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Food storage, prey remains and notes on occasional vertebrates in the diet of the Eurasian water shrew, *Neomys fodiens*

Werner HABERL

Hamburgerstrasse 11, A-1050 Vienna, Austria; e-mail: shrewbib@sorex.vienna.at

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A b s t r a c t . The food remains of *Neomys fodiens* (particularly trichopteran larvae, Gastropoda and Amphibia) found on the banks of ponds and small creeks in Lower Austria are described. Characteristic bite marks, the manner of opening the cases and shells, as well as data on feeding patterns are presented. Food caches mainly consisted of caddis fly larvae and snails, but also contained non-palatable items which shrews apparently had confused with real prey and retrieved. The composition of the caches varied seasonally, showing a marked mid-summer decline and a shift in the proportion of Trichoptera and Mollusca in late summer and autumn. Shrews employed particular methods when breaking snail shells and opening caddis fly cases, and in the consumption of vertebrate carcasses.

Key words: shrews, ecology, foraging behaviour, food cache, frogs, carrion

Introduction

The Eurasian water shrew *Neomys fodiens* (Pennant, 1771) inhabits various riparian and littoral habitats of the Palaearctic including the shores of marine habitats, lakes and rivers, but also lives in swamps, humid woodland, wet meadows and, in the northern part of its range, even fields and drainage ditches (C h u r c h f i e l d 1990, S p i t z e n b e r g e r 1999). In the south it is confined to mountainous areas where it lives in the reedbeds of lakes, mountain brooks, small rivers and riverine forests.

Water shrews take both terrestrial and aquatic prey, the latter particularly including caddis fly larvae, crustaceans and snails. Whereas most small prey items can easily be detected by gut or faecal analysis from undigested chitinous exoskeletal fragments (C h u r c h f i e l d 1985), other prey are difficult to detect from such analyses, even though their mass intake may be high. This is especially true for snails and occasional vertebrate prey such as amphibians, fish and occasionally utilised small mammal carcasses (H a b e r l 1993).

Water shrews usually have favourite landing and feeding places as well as “caches” in secluded places amongst vegetation or under stones and logs, where it is possible to find immobilised prey and prey remains. The literature (see H a b e r l 1995) includes only a few reports on water shrew food storage places, and all refer to *N. fodiens* rather than *N. anomalus*. F o r m o z o v (1948) found a few snails in a shrew burrow, but the first reports of larger prey accumulations are from the Bialowieza National Park in Poland (B u c h a l c z y k & P u c e k 1963, W o l k 1976). These storage places included caddis fly larvae, snails, partly eaten frogs and fish. Amongst caddis fly and fish remains, K r a f t & P l e y e r (1978) found over 4,000 snail shells at ca. 60 feeding places on the banks of German fishponds.

Descriptions of the behaviour of water shrews when opening snail shells are sparse, controversial and limited to Lymnaeidae (B u c h a l c z y k & P u c e k 1963, W o l k 1976, K r a f t & P l e y e r 1978, K r a f t 1980, K ö h l e r 1984). However, fixed patterns of prey handling have been described for other shrew species (*N. anomalus*, *Sorex araneus*, *S. minutus*, *Crocidura suaveolens*) including predation on snails and other prey items (H u t t e r e r 1976, H a b e r l 1998).

This paper deals with the food remains of *Neomys fodiens* found in a study area in Austria. The main concerns of the study were prey composition at storage places during different parts of the year, the positioning of prey storage places, and the description of patterns of prey utilisation.

Material and Methods

The data were collected in the course of a study of small mammals in a wetland habitat in the Waldviertel (Schönbach, Lower Austria; H:48°27,33', V:15°2,44') between 1988–1990. This wetland was characterized by several underground springs and brooks leading into two small ponds that drained into the plain of the "Kleiner Kamp" river. Dominant plants on the study plot were *Polygonum bistorta*, *Filipendula ulmaria*, *Deschampsia caespitosa* and several *Carex* species (see H a b e r l 1993 for details).

Live trapping was conducted in addition to collecting tracks on smoked paper. The banks of streams and ponds in and around the study area were regularly searched for storage places and the food remains found were collected. Prey items were classified as being those of *N. fodiens* on the following criteria: (1) The storage places conformed to those described in the literature, (2) they were close to water, (3) live traps placed near the storage places yielded only *N. fodiens*, (4) tracks on smoked paper were found to be those of *N. fodiens* when compared with reference tracks from captive *N. fodiens* and *N. anomalus*, (5) faeces found nearby were those of *N. fodiens* (containing aquatic prey, mainly *Gammarus* sp.), and (6) snail shells showed the same bite marks as found on snails fed to captive *Neomys*, and as described by B u c h a l c z y k & P u c e k (1963) and K r a f t & P l e y e r (1978).

In order to obtain reference material on patterns of prey handling and carcass consumption, behavioural observations and experiments were conducted upon captive shrews. Animals were caged separately in glass vivaria containing a small water bowl, a ground layer of 5–10 cm of peat, soil and adequate cover (pieces of wood, stones, foliage and grass-tufts with rootstocks). Captive shrews were fed a basic diet of *Tenebrio* larvae *ad libitum*. Additional food items, particularly snails, and also fish and small mammal carrion were offered to captive shrews, and their utilisation was documented. Single experiments were conducted using prey dummies presented to the shrews in dry bowls: pieces of plastic drinking straws and gelatine capsules (either empty or filled with mealworms), clean cigarette filters and balls of aluminium foil.

Small mammal carrion was also laid out in the field. Rodent carcasses (Murinae, Microtinae) (n = 64) and tracking tunnels (smoked paper placed in PVC pipes) were randomly deposited in the study area. Carrion was fixed to the ground by a stake and sheltered from rain by a plastic dish placed ca. 5 cm above ground. Carrion was inspected regularly, weighed and photographed, and the presence of bite marks and faeces were documented.

Results

F o o d c a c h e s a n d p r e y r e m a i n s

A few empty trichopteran larval cases were found in a clump close to a fishpond in 1988. Larger accumulations were discovered along the banks of a small pond (ca. 30 m^2) in the Lower Austrian study area from May 1989. The majority of the feeding places were on the very steep banks of this pond (slope >60º), located 5–30 cm away from the water (d_{max} = 90 cm). Prey remains were concentrated in a small area of 5–10 cm in diameter, and these often were very difficult to find when hidden amongst vegetation. Live-trapping showed that the banks of this small pond were inhabited by 1–3 water shrews (captures from July to November 1989).

In total, 568 items from 66 food caches in the study area were found between July 1988 and June 1990. For the most part, these included trichopteran larvae (79.2%, mostly Limnephilidae: *Limnephilus* sp., *Glyphotelius* sp.) and aquatic Mollusca (9.7%, mostly *Radix peregra*). Terrestrial Gastropoda (*Succinea putris*, *Perforatella incarnata, Cepea hortensis*, *Eucobresia diaphana*, *Vitrina pellucida*) constituted only 4%. Other aquatic and terrestrial invertebrates were Hirudinea and the larvae and pupae of Ephemeroptera, Odonata and Coleoptera (mainly Curculionidae, Carabidae, Dytiscidae) (3,2%). Non-palatable items such as twigs, stones and artificial objects such as a broken ping-pong ball and a rubber ring were also identified (3,9%). The caches also contained two colour-marked prey dummies (empty snail shells) that I had positioned near the pond during an earlier experiment.

In winter (November to April), even in snowless periods, there were no caches evident and the only finds were two partly eaten frogs (*Rana temporaria*) collected on 2. 4. 1989 and 20. 4. 1989 (not included in calculations).

All years combined, the largest numbers of food remains were found between May and June and again in October. During late summer (August to September) such finds were rare. Considering Trichoptera and aquatic Mollusca only, a seasonal separation of the data reveals that from August to October Trichoptera predominated (54.1%) but there was a significantly higher proportion of limnic gastropods than in late spring and early summer. In contrast, from May to July limnic gastropods represented 2.3% of the prey found, whilst Trichoptera comprised 87.1% of the food remains (χ^2 = 118; df = 1; P = 0.05) (Fig. 1).

Feeding patterns and experimental studies

Trichoptera

The caddis fly cases found (most were those of pupae) consisted of either crude sand or small stones or small twigs (Limnephilidae use a combination of these materials). Trichopteran

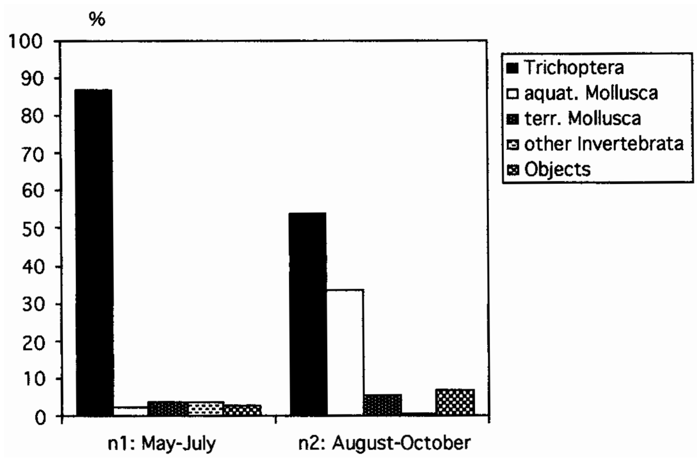

Fig. 1. Seasonal changes in the composition of food remains of *N. fodiens* at the feeding places (n1=433, n2=135) (all years combined).

cases were sorted and evaluated according to eight categories: (A) intact (5%) – (B) opened to a small extent from one end (22,6%) – (C) opened from one end to a maximum extent of half the case (26,1%) – (D) opened from one end and leaving less than half the case (20,3%) – (E) opened from both ends (1,7%) – (F) small middle parts (7,9%) – (G) opened from the side (12,6%) – (H) opened from the side and from one end (3,8%). The distribution deviated significantly from random (χ^2 = 257; df = 7; P = 0.01; n = 522). Shrews mainly opened trichopteran cases from either on one end (patterns B, C, and D) or from the side (patterns G and H) (69% and 16.4%, respectively) (Fig. 2).

Mollusca

The 55 *Radix peregra* found at the storage places included 21 that were alive and obviously uninjured and one shell-less body, which had been pulled out of its shell and cached by a water shrew. 29% of the empty shells had been opened from the apex by breaking at least one turn of the shell. Another 15% were opened from the side, but leaving the lip intact. The remainder were not broken or only the apex was missing. This pattern, employed when breaking conical shells, and also observed in captivity (e.g. *Radix*, *Limnaea*, *Succinea*) was not used for larger, spherical terrestrial snails (e.g. *Helix*, *Arianta*, *Cepea*). The latter were either eaten without the shell being broken or, occasionally, by the opening of the shell from the lip, thus breaking away up to one half of the final whorl or more (a method similar to that employed by *Sorex araneus*) (Fig. 2). There seems to be great intra-individual variation in the pattern in which their shells are opened (also see K r a f t 1980). There were also marked individual differences in the time of the shrew's first acceptance of snails as prey. Snails were immediately smelled and „investigated" when new objects in vivaria and sometimes marked with faeces, however, they were usually attacked and eaten on only after several days or even sometimes weeks.

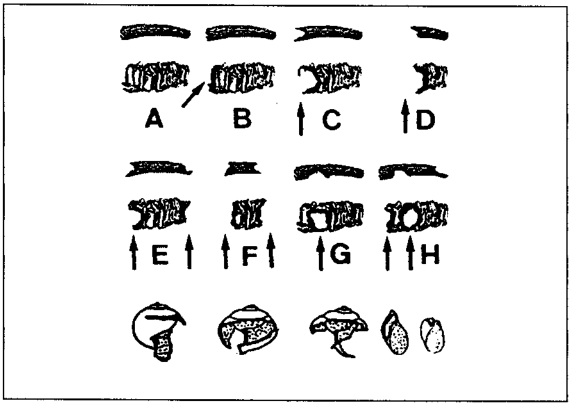

Fig. 2. The most characteristic patterns for opening trichopteran larvae cases and shelled Mollusca.

Experiments using prey dummies

In captivity, prey dummies (see Material and Methods) were removed by the shrews from feeding bowls and accumulated ("hoarded") in small groups of 3–17 objects (occasionally mixed with meal worms or snails) in different places in the vivarium. The position of these caches varied: most were in runways or under pieces of wood, some were placed in the open or near or even in water bowls. In the course of several days these "caches" were “reorganised”, i.e. individual pieces were shifted from one place to another – usually over night. It is remarkable that in some cases a few dummies of similar size and make were found “cached” next to each other, although they were initially mixed when dispensed in the bowl.

The plastic straw dummies remained unopened, but gelatine capsules and cigarette filters showed distinct bite marks. 55% of the gelatine capsules (n=40) were opened from the side – a pattern similar to that seen in trichopteran cases.

Vertebrate prey and carcass consumption

Studies both in captivity and in the field showed that distinct eating patterns are not only employed in the consumption of invertebrates, but also of vertebrate prey. The carcasses of small mammals (e.g. *Microtus*, *Apodemus*, *Mus*) usually were cut open, starting with the area behind the head and subsequently opening the thorax by nibbling through the rib-cage (Fig. 3). The lungs, the heart and the liver were consumed first. The limbs were sometimes “skinned” from inside the thoracic cavity by the shrews’ pulling them inwards and eating the muscles, so leaving the skin turned inside out. The carrion continued to be eaten for several days.

Fig. 3. A field mouse carcass (*Microtus arvalis*) utilised by shrews. (Photo by W. Haberl)

In the field, 59% (n = 64) of the murid carcasses laid out in the study area were utilised by shrews (*Sorex* and *Neomys*), at least in part within the first 4–7 days (March – November). That this was the work of shrews was obvious from comparing the eating patterns with those found in captive shrews, from faeces deposited on or near the carcasses, and from tracks on smoked paper. After 2–3 weeks most pieces were almost completely consumed so that mainly the skeleton and the skin remained. Some carrion was eaten on the first day or even within a few hours, whereas other carcasses, placed only a few metres away, remained untouched for long periods, even if defecated on by shrews. However, according to the shrews’ home ranges within the study grid (see H a b e r l 1993), most carrion utilisation, except for corpses placed on the banks of the pond, could be attributed to *Sorex* spp., presumably *S. araneus*.

Dead fish fed to captive water shrews were eaten starting from behind the head and continuing in a distinct pattern along the dorsal muscles (Fig. 4). This was also observed in a large trout (*Salmo gairdneri*) found caught in the drainage net of a small fishpond after drainage; here consumption continued for several days.

Of particular interest were the remains of two partially eaten adult frogs (*Rana temporaria*) found in April 1989. Although still breathing, the frogs were immobile and stiff, showed numerous bite marks, and had their hind legs stretched open; spawn protruded from wounds. About one week later I found the remains of one of the frogs about one metre away; it had been almost completely consumed apart from the skin and skeleton. These frog remains closely resembled those reported by S c h m i d t (1986).

Discussion

Although live-trapping and the collection of tracks on smoked paper revealed the presence of water shrews along the banks of most creeks and ponds in the study area, it is notable that feeding places were found only in certain areas. The majority were located on a small pond in the main capture grid. The reasons for this may be twofold: (1) the particularly steep bank of this pond provided dry nesting places, and (2) the steepness of the slope provided ideal diving conditions, shown to be of great importance for successful shrew foraging (see R u t h a r d t & S c h r ö p f e r 1985, S c h r ö p f e r 1985), although L a r d e t (1988) has shown that *N. fodiens* prefers shallow water. Underwater burrow exits (S p a n n h o f 1952) could not be found in this study (also see I l l i n g et al. 1981). I carefully searched the banks of all other water bodies in and around the study area (small creeks, lakes and fishponds) for over two years but could not find any other similar accumulation of caches. On one occasion I did find a few empty caddis fly cases on a large rock in a creek close to the main study area (Kleiner Kamp). This suggests that a shrew had used the rock as a place for landing prey (and had probably started foraging dives from there) as previously observed by S c h l o e t h (1980), D. C a n t o n i (pers. comm. by P. V o g e l) and P. V o g e l (pers. comm.).

The scarcity of feeding places in summer (July to September) might be connected to the abundance and availability of terrestrial invertebrate prey. The observed seasonal shift in the ratio of Trichoptera / Mollusca (a higher proportion of snails in late summer and autumn) was also reported by W o l k (1976). The limited numbers of Trichoptera in small ponds, as

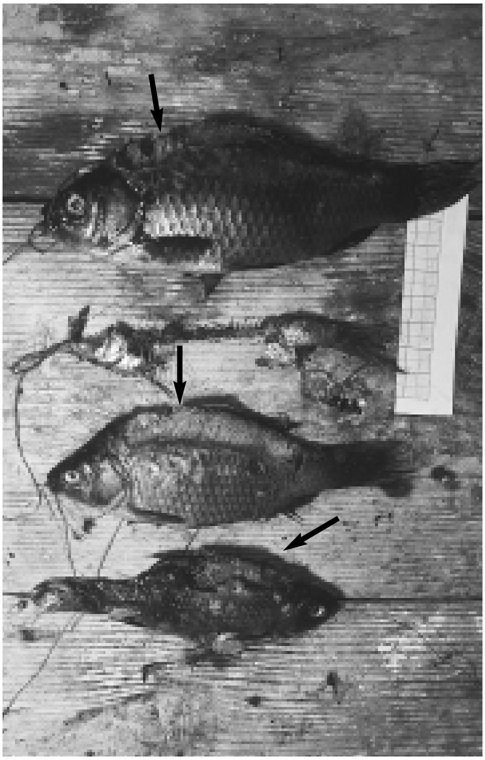

Fig. 4. Fish carrion (Cyprinidae) utilised by *Neomys fodiens*. (Photo by W. Haberl)

well as the timing of metamorphosis, may well account for the higher percentage of Mollusca caught in late summer and autumn (see also Kraft & Pleyer 1978).

Although I found a steady decline in trichopteran case numbers over the course of the year, the comparative rarity of findings in mid summer represents a notable decrease that cannot be explained by a progressively diminishing population (*sensu* Wolk 1976) alone. One possible explanation would be a higher predation by young shrews before they disperse from their mothers' home ranges. This effect may also account for the larger numbers of food remains found in caches in late spring and early summer. In addition, the abundance of terrestrial prey in mid summer and late summer and a corresponding dietary shift could be responsible. Churchfield (1984) also reports of two peaks (May and October) and a mid-summer decline in the trichopteran diet of *N. fodiens*.

Shrews are generalists in terms of the spectrum of food types taken, and yet some degree of specialisation does occur (Churchfield 1990). In summer Trichoptera pupae may represent an easy, defenceless and valuable prey resource. Thus, when Trichoptera are pupating, foraging by *N. fodiens* could be regarded as "harvesting" – a foraging mode that has already been reported for *Sorex* spp. (Hutterer 1982, Kuvikova 1986, Pierce 1987).

The patterns of removal of the bodies of larger snails have been reported by Cranbrook (1959), Kraft (1980) and Köhler (1984). The maximum size of broken snail shells was within the range of the largest shells offered to captive animals and found in nature. The 1–1.5 mm strong lip of adult Helicidae can easily be broken by *N. fodiens* and by *S. araneus*. This confirms that shrews can break even thicker shells (see Broadbrooks 1939, Crowcroft 1957, Cranbrook 1959). The critical thickness of 0.3 mm for *N. fodiens* as reported by Köhler (1984) is even outperformed by *S. araneus* and the size limits of snails (3–5 cm in Lymnaeidae) may well represent realistic values when compared to those given by Cranbrook (1959).

The opening patterns found for *Radix peregra* in this study show a higher degree of variability than those described for *Lymnea stagnalis* (Kraft & Pleyer 1978, Kraft 1980). The overall picture presented by Buchalczyk & Pucek (1963) shows a much greater similarity to my findings.

While the main bulk of the water shrew's diet comprise small invertebrates, there are many examples of vertebrate prey being caught and eaten. Although there is no evidence from food remains that water shrews kill and eat small rodents in the wild, they may well feed on mice and microtines that have died in their nests or have been left by cats or other predators (Schlüter 1980, Kosoi 1982, Haberl 1993). However, my studies on both captive and free-ranging shrews, in which I offered rodent carcasses and observed their utilisation, reveals a distinct eating pattern. Interestingly, feeding on carcasses is not due to lack of other food, since both in the wild and in captivity additional food was abundant. The carcasses are fed on continuously over several days even if, especially in summer, the state of decay is obvious and the carrion smells strongly. This contradicts Crowcroft (1957) who stated that "...the meat supplied to shrews must be fresh for they will starve to death rather than feed on tainted flesh" (also see Spannhof 1952, Baxter & Meester 1980, 1982). However, in foraging theory such carrion represents a food patch that ensures a continuous food supply. Schlüter (1980) suggests that carrion eating by *Sorex araneus* and *N. fodiens* may be most important in winter.

Carcasses of reptiles were never found in the study area but small lizards should be considered as easy prey for water shrews (see Mezhzerin 1958) and even *Suncus etruscus* can kill small lizards with bites to the throat (Geraets 1972). Larger lizards are unlikely to be killed by water shrews: an adult male *Lacerta agilis* and a toad, *Bufo bufo*, survived three weeks in the vivarium of a water shrew (Haberl 1993).

The finding of the remains of the two partially eaten adult *R. temporaria* are of interest. Frogs seem to be distasteful to shrews because of their slimy and toxic skin secretions (Formanowicz & Brodie 1979, Brodie & Formanowicz 1981, Köhler 1984). In this study predated frogs were found in April 1989. March had been unusally warm and the frogs had started to breed, however, there was a sudden cold snap in April. Both frogs were discoverd early in the morning, when ambient temperatures were around freezing, causing immobility and a reduction in skin secretion production (also see Haberl & Wilkinson 1997). This suggests that random climatic fluctuations can make adult frogs vulnerable to shrew predation.

Rozmus (1961) states that it is likely that young frogs dispersing and occurring in masses after metamorphosis temporarily represent the main source of food for shrews (also see Rörig 1905, Wilcke 1938, Sergeev 1973). Ognev (1959) counts amphibians to the preferred prey of *N. fodiens*. Buchalczyk & Pucek (1963) and Wolk (1976) report of approximately 20–42% of frogs in the water shrew's diet, whereas Kraft & Pleyer (1978) found no frog remains. Lorenz (1952) and Pucek (1959) report that also adult, medium-sized frogs can be killed by *N. fodiens* and Pernetta (1976) reports the predation on newts (*Triturus vulgaris*).

It is significant that other, non-palatable, objects found in the feeding places closely resembled real prey. The size of found objects was slightly above the mean size of Trichoptera larvae. This suggests a preference for supra-optimal prey size and, hence the strong effect of supra-optimal dummies. According to Churchfield (1990), a surplus of prey seems to stimulate caching behaviour.

Hitherto only a few experiments using prey dummies have been conducted with shrews: Shull (1907) used sand-filled snail shells with *Blarina brevicauda*; Dummies made of yarn and tissue resembling *Calliphora* larvae could not be discriminated by *N. fodiens* under water in the experiments by Churchfield & White (unpublished data, c.f. Churchfield 1985). Pierce (1987) used meal-worm segments in pieces of straws in order to examine the foraging strategy of *S. araneus*. Crowcroft (1955) observed that *S. araneus* carried small stones into their nest and interpreted this behaviour as „food hoarding" that was triggered by an object resembling real prey, once it has been seized and taken into the mouth.

As in former studies on *N. fodiens*, the terms "feeding place" and "storage place" / "cache" have been used synonymously in this report. However, it is recommended that, in future, these terms should be used more specifically whenever possible. It is very difficult to draw a line between the terms as, when finding food remains in the wild, it is almost impossible to differentiate between a "storage place" (i.e. caught prey that is immobilised and kept for later usage) and a "feeding place" (i.e. an area where prey is taken to shore and is eaten, leaving only the unpalatable parts). Finds of prey remains can only be evaluated with the aid of direct observations and frequent monitoring of known landing places, preferably by colour marking the remains found and keeping a record of their position. The results also suggest that monitoring should continue over longer periods of time, since the occurrence of feeding places may be sporadic and their composition may undergo seasonal changes. In this respect it is interesting that other studies on the diet and habitat of water shrews do not mention food caches at all (e.g. Niethammer 1977, 1978, Schloeth 1980, Churchfield 1984, Kuvikova 1985, Lardet 1988, DuPasquier & Cantoni 1992).

In order to evaluate the complete dietary spectrum of *N. fodiens* and knowledge of its foraging behaviour and habitat preferences, it would be necessary to search its habitats for storage places and prey remains regularly, as well as to conduct experiments using captive shrews.

A c k n o w l e d g e m e n t s

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