x
- Illius AW, Gordon IJ (1987) The allometry of food intake in grazing ruminants. *J Anim Ecol* 56:989–999
- Kie JG (1999) Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *J Mammal* 80:1114–1129
- Luterbacher J, Dietrich D, Xoplaki E, Grosjean M, Wanner H (2004) European seasonal and annual temperature variability, trends, and extremes since 1500. *Science* 303:1499–1503. doi:10.1126/science.1093877
- Malechek JC, Smith BM (1976) Behavior of winter cows in response to winter weather. *J Range Manag* 29:9–12
- Maloney SK, Moss G, Cartmell T, Mitchell D (2005) Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*). *J Comp Physiol A* 191:1055–1064. doi:10.1007/s00359-005-0030-4
- McCarty JP (2001) Ecological consequences of recent climate change. *Conserv Biol* 15:320–331. doi:10.1046/j.1523-1739.2001.015002320.x
- McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock TH (2006) Lifetime reproductive success and density dependent, multi-variable resource selection. *Proc R Soc Lond B* 273:1449–1454
- Mysterud A (1998) The relative roles of body size and feeding type on activity time of temperate ruminants. *Oecologia* 113:442–446. doi:10.1007/s004420050396
- Mysterud A (1999) Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *J Zool Lond* 247:479–486. doi:10.1111/j.1469-7998.1999.tb01011.x
- Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC (2001) Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *J Anim Ecol* 70:915–923. doi:10.1046/j.0021-8790.2001.00559.x
- Neuhaus P, Ruckstuhl KE (2002) Foraging behaviour in Alpine ibex (*Capra ibex*): consequences of reproductive status, body size, age and sex. *Ethol Ecol Evol* 14:373–381
- Oechel WC et al (1997) *Global change and Arctic terrestrial ecosystems*. Springer, New York
- Oosenberg SM, Theberge JB (1980) Altitudinal movements and summer habitat preferences of woodland caribou in the Klunne range, Yukon territory. *Arctic* 33:59–72
- Owen-Smith NR (1988) *Megaherbivores*. Cambridge University Press, Cambridge
- Owen-Smith NR (1992) Grazers and browsers: ecological and social contrast among African ruminants. In: Spitz F, Janeau G, Gonzalez G, Aulagnier S (eds) *Ongulés/Ungulates 91*. S.F.E.P.M.-I.R.G.M, Paris, pp 175–181
- Owen-Smith NR (1994) Foraging responses of kudu to seasonal changes in food resources: elasticity in constraints. *Ecology* 75:1050–1062
- Owen-Smith NR (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *J Zool Lond* 246:183–192. doi:10.1111/j.1469-7998.1998.tb00147.x
- Parker KL, Gillingham MP, Hanley TA, Robbins CT (1996) Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Can J Zool* 74:442–450. doi:10.1139/CJZ-74-3-442
- Parker KL, Robbins CT (1984) Thermoregulation in mule deer and elk. *Can J Zool* 62:1409–1422. doi:10.1139/CJZ-62-7-1409
- Pelletier F, Festa-Bianchet M (2004) Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. *Behav Ecol Sociobiol* 56:546–551. doi:10.1007/s00265-004-0820-7
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-plus*. Springer, New York
- Post E, Stenseth NC (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology* 80:1322–1339. doi:10.1890/0012-9658(1999)080[1322:CVPPAN]2.0.CO;2
- Pyke GH (1984) Optimal foraging theory: a critical review. *Ann Rev Ecol Syst* 15:523–575
- Renecker LA, Hudson RJ (1986) Seasonal energy expenditures and thermoregulation responses of moose. *Can J Zool* 64:322–327. doi:10.1139/CJZ-64-2-322
- Roberts SC, Dunbar RIM (1991) Climatic influences on the behavioral ecology of Chanler mountain reedbeek in Kenya. *Afr J Ecol* 29:316–329
- Ruckstuhl KE (1998) Foraging behaviour and sexual segregation in bighorn sheep. *Anim Behav* 56:99–106. doi:10.1006/anim-be.1998.0745
- Ruckstuhl KE, Festa-Bianchet M, Jorgenson JT (2003) Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season,

- age, sex and reproductive status. *Behav Ecol Sociobiol* 54:167–173. doi:[10.1007/s00265-003-0615-2](https://doi.org/10.1007/s00265-003-0615-2)
- Schab FE, Pitt MD (1991) Moose selection of canopy cover types related to operative temperature, forage, and snow depth. *Can J Zool* 69:3071–3077. doi:[10.1139/CJZ-69-12-3071](https://doi.org/10.1139/CJZ-69-12-3071)
- Schemper M (1990) The explained variation in proportional hazards regression. *Biometrika* 77:216–218
- Seip DR, Bunnell FL (1985) Foraging behaviour and food habits of Stone's sheep. *Can J Zool* 63:1638–1646. doi:[10.1139/CJZ-63-7-1634](https://doi.org/10.1139/CJZ-63-7-1634)
- Shi JB, Dunbar RIM, Buckland D, Miller D (2003) Daytime activity budgets of feral goats (*Capra hircus*) on the Isle of Rum: influence of season, age, and sex. *Can J Zool* 81:803–815. doi:[10.1139/z03-055](https://doi.org/10.1139/z03-055)
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edn. Freeman, San Francisco
- Steele BM, Hogg JT (2003) Measuring individual quality in conservation and behavior. In: Festa-Bianchet M, Apollonio M (eds) *Animal behavior and wildlife conservation*. Island Presse, Washington, pp 243–269
- Van Soest PJ (1963) Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *J Ass Offic Agr Chem* 46:829–835
- Van Soest PJ (1994) *Nutritional ecology of the ruminant*, 2nd edn. Comstock, Ithaca
- Van Soest PJ, Robertson JB, Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *J Dairy Sci* 74:3583–3597
- von Hardenberg A (2005) *Sénescence, sélection sexuelle et dynamique de population du bouquetin des Alpes (Capra ibex)*. PhD thesis, Département de Biologie, Université de Sherbrooke, Sherbrooke, p 200
- Walther G-R et al (2002) Ecological responses to recent climate change. *Nature* 416:389–395. doi:[10.1038/416389a](https://doi.org/10.1038/416389a)
- White RG (1983) Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377–384
- Winterbach HEK, Bothma JD (1998) Activity patterns of the Cape buffalo *Syncerus caffer caffer* in the Willem Pretorius Game Reserve, Free State. *S Afr J Wildl Res* 28:73–81