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Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment

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Abstract Optimality models of food selection by herbivores assume that individuals are capable of assessing forage value, either directly through the currency used in the model or indirectly through other variables correlated with the currency. Although energy and protein are the two currencies most often used, controversy exists regarding their respective influence on food choice. Part of the debate is due to the difficulty of teasing apart these two nutrients, which are closely correlated in most natural forages. Here we offer a test of the assumption that energy and protein contents of the forage are both currencies that large mammalian herbivores can use when selecting their food. We observed feeding behavior of 47 wild white-tailed deer (*Odocoileus virginianus*) during winter while individuals were presented with four experimental foods representing two levels of energy and protein (dry matter digestibility: 40–50%; crude protein: 12–16%). Using experimental foods allowed us to separate the influences of energy and protein and clearly distinguish between the roles of these two nutrients. Deer discriminated between foods through partial selection, and selected diets higher in energy but lower in protein. The observed choices appeared consistent with physiological needs of deer wintering at the study site, where digestible energy was in short supply in the natural environment while protein was probably not. Results are in good agreement with recent findings on domesticated ruminants. They support a basic assumption of optimality models of food selection that use energy and/or protein as a currency, although the physiological mechanisms behind the food selection process remain unclear. We urge students of food selection by herbivores to replicate our experiment with other foods and/or in other circumstances before more general conclusions are drawn.

Key words Energy · Herbivore-plant interactions · Ruminants · *Odocoileus virginianus* · Protein

Introduction

The trophic relationship between plants and large mammalian herbivores is an area of intense empirical and theoretical investigation (Stephens and Krebs 1986; Hughes 1990; Robbins 1993). Accordingly, the behavior and ecology literature is now replete with observations on food habits of large herbivores, suggesting correlations between diet preferences and a list of food constituents. Proof of causality in food selection studies, however, cannot be inferred from correlations alone (Romesburg 1981). The focus has thus recently shifted from purely descriptive to analytical (Robbins 1993).

Diet selection is often approached within the context of an optimal foraging problem (Stephens and Krebs 1986). Two basic assumptions with such an approach are that (1) forage value can be measured in one or several currencies of importance to the herbivore, and (2) the herbivore is capable of assessing forage value, either directly through the chosen currency or indirectly through other variables correlated with the currency (Stephens 1990; Hanley 1997). Digestible energy and protein are the two currencies that clearly appear to be most limiting for large herbivores (Robbins 1993). Hence most models of food selection use one or both of

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these currencies (Pyke 1984; Stephens and Krebs 1986). However, because energy and protein contents are closely correlated in most natural forages (Westoby 1974; Owen-Smith and Novellie 1982; Robbins 1993), controversy exists regarding their relative role in the food selection process (Langvatn and Hanley 1993; Wilmshurst and Fryxell 1995). When choosing their food, do herbivores assess its value according to its energy content, protein content, or both? Recent results from domesticated species suggest that herbivores have the ability to select their food according to both its energy and protein contents, and tend to maximize or minimize the ingestion of these nutrients according to their needs (Hou et al. 1991; Kyriazakis and Oldham 1993; Provenza et al. 1996; Wang and Provenza 1996; Villalba and Provenza 1997). Unfortunately, tests performed on wild species have been much more difficult to interpret (e.g., Langvatn and Hanley 1993; Wilmshurst and Fryxell 1995).

Here we go back to the basics of the food selection theory to offer a simple test of the assumption that protein and energy contents of the forage (or some of their correlates) are two currencies that wild large mammalian herbivores can use when selecting their food. We performed choice experiments with free-living white-tailed deer, *Odocoileus virginianus*, provided with a range of experimental feeds of manipulated protein and digestible energy contents. Using experimental foods allowed us to bypass the protein-energy correlation that usually exists in plants, thus offering the opportunity to clearly distinguish between the roles of these two currencies. To our knowledge, this approach has never been used with large herbivores studied in the wild.

Our design allowed us to first detect whether there was an over-all difference among four foods offered for deer choice. Based on these results, we then picked pairs of rations to test specific hypotheses about differences between diets. We made three predictions: (1) if deer select their food according to its energy content only (or one of its correlates), we should see no difference in consumption of isoenergetic foods differing in protein density; (2) if protein (or one of its correlates) is the currency used in food choice, we should observe an equal consumption of isoproteic foods of varying energy content; and (3) if both currencies (or some of their correlates) are used by individuals when selecting their food, then energy and protein content of the experimental foods should both affect choice of deer.

Methods

Study area and animals

We conducted the research in the Pohénégamook deer yard, located 200 km east of Québec City, Canada. During the study (15 January–5 April 1996) this 25-km^2 wintering area supported a population of *c.* 520 deer (A. Dumont, unpublished work). Potvin et al. (1981) give a description of the physiography and the vegetation of the study area.

Experimental diets

Experimental diets consisted of commercial feeds (Table 1) formed into 0.3 × 1-cm cylindrical pellets. Ingredients were chosen to provide 2 levels of energy and protein. We named experimental foods according to relative energy and protein levels: Ep (high energy, low protein), ep (low energy, low protein), EP (high energy, high protein), and eP (low energy, high protein).

To obtain a detailed description of the chemical composition of our experimental foods, samples were ground to pass through a 20-mesh screen in a Wiley Mill and analyzed for energy, nitrogen, fiber and total phenolic contents. Gross energy and total nitrogen contents were determined with an adiabatic calorimeter (Parr, Model 1241) and an automated Macro-Kjehldahl analyzer (Association of Official Analytical Chemists 1984), respectively. The crude protein content (CP) was estimated by multiplying the nitrogen content by 6.25. Fiber content (NDF, neutral detergent fiber; ADF, acid detergent fiber; and ADL, acid detergent lignin) was determined using the detergent method (Goering and Van Soest 1970; Gauthier et al. 1991). We used sodium sulfite in forage analyses. Ash content was determined by incinerating 1-g samples for 3 h at 500°C. All analyses were done in duplicate using 0.7 g samples or in triplicate whenever a difference of more than 2% was found between the first two samples. The concentration of total phenolic compounds was obtained by colorimetric method using the Folin-Ciocalteu reagent (Marigo 1973; Sauvesty et al. 1991). Results are expressed in percentage of total phenolic compounds in reference to a gallic acid standard. Determination of nitrogen, NDF, ADF, ADL and phenols was based on the dry organic mass of the sample. The percent dry matter digestibility (DMD) of each ration was calculated using summative equations of Robbins et al. (1987) and assuming zero values for the protein-precipitating capacity of tannins in the rations. The energy digestibility coefficient was assumed to equal DMD (Robbins 1993). Chemical composition of our experimental diets is summarized in Table 2. Levels of energy and protein were well within the range of what white-tailed deer consume in the wild on a year-round basis, but exceeded levels found in forage consumed by Pohénégamook deer during the winter period (A. Dumont, unpublished work; see also Discussion).

Choice experiments

Twelve experimental sites, regularly distributed across the deer yard, were first selected according to signs of deer presence. Distance between sites was ⩾ 1 km in order to minimize the likelihood that some individuals attended several of them. We placed a

Table 1 Percentage of the different ingredients used to prepare four experimental feeds offered to white-tailed deer in choice experiments performed at Pohénégamook, Québec, 1996

Ingredients	Experimental diets			
	Ep	ep	EP	eP
Oat grain	17.3	43.3	17.2	30.3
Sawdust[a]	26.0	35.0	26.0	35.0
Beet pulp	5.8	5.8	5.8	5.8
Ground soy bean (48%)	7.0	7.0	19.0	20.0
Ground yellow corn grain	29.0	6.0	23.1	6.0
Barley feed grain	6.0	6.0	6.0	6.0
Cane molasse	5.5	5.5	5.5	5.5
Monoammonium phosphate	1.3	1.3	1.3	1.3
Binding agent[b]	0.5	0.5	0.5	0.5
Calcium carbonate	0.8	0.8	0.8	0.8
Salt	0.8	0.8	0.8	0.8

[a] Sawdust composed of several species of deciduous hardwoods, including mainly Birch (*Betula* sp.) and Maple (*Acer* sp.)
[b] Lignosulfonate

Table 2 Composition (100% dry matter basis) of the four experimental feeds used in feeding trials performed on free-living white-tailed deer wintering at Pohénégamook, Québec, 1996 (*CP* crude protein, *NDF* neutral detergent fiber, *ADL* acid detergent lignin, *DMD* dry matter digestibility, *GE* gross energy (kcal/g), *DE* digestible energy, kcal/g)

Constituents	Experimental diets			
	Ep	ep	EP	eP
CP	11.89	11.52	15.91	16.33
NDF	34.82	46.68	33.77	44.96
ADF	23.10	32.42	23.48	32.55
ADL	25.64	28.20	23.53	26.28
DMD	51.61	41.19	52.87	43.33
GE	3.93	4.01	3.93	4.03
DE	2.03	1.65	2.08	1.74
Total phenolics	0.43	0.57	0.40	0.50
Ash	5.32	6.41	6.30	6.32

feeding station at each site on 15 January. For 3 weeks, we habituated animals to use the stations by filling feeders every day with 2 kg of a baby beef ration (16% protein, 68% digestible energy; Deschênes and Landry Inc.). We subsequently chose the seven sites that were more often visited by deer for detailed observation of feeding behavior. We conducted three successive experiments at these seven sites.

Experiment 1

From 7 February to 19 March, individuals were presented virtually every day, at each site, with four samples of each experimental ration (800 g each). Feeds were presented simultaneously to animals in cafeteria feeding trials. We used feeders made of a wooden box (length: 40 cm, width: 16 cm, height: 10 cm), divided into four adjacent partitions of equal size (10 × 16 × 10 cm). Feeders were placed 1 m above ground. A wire mesh screen surrounded three sides of the feeder so that a deer could only reach feeds by approaching the feeder by its largest, front side. Feeder design thus ensured that observed individuals had the opportunity to sample all four rations during a feeding trial. Each feed was randomly assigned to a partition at the beginning of a test period.

We observed animals from elevated platforms, at a distance of 10–70 m, between 0800 and 1800 hours. Deer were recognized individually, either from radio-collars and ear tags, or from naturally distinctive markings (mainly shape and color of the head or presence of scars). Observed animals were classified into three categories: fawns (easily recognized because of their small size), males (large size, presence of antler scars) and females. Yearling males were roughly the same size as does and were often difficult to distinguish from them. We thus classified all yearling males as "females" for data analysis.

During each feeding trial, we measured individual behavior using a continuous recording technique (Martin and Bateson 1993). Two behavioral categories were used: "Feeding" when the focal animal was actually eating pellets, and "Break" when it had its head up, processing the food or being alert. The first category was further divided into four sub-categories according to which partition the animal was using (partitions 1 and 4 were on the sides and partitions 2 and 3 were in the middle). We set the maximum duration of focal sampling at 12 min because Ozoga and Verme (1982) showed that the mean duration of undisturbed visits to feeders by supplementally fed white-tailed deer was $\leqslant$ 10 min in January–February. We stopped observations before 12 min if the focal individual consumed all the feed in a partition, in order to avoid "non-preferred" foods being eaten simply because "preferred" foods were no longer available. We also stopped observations when a second individual began to eat at the feeder, because this event made some of the partitions no longer available to the focal deer.

Observers dictated the behavioral events into a portable tape recorder. The sequence and duration of events were subsequently analyzed with "The Observer" software (Noldus 1991). The between-observer reliability for each category of behavior was $\geqslant 95\%$. After each trial, the food that remained in each partition was collected to be later weighed (± 1 g). Data of a typical trial therefore consisted of the identity of the focal individual and, for each of four partition/diet combinations, the number of feeding bouts, the time spent feeding (s), and the food intake (g).

Experiment 2

Because behavioral data often exhibit considerable variability, we wished to test the repeatability of our results before going further in our analysis of preferences. We thus presented individuals with only two rations, those most and least preferred in experiment 1 (Ep and eP, respectively). We followed the same procedure as in experiment 1, except that we used only the two central partitions of the feeders. Each food was randomly assigned to a partition at the beginning of the feeding trial. We predicted that Ep would be more consumed than eP. Experiment 2 lasted from 25 to 30 March.

Experiment 3

The results of the two previous experiments consistently showed that individuals preferred the diets higher in digestible energy. Results also suggested that animals preferred the feeds with lower protein content. Our third experiment thus specifically tested the hypothesis that individuals, when offered a choice between isocaloric diets differing in protein content, would prefer the food with less protein. We thus offered Ep and EP to deer in feeders, following the same procedure as in experiment 2. The experiment lasted from 1 to 5 April.

Statistical analyses

Two factors complicated the data analysis. First, data on the mass of ingested food was lacking for *c*. one-sixth of the trials, because we did not replace rations when a deer fed for only a few seconds before leaving. In such a case, the observer remained hidden waiting for a second individual to come. When we observed feeding behavior of a second individual, feeding times for each partition/feed combination were recorded but food intake could not be measured. We thus regressed feeding time on food intake for all ration/feed combinations for which we had data on both variables (all three experiments combined). This allowed us to evaluate whether the two variables were correlated enough to use feeding time as a reliable index of food consumption. Since food intake rate depends on incisor breadth (Illius and Gordon 1987), independent regressions were performed for the three classes of individuals (fawns, females, and males). Linear regressions (Fig. 1) showed good correlations between feeding time and food intake (inclusion of polynomial factors did not significantly improve the variation explained). Subsequent analyses were thus performed on feeding time alone, including those trials where ingested food mass could not be precisely determined.

Second, for the results of our experiment to be meaningful, we were concerned that analyses should be performed only on those feeding trials in which total feeding time was large enough to be compatible with the scale at which deer actually performed their choices. Unfortunately, to our knowledge no data exist as to the minimum time scale at which deer preferences can reliably be measured. We thus decided arbitrarily to keep for our analyses only the tests in which individuals ingested $\geqslant$ one-tenth of their daily energy requirements. We estimated daily energy requirements R (kJ/day) in mid-winter according to the following equation (Schmitz 1990):

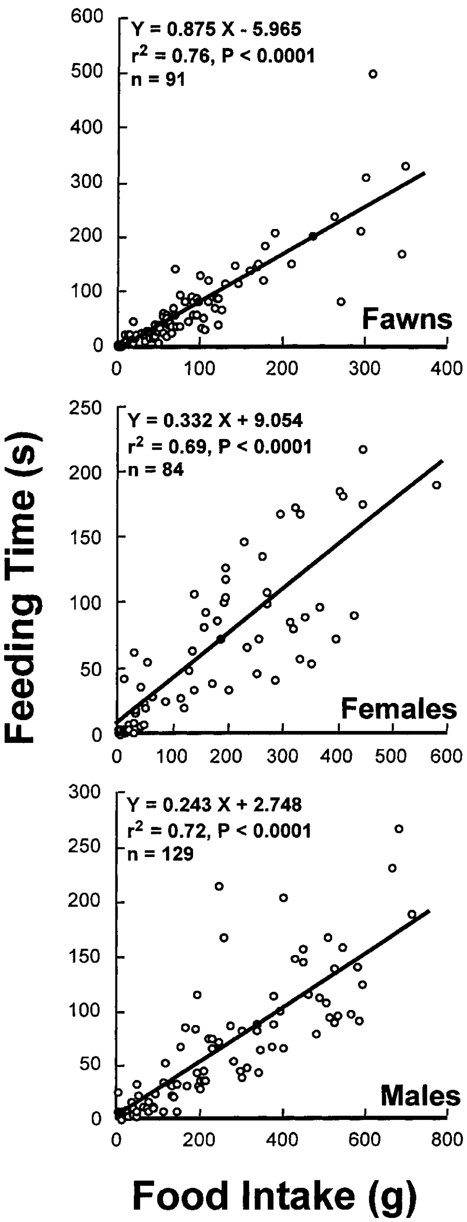

Fig. 1 Relationship between food intake and feeding time in white-tailed deer feeding on experimental rations. Each *point* represents a partition/feed combination for a given feeding trial (*Females* includes yearling males)

$R = 605.7\ W^{0.75}$,

where W is body mass. We used body masses of 30, 60 and 85 kg for fawns, females and males, respectively (C. Bois et al., unpublished work), which yielded respective daily requirements of 7,764, 13,058 and 16,956 kJ/day. The experimental foods contained on average 7,838 kJ of digestible energy per kg. The respective total pelleted feed requirements for individuals were thus estimated at 991, 1,666 and 2,163 g/day. Fitting one-tenth of these values in the regression equations relating feeding time to ingested biomass (Fig. 1) gave minimum feeding times of 81, 64 and 55 s for fawns, females and males, respectively, for a trial to be included in the analyses.

Trials were sometimes performed several times on the same individual. We averaged data across trials when these replicates were performed with the same partition/feed combinations. When a given individual was observed more than once, but replicates were performed with different partition/feed combinations, we considered these data as independent in further analyses. Sample sizes (number of tests performed, number of tests included in the analyses, and number of individuals) are given for each experiment in Table 3.

In experiment 1, a given feed consumption was possibly affected by two factors; its composition and its position in the feeder. Furthermore, comparing consumption times across trials necessitated that raw data were first transformed into percentages, since total feeding time varied between trials. This made consumption of a diet dependent on the consumption of the others. As a result, the appropriate analysis for testing the existence of preferences was a nonparametric method used for randomized blocks; the Friedman 2-way analysis of variance (Siegel 1956). In our design, the first factor was diet composition, while the other one (position in the feeder) represented the blocks in the experiment. Multiple comparisons among pairs of means, which would allow post-hoc analysis of the origin of the difference between diets, are not possible after a Friedman analysis of variance. However, sample sizes were roughly the same for the four diets in each of the four blocks of the experiment (Table 4), which allowed us to use unpaired Wilcoxon two-sample tests for multiple comparisons (Sokal and Rohlf 1981).

In experiments 2 and 3, comparison of consumption times across feeds were performed with Wilcoxon tests (one-tailed), after averaging data when several replicates were performed on the same individual. Length and number of foraging bouts were compared between feeds (one-tailed paired *t*-tests) as another mean of detecting preferences.

All statistical analyses were performed on SAS version 6 (SAS Institute 1990) or JMP version 3.0 (SAS Institute 1994). Values are means ± SD.

Table 3 Sample size (number of tests and number of individuals) for three sets of feeding trials performed on white-tailed deer wintering at Pohénégamook, Québec, 1996

	Exp. 1	Exp. 2	Exp. 3
Number of tests performed	125	28	18
Number of tests analyzed[a]	77	27	17
Number of individuals:			
Fawns (number of tests)	12 (28)	5 (7)	4 (4)
Females (number of tests)	9 (21)	6 (8)	3 (3)
Males (number of tests)	11 (28)	7 (12)	6 (10)
Total[b]	32	18	13

[a] See the Methods section for a full description of the criteria used to exclude some of the tests from the statistical analyses

[b] Four individuals were common to all three experiments. 4, 2 and 2 other individuals were observed in both experiments 1 and 2, 1 and 3, and 2 and 3, respectively

Table 4 Number of times each partition/feed combination was offered to white-tailed deer in the 77 feeding choice tests involved in experiment 1. The last row indicates *G*-values testing for an equal frequency of occurence of feeds in each of the four partitions

	Experimental diets				Total
	Ep	ep	EP	eP	
Partition 1	19	20	21	17	77
Partition 2	22	20	18	17	77
Partition 3	18	20	20	19	77
Partition 4	19	17	18	24	77
G-values	0.54[a]	0.17[a]	0.34[a]	1.64[a]	–

[a] $P > 0.05$

Results

Experiment 1

Feeding trials lasted on average 7 min 40 s (± 107 s), whereas total feeding time averaged 3 min 10 s ± 71 s (41.3% of the feeding trial length). Focal animals consumed $\geqslant$ three rations in 73% of the trials ($n = 77$). They fed on a single ration in only 3% of the tests. Deer food choices thus did not follow a "zero-one" rule, indicating that any significant food selection could only be a partial selection. Deer spent less time feeding in lateral partitions (Fig. 2). Mean consumption times were 8.6%, 41.8%, 38.7% and 9.6% for partitions 1–4, respectively.

The comparison of the consumption times (%) across all partition/feed combinations (Fig. 2) showed a significant difference in the proportion of time animals spent consuming the different experimental rations (Table 5). Within each block of the experiment (partitions of the feeders), deer preferred the two rations with greater digestible energy content (Ep and EP) over the two diets containing less energy (ep and eP). Consumption times of the two high-energy feeds (pooled for analysis) were significantly higher than consumption times of the two low-energy ones (30.2 ± 19.8% versus 19.8 ± 24.5%; Wilcoxon $z = -2.675$, $P = 0.008$). The ranks of preference of feeds of similar energy content but different protein level (Ep vs. EP and ep vs. eP) suggested that diets lower in protein tended to be preferred (Table 5). Post hoc analysis, however, demonstrated no significant difference in mean consumption times according to protein content of the food (Ep versus EP: 31.7 ± 31.2% versus 28.6 ± 31.7%, Wilcoxon $z = -0.689$, $P = 0.245$; ep versus eP: 24.0 ± 28.2% versus 15.7 ± 19.4%, Wilcoxon $z = -1.538$, $P = 0.062$).

The generally higher ranking of foods of highest energy content did persist when we analyzed separately the data from fawns, females, and males (Table 5). Differences between feeds, however, were no longer significant. The fact that significant results emerged only when the analysis was performed on the whole data set reflects the large between-trial variability in food selection patterns, which probably masked preferences when sample size was reduced. Because no power analyses exist for the Friedman analysis of variance (Siegel 1956), we cannot calculate what minimum sample size was necessary before significant differences could be detected.

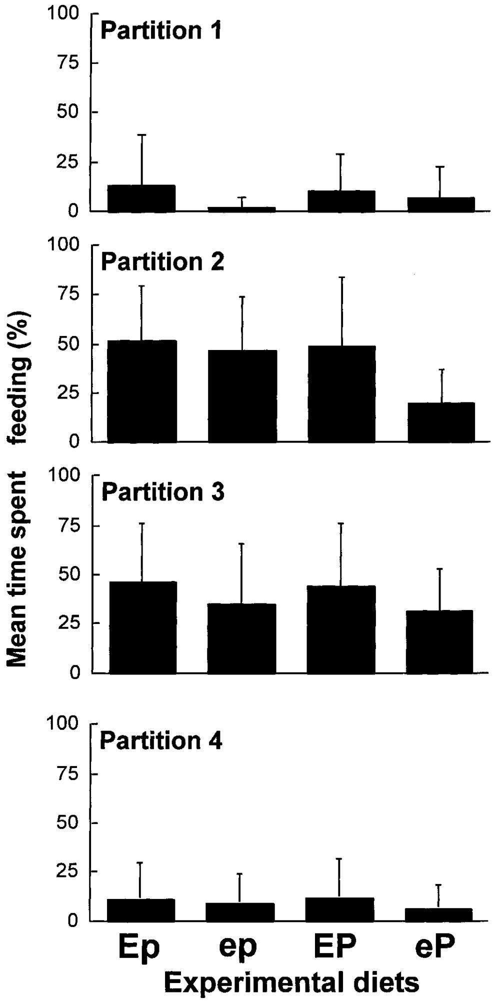

Fig. 2 Mean percentage (± SD) of time spent feeding in each partition/feed combination. Percentages were first calculated within each of 77 feeding trials, and then averaged across trials for each partition/feed combination

Table 5 Preference ranks of four experimental feeds offered to free-living white-tailed deer in feeders composed of four partitions. Ranks are given for each of three classes of individuals and for all individuals pooled together. Last row indicates the outcome of Friedman 2-way analyses of variance testing for the existence of consistent preferences among the four experimental diets

	Fawns				Females				Males				All individuals			
	Ep	ep	EP	eP	Ep	ep	EP	eP	Ep	ep	EP	eP	Ep	ep	EP	eP
Partition 1	1	4	2	3	4	3	1	2	1	4	3	2	1	4	2	3
Partition 2	1	3	2	4	3	2	1	4	2	1	3	4	1	3	2	4
Partition 3	1	3	4	2	2	3	1	4	2	4	1	3	1	3	2	4
Partition 4	3	4	1	2	1	2	4	3	3	1	2	4	2	3	1	4
Mean rank	1.5	3.5	2.25	2.75	2.5	2.5	1.75	3.25	2	2.5	2.25	3.25	1.25	3.25	1.75	3.75
Fried. ANOVA	$X_r^2 = 5.1$, $P = 0.190$				$X_r^2 = 2.7$, $P = 0.508$				$X_r^2 = 2.1$, $P = 0.649$				$X_r^2 = 11.1$, $P = 0.003$			

Table 6 Time spent feeding, number of feeding bouts, and bout duration recorded in two white-tailed deer choice experiments where individuals were presented with 2 feeds of varying energy or protein level, Pohénégamook, Québec, 1996

	Experiment 2		Experiment 3	
	Ep	eP	Ep	EP
Time spent feeding (%) (Wicoxon test)[a]	64.2 ± 26.7 ($z = -1.85$, $P = 0.032$)	35.8 ± 26.7	67.5 ± 25.5 ($z = -1.99$, $P = 0.023$)	32.5 ± 25.5
Mean number of bouts (t-test)[b]	9.30 ± 5.6 ($t = 1.53$, $P = 0.072$)	6.85 ± 5.7	12.44 ± 6.5 ($t = 2.95$, $P < 0.01$)	6.03 ± 3.4
Mean bout length (s) (t-test)[b]	11.22 ± 8.0 ($t = 1.07$, $P = 0.151$)	8.01 ± 5.9	10.38 ± 6.9 ($t = 0.082$, $P = 0.468$)	10.23 ± 8.8
Sample size	18	18	13	13

[a] Wilcoxon matched-pairs signed-ranks test. P-values are one-tailed
[b] One-tailed paired t-test

Experiment 2

The mean length of feeding trials was 6 min 57 s (±191 s) and total feeding time averaged 2 min 17 s (±100 s) (32.8% of feeding trial length). Animals used both partitions in 88.9% of the tests ($n = 27$). They spent a significantly higher percentage of time eating food Ep than eP, showing that the major trend observed in experiment 1 was repeatable. The mean number of feeding bouts, however, did not differ across treatments, nor did the mean length of feeding bouts (Table 6).

Experiment 3

The mean length of feeding trials was 7 min 20 s (±112 s) whereas the average feeding time per meal was 2 min 43 s (±74 s) (37.0% of feeding trial length). Deer used both partitions in 94.1% of the tests ($n = 17$). The mean percentage of time spent eating was significantly higher for the food containing less protein (Ep), and deer performed significantly more feeding bouts on this food (Table 6). Mean length of feeding bouts, however, did not significantly differ according to the food composition (Table 6). This experiment confirmed that animals, when offered the choice between isocaloric rations, preferred the food with less protein.

Discussion

Four main patterns emerged from our experiments: (1) deer were able to discriminate among experimental foods; (2) they consumed more of the foods higher in digestible energy; (3) at each given level of digestible energy, they consumed more of the foods lower in crude protein; and (4) the patterns of food selection that we observed were not absolute but partial.

First, we place our results within the natural context of the experiment, that is the energy and protein needs of deer during winter and the availability of these nutrients in natural forages at the same period. Energy available to white-tailed deer is at its lowest point in the annual cycle during the winter season (Moen 1976). During winter, deer living at northern latitudes have to maintain a positive energy balance in spite of their movements in deep snow (Moen 1976; Parker et al. 1984) and prolonged periods of cold temperatures (Halls 1978; Short 1981; Verme and Ullrey 1984). Individuals meet their energy requirements from catabolism of body reserves (DelGiudice et al. 1988) and ingestion of woody browse which is low in energy content (Ullrey et al. 1970). In these conditions, winter is obviously energetically stressful for deer (Hanley and McKendrick 1985; Worden and Pekins 1995). Massive starvation can occur during snowy winters, as has already been observed at the study site (Potvin et al. 1981). Crude protein requirements for maintenance of yearling or adult white-tailed deer have been estimated at 7–8% (French et al. 1956), 5–6% (Holter et al. 1979) or 4–5% (Asleson et al. 1996). These figures are consistent with the 6% need proposed by Schwartz et al. (1988) for maintenance of moose, but lower than the 10% requirement proposed by Short (1981) for black-tailed deer. Crude protein content of natural browse used by deer in the Pohénégamook area was measured over three winters (A. Dumont, unpublished work) and averaged 7.8%. Natural food thus likely provided an adequate source of protein to our study animals, and the protein contents of experimental foods (12–16%) were probably much higher than maintenance needs of deer.

Given the above, the mechanisms allowing selection of high energy foods by wintering deer may be under strong selective pressure. The observed preference for foods of higher energy content is thus not surprising, at least with regard to its function. It parallels observations on captive ruminants showing that animals can select, among novel foods, those that complement the macronutrient composition of their basal diet (Wang and Provenza 1996). Sheep can discriminate among foods containing different levels of digestible energy, and prefer the ones with high energy density (Provenza et al. 1996). They typically show stronger preferences for energy than protein (Villalba and Provenza 1997; Wang and Provenza 1997).

The fact that, at each given level of digestible energy, deer preferred foods with less protein may appear surprising, given that herbivores are generally thought to maximize rather than minimize protein ingestion (Robbins 1993). Two lines of evidence suggest that deer tended to avoid an excess of protein intake. First, feeding trials performed on captive ruminants and nonruminants have shown that animals do avoid an excess of nitrogen intake when given the possibility. Growing lambs are able to select a diet that meets their protein requirements and avoid excess of protein intake (Kyriazakis and Oldham 1993). Sheep select foods of intermediate protein density when offered rations below, equal to, or above their requirements (Hou et al. 1991). Cattle regulate intake of foods with high levels of nonprotein nitrogen to maintain blood ammonia levels below a fixed limit (Nicholson et al. 1992). Pigs prefer the food lower in protein when they are given the choice between a food with protein concentrations close to requirements and a food with richer protein content (Kyriazakis et al. 1990). Evidence for an avoidance of excessive nitrogen intake is scarcer for wild animals. Prins and Beekman (1989) showed that buffalo avoid eating too much protein-rich plants after a period of poor food, likely reflecting the slow adaptation of the rumen to new foods rich in nitrogen. Vickery et al. (1994) demonstrated that wild deer mice avoid a protein-rich (20%) diet when this is simultaneously offered with other foods lower in protein. Second, an apparent cost of excessive ingestion of protein in wintering cervidae was reported by Soppela et al. (1992). They studied captive reindeer during winter and found that protein intake was directly related to daily water inflow, surplus protein being eliminated by renal excretion. Increased daily water intake led to increased energy expenditure because reindeer had to warm ingested water or snow up to body temperature. There are no such physiological data for wintering white-tailed deer, but a similar consequence may be expected.

Which physiological mechanisms allowed deer to select foods in a way consistent with differences in energy and protein contents is far from clear. Verme and Ullrey (1984) attributed no "nutritional wisdom" to deer, whereas Galef (1991) gave an extensive criticism of nutritional wisdom in animals. Stephens and Krebs (1986) stated that herbivores do not seem to be able to detect specific nutrients, apart from sodium and water. Ruminants quickly experience postingestive effects of nutrients and toxins, and some metabolites like volatile fatty acids or ammonia signal postingestive effects of food ingestion very early in a meal (e.g., Villalba and Provenza 1996, 1997). Hence some propose that postingestive feedbacks explain most of the mechanism of food selection by ruminants (Provenza 1995). Too little is understood on such feedbacks, however, to know if they can explain preferences observed within the short time frame of our tests.

The pattern of food selection that we observed in our experiment was partial rather than absolute, thus corresponding to a matching rather than maximizing behavior. Partial selection is observed very consistently in all studies of food selection conducted on herbivores (e.g., Langvatn and Hanley 1993; Wilmshurst et al. 1995; Provenza et al. 1996). Many hypotheses have been proposed as to the various benefits that may accrue to individuals performing partial selection (reviews in Krebs and McCleery 1984; Parsons et al. 1994), but no consensus has emerged as to why matching behavior seems to be the rule when herbivores are selecting their food (e.g., Rolls 1986; Illius and Gordon 1990; Provenza 1996). In our first experiment, partial selection resulted in intakes of energy that were about 11% lower than maximum possible with absolute selection, and only 2% higher than random consumption. The respective percentages were 8 and 3% in experiment 2. Selective feeding thus made only small changes in quality of food intake. This could be interpreted as an indication of the poor precision of currencies in optimal foraging theory. Such small changes, however, can have a strong influence on animal performance through multiplier effects (White 1983). The physiological consequences of the pattern of food selection observed in our study should thus not be regarded as trivial.

We have interpreted differences in consumption of the different feeds as being due to our experimental manipulation of digestible energy and protein densities. An alternative explanation is that the differences were due to some other factor that differed between the diets, e.g., the taste of some particular ingredients. Without experimental replication with other feeds of similar energy and protein contents, but made of different ingredients, we cannot rule out this possibility. For example, our results could partly be explained by high palatability of corn meal. Ground soy bean was used to manipulate protein density of the feeds, and one could also propose that ruminants simply do not like the taste of soy bean, which drove deer toward the feeds lower in protein. Growing lambs and pregnant ewes, however, do prefer the rations containing the highest percentage of soy bean, a reflection of their high nitrogen needs (Cooper et al. 1994; Provenza et al. 1996). This observation, coupled with the fact that food choice experiments performed on domesticated ruminants give very consistent results in spite of the use of different ingredients to manipulate energy or protein content of the feeds (Provenza 1995), suggests that the response of deer was related to the variables under study. This discussion illustrates the need for our study to be repeated with other rations and in different conditions.

In conclusion, our study suggests that both energy and protein contents of experimental foods influenced food choice by wild white-tailed deer. Although it is always difficult with wild animals to gain control on all the variables that can influence food choice, the order of preference of the rations likely reflected deer's physiological needs. Our results thus support a basic assumption of optimality models of food selection, namely that herbivores are capable of assessing forage "value", either directly through the currencies we think are of importance or indirectly through other variables correlated with these currencies. Although energy and protein density are generally correlated in natural forages, our experimental approach suggests, in good agreement with results from domesticated species, that wild large herbivores are able to discriminate between these two currencies of high physiological importance.

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