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The relative roles of body size and feeding type on activity time of temperate ruminants

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Abstract Recently, there has been some critical testing of whether body size or feeding type (CS: concentrate selectors, IF: intermediate feeders, GR: grass-roughage eaters) is the most important determinant of physiological aspects of ruminant ecology, whereas little has been done on behavioral aspects like activity time. Different predictions regarding the relationships between activity time and body weight/feeding type were tested with activity time data from 18 temperate ruminants. Activity time decreased allometrically with increasing body weight, but there was also a tendency for an effect of feeding type. Exclusion of one statistically defined outlier (mountain goat) made the effect of feeding type highly significant. GR and CS were about equally active. Surprisingly, IF were more active than both GR and CS. The hypothesis is put forward that IF are more active than GR/CS due to their opportunistic use of high-quality forage of both types (concentrate and grass-roughage; on average better quality and hence shorter rumination time), though possible confounding effects of observation methods and varied behavior with respect to cover among CS, IF, and GR should also be evaluated.

Key words Activity patterns · Body size · Browsers · Grazers · Ruminants

Introduction

Most ecologists classify the diversity of ruminants into three feeding-type categories: concentrate selectors (CS/browsers), intermediate feeders (IF) and grass-roughage eaters (GR/grazers), following the pioneering work of Hofmann (1973, 1989). According to his classification, the major determinant of ruminant ecology is in their adaptations for consuming a bulk/roughage diet of primarily grasses (GR) versus a concentrate diet of browse/forbs/fruits (CS), with IF always intermediate. The CS strategy is characterized by a rapid turnover of easily digestible forage (cell solubles), the GR strategy by a slow turnover of plant material rich in cellulose (cell walls) (Hofmann 1989).

However, it has also long been recognized that body size is an important determinant of ruminant nutritional ecology, since nutrient requirements are allometrically related to body size ($W^{0.75}$), while rumen volume and gut capacity are isometric with body size (e.g., Bell 1971; Jarman 1974; Demment and Van Soest 1985; Illius and Gordon 1987; Owen-Smith 1988). Although there was an early report of a tendency for small species to be browsers and large species to be grazers (Case 1979), it was not until recently that critical empirical testing of these two hypotheses has been undertaken (Gordon and Illius 1994, 1996; Robbins et al. 1995). These studies conclude that, in comparison to body size, several of Hofmann's nutritional and physiological interpretations of anatomical differences amongst ruminants can play only a subtle role in determining the economics of diet selection (Gordon and Illius 1994, 1996; Robbins et al. 1995). No study has, however, tested these competing hypotheses for behavioral characteristics such as activity patterns.

Ruminants typically have a simple serial foraging-resting-foraging activity pattern. It is well documented that activity time of ruminants is influenced by a number of factors, like temperature (Belovsky 1981; Belovsky and Slade 1986; Beier and McCullough 1990; Schmitz 1991; Demarchi and Bunnell 1995), time of day/light conditions (Beier and McCullough 1990), and disturbance by predators and humans (Singer et al. 1991), insects (Espmark and Langvatn 1979) and dominant conspecifics (Wahlström 1994). However, a major determinant of rumination time, and hence time left for overall activity, is the quality of the food (e.g., Hanley 1982; Demment and Van Soest 1985; Cederlund 1989).

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Different predictions have been made concerning relationships between total time active (of which foraging time is the dominant component) and body weight among herbivores (reviewed in Table 1). These competing hypotheses were tested by comparing data from the literature on activity budgets of free-ranging ruminants in North America and Europe. Both Bunnell and Gillingham (1985) and Owen-Smith (1992) have plotted total time feeding for tropical and temperate ruminants and daylight foraging time for African ruminants, respectively, against body weight and marked out feeding types. Their analyses, however, were graphical with no test for different intercepts for feeding types (i.e., by the use of ANCOVA), and their conclusions were opposite with regard to both body size and feeding type (Table 1). I therefore also include a reanalysis of their data to validate their conclusions and establish if these relationships are similar for temperate and tropical ruminants.

Materials and methods

The literature was reviewed for studies measuring activity time of ruminants in North America and Europe. Preferentially, data from adult females recorded during June and July were used. Studies from rutting and winter periods were excluded. I regarded total active time as the time spent in a non-lying position.

Information about feeding types was retrieved from Hofmann (1989) and Loison et al. (1997). Data on body weights were taken from Loison et al. (1997), except for sheep (*Ovis aries*) (Sæther and Gordon 1994) and cattle (*Bos taurus*) (Mofareh et al. 1997). Data from Bunnell and Gillingham (1985, p 59) and Owen-Smith (1992, p 177) were extracted from graphs in the respective papers. Note that Bunnell and Gillingham (1985) used activity budgets (and not number of species) as replicates. Their data set includes a large number of citations of unpublished work which precludes rearrangement of the data. I therefore used their original data set. Note also that data from Bunnell and Gillingham (1985) were on total time feeding per day, and Owen-Smith (1992) on daylight foraging time.

Statistical analyses

Analyses were done with ANCOVA models. Within-model differences between feeding types were tested using Scheffe tests that adjust for multiple comparisons (Wilkinson et al. 1992). Activity time was recorded as percentage of total time, and was hence transformed before the analyses {arcsin [sqrt (activity time/100)]}. Since the relationship between activity and body weight is expected to be allometric (Illius and Gordon 1987), body weights were log-transformed. If there was more than one study for a species, the average activity reported was used. Each estimate was therefore weighted with the square root of the number of activity budgets per species. The main model was checked for assumptions of linearity, homogeneity of variance, and influential values were detected by the use of Cook's distances (Venables and Ripley 1994).

Results

Data from 18 temperate ruminant species were obtained (20–331 kg; 5 CS, 9 IF, 4 GR; Table 2). The ANCOVA model explained 54.8% of the variation. There was a significant negative allometric relationship between activity time and body weight (Fig. 1; F-ratio = 11.468, P = 0.004), but there was also a tendency for an effect of feeding type (F-ratio = 2.768, P = 0.097). Excluding mountain goat (*Oreamnos americanus*), which was identified as an outlier with a high Cook-d-value greatly strengthened the effect of both body weight (r^2 = 73.5, F-ratio = 22.111, P = 0.000) and feeding type (F-value = 6.955, P = 0.009). GR and CS were equally active (Scheffe, $P > 0.05$), but IF were more active than both GR and CS (Scheffe, $P < 0.05$).

Table 1 Summary of predictions made about the relationships between body size, feeding type and total time spent active in ruminants. Note that the two hypotheses concerning body size and feeding type can be combined in four different hypotheses, as has actually been done by some authors (*CS* concentrate selectors, *GR* grass-roughage eaters)

Prediction	Observation	Organisms/groups originally compared	Reference
Active time decrease with increasing body size	(a) Retention time of digesta in the alimentary tract positively correlated to body mass	African ruminants	Gordon and Illius 1994
	(b) Include lower-quality foods, longer rumination time	Large hindgut-fermenting and ruminant herbivores	Bell 1971; Jarman 1974; Demment and Van Soest 1985
Active time increase with increasing body size	(a) Large herbivores have a larger stomach/rumen, they could feed for a longer time	Large hindgut-fermenting and ruminant herbivores	Demment and Van Soest 1985; Hudson 1985; Owen-Smith 1988, 1992
	(b) Increased tolerance to extreme thermal regimes with increasing body size	Insects to ruminants	Belovsky and Slade 1986
CS more active than GR	(a) CS eat easily digestible forage, short rumination time	Ruminants	Hofmann 1989
	(b) CS more scattered forage (increased searching time)	African ruminants	Owen-Smith 1992
GR more active than CS	(a) CS more scattered forage (less time spent foraging)	Ruminants	Bunnell and Gillingham 1985
	(b) Rumen volume of GR larger than CS, need to forage for a longer time to fill gut		

Table 2 Body weight (*BW*), feeding type (*FT*; *CS* concentrate selectors, *IF* intermediate feeders, *GR* grass roughage eaters), sex (*M* male, *F* female, *B* both sexes), and total activity time (*AT*) of temperate ruminants recorded with different methods (*RT* radio-telemetry, *DO* direct observation)

Species	BW (g)	FT	AT (%)	Period	Sex	Method	Reference[1]
Alces alces	330 500	CS	43.25	Jun–Jul	F	RT	1
			42.08	May–Aug	B	RT	2
Antilocapra americana	46 844	IF	58.00	Jul–Aug	M	DO	3
Bison bison	274 750	GR	45.83	May–Sep	B	DO	4
Bos taurus	225 000	GR	47.00	Summer	F	RT	5
Capra aegagrus	20 125	IF	64.70	Aug–Sep	F	DO	6
Capreolus capreolus	26 730	CS	50.00	Jun–Jul	F	RT	7
			60.21	May–Aug	B	RT	8
			51.00	Jun–Jul	B	RT	9
Cervus canadensis	238 667	IF	53.50	Summer	F	RT	10
			43.26	Aug–Sep	B	DO	4
			53.00	Summer	B	DO	11
Cervus elaphus	107 500	IF	53.63	Jun–Jul	F	RT	12
Muntiacus reevesi	20 000	CS	66.81	May–Aug	B	RT	8
Odocoileus hemionus	56 000	CS	43.00	Summer	F	RT	5
			51.18	Aug–Sep	B	DO	4
			52.00	Summer	F	DO	13
Odocoileus virginianus	45 000	CS	58.50	Jun–Jul	F	RT	14
			42.78	Aug–Sep	B	DO	4
Oreamnos americanus	53 000	IF	45.00	Summer	F	DO	13
			43.80	Jul–Aug	B	DO	15
Ovibos moschatus	266 000	IF	53.40	Jul	B	DO	16
			48.10	Jun–Aug	F	DO	17
Ovis aries	50 000	GR	58.53	Jun–Sep	F	RT	18
Ovis canadensis	72 107	GR	37.50	Summer	F	RT	19
			53.68	May–Aug	B	DO	4
Rangifer tarandus	88 867	IF	70.10	Summer	B	DO	20
Rupicapra pyrenaica	24 000	IF	74.00	Jun–Jul	F	DO	21
Rupicapra rupicapra	26 000	IF	75.00	Summer	M	RT	22
			59.00	Jul–Aug	F	DO	23

1 Cederlund 1989, *2* Van Ballenberghe and Miquelle 1990, *3* Maher 1991 *4* Belovsky and Slade 1986, *5* Kie et al. 1991, *6* Nicholson and Husband 1992, *7* Cederlund 1981, *8* Chapman et al. 1993, *9* Jeppesen 1989, *10* Craighead et al. 1973, *11* Collins et al. 1978, *12* Georgii 1981, *13* Carl and Robbins 1988, *14* Beier and McCullough 1990, *15* Romeo and Lovari 1996, *16* Jingfors 1982, *17* Oakes et al. 1992, *18* Warren and Mysterud 1991, *19* Alderman et al. 1989, *20* Reimers 1980, *21* Pépin et al. 1991, *22* Hamr and Czakert 1986, *23* Pachlatko and Nievergelt 1985

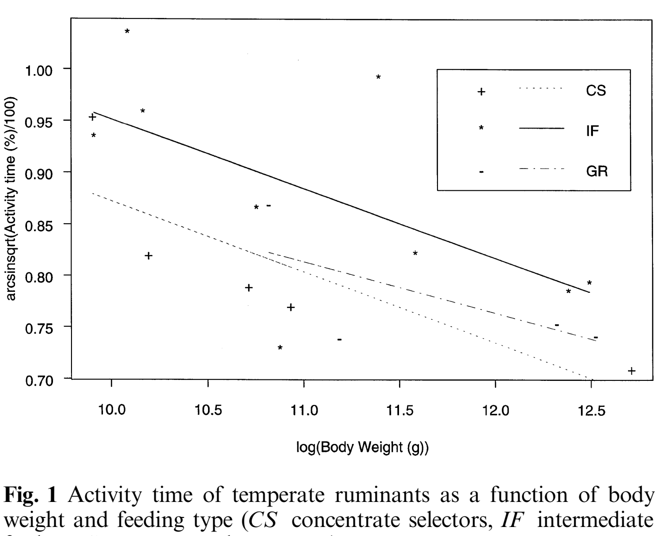

Fig. 1 Activity time of temperate ruminants as a function of body weight and feeding type (*CS* concentrate selectors, *IF* intermediate feeders, *GR* grass-roughage eaters)

Reanalysis of Bunnell and Gillingham's (1985) data

The reanalysis of data on both temperate and African ruminants from Bunnell and Gillingham (1985) showed that both body weight (ANCOVA, n = 187, r^2 = 0.205, F-ratio = 18.832, P = 0.000) and feeding type (F-ratio = 15.985, P = 0.000) influenced feeding time. Time spent feeding decreased allometrically with increasing body weight. GR were more active than CS (Scheffe, P = 0.000), and IF were more active than both CS (Scheffe, P = 0.046) and GR (Scheffe, P = 0.001). Average body weights of the 21 CS, 68 IF, and 98 GR were 148 kg (10–800), 122 kg (25–335) and 124 kg (20–600), respectively.

Reanalysis of Owen-Smith's (1992) data

The recalculation of data on African ruminants from Owen-Smith (1992) showed that daylight foraging time was influenced by body size (ANCOVA, n = 17, r^2 = 0.540, F-ratio = 13.096, P = 0.001), and tended also to be influenced by feeding type (F-ratio = 3.490, P = 0.061). However, total time spent feeding increased with increasing body weight. IF tended to forage more than GR (Scheffe, P = 0.062), while there was no difference between GR and CS (Scheffe, P = 0.679) or

IF and CS (Scheffe, $P = 0.268$). Average body weights of the 5 CS, 5 IF, and 7 GR were 218 kg (5–850), 35 kg (10–130) and 86 kg (12–145), respectively.

Discussion

Activity time of temperate ruminants decreased allometrically with increasing body size. Nutrient requirements are known to be allometrically related to body size ($W^{0.75}$), while rumen volume and gut capacity are isometric with body size (See Introduction). Demment and Van Soest (1985, p. 648) therefore suggested that with increasing body size, animals will expand their diets to include lower-quality foods. Alternatively, they could expand their feeding area and eat the same diet or feed longer. It has been shown that the size of the feeding area (home range) scales allometrically with body size (McNab 1963; Harestad and Bunnell 1979; Lindstedt et al. 1986; Swihart et al. 1988). Large African herbivores, however, have been observed to choose a lower-quality diet as well (Bell 1971; Jarman 1974) even if there is no reason for doing so unless compelled (Illius and Gordon 1987). The negative relationship between body size and activity suggests that larger ruminants in the temperate region indeed include a lower-quality diet leading to longer rumination time and hence less time spent active. The different result for data on daylight activity for African ruminants (Owen-Smith 1992) may be due to the observation that large herbivores feed more during the day (Bunnell and Gillingham 1985; Owen-Smith 1988).

There was an effect of feeding type on activity time, although not as equally pronounced as the effect of body weight. However, the effect of feeding type was not as predicted by Hofmann (1989). GR and CS were about equally active in the sample with only temperate ruminants (Fig. 1), whereas GR were more active than CS for the sample including tropical ruminants (data from Bunnell and Gillingham 1985). This supports a study that found that increased dietary browse levels increased retention time in both mule deer, bighorn sheep and elk (Baker and Hobbs 1987). High levels of lignin and secondary compounds like tannins (Robbins et al. 1987a, b; Hanley et al. 1992) make "concentrate" a misleading term of browse and herbs (Robbins et al. 1995). More surprisingly, IF were more active than both CS and GR (Fig. 1). I hypothesize that this might be due to the opportunistic use of high-quality forage of either kind (concentrate and grass-roughage) by IF, leading to an on average better-quality intake and hence shorter digestion times.

Most studies using radio-telemetry included 24-h activity patterns, whereas studies using different measures of direct observation (Altmann 1974) usually included only periods of daylight of various lengths. The ratio of day to night activity may vary with feeding type (Bunnell and Gillingham 1985). Perhaps even more important, differential behavior with respect to cover (Turner 1979) among CS, IF, and GR may be an important source of error when relying on direct observation for estimating activity time. More studies, especially on GR and IF using radio-telemetry are needed before firm conclusions can be drawn for general relationships between activity time and feeding type of temperate ruminants.

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