



# The effect of food quality and relative abundance on food choice in fallow deer

ULRIKA ALM, BJÖRN BIRGERSSON & OLOF LEIMAR

Department of Zoology, Stockholm University

(Received 20 June 2001; initial acceptance 22 August 2001;

final acceptance 4 February 2002; MS. number: 6967R)

The diet choice of large herbivores is influenced by the presence of nutrients and toxins in available plants. It is generally assumed that herbivores ingest food that contains higher amounts of nutrients and lower amounts of toxins than the average of the food available. We studied the effects of quality and relative abundance on food choice in fallow deer, *Dama dama*. Preferences for and aversions against different compounds were first examined in two-choice tests with food and water. We then did cafeteria (multiple-choice) tests with hydrolysable tannin and sucrose added to food to investigate the influence of the frequency of occurrence. We found that food choice was biased towards lower tannin content. Consumption with respect to tannin content was relative rather than absolute, however, in that the intake of a given concentration depended on which other concentrations were present. In addition, the relative preference for low-tannin food was weaker in the cafeteria test, where this food had a smaller frequency of occurrence, indicating that frequency of occurrence influences food choice. We discuss these results from the perspective of optimal foraging theory and suggest that a changing and complex distribution of food types in nature may make it advantageous for large herbivores to show intermediate selectivity, rather than attempting to ingest only the highest quality food possible.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

Since many large herbivores are able to use micro-organisms to process cellulose, a large number of plants are potential food resources. As the concentrations of nutrients and metabolizable energy in plants can be low, herbivores typically need to ingest large amounts. The majority of mammalian herbivores are generalists (Freeland 1991), implying that they encounter a large range of different plants of varying quality, in terms of the content of energy, nutrients and toxins in the form of secondary compounds. Generalist herbivores may eat a mix of different plants to get a balanced diet or because their detoxification mechanisms do not allow them to cope with large amounts of a single toxin (Moss 1991). Diet choice in mammalian herbivores is thought to be influenced by the presence of nutrients as well as toxins (Palo & Robbins 1991; Provenza 1995) and their diet to contain higher amounts of nutrients and lower amounts of toxins than the average of the food available (Freeland & Janzen 1974).

In broad terms, the herbivore diet choice problem is to select food based on the perceived qualities of available food types and on their frequencies of occurrence. The complexity of the situation encountered by mammalian

Correspondence: U. Alm, Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden (email: [Ulrika.Alm@zoologi.su.se](mailto:Ulrika.Alm@zoologi.su.se)).

herbivores, in particular the great number of secondary substances, with concentrations that vary between plants, plant parts and times in the season, makes it likely that they are sensitive to many aspects of the distribution of plant food. Some data suggest that generalist herbivores are willing to try new foods. For instance, after being exposed to food with a particular flavour, lambs, *Ovis aries*, prefer to eat similar food with a different flavour (Early & Provenza 1998). Animals living in a seasonal environment are also forced to change their diet between seasons (Iason & Van Wieren 1999). Herbivores eat from previously avoided tannin-rich leaves instead of the usually preferred grass at times in the season when the grass becomes less nutritious (Hofmann 1989). Conversely, high-quality diet supplementation can make herbivores more selective when feeding on natural forage (Murden & Risenhoover 1993). The fact that the diet can be changed over time indicates that the decision of what to eat is likely to be relative rather than absolute.

Mammalian herbivores are thought to sample the food in their environment (Provenza et al. 1992), which could provide information about the relative abundance of different foods. Some data suggest a strong influence of the frequency of occurrence on food choice. Parsons et al. (1994) found that sheep ingested less clover than grass when the abundance of clover was low, although they

preferred clover to grass when the abundances were equal. Since there was enough clover for the animals' needs in the low-abundance treatment (Parsons et al. 1994), this supports the idea that the frequency of different food types affects the food choice. In general, however, there seems to be a lack of studies on the response of mammalian herbivores to frequency of occurrence.

Animals could respond to variation in frequency in different ways. One possibility would be to eat the same distribution of food types independently of their frequency of occurrence, which would require that none of these food types is absent or rare. Another possibility would be to eat proportional to frequency, which means that as a food type becomes more common it makes up a larger part of the diet. There could also be responses to frequency that deviate from proportionality, for instance exploiting common food types either more or less than proportional to abundance. The latter issue has been thoroughly investigated for predators hunting by sight (so-called apostatic and antiapostatic selection, reviewed in Allen 1988).

We experimentally examined some factors potentially influencing food choice in fallow deer, *Dama dama*. Using manipulated foods, presented to individual, tame fallow deer hinds in two-choice and cafeteria tests, we investigated how quality and frequency of occurrence affected their food choice.

## METHODS

The fallow deer is a generalist herbivore with a broad food spectrum, consisting of, for example grass, leaves and bark, depending on the season (Chapman & Chapman 1975). We studied six adult female fallow deer. They were kept in a 4-ha enclosure with forest and meadow at Tovetorp zoological field station, in south-central Sweden. Since they were reared by hand they were tame and could be handled individually. During the study, the deer had ad libitum access to silage and pasture, water, minerals and salt stone, and there was no fasting before the experiments. The experiments were performed with permission from the Swedish National Board for Laboratory Animals.

The experiments took place from February to May 2000. A small experimental enclosure (100 m<sup>2</sup>) was placed within the larger enclosure where the deer were kept. The entrance to the experimental enclosure had a small vestibule into which the deer could be led. To start a trial we released a female from the vestibule into the experimental enclosure. The walls of this enclosure were solid and 1.4 m high, so that the deer were prevented from seeing through or over the wall.

### Two-choice Tests

To investigate binary taste preferences, we added different compounds to food or water in two bowls placed 12 cm apart in the experimental enclosure. The concentrations in water of acetic acid, saccharine and sucrose were chosen to be above the sensitivity level in black-

**Table 1.** Compounds and concentrations used in the two-choice tests

Compound	Order*	Concentration in water (g/litre) or food (g/kg)	
Acetic acid	4	Water	0–1
Acetic acid	17	Food	0.3–1.5
Ascorbic acid	5	Water	0–2
Ascorbic acid	7	Food	0.6–3
Ascorbic acid	15	Food	0.4–4
Methyl salicylate	12	Water	0–0.3
Methyl salicylate	13	Food	0.4–2
Monosodium glutamate	10	Water	0–1.9
Monosodium glutamate	11	Food	0–5
Saccharine	3	Water	0–0.8
Saccharine	9	Food	0.03–0.2
Saccharine	8	Food	0.007–0.03
Sucrose	1	Water	0–34
Sucrose	16	Food	9.0–30
Tannin†	2	Water	0–16
Tannin†	6	Food	6.0–30
Tannin†	14	Food	1.2–6.0

\*The order in which the tests were performed.

†Tannic acid (chemical formula: C<sub>19</sub>nH<sub>13</sub>nO<sub>12</sub>n).

tailed deer, *Odocoileus hemionus* (Crawford & Church 1971). In the tests with water one bowl contained pure water and the other water with the compound and in the tests with food the bowls contained pellets with different amounts of compound added (Table 1). The compounds were tested one at a time, either in water or in pellets, in the order given in Table 1. The pellets used were of a type intended for wild cervids and contained 10.5 MJ digestible energy and 120 g crude protein per kg. The compounds were dissolved in water and sprayed over the pellets. At the start of a trial, a bowl contained either 350 g pellets or 2 litres of water, and the bowls were alternated right and left every trial. A trial was considered finished when the deer stopped eating or drinking for more than 1 min or when either bowl became empty. For each of the two-choice tests in Table 1, each deer had six trials, with one to three trials per day.

### Cafeteria Tests

To investigate whether food choice depended on the relative abundance of different food types, we increased the number of bowls to eight. In these tests we used pellets with different concentrations of tannin or sucrose. These two compounds were chosen because we expected the deer either to avoid (tannin) or to prefer (sucrose) higher concentrations of the substance. To determine the extent to which the deer were searching among the bowls, and therefore could have tasted the content of the different bowls, we also measured the number of bowls visited and the number of shifts between the bowls during a trial.

The pellets and the concentrations were the same as in the two-choice tests and each bowl contained 400 g of pellets. The eight bowls were placed equally spaced along the perimeter of a circle and numbered clockwise. The

**Table 2.** The design used for the placement of bowls with different concentrations in the cafeteria test with tannin

Position	1	2	3	4	5	6	7	8	Circle position
Trial 1	L	H	M	H	M	H	M	H	Right
Trial 2	H	M	H	M	H	L	H	M	Left
Trial 3	M	H	M	H	M	H	L	H	Right
Trial 4	H	M	H	M	H	M	H	L	Left
Trial 5	M	H	M	H	L	H	M	H	Right
Trial 6	H	L	H	M	H	M	H	M	Left
Trial 7	M	H	L	H	M	H	M	H	Right
Trial 8	H	M	H	L	H	M	H	M	Left

The positions along the perimeter of the circle were numbered clockwise so that either 5 or 6 was closest to the entrance of the experimental enclosure. The letters L, M and H refer to low, medium and high concentrations.

diameter of the circle was 3 m and it was positioned alternately on the right or the left side of the experimental enclosure. Each deer had eight trials in a test, at the rate of one or two trials per day. A trial was considered finished when the animal stopped eating for more than 1 min. For the experiment with tannin we used three concentrations, referred to as low, medium and high. Out of the eight bowls one had the low, three the medium and four the high concentration. The idea behind this design, with only one bowl out of eight containing the conceivably most attractive low concentration, was to test the hypothesis that food types with low relative abundance tend to be exploited to a lesser extent. Table 2 gives the design for the sequence of trials. Each deer experienced each of the eight arrangements. After the cafeteria test with tannin a supplementary two-choice test was carried out to see if there had been an overall change in the preference for low- over medium-tannin food. In this test the two bowls each contained 300 g of pellets.

The cafeteria test with sucrose was done in the same way as the test with tannin except that we used only two concentrations, low and high. Out of the eight bowls, only one contained the high concentration and the remaining seven contained the low concentration of sucrose. The design for the sequence of trials followed the same schedule as for tannin, with the high-sucrose bowl placed in the position of the low-tannin bowl (Table 2). The idea for the design was again to have the conceivably most attractive food type occur at a low frequency.

### Statistical Analysis

For our statistical tests, we used nonparametric comparisons (Wilcoxon signed-ranks tests). The individual animal was the sampling unit ( $N=6$ ) for all analyses, including the calculation of standard errors. We calculated data points by averaging over the trials of a given set-up. To reach statistical significance in a two-sided test, each of the six individuals must then show a difference in the same direction (yielding  $T=0$ ,  $P=0.03$ ). We followed a procedure of planned comparisons (Sokal & Rohlf 1995),

limiting the number of comparisons to the degrees of freedom available for testing (i.e. the total number of amounts minus one). The most basic hypothesis we tested is whether the concentration of a compound influences intake. If this is the case, two other hypotheses are of interest, namely whether the intake of food with a given concentration of compound depends on which other concentrations are present and whether the relative preference of one concentration over another differed between the cafeteria and the two-choice tests.

## RESULTS

### Reactions to Different Compounds

The different substances and concentrations used in the two-choice tests (Table 1) resulted in a diverse spectrum of preferences and aversions, although in no case was there an absolute discrimination against one of the alternatives (Fig. 1). Tannin was the most strongly avoided compound both in pellets and in water, whereas sucrose in water was the most preferred. The sour tastes produced negative or neutral responses and monosodium glutamate, saccharine and methyl salicylate were neither strongly preferred nor avoided (Fig. 1).

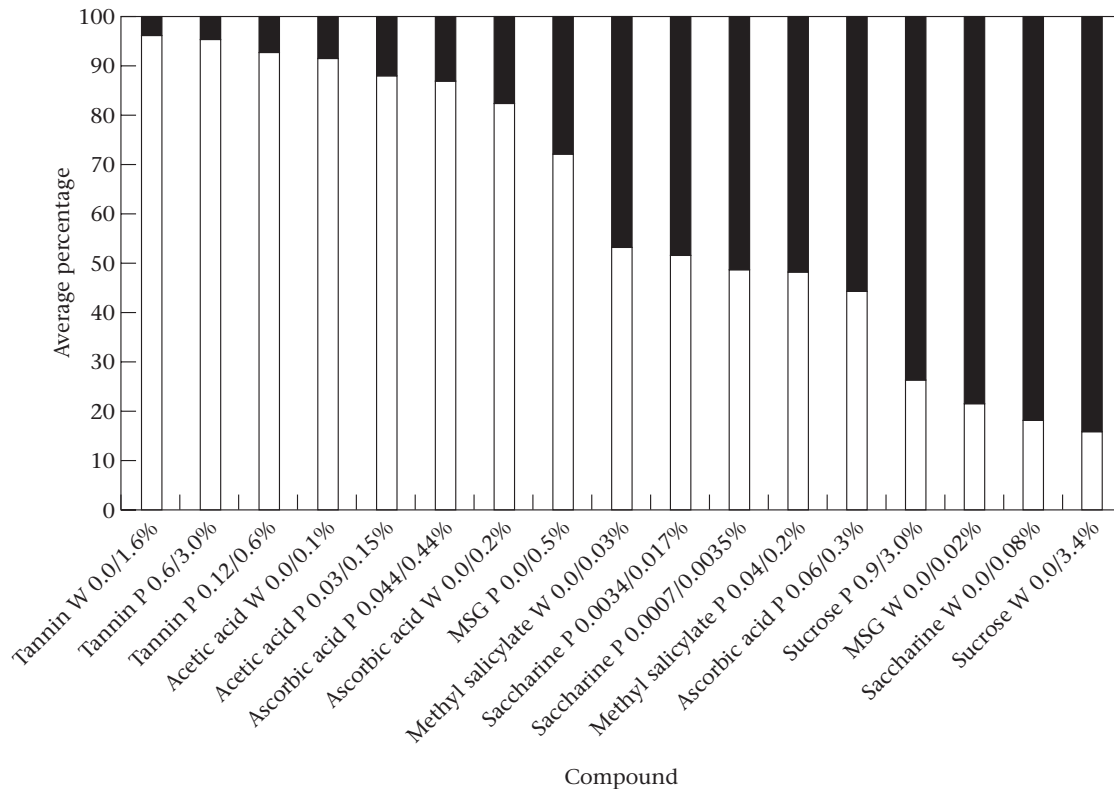
### Tests with Tannin and Sucrose

The concentration of tannin influenced the amount of pellets consumed per bowl in the different experimental set-ups (Fig. 2a). In each of the three two-choice tests, all individuals consumed more of the lower concentration food ( $P=0.03$  in each case). Similarly, in the cafeteria test (Fig. 2a), all individuals consumed more from a low-tannin bowl than from a medium-tannin bowl ( $P=0.03$ ), but also more from a medium-tannin bowl than from a high-tannin bowl ( $P=0.03$ ). Thus, higher tannin concentration consistently reduced intake.

The medium/high and the first low/medium two-choice tests both contained the same medium-tannin food, but this was paired with either a higher or a lower concentration. All individuals consumed more medium-tannin food per bowl when paired with a high than a low concentration ( $P=0.03$ ). The difference was large (Fig. 2a), with on average about 12 times as much medium-tannin food consumed when paired with the high concentration.

Low- and medium-tannin food were present in the first and final low/medium two-choice test and in the intervening cafeteria test. We can express a relative preference as the ratio between the amount consumed from a low-tannin bowl and the amount consumed from a medium-tannin bowl. For all individuals, this ratio was smaller in the cafeteria test than in either of the two-choice tests ( $P=0.03$  in each case; Fig. 2a), which shows that the relative preference for low over medium-tannin food was weaker in the cafeteria test.

From this we can conclude that all individuals must have consumed a smaller total proportion of low-tannin food in the cafeteria test (Fig. 2b), since there was only a



**Figure 1.** Average percentage ingested from lower (□) and higher (■) concentrations in two-choice tests with different compounds. The letters W and P denote compounds in water and in pellets. The concentrations are given in percentages for each compound.

single low-tannin bowl in that set-up. The reason for the relatively lower consumption of low-tannin food in the cafeteria test was not that the deer ran out of low-tannin food, since in this set-up all bowls still contained some food at the end of a trial. A change over time in the overall preference for low-tannin food is also ruled out, since there was a two-choice test both before and after the cafeteria test. It thus seems that the frequency of occurrence influenced the intake of the low-tannin food.

We could not establish a statistically significant influence of sucrose concentration on the amount of pellets consumed per bowl (Fig. 3). For the two-choice test, there was a nonsignificant tendency towards higher consumption from the high-sucrose bowl ( $T=1$ ,  $P=0.06$ ), but no effect in the cafeteria test ( $T=7$ ,  $P=0.89$ ). All individuals consumed a smaller proportion of high-sucrose pellets in the cafeteria test than in the two-choice test, suggesting an effect of frequency of occurrence, but since we could not establish an effect of concentration on the consumption per bowl, this result should be regarded as tentative.

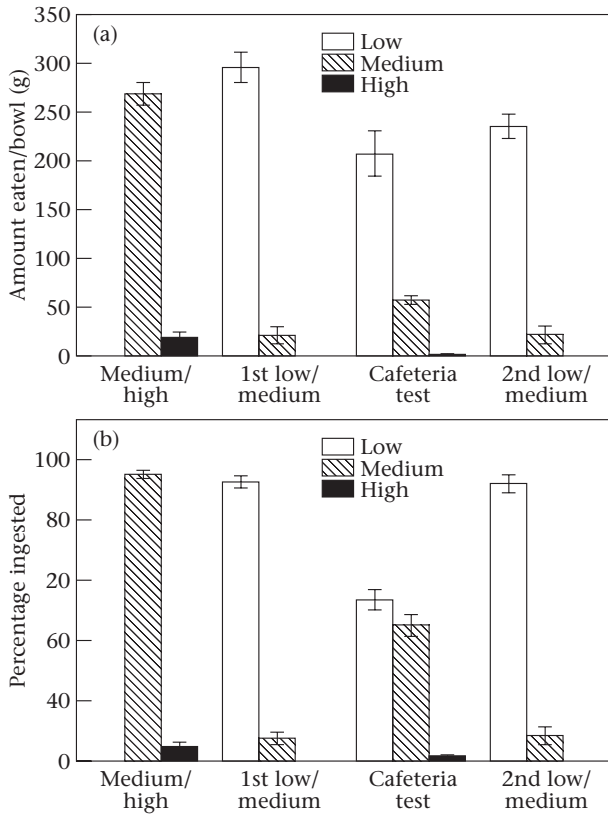
We also looked for consistent trends over time in the cafeteria test consumption patterns. We computed the rank correlation between proportion consumed and trial number (1–8), separately for each individual. For two-tailed statistical significance, each correlation would then need to be of the same sign. However, we found no consistent trends, either for the proportion of low-tannin food ( $r_s = -0.26 \pm 0.20$ ) or for the proportion of high-sucrose food ( $r_s = 0.10 \pm 0.16$ ).

## Searching Behaviour

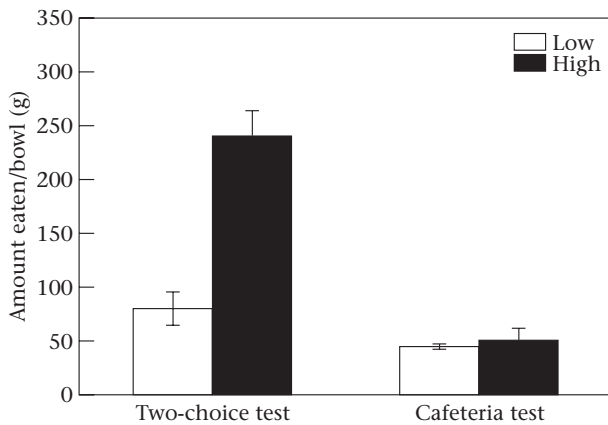
The deer showed different searching behaviour in the cafeteria test with tannin than in the cafeteria test with sucrose. All individuals visited more bowls at least once in a trial in the test with tannin ( $P=0.03$ ; Fig. 4a), and usually visited all eight. Part of the reason for this result was that all individuals changed bowls more during a trial in the tannin test (Fig. 4b). The deer could have moved to a random bowl or preferentially to an untried bowl. We investigated whether they tended to search systematically in this manner, by comparing the observed number of bowls with the random expected number based on the actual number of shifts in that trial. In the test with tannin, all individuals found more bowls than expected from random search, but this was not the case for sucrose (tannin:  $T=0$ ,  $N=6$ ,  $P=0.03$ ; sucrose:  $T=1$ ,  $N=6$ ,  $P=0.06$ ).

## DISCUSSION

The most striking overall result from our study was that the amount of a food type consumed during a trial depended strongly on the context in which the food was presented. For instance, food choice in relation to tannin content was relative rather than absolute, so that considerably more medium-concentration food was consumed in the medium/high test than in the low/medium test (Fig. 2). Although large herbivores are known to change their diet as a response to seasonal changes in availability and quality (Hofmann 1989), there seems to be a lack of

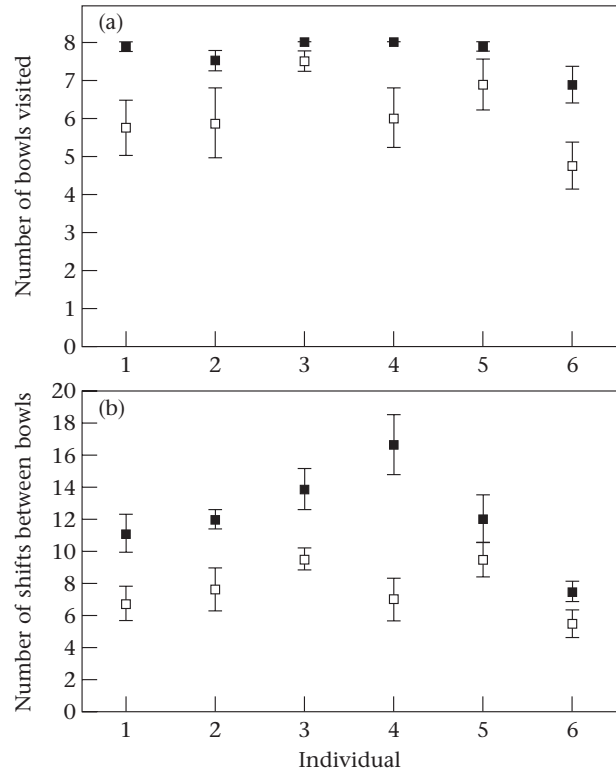


**Figure 2.** Food choice of six deer in three two-choice tests and one cafeteria test, with low, medium and high concentrations of tannin (0.12/0.6/3.0%). Of the eight bowls in the cafeteria test, one contained a low, three a medium and four a high concentration. (a) The amount of pellets eaten per bowl. (b) The percentage of total pellets ingested. Means are given  $\pm$ SE.



**Figure 3.** Food choice of six deer in one two-choice test and one cafeteria test, with low and high concentrations of sucrose (0.9/3.0%). Of the eight bowls in the cafeteria test, only one contained a high concentration and the remaining seven a low concentration of sucrose. The amount of pellets eaten per bowl ( $\bar{X} \pm$ SE) is shown.

experimental studies of the phenomenon. Our experiments show that fallow deer can adapt rapidly to changes in the distribution of food types. From the cafeteria tests, we also found that the deer tended to use more common foods to a higher degree, at least if the quality was above



**Figure 4.** Aspects of the search strategies used by the deer in the cafeteria tests with tannin (■) and sucrose (□). (a) The number of bowls visited at least once per trial ( $\bar{X} \pm$ SE). (b) The total number of shifts between bowls ( $\bar{X} \pm$ SE) for each individual.

some minimum level (Figs 2, 3). To describe such effects, it may be useful to make a distinction between preference and choice (Parsons et al. 1994). The first low/medium tannin concentration two-choice test can be interpreted as showing a preference for lower tannin content, and the supplemental low/medium test then showed that this preference remained throughout the experiment. The greater consumption from the low-concentration bowl in the cafeteria test with tannin was also consistent with this preference, but the influence of the relative abundances affected the choice of foods so that the total consumption of low- and medium-concentration foods was about the same. Similar effects of relative abundance have been found for sheep grazing on clover and grass (Parsons et al. 1994).

For predators hunting by sight, the influence of frequency of occurrence on consumption has been examined in several studies (e.g. Allen 1988; Weale et al. 2000). These studies have mostly investigated birds feeding on two types of artificial prey of different colour but identical nutritional value and palatability. From these studies it seems that predators usually consume more than proportional to the frequency of common types, at least for low or moderate prey densities, and this corresponds to apostatic selection. In connection with investigations of warning coloration and mimicry, there are also studies of the influence of the frequency of occurrence on consumption of prey types that differ in palatability (e.g. Speed et al. 2000; Lindström et al. 2001). These studies

have found antiapostatic selection acting on conspicuously coloured and unpalatable prey types. Since these phenomena depend on different visual stimuli triggering attacks by predators, the connection with herbivory is an open question, but it is at least clear that there can be diverse effects of frequency of occurrence on consumption.

Preferences and aversions to different tastes, which can be either innate or acquired through learning, are generally thought to derive from an association between the taste and the benefit or harm to the animal of ingesting the food. For instance, unripe fruits and rotting materials are sour (Lindemann 1996), whereas a sweet taste indicates readily digestible energy. Similarly, the avoidance of food with high tannin content could be an evolved response to the negative effects of tannins on fitness (Rhoades 1979). Tannins are divided into two major structural groups: condensed and hydrolysable tannins. Previous studies of ruminant reactions to tannin have been done with condensed tannins (Provenza et al. 1990; Landau et al. 2000), whereas we used hydrolysable tannins. The latter are found only among the dicotyledons and have the same ability *in vitro* to bind to proteins as condensed tannins (Meyer & Karasov 1991). Thus, adding hydrolysable tannin probably reduced the quality of the food. Both in the tests with tannin and in the tests with sucrose it then seems likely that the deer encountered a simple spectrum from lower to higher quality food. From our results (Figs 2, 3), there appeared to be a stronger selectivity for tannin than for sucrose with respect to different concentrations. This might simply have been a consequence of the concentrations used, but it could be that it is more important to avoid unsuitable food than to consume the highest quality. The deer also searched more thoroughly in the cafeteria test with tannin than in the one with sucrose (Fig. 4).

If we focus on the tests where tannin was added to pellets, for which the results were consistent between individuals, it is clear that the deer had a fairly extensive experience of the different concentrations. In these tests, including the final supplementary two-choice test, each individual had 26 trials over several weeks, usually sampling all the bowls in a trial, and consuming a total of around 6 kg of pellets. It thus seems reasonable to regard the patterns of food choice observed as being long term or, at least, medium term. One might then wonder why we found no trends over time in the different tests, or between the two low/medium two-choice tests. Postingestive learning can cause ruminants to modify their diet relatively quickly, over periods of a few days to a week (Villalba & Provenza 2000), and this is also true for fallow deer (U. Alm, B. Birgersson & O. Leimar, unpublished data). Thus, we cannot conclude that no learning took place. An alternative possibility is that the deer gradually became more informed about the postingestive properties of the food types, but that this did not cause them to revise substantially their initial estimates of the relative qualities. Since tannins occur in many plants, the deer might have been skilled at estimating their effects.

Overall, the deer in our experiments managed to ingest food that contained higher amounts of nutrients and

lower amounts of toxins than the average of the food available. One natural way of achieving such selectivity would be to sample available foods and to shift exploitation continuously towards the high-quality end of the available spectrum. The outcome of such a process might be to consume foods only above the highest possible quality threshold consistent with the animal's intake requirements. However, we did not find such ongoing shifts towards selection of only the high-quality end of the spectrum. Instead, the deer quickly reached an intermediate degree of selectivity and then seemed to maintain this pattern of exploitation.

This kind of frequency-dependent selectivity, with only a partial shift towards the high-quality end of the available distribution of food, might be common among large herbivores. From the point of view of optimal foraging theory (Stephen & Krebs 1986), there could be different explanations for such a pattern of exploitation. Herbivores may be fairly inaccurate in identifying food types, leading to imperfect selectivity, but this alternative fails to explain the observed effects of frequency of occurrence. For instance, from Fig. 2a it is clear that the deer could identify the low-tannin bowl. A more likely possibility is that the pattern of selectivity is an adaptation to changing quality distributions (see Inglis et al. 2001). Although herbivores might quickly distinguish food types by taste and odour, it will be considerably more time consuming to determine the precise quality of a food type by postingestive analysis, in particular if the diet is mixed. In addition, it can take time to build up the gut flora needed to exploit efficiently previously unused food types. As a consequence of such time constraints it might be unwise to rely on consumption of only a small and possibly ephemeral segment of the available distribution of food types.

A number of other suggested explanations for diet breadth in large herbivores, such as the need for a balanced diet or avoiding excessive consumption of a single toxin, could well be valid in general, but do not explain our observations. The main discrepancy is that these other explanations do not predict the kind of frequency-dependent selectivity that we observed. For instance, a herbivore that attempts to maintain a certain balanced diet ought not to respond strongly to changes in relative abundance. Further studies are needed to clarify which principles are most important to explain diet choice of large herbivores in nature.

### Acknowledgments

We thank Anders Bylin for help in constructing the experimental set-up. This study was supported by grants from the Swedish Natural Science Research Council (to O.L.).

### References

- Allen, J. A. 1988. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society of London*, **219**, 485–503.

- Chapman, D. & Chapman, N.** 1975. *Fallow Deer: their History, Distribution and Biology*. Lavenham: T. Dalton.
- Crawford, J. C. & Church, D. C.** 1971. Response of black-tailed deer to various chemical taste stimuli. *Journal of Wildlife Management*, **35**, 210–215.
- Early, D. M. & Provenza, F. D.** 1998. Food flavor and nutritional characteristics alter dynamics of food preference in lambs. *Journal of Animal Science*, **76**, 728–734.
- Freeland, W. J.** 1991. Plant secondary metabolites: biochemical coevolution with herbivores. In: *Plant Defenses against Mammalian Herbivory* (Ed. by R. T. Palo & C. T. Robbins), pp. 61–81. Boca Raton: CRC Press.
- Freeland, W. J. & Janzen, D. H.** 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist*, **108**, 269–289.
- Hofmann, R. R.** 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive-system. *Oecologia*, **78**, 443–457.
- Iason, G. R. & Van Wieren, S. E.** 1999. Digestive and ingestive adaptations of mammalian herbivores to low quality forage. In: *Herbivores: Between Plants and Predators* (Ed. by H. Olff, V. K. Brown & R. H. Drent), pp. 337–369. Oxford: Blackwell Scientific.
- Inglis, I. R., Langton, S., Forkman, B. & Lazarus, J.** 2001. An information primacy model of exploratory and foraging behaviour. *Animal Behaviour*, **62**, 543–557.
- Landau, S., Silanikove, N., Nitsan, Z., Barkai, D., Baram, H., Provenza, F. D. & Perevolotsky, A.** 2000. Short-term changes in eating patterns explain the effects of condensed tannins on feed intake in heifers. *Applied Animal Behaviour Science*, **69**, 199–213.
- Lindemann, B.** 1996. Taste perception. *Physiological Reviews*, **76**, 719–766.
- Lindström, L., Alatalo, R. V., Lytinen, A. & Mappes, J.** 2001. Strong anti-apostatic selection against novel rare aposematic prey. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 9181–9184.
- Meyer, M. W. & Karasov, W. H.** 1991. Chemical aspects of herbivory in arid and semiarid habitats. In: *Plant Defenses against Mammalian Herbivory* (Ed. by R. T. Palo & C. T. Robbins), pp. 167–187. Boca Raton: CRC Press.
- Moss, R.** 1991. Diet selection: an ecological perspective. *Proceedings of the Nutrition Society*, **50**, 71–75.
- Murden, S. B. & Risenhoover, K. L.** 1993. Effects of habitat enrichment on patterns of diet selection. *Ecological Applications*, **3**, 497–505.
- Palo, R. T. & Robbins, C. T.** 1991. *Plant Defenses against Mammalian Herbivory*. Boca Raton: CRC Press.
- Parsons, A. J., Newman, J. A., Penning, P. D., Harvey, A. & Orr, R. J.** 1994. Diet preference of sheep: effects of recent diet, physiological state and species abundance. *Journal of Animal Ecology*, **63**, 465–478.
- Provenza, F. D.** 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *Journal of Range Management*, **48**, 2–17.
- Provenza, F. D., Burrit, E. A., Clausen, T. P., Bryant, J. P., Reichardt, P. B. & Distel, R. A.** 1990. Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. *American Naturalist*, **136**, 810–828.
- Provenza, F. D., Pfister, J. A. & Cheney, C. D.** 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. *Journal of Range Management*, **45**, 36–45.
- Rhoades, D. F.** 1979. Evolution of plant chemical defense against herbivores. In: *Herbivores: their Interactions with Secondary Plant Metabolites* (Ed. by G. A. Rosenthal & D. H. Janzen), pp. 3–54. New York: Academic Press.
- Sokal, R. R. & Rohlf, F. J.** 1995. *Biometry*. New York: W. H. Freeman.
- Speed, M. P., Alderson, N. J., Hardman, C. & Ruxton, G. D.** 2000. Testing Müllerian mimicry: an experiment with wild birds. *Proceedings of the Royal Society of London, Series B*, **267**, 725–731.
- Stephen, D. W. & Krebs, J. R.** 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Villalba, J. J. & Provenza, F. D.** 2000. Postingestive feedback from starch influences the ingestive behaviour of sheep consuming wheat straw. *Applied Animal Behaviour Science*, **66**, 49–63.
- Weale, M. E., Whitwell, D., Raison, H. E., Raymond, D. L. & Allen, J. A.** 2000. The influence of density on frequency-dependent food selection: a comparison of four experiments with wild birds. *Oecologia*, **124**, 391–395.