Oecologia (1996) 107:170–178

John E. Gross · Philip U. Alkon
Montague W. Demment

Nutritional ecology of dimorphic herbivores: digestion and passage rates in Nubian ibex

Received: 1 September 1995 / Accepted: 26 December 1995

Abstract We compared forage digestion and passage rates among three groups of Nubian ibex (*Capra ibex nubiana*) – mature males, non-lactating females, and lactating females – to test hypotheses relating intraspecific digestive ability to body mass and reproduction costs. We hypothesized that large males (60 kg) would exhibit longer forage retention times and more complete digestion of fermentable cell walls than adult females (23 kg). We tested these predictions by measuring digestion and retention of a grass hay and an alfalfa hay, forages that exhibited contrasting rates and extents of cell wall digestion. Consistent with predictions, males retained both forages longer than non-lactating females. However, by substantially increasing gut fill, lactating females increased both intake and retention time with respect to non-lactating females. Contrary to predictions, all three groups digested the grass (66% digestible) and alfalfa hay (63%) equally well. Alfalfa cell wall was less digestible than that of grass hay (60% vs 69% digestible), and retention time of alfalfa was consistently, but not statistically significantly, shorter. Fiber digestion was not correlated with retention time, emphasizing the ability of behavioral processes to modify digestion rate. We postulate that females achieved their greater digestion rate by masticating forages much more thoroughly than males.

J. E. Gross (✉)[1] · M. W. Demment
Department of Agronomy and Range Science,
University of California
Davis, CA 95616, USA

P. U. Alkon
Mitrani Center for Desert Ecology
The Jacob Blaustein Institute for Desert Research,
Ben-Gurion University of the Negev,
Sede Boqer Campus, 84993 Israel

Current address:
[1] Natural Resource Ecology Laboratory,
Colorado State University,
Ft. Collins, CO 80523-1499, USA
fax: 970 491 1965
e-mail: Johng@NREL.ColoState.edu

Key words Herbivore · Digestion · Retention time · Body size · Allometry

Introduction

Demment (1983) suggested that differences in diet and habitat selection in sexually dimorphic herbivores would result from the scaling of gut size and metabolism with body size. Because gut capacity increases linearly with body size (Parra 1978; Demment and Van Soest 1985; Justice and Smith 1992) and metabolism increases as a fractional power of mass, smaller animals have less digestive capacity per unit of metabolic need (Parra 1978). Theory thus predicts that small-bodied herbivores must compensate by selecting diets that are more readily digested, or they must excrete digesta more rapidly in order to maintain an intake sufficient to meet metabolic needs. The extent of digestion is determined in part by retention time in the gut; thus smaller herbivores should exhibit higher rates of passage and lower digestibilities when diet quality is held constant (Parra 1978). In species with a large degree of sexual dimorphism in size, smaller females would be constrained by their lower digestive capacity to foods that digest quickly, while large males would require higher intake rates to meet greater total metabolic requirements. During lactation these differences are amplified; lactating females were projected to have very short retention times and a reduced ability to ferment cell wall. Theory has uniformly assumed that gut fill remains constant, and that the rate of digestion of a particular forage is independent of body size.

There has been considerable speculation about the role of digestive processes in shaping the ecology of herbivores (e.g. Parra 1978; Milton 1979; Demment and Van Soest 1985; Beier 1987; Duncan et al. 1990; Fryxell 1991; Hodgson et al. 1991; LaGory et al. 1991; Weckerly 1993), but few direct measures of the most relevant processes linking nutrition to behavior (Baker and Hobbs 1987). Differences in digestive function are likely to promote variation in foraging behavior (Demment and

Greenwood 1988) and, depending on the spatial relationship between food quality and quantity, differences in the habitats selected by males and females (Clutton-Brock et al. 1982; Demment 1983; McCullough et al. 1989; LaGory et al. 1991; Miller and Litvaitis 1992; Gross et al. 1995a). Although sex-based differences in digestive capabilities have frequently been cited as a potential cause of sexual segregation, this is apparently the first test of the underlying mechanisms. Most theory concerning the influence of size-related nutritional constraints rests on a comparison of the retention and digestion kinetics of males, non-lactating and lactating females. Here, we examine the hypotheses that (1) males retain forages in the gut longer than females; (2) males digest forages more completely than females; (3) lactating females have higher food passage rates and lower forage digestibilities than non-lactating females; and (4) test forages differ in the extent of cell wall digested by ibex.

We tested these predictions by conducting digestion trials with highly size-dimorphic Nubian ibex (*Capra ibex nubiana*). We measured intake, digestive coefficients, and forage passage kinetics of male, non-lactating female, and lactating female Nubian ibex fed forages that contrasted in their rate and extent of cell wall digestion.

Materials and methods

Animals and forages

We conducted full balance digestion trials (Van Soest 1994) using four adult female ibex (average mass 23.0 kg, SD =3.2 kg) and four adult male ibex (average mass 60.2 kg, SD =6.8 kg) previously habituated to the experimental protocols. Each animal was fed either a coarse grass hay (*Pennisetum americanum*) or alfalfa hay (*Medicago sativa*) diet during all phases of a trial. Grass hay typically contains a relatively large amount of digestible cell wall, but with a slow rate of digestion, while alfalfa hay is composed of relatively indigestible cell wall, but the portion of cell wall that is digested does so rapidly. Fiber composition of the test diets was determined by sequentially removing fractions with detergent solutions (Goering and Van Soest 1970). Lignin content was estimated from the residue after forage samples were digested in concentrated (72%) sulfuric acid. We estimated organic matter (OM) by ashing forage samples at 540°C for 3–4 h, and determined protein content from forage N (Kjeldahl N×6.25, AOAC 1980). Composition of the grass diet (percent of 100°C dry matter) was 88.2% OM, 64.7% neutral detergent fiber (NDF), 34.3% acid detergent fiber (ADF), 5.4% lignin, and 9.8% protein. The alfalfa diet consisted of 89.0% OM, 48.5% NDF, 34.3% ADF, 8.0% lignin, and 19.4% protein. NDF includes cellulose, hemicellulose, and lignin, approximating total cell wall content. ADF consists primarily of cellulose and lignin. Digestion trials were timed to include the period of peak lactation by ibex. We were able to acquire a limited number of female ibex; thus females were tested first in the spring/early summer during the period of peak lactation (30–60 days postpartum, Maltz and Shkolnik 1984) with a single kid, and again during the autumn more than 1 month following separation from their kids. Males were tested only in the spring and early summer.

Each digestion trial consisted of three phases: adaptation to the test diet, determination of voluntary ad libitum intake, and determination of digestion coefficients. In the adaptation phase animals were weighed, then isolated in pens (about 80 m^2) and habituated to the grass hay diet for at least 3 weeks prior to initiation of the first trial. Five to 7 days before placing ibex in individual digestion cages (1.5×3.0 m), and for the first 3–5 days while in the digestion cages, voluntary intake was determined by reducing meals until refusals were less than 200 g/day. Ibex were fed twice daily (0700 and 1700 hours) during all phases of the trial. Full balance trials were initiated after intake stabilized in the digestion cages, and thereafter animals were fed 95% of their voluntary intake for the duration of each trial. Ibex were weighed (+ 0.05 kg) at the start and all feces, urine, feed, and refusals were collected for at least 7 days. Ibex were weighed and metabolism cages thoroughly cleaned at the end of each trial. Feeds, feces, and refused feed samples were analyzed for dry matter, ash, NDF, ADF, acid detergent lignin (Goering and Van Soest 1970), and for crude protein (Kjeldahl N×6.25, AOAC 1980).

After a grass hay trial, the animal's diet was gradually changed to alfalfa hay over a 7 day period. Following at least 2 weeks of habituation to alfalfa hay, the preparatory and experimental protocols outlined above were repeated. Grass hay trials were always conducted first because ibex greatly preferred alfalfa such that a prohibitively long adaptation period would have been necessary if the order of diets was reversed.

We measured in vitro digestion rates using rumen inoculant from a grass-fed cow to confirm the validity of our assumptions about the relative rate and extent of cell wall digestion of forages. Forage samples ground to pass through a 1 mm screen were incubated in a rumen fluid/buffer system under CO_2 for periods up to 96 h (Mertens 1973). For each forage, fermentation of three replicate samples was arrested after 0, 3, 6, 12, 18, 24, 26, 48, 72, and 96 h. The mass of cell wall residue from these samples was determined by refluxing in neutral detergent solution (Mertens 1973). Rumen fluid was obtained from a rumen-fistulated cow fed a grass hay diet. Previous studies have shown that in vitro digestibility results are not influenced by the species of animal that donates rumen fluid (Robbins et al. 1975; Palmer et al. 1976; Brooks and Urness 1984), but the diet of the donor animal can affect the extent of digestion.

Passage markers and calculations

We used two digesta markers to interpret retention times in ibex. First, we marked the large particle pool using Cr-mordanted fiber (Uden et al. 1980). The large particle pool represents that fraction of the forage that is physically too large to pass through the rumen without further breakdown. Particles size can be reduced by chemical digestion, or by mastication either at the time of consumption or later during rumination. We used Co-EDTA, a liquid phase marker, to represent passage dynamics of the small particle pool (Uden et al. 1980). Cr-mordanted fiber was fed to ibex prior to the morning meal on the second day of each digestion trial, and Co-EDTA in solution was offered to the animals several hours later. We recorded the time of marker consumption by each animal. Fecal samples were collected immediately before dosing, 6 h later, and every 3 h thereafter until 51 h post-dosing. Additional samples were collected at 55, 59, 65, 71, 79, 87, 97, 107, 119, 131, 144 h post-dosing. Midpoints between collection times were used to calculate marker excretion rates. Fecal samples were dried immediately at 55°C or frozen for later processing.

Cr and Co concentrations in fecal samples were determined by atomic absorption spectrophotometry. Fecal samples were ground, ashed for 8 h at 600°C, and digested in concentrated nitric and perchloric acids (Uden et al. 1980). Because of uncertainties regarding estimation techniques, we used two methods of contrasting complexity to analyze marker excretion rates. First, we used the summation method (Faichney 1975), which makes no assumptions about digestive processes or statistical distributions, to estimate total tract mean retention time (TMRT). TMRT is the average residence time of a digesta particle in the gut, and is calculated as:

$$\mathrm{TMRT} = \frac{\sum_{n=1}^{\infty}(\text{hours} \times \text{concentration} \times \text{fecal DM})}{\sum_{n=1}^{\infty}(\text{concentration} \times \text{fecal DM})} \quad (1)$$

where hours is the time since dosing for sample n (in hours), concentration is marker concentration in sample n (PPM), and fecal DM is the mass of dried fecal material. The summation technique provides no statistical estimate of transit time (TT, first appearance of the marker in feces).

We also estimated total tract transit time (total tract TT) and rumen mean retention time (rumen MRT) by fitting a gamma-2 age-dependent model (Matis 1972; Fadel et al. 1987) to concentrations of forage markers in fecal samples. This model more appropriately represents the dynamics of particle flow in a compartmental system where the probability of outflow from a compartment (e.g. the rumen) increases with residence time. Parameters of the gamma-2 model were fitted using non-linear regression (SAS 1988).

We calculated total tract digestible and indigestible fill from diet fractional digestibility, particulate MRT, and daily intake using the occupancy principle (Eqs. 5 and 6 from Holleman and White 1989). Indigestible fill (V_N, g dry matter) was calculated as the product of fecal output (F, g dry matter/h) and total mean retention time (TMRT, h):

$$V_N = F\,\mathrm{TMRT} \quad (2)$$

The total dry matter fill (V, g dry matter) of the alimentary tract was then estimated as:

$$V = V_N + \frac{V_N A}{2(1-A)} \quad (3)$$

where A is the dry matter digestibility of the diet.

Milk production

Milk production was estimated by determining body water turnover rates of kids, who obtained virtually all their free water via milk from their mother. Water turnover was calculated using the isotope dilution technique (Macfarlane et al. 1969). Kids were injected with 1.11 MBq/kg of tritiated water and held in digestion cages with their mothers during trials. All free water consumption was measured. Because some kids grew appreciably during a digestion trial we calculated water turnover with a model that incorporated changes in the size of the body water pool (Dove and Freer 1979). Our estimates accounted for metabolic water production, milk composition (Mitchell 1962; Maltz and Shkolnik 1984), and free water intake. All calculations of milk energy yield are based on an estimated milk energy content of 6284 kJ/kg (Maltz and Shkolnik 1984).

Statistical analysis

Differences due to sex (male or female), lactation within sex, forage type (diet), and the interaction of forage with sex were evaluated using a two-stage, repeated-measures ANOVA for an unbalanced design. This design accounted for multiple measurement from the same animal, which can result in correlated data. The first stage of the ANOVA separated all potential sources of variance (Table 1, upper chart). We then tested the necessity of splitting out the variance contributed by animals within each sex (MS_2 in Table 1, upper chart) using an F test (MS_2/MS_4, Table 1, upper chart). This test was not significant for 16 of 18 cases, and we thus report results from a reduced ANOVA model (Table 1, lower chart; SPSS/PC, Norvšis 1990). Cell sizes in our ANOVA were unequal because one kid died between the first and third digestion trial, and one female refused to consume the liquid marker (Co-EDTA) in two trials. Thus there were three females in these cells and four in all others.

We scaled variables to body mass by performing linear regression on $\log_{10}$ transformed data ($\log y = \log a + b \log x$, SAS 1988).

Table 1 ANOVA designs used to test for effects of sex, diet, and lactation. We examined results from the full model ANOVA shown in the upper chart and determined the appropriateness of a reduced model from the significance (F-test) of MS_2/MS_4. The design of the reduced model is shown in the lower chart

Source	*df*	MS	*F*
Sex	1	1	MS_1/MS_2
Animal within sex	6	2	
Lactation within sex	1	3	MS_3/MS_4
Animal * (lactation within sex)	3	4	
Diet	1	5	MS_5/MS_7
Diet * sex	1	6	MS_6/MS_7
Diet * (animal within sex)	6	7	
Residual	3		
Total	22		
Sex	1	1	MS_1/MS_3
Lactation within sex	1	2	MS_2/MS_3
(Animal within sex) + animal * (lactation within sex)	9	3	
Diet	1	4	MS_4/MS_6
Diet * sex	1	5	MS_5/MS_6
Diet * (animal within sex)	6	6	
Residual	3		
Total	22		

Results

Forage intake and digestion

Daily dry matter (DM) intake expressed in terms of metabolic body mass ($W^{0.75}$; W = body mass in kg) did not differ with sex or forage (Table 2). However, daily intake rates of females increased by 25% to 75% ($P < 0.05$) with lactation, and DM consumption by males was intermediate to that of the two female groups. Males and non-lactating females consumed similar amounts of feed per kilogramm of body mass, but lactating females consumed about 50% more than other groups (38 g kg^{-1} day^{-1}, Table 2, $P < 0.05$). Dry matter intake scaled to $W^{0.82}$ ($r^2 = 0.78$, $n = 23$) when all animals were included in the regression, but different exponents resulted when only males and lactating females ($W^{0.63}$, $r^2 = 0.91$, $n = 15$) or males and non-lactating females ($W^{1.04}$, $r^2 = 0.94$, $n = 16$) were included in the regression.

Neither sex nor lactation significantly influenced apparent DM digestion, but alfalfa hay was consistently less digestible than grass hay (Table 2). Sex and lactation had no effect on either NDF or ADF digestion. Alfalfa hay NDF and ADF digestion coefficients (60% and 56%) were significantly lower than those of grass hay (69% and 63%, respectively). Digestion of NDF was not correlated with total MRT ($r^2 = 0.08$).

The rate and extent of cell wall (NDF) digestion differed in the alfalfa and grass hays (Fig. 1). Cell wall of alfalfa was less digestible overall, but the fermentable portion of the alfalfa cell wall digested rapidly. After 18 h of incubation, 86% of the digestible cell wall of al-

Table 2 Daily intake and digestion (mean and SE) of forage dry matter (*DM*), neutral detergent fiber (*NDF*), and acid detergent fiber (*ADF*) by Nubian ibex fed a grass hay (*GH*) or alfalfa hay (*AAH*)

	DM intake ($g\ kg^{-0.75}$)		DM intake (g/kg)		NDF intake (g/kg)		DM digestion		NDF digestion		ADF digestion	
Non-lactating females												
GH	59.2	5.44	26.7	2.22	16.9	1.50	0.66	0.01	0.68	0.01	0.63	0.01
AAH	50.1	4.68	22.6	1.87	9.9	0.89	0.64	0.02	0.58	0.02	0.54	0.02
Lactating females												
GH	73.8	3.52	34.2	2.05	22.8	1.30	0.67	0.02	0.70	0.03	0.64	0.03
AAH	87.3	6.28	40.6	2.57	20.1	1.59	0.62	0.02	0.59	0.04	0.58	0.04
Adult males												
GH	67.4	2.63	24.3	0.82	15.6	0.50	0.66	0.00	0.69	0.00	0.63	0.00
AAH	71.2	3.29	25.6	1.24	13.0	0.86	0.65	0.00	0.63	0.01	0.56	0.03
Effects:												
Sex			**		**							
Lactation	*		*		*							
Forage			*		**				**		*	

* = $P<0.05$, ** = $P<0.01$

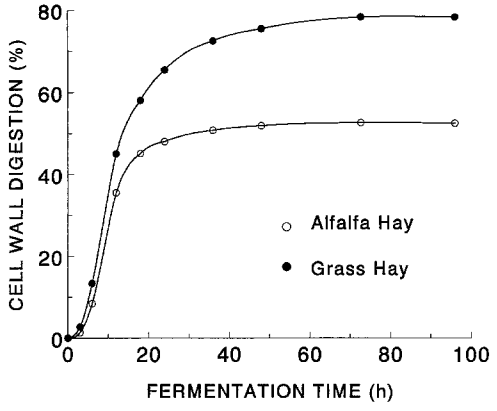

Fig. 1 In vitro rate of digestion of plant cell wall (*NDF*) from alfalfa and grass hay

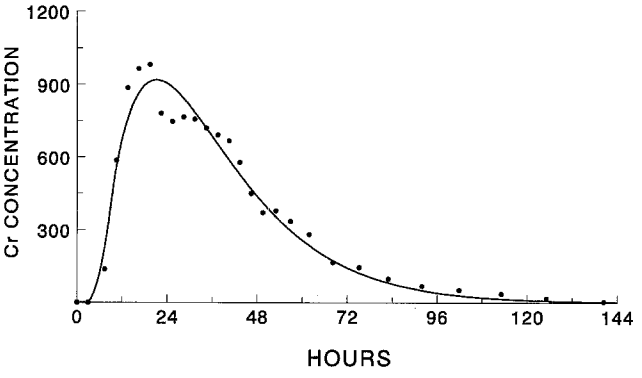

Fig. 2 A representative example of the excretion pattern of the large particle forage marker (Cr-mordanted fiber; *solid circles*) and the least-squares fit of the gamma-2 model (*line*)

Table 3 Transit time (*TT*, h) and mean retention time (*MRT*, h) of the large particle pool (Cr-mordanted fiber) for Nubian ibex as estimated by a gamma-2 model or summation method (Eq. 1). Values in the Table are means and SE

	Gamma-2 model						Summation method					
	TT		Rumen MRT		Total MRT		TT		Rumen MRT		Total MRT	
Non-lactating females												
GH	13.4	0.61	20.8	4.40	34.2	4.69	13.0	1.76	22.4	4.22	35.4	3.52
AAH	10.3	0.83	19.2	3.46	29.5	3.47	13.4	1.12	21.3	2.31	34.7	2.45
Lactating females												
GH	9.3	0.98	31.0	4.10	40.3	3.99	9.7	0.89	30.1	3.02	39.8	2.80
AAH	8.2	1.50	28.9	2.88	37.1	3.72	9.4	1.29	29.9	2.45	39.3	2.99
Adult males												
GH	11.1	0.55	45.4	7.77	56.5	7.60	12.0	0.34	41.6	4.58	53.6	4.69
AAH	9.2	1.77	28.8	1.89	38.0	3.29	12.5	2.05	31.8	4.07	44.3	5.36
Effects:												
Sex			*		*				*		*	
Lactation	*						*					
Forage	**		*		*				*			

* = $P<0.05$, ** = $P<0.01$

Table 4 Transit time (*TT*, h) and mean retention time (*MRT*, h) of the small particle pool (Co-EDTA) for Nubian ibex as estimated by a gamma-2 model or summation method (Eq. 1). Values in the Table are means and SE

	Gamma-2 model						Summation method					
	TT		Rumen MRT		Total MRT		TT		Rumen MRT		Total MRT	
Non-lactating females												
GH	10.3	0.93	11.1	2.47	21.4	1.53	9.4	1.64	13.5	2.86	22.9	1.23
AAH	9.1	1.40	11.1	1.45	20.1	1.80	10.4	1.29	12.4	2.04	22.8	2.38
Lactating females												
GH	6.9	0.74	14.2	0.87	21.1	1.59	7.3	1.23	15.0	0.61	22.3	1.48
AAH	7.5	1.83	11.4	1.08	18.9	0.74	8.4	1.25	13.3	0.98	21.7	0.78
Adult males												
GH	9.0	0.86	19.1	1.46	28.1	1.71	11.4	1.26	20.5	1.81	31.9	1.42
AAH	8.3	1.78	16.6	1.73	24.9	3.26	9.7	1.90	18.5	1.35	28.1	2.99
Effects:												
Sex			*						*			
Lactation												
Forage							[a]					

* = $P < 0.05$; [a] $P = 0.056$

Table 5 Gut fill (g dry matter, mean and SE) of ibex consuming grass hay (*GH*) or alfalfa hay (*AAH*). Calculations were based on mean retention time estimated by a gamma-2 model or summation method. Mass-specific gut fill is the average of the two estimates

	Gamma model		Summation		Gut fill (g/kg body mass)		Gut fill (g/kg$^{.75}$ body mass)	
Non-lactating females								
GH	583	16	615	34	25.2	1.2	55.5	1.7
AAH	439	33	525	51	20.2	0.9	44.6	1.9
Lactating females								
GH	831	85	822	61	37.4	1.3	81.0	3.3
AAH	917	93	976	108	43.9	1.7	94.3	3.4
Adult males								
GH	2229	175	2131	99	36.8	2.8	102.3	6.9
AAH	1638	111	1899	182	29.3	1.9	81.5	5.3
Effects:								
Sex	***		***				**	
Lactation	*		*		**		**	
Forage	**		[a]		*		**	

* = $P<0.05$, ** = $P<0.01$, *** $P<0.001$, [a] $P = 0.056$

falfa had been fermented, compared to only 58% of the grass hay.

Passage rates

Rumen MRT and total MRT of Cr-mordanted fiber (the large particle marker) was longer in males than females ($P < 0.05$, Table 3), an effect due primarily to the much longer retention of the grass hay fiber (rumen MRT >40 h for males). Large particle rumen MRT was shorter in non-lactating females (22 h) than any other group. Average transit time of Cr-mordanted fiber in lactating females was about 2 h shorter than in non-lactating females ($P < 0.05$) and males ($P > 0.05$), but there was no significant difference by sex (Table 3).

There was a significant forage effect when Cr TT was estimated by the gamma model, but not when estimated by summation (Table 3). This discrepancy is likely due to the failure of two non-lactating females to defecate for one or two sampling periods in which the marker would have been expected to appear in the feces. Therefore, TT estimated from the gamma model likely provided a more realistic approximation of TT for these animals. Overall, the gamma model provided a good fit to excretion patterns of both markers (Fig. 2), and it accounted for an average of 93% and 97% of the variance of Cr and Co concentration in fecal matter.

Rumen MRT of CoEDTA was longer in males than females ($P < 0.05$), but TT and total MRT did not differ among treatments (Table 4). Forage type and lactation had no effect on CoEDTA dynamics.

Retention times of Co and Cr were significantly correlated (Cr rumen MRT =2.65 + 1.86 Co rumen MRT, r =0.62, $P < 0.01$, n =21; Cr total MRT =2.71 + 1.60 Co total MRT, r =0.62, $P < 0.01$, n =21). With lactation there was a shift in the relationship of large and small particle passage that was indicated by an increase in the residence time of large particles, but constant turnover rate of the small particle pool.

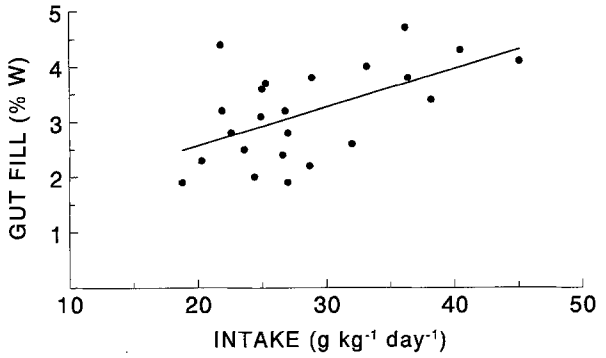

Fig. 3 The relationship between gut fill (% of body mass, W) and daily intake rate [g (kg body mass^{-1}) day^{-1}] for Nubian ibex. Gut fill increased with daily intake ($y = 1.19 + 0.07x$, $r^2 = 0.32$, $P < 0.001$)

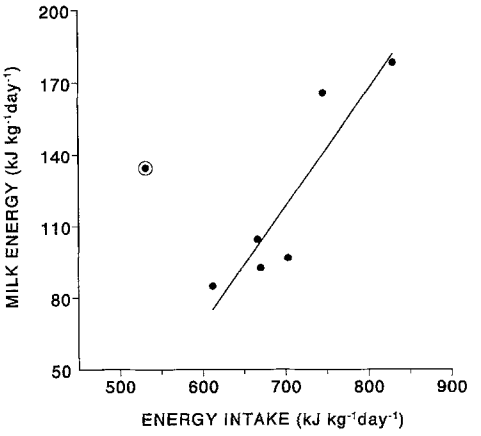

Fig. 4 Milk production and energy intake by Nubian ibex. Milk production was strongly correlated with energy intake ($y = -224 + 0.49x$, $r^2 = 0.83$, $P = 0.01$, excluding the *circled value*)

Gut fill

Compared to non-lactating females, gut fill (g DM/kg W) of lactating females was 50% greater for ibex fed grass hay, and gut fill was more than doubled for ibex fed alfalfa hay (Table 5). Correlations of gut fill to DM intake (g kg^{-1} day^{-1}, $r^2 = 0.32$, $P < 0.01$, $n = 23$) and NDF intake ($r^2 = 0.33$, $P < 0.01$, $n = 23$) were statistically significant, but had little predictive power. When gut fill was analyzed as a linear function of body size (e.g. W^1), there was no direct effect attributable to sex. However, when expressed as a function of metabolic body size ($W^{0.75}$), male gut capacity was significantly greater than that of females ($P < 0.01$; Table 5). We could discern no clear upper limit to gut fill, but there was a distinct lower limit for animals with intakes of more than 25 g kg^{-1} day^{-1} (Fig. 3).

Lactation

Milk production per female increased by 46% between the grass and alfalfa hay trials (Table 6), from 16.1 to 23.5 ml kg^{-1} day^{-1}. The energy content of milk produced by each lactating ibex (based on 6284 kJ/kg milk; Maltz and Shkolnik 1984) averaged 2740 kJ/day over both trials, but varied with animal and forage from 1678 to 4397 kJ/day. Milk energy production was significantly related to kid body mass (ME = 318 + 522 W; ME = kJ milk/day, W = kid body mass in kg; $r^2 = 0.74$, $P = 0.01$, $n = 7$) and to daily intake by ewes (Fig. 4). Lactating ibex consumed an average of 231 kJ kg^{-1} day^{-1} more energy than when barren, and produced an average of 122 kJ kg^{-1} day^{-1} of milk. Lactating ewes thus converted about 53% of the additional energy consumed during lactation into milk energy.

Discussion

Digestion and passage rates

An allometric-based theory on herbivore nutritional ecology (Clutton-Brock et al. 1982; Demment 1983; Demment and Van Soest 1985; Illius and Gordon 1991; Justice and Smith 1992) was supported by several of the results from our experiments. This theory, founded on the scaling relationships of intake and gut volume with body size, incorporates the well-established increase in cell wall digestion with retention time (Fig. 1). Consistent with theory, males did consume more forage on an absolute basis than did the smaller-bodied females, and daily intakes were not different when corrected to metabolic body size ($W^{0.75}$). We also found that male ibex retained forages in the digestive tract longer than females, extending results from interspecific comparisons of other ruminants (Robbins 1983; Van Soest et al. 1983; Illius and Gordon 1991).

Our estimates of gut fill were also consistent with scaling relationships derived from interspecific comparisons (Parra 1978; Demment 1982; Justice and Smith 1992). When we expressed gut fill as a linear function of body size (e.g., W^1), there was no statistical difference in gut fill due to sex (Table 5). However, gut fill as a por-

Table 6 Daily milk production (mean and SE) by lactating Nubian ibex fed grass hay or alfalfa hay

Diet	ml		kJ		ml/kg body mass		kJ/kg body mass	
Grass hay	364	88	2314	559	16.1	2.13	102	13
Alfalfa hay	518	93	3293	592	23.5	2.91	149	18

tion of metabolic body size (e.g., $W^{0.75}$) was greater for males than for females. The gut fill of lactating females approached that of males, but we have no reason to believe that males were any less able than females to enhance gut fill in response to an increase in energy needs or a decrease in diet quality.

Because of the difference between MRT of male and female ibex, we were surprised to find that all groups of ibex digested the fiber components of forages to the same extent, and there was no correlation of NDF digestion with RMRT (r^2 = 0.08). This result was especially perplexing in light of rumen retention times we observed, which fell on the steeply ascending portion of the cell wall digestion curve for grass hay (Fig. 1). Thus, cell wall digestion coefficients for grass hay should have been quite sensitive to the variation we observed in retention times, but they were not. Previous studies of both ruminant and non-ruminant herbivores have inextricably linked the total extent of cell wall digestion to retention time (reviewed by Parra 1978; Allen and Mertens 1988; Van Soest 1994). Forage retention time in the gut is seen as an important determinant of digestion because passage and digestion of fiber are viewed as competing processes (Mertens 1977; Robbins 1983; Huston et al. 1986; Allen and Mertens 1988; Van Soest 1994). However, other processes clearly influence the rate of digestion for cell wall.

Mastication is such a process. We believe that female ibex in our experiments comminuted food particles more completely than males, thereby increasing the rate of cell wall digestion in the rumen relative to that of males. Robbins' summary (1983, p320) suggests that fiber intake by all ibex in this experiment was sufficient to elicit maximal rumination activity (9–10 h/day). We calculated that if our ibex ruminated for 9.5 h/day at a rate of 55 or 61 chews/min (for females and males, respectively; Gross et al. 1995b), then even lactating females were capable of chewing each gram of intake almost twice as many times as males while ruminating. We estimate that chewing during rumination would have resulted in a total of 22, 41, and 58 chew/g for males, lactating females, and non-lactating females, respectively. A reduction of ingesta particle size due to mastication would not influence the total extent of cell wall digestion, but it would change the rate of digestion and reduce the lag time before fermentation of cell wall (Poppi et al. 1981; Bjorndal et al. 1990). Mastication damages cell wall surfaces and enhances penetration by cellulase-producing bacteria (Akin 1979), thereby increasing digestion rate and reducing the lag time between ingestion and the initiation of cell wall digestion. In vitro digestion trials revealed that significant digestion of cell wall from masticated forages took place after 3.1 h, in contrast to 15 h required for unmasticated samples (Reid et al. 1979; Poppi et al. 1981). Therefore, in comparison with male ibex, females were apparently capable of compensating for shorter retention times by virtue of a greater chewing investment.

Our hypothesis for the role of mastication in modifying digestion rate also finds support from an interspecific comparison of mastication rates, ingested particle size, and fiber digestion by sheep (67 kg) and goats (45 kg; Domingue et al. 1991a, b). Relative to sheep, the smaller goats more efficiently reduced particle size at the time of ingestion by chewing each gram of intake more. Goats ingested a larger portion of small forage particles, thereby accounting for their higher rates of digestion of plant cell wall (Domingue et al. 1991a). These results are consistent with observations of male and female ibex: when fed a wheat/rye hay, female Nubian ibex chewed each gram of intake about 50% more than males both at the time of ingestion, and during rumination (Gross et al. 1995b). Size-related changes in molar surface area or chewing force do not compensate for these differences in chewing investment (Fortelius 1985; Gross et al. 1995b).

Gut fill

Our results indicated that animals modified behaviors to compensate for digestive constraints imposed by lactation. Lactating ibex were able to maintain retention time in the face of increased intake through enhanced gut fill. During lactation, dairy cattle typically more than double intake, resulting in a decrease in forage retention time and a consequent reduction in cell wall digestion (Fig. 1; reviewed by Tyrrell and Moe 1975; Van Soest et al. 1979; Van Soest 1994). Forage retention by ibex may be less influenced by lactation simply because they exhibited a relatively small increase in intake with lactation (Table 2) and they have a great ability to increase gut fill over maintenance levels. Increased gut fill is a common, but not universal, response to increased energy demands or to a decrease in forage quality (Fell et al. 1972; Hartnell and Satter 1979; Hofmann 1982; Gross et al. 1985; Baker and Hobbs 1987; Hammond and Wunder 1991). Ibex may be unusual among wild ruminants in the extent to which they can respond by increasing gut fill: maximum gut fill of ibex (> 4.0% of body mass, Fig. 3) was greater than that reported for mule deer (*Odocoileus hemionus*, 3.6%, Baker and Hobbs 1987), elk and mountain sheep (*Cervus elaphus canadensis* and *Ovis canadensis*, 2.1%, Baker and Hobbs 1987), red deer (*C. elaphus elaphus*, 3.4%, Milne et al. 1978), or a variety of African ruminants (maximum of 3.4%, Gordon and Illius 1994). Elk and mountain sheep were apparently unable to increase gut fill in response to digestive limitations, and digestible energy intake declined as forage quality was reduced (Baker and Hobbs 1987).

We calculated that ibex fed our experimental diets consumed adequate fiber to elicit high levels of rumination, yet forage nutrient density (*sensu* Montgomery and Baumgardt 1965) was apparently sufficient in our experiments to allow animals to regulate intake via physiological rather than physical stimuli. If males can modify gut fill to the same extent as females, only lactating females

were potentially limited by digestive volume (Ammann et al. 1973). The poor relationship of gut fill to fiber (NDF) intake (g kg^{-1} day^{-1}, r^2 = 0.31) or DM intake (Fig. 3) suggests that ibex had considerable flexibility with respect to intake or passage (see also Demment and Greenwood 1988). We were unable to use diets as poor as those commonly consumed by free-ranging ibex (J. Gross, P. Alkon, M. Demment, unpublished data), thus the ultimate ability of male and female ibex to digest very low quality forages remains unknown. Nubian ibex have subsisted on wheat straw (Choshniak et al. 1984), but they lost weight even after a 3-month habituation period. A more demanding test would include a very high-fiber diet containing a large fraction of digestible cell wall. However, in a pretrial we found that lactating ibex rejected their kids when fed a lower quality diet than the grass hay used in our experiments.

Passage dynamics

The gamma model and summation technique produced similar estimates of TT, rumen MRT, and total MRT, but gamma model estimates were less subject to biases introduced by sampling frequency, small errors at long sampling times, and missing samples when an animal fails to defecate between fecal collections. Thus, under the conditions of our experiments, the gamma model was more likely to produce biologically relevant estimates for rates of passage.

Extant theory for the nutritional ecology of herbivores has provided a valuable framework for identifying and examining the potential constraints related to body size (e.g. Parra 1978; Demment 1983; Demment and Van Soest 1985; Penry and Jumars 1987; Illius and Gordon 1991; Fryxell 1991). However, models of digestion that form the foundation of this theory have uniformly ignored the ability of animals to compensate for digestive constraints by increasing digestion rate as well as gut fill. Our results clearly show that these behavioral adaptations are of sufficient magnitude to alter conclusions from previous modelling exercises, and they emphasize the need for further study to quantify these relationships.

Acknowledgements We thank Dr. Mandy Kotzman, Etan Jackson, Raid Moalem, Sonia Rosen, Marc Goldberg, and Dr. Ganga Deo for their help collecting and processing samples. Dr. Jim Fadel helped with passage marker analysis. Dr. Neil Willits and Jim ZumBrunnen provided invaluable advice on statistical analyses. The manuscript was improved by suggestions from Drs. M. Kotzman, E.A. Laca, J.G. Fadel, and B.A. Wunder. We thank The Israel Nature Reserves Authority for permits and animals, and Prof. Amiram Shkolnik and Tel Aviv University for the use of facilities and animals. The National Geographic Society, the U.S.-Israel Binational Science Foundation, the Department of Agronomy and Range Science, University of California-Davis, and the Blaustein Institute for Desert Research provided financial support. This is contribution No. 213 of the Mitrani Center for Desert Ecology.

References

Akin DE (1979) Microscopic evaluation of forage digestion by rumen microorganisms – a review. J Anim Sci 48: 701–710

Allen MS, Mertens DR (1988) Evaluating constraints on fiber digestion by rumen microbes. J Nutr 118: 261–270

Ammann AP, Cowan RL, Mothershead CL, Baumgardt BR (1973) Dry matter and energy intake in relation to digestibility in white-tailed deer. J Wildl Manage 37: 195–201

AOAC (1980) Official methods of analysis. Assoc Official Anal Chem, Washington, D.C.

Baker DL, Hobbs NT (1987) Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Can J Zool 65: 1978–1984

Beier P (1987) Sex differences in quality of white-tailed deer diets. J Mammal 68: 323–329

Bjorndal KA, Bolten AB, Moore JE (1990) Digestive fermentation in herbivores: effect of food particle size. Physiol Zool 63: 710–721

Brooks J III, Urness PJ (1984) Comparison of in vivo and in vitro digestibility of forages by elk. J Anim Sci 58: 963–970

Choshniak I, Arnon H, Shkolnik A (1984) Digestive efficiency in a wild goat the Nubian ibex. Can J Anim Sci 64 [Suppl]: 160–162

Clutton-Brock TH, Guinness FE, Albon D (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago

Demment MW (1982) The scaling of ruminoreticulum size with body weight in East African ungulates. Afr J Ecol 20: 43–47

Demment MW (1983) Feeding ecology and the evolution of body size of baboons. Afr J Ecol 21: 219–233

Demment MW, Greenwood GB (1988) Forage ingestion: effects of sward characteristics and body size. J Anim Sci 66: 2380–2392

Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am Nat 125: 641–672

Domingue BMF, Dellow DW, Barry TN (1991a) The efficiency of chewing during eating and ruminating in goats and sheep. Br J Nutr 65: 355–363

Domingue BMF, Dellow DW, Barry TN (1991b) Voluntary intake and rumen digestion of a low-quality roughage by goats and sheep. J Agric Sci 117: 111–120

Dove H, Freer M (1979) The accuracy of tritiated water turnover rate as an estimate of milk intake in lambs. Aust J Agric Res 30: 725–739

Duncan P, Foose TJ, Gordon IJ, Gakahu CG, Lloyd M (1990) Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia 84: 411–418

Fadel JG, Uden P, Robinson PH (1987) Effect of nitrogen and energy supplements on intake and digestion of oat straw by non-lactating dairy cows. J Agric Sci 109: 503–511

Faichney GJ (1975) The use of markers to partition digestion within the gastro-intestinal tract of ruminants. In: McDonald IW, Warner ACI (eds) Digestion and metabolism in the ruminant. University of New England Publication Unit, Armidale, N.S.W., Australia

Fell BF, Campbell RM, Mackie WS, Weekes TEC (1972) Changes associated with pregnancy and lactation in some extra-reproductive organs of the ewe. J Agric Sci 79: 397–407

Fortelius M (1985) Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. Acta Zool Fenn 180: 1–76

Fryxell JM (1991) Forage quality and aggregation by large herbivores. Am Nat 138: 478–498

Goering HK, Van Soest PJ (1970) Forage fiber analyses. U S Dep Agric Res Serv Agric Handb 379: 1–20

Gordon, IJ, Illius AW (1994) The functional significnce of the browser-grazer dichotomy in African ruminants. Oecologia 98: 167–175

Gross JE, Wang Z, Wunder BA (1985) Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. J Mammal 66: 661–667

Gross JE, Alkon PU, Demment MW (1995a) Grouping patterns and spatial segregation by Nubian ibex. J Arid Environ 30: 423–439

Gross JE, Demment MW, Alkon PU, Kotzman M (1995b) Feeding and chewing behaviours of Nubian ibex: compensation for sex-related differences in body size. Funct Ecol 9: 385–393

Hammond KA, Wunder BA (1991) The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. Physiol Zool 64: 541–567

Hartnell GF, Satter LD (1979) Determination of rumen fill, retention time and ruminal turnover rates of ingesta at different stages of lactation in dairy cows. J Anim Sci 48: 381–392

Hodgson J, Forbes TDA, Armstrong RH, Beattie MM, Hunter EA (1991) Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. J Appl Ecol 28: 205–227

Hofmann RR (1982) Zyklische Umbauvorgänge am Verdauungsapparat des Gamswildes als Ausdruck evolutionärer Anpassung an extreme Lebensräume. Allg Forst Z 51/52: 1562–1564

Holleman DF, White RG (1989) Determination of digesta fill and passage rate from nonabsorbed particulate phase markers using the single dosing method. Can J Zool 67: 488–494

Huston JE, Rector BS, Ellis WC, Allen ML (1986) Dynamics of digestion in cattle, sheep, goats and deer. J Anim Sci 62: 208–215

Illius AW, Gordon IJ (1991) Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. J Agric Sci 116: 145–157

Justice KE, Smith FA (1992) A model of dietary fiber utilization by small mammalian herbivores, with empirical results for *Neotoma*. Am Nat 139: 398–416

LaGory KE, Bagshaw III C, Brisbin Jr. IL (1991) Niche differences between male and female white-tailed deer on Ossabaw Island, Georgia. Appl Anim Behav 29: 205–214

Macfarlane WV, Howard B, Siebert BD (1969) Tritiated water in the measurement of milk intake and tissue growth of ruminants in the field. Nature 221: 578–579

Maltz E, Shkolnik A (1984) Lactational strategies of desert ruminants: the Bedouin goat, ibex, and desert gazelle. Symp Zool Soc Lond 51: 193–213

Matis JH (1972) Gamma time-dependency in Blaxter's compartmental model. Biometrics 28: 597–602

McCullough DR, Hirth DH, Newhouse SJ (1989) Resource partitioning between sexes in white-tailed deer. J Wildl Manage 52: 277–283

Mertens DR (1973) Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. PhD thesis, Cornell University, Ithaca, New York

Mertens DR (1977) Dietary fibre components: relationship to the rate and extent of ruminal digestion. Fed Proc 36: 187–192

Miller BK, Litvaitis JA (1992) Habitat segregation by moose in a boreal forest ecotone. Acta Theriol 37: 41–50

Milne JA, MacRae JC, Spence AM, Wilson S (1978) A comparison of the voluntary intake and digestion of a range of forages at different times of the year by the sheep and red deer (*Cervus elaphus*). Br J Nutr 40: 347–357

Milton K (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Am Nat 114: 362–378

Mitchell HH (1962) Comparative nutrition of man and domestic animals. Academic Press, New York

Montgomery MJ, Baumgardt BR (1965) Regulation of food intake in ruminants. I. Pelleted rations varying in energy concentration. J Dairy Sci 48: 569–574

Norvsis M J (1990) SPSS/PC+ Advanced statistics 4.0. SPSS, Chicago, Illinois

Palmer WL, Cowan RL, Ammann AP (1976) Effect of innoculum source on in vitro digestion of deer foods. J Wildl Manage 40: 301–307

Parra R (1978) Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, D.C., pp 209–229

Penry DL, Jumars PA (1987) Modeling animal guts as chemical reactors. Am Nat 129: 69–96

Poppi DP, Minson KJ, Ternouth JH (1981) Studies of cattle and sheep eating leaf and stem fractions of grasses. II. Factors controlling the retention of feed in the reticulo-rumen. Aust J Agric Res 32: 109–121

Reid CSW, Ulyatt MJ, Waghorn GC, Milligan LP (1979) Chewing and the physical breakdown of feed in sheep. Ann Rech Vet 10: 205–207

Robbins CT (1983) Wildlife feeding and nutrition. Academic Press, New York

Robbins CT, Van Soest PJ, Mautz WW, Moen AN (1975) Feed analysis and digestion with reference to white-tailed deer. J Wildl Manage 39: 67–79

SAS Institute Inc. (1988) SAS Institute, Cary, N.C.

Tyrrell HF, Moe PW (1975) Effect of intake on digestive efficiency. J Dairy Sci 58: 1151–1163

Uden P, Colucci PE, Van Soest PJ (1980) Investigation of chromium, cerium, and cobalt as markers in digesta: rate of passage studies. J Sci Food Agric 31: 625–632

Van Soest PJ (1994) Nutritional ecology of the ruminant. Cornell University Press, Ithaca, New York

Van Soest PJ, Fadel J, Sniffen CJ (1979) Discount factors for energy and protein in ruminant feeds. Proc Cornell Nutr Conf 1979: 63–75

Van Soest PJ, Foose T, Robertson JB (1983) Comparative digestive capacities of herbivores. Proc Cornell Nutr Conf 1983: 51–59

Weckerly FW (1993) Intersexual resource partitioning in black-tailed deer – a test of the body size hypothesis. J Wildl Manage 57: 475–494