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Adaptive food choice of bank voles in a novel environment: choices enhance reproductive status in winter and spring

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Using wild and laboratory animals, we studied the food preference of bank voles, *Clethrionomys glareolus*, as a function of sex and reproductive status. Wild voles were captured in winter and early spring in central Finland, and during one day of captivity, were examined for food preferences. Pregnant females consumed significantly larger quantities of food rich in animal oil and protein than did non-reproductive females and males. Food preferences of pregnant females may indicate that spring breeding is constrained by access to fat and animal protein. Non-reproductive males showed a preference for spruce seeds, which may indicate a specific value of spruce seeds for this group, possibly related to the maturation process. Species-specific food constraints can differ between sexes and across seasons. Tests with laboratory animals revealed that voles prefer both artificial and unfamiliar food items over their staple diet. These data suggest that food choice in voles may have an unlearned component, and that animals can make adaptive food choices under experimental conditions. We suggest that food preference under experimental conditions can be a useful indicator for food constraints in the wild.

Introduction

In temperate environments, the life histories of terrestrial vertebrates are influenced by food availability (Boutin 1990). In extreme environments characterized by low temperatures and short growing seasons, iteroparous breeders are restricted to reproducing within a few months (Millar 1987, Sharpe & Millar 1991). Food supply during the non-breeding season may thus be essential for the onset of breeding and subsequent fitness in a breeding season (e.g. Tait 1981, Taitt & Krebs 1981, Eccard & Ylönen 2001, Ylönen & Eccard 2004). Seasonal animals must time their breeding so that the highest food demands coincide with food availability peaks. However, reproductive activation in boreal habitats occurs long before the onset of new plant material growth, and is based solely on consumption of partly depleted, late winter resources.

Food limitation in wild populations is usually studied by food supplementation (for review *see* Boutin 1990). Most studies supplementing small rodent populations have used grain in large quantities (e.g. Andrzjewski 1975, Banach 1986), although grain is a low energy supplemental food and a poor supporter of maturation and breeding (e.g. Batzli 1983, Prevot-Julliard *et al.* 1999). Other studies have used lab chow (e.g. Cole & Batzli 1978, Taitt & Krebs 1981), a food mixture high in proteins and designed to provide rodents with all necessary vitamins, nutrients, and trace elements. Sheer quantity of poor food or a mixture of ingredients might nevertheless mask what would be the limiting factor without supplementation.

The natural food of small wild animals is mostly studied by analysing stomach contents of snap-trapped specimens (e.g. Holisova 1971, Hansson & Larsson 1978) or by analysing faeces (e.g. Ferns 1976). These forms of analyses may show a preference for a food type, providing the type falls within the often marginal fraction of identifiable food items, or may be useful to indicate which food items are readily available (for a review on methods and relevance *see* Hansson 1985: 156–157). Given that these methods are based on analysis of foraged items, the suitability of faecal analysis for the determination of food preference can be questioned (Phillipson *et al.* 1983). If the preferred food type is scarce, it cannot be identified through the study of ingested food.

Although bank voles are omnivores, past research on food limitations has concentrated on the impact of seeds (Boutin 1990 for a review, Eccard & Ylönen 2001). Only few studies have concentrated on animal protein supplementation of boreal rodents during winter and spring, and these showed that increased protein availability allows earlier maturation and breeding of females (McAdam & Millar 1999, von Blanckenhagen *et al.* 2001). Protein rich food sources are available also in boreal environments, as a considerable number of invertebrate species are available for consumption under the winter snow (Aitchinson 1984, 1989).

To investigate food preferences during winter and spring in bank voles, we conducted a food choice experiment with field caught animals. Comparisons were made with regard to sex and reproductive status. Naturally, the usefulness of any food preference test depends on the food types offered. In our experiment, we tried to find a balance between naturally available and artificial, concentrated food types. In our analysis, we distinguish food types based on animals — that is, containing animal-based oils and protein — from food types based on seeds. Although small mammals are thought to benefit from sampling novel foods to assess their nutritional value (Vickery 1984) we wanted to guard against the possibility that animals choose the food they are habituated to, over food types they might be missing, and against the possibility of neophobia towards novel food. We thus conducted a control test with bank voles from a laboratory colony. These voles were on a limited diet which was known to us.

Material and methods

The bank vole is an omnivore, intermediate between pronounced granivores and folivores (Hansson 1985). Analysis of ingested food items revealed that the percentage of animal food — consisting of invertebrates like insects, centipedes, molluscs, annelids, and small vertebrates — is between 5% and 10%, with a peak in spring (Hansson 1985). Food can be considered a limiting factor in boreal bank vole populations, since food supplementation increased the proportion of year-born females able to mature in open populations (Prevot-Julliard *et al.* 1999), and led to an earlier start of breeding season in enclosed populations (Ylönen *et al.* 1988, Eccard & Ylönen 2001). Similarly, small amounts of supplemental spruce seeds were able to induce earlier maturation in male bank voles (Kaikusalo 1972, Eccard & Ylönen 2001). Supplemental animal protein induced an earlier increase in male body weight and an earlier maturation and breeding in open populations (von Blanckenhagen *et al.* 2001). Interestingly, litter size and pup weights were not affected. In other studies, voles provided with large quantities of poor quality food (barley) had earlier but smaller litters than unsupplemented controls (Ylönen & Eccard 2004). These findings indicate that food quantity and quality may be a limiting factor in the growth of bank vole spring populations.

Food choice experiments were conducted in an experimental arena (50 × 30 cm). Food was offered in small plastic cups embedded in a wooden tray (50 × 15), and was weighed before the trial on an electric scale (± 0.05 g). Food types were randomly assigned to cups in the feeding tray. We offered two types of animal-based foods: dried *Chironomid* larvae (food for aquarium fish) that resemble insect larvae available in nature, and fish pellets that contained animal oil and protein in an artificial, concentrated form. We also offered four types of plant-based foods: spruce and birch seeds, which are likely to be available in nature, barley seeds, and a seed mixture (mix containing millet, hemp and oat) that resembles an artificial, concentrated source of rich plant food. Leftovers were collected and weighed the next morning. All food was dry and had been stored in open containers before the trial, thus no correction for water content was needed. Voles were weighed before and after the experiment.

Between mid-February and mid-April 1997, Ugglan special traps baited with sunflower seeds were used to trap wild bank voles around Konnevesi research station in central Finland (62°N). Traps were controlled twice a day, and animals captured in the morning were transferred to the laboratory where the voles were kept in a standard mouse cage with lab chow and water for the rest of the day (6–8 h). In the evening they were transferred to the experimental arena and provided with water, hay, and the feeding tray. The experiment lasted until next morning (10–12 h). Ten animals were tested while in non-breeding wintering condition (6 non-pregnant females, 4 males with abdominal testes) and 14 animals in breeding condition (6 pregnant females, 7 males with scrotal testes). Body weight differed between reproductive voles (22 ± 4 g) and non-reproductive voles (17 ± 3 g, $t_{14} = 2.9$, $p = 0.010$). All animals were released at the place of capture the next day.

Laboratory animals ($n = 28$) were captured in November 1996 and kept in the laboratory on an *ad libitum* diet of barley, potatoes and water, with weekly rations of spruce seed pellets glued together with potato starch. Food preference tests of laboratory individuals were conducted from late January to late March 1997. Experimental procedure was identical to the tests of the wild animals, with the exception that these animals were not released at the conclusion of the experiment. Laboratory kept females ($n = 16$) were not reproductive. Males were either reproductive ($n = 7$) or non-reproductive ($n = 5$) during the test trials. The body weight of lab voles differed between reproductive males (20 ± 3 g) and non-reproductive voles (females: 17 ± 2 g, males: 17 ± 1 g, $F_{2,23} = 4.2$, $p = 0.028$).

We analysed the total consumption, consumption of each item, percentage of plant food versus animal food consumption, and the diversity of chosen food. Some foods had different net energetic returns than others — for example, it is more time consuming to handle seeds that need to be husked than eating fish pellets. Husks of consumed bird food and spruce seeds were removed before weighing, therefore the consumption of these foods may actually be overestimated. Similarly, small, lightweight items like dried *Chironomid* larvae and birch seeds require more handling effort than large fish pellets. Furthermore, it was impossible to assess which seed the voles had picked from the seed mix. To overcome these problems, we analysed the percentage of foods containing animal protein versus foods containing plant protein. Diversity of food choice was assessed by counting the number of food types of which the animal had consumed more than 0.05 g.

Comparisons were conducted as a function of sex and reproductive status, using *t*-test, χ^2-test, One-Way ANOVA, and Tukey-Kramer post-hoc tests where appropriate. Non-parametric Mann-Whitney *U*-test, Fisher's exact test, and Kruskal-Wallis *H*-test were used if counts or proportions were compared, or if variances were not similar.

Results

Laboratory voles

Lab voles chose a very diverse diet consisting of an average of 4.5 different food types, and had an average total food intake of 1.5 g (Table 1). All lab voles consumed seed mix (Table 1), and this food was consumed in the highest amount (Fig. 1). Fish pellets and spruce seeds were consumed in similar proportions (82% and 86% of voles) and in similar amounts. The staple diet of the laboratory animals, i.e. spruce seeds and barley, was consumed by many animals (86% and 75 % of voles) but constituted only a combined 33% ± 18% of the total food intake. Most voles lost body weight during the experiment. Total intake and intake of different food types did not differ among females, non-reproductive males, and reproductive males (One-Way ANOVA: $F_{2,25} < 1.7$, $p > 0.205$).

Wild voles

Field caught voles chose a less diverse diet (3.4 food types) than did the lab animals (Table 1 and Fig. 1). A smaller proportion of wild voles consumed chironomids, fish, seeds, and birch as compared with the lab voles. The total food intake (g) did not differ. Proportions of voles that consumed barley and spruce seeds did not differ, however, wild voles on average consumed a higher amount and a larger percentage of spruce seeds (70%) than did the lab voles (20%). Wild voles consumed lower percentages of animal foods than the lab voles. On average, wild voles gained body weight during the experiment (descriptives and statistics in Table 1).

Pregnant females consumed a significantly higher proportion of the animal-based food (Kruskal-Wallis test: $H = 11.4$, df = 3, $p = 0.009$) than reproductive males (post-hoc: $p = 0.005$, Fig. 2), but not when compared with non-reproductive males and females. Non-reproductive males consumed significantly more spruce seeds (1.0 ±

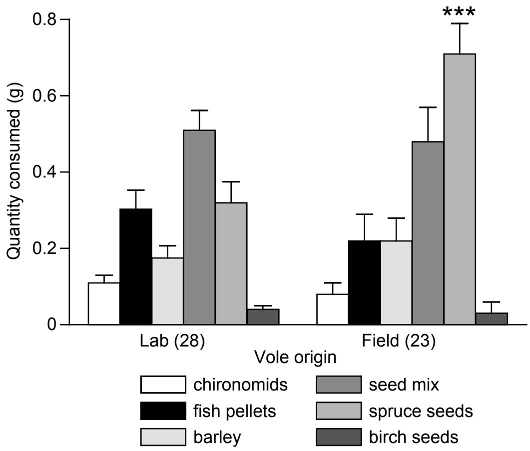

Fig. 1. Food choice (mean + SE) of wild-caught boreal bank voles in winter and spring as compared with that of voles kept many weeks in the laboratory on a diet of barley, spruce seeds and potatoes. Wild voles consumed smaller quantities of chironomids, fish pellets and birch seeds (Mann-Whitney *U*-test: $p = 0.035$, 0.054, 0.001), and larger amounts of spruce seeds ($p < 0.001$) than lab voles. Consumed amounts of barley and seed mix did not differ.

Table 1. Food choice of bank voles in central Finland in winter and spring. Laboratory: 28 bank voles kept on a diet of potatoes, barley, and spruce seeds for 2–4 months before the feeding experiment, Wild: 23 voles that were tested on the day of capture. Six food types were offered.

	Laboratory		Wild				
	n	%	*n*	%	Statistic	*p*	df
Single food type chosen by *n*/%) voles							
seeds	28	100	18	78	Fishers	0.014	1
spruce	24	86	22	96	Fishers	0.362	1
fish	23	82	12	52	$\chi^2 = 5.3$	0.022	1
barley	21	75	14	61	$\chi^2 = 1.2$	0.279	1
chironomids	20	71	9	39	$\chi^2 = 5.3$	0.02	1
birch	13	46	1	4	Fishers	0.001	1
	Mean	SD	Mean	SD			
Diversity of diet (number of consumed food types)	4.6	1.1	3.4	1	$U = 180$	< 0.001	51
Food intake (g/night)	1.4	0.6	1.8	0.8	$t = 1.7$	0.101	49
Spruce seed, staple diet of lab voles (%)	20	16	57	20	$U = 138$	< 0.001	51
Barley, staple diet of laboratory voles (%)	11	11	12	14	$U = 342$	0.536	51
Animal food (fish pellets + Insect larvae) (%)	28	17	15	17	$U = 195.5$	0.002	51
Weight difference after – before experiment (g)	–0.6	1.2	0.6	1.2	$t = 2.4$	0.02	33

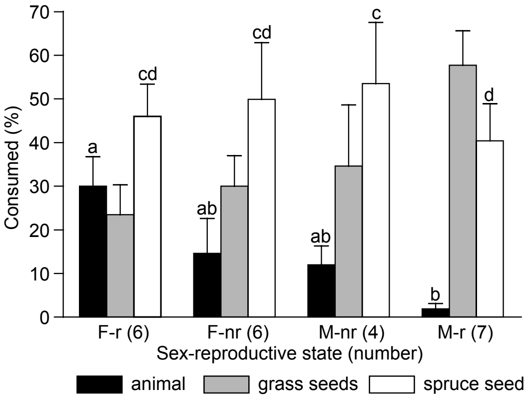

Fig. 2. Food choice (mean + SE) of wild-caught bank voles of different sex and reproductive state in a cafeteria test during winter and spring on the day of capture. Animal-based foods consisted of fish pellets and chironomid larvae, grass seeds (and forb seeds) included barley, hemp, millet and oat. F = female, M = male, r = reproductive (testes visible/pregnant), nr = non-reproductive (testes abdominal/vagina closed). Differences between a and b in the consumption of animal food (Tukey-Kramer post-hoc test: $p = 0.005$), and between c and d in the consumption of spruce seeds ($p < 0.05$).

0.5 g, $F = 4.1$, $p = 0.022$) than did reproductive males (0.5 ± 0.2 g, post-hoc: $p < 0.05$, Fig. 2), but not more than females (non reproductive: 0.6 ± 0.3 g, pregnant: 0.9 ± 0.2 g, both $p > 0.05$). The total food intake did not differ based on sex or reproductive status ($F = 2.0$, $p = 0.143$).

Discussion

Our data suggest that bank voles prefer food types that benefit them most, given their standard diet, their sex, and their reproductive status. Given that this preference is often expressed for unfamiliar and artificial food types, our results suggest that animals make adaptive choices in novel environments, and that food choice trials can be used as a tool to indicate food scarcity and food requirements in the wild. Depending on the food types offered, choice trials may offer additional information as compared with the analysis of faeces or stomach contents. These latter methods allow for only a fraction of the ingested material to be identified, and this fraction indicates the availability of food types rather than food preferences.

The laboratory and wild caught animals were roughly the same weight. The laboratory animals lost a small amount of weight during the one-night experiment. This raises the possibility that absent but necessary food types were chosen over the standard diet. Alternatively, the wild captured voles gained weight, which may suggest that these animals had fewer nutritional deficits to compensate for, and were thus able to choose a nutritionally adequate diet during the test.

The preferences exhibited by the bank voles support the hypothesis that animal-based food may play an important role in the reproduction of females in the spring (Fig. 2). Animal protein, for an omnivore species like the bank vole, may be an essential food during pregnancy and lactation, when protein requirements reach their peak (Clutton-Brock *et al.* 1989). Most studies that supplement food to wild rodent populations concentrate on seeds (Boutin 1990), and we know of only two studies that focused on animal protein supplementation of boreal rodents during winter and spring. These studies show that increased protein availability allows earlier maturation and breeding of females. Animal protein diet also enhanced nestling growth and nestling survival, indicating particular high needs of lactating females for protein (McAdam & Millar 1999, von Blanckenhagen *et al.* 2001). However, other food choice studies suggest that small mammals attempt to maximise their energy intake (e.g. Kerley & Erasmus 1991). Thus fish pellets, which where rich in fish oil, may have been taken mainly for their high caloric value. We cannot distinguish whether fish pellets were eaten because of their oil or protein content or possibly other special compounds such as steroids or calcium. Unfortunately, this problem applies to any natural invertebrate food item.

Wild caught voles consumed high amounts of spruce seeds (Fig. 1). Spruce seeds can be found on top of the snow on sunny spring days, but seed yield had been very low during this study year (Eccard & Ylönen 2001). Laboratory studies have shown that spruce seeds are important for activation of maturation in bank vole males (Kaikusalo 1972 in the laboratory, and Eccard & Ylönen 2001 in a food supplementation experiment). Indeed, non-reproductive males consumed higher amounts of spruce seeds in the food-choice tests than did reproductively mature males. The attractiveness of spruce seeds may be related to findings that conifer tissue contains secondary plant compounds and mammalian steroid hormones (Sahden-Krehula *et al*. 1971, Simons & Grinwich 1989), although many tree seeds also contain deterrent compounds (Grodzinski & Sawicka-Kapusta 1970). Our finding that spruce seeds are preferred by non-reproductive males may indicate that spruce seeds provide an important compound for the onset of maturation for wild bank voles. However, females also consumed high quantities of spruce seeds. The effects of spruce seeds on females is not well-studied (Eccard & Ylönen 2001).

In conclusion, food-preference trials can be used to identify preferred food types in wild animal populations. Voles in our study made adaptive choices that indicated scarce but nutritionally important food types. Animals prefer food items that benefit them most given their standard diet, sex, and reproductive status. In bank voles, we found that animal oil or protein, which is probably limited in the field, was a preferred resource during spring for pregnant females. Our data also suggest that spruce seeds may be important for the onset of reproduction in bank voles, since they may play a role in maturation of males.

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