Temporal changes in food preferences of wood mice (*Apodemus sylvaticus* L.)

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Abstract. Diet choice was determined for wild-caught wood mice (*Apodemus sylvaticus* L.), temporarily confined to cages in the field and offered a choice of 24–26 types of seeds and fruits in 2-h sessions throughout the night. The mice showed an overall preference for some foods over others. The set-up minimized influences on food preferences of predation risk, hunger, food availability and competition. Variation in food preferences was not attributable to differences between individuals, but followed a temporal pattern. The variety of foods eaten showed a bimodal pattern with peaks corresponding to the two most active periods at the beginning and end of the night. Both the amount of food eaten and variation in the amount diminished from the first to the second active period. An expected selection for carbohydrates early in the night and proteins at the end of the night was not found, but sugars were selected for early in the night. These results are discussed in relation to the conflict between an animal's continuous energy requirements and the essentially periodic activity of foraging.

Food choice and feeding behaviour studies play an important role in both our understanding of population dynamics (e.g. Hansson 1971; Schaffer and Tamarin 1973) and the psychology of animal motivation (e.g. Machlis 1977; Toates 1980). Identifying the factors that determine which foods an animal chooses to eat has been a central concern in many ecological and psychological studies. An animal's food preference is widely assumed to be a function of the properties of both the food and the internal state of the animal (e.g. Rozin 1976) and therefore open to investigation through trials in which both animal and food are controlled. The underlying factors that lead to these preferences are often difficult to determine, however, even

when clear preferences are shown in choice tests under controlled conditions (e.g. Brown 1969; Moon and Ziegler 1979). Many studies have focused on the selection for certain food types as measured by the abundance of foods in the animal's diet relative to that in its habitat [e.g. Evans 1973; Ferns 1976; Godfrey 1953 (faecal analysis); Drozdz 1966; Faber and Ma 1986; Flowerdew and Garner 1978; Green 1979; Hansson 1971; Holišová 1960; Miller 1954; Obrtel and Holišová 1979; Pelz 1979; Reichman 1977; Smal and Fairley 1980; Watts 1968; Zemanek 1972 (stomach and caecal analysis); Chitty et al. 1968 (enclosure experiment)]. Differences between distributions of items in an animal's habitat and in its diet have often been explained by selection for items with highest calorific gain per unit time spent foraging (e.g. Hansson 1985), but other factors may affect selectivity, such as predation risk (Lima and Valone 1986), the need for a balanced diet (Ashworth and Watson 1970; Gibb 1962; Goss-Custard 1977; Moss 1968; Tinbergen 1960) and toxicity of the foods (Drōżdż 1966; Zemanek 1972), sometimes resulting in items with greatest calorific yield being underselected.

As foraging is essentially a periodic activity (Le Magnen 1985) and an animal needs a continuous supply of energy, it has to rely on energy stored in the body to supply its needs during periods of rest. It would therefore be expected to choose a diet high in readily available energy at the start of a foraging period in order to supply its needs during this period and to select for more slowly digestible energy towards the end of the period to supply its needs during periods of inactivity (e.g. Hayne et al. 1986; Tempel et al. 1985). The wood mouse, *Apodemus sylvaticus* L. is a highly motile forager (Wolton 1985) with a simple digestive system (Campbell 1974), which in its natural habitat feeds on a wide selection of species (Bailey 1970; Eldridge 1969; Hansson 1971; Miller 1954; Watts 1968). In the present study, wild-caught animals were temporarily confined to cages at the site of capture and offered a selection of seeds and fruits collected locally to determine (1) preferences for some foods over others; (2) changes in preferences during the period of foraging; and (3) the relation of temporal changes to nutrient contents of the foods.

Methods

Wild wood mice were captured in cereal fields and surrounding hedgerows during 10 nights in October 1990 using 50 Longworth live-traps. These were baited with wheat and filled with hay for bedding and were checked every 2 h throughout the night. Captured wood mice were weighed, sexed and numbered using a fur-clip method (Twigg 1975) and sub-adults (females which were neither perforate, pregnant or lactating and males without descended testes, weighing between 15 g and 20 g) were transferred to individual wire cages (20 cm × 30 cm × 15 cm) at the site of capture. Juveniles were not used as they may not have been familiar with all the foods offered in the tests, and nor were adults in breeding condition which would introduce an extra variable due to sex-based differences in nutritional requirements (Campbell 1974).

Twenty-five trials involving eight animals were conducted, each trial lasting 2 h. Each study animal was presented with a single layer of 50 seeds or fruits of each of 24–26 plant species, distributed on the metal base of each cage (only 10 each of the larger fruits). The food items had been collected locally within the previous 3 days. Care was taken to collect seeds that appeared healthy and at the stage of ripeness characteristic of that species in the vicinity. Seeds were not de-husked so as not to affect appearance or handling time by the animal. Bedding (hay) and drinking water were provided *ad libitum* except in five trials in which water was unavailable. The animal was released at the end of a trial and the remaining seeds and seed-husks collected in a polythene bag for subsequent counting. The trials were carried out on dry, still nights (6° C–15.5° C) to avoid unnecessary soaking and chilling of the study animals and to prevent the seeds from being blown or washed away.

Recovered seeds were counted and weighed within hours of the field trial, and each type assigned a preference rank from the number of items chewed or eaten, as these rankings were found to correspond to those based on wet weights. "Items" were defined as individual seeds, while "types" were defined as the plant species from which fruiting bodies were taken. In the case of larger fruits, which were never eaten entirely, bites were counted as items eaten, as they represented numbers of selections of that fruit. If only one seed or fruit of a certain type showed toothmarks, it would be recorded as not selected, as it might have been sampled but found unpalatable. In order to minimize handling error, the very smallest seeds found in the hedgerows were excluded from the trials. By basing the comparisons between and within individuals on rankings rather than on absolute measures, variations due to differences in amounts eaten were controlled for. Seeds were used once only, lest they had been tainted with mouse odour during the trial, or had been rejected by the first subject for being unripe, diseased or infected by insect pests. Measurements of temperature at the time of the trials were obtained from a weather station situated on the farm.

Preference rankings were compared using Spearman's rank-order correlation coefficient, r_s, for pairs of trials in which an identical selection of foods had been offered. Variations in the magnitude of r_s were investigated by general linear modelling (GLM; SAS Institute Inc. 1988) in a factorial model with classification variables of sex (males, females, mixed), same/different night, same/different individual, and continuous variables of temperature difference and difference in time of night of the trials.

Variations in numbers of food types eaten with time were analysed using a procedure described in the Appendix.

The activity rhythm of animals used in the trials was compared to that of four free-ranging mice (two females, two males), radio-tracked on the farm for five nights each.

The nutritional values of the six most preferred food were obtained from the literature (Money and Christian 1950; McCance et al. 1978; Niewiadomski 1983; Herrera 1987; Holland et al. 1988; Sosulski et al. 1985). These six foods (blackberries, oilseed rape, wild oats, sweetcorn, wheat and barley) made up between 90% and 100% of the foods eaten in 20 of the 25 trials, with only one trial in which the six foods constituted less than 80% (76.5%). The percentage contents in the diet of various nutrients were compared for trials early and late in the night with a permutation test (Siegel and Castellan 1988). Information on plant toxins was also gained from the literature.

Results

Preference

Of the 26 food types offered, 13 were taken by at least one animal (Table 1). No one species was ranked first on every occasion it was presented, but sweetcorn was amongst the three most favoured foods in all the trials in which it was presented, wheat in 88% of trials, blackberries in 81% and oilseed rape in 65% of trials. Of the 14 foods recorded as not eaten (Table 2), 11 had not been sampled, showing no tooth-marks. Of the remainder, onion garlic had been sampled by three animals, and sterile brome and privet by two animals each. At least six of the foods not eaten during trials contain compounds toxic to mammals, and several of the foods eaten also contain toxins (Table 1) but the data were insufficient to analyse further the relationship between toxins and food preference.

Pair-wise comparisons between preference rankings from different trials in which the same selection of food had been offered gave significant correlations (all positive) in 6 of 38 comparisons only. These all involved females. The sex of the animals involved (five females and three males), did not, however, contribute significantly to variation in the strength of the correlation coefficient (sex effect $F_{2, 31} = 0.82$, $P = 0.5$; model $F_{6, 31} = 4.43$, $P = 0.002$). Similarly, comparisons between the same and different individuals did not significantly influence variation in the coefficient ($F_{1, 31} = 0.58$, $P = 0.5$).

Temporal changes in preference

The degree of correlation between rankings of foods was independent of whether trials were done on the same night or on different nights ($F_{1, 31} = 3.72$, $P = 0.06$), but it was dependent on the time of night at which the trials were carried out (Fig. 1: $F_{1, 31} = 6.87$, $P = 0.01$). The absolute length of time between trials was not a significant factor ($F_{1, 31} = 2.23$, $P = 0.1$), nor was the difference in temperature at the time of the trials ($F_{1, 31} = 2.19$, $P = 0.1$).

A low value of r_s for the pairwise comparisons could be a result of a difference between the ranking of the foods eaten by both animals, but also in the number of types eaten. The numbers of food types eaten during the night (Fig. 2) shows a bimodal pattern with one peak towards the beginning of the night, a trough around 0130 hours and a second peak towards the end of the night. Bimodality was confirmed at $P = 0.05$ (broken line, Fig. 2), using the procedure described in the Appendix. The trough in the middle of the night coincides with a drop in percentage active radio-fixes recorded for four wood mice (two females, two males) radio-tracked for 5 nights on the farm, and with a drop in the success in trapping subjects for the study (Fig. 3). The radio-tracked animals all spent 2–4 h in the middle of the night in their burrows.

Preferences differed between the two active periods (defined as the two periods on either side of the trough in the feeding pattern-curve (Fig. 2), i.e 2130–0000 and 0230–0530 hours). Rankings from pairs of trials conducted within the same active period showed a greater degree of concordance than rankings from pairs of trials of which

Table 1. Content of nutrients and toxins of foods eaten

Food types eaten by one or more wood nice	g/100 g wet weight							
	Times offered	Mean rank when eaten	Total carbon	Sugar alone	Protein	Lipids	Water	Toxins
Sweetcorn var. LG 20/80 (*Zea mays* L.)[a]	6	1.3	17.0	2.0	3.4	1.8	76.0	
Winter wheat var. Galahad (*Triticum aestivum* L.)[b]	24	1.7	63.9	2.1	12.7	2.2	14.0	phytohaemagglutenins[g]
Bramble (blackberry) (*Rubus* sp.)[e]	21	2.1	5.1	5.1	0.9	0.2	85.0	
Oilseed rape var. Libravo (*Brassica napus* L.)[d]	26	2.9	22.7	4.1	22.7	36.0	10.0	glucosinolates[h]
Winter barley var. Marinka (*Hordeum vulgare* L.)[b]	26	3.5	64.0	1.8	10.6	2.1	11.0	phytohaemagglutenins[g]
Common wild oats (*Avena fatua* L.)[e]	22	3.9	32.0	Tr	13.6	5.7	13.0	
Greater plantain (*Plantago major* L.)	26	4.0	–	–	–	–	–	
Yellow oatgrass *Trisetum flavescens* (L.) Beauv.	26	4.0	–	–	–	–	–	
Wild rose (rosehip) (*Rosa* sp.)[f]	26	4.2	–	–	1.2	0.8	55.2[k]	tannins[j]
Elder (elderberry) (*Sambucus nigra* L.)[f]	9	5.0	–	–	1.9	0.3	81.6[k]	cyanogenic glycosides[i]
Hawthorn (haw) (*Crataegus monogyna* Jacq.)[f]	25	5.0	–	–	1.6	0.6	56.4[k]	tannins[j]
Blackthorn (sloe) (*Prunus spinosa* L.)[f]	7	5.5	–	–	0.6	0.4	68.9[k]	
Field maple (*Acer campestre* L.)	26	6.0	–	–	–	–	–	

[a] Holland Buss and Unwin (1992) [d] Niewiadowski (1983) [g] Liener (1979) [j] Herrera (1984)
[b] Holland et al. (1988) [e] Sosulski and Sosulski (1985) [h] MAFF (1983) [k] Snow and Snow (1988)
[c] Holland, Unwin and Buss (1992) [f] Herrera (1987) [i] Cooper and Johnson (1988)

Table 2. Food types not eaten

Species	Times offered	Toxins
Autumn hawkbit (*Leodonton autumnalis* L.)	26	
Cleavers (*Gallium aparine* L.)	24	
Common agrimony (*Agrimona euptoria* L.)	25	
Common knapweed (*Centaurea nigra* L.)	26	
Crow garlic (*Allium vineale* L.)	23	n-propyl disulphide[a]
Giant hogweed (*Heracleum mantagazzianum* Som. and Lev.)	25	furanocoumarin[b]
Greater knapweed (*Centaurea scabiosa* L.)	26	
Hedge parsley (*Anthriscus sylvestris* (L.) Hoffm.)	26	furanocoumarin[b]
Hogweed (*Heracleum sphondylium* L.)	26	furanocoumarin[b]
Marsh thistle (*Cirsium palustre* (L.) Scop.)	25	
Privet (*Ligustrum vulgare* L.)	24	ligustrin[c]
Ribwort plantain (*Plantago lanceolata* L.)	26	
Sterile brome (*Bromus sterilis* L.)	24	
Woody nightshade (*Solanum dulcamara* L.)	23	solanine[c]

[a] Cooper and Johnson (1988)
[b] Berenbaum (1981)
[c] Kear (1968)

one was conducted in the first active period and the other in the second ($t_{23} = -3.43$, $P = 0.002$).

The numbers of food types taken per trial showed a positive correlation with the number of captures within the same time blocks ($r_6 = 0.72$, $P = 0.04$). As expected, the numbers of items taken per trial were positively correlated with the mass of the foods eaten ($r_{24} = 0.93$, $P = 0.0001$), justifying the use of numbers of items eaten as the basis for the rankings. Neither the numbers of items nor the mass of food eaten per trial showed any bimodality (fit of quartic curve: $F_{4,18} = 2.01$, $P = 0.1$, and $F_{4,18} = 1.02$, $P = 0.4$, respectively, Fig. 4), but from the first to the second active period the mass of the food eaten decreased ($P = 0.02$, permutation test) as did the variance in mass (adjusted $\chi_1^2 = 4.68$, $P = 0.03$, Bartlett's test of homogeneity).
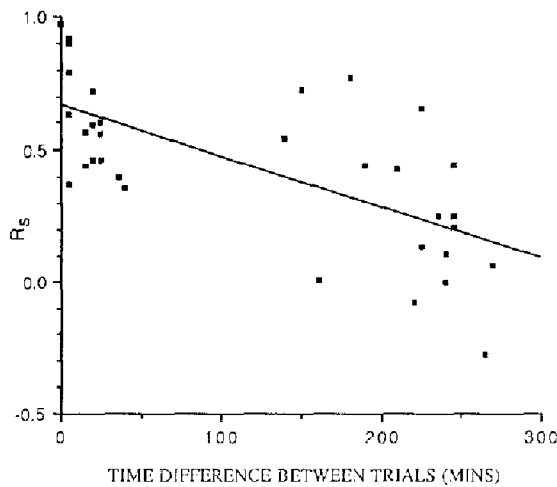
Fig. 1. Spearman rank-order correlation coefficient (r_s) as a function of the difference in the time of night between pairs of trials compared $(F_{1,31} = 6.87, P = 0.01)$
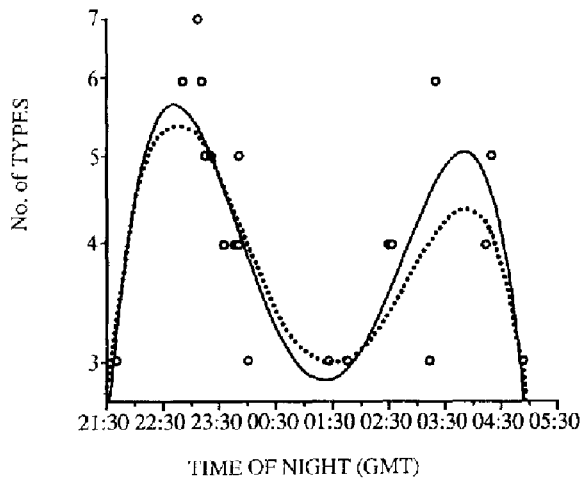

Fig. 2. Variation in number of food types taken throughout the night. The regression is best described by a quartic equation (fourth-order polynomial, $F_{4,18} = 8.05$, $P = 0.0007$), equations of lower orders not providing significant fits. Values of y were logged to bring the regression to zero at the beginning and at the end of the active periods. *Broken line* gives the flatter 95% confidence limit for the quartic (see Appendix)

Nutritional value

The percentage contents of carbohydrates and of protein in the six most preferred foods (Fig. 5a, b) did not differ between the two active periods (permutation test, $n = 8$ and 5, $P = 0.7$ for both, permutation test) and neither did water or lipid contents ($P = 0.4$ and $P = 0.5$), whereas the percentage content of sugar alone decreased significantly from the first to the second active period (Fig. 5c, $P = 0.02$). The percentage content of all the above mentioned components differed significantly between inactive and active periods: foods chosen during the active periods were higher in carbohydrates and proteins (permutation test, $n = 13$ and 8, $P = 0.002$ for both) while those chosen during the inactive period were higher in sugars and water ($P = 0.02$ for both). This might suggest an underlying
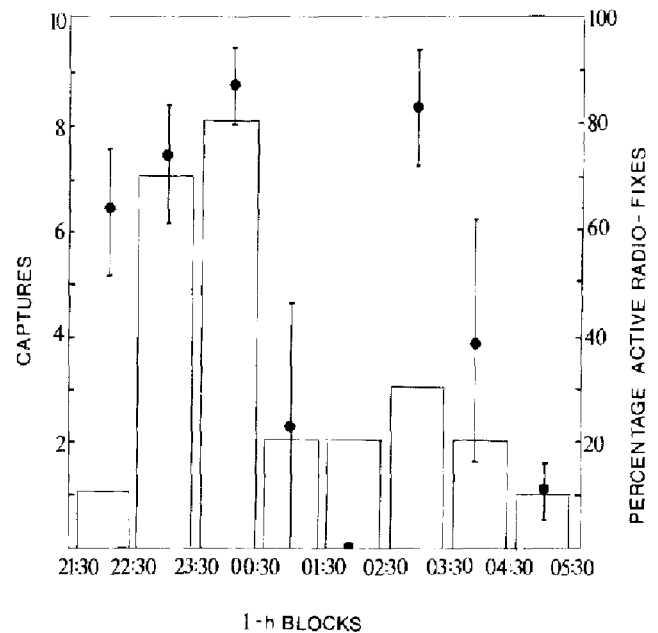

Fig. 3. Variation in number of captures throughout the night (*histogram*) and mean percentage active radio-tracking fixes for 4 mice (*spots* and *bars* indicate mean $\pm$ SE)
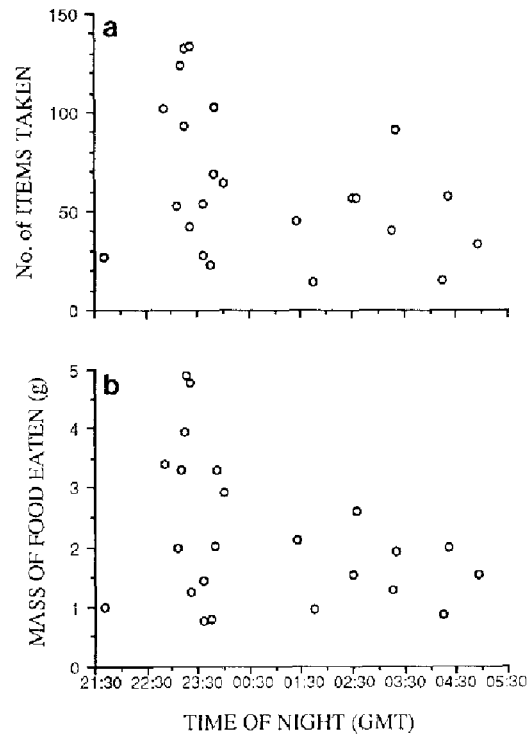

Fig. 4a, b. Variation in the number of food items (a) and the mass of food taken (b) with time of night

dependency between the carbohydrate and protein contents and between water and sugar contents in each of the food types eaten. The carbohydrate and the protein contents are indeed strongly correlated in the diets chosen (Fig. 6a, $r_{24} = 0.99$, $P = 0.0001$) as are the water and sugar contents ($r_{24} = 0.94$, $P = 0.0001$), but such correlations are not found in the individual food types offered (Fig. 6b), the
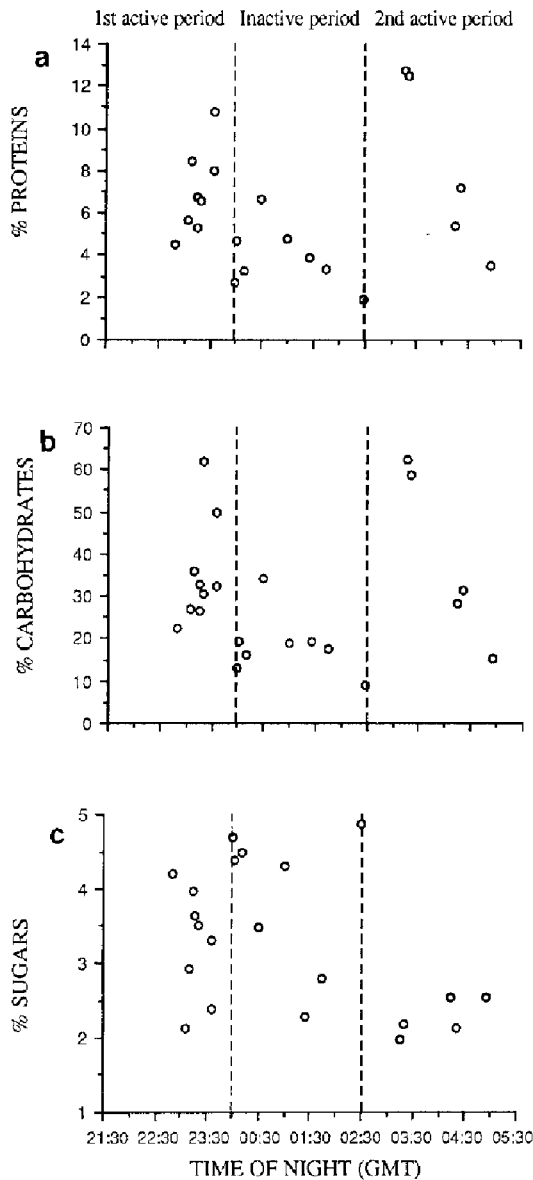
Fig. 5a–c. Percentage proteins (a), carbohydrates (b), and sugars (c) in diets chosen throughout the night. Trials in which blackberries were not offered are excluded
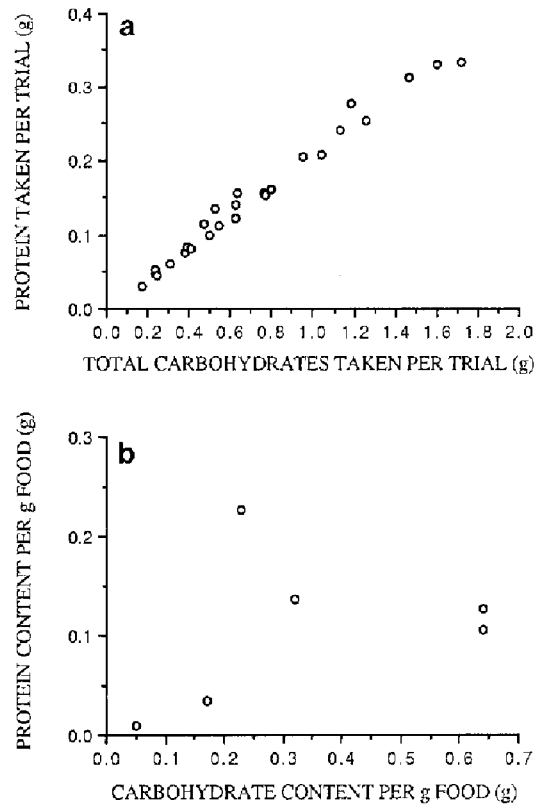

Fig. 6a, b. Variation in protein content with total carbohydrate content in diet chosen (a) and (b) in the six most favoured foods (blackberries, sweetcorn, oilseed rape, wild oats, wheat and barley)

only positive correlation being that of protein with water contents ($r_3 = -0.86$, $P = 0.03$). The mice seem therefore to be selecting for both carbohydrates and proteins in the active periods and for both water and sugars in the inactive period. Trials in which blackberries were not offered were excluded from the calculations as they showed significantly different results from trials which included blackberries, with higher percentages of carbohydrates and proteins and lower percentages of sugars and water (permutation test, $n = 5$ and 21, $P = 0.009$) in each case.

Discussion

Some studies have tested preferences for certain foods by recording the amount taken from feeding stations in the field by unknown individuals (e.g. Vickery 1984), while in

others, foods have been offered to known animals in the laboratory (e.g. Kerley and Erasmus 1991; Miller 1954; Partridge and MacLean 1981; Tempel et al. 1985). The technique adopted in this paper combines the advantages of using wild rodents restrained within their natural environment for a maximum of 4 h (2 h in trap plus 2 h in cage) and testing for their preference for local, wild-growing foods, with the advantages of using animals of known weight, sex, breeding condition and approximate age, and being able to repeat the tests on the same animals. Using this technique moreover circumvents a number of methodological difficulties encountered in diet choice tests, including (1) differential breeding status and nutritional requirements of the animals tested, (2) previous experience and background diet, and (3) the effects of depletion of preferred food types and a resulting decrease in encounter rates throughout trials. The effect of previous experience and of the background diet of the study animal prior to food choice tests has been discussed by Muetzelfeldt (1975), Partridge (1981) and Partridge and MacLean (1981). Test animals that have been given a nutrient supplement make physiological adaptations to a diet of one type and will show a preference for that food, as in the case of the voles in Partridge's study (1981), whereas those that have been fed on a nutritionally insufficient diet of one cereal will subsequently select for alternative food types in order to restore their nutrient balance, as was the case in Muetzelfeldt's study (Muetzelfeldt 1975; Partridge and MacLean 1981). The animals tested in the present study had access to wheat for up to 2 h in the traps in which they

had been caught which is unlikely to have been sufficient time for the mice to become deficient in some nutrient. As the majority of the animals had been caught in fields with ripe wheat, their diet in the traps would not have differed greatly from that experienced in the field. This procedure also permitted the assumptions, that (1) wood mice did not consume enough to reduce the density of any food sufficiently to affect the encounter rates, and (2) search time was comparable for each food type. A number of papers on food preference of seed-eating rodents have been criticized on the basis that the authors failed to distinguish between the different parts of the seeds when calculating nutrient contents (e.g. Jenkins 1988; Kerley and Erasmus 1991). Of the seeds used in the present analysis, grains of wheat and barley were either eaten in their entirety or chewed randomly (the mice would begin chewing at either end, often leaving half the seed uneaten), rape seeds were always eaten entirely, and the pulp of blackberries is fairly homogeneous in its nutrient content.

The results of the trials show that (1) wild wood mice preferred some of the foods available in fields and hedgerows to others, and avoided some completely; (2) variation in food preferences was not attributable to differences between individuals, but followed a temporal pattern; (3) the number of food types eaten peaked early and late in the night with a trough in the middle of the night; (4) the amount of food eaten did not reflect this pattern, being greatest but most variable early in the night and more consistently lower in the second active period; and (5) carbohydrate, protein, lipid and water contents of the diets differed between active and inactive periods but not between the two active periods early and late in the night, whereas sugars were selected for early in the night.

Two laboratory-based studies have revealed that laboratory rats (Tempel et al. 1985) and domestic chicks (Hayne et al. 1986) selected for a diet high in carbohydrates at the beginning of their active period and changed to a diet high in proteins prior to their period of rest (i.e. towards the end of a dark phase for rats, and towards the end of a light phase for chicks). In both these experiments, however, the animals were offered homogenised feeds made up to differ only in carbohydrate and protein contents (the rats had an additional choice of a fatty diet), while vitamin and mineral contents and caloric values were kept constant. In both cases sugars and other carbohydrates were linked in the diets offered, and if the rats and chicks were selecting for sugars, they had to choose the carbohydrate diet. In this study the sugar and the total carbohydrate contents of the foods offered were not correlated ($r_4 = 0.50$, $P = 0.3$), and the mice selected for sugars only at the beginning of the night rather than carbohydrates as a whole. Studies on rats under self-selection conditions (Theall et al. 1984) have revealed that a constant protein:carbohydrate ratio is maintained over a 24-h period of feeding. The actual ratio chosen is that which can be expected neither to increase nor to decrease the rats' brain serotonin (Fernstrom and Wurtman 1972). In this study, wild wood mice under self-selection conditions maintained a markedly constant protein:carbohydrate ratio throughout the night, while varying their choice of specific carbohydrates. As sugar is more quickly digestible than other carbohydrates (Stryer 1981) they may be selecting for a quick source of energy at the beginning of their first active period to help elevate their body temperature (Collier and Squibb 1967).

Appendix

Given some *a priori* reason for expecting a data set to have a bimodal pattern, the following procedure provides a confidence limit for the bimodality, provided that when the data are fitted to the quartic equation:

$$y = a + b_1 x + b_2 x^2 + b_3 x^3 + b_4 x^4,$$

the constant b_4 is negative and significant. Confidence intervals are constructed around b_4 from its standard error ($b_4 \pm SE = b_{4a}$ and b_{4b}). Supposing b_{4a} is numerically the smaller (closer to zero), a new dependent variable, z, is determined as

$$z = y - b_{4a} x^4.$$

A new set of parameters, a^*, b_1^*, b_2^* and b_3^* are estimated from z:

$$z = a^* + b_1^* x + b_2^* x^2 + b_3^* x^3.$$

$b_{4a} x^4$ is now recombined with these parameters to give

$$y = a^* + b_1^* x + b_2^* x^2 + b_3^* x^3 + b_{4a} x^4.$$

This is the flattest quartic having an acceptable fit. This curve being bimodal will be evidence that bimodality is a genuine feature of the data.

Example using data shown in Fig. 2

The observed data were logged and fitted to a quartic equation using Proc Reg (SAS Institute Inc. 1988) giving:

$$y = 9.07 \times 10^{-1} + 2.74 \times 10^{-2} x - 2.86 \times 10^{-4} x^2$$
$$+ 9.86 \times 10^{-7} x^3 - 1.07 \times 10^{-9} x^4,$$

($P = 0.0004$, 0.0001, 0.0001, 0.0001, and 0.0001).

SE for $b_4 = 2.12 \times 10^{-10}$, giving upper and lower confidence limits of 1.29×10^{-9} and 8.68×10^{-10}. The latter value, being closer to zero, becomes b_{4a}, which, for each value of y gives a value, $z = y - 8.68 \times 10^{-10} x_4$. Fitting a 3rd-order polynomial to this new set of z values gives: $z = 1.00 + 2.26 \times 10^{-2} x - 2.34 \times 10^{-4} x^2 + 7.96 \times 10^{-7} x^3$. Re-entering the value for b_{4a} gives the formula for the flatter 95% confidence limit for the quartic:

$$y = 1.00 + 2.26 \times 10^{-2} x - 2.34 \times 10^{-4} x^2 + 7.96$$
$$\times 10^{-7} x^3 - 8.68 \times 10^{-10} x^4.$$

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