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Foraging decisions in a capital breeder: trade-offs between mass gain and lactation

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Abstract The high energetic costs of lactation can lead to fundamental trade-offs in life-history traits, particularly in young females that reproduce before completing body growth. We assessed whether lactating female mountain goats (*Oreamnos americanus*) used behavioural tactics at fine spatio-temporal scales to increase energy intake to compensate for the costs of lactation. Lactating females increased bite rate and chewing rate compared with non-lactating females, but selected similar foraging sites in terms of plant quality and abundance. At peak lactation, forage intake of lactating females was >40% greater than that of non-lactating females. For females that had reached asymptotic body mass (i.e. ≥6 years old), summer mass gain of lactating females was similar to that of non-lactating females. At 4 and 5 years of age, however, daily mass gain of lactating females was about 20% lower than that of non-lactating females. We conclude that increased foraging may allow fully-grown lactating females to compensate for the energetic costs of lactation, but that there is a major trade-off between mass gain and lactation for younger females.

Keywords Bite rate and size · Chewing rate · Growth · Mountain goats · Rumination

Introduction

Life-history theory predicts that current reproduction leads to trade-offs in growth, future reproduction and/or survival because time and energy are limited (Stearns 1992). In female mammals, lactation entails high energetic costs that can increase energetic requirements by two to fivefold during the peak of lactation (Oftedal 1985; Gittleman and Thompson 1988). While lactating females of some species may compensate by reducing metabolic expenditures (e.g. by reducing locomotor activities, Miller et al. 2006; fasting, Mellish et al. 2000; entering periodic torpor, Racey and Speakman 1987) or by increasing metabolic efficiency (Mellish et al. 2000), females of most species are expected to increase nutrient intake during lactation (Bunnell and Gillingham 1985). For example, increase nutrient intake has been observed in guinea pigs (*Cavia porcellus*; Künkele and Trillmich 1997), koalas (*Phascolarctos cinereus*; Krockenberger 2003), cheetahs (*Acinonyx jubatus*; Laurenson 1995), ruminants (Arnold 1985) and humans (Dufour et al. 2002).

In herbivores, although the lactation period usually occurs when food is more abundant and of higher quality, this increased availability is usually insufficient for females to meet the high energetic requirements of lactation. To achieve a higher nutrient intake, lactating females are therefore expected to modify their foraging behaviour. Herbivores with high energetic requirements should forage

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longer than those with lower energetic needs when foraging on the same type of vegetation or in similar habitats (Bunnell and Gillingham 1985; Shipley et al. 1994, 1999). Females with young often increase forage intake by spending more time foraging than non-lactating females (Clutton-Brock et al. 1982; MacWhirter 1991; Komers et al. 1993; Ruckstuhl and Festa-Bianchet 1998). At a finer scale, however, nutrient intake is controlled by the consumption rate achieved while foraging as well as by digestive capacities and excretion rates.

Consumption rate can be limited in four ways. Firstly, an animal can increase nutrient intake by increasing foraging intensity (Spalinger and Hobbs 1992). As predicted by Bunnell and Gillingham (1985), lactating females have been shown to increase bite rate (Ruckstuhl and Festa-Bianchet 1998). Secondly, bite size also influences consumption rate (Shipley et al. 1999) and, in herbivores both the type and size of plants eaten as well as mouth morphology determine bite size (Shipley et al. 1994). Because bite size is difficult to estimate in free-ranging herbivores (but see Renecker and Hudson 1986), plant biomass, which correlates with plant type and size (Gross et al. 1993; Iason et al. 2000), has often been used as a surrogate because animals have been shown to increase bite size with increasing plant biomass (Wickstrom et al. 1984; Murray 1991). Thirdly, fibre and protein content, which influence plant digestibility, can also affect consumption rate. To increase nutrient intake, individuals can therefore be more selective and forage on plants with high protein and digestible contents (Shipley et al. 1999). Fourthly, chewing while foraging greatly reduces forage intake because animals have less time to crop new bites (Spalinger and Hobbs 1992; Shipley et al. 1994). Although chewing while foraging may slightly increase nutrient intake by improving digestion, rumination has a much greater influence on digestion efficiency (see below), and thus the benefit of increasing chewing while foraging is fairly small compared with that of increasing forage intake. Therefore, individuals that chew faster or allocate fewer chews per gram of forage eaten may increase consumption rate (Gross et al. 1995; Ginnett and Demment 1997).

The ultimate factors restricting nutrient intake are the rates of digestion and excretion. Rumen fill, retention time and rumination directly influence the rates of digestion and excretion (Pérez-Barbería and Gordon 1998). Rumen fill is determined by the quantity of vegetation ingested and foraging bout frequency, which in turn are limited by retention time, because short transit times allow more vegetation to be ingested (Renecker and Hudson 1986; Domingue et al. 1991). Retention time is influenced by vegetation quality, since the digestion of cell walls increases with retention time (Côté 1998). Hence, an animal foraging on poor quality vegetation—for example, during winter—will tend to increase retention time (Gross et al. 1996). Therefore, if lactating females increase intake rate, they are expected to decrease retention time and, concomitantly, digestive efficiency should decrease (van Hoven and Boomker 1985). In Nubian ibex (*Capra ibex nubiana*), however, lactating females have been observed to increase both intake and retention time compared with non-lactating females by increasing gut fill over the level required for maintenance (Gross et al. 1996). Nevertheless, plasticity in gut fill does not seem to be widespread, as elk (*Cervus elaphus elaphus*) and bighorn sheep (*Ovis Canadensis*) cannot increase gut fill in response to digestive restrictions (Baker and Hobbs 1987). Herbivores, however, may show plasticity in rumination, which decreases the size of forage particles and increases the surface area of forage, thus enhancing digestive efficiency (Pérez-Barbería and Gordon 1998). Individuals who ruminate for longer periods or show greater chewing rates while ruminating could increase the rate of forage passage in the rumen (Pan et al. 2003).

If lactating females cannot fully compensate for the energetic requirements of lactation by modifying their foraging behaviour, their body condition might be adversely affected. Because body condition is a fundamental determinant of reproduction (Parker et al. 2009), lower mass gain may result in the lactating females skipping the next reproductive event. Indeed, yeld red deer hinds (*Cervus elaphus*) experience a steady increase in body mass and condition during the summer, usually reproduce the following year and show higher survival, especially for young and old individuals, compared with milk hinds (Clutton-Brock et al. 1983; Moyes et al. 2006). In bighorn sheep, lactation also negatively affects ewe mass gain, and a small mass in late summer decreases reproductive success the subsequent year (Festa-Bianchet et al. 1998). Because the accumulation of body reserves during summer can greatly influence future reproduction and survival, lactating females should face important trade-offs during lactation.

Mountain goats (*Oreamnos americanus*) are capital breeders. Females lose 30% of their late summer body mass over winter and regain it during the summer (Festa-Bianchet and Côté 2008). Body mass is important for their reproduction since heavy female goats produce heavier kids and have lower costs of reproduction than light females (Côté and Festa-Bianchet 2001b; Hamel et al. 2009). Female goats experience short and cool summers and very long winters (Festa-Bianchet and Côté 2008); consequently, they have access to high-quality vegetation for a few weeks only, during which time they must compensate for the energetic costs of lactation and accumulate body reserves to survive the winter and reproduce successfully the following year. We have previously shown that lactating females modify their foraging behaviour at a large scale (i.e. their daily activity budget) as they increase time spent foraging and ruminating (Hamel and Côté 2008). The objective of the study reported here was to determine whether lactating mountain goats use other tactics at fine spatio–temporal scales to increase their energy intake and compensate for the high energetic costs of lactation. Specifically, we compared bite rates while foraging and chewing rates while ruminating between lactating and non-lactating females throughout the lactation period. We estimated the biomass and quality of plants at foraging sites. In addition, we determined the average bite size of adult female mountain goats in captivity (see Appendix S2) to estimate the difference in biomass intake between lactating and non-lactating females based on differences in time spent foraging and biting rate. Finally, we assessed the summer mass gain of lactating and non-lactating females to verify if females were able to compensate for the energetic costs of lactation. We predicted that lactating females would increase bite rate and chewing rate compared with non-lactating females, but that both would select similar foraging sites because vegetation in the alpine habitat is relatively homogenous and all females forage in the same groups. Adult female mountain goats often take reproductive pauses (approx. 25% of years; Festa-Bianchet and Côté 2008), and we therefore hypothesized that lactating females would show greater forage intake than non-lactating ones, but not sufficiently so to reach a similar summer mass gain. Also, because young lactating females have to allocate resources to both growth and reproduction, we expected to find a lower summer mass gain in lactating goats that have not reached asymptotic body mass (i.e. 6 years and younger; Côté and Festa-Bianchet 2001a) than in fully grown females. Our study is unique since it combines observations of foraging behaviour at a fine scale and forage biomass and quality under natural conditions, with seasonal changes in body mass in a capital breeder monitored over several years.

Materials and methods

Study area

We studied a population of mountain goats located at Caw Ridge (54°N, 119°W), west central Alberta, Canada, in the front range of the Rocky Mountains. Goats use 28 km^2 of alpine tundra and subalpine open forest of Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) at 1750–2170 m elevation. The landscape includes gently rolling hills and steep grassy slopes as well as rockslides and a few cliff faces that are crucial escape terrains for mountain goats. The climate is subarctic–arctic, and snowfall can occur during any month of the year. The main predators are wolves (*Canis lupus*), grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*), but also potentially black bears (*Ursus americanus*), coyotes (*Canis latrans*), wolverines (*Gulo gulo*) and golden eagles (*Aquila chrysaetos*) (Festa-Bianchet and Côté 2008).

Goats are generalist herbivores that mainly eat grass (>50%), forbs (30%), and browse (15%) in alpine meadows near cliffs and rocky ledges (Côté and Festa-Bianchet 2003). At Caw Ridge, the main grass and sedge species include *Agropyron* sp., *Carex* spp., *Festuca* spp., *Kobresia* spp., *Poa* spp. and *Phleum* sp. The most important consumed forbs are *Aconitum delphiniifolium*, *Anemone drummondii*, *Astragalus* spp., *Campanula lasiocarpa*, *Castilleja* spp., *Epilobium* spp., *Gentiana* spp., *Myosotis alpestris*, *Oxyria* spp., *Oxytropis* spp., *Pedicularis* spp., *Polemonium* sp., *Polygonum viviparum* and *Potentilla* spp. Palatable shrubs consist mainly of *Betula glandulosa*, *Salix* spp. and *Vaccinium* spp.

Captures and body mass measurements

Between 1988 and 2006 we captured goats in remotely controlled box traps and self-tripping Clover traps baited with salt. We immobilized adult goats with xylazine hydrochloride and reversed the effects of xylazine with an injection of idazoxan (Haviernick et al. 1998). Adult females were marked with plastic ear tags and collars. From 1993 onwards, 98% of goats aged $\geq$1 year were marked. We aged adult goats not marked as juveniles by counting their horn annuli, a technique reliable up to 7 years of age (Stevens and Houston 1989). Of the female goats included in this study, 12% were marked between 2 and 7 years of age, but no female was marked after age 7. We weighed captured goats with a spring scale (±0.5 kg). Because most females were not captured when adults ($\geq$3 years of age) to prevent kid abandonment (Côté et al. 1998a), we also recorded mass (±0.5 kg) of adult females using three remotely controlled electronic platform scales (50 × 130 cm) baited with salt. These scales allowed us to weigh goats without handling them and to collect repeated measures of mass ($n = 505$) during the summer for the same individuals ($n = 84$ female-years). Further descriptions of capture techniques can be found in Côté et al. (1998a).

Behavioural observations

From mid-May to late September 2001–2006, we recorded daily behavioural observations on adult females and their offspring using spotting scopes (15–45×) from 0600 to 2300 hours. The number of adult females each year ranged between 45 and 61, and total population size ranged between 124 and 159 individuals. For all groups, we noted the identity of each individual and determined the reproductive status of females from observations of nursing behaviour. Reproducing females always gave birth to a single kid, with 80% of births occurring during a 2-week period in late May–early June. Most females usually weaned their offspring in late September–early October. We considered a female as non-lactating 10 days after she had lost her kid ($n = 17$ cases out of 318 female-years). The exclusion of these females from the analyses provided similar results. We recorded group size excluding kids, as kids are not independent of their mothers.

Mountain goats are very aggressive compared with similar-sized ungulates (Fournier and Festa-Bianchet 1995), and social dominance greatly influences female reproduction (Côté and Festa-Bianchet 2001a; Hamel et al. 2009). Because social rank may also influence foraging behaviour, we recorded agonistic encounters between adult females using *ad libitum* sampling ($n = 9061$ interactions from 2001 to 2006) (Altmann 1974). During each encounter, we recorded the identity of the initiator, winner and loser. We considered an encounter resolved when one of the opponents withdrew and, for each dyad, we considered an individual dominant if it won more than 50% of the interactions with the other individual (Côté 2000). We then organized interactions in yearly dominance matrices that we tested for linearity using a sampling process and performing 10,000 randomizations (de Vries 1995). Dominance relationships were significantly linear for all years (all h' values ≥ 0.2, all P values <0.001). Thus, we ordered adult females in annual hierarchies according to de Vries (1998) using Matman 1.0 for Windows (Noldus Information Technology 1998). Briefly, we ordered all females in the population using an iterative procedure (1000 randomizations) that ranked individuals by minimizing the number and strength of inconsistencies in the matrix. An inconsistency occurs when individual j dominates i, and j is ranked below i; the absolute difference between the ranks of two individuals involved in an inconsistency is called the strength of that inconsistency (de Vries 1998). By taking into account the number and strength of inconsistencies, this method can include unknown and tied dominance relationships (de Vries 1998). Because the number of adult females varied annually, we transformed social ranks according to 1-rank/N_I, where N_I is the number of adult females during year I (Côté 2000). Hence, social rank varied from 0 to 1, from subordinate to dominant. Further descriptions of these methods are provided in Côté (2000).

Bite rate

To measure individual foraging intensity, we counted the number of bites a female took during a 2-min focal while foraging (Altmann 1974). We chose 2 min because most variability seen during 5-min focals was captured after 2 min [mean ± standard deviation (SD) 2 min: 44.3 ± 11.1 bites/min; 3 min: 44.3 ± 11.2 bites/min; 4 min: 44.2 ± 11.2 bites/min; 5 min: 44.2 ± 10.8 bites/min; $n = 113$, 5-min focals]. Both lactating and non-lactating mountain goats spent a similar amount of time in vigilance (when a goat stands, head upright with ears raised, scanning around; Hamel and Côté 2008); consequently, we discarded observations in which a female spent more than 5 consecutive seconds vigilant in order to exclude vigilance behaviour and specifically measure foraging intensity. In addition, we recorded focals only when females were foraging actively, i.e. not travelling (that is <75 steps per 2 min, S. Hamel unpublished data). We sampled every adult female in the population at the beginning of each month in June, July, August and September 2002 and 2003, and in July and August in 2001 ($n = 524$ focals on 61 females).

We also recorded the following variables that may influence the number of bites taken by females: distance to escape terrain (m), number of neighbours, period during a foraging bout, and habitat type. We recorded the number of neighbours on an integer scale from 0 to 4, where 0 was no goat within 5 m, and 1–4 were at least one goat within 5 m of the focal female in, respectively, one, two, three, or four of the directions around her (i.e. in front, behind, to the left, and to the right). To account for variability in bite rate during the foraging bout, we divided it into three periods: (1) *early*, when a goat had just started foraging; (2) *middle*, when a goat had been foraging for a minimum of 10 min; (3) *late*, when a goat stopped foraging within approximately 10 min of the completion of the focal. We assigned habitat to one of the four following categories: (1) *short grass*, the bite cropped fitted entirely in a female's mouth; (2) *long grass*, the bite cropped protruded outside a female's mouth; (3) *short grass/rocky*, approximately 50% short grass and 50% rocks; (4) *open forest*, grassy areas interspersed with conifers. Grass height averaged (±SD) 6.6 ± 4.5 cm.

Chewing rate

We determined rumination intensity by observing a focal female chewing ten consecutive boluses. A bolus began with the regurgitation of forage in the mouth and ended once the female had stopped chewing and all of the food had been swallowed back. For each bolus, we recorded the duration and the number of chews as well as the time between boluses in order to compute the number of chews per minute spent ruminating. We also recorded the ruminating bout period: (1) *early*, when a goat just started ruminating; (2) *middle*, when a goat had been ruminating for a minimum of 10 min; (3) *late*, when a goat stopped ruminating within approximately 10 min of the completion of the focal. We sampled most adult females twice each year (before and after 31 July) from 2002 to 2005 ($n = 338$ focals on 73 different females).

Vegetation quality and quantity at foraging sites

In 2002 and 2003, we randomly selected 12 lactating and 12 non-lactating females (40 different females over 2 years) and estimated the available biomass and the quality of the vegetation where they foraged. For each month and each female, we recorded the central point where they foraged during the 2-min focal observations for bite rate ($n = 191$). Within 4 m of the central point, we randomly placed five 20 × 20-cm quadrats, and in each quadrat, we estimated the percentage cover of live grasses/sedges, live forbs, live shrubs and dead plants in 5% classes as well as vegetation height in centimetres. We averaged height among plant clusters when it was heterogeneous. We randomly chose one of the five quadrats to clip grasses/sedges, forbs, shrubs and dead plants at 1 cm above ground. Shrubs consisted of buds in June and annual leaves for the rest of the summer. Vegetation was first air-dried in the field and then oven-dried at 45°C for 48 h to determine aboveground biomass. For each plant category, we used a regression analysis to calculate the relationship between percentage plant cover and height, and aboveground biomass (Appendix S1; Bonham 1989). We then used these equations to estimate plant biomass for quadrats not clipped. We calculated the mean biomass of each forage category at each foraging site and plant biomass between foraging sites of lactating and non-lactating females was compared.

To assess vegetation quality, we estimated digestible plant content [%NDS, the fraction of the plant cell that dissolves in neutral detergent; %ADS, the fraction that dissolves in acidic detergent; %ADL, the fraction that does not dissolve in H_2SO_4 (mostly lignin); Van Soest 1994] and protein content (macro-Kjeldhal acid digestion technique; Association of Official Analytical Chemists 1984) of all plant categories found in each clipped quadrat (grasses/sedges: $n = 148$ for 40 different females; forbs: $n = 93$ for 35 females; shrubs: $n = 56$ for 30 females; dead plants: $n = 44$ for 30 different females). Because these analyses required about 8 g of dried vegetation per sample and quadrats never contained that much (see Table 1 and Hamel and Côté 2007), we collected additional vegetation within 1 m of the quadrat.

Data analyses

We performed linear mixed models (LMM) to control for year and individual variations (see below) in order to assess the effects of date, time of day (min), female age years), social rank, reproductive status, foraging bout period, distance to escape terrain, group size, number of neighbours, habitat type and a number of important two-way interactions on bite rate (see Appendix S3). For example, we tested the interactions (1) “reproductive status × female age” and (2) “reproductive status × date” because we expected to find variations in foraging decisions between lactating and non-lactating females (1) whether females were fully-grown or not, and (2) as the summer progressed (because of decreasing energetic demands for lactating females as offspring age). We therefore defined a set of a priori models that made biological sense (see Appendix S3) and used the Akaike Information Criterion (AIC) to select the most parsimonious model explaining variation in bite rates (Burnham and Anderson 2002). We computed ΔAIC to select the best model and present effects included in the best model with 95% confidence intervals (CI). We considered models with $\Delta\text{AIC} \leq 2$ to be equivalent. When the models were equivalent, we selected the model with the fewer parameters as the best one, but also presented the 95% CI of the other variables included in equivalent models.

Because we only sampled vegetation quality and abundance in a subset of focals for which we had measured bite rates ($n = 191$ focals out of 524), we could not assess the influence of plant biomass, % protein, %NDS, %ADS and %ADL on bite rate using the same model as that described above. We therefore used a reduced data set excluding observations with missing values and compared AICc values (i.e. AIC values adjusted for small sample size) of models excluding and including vegetation attributes. We used the best model selected with the complete data set as our initial model. First, we compared the initial model with models including the effects of the initial model plus a single vegetation attribute. Because none of these models provided a better fit than the initial model (based on ΔAICc and number of parameters; see Appendix S4), there was no need to further compare models including two or more additive effects of vegetation attributes. Finally, because plant composition differed for each focal, sample sizes for plant quality and abundance varied for each plant category. Hence, AICc values were not comparable for models that included vegetation attributes of different plant categories; consequently, we performed the analyses separately for each plant category (see Appendix S4).

For determining rumination intensity, we used LMM to assess the influence of the summer period (before and after 31 July), time of day, female age, social rank, reproductive status, ruminating bout period, and a number of interactions on chewing rate (see above for examples of interactions tested and Appendix S5). We defined a set of a priori models (see Appendix S5) and used the AIC to select the most parsimonious model, as described above.

For plant quality and biomass analyses, we used LMM to test the relationships between female reproductive status

Table 1 Estimates of plant biomass and quality collected at foraging sites of lactating and non-lactating female mountain goats at Caw Ridge, Alberta (2002–2003), based on LMM performed for each plant attribute (i.e. biomass, %NDS, %ADS, %ADL and %protein) and each plant category, after accounting for month and distance to escape terrain (see Sect. Data analyses)

Dependent variables	Estimates for lactating females	Estimates for non-lactating females	*df*	*F* values	*P* values
Plant biomass ($n = 191$)					
Grasses/sedges (g/400 cm^2)	0.57 ± 0.11	0.54 ± 0.11	1, 31	0.2	0.6
Forbs (g/400 cm^2)	0.33 ± 0.03	0.29 ± 0.03	1, 26	0.02	0.9
Shrubs (g/400 cm^2)	0.36 ± 0.06	0.33 ± 0.07	1, 21	0.01	0.9
Dead plants (g/400 cm^2)	0.36 ± 0.10	0.30 ± 0.10	1, 21	1.1	0.3
All species (g/400 cm^2)	1.62 ± 0.11	1.49 ± 0.11	1, 31	1.9	0.2
Plant quality					
Grasses/sedges ($n = 148$)					
NDS (%)	49.3 ± 1.2	49.6 ± 1.2	1, 31	0.2	0.7
ADS (%)	77.9 ± 2.0	77.5 ± 2.0	1, 31	1.3	0.3
ADL (%)	1.2 ± 0.6	1.4 ± 0.6	1, 31	0.6	0.4
Protein (%)	14.1 ± 0.4	14.3 ± 0.4	1, 31	0.3	0.6
Forbs ($n = 93$)					
NDS (%)	78.1 ± 0.6	77.7 ± 0.6	1, 26	0.3	0.6
ADS (%)	84.6 ± 0.7	83.4 ± 0.7	1, 26	3.7	0.07
ADL (%)	4.6 ± 0.5	4.7 ± 0.5	1, 26	0.1	0.8
Protein (%)	18.9 ± 0.8	17.5 ± 0.8	1, 26	3.7	0.07
Shrubs ($n = 56$)					
NDS (%)	70.3 ± 0.8	70.9 ± 0.8	1, 21	0.2	0.6
ADS (%)	78.1 ± 2.4	78.7 ± 2.3	1, 21	0.2	0.7
ADL (%)	11.0 ± 1.0	10.8 ± 1.0	1, 21	0.02	0.9
Protein (%)	14.6 ± 1.4	15.7 ± 1.3	1, 21	1.6	0.2
Dead plants ($n = 44$)					
NDS (%)	34.2 ± 3.5	30.4 ± 3.5	1, 21	2.2	0.2
ADS (%)	67.8 ± 3.0	65.8 ± 3.0	1, 21	1.9	0.2
ADL (%)	2.0 ± 0.5	2.7 ± 0.5	1, 21	3.0	0.1
Protein (%)	5.1 ± 0.6	4.9 ± 0.6	1, 21	0.04	0.8

Values are given as the mean ± standard error (SE)

LMM, Linear mixed models; NDS, fraction of the plant cell that dissolves in neutral detergent; ADS, fraction that dissolves in acidic detergent; ADL, fraction that does not dissolve in H_2SO_4 (mostly lignin)

and biomass, %protein, %NDS, %ADS and %ADL of each plant category. As we have previously shown that plant quality and abundance vary with month and distance to escape terrain (likely because of increased grazing pressure near escape terrain as well as the deposition of faeces and urine; Hamel and Côté 2007), we included month, distance to escape terrain and their interaction as covariables in these LMM to control for their potential confounding effects.

We estimated the daily forage intake of lactating and non-lactating females during the summer according to:

$$I_{ds} = T_{ds}\mathrm{BR}_{ds}\mathrm{BS} \qquad (1)$$

where I_{ds} is the daily intake in terms of plant biomass at a specific date (d) and for a specific reproductive status (s), T_{ds} is the time spent foraging during the day (accounting for variations in day length during the summer d and reproductive status s; from Hamel and Côté 2008), BR_{ds} is the bite rate at a specific date (d) and for a specific reproductive status (s) and BS is the average bite size (Appendix S2).

To compare individual mass gain of lactating and non-lactating females during the summer, we calculated mass gain for females weighed at least twice at intervals of >30 days, and at least once early (≤22 July) and once late (≥23 July) in the summer. Since mass gain in capital breeders is faster in early than in late summer (e.g. Festa-Bianchet et al. 1996), we adjusted body mass to either 15 June (if collected ≤22 July) or 25 August (if collected ≥23 July) using regression equations calculated from body mass records obtained between 25 May and 22 July, and between 23 July and 15 September, respectively. We thus used individual slopes between 15 June and 25 August as estimates of summer mass gain ($n = 84$ female-years). We used a LMM to assess the influence of female age, reproductive status, and age × status on individual summer mass gain and included early-summer mass as a covariable to account for individual differences in mass in early summer. Our comparison of masses ($n = 505$) of lactating females with non-lactating females throughout summer—i.e. comparing the slope of mass gain for all lactating females with that of all non-lactating females—yielded the same results, and thus we do not present them here.

We performed all analyses in SAS (Littell et al. 2006). For all LMM analyses, we included both "year" and "female identity" as random effects to control for stochastic between-year variation and pseudo-replication (Machlis et al. 1985). We used the PROC Mixed procedure with a compound symmetry as the covariance structure to control for the correlation between measurements recorded on the same individual, assuming an equal correlation among all within-group errors related to the same group (Littell et al. 2006). As this procedure does not provide R^2 values, we computed the explained variance as: $R^2 = 1 - (\mathrm{SSR}/\mathrm{SSTO})$ where $\mathrm{SSR} = \sum\left((Y_{\mathrm{observed}} - Y_{\mathrm{predicted}})^2\right)$ and $\mathrm{SSTO} = \sum\left((Y_{\mathrm{observed}} - \bar{Y}_{\mathrm{observed}})^2\right)$ (Xu 2003). Collinearity diagnostic tests for all models revealed no multicollinearity problems: the highest condition index was 3.4, and the highest variance inflation factor (VIF) was 3.5 (multicollinearity begins to affect parameter estimates when the condition index and VIF values are ≥ 10; Freund and Littell 1992; Belsley et al. 2005). All variables were normally distributed, except plant biomass, which we normalized with a logarithmic transformation after adding 0.1 (Sokal and Rohlf 1981). We excluded 3-year-old females because only two of the 48 were lactating between 2001 and 2006. Age at primiparity was 4.6 ± 0.9 years on average (Côté and Festa-Bianchet 2001a). Because we expected females that were still growing to have different foraging tactics than females that had completed body growth, we analysed age in two categories: young, growing females (4 and 5 years old) and adult females that have reached asymptotic body mass (≥ 6 years; Côté and Festa-Bianchet 2001a). All results are presented as means ± standard error based on model predictions, unless otherwise stated.

Results

The best model explaining variations in bite rate (AIC weight 0.43, R^2 0.43, Appendix S3) included female age (95% CI 0.82–4.00), date (−0.04 to 0.03), female reproductive status (11.90–17.12), date × reproductive status (−0.09 to −0.01) and the number of neighbours (0.004–1.086). Females that were still growing had higher bite rates than those that had reached asymptotic body mass (young 47.8 ± 0.9, adult 45.4 ± 0.9 bites/min). Bite rate was on average 27% higher for lactating than non-lactating females, but this difference varied from 32% at the beginning of the summer to 23% at the end of the summer (Fig. 1a). A decrease through time was only seen in lactating females, as bite rates of non-lactating females remained stable during the summer (Fig. 1a). Females took more bites per minute spent foraging as the number of neighbours found within 5 m increased (no neighbour 45.8 ± 0.9, four neighbours 47.9 ± 1.4 bites/min). Using reduced data sets excluding missing values to assess the influence of vegetation attributes on bite rate, we found a poorer fit for about half of the models including a single additive effect of vegetation characteristic (i.e. plant biomass, %NDS, %ADS, %ADL and %protein of each plant category) than for that excluding these effects (i.e. the initial model; see Appendix S4). The other half presented

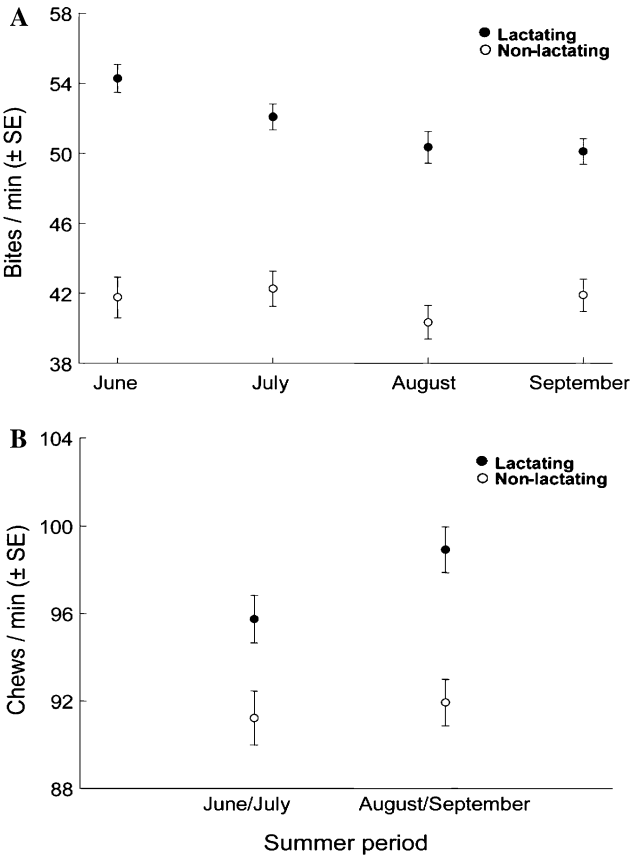

Fig. 1 Effects of female reproductive status and date during summer on the number of bites taken per minute spent foraging (**a**; means ± standard error (SE) of observed values collected monthly) and the number of chews performed per minute spent ruminating (**b**; means ± SE of observed values collected bimonthly), in adult female mountain goats at Caw Ridge, Alberta

an equivalent fit to the initial model, but these models were less parsimonious, and the 95% CI of the variables included in these models included 0 (Appendix S4).

For chewing rate, the best model (AIC weight 0.37, R^2 0.21; Appendix S5) included female age (95% CI 2.28–6.99), summer period (−2.71 to 1.90), female reproductive status (4.85–9.88), summer period × reproductive status (−6.00 to −0.05) and time of day (0.25–0.85). Equivalent models (Appendix S5) included the interaction between female age and reproductive status (95% CI −7.03 to 0.80) and the ruminating bout period (95% CI early vs. late −1.09 to 3.96; middle vs. late −2.29 to 2.87), but the confidence interval estimates for these effects all included 0. Females that had not reached asymptotic body mass had higher chewing rates than adult females (young 97.1 ± 1.0; adult = 92.5 ± 0.9 chews/min). Lactating females performed four more chews/min than non-lactating females in early summer, and this difference increased to seven more chews/min in late summer (Fig. 1b). Females also increased chewing rate from the beginning to the end of the day (0800 hours 90.7 ± 1.4; 2000 hours 97.4 ± 1.2 chews/min).

After accounting for collection date and distance to escape terrain, plant biomass at foraging sites was similar for lactating and non-lactating females for all plant categories (Table 1). Plant quality did not vary between foraging sites of females for grasses/sedges, shrubs and dead plants (Table 1). For forbs, plant quality was similar between females except that %ADS and protein tended to be higher at the foraging sites of lactating than non-lactating females (Table 1), although this difference was small (approx. 1%; see Table 1).

The average bite size estimated in captivity was 0.12 ± 0.01 g of dry biomass (Appendix S2). The estimated forage intake during daytime was about 1.5-fold greater in lactating than in non-lactating females (Eq. 1; Fig. 2). In early summer, females with a kid ingested about 1 kg more dry biomass during the daytime than non-lactating females; in late summer, this difference was about 0.5 kg (Fig. 2). About 85% of the difference in dry biomass intake between lactating and non-lactating females resulted from an increase in bite rate, while the rest was the result of an increase in time spent foraging. Assuming that goats also forage at night, total daily forage intake at the peak of lactation was estimated at about 4.5 and 3 kg for lactating and non-lactating females, respectively. Forage intake for all females decreased in mid-summer (Fig. 2).

After accounting for early summer mass, individual mass gain during the summer varied with female reproductive status and age (status $F_{1,46} = 9.9$, $P = 0.003$; age $F_{1,46} = 7.0, P = 0.01$; status × age $F_{1,46} = 4.5, P = 0.04$; $n = 84$ female-years; R^2 0.30; Fig. 3). When females had reached asymptotic body mass (i.e. ≥6 years old), the mass gain of lactating and non-lactating females was similar (Fig. 3). When females were still growing (i.e. 4 and 5 years old), however, lactating females gained about 50 g less per day than non-lactating females (Fig. 3).

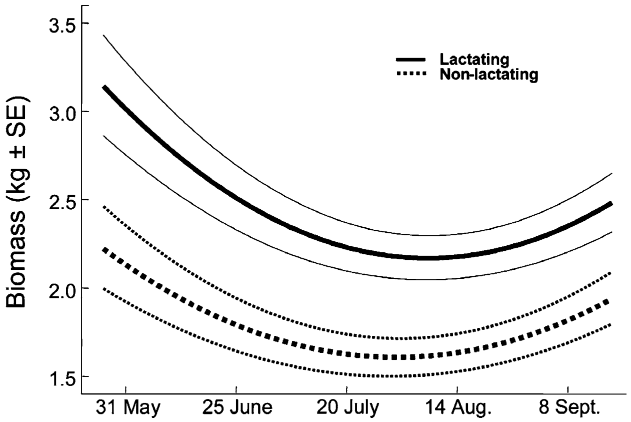

Fig. 2 Estimations of forage intake (kg ± SE of dry biomass) during the daytime for lactating and non-lactating female mountain goats in relation to date during summer, at Caw Ridge, Alberta. The curves are from the estimates predicted from linear mixed models (LMM; with covariables centered on their means) used to determine time spent foraging and bite rate at a specific date and for a specific reproductive status

Discussion

Lactating mountain goats modified their foraging behaviour by increasing bite rate (this study) as well as time spent foraging (Hamel and Côté 2008). This resulted in a >40% increase in forage intake compared with non-lactating females at the peak of lactation. To process this additional forage intake, females also modified their

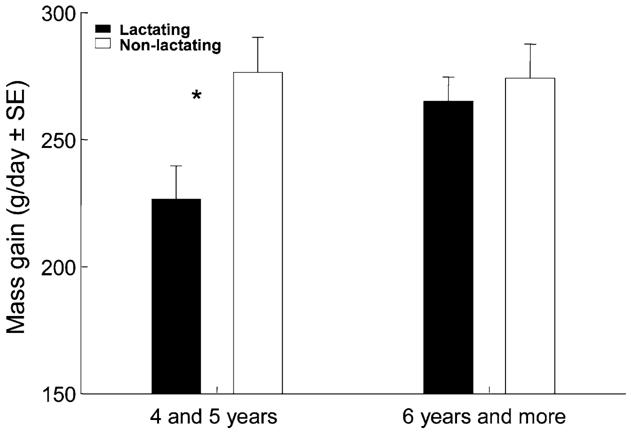

Fig. 3 Individual summer mass gain (g/day ± SE) in relation to age and reproductive status in adult female mountain goats at Caw Ridge, Alberta (2001–2006). $n = 84$ individual mass gains for 51 different females

ruminating behaviour by increasing chewing rate (this study) as well as time spent ruminating (Hamel and Côté 2008). These changes in foraging and ruminating behaviours seem to have allowed lactating females that had reached asymptotic body mass to compensate for the energetic costs of lactation since they achieved a similar summer mass gain as non-lactating females. However, females that were still growing appeared to face an important trade-off between growth and lactation since their mass gain was lower than non-lactating females, even if they achieved higher biting and chewing rates than fully grown females.

Foraging decisions

At a fine scale, the consumption rate of lactating mountain goats was augmented by increasing bite rate rather than by foraging more selectively on plants of higher quality. Indeed, lactating females took 27% more bites per minute foraging than non-lactating females. Interestingly, the influence of lactation on bite rate was lower in late lactation than in early lactation, a time when energetic demands are expected to be greater since milk yield is higher (Oftedal 1985; Landete-Castillejos et al. 2000). Bite rate has also been shown to be higher in lactating than in non-lactating females in bighorn sheep (Ruckstuhl et al. 2003), plain zebra (*Equus burchelli*; Neuhaus and Ruckstuhl 2002a) and Alpine ibex (*Capra ibex*; Neuhaus and Ruckstuhl 2002b), but no study has demonstrated variation in bite rate throughout the lactation period. Hudson and Frank (1987) demonstrated that bite rate of bison (*Bison bison*) increased when available biomass decreased and suggested that this increase was to compensate for reduced forage intake per bite. As plant biomass did not influence bite rate in mountain goats, our results suggest that lactating females did increase forage intake by increasing bite rate.

In ungulate species for which selectivity has been assessed according to female reproductive status, females were shown to maintain similar selectivity when non-lactating (e.g. Komers et al. 1993; Ruckstuhl et al. 2003), except in red deer where lactating females selected sites with higher quality forage than non-lactating females (Clutton-Brock et al. 1982). In most studies, however, selectivity is only indirectly determined by assessing travel velocity, through stepping rate, assuming that a more selective individual would have a higher stepping rate. We believe this assumption may not always be respected because although step rate varies with habitat type at a large scale, step rate is not influenced by plant quality at a finer scale, rather, it increases with decreasing plant biomass (S. Hamel, unpublished data). Therefore, it may be more appropriate to directly measure selectivity at a fine scale rather than measuring stepping rate. Overall, our estimates of protein and digestible contents in plants collected at foraging sites suggested that lactating mountain goats foraged on sites of similar plant quality as non-lactating females. These results are consistent with our expectation of a low potential for females of this species to increase selectivity when lactating that was based on (1) mountain goats being generalist herbivores (Côté and Festa-Bianchet 2003) that forage in a relatively homogeneous alpine tundra habitat (Hamel and Côté 2007), and (2) lactating and non-lactating females foraging in the same groups.

Lactating females increased forage intake by ingesting about 1 kg of dry biomass more than non-lactating females each day, mainly by increasing bite rate (this study) but also by increasing time spent foraging (Hamel and Côté 2008). This increase, from 42 to 28% from early to late lactation, is in the range reported for other ungulate species. In black-tailed deer (*Odocoileus hemionus columbianus*), lactating females were observed to increase daily food intake by 35% when nursing a single fawn and by 70% when nursing twins, and intake decreased after the early peak of lactation (Sadleir 1982). Female domestic sheep (*Ovis aries*) also increased their dry organic matter intake—by 25–50%—when lactating (Arnold and Dudzinski 1967), as did Nubian ibex (by 25–75%; Gross et al. 1996). Not surprisingly, our estimation of forage intake for all females was lower in mid-summer. This occurred because of the reduced time spent foraging in mid-summer, which likely resulted from greater forage abundance and quality at that time of the year (Hamel and Côté 2008). Nevertheless, lower forage intake is unlikely to result in lower nutrient intake because vegetation quality is high in mid-summer.

Because digestion is the ultimate factor limiting nutrient intake, lactating females had to increase their digestive efficiency to process the additional vegetation they ingested compared with non-lactating females. It was therefore not surprising to find that lactating females increased vegetation processing by increasing chewing intensity while ruminating (this study) and by spending more time ruminating than non-lactating females (Hamel and Côté 2008). Blanchard (2005) also found an increase in chewing rate in lactating bighorn sheep. One of his hypotheses was that this increase in chewing rate could enhance nutrient assimilation and hence help lactating females to partly compensate for the costs of lactation. As bighorn ewes also increase bite rate when lactating (Ruckstuhl et al. 2003), increased chewing rate may also be the direct result of additional food intake that needs to be processed (Blanchard 2005). Although it is difficult to disentangle these two non-exclusive hypotheses, our findings suggest that increases in rumination time (Hamel and Côté 2008) and intensity were primarily the results of increased forage intake.

Mass gain and costs of lactation

Young females that reproduce while they are still growing require energy for both reproduction and growth, two of the most energetically demanding activities (Stearns 1992). We should therefore expect greater costs of lactation in females that have not reached asymptotic body mass than in fully grown ones. Indeed, although young female goats increased nutrient intake by foraging and ruminating more intensively than older females, they accumulated less mass during the summer when they were lactating than when they were barren. Young lactating females therefore appeared to be unable to compensate for the energetic costs of lactation. Although this lower mass gain in growing females may result from lower fat reserves and/or body growth, lactation also has a negative effect on the annual growth increments of horns of 4- and 5-year-old females (Côté et al. 1998b), which suggests that a fundamental short-term compromise exists between growth and lactation in young adult mountain goats. Female moose (*Alces alces*) that started reproducing as yearlings also experienced lower body growth than females that delayed reproduction (Sæther and Haagenrud 1985). In bison, females reach asymptotic body mass at around 6 years of age but start reproducing between 2 and 4 years, and those that reproduced at 2 years of age reached a smaller asymptotic body mass than females that delayed reproduction until 4 years old (Green and Rothstein 1991). The negative effect of early reproduction on body mass can also impact other life-history traits, since body mass may affect the survival and reproduction of females as well as the body mass and survival of the offspring produced (Gaillard et al. 2000). Because of the trade-off between growth and lactation, we should expect young growing females to have greater costs of reproduction than older females, as found, for example, in Soay sheep (*Ovis aries*; Tavecchia et al. 2005) and in mountain goats (Hamel 2008).

As the summer mass gain was similar for lactating and non-lactating females $\geq$6 years old, increased foraging by lactating mature females seems to have allowed them to compensate for the energetic costs of lactation. However, fully grown female mountain goats still take reproductive pauses once every 4 years (Festa-Bianchet and Côté 2008), suggesting that the short-term compensation for the energetic costs of lactation may not be sufficient over the long-term. Indeed, cumulative costs of reproduction may occur (Moyes et al. 2006), and they may involve other physiological processes than mass gain. Furthermore, a fundamental question remains “Why don’t non-lactating females also increase forage intake in the expectation of the following breeding season?” Body mass loss in winter may be compensatory, so that individuals that accumulate more mass in summer also lose more mass during winter (Festa-Bianchet et al. 1995). It may therefore be costly to increase mass and fat beyond a certain threshold. Increasing forage intake should also result in greater rumination processing that can accelerate tooth wear (Gross et al. 1995; Veiberg et al. 2007).

Our results illustrate the importance of integrating several variables at different scales to better understand the complexity of foraging behaviour. For example, lactation did not affect all aspects of the foraging behaviour of females (e.g. no difference in plant quality and biomass at foraging sites), and the importance of each variable varied according to different spatio–temporal scales (e.g. the stronger influence of bite rate than daily activity budget). On a short time scale, we demonstrated that lactating mountain goats could compensate for the costs of lactation when they had reached asymptotic body mass by adjusting foraging behaviour. A major trade-off, however, existed between growth and lactation for younger females that appeared unable to compensate for the costs of lactation.

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