Retention Time and the Functional Response of Beavers

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Oikos, Vol. 71, No. 2. (Nov., 1994), pp. 207-214.

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Fryxell, J. M., Vamosi, S. M., Walton, R. A. and Doucet, C. M. 1994. Retention time and the functional response of beavers. – Oikos 71: 207–214.

We investigated the effects of interspecific variation in forage retention time on rates of food intake and energy gain by beavers. Ad libitum intake rates by beavers were a hyperbolic function of retention time in the digestive tract and a positive linear function of beaver live mass. Mean retention times of animals on mixed diets varied proportionately with diet composition. Daily intake rates by beavers provided with monospecific stands of trembling aspen or speckled alder saplings showed a monotonically decelerating (type 2) functional response to changes in sapling biomass density. Daily intake rates differed between these two forage species, such that alder with a long retention time produced lower consumption rates than aspen with a short retention time. Net rates of energy gain were also reduced when animals foraged on species with long retention time. Our results suggest that interspecific variation in retention time plays an important role in determining rates of dry matter intake and energy gain by beavers, which could influence the stability of beaver-vegetation interactions.

J. M. Fryxell, S. M. Vamosi, R. A. Walton and C. M. Doucet, Dept of Zoology, Univ. of Guelph, Guelph, Ontario, Canada N1G 2W1 (present address of CMD: Dept of Wildlife and Fisheries Sciences, Texas A & M Univ., College Station, TX 77843-2258, USA).

Theoretical considerations of predation rates in relation to changes in prey availability (the functional response) commonly include constraints due to handling time (Holling 1959, Lundberg and Åström 1990, Spalinger and Hobbs 1992). There are numerous possible components to handling time, including time investment in killing and dismembering prey, carrying prey to feeding sites, consumption, and digestion of prey. The behavioral components of handling time are readily measured, whereas digestion or retention time is more difficult to measure. Hence, ecologists often tend to overlook or not examine retention time as a constraint on feeding rates.

In the case of herbivores, however, retention time in the digestive tract can be of considerable magnitude, ranging from a matter of hours to several days (Warner 1981). There is also evidence that interspecific variation in retention time can influence herbivore diet preferences (Belovsky 1978, 1984, 1986, Doucet and Fryxell 1993). This suggests that digestive constraints could play a critical role in determining maximum rates of food consump-

tion and energy gain by herbivores. However, few studies have measured variation in retention times of naturally occurring forage species or their effect on rates of food consumption.

Beavers (*Castor canadensis*) feed on a wide variety of aquatic, herbaceous, and woody plant species. Previous observational studies (Jenkins 1975, 1980, Pinkowski 1983, Belovsky 1984, McGinley and Whitham 1985, Basey et al. 1988) and experimental studies (Basey et al. 1990, Fryxell and Doucet 1991, 1993, Fryxell 1992, Doucet and Fryxell 1993) suggest that diet preferences are adaptively related to interspecific and intraspecific variation in plant size, spatial distribution and nutritional characteristics. Of particular interest, Doucet and Fryxell (1993) recorded substantial variation in retention time among common forage species for beavers and showed that dietary preferences were at least partially influenced by retention time. Our objectives in this study were (1) to test whether retention time constrains ad libitum consumption rates by captive beavers, (2) to test whether

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mean retention times for mixed diets vary proportionately with diet composition, and (3) to test whether retention time influences rates of consumption and energy gain by beavers foraging under semi-natural conditions.

Methods

All experiments were conducted at the Wildlife Research Station in Algonquin Provincial Park, Ontario (48°30'N, 78°40'W). Beavers were livetrapped from local streams and ponds using Hancock traps and transferred either to 0.9-m³ cages (for retention time experiments) or 30 × 50 m enclosures (for functional response experiments). The cages had a wire mesh floor (2.5 cm²) allowing feces to fall onto a galvanized steel tray for collection. Beavers were acclimated to cages and enclosures for 1–2 weeks before experiments. During this time, and between trials, captive animals were maintained on an ad libitum mixed diet of woody and herbaceous plants, including trembling aspen (*Populus tremuloides*), raspberries (*Rubus idaeus*), beaked hazel (*Corylus cornuta*), and ferns. Drinking water was provided ad libitum at all times. Beavers were held in the cages for no more than 9 weeks.

Retention times and ad libitum intake rates were recorded for 16 beavers fed pure diets, 8 animals in 1991 and 8 animals in 1992. In 1991, retention times and intake rates were recorded for beavers fed 5 common forage species: trembling aspen, speckled alder (*Alnus rugosa*), red maple (*Acer rubrum*), raspberry, and white water lily (*Nymphea odorata*). In 1992, retention time and intake measurements were repeated for 8 animals fed the following species (in order of presentation): trembling aspen, speckled alder and red maple. Following these monospecific feeding trials in 1992, we recorded retention times for the same eight animals fed mixed diets of aspen and alder. In these mixed diet experiments, beavers were fed initially 1/3 or 2/3 the dry mass of aspen consumed in the pure diet trials and then presented with an ad libitum supply of alder. The resulting mixed diets ranged between 30–75% aspen, by dry mass.

Retention time was estimated using the method described in Doucet and Fryxell (1993). Before trials, beavers were fasted for 12 h. Animals were then provided with vegetation samples which had 100 soft plastic beads (Hama melt beads, produced in Denmark by Malte Haaning, DK-7900 Nykobing Mors) glued onto the leaves with a flour and water paste. The purpose of the beads was to provide an indigestible marker that would pass along with ingesta through the digestive tract. Feces were collected at 2-h intervals over the following 30–90 h. Feces were placed in a bucket of water, broken up, and the floating beads were then recovered from the surface. Although beavers are coprophagous (Buech 1984), this did not bias our estimates of retention time. After the first passage through the gut, beavers used their tails to catch

feces before reingestion. After the second passage, beavers simply let the feces fall through the mesh floor of the cages to a collection tray. We calculated the mean retention time by averaging over all times of bead emergence within 90 h of initial ingestion.

During retention time experiments, daily rates of ad libitum intake were estimated by subtracting the wet mass of rejected forage from the wet mass presented initially. This value was then converted to a dry matter equivalent by dividing by the wet-dry ratio appropriate to these woody plant species (1.74; Doucet and Fryxell 1993).

Functional response experiments were conducted during May–October 1992. Experimental enclosures were constructed in mixed deciduous-coniferous woodland with numerous mature trees (the lower trunks of which were wrapped in wire mesh to limit feeding to experimentally provided food). Beavers in each enclosure were housed in a plywood lodge beside a small, concrete-lined pond. Small saplings (2.0–3.0 cm diameter) were randomly positioned within the enclosures, with saplings pushed 15–25 cm into the ground to anchor them. Uneaten saplings were replaced every 5 d, to reduce the potential for changes in plant nutritional quality over time. Subsequent observations verified that beavers usually cut saplings and dragged them to the pond before consuming them, as they commonly do in natural settings.

A pair of yearling or adult beavers trapped from the same colony were used in each functional response trial. Beavers were presented with monospecific stands of aspen saplings during the first 8 trials and presented with alder saplings during the last 8 trials. Before each experimental trial, beavers were presented for 5–7 d with 6–10 saplings of the appropriate species, to acquaint them with the enclosures and the experimental procedures. A total of 16 beavers were used in feeding trials, with all animals tested with both forage species. Feeding trials were conducted for 1 d at each of 6 sapling densities (5, 10, 15, 20, 25, or 30 saplings per 0.15 ha), with sapling density randomly chosen every day. Such sapling densities are fairly typical of food availability recorded at our field study sites in Algonquin Park (Fryxell, unpubl.). The number and location of saplings removed during the preceding 24 h was recorded each morning. Sapling density and sapling consumption rates were converted to dry matter equivalents using an allometric regression (y = 0.017x²·⁵⁰, r² = 0.95, P < 0.001) for the dry mass of edible components (kg dry mass of leaves, twigs, and bark) in relation to stem diameter (in cm) (Fryxell and Doucet 1991).

We used an experimental design which could be analysed, in principle, using either univariate or multivariate (repeated measures) techniques. The repeated measures analysis allows subtle partitioning of variance between subject and treatment effects (Gurevitch and Chester 1986), but was unnecessary in our case because of strong treatment effects. Hence, we used simple univariate
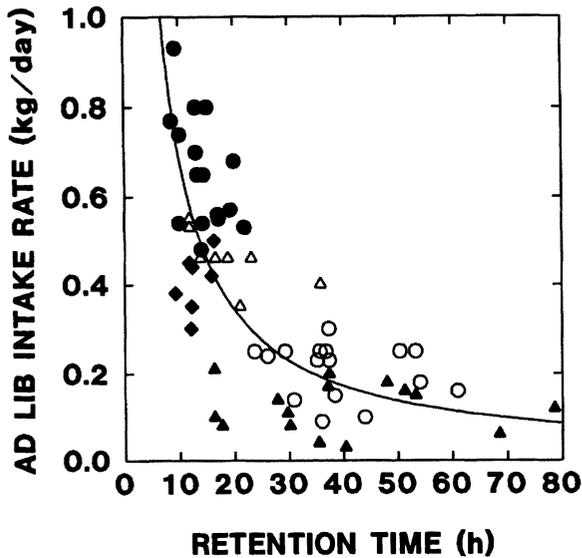
Fig. 1. Ad libitum rate of food intake by captive beavers in relation to variation in retention time for 5 species of common food plants (filled circles: trembling aspen, open circles: speckled alder, filled triangles: red maple, open triangles: white water lily, filled diamonds: wild raspberry). Fitted hyperbolic curve is given in Results.
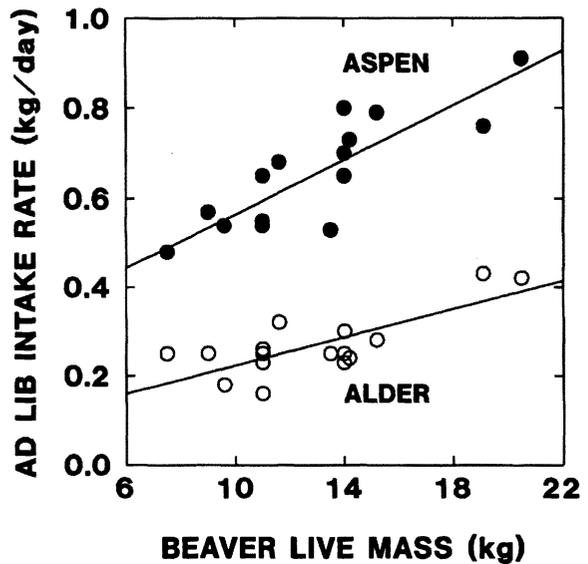

Fig. 2. Ad libitum rate of food intake by captive beavers in relation to live body mass of beavers (filled circles: trembling aspen, open circles: speckled alder). The same animals were tested with both diets. Regression equations are given in Results.

statistics and nonlinear parameter-fitting algorithms to evaluate our experimental results.

Results

Measurements conducted on 5 forage species suggest that both retention time and ad libitum food intake varied over nearly an order of magnitude, with intake inversely correlated with retention time (Fig. 1). A hyperbolic function ($y = 6.881/x$) explained 87.5% of the observed variation in ad libitum intake (in kg dry mass) in relation to retention time (in h). More detailed analysis of intake rates for animals fed pure diets (Fig. 2) suggested that body size of beavers was also positively related to daily consumption of aspen ($y = 0.262 + 0.030x$, $r^2 = 0.716$, $t = 5.942$, P < 0.001) and alder ($y = 0.064 + 0.016x$, $r^2 = 0.576$, $t = 4.357$, P $= 0.001$). Both of these patterns are consistent with the hypothesis that ad libitum intake rates are affected by digestive constraints, with retention time directly dictating the rate of clearance of ingesta and body mass affecting the gut capacity.

We tested whether mean retention time was an additive function of the proportion of dietary components by recording retention times for animals fed mixtures of alders and aspens (Fig. 3). Mean retention time declined linearly with increasing aspen content ($y = 43.687 - 31.382x$, $r^2 = 0.731$, $t = -9.038$, P < 0.001; higher order polynomial terms, P > 0.05), suggesting that the mean retention time for animals on a mixed diet can be estimated from the

retention times of each dietary component, weighted by their proportion in the diet. Given this additive relationship, one might expect that ad libitum intake by the animals on mixed diets should also follow the hyperbolic function in Fig. 1. Our results confirmed that ad libitum
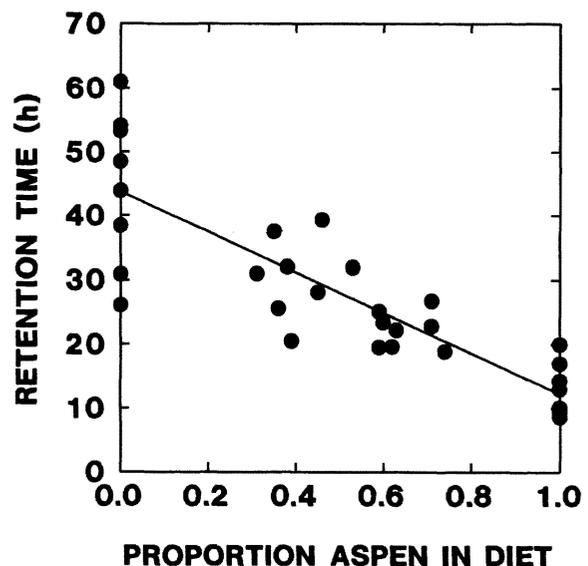

Fig. 3. Mean retention time in the alimentary tract by captive beavers fed varying proportions of trembling aspen and speckled alder. The same animals were tested with all three diets. Regression equation is given in Results.
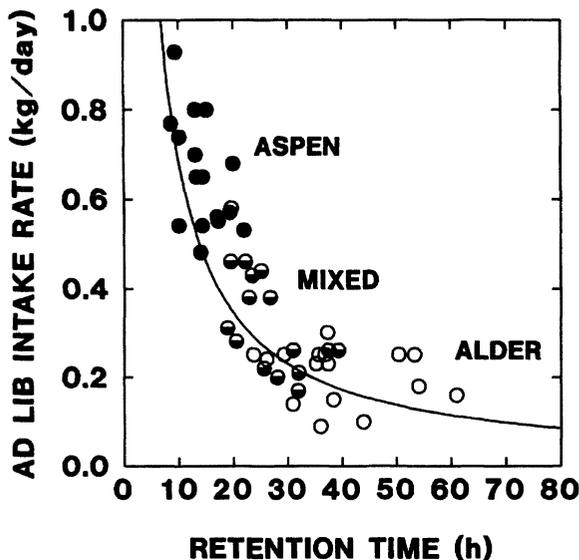
Fig. 4. Ad libitum rate of food intake by captive beavers in relation to variation in retention time for animals fed a pure diet of trembling aspen (filled circles), a pure diet of speckled alder (open circles), or a mixed diet of aspen and alder (half-filled circles). The same animals were tested with both diets. Data for the pure diets come from Fig. 1. Fitted hyperbolic curve is based on data in Fig. 1.

intake by animals on mixed diets was intermediate to that by animals on pure aspen or alder diets (Fig. 4). Moreover, the recorded values straddled the hyperbolic function determined from the multi-species data.

Our experimental studies showed that the retention time of aspen (mean = 14.42 h, SE = 0.98) was 37% that of alder (mean = 39.34 h, SE = 2.64). If retention time influences consumption rates when beavers must forage for their food (i.e. food availability is potentially limiting), then maximum consumption rates should be 2.7 times higher when beavers feed on aspens than when feeding on alders. Functional response curves should differ most strongly among forage species when resource availability is high (because handling time should be limiting), whereas functional responses should be similar among species when resource availability is low (because encounter rates should be limiting). Note that the latter prediction assumes that the area searched per unit time and the probability of cutting a sapling once encountered by a beaver are constant across species.

Daily rates of consumption by beavers varied substantially between aspen and alder treatments (Fig. 5; $F_{1,94} = 74.675$, $P < 0.001$). In both sets of single-species trials, consumption rates varied with sapling biomass density (aspen: $t = 3.253$, $P = 0.002$; alder: $t = 2.070$, $P = 0.044$). We therefore fit our empirical data to two functional response models, using a nonlinear parameter estimation algorithm (Wilkinson 1990). In the first model, Holling's (1959) disc equation ($y = ax/1 + ahx$), the consumption rate at low prey density is a linear function of

prey density, but independent of handling time. In the second model ($y = ax/h + ahx$), the consumption rate at low prey density is a linear function of the ratio of prey density to handling time. In both models, the maximum rate of consumption at high prey density should be proportionate to the reciprocal of handling time.

Both models fit the empirical data equally well (aspen: $r^2 = 0.879$; alder: $r^2 = 0.673$), which is not surprising because both models have similar form and are based on two parameters. However, the standard errors of encounter rate estimates were considerably smaller for the disc equation model (aspen: a = 0.762, SE = 0.294; alder: a = 0.214, SE = 0.141) than for the second model (aspen: a = 0.915, SE = 0.479; alder: a = 0.626, SE = 0.615). Both models yielded identical estimates of handling time (aspen: h = 1.201, SE = 0.183; alder: h = 2.922, SE = 1.017). On the basis of differences in the standard errors of fitted parameters, we conclude that the disc equation ($y = ax/1 + ahx$) provided the most reasonable description of our functional response data.

The estimates of handling time derived from the curve-fitting procedure differed by roughly the same ratio (aspen/alder = 1.20/2.92 = 0.41) as the experimentally derived estimates of retention time (aspen/alder = 14.42/39.34 = 0.37). The estimated maximum consumption rate of beavers foraging on aspens (1/1.20 = 0.84) was 2.5 times that of beavers foraging on alders (1/2.92 = 0.34), close to the value predicted by the retention time hypothesis. However, there was evidence that sapling encounter rates also varied among forage species (aspen =

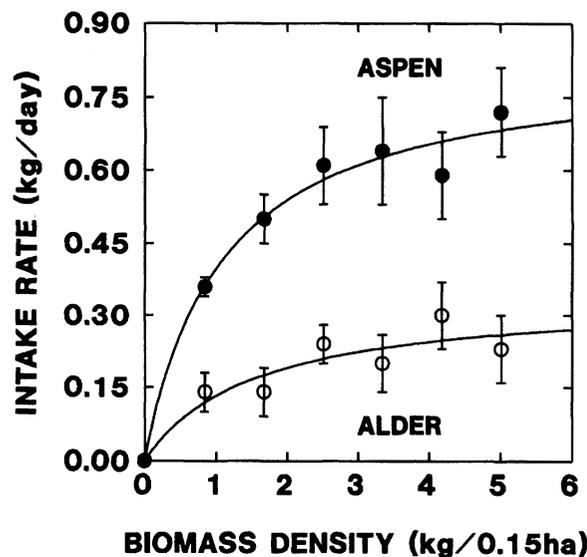Fig. 5. Daily rate of dry matter intake per beaver in relation to sapling biomass density in 0.15 ha enclosures. Beavers were presented with saplings of constant size of either trembling aspen (filled circles) or speckled alder (open circles). The same animals were tested with both diets. Vertical lines are 1 SE around the means. Fitted type-2 functional response curves are given in Results.
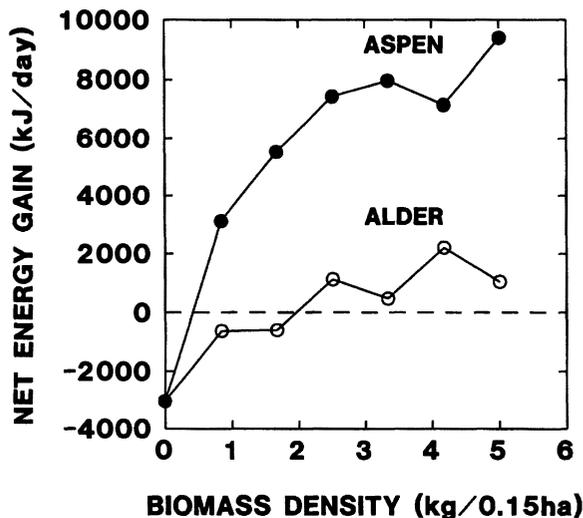
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Fig. 6. Net daily rate of energy intake per beaver in relation to sapling biomass density in 0.15 ha enclosures. Beavers were presented with saplings of constant size of either trembling aspen (filled circles) or speckled alder (open circles).

0.762; alder = 0.214). As a result, consumption rates did not converge for both treatments at low resource availability, contrary to our expectations.

Our previous studies of activity patterns of beavers (Fryxell and Doucet 1993) showed that foraging time (in h) was negatively related to resource availability (in kg dry mass per 0.15 ha) ($y = 3.660 - 0.13x$, $r^2 = 0.334$, $t = -3.248$, $P = 0.004$). Not surprisingly, the distance travelled by beavers (in km) was positively related to foraging time (in h) ($y = 0.355 + 0.502x$, $r^2 = 0.722$, $t = 7.389$, $P < 0.001$). Hence, energetic expenditures might be expected to be correlated negatively with resource availability, if movement costs exceed sedentary costs.

We did not directly estimate energetic expenditures in this study. However, other published studies suggest that the resting metabolic rate of beavers is 1.71 W/kg mass (MacArthur 1989), which is close to the value predicted by allometric relations (Kleiber 1975, see MacArthur 1989 for comparison). A recent review (Karasov 1992) suggests that vertebrate metabolic rates during periods of activity are roughly 4.1 times the resting metabolic rate. We used these parameter values to estimate energetic costs for beavers in relation to resource availability.

Body mass of beavers used during the functional response trials averaged 14.0 kg, implying a metabolic cost of 86.2 kJ/h while inactive and 353.4 kJ/h while active. Our previous nutritional studies showed that aspen and alder saplings provided 17.02 kJ of digestible energy per g ingested (Doucet and Fryxell 1993, Fryxell and Doucet 1993). We multiplied these estimates of energy content by functional response data to estimate gross energetic gain and subtracted energetic costs associated with foraging activity as a function of sapling availability to estimate net energetic gain.

Our results suggest that beavers feeding on monospecific stands of alder were barely able to meet their energetic demand at any resource density, whereas gains readily exceeded costs for beavers feeding on aspen saplings (Fig. 6). Hence, diet composition had a strong impact on rates of energy gain and the level of resource availability at which animals made the transition from negative to positive energy budgets.

Discussion

Our results were largely consistent with the hypothesis that digestive constraints influence rates of food intake by beavers under ecologically relevant conditions. Four predictions of the digestive contraint hypothesis were supported, at least in part.

First, daily rates of consumption by beavers presented with unlimited supplies of food were inversely related to interspecific variation in retention time in the gut. This relationship was hyperbolic, which is expected if maximum intake rate is a function of the volume of the stomach multiplied by the rate of turnover, the latter of which is the reciprocal of retention time.

Second, daily rates of consumption were positively related to body mass. Stomach volume is a constant proportion of body mass for a wide variety of vertebrate herbivores (Demment and Van Soest 1985, Justice and Smith 1992), so processing rates should increase linearly with herbivore mass, all other factors being equal.

Third, mean retention times for animals fed mixed diets were a linear function of the proportion of dietary components. This would be expected if retention time of each forage species is constant (i.e. unaffected by other items present concurrently in the digestive tract).

Fourth, consumption rates of beavers foraging under semi-natural conditions varied between forage species presented to study animals. Maximum consumption rates of beavers feeding on trembling aspen were 2.5 times those of beavers feeding on speckled alder, which scales closely with the difference in retention times between the two forage species. Hence, there was strong evidence that retention time influenced rates of resource use. However, there was also evidence that encounter rates by beavers were lower for speckled alder than for trembling aspen. It is possible that interspecific differences in encounter rates could relate to variation in olfactory signal strength, because we know that beavers largely detect prey on the basis of smell (Doucet et al. 1994). Alternatively, the probability of acceptance by beavers once a sapling has been encountered may differ between prey species, perhaps based on interspecific variation in nutritional characteristics.

Previous studies of mammalian herbivores suggest that retention time in the gut can be of considerable magnitude, often on the order of days (Warner 1981). There are relatively few studies in which variation in retention time

among indigenous plant species have been compared. The limited data that are available suggest considerable interspecific variation (e.g. Spalinger et al. 1986, Baker and Hobbs 1987). These findings are generally echoed by studies of domesticated ungulates (Alwash and Thomas 1971, Mertens 1973) and ungulates in zoos maintained on nonindigenous diets (reviews in Duncan et al. 1990, Illius and Gordon 1992).

Measurements of ad libitum intake in relation to retention time are even less common. Alwash and Thomas (1971) showed an inverse correlation between intake and retention time in domesticated sheep, and similar relations were recorded by Baker and Hobbs (1987) for mule deer, wapiti, and mountain sheep fed natural diets. Duncan et al. (1990) and Illius and Gordon (1992) reviewed data on ad libitum dry matter and energy intake by several bovid and equid species, showing that ad libitum intake was generally higher in equids than bovids, and these differences were related to shorter retention times by equids than bovids. Hence, our results are consistent with previous studies, showing that retention time can potentially constrain rates of consumption by herbivores, at least when herbivores are provided with unlimited food supplies.

Our estimate of mean retention time of aspen leaf, bark, and twig tissues was somewhat shorter than the 34 h reported in a previous study (Buech 1984). Buech's work was based on a single animal fed bark only. Hence, the recorded difference our results and Buech's results could stem either from substantial variability among individuals (Fig. 1) or differences in the nutritional characteristics of bark vs twig and leaf tissues.

Previous studies of some vertebrate herbivores and omnivores have suggested that the retention times of individual components can vary as a function of overall diet composition (Bines and Davey 1970, Milne and Bagley 1976, Ledoux et al. 1985, Baker and Hobbs 1987, Bjorndal 1991). However, this does not necessarily imply that mean retention time is nonlinearly related to diet composition. For example, Baker and Hobbs (1987) marked samples of grass and browse species and then measured retention times of each component as the proportion of browse in the diet was varied from 0 to 75%. Grasses showed increased retention time when eaten in conjunction with browse, but the converse occurred for browse. The net effect was a linear relation between mean retention time and the proportion of browse in the diet, similar to the relationships recorded in our study. This suggests that mean retention time can be treated as an additive process, if associative effects on different dietary components are compensatory. As we did not give each forage species its own marker in our retention time experiments, we have no means of knowing whether associative effects occurred. Nonetheless, our data do suggest that mean retention time by beavers can be treated as if it were an additive process.

Previous studies suggest that retention time is associated positively with digestible fibre content, lignin con-

tent, cell wall content, and cell wall thickness (Spalinger et al. 1986, Baker and Hobbs 1987). Many of these same factors have been shown to influence ad libitum consumption rates (e.g. Spalinger et al. 1986, 1988, Baker and Hobbs 1987, Hobbs 1990), presumably because of their effects on retention time in the digestive tract. Our previous nutritional studies indicated that alders are more fibrous and lignified than aspens (Doucet and Fryxell 1993). It therefore seems likely that the recorded differences in forage retention time and ad libitum intake by beavers are, at least partially, linked to interspecific variation in plant chemical composition.

New insights have emerged recently regarding the multiplicity of factors shaping herbivore functional responses (Lundberg and Åström 1990, Spalinger and Hobbs 1992). Much of this work has focussed on factors constraining short-term rates of food ingestion, such as trade-offs between mastication and bite rate and the influence of plant size and spacing on these mechanistic constraints (Lundberg and Åström 1990, Spalinger and Hobbs 1992). There is mounting experimental evidence that such factors are critical over short time horizons (Åström et al. 1990, Shipley and Spalinger 1992, Gross et al. 1993). Over longer time horizons, however, there are good reasons to expect that digestive constraints should also influence intake rates (Belovsky 1978, Owen-Smith and Novellie 1982, Hobbs and Swift 1988, Fryxell 1991, Owen-Smith 1993).

To our knowledge, no previous study has demonstrated that interspecific variation in retention time influences rates of consumption or energy gain by herbivores under natural or even semi-natural conditions (i.e. when animals have limited food supplies and animals must actively forage to meet their needs). Our work suggests that such variation substantially affected intake rates by beavers foraging under conditions approximating those in nature. Hence, adequate understanding of interspecific variation in processing rates, as well as other nutritional parameters, is critical for predicting patterns of diet composition and consumption rates by beavers feeding in complex vegetation communities (Doucet and Fryxell 1993, Fryxell and Doucet 1993). In view of the generality of the underlying mechanisms, we would be surprised if processing constraints were not ecologically relevant to other terrestrial herbivores as well.

Interspecific variation in processing and consumption rates could have important implications for the long-term dynamics of plant-herbivore systems. A critical determinant of local stability in many analytical models of consumer-resource interactions is the threshold resource density required for consumers to just replace themselves each generation (the consumer zero isocline) relative to the resource zero isocline (Rosenzweig and MacArthur 1963, May 1974, Tanner 1975, Caughley 1976). Factors that shift the consumer zero isocline to higher resource levels tend to have a stabilizing effect (Caughley 1976) as a result of increased density-dependence in resource mortality rates due to intraspecific competition and decreased

inverse density-dependence due to consumption (the latter being implicit in decelerating functional responses). Hence, beaver populations living in ecosystems predominated by relatively unprofitable plants, such as alders, should be more stable than populations of beavers in ecosystems predominated by highly profitable plants, such as aspens.

A similar prediction should apply to more complex ecosystems with a mixture of plants of varying profitability. Beavers have been shown to select adaptively among woody plants on the basis of energetic profitability (Doucet and Fryxell 1993, Fryxell and Doucet 1993). Analytical models incorporating such adaptive diet selection by consumers suggest that local stability can only arise if the lowest-ranking resources are barely sufficient for individual consumers to persist (Fryxell and Lundberg 1994), as was apparently the case for beavers fed alders (Fig. 6). This suggests that beaver populations in areas predominated by mixtures of profitable and unprofitable plants, such as aspens and alders, should tend to be more stable than beaver populations in areas dominated by aspens, provided that other key plant parameters, such as recruitment rates or carrying capacities of plants, remain the same.

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