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Foraging behaviour of shrews

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This paper reviews the foraging behaviour of temperate shrews, including the ecological and physiological constraints on foraging decisions. Ecological constraints limit food availability through resource competition and predation. The physiological constraints include the sensory capabilities of shrews, their energy requirements and their physiological capacity for food processing. Several kinds of foraging situations have been studied with shrews. This paper reviews experiments on prey selection and factors affecting it, risk-sensitive foraging, and the effects of temporal and spatial variation in prey availability on foraging decisions.

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1. Introduction

Shrews comprise the family Soricidae of the order Insectivora, with some 250 described species (Corbet & Hill 1980), some of which have rather restricted distributions (many tropical species) while others have continent-wide distributions (especially many temperate species). The Soricidae is divided into two subfamilies: Soricinae and Crocidurinae. Crocidurinae have a more southern distribution and they are more sociable than Soricinae. For a detailed comparison of the two subfamilies see Vogel (1980) and Genoud (1988). This paper is restricted to the foraging behaviour of Soricinae shrews.

Shrews have an exceptionally high mass-specific metabolic rate, and they are so small that they are unable to store large energy reserves in their bodies (Vogel 1976, Hanski 1984). This means that shrews are unable to sleep for longer than a few hours at a time. The Soricinae shrews have a higher mass-specific metabolic rate than Crocidurinae (Vogel 1976), and lack the ability to enter torpor (except for *Notiosorex crawfordi*; Lindstedt 1980, and possibly *Sorex sinuosus*; Newman & Rudd 1978), while many species of Crocidurinae can make use of torpor to save energy whileasleep or during unfavourable environmental circumstances (Newman & Rudd 1978).

Because of their constant need for food and wide range of potential prey items (e.g. Pernetta 1977, Aitchison 1984), shrews have to make hourly vitally important decisions about foraging. Optimal foraging theories (Stephens & Krebs 1986) have been developed to study the adaptive value of foraging decisions. In the long term, an individual which maximizes its short- and medium-term foraging efficiency may increase its rate of reproduction and thus its fitness. Classical optimal foraging theory assumes that only the mean reward rate affects foraging decisions, while models based on the risk of starvation assume that both the mean and the variance are important (Barnard et al. 1985). The risk-sensitive foraging theory (Caraco et al. 1980, Caraco 1981, Houston & McNamara 1985) predicts that when an individual is running below its estimated energy balance, and when the average reward rate at the feeding sites is lower than the requirement, the individual is likely to choose the option with a high variance in reward rate, which would give it a higher chance of survival. In contrast, when an individual is running above its estimated energy balance it will choose low reward variability (Barnard & Brown 1987).

The two basic models of optimal foraging, on prey and patch selection, assume that the foraging individual attempts to maximize the average rate of energy intake. The prey model makes three main predictions (Stephens & Krebs 1986). First, the zero-one rule, according to which a prey type is always taken or is always ignored in a given foraging situation. Second, the prey types are ranked by profitability (energy gained per energy expended in procuring the prey),

and the prey are added to the diet in the order of their rank. Third, inclusion of a prey type in the diet does not depend on its own encounter rate. The patch model's main result is the marginal value theorem, according to which the rate of gain in a patch at a point when it is left equals the long-term average rate of gain in the environment (Stephens & Krebs 1986).

There are several limitations to the basic models, such as the assumption about separate encounters with prey and about complete information, the forager's state is not considered, etc. (Stephens & Krebs 1986). In spite of these limitations, optimal foraging models are often successful in predicting decision rules for predators in simple situations (Krebs 1978).

I will now firstly examine the environmental constraints, comprising mainly other animals of the same and other species, which as competitors, predators or prey of shrews affect their foraging decisions. I shall next look at the internal factors, such as the energetic requirements, sensory capabilities and the physiology of food processing, that may limit or affect the shrews' foraging decisions. The fourth section of this paper will review experiments testing various foraging problems with shrews.

2. Ecological constraints on foraging

2.1. Assemblages of coexisting shrews

Several species of shrew are usually found together in the same habitat (Moraleva 1987, Sheftel 1989). Assemblages of coexisting shrews usually consist of species of different sizes (Hanski 1990). Size differences are often considered to represent ecological niche differentiation, for example different-sized species specialize in different-sized prey. Similar assemblages of shrews are found both in the palearctic and the nearctic regions (Hanski 1990). In the palearctic region, the numerically dominant species is the common shrew *Sorex araneus*, which is much larger than the dominant species in the nearctic region, the masked shrew *Sorex cinereus* (Kirkland & Kirkland 1989, Virtanen 1989, Hanski 1990).

Apart from size divergence, coexisting shrew species may show other ecological specializations. Most Soricinae species seem to be active around the clock, while many Crocidurinae are nocturnal according to both laboratory (Crowcroft 1954, Martinsen 1969, Buchalczyk 1972, Golden & Meester 1976, Vogel et al. 1981) and field data (Genoud & Vogel 1980, Khlyap 1983, Genoud 1984). Croin Michielsen (1966) and Grainger & Fairley (1978) have shown that the common shrew lives and forages more commonly underground than the pygmy shrew *Sorex minutus*, which forages in the litter-zone, and generally the large species of shrew tend to forage underground to a greater extent than the smaller species (Hanski 1990). Ellenbroek (1980) expected a shift towards more underground activity as proof of a habitat switch in the pygmy shrew in the absence of the common shrew in Ireland, but he did not observe such a shift, suggesting that the difference in the foraging habitat is not caused by present competition, but that the species are genetically adapted to living in a particular microhabitat. However, Dickman (1988) found that when common shrews were removed from an experimental plot, pygmy shrews tended to move into microhabitats previously occupied by the common shrews, and the mean prey size eaten by the pygmy shrew increased from 6.2 to 7.9 mm (27%), while that of control individuals increased by only 2%. Similarly, when Malmquist (1985) selectively removed all the common shrews from an experimental area and found that the density of the pygmy shrew doubled. The larger species of shrew are often more abundant than the smaller species in the most productive habitats, sometimes inhabiting them exclusively, while the smaller species are relatively more abundant in the poorer habitats, probably being negatively affected by the larger species in the best habitats (Malmquist 1985, Hanski 1990).

2.2. Social structure of shrew populations

Territoriality

Shrews are very aggressive in defending their solitary way of life. Young immature shrews start defending territories in late summer; if they do not find a territory of their own they are usually doomed to death (Hawes 1977). The main reason for strict territoriality in immature shrews is probably the need to secure sufficient food resources for winter (Randolph 1973, Hawes 1977). Possessing a territory which the shrew knows thoroughly may be essential also for short-term survival.

The size of the territory is expected to depend on the energy demands of the shrew, on the availability and quality of food, and on the foraging efficiency of the shrew (McNab 1963, Hawes 1977). Croin Michielsen (1966) found that, unexpectedly, the territories of the small pygmy shrews were twice as large as those of the much larger common shrews. This was

explained by the better accessibility of the common shrew to underground food sources, e.g. earthworms, which the pygmy shrews do not make use of.

Wide overlap often exists in the observed food selection of sympatric shrew species, possibly leading to resource competition (e.g. Hamilton 1930, Dickman 1988). In this situation, defending a territory against members of other species may be worth the costs of defence (Hawes 1977). Coexistence is allowed because each species may have one or several microhabitat types where it is a superior competitor (Hawes 1977). Interspecific territoriality between shrew species has been reported by Croin Michielsen (1966), Hawes (1977), Malmquist (1985) and Moraleva (1989).

Mating system

Practically all shrews delay maturation until the spring following their birth (Dokuchaev 1989, Sheftel 1989 and references therein). In spring, females remain territorial while males expand their home ranges (Hawes 1977). The mating system is promiscuity. During lactation the energy requirements of females greatly increase (Glazier 1985, Genoud pers. comm.), explaining why the females expand their territory in spring, though not as much as males (Hawes 1977). Later in summer the old shrews seem to be non-territorial, at least towards juveniles (Croin Michielsen 1966, Moraleva 1989). Females have a post-partum oestrus, and are able to produce two to four litters in rapid succession right up until their death (Crowcroft 1957).

2.3. Predators of shrews

Predation risk may affect foraging in several ways, for example the patch residence time (Stephens & Krebs 1986). Shrews may cache extra food items under cover in safe places or in the nest to avoid predation risk while ingesting food (Dehnel 1961, Maser & Hooven 1974, Skarén 1978, Robinson & Brodie 1982, Martin 1984). The main predators of shrews in Europe are some predatory birds such as owls, harriers and the kestrel (*Falco tinnunculus*), while mustelids do not seem to be important, not at least in Central Finland (Korpimäki & Norrdahl 1987, 1989a). Small mammalian predators dislike the strong smell and taste of shrews (Erlinge 1981). Avian predation on shrews is independent of the density of shrews, which are the second choice for predators strongly preferring voles (Erlinge 1981, Korpimäki & Norrdahl 1989a). This result supports one of the main predictions of the prey models: prey selection should depend only on the density of the prey with higher profitability than that of the target species (Stephens & Krebs 1986). Korpimäki & Norrdahl (1989b) review the predators of shrews in detail.

Most shrew species share the same intestinal parasites over their entire geographical ranges (Haukisalmi 1989). This observation lends further support to the idea that different shrews share the same prey species (next section). The main intermediate hosts of the parasites are Mollusca, Collembola and Lumbricidae. In Poland, the Catopidae (Coleoptera), common insects in small mammal nests, are important intermediate hosts of the parasites of the common shrew (Kisielevska 1963).

2.4. Type and availability of prey

There are no distinct differences in the prey selection of different shrew species. The smaller species usually eat larger quantities of smaller arachnids or opilionids, while the larger species eat, in addition to the smaller prey, earthworms, frogs and even other mammals (Ackefors 1974, Pernetta 1976, Aitchison 1987). The carcasses of dead voles and mice may be an important prey type during winter (Schlüter 1980), and some shrews actively hunt young vole sucklings in their nest (Ružić 1972). Shrews are obviously able to discriminate between different prey types but what is encountered and rejected is not really known (Crowcroft 1957). Shrews will probably eat any animal which they can catch and handle (Pernetta 1976, Aitchison 1984).

The availability of suitable prey is often limited and several investigators have concluded that food availability may limit shrew populations (Holling 1959, Judin 1962, Hawes 1977, Butterfield et al. 1981).

3. Physiological constraints on foraging

3.1. Energetic requirements

Because of their very high mass-specific metabolic rate (Vogel 1976, 1980, Hanski 1984) and small body reserves, shrews need a constant supply of food. A common shrew will survive in the laboratory for less than eight hours without food and water (Crowcroft 1954), and the smaller species starve in even

shorter periods of time (Gebczynski 1971). In the wild survival times may be even shorter. However, the lack of body reserves may be compensated for by short-term food caches (Section 4.6).

In autumn and winter, at below freezing point, the energy cost of maintaining homeostasis at rest is much greater than in summer. The weight of *Sorex* shrews usually drops during winter and their skull and body measurements decrease (Pucek 1970, Hyvärinen 1969). The reduction of body length is induced by histolysis of cartilage and bone tissues on the edges of intervertebral discs. The height of the skull is reduced by actively dissolving the skull bones at the joints, which is carried out from September until January (Hyvärinen 1969). The decrease in body size in winter seems to be an adaptation in Soricinae shrews to save energy, since the energy expenditure is closely related to body size (Genoud 1985, 1988). It is noteworthy that the shrew species inhabiting the coldest regions are, on average, smaller and lighter than the southern species (Mezhzherin 1964).

Shrews have the highest measured quantities of brown fat among mammals (Brown Adipose Tissue, the heat generating tissue which is dispersed all over the body). High concentrations of BAT can be found around the oesophagus and in the thighs around large veins. A large amount of BAT is thought to be another adaptation increasing survival over the winter.

Foraging takes up most of the active time of shrews, especially in winter. Genoud & Vogel (1980) were able by artificial feeding to decrease the daily activity of free-living shrews in winter (*Crocidura russula*) from 495 min (34%) to 208 min (14%), which is close to the activity level of captive shrews. In captivity, the activity level of shrews depends mainly on their energy requirements (Crowcroft 1954, Girons 1959, Genoud 1988).

Refection, or coprophagy, has been observed in many species of shrew (Crowcroft 1952, 1957, Maser & Hooven 1974). In refection the rectum is everted by rapid abdominal contractions to a distance of about 5 mm and then licked and gently nibbled. It has been suggested that refection is a method of increasing the assimilation of essential substances otherwise lost in the faeces (Crowcroft 1952, Goulden & Meester 1978, Skarén 1978).

3.2. The senses

Vision

The poor eyesight of shrews has been confirmed by moving prey items quietly near a shrew, which usually does not notice anything (e.g. Crowcroft 1957). The eyes of shrews lack the *fovea*, the spot of maximal visual acuity (Branis 1985). Shrews do not use vision in finding prey but vision may be used in close contact, for example when deciding whether a prey will be pursued or not depending on its size (Barnard & Brown 1982). The rearing up on two feet in aggressive disputes, thus exposing the white belly, is a visual signal to a competitor, which demonstrates that shrews do use visual information (Crowcroft 1957, Saarikko 1988).

Smell

Like most mammals, shrews have a good sense of smell, enabling them, for example, to follow the scent tracts of beetles and pursue the prey even underground (Maser & Hooven 1974). Yoshino & Abe (1984) found in their experiments with *Sorex unguiculatus* and *S. cinereus* that in the detection of inactive prey, such as fly pupae, scent was important in shallow soils less than 2 cm in depth, but in deep soil (5 to 30 cm) the finding of pupae appeared to depend on chance, though *S. unguiculatus* did actively dig in deep soil. Holling (1958), working with *S. cinereus* and *Blarina brevicauda*, found that shrews used olfaction for locating sawfly cocoons or any new object placed under 2 cm of sand. The locating behaviour seemed to be innate while prey selection in the eating phase was learned. Thus the shrews learned to recognize the odour of inedible, parasitized cocoons and stopped digging them up (Holling 1958).

In Crowcroft's (1957) experiments shrews preferred mealworms to earthworms, and woodlice to mealworms. Crowcroft (1957) offered four species of woodlice to his experimental subjects. The shrews usually sniffed at the animals offered and then selected *Philoscia*, while *Armadillium* was always eaten last. The order of preference seemed to be primarily due to taste, for *Armadillium* was often rejected after being crushed in the jaws.

Sound

Rudge (1968) found that in most cases the common shrew located its prey by nasal contact, but occasionally shrews oriented to the slight sounds of moving Isopoda and Chilopoda in the dish where they were offered.

Shrews are able to emit and hear ultrasonic sounds and probably use these for locating prey in underground tunnels and at short distances (Forsman & Malmquist 1989). Maser & Hooven (1974) found that the Pacific shrew *Sorex pacificus* occasionally managed to catch flying insects by orienting to their sounds; more often the shrews would jump over

alighted insects or grab them from the sides of the cage. Shrews jumping on top of prey have also been observed by Pernetta (1977), especially after an unsuccessful first approach. A warning sound emitted by some insects keeps the shrews from attacking, but when some individuals failed to create the sound they were immediately attacked by the shrews (Maser & Hooven 1974).

Touch

Shrews mainly find their prey by touch (Crowcroft 1957, Rudge 1968, Yoshino & Abe 1984, Burda & Bauerová 1985, Pierce 1987). After contact, prey may be followed, perhaps by the sound or odour, and the decision whether to take the prey is mainly based on the sense of smell or taste.

3.3. Morphological constraints

The digestive tract

The Soricinae shrews have a relatively larger stomach than other insectivores. The pyloric gland section of the stomach, where protein rich meat is digested, is particularly elongated and large in *Sorex* (Myrcha 1968). Stomach size and the ratio of the surface area of the stomach to the body weight are largest in the smallest species of shrew.

According to Myrcha (1968) the main reason for the differences in the relative stomach sizes is differences in the amount of food eaten. Shrews that weigh less than 5 g eat proportionately much more than the larger species (*Sorex minutissimus* up to 200% of its body weight in 24 hours; Hanski 1984). The smallest shrews may also need a proportionately larger stomach than large species to store food in order to survive over the sleep periods (Hanski 1984).

The relative length of the intestine decreases with decreasing body size in shrews (Okhotina 1974). The smaller species have a higher assimilation efficiency than the larger ones, excepting the very smallest species (Hanski 1984). A short digestive tract, rapid throughput and high assimilation efficiency in the smaller species may be related to the kind of food consumed by them. The very smallest shrews have a lower assimilation efficiency than medium-sized species. The smallest species may have to maximize net energy gain rather than to minimize foraging time, because of their exceptionally high mass-specific metabolic rate. A decrease in throughput time may decrease assimilation efficiency but increase net energy gain. This assumes that ingestion rate is not a limiting factor (Hanski 1984).

Digestive or absorptive 'bottlenecks' and other such constraints may mean that the optimal ingestion rate is below the maximum possible (Barnard et al. 1983). Saarikko & Hanski (1989) found that the length of short rest periods during foraging bouts, observed for several species of shrew (Crowcroft 1954, Barnard et al. 1983), is positively correlated with the amount of food eaten immediately before the short rest period. This observation implies that a shrew enters a short rest period when its digestive tract is so full that no more food can be profitably ingested.

One way around digestive constraints and a way of ensuring sufficient short-term food supplies is to cache the food items that cannot be ingested immediately (Section 4.6).

Tooth wear

The teeth of shrews wear down rapidly and they do not grow as in e.g. microtine rodents. Age groups of shrews can be easily separated by tooth wear (Pearson 1945, Dapson 1968, Pankakoski 1989). Dapson (1968) found that in *Blarina brevicauda* the sharp points of teeth wear off rapidly in early age, after which the rate of wear slows down, while Pankakoski (1989) found that the wear is accelerated in old age, as the hard surface of the teeth wears off. Others (Conaway 1952, Rudd 1955) have found that tooth wear is constant throughout life.

Most investigators agree that the quality of habitat and diet strongly affect the rate of tooth wear. The teeth of individuals eating more grit-filled earthworms or biting the hard exoskeleton of beetles may wear off faster. *Sorex obscurus* has slightly larger and more slowly wearing teeth than *S. vagrans*. Robust teeth may be an adaptation to masticating small chitinous insects, which are proportionally more numerous in poorer soils. This and perhaps different hunting techniques may give *S. obscurus* a competitive advantage over *S. vagrans* on poor soils (Hawes 1977).

4. Experiments on foraging behaviour of shrews

4.1. Prey species selection

Shrews are able to discriminate between different kinds of prey, and as noted in Section 3.1, sometimes they show a distinct food preference (Crowcroft 1957). Usually, however, all litter- and ground-dwelling invertebrates, with the possible exception of e.g. some millipedes, are pursued and ingested (Pernetta

1976, Aitchison 1984). For example, captive black shrews *Sorex isodon* (Skarén 1979) consumed bees, ants, aphids, beetles, moths, flies, sowbugs, spiders, chilopods, lumbricids and the carcasses of fish, frogs, small passerines and voles (see also Maser & Hooven 1974).

A general rule emerging from the experiments by Rudge (1968) was 'first encountered, first eaten'. The range of prey available was not examined by shrews, although sometimes an item was dropped in favour of another one if the two were found close together. These results support the basic assumption of optimal foraging models that prey items are encountered sequentially (Introduction). Rudge (1968) concluded that the level of hunger affected the selectivity of shrews, especially at the beginning of a feeding period, because after eating a large lepidopteran larva the shrews ignored previously accepted prey.

Most analyses of food selection by shrews are based on stomach samples, which do not give an accurate picture of food selection, because of varying digestibility and availability of different prey types (Crowcroft 1957). However, stomach analyses may be used to compare diets of shrew species living in the same habitat (Butterfield et al. 1981). This kind of comparative approach has revealed that pygmy shrews *Sorex minutus* do not usually eat lumbricids, while common shrews *S. araneus* do (Butterfield et al. 1981).

Shrews have also been observed to eat plant material, though this generally has little energy or nutritional value to shrews (Judin 1962). However, seeds may be an important part of the diet for some species of shrew, especially in winter (Dokuchaev 1989). Terry (1978) gave *Sorex trowbridgii*, *S. vagrans* and *Neurotrichus gibbsi* different kinds of conifer seeds, which the shrews ate willingly; seeds of *Picea sitchensis* and *Pinus monticola* were eaten in large quantities. Because the shrews often peeled the seeds, there would remain only traces of endosperm in their digestive tract, if any, proving the diet. Terry (1978) agreed with Moore (1942) and Gashwiler (1970) that shrews may be major predators of the seeds of the Douglas fir *Pseudotsuga menziesii* and other conifers. Terry (1978) also fed her shrews with some berries and mushrooms, which were also eaten.

4.2. Prey size selection

Optimal foraging theories assume that the predator selects its prey from a range of possible choices according to prey profitability, the net gain of energy per unit of handling time. In most experiments shrews have been offered two kinds of prey, which have been made unequally profitable by increasing either prey handling time or recognition time (Barnard & Brown 1981).

Barnard & Brown (1981) suggest that in some cases the predator may not evaluate profitability based on net energy gain, but may use a simpler "rule of thumb", which, on average, would result in selecting the most profitable prey. This would be especially reasonable for predators with a wide range of prey types available. Barnard & Brown (1981) tested this idea with common shrews *S. araneus*, which were given a choice of large and small prey types. In the experiment the larger prey type (4 mealworm segments) was less profitable than the smaller one (2 mealworm segments), because of its longer handling time (4.3 and 2.9 cal/s handling time, respectively). The shrews more often selected the larger prey type when its encounter rate was greater than 0.03/s; at lower encounter rates the two types were taken equally. The encounter rate with the smaller prey did not affect prey selection (Barnard & Brown 1981).

Holling (1958) found that shrews were able to recognize the larger female diprionid cocoons from male cocoons, because of their stronger odour due to their larger size, and then to dig them up selectively. In the field, all small mammals opened significantly more female than male cocoons, and the larger small mammal species opened proportionately more female cocoons than the smaller species. In the laboratory, *Sorex cinereus*, which previously had been fed with male cocoons for seven days, opened significantly more male than female cocoons. Holling (1958) drew the conclusion that it was more profitable for the smaller species of shrew to eat cocoons less selectively in the field because for them the shorter handling time of the smaller male cocoons would make up the loss in the quantity of reward.

The profitability of many prey types is approximately the same for small and large shrew species (Dickman 1988), though the largest species seem to gain less profit from the very smallest prey items than the smaller species (Fig. 1), and the smallest shrews cannot kill the largest insects (Dickman 1988, Hanski 1990). However, the results in Fig. 1 show that relatively large prey items are most profitable for all shrew species (Hanski 1990). These results provide a functional explanation to the conclusion by Barnard & Brown (1981) that shrews would generally choose the larger of two prey items. The results of Dickman

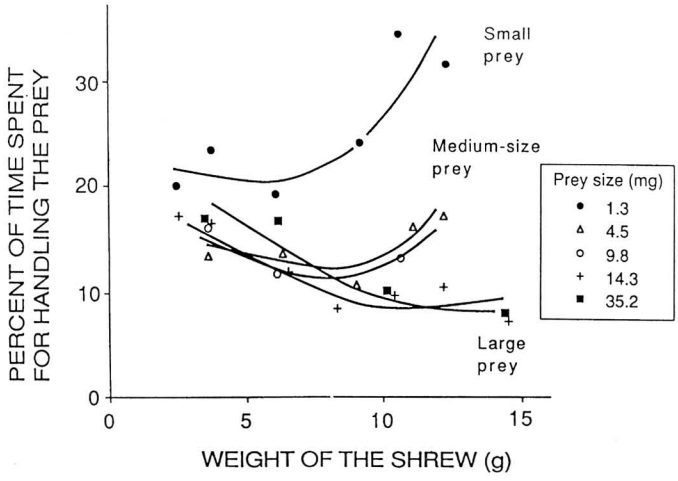

Fig. 1. Profitabilities of different-sized beetles to six species of shrew varying in size. The prey profitability is measured on the vertical axis, by the percentage of 24 hours needed for killing, handling and eating the prey type to satisfy the size-dependent energy demands of the shrew. The shrew species are *Sorex minutissimus*, *S. minutus*, *S. caecutiens*, *S. araneus*, *S. isodon* and *Neomys fodiens*. The beetle species are *Cercyon* sp., *Aphodius prodromus*, *A. fimetarius*, *Sphaeridium* sp. and *A. fossor* (from Hanski 1990).

(1988) also show that large prey are preferred by all species when a choice of prey sizes is available.

4.3. Competition and prey selection

Barnard & Brown (1981) predicted that the presence of another individual would make a foraging shrew less selective in its food choice, because of an expected additional depletion of food. In their experiment, access to the food source by the competitor was denied and so competition was only apparent, and any change in prey selection would be based on an expectation of food depletion by the competitor rather than actual depletion. The presence of a competitor did not affect the time spent foraging or prey handling time; but shrews tended to include more small prey in their diet when a competitor was present, in other words they became less selective (Barnard & Brown 1981).

Later, Barnard et al. (1983) came to the conclusion that when food availability is low, the presence of a competitor might increase the proportion of foraging behaviour in the time budget of a shrew, because a competitor might affect food availability and quality of the territory of the shrew. Barnard et al. (1983) measured the proportions of different kinds of behaviour during two one-hour periods per day for four days in the presence and absence of an apparent competitor. The result was that during the presence of a competitor the bout-length of some behaviour types, e.g. prey catching and ingestion, remained the same while the frequency of performing those types of behaviour increased. This means that the fraction of the total time spent on these types of behaviour increased significantly, thus increasing total energy gain (Barnard et al. 1983).

In another experiment Barnard & Brown (1982) studied the effect of the amount of food available on the competitive ability of resident common shrews. The shrews were provided with three quantities of blowfly pupae (318, 109 and 0). In dual fights between a resident and an animal new to the arena, food density affected the resident advantage, which was greater when there was less food on the arena. Barnard & Brown (1982) thus concluded that residents invest more in defending a territory when the cost of intrusion is high (possible food depletion).

Barnard & Brown (1984) tested the effect of food availability when both contestants were residents, but experienced either a low or high food availability. They found that the animal experiencing the lower food availability won significantly more fights, though differences in competitive ability also affected this advantage. Saarikko (1988) found in a similar experiment that the shrew which first experienced the lower food availability started to win the contests, but when the food availabilities were changed amongst the two individuals, the first winner continued to win and no significant turnover was observed.

4.4. Risk-sensitive foraging

Risk-sensitive foraging theories have been mostly tested with small passerine birds, which have to find a certain amount of food to avoid starvation before they

stop foraging for the night (Caraco et al. 1980, Caraco 1981). Barnard & Brown (1985a) tested the theory with common shrews by presenting them with a choice of a constant and a variable feeding station, which were rewarding with the same average rate. They used shrews because they have a short starvation time (Crowcroft 1957, Gebczynski 1971), and should therefore be sensitive to reward characteristics that influence short-term food intake.

When the shrews had previously experienced an intake below their estimated individual food requirement, they were more likely to choose a feeding station in which the variance of food availability was high than a station where it was low (60% preference). When the shrews met or exceeded their requirement, they showed a preference (74%) for the constant station. These results support the risk-sensitive foraging theory, but they agree only with models which consider limited interval rather than continuous foraging (Barnard & Brown 1985a, Barnard et al. 1985).

Houston & McNamara (1985) examined risk-sensitive prey choice in a continuously foraging predator, such as the common shrew, in which the risk of starvation comes from a run of bad luck during foraging, rather than from starvation during the night. In this model the probability of survival is maximized by accepting any prey item that results in a net gain in energy, and the optimal choice should not depend on the predator's energy reserves. In particular, when two options have the same mean reward rate, but different variances, the option with the smaller variance should always be preferred (Barnard et al. 1985). Barnard & Brown (1985a) found that their common shrews preferred the less variable reward option when they met their estimated requirement. According to the models without the time constraint, choice should not be dependent on the energy reserves. Barnard et al. (1985) developed a new model to fit between the two extreme models (either foraging continuously or stopping foraging for one long period). In the new model, the foraging period was randomly interrupted for randomly selected periods. The shrews now need to have sufficient reserves to survive through an unpredictably long interruption in their foraging (Barnard et al. 1985). In the new model, the mean is more important than variance, so that the higher mean should nearly always be preferred. When the interruption probability is high the animal should take risks to obtain food to avoid starvation, However, when energy reserves are very low, the danger of immediate starvation makes it optimal to be risk-averse. When reserves are high, risk should also be avoided (Barnard et al. 1985).

The shrews tended to choose the option with the higher mean as predicted by intake maximization models and the model of Barnard et al. (1985). This choice was influenced by the shrews' experience of variance of the option with the higher mean, especially when shrews were running below their estimated requirement.

The previous studies have concentrated on the effects of energy requirements on the selection of feeding stations. Barnard & Brown (1985b) showed that competition may also affect the risk-sensitivity of shrews. Competition may affect the predictability of food resources and increase the risk of doing badly in the future. In shrews risk-aversion tends to increase with increasing intake relative to requirement (Barnard & Brown 1985a). In the presence of an apparent competitor this shift was not observed (Barnard & Brown 1985b). While running below requirement there was no tendency in the shrews for risk-proneness either with or without a competitor. In the presence of a competitor the shrews shifted from risk-aversion to risk-indifference rather than risk-proneness (Barnard & Brown 1985b).

4.5. Temporal variation in prey availability

Because of their short starvation time shrews are very sensitive to short-term temporal variation in food availability. Hanski (1985) experimentally induced an energy crisis to captive shrews. The shrews were rewarded either for increasing or for decreasing their activity, but were given 5% less food than their requirement if they retained their previous level of activity. Large shrews decreased their activity while small species increased it. This result may be explained by the fact that larger shrews have larger energy reserves and can rely on them during a short period of bad luck in foraging, due to e.g. bad weather. Smaller shrews do not have such reserves and have to increase their activity when food availability decreases (Hanski 1985).

In another experiment Saarikko and Hanski (unpubl.) found that when food availability changed between high and low levels, the length of the sleep period remained unchanged, but the length of the foraging period altered. If food availability remained low for a long period of time, the foraging period was longer than if food availability was equally low for only a short time.

4.6. Food caching

Food caching is one solution to temporal variation in food availability. Short-term food caching may be energetically important especially for the smaller species of shrew, which are not able to store much energy in their body. Caching has been observed in shrews both in the laboratory and in the field. Some shrew species have venom in their saliva, which prevents prey from moving, or the shrew may bite the prey around the head thus paralysing it (Ingram 1942, Tomasi 1978, Martin 1981).

Two types of food caching can be distinguished. In scatter hoarding a short-term cache may be used to cover temporary bad luck in foraging; short-term food caches may also be accumulated when the shrew has found a good batch of food and cannot or does not have to consume it immediately (Goulden & Meester 1978, Robinson & Brodie 1982). Crowcroft (1957) described how some shrews stored food by just putting it out of sight or burying it in the soil in the cage. Later the shrews could retrieve such cached food.

In larder hoarding food is stored within a small area, and usually in a secure place, for long periods of time (Crowcroft 1957, Platt 1976, Robinson & Brodie 1982, Martin 1984). This kind of caching is affected, or induced, by the season, ambient temperature, food abundance and proximity of conspecifics (Martin 1984). The long-term caches are actively maintained, new items are added while others are removed (Ingram 1942). The cached items may also be moved to another location (Robinson & Brodie 1982, Skarén 1982).

Martin (1984) showed that short-tailed shrews *Blarina brevicauda* hoarded in semi-natural conditions in summer for a few days only and in winter for long periods of time. Summer hoarding was seen only when food abundance was increased over a certain level. Larder hoarding for winter was first observed in late autumn. The stores increased in size until late winter and disappeared in April. Buchalczyk & Pucek (1963) also reported an increase in the size of the food caches of the European water shrew *Neomys fodiens* during consecutive observations in October and November.

The size and type of prey affects caching. Usually shrews do not cache food items smaller than a certain size (Crowcroft 1955, Robinson & Brodie 1982). Barnard & Brown (1985a) did not observe caching in common shrews fed with single mealworm segments, which were probably too small to be worth caching. The short-tailed shrews tended not to cache mealworms, while they cached items of all larger prey types (Robinson & Brodie 1982). Martin (1984) found that short-tailed shrews first began hoarding well preservable prey and only later perishable prey and that the order of hoarding was opposite to the order of preference.

Table 1. The numbers of eaten and cached blowfly pupae per individual per hour in the common shrew *Sorex araneus*. Each experiment lasted for 7.5 hours. *P*-values (*t*-test) are for differences between the previous and the following stage (from Barnard et al. 1983).

	Competitor absent	*P*	Competitor present	*P*	Competitor removed
Eaten	3.5	<0.01	4.6	<0.02	3.8
Cached	1.3	<0.001	10.8	<0.001	0.7

Barnard et al. (1983) found that the presence of an apparent competitor significantly increased caching behaviour (Table 1). In this experiment shrews were foraging on blowfly pupae, which are better quality food to shrews and which can be stored for long periods of time. Hanski (1989) found captive *Sorex caecutiens* to cache blowfly pupae.

Caching behaviour increases the value of territoriality. By storing food an animal can place it out of reach of possible competitors, or make it easier to defend. If the animal is scatter hoarding the value of knowing the territory well also increases. In winter, a food cache near or in the nest allows the shrew to decrease activity and thus to save energy during extreme cold periods.

4.7. Spatial variation in prey availability

Hanski (1989) studied habitat selection of shrews on an arena divided into two halves. On one side the probability of obtaining food was constant in 5 feeders, while on the other side, the reward probability in the 5 feeders alternated between 0.5 and 0.1 in such a way that the average was 0.23. The reward probability on the "constant" side was gradually changed from 0.1 to 0.5. The shrews shifted their preference from the "variable" to the constant side when the reward probability was higher than 0.23. As expected, the point of switching was affected by the success of individual shrews on the variable side, in such a way that the more successful individuals switched to the constant side at a higher reward probability level than

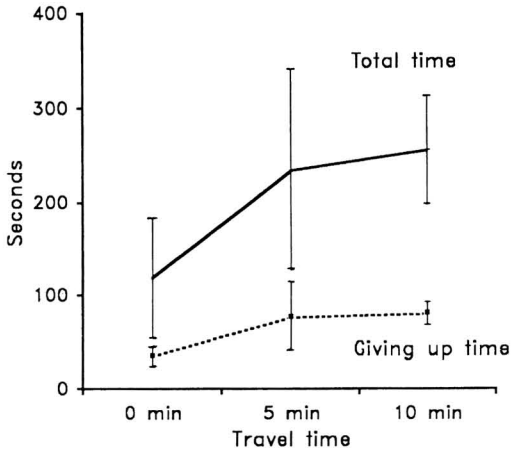

Fig. 2. The giving up time (time from last discovery of a food item till patch-leaving) and total patch residence time in four *S. araneus* individuals with three different travel times (time from leaving a patch to entering the next patch). The vertical lines give one *SD* (one way analysis of variance; from Landén 1989).

the less successful individuals. In fact, the shrews with the best performance on the variable side preferred the variable side even when they had obtained a substantially higher (up to 50%) food intake on the constant side, suggesting that they did not base their habitat selection exclusively on the average-rate maximization principle as predicted by optimal foraging theories (Stephens and Krebs 1986).

Landén (1989) found that common shrews tended to stay longer in a food patch when the travel time to other patches was experimentally increased (Fig. 2), as would be expected by the marginal value theorem (Charnov 1976b, Stephens & Krebs 1986). However, she also found that individual shrews probably used different decision criteria for leaving the patch.

5. Conclusions

Soricinae shrews have high mass-specific metabolic rates. Because of their small body size they cannot store much energy in their bodies, and they have a short starvation time of only a few hours, with major consequences to their foraging behaviour. Shrews have to forage both day and night throughout the year and they cannot sleep for more than a few hours at a time. Shrews have to make vitally important decisions about foraging on a daily or even on an hourly basis. A large proportion of the active time is spent in foraging, especially in winter, when the total active time is lowest.

Possessing a territory in winter when food availability is usually low is vital for Soricinae shrews. They live solitarily defending a territory through most of their non-reproductive season (summer to spring). Protecting a long-term food supply over autumn and winter months may be the most important reason for territoriality in Soricinae shrews. Both short- and long-term food supplies may be enhanced by food caching within the territory.

The availability of high quality prey is highly variable. Perhaps due to this reason, shrews are opportunistic foragers, consuming almost any prey item that they are able to catch and ingest. However, if they are given a choice, they may show selection by both prey size and quality, depending on their current energy budget and environmental factors such as presence of competitors. In simple experiments Soricinae shrews have been shown to be risk-averse when running above their energy requirement, and risk-prone, when running below their requirements, as predicted by risk-sensitive foraging theories.

Soricinae shrews show physiological adaptations that facilitate their survival under adverse environmental conditions in autumn and winter and during periods of low food availability. The shrinking of body and skull in winter decreases the total energy expenditure and hence food requirements of shrews, while their digestive ability remains unchanged.

Shrews are sensitive to short-term temporal variation in food availability because of their limited energetic autonomy. They may react to temporal variation in food availability by changing their activity. During an energy crisis, when shrews are running below their energy requirements, larger shrew species may decrease their activity, while smaller species cannot rely on the energy stored in their body and need thus increase their activity. Another solution to short-term energy crises is to decrease activity and to use previously cached food.

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References

Ackefors, H. 1964: Vinteraktiva näbbmöss under snön. — Zool. Revy 26:16–22.

Aitchison, C. W. 1984: A possible subnivean food chain. — In: Merritt, J. F. (ed.), Winter ecology of small mammals. Carnegie Mus. Nat. Hist., Sp. Publ. 10:363–371. Pittsburgh.

—"— 1987: Review of winter trophic relations of soricine shrews. — Mammal. Rev. 17:1–24.

Barnard, C. J. & Brown, C. A. J. 1981: Prey size selection and competition in the Common shrew (Sorex araneus L.). — Behav. Ecol. Sociobiol. 8:239–243.

—"— 1982: The effects of prior residence, competitive ability and food availability on the outcome of interactions between shrews (Sorex araneus L.). — Behav. Ecol. Sociobiol. 10:307–312.

—"— 1984: A payoff asymmetry in resident-resident disputes between shrews. — Anim. Behav. 32:302–304.

—"— 1985a: Risk-sensitive foraging in common shrews (Sorex araneus L.). — Behav. Ecol. Sociobiol. 16:161–164.

—"— 1985b: Competition affects risk-sensitivity in foraging shrews. — Behav. Ecol. Sociobiol. 16:379–382.

—"— 1987: Risk-sensitive foraging and patch residence time in common shrews, Sorex araneus, L. — Anim. Behav. 35:1255–1257.

Barnard, C. J. & Brown, C. A. J. & Gray-Wallis, J. 1983: Time and energy budgets and competition in the common shrew (Sorex araneus L.). — Behav. Ecol. Sociobiol. 13:13–18.

Barnard, C. J., Brown, C. A. J., Houston, A. I. & McNamara, J. M. 1985: Risk-sensitive foraging in common shrews: an interruption model and the effects of mean and variance in reward rate. — Behav. Ecol. Sociobiol. 18:139–146

Branis, M. 1985: Postnatal development of the eye of Sorex araneus. — Acta Zool. Fennica 173:247–248.

Buchalczyk, A. 1972: Seasonal variations in the activity of shrews. — Acta Theriol. 17:221–243.

Buchalczyk, T. & Pucek, Z. 1963: Food storage of the European water shrew, Neomys fodiens (Pennant, 1771). — Acta Theriol. 7:376–379.

Burda, H. & Bauerová, Z. 1985: Hearing adaptations and feeding ecology in Sorex araneus and Crocidura suaveolens (Soricidae). — Acta Zool. Fennica 173:253–254.

Butterfield, J., Coulson, J. C. & Wanless, S. 1981: Studies on the distribution, food, breeding biology and relative abundance of the pygmy and common shrews (Sorex minutus and S. araneus) in upland areas of Northern England. — J. Zool., Lond. 195:169–180.

Caraco, T. 1981: Energy budgets, risk and foraging preferences in dark eyed juncos (Junco hyemalis). — Behav. Ecol. Sociobiol. 8:213–217.

—"— 1982: Aspects of risk-aversion in foraging white-crowned sparrows. — Anim. Behav. 30:719–727.

Caraco, T., Martindale, S. & Whittam, T. S. 1980: An empirical demonstration of risk-sensitive foraging preferences. — Anim. Behav. 28:820–830.

Charnov, E. L. 1976a: Optimal foraging: attack strategy of mantid. — Amer. Nat. 110:141–151.

—"— 1976b: Optimal foraging: the marginal value theorem. — Theor. Popul. Biol. 9:129–136.

Corbet, G. B. & Hill, J. E. 1980: A world list of mammalian species. — British Museum (Natural History), Publication 813:1–229. London.

Croin Michielsen, N. 1966: Intraspecific and interspecific competition in the shrews Sorex araneus L. and S. minutus L. — Arch. Neerl. Zool. 17:73–174.

Crowcroft, P. 1952: Refection in the common shrew. — Nature, London 170:627.

—"— 1954: The daily cycle of activity in British shrews. — Proc. Zool. Soc. Lond. 123:715–729.

—"— 1955: Notes on the behaviour of shrews. — Behaviour 8:63–80.

—"— 1957: The life of the shrew. — 166 p. Max Reinhardt, London.

Dapson, R. W. 1968. Reproduction and age structure in a population of short-tailed shrews, Blarina brevicauda. — J. Mammal. 49:205–214.

Dehnel, A. 1961: Aufspeicherung von Nahrungsvorräten durch Sorex araneus Linnaeus, 1758. — Acta Theriol. 14: 265–268.

Dickman, C. R. 1988: Body size, prey size and community structure in insectivorous mammals. — Ecology 69: 569–580.

Dokuchaev, N. E. 1989: Population ecology of Sorex shrews in North-East Siberia. — Ann. Zool. Fennici 26:371–379.

Ellenbroek, F. J. 1980: Interspecific competition in the shrews Sorex araneus and Sorex minutus (Soricidae, Insectivora): a population study of the Irish pygmy shrew. — J. Zool., Lond. 192:119–136.

Erlinge, S. 1981: Food preference, optimal diet and reproductive output in stoats Mustela erminea in Sweden. — Oikos 36:303–315.

Forsman, K. A. & Malmquist, M. G. 1989: Evidence for echolocation in the common shrew, Sorex araneus. — J. Zool. 216:655–663.

Gashwiler, J. S. 1970: Further study of conifer seed survival in a western Oregon clearcut. — Ecology 51:849–854.

Gebczynski, M. 1971: Oxygen consumption in starving shrews. — Acta Theriol. 16:288–292.

Genoud, M. 1984: Activity of Sorex coronatus (Insectivora, Soricidae) in the field. — Zeitschr. Säugetierk. 49:74–78.

—"— 1988: Energetic strategies of shrews: ecological constraints and evolutionary implications. — Mammal Rev. 18:173–193.

Genoud, M. & Vogel, P. 1980: The activity of Crocidura russula (Insectivora, Soricidae) in the field and in captivity. — Zeitschr. Säugetierk. 46:222–232.

Glazier, D. S. 1985: Energetics of litter size in five species of Peromyscus with generalizations for other mammals. — J. Mammal. 66:629–642.

Golden, E. A. & Meester, J. 1976: Notes on the behaviour of Crocidura and Myosorex (Mammalia: Soricidae) in captivity. — Mammalia 42:197–207.

Grainger, J. P. & Fairley, J. S. 1978: Studies on the biology of the pygmy shrew Sorex minutus in the west of Ireland. — J. Zool., Lond. 186:109–141.

Hamilton, W. J. Jr. 1930: The food of the Soricidae. — J. Mammal. 11:26–39.

Hanski, I. 1984: Food consumption, assimilation and metabolic rate in six species of shrews from Finland (Sorex and Neomys). — Ann. Zool. Fennici 21:157–165.

—"— 1985: What does a shrew do in an energy crisis? — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural Ecology: 247–252. Symp. Brit. Ecol. Soc., Blackwell, Oxford.

—"— 1989: Habitat selection in a patchy environment: individual differences in common shrews. — Anim. Behav. 38:414–422.

—"— 1990: Insectivorous mammals. — In: Crawley, M. J. (ed.), Natural enemies: The population biology of predators, parasites and diseases. Blackwell, Oxford. (in press).

Haukisalmi, V. 1989: Intestinal helminth communities of Sorex shrews in Finland. — Ann. Zool. Fennici 26:401–409.

Hawes, M. L. 1977: Home range, territoriality and ecological separation in sympatric shrews, Sorex vagrans and Sorex obscurus. — J. Mammal. 58:354–367.

Holling, C. S. 1958: Sensory stimuli involved in the location and selection of sawfly cocoons by small mammals. — Can. J. Zool. 36:633–653.

—"— 1959: The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. — Can. Entomol. 91:293–320.

Houston, A. I. & McNamara, J. M. 1985: The choice of two prey types that minimises the probability of starvation. — Behav. Ecol. Sociobiol. 17:135–141.

Hyvärinen, H. 1969: On the seasonal changes in the skeleton of the common shrew (Sorex araneus L.) and their physiological background. — Aquilo, Ser. Zool. 7:1–32.

Ingram, W. M. 1942: Snail associates of Blarina brevicauda talpoides (Say). — J. Mammal. 23:255–258.

Judin, B. S. 1962: Ecology of shrews (genus Sorex) of Western Siberia. — In: Voprosy Ekologii, Zoogeografii, i Sistematiki Zhiyotnykh (Trudy Biologichoskogo Instituta, Akademia Nauk SSR, Sibirskoye Obdolaniyo). Vol VIII, Novosibirsk: 33–134. (U.S. Dept. of Commerce, Office of Tech. Serv., Joint Publ. Res. Service, translation no. 17,973, 1963).

Khlyap, L. A. (Хлап, Л. А.) 1983: [Peculiarities of structure of home ranges and their use by shrews and forest voles.] (in Russian) — Fauna and Ecology of Rodents 15:162–203.

Kirkland, G. L. & Kirkland, C. J. 1989: Patterns of community convergence in forest-dwelling soricids from the mountains of Eastern North America and Central Europe: an ecomorphological approach. — In: 5. International Theriological Congress, Rome 1989. Abstracts of papers and posters, Vol. II:672.

Kisielevska, K. 1963: Food composition and reproduction of Sorex araneus, Linnaeus 1758, in the light of parasitological research. — Acta Theriol. 7:127–153.

Korpimäki, E. & Norrdahl, K. 1987: Low proportion of shrews in the diet of small mustelids in western Finland. — Zeitschr. Säugetierk. 52:257–260.

—"— 1989a: Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. — Oikos 54: 154–164.

—"— 1989b: Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. — Ann. Zool. Fennici 26:389–400.

Krebs, J. R. 1978: Optimal foraging: decision rules for predators. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach. Blackwell, Oxford.

Krebs, J. R., Erichsen, J. T., Webber, M. I. & Charnov, E. L. 1977: Optimal prey selection in the great tit, Parus major. — Anim. Behav. 25:30–38.

Landén, T. 1989: Foraging behaviour of the common shrew (Sorex araneus) in a patchy environment. — M.Sc. thesis, Department of Zoology, University of Helsinki. 41 pp. (in Finnish)

Lindstedt, S. L. 1980: Regulated hypothermia in the desert shrew. — J. Comp. Physiol. B. 137:173–176.

Malmquist, M. 1985: Interspecific competition in shrews (Soricidae): evolutionary and ecological consequences. — Acta Univ. Uppsala, Dissertations from the faculty of Science, 794, Uppsala, Sweden.

Martin, I. G. 1981: Venom of the short-tailed shrew (Blarina brevicauda) as an insect immobilizing agent. — J. Mamm. 62:189–192.

—"— 1984: Factors affecting food hoarding in the short- tailed shrew Blarina brevicauda. — Mammalia 48:65–71.

Martinsen, D. L. 1969: Energetics and activity patterns of short-tailed shrews (Blarina) on restricted diets. — Ecology 50:505–510.

Maser, C. & Hooven, E. F. 1974: Notes on the behavior and food habits of captive pacific shrews, Sorex pacificus pacificus. — Northwest Sci. 48:81–95.

McNab, B. K. 1963: Bioenergetics and the determination of home range size. — Amer. Nat. 97:133–141.

Merritt, J. F. 1986: Winter survival adaptations of the short-tailed shrew (Blarina brevicauda) in an Appalachian montane forest. — J. Mammal. 67:450–464.

Mezhzherin, A. 1964. Dehnel's phenomenon and its possible explanation. — Acta Theriol. 8:95–114.

Michalak, I. 1983: Reproduction, maternal and social behaviour of the European water shrew under laboratory conditions. — Acta Theriol. 28:22–29.

Moore, A. W. 1942: Shrews as a check on Douglas fir regeneration. — J. Mammal. 23:37–41.

Moraleva, N. V. (Моралева, Н. В.) 1987: К проблеме межвидовых отношений близких видов землероек-бурозубок (Insectivora, Sorex) (in Russian). — Fauna i ekologija 1987:213–228.

—"— 1989: Intraspecific interactions in the common shrew Sorex araneus in Central Siberia. — Ann. Zool. Fennici 26:425–432.

Myrcha, A. 1968: Comparative studies on the morphology of the stomach in the Insectivora. — Acta Theriol. 12:223–244.

Newman, J. R. & Rudd, R. L. 1978: Observations of torpor-like behavior in the shrew, Sorex sinuosus. — Acta Theriol. 23:436–438.

Okhotina, M. V. (Охотина, М. В.) 1974: Morpho-ecological features making possible joint habitation for shrews of the genus Sorex (Soricidae, Insectivora). — In: Okhotina, M. V. (ed.), Fauna and flora of the terrestrial verte-

brates of the Southern part of the Soviet Far East. Vladivostok: 42–57.

Pankakoski, E. 1989: Variation in the tooth wear of the shrews Sorex araneus and S. minutus. — Ann. Zool. Fennici 26:445–457.

Pearson, O. P. 1945: Longevity of the short-tailed shrew. — Amer. Midl. Nat. 34:531–546.

Pernetta, J. C. 1976: Diets of the shrews Sorex araneus L. and Sorex minutus L. in Wytham grassland. — J. Anim. Ecol. 45:899–912.

—"— 1977: Anatomical and behavioural specialisations of shrews in relation to their diet. — Can. J. Zool. 55: 1442–1453.

Pierce, G. J. 1987: Search paths of foraging common shrews Sorex araneus. — Anim. Behav. 35:1215–1224.

Platt, W. J. 1976: The social organization and territoriality of short-tailed shrew populations in old field habitats. — Anim. Behav. 24:305–318.

Pucek, Z. 1970: Seasonal and age change in shrews as an adaptive process. — Symp. Zool. Soc. London 26:189–207.

Pyke, G. H. 1978: Are animals efficient harvesters? — Anim. Behav. 26:241–250.

Randolph, J. C. 1973: Ecological energetics of a homeothermic predator the short-tailed shrew. — Ecology 54:1166–1187.

Richardson, J. H. 1973: Locomotory and feeding activity of the shrews, Blarina brevicauda and Suncus murinus. — Amer. Midl. Nat. 90:224–227.

Robinson, D. E. & Brodie, E. D. Jr. 1982: Food hoarding behavior in the short-tailed shrew Blarina brevicauda. — Amer. Midl. Nat. 108:369–375.

Rudd, R. L. 1955: Age, sex, and weight comparisons in three species of shrews. — J. Mammal. 36:323–339.

Rudge, M. R. 1968: The food of the common shrew Sorex araneus L. (Insectivora: Soricidae) in Britain. — J. Anim. Ecol. 37:565–581.

Ružić, A. 1972: Spitzmäuse (Soricidae) als Räuber der Feldmaus, Microtus arvalis (Pallas 1779). — Säugetierk. Mitt. 20:366–370.

Saarikko, J. 1988: The effect of dominance and food availability in territorial disputes of shrews. — M.Sc. thesis, Department of Zoology, University of Helsinki. (in Finnish). 70 pp.

Sheftel, B. I. 1989: Long-term and seasonal dynamics of shrews in Central Siberia. — Ann. Zool. Fennici 26:357–369.

Schlüter, A. 1980: Waldspitzmaus (Sorex araneus) und Wasserspitzmaus (Neomys fodiens) als Aasfresser im Winter. — Säugetierk. Mitt. 40:45–54.

Skarén, U. 1978: Feeding behaviour, coprophagy and passage of foodstuffs in a captive least shrew. — Acta Theriol. 23:131–140.

—"— 1979: Variation, breeding and moulting of Sorex isodon Turov in Finland. — Acta Zool. Fennica 159:1–30.

—"— 1982: Intraspecific aggression and postnatal development in the shrew Sorex isodon Turov. — Ann. Zool. Fennici 19:87–91.

Stephens, D. W. & Krebs, J. R. 1986. Foraging theory. — 248 pp. Princeton Univ. Press, Princeton, N.J.

Terry, C. J. 1978: Food habits of three sympatric species of Insectivora in Western Washington. — Can. Field Nat. 92:38–44.

Tomasi, T. E. 1978: Function of venom in the short-tailed shrew, Blarina brevicauda. — J. Mammal. 59:852–854.

Virtanen, H. 1989: Morphological variation in Eurasian and North-American shrews. — M.Sc. thesis, Department of Zoology, University of Helsinki (in Finnish).

Vogel, P. 1976: Energy consumption of European and African shrews. — Acta Theriol. 21:195–206.

—"— 1980: Metabolic levels and biological strategies in shrews. — In: Schmidt-Nielsen, K., Bolis, L. & Taylor, C. R. (eds.), Comparative physiology: primitive mammals: 170–180. Cambridge Univ. Press, Cambridge.

Vogel, P., Genoud, M. & Frey, H. 1981: Rythme journalier d'activite chez quelques Crocidurinae africains et europeens (Soricidae, Insectivora). — Rev. Ecol. (Terre et Vie) 35:97–108.

Yoshino, H. & Abe, H. 1984: Comparative study on the foraging habits of two species of soricine shrews. — Acta Theriol. 29:35–43.

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