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Prey Handling Times and Partial Prey Consumption in Five Species of European Shrews (Soricidae, Insectivora)

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Abstract
Prey handling times for meal-worms were measured in the common shrew (*Sorex araneus* Linnaeus, 1758), the pygmy shrew (*S. minutus* Linnaeus, 1766), the European water shrew (*Neomys fodiens* Pennant, 1771). Miller's water shrew (*N. anomalus* Cabrera, 1907) and the lesser white-toothed shrew (*Crocidura suaveolens* Pallas, 1811). The ranking corresponds with the body mass of the shrew species, water shrews eating fastest and pygmy shrews slowest. Eating patterns as revealed by food remains are evaluated and the significance of partial prey consumption is discussed.

Key words: Sorex, Neomys, Crocidura, shrews, prey, behaviour, foraging strategy

Introduction
Information on the time it takes a predator to devour various prey items is essential for testing predictions derived from the prey and patch models of optimal foraging theory. A prey yields a fixed amount of energy and requires a fixed amount of time to handle. This is a threshold in a predator's time budget. In sensu stricto, prey handling time comprises the duration of pursuit, capture and consumption (Stephens and Krebs, 1986). These activities can be treated separately only when prey is large and defensive. Considering a shrew eating a small invertebrate, however, this distinction is difficult. Barnard and Hurst (1987) measured handling times in common shrews for meal-worm segments.

Due to their high metabolic rate shrews are ideal experimental animals for eco-ethological investigations concerning the question of maximization of net energy intake. According to my recent review of the literature on shrew research (Haberl, 1995), exceptionally few scientists have investigated foraging strategies in Soricidae (e.g. Barnard and Brown, 1981, 1985a, 1985b, 1987; Barnard *et al*., 1983, 1985; Arditi *et al*., 1983; Pierce, 1987; Pierce *et al*., 1993; Saarikko, 1989; Ruthardt, 1990). It is of great wonder, that these animals have not stimulated wider research in this field. The reason for this can only be attributed to the difficulties inherent in maintenance and observation of shrews.

Materials and Methods
In this study, I measured prey handling times for *Tenebrio molitor* larvae in five common shrews (*Sorex araneus* Linnaeus, 1758), one pygmy shrew (*S. minutes* Linnaeus, 1766), four European water shrews (*Neomys fodiens* Pennant, 1771), two Miller's water shrews (*N. anomalus* Cabrera, 1907) and one lesser white-toothed shrew (*Crocidura suaveolens* Pallas, 1811). The experimental animals had been *suaveolens* (Pallas, 1811). The experimental animals had been trapped live in 1988 and 1989 in Schönbach (Lower Austria) and were caged separately in glass terraria containing a ground layer of 5-10 cm of peat and sufficient cover, provided by pieces of wood, stones, foliage and grass-tuft with rootstocks. The shrews were supplied ad libitum with various invertebrates (meal-worms, snails, earthworms) and rodent caresses. Cotton wool was provided as additional nesting material. The enclosures were accommodated in a brick building with large windows on two sides, providing a natural day and night light cycle and almost ambient temperatures. The captive animals were returned to the wild at the end of each study period (November 1988 and 1989), if they did not die earlier of natural causes.

For measurements of handling times, the shrews were temporarily transferred to smaller containers (42×22×25 cm) lined with cotton wool. The shrews were deprived of food for 1-4 hours before measurement (until the faces turned green and contained no cuticula). Timing was conducted from the moment of seizure of a meal-worm to the termination of chewing and swallowing according to the obvious cessation of mastication and sounds derived from crunching the cuticula. The completion of this procedure was usually marked by the shrew moving to either pick up another meal-worm or take cover. To standardize the data, only meal-worms of approximately the same size were used for this experiment (approximate length 23-28 mm; X = 122.5 mg, SE = 13 mg fresh weight). Live larvae yield about 2300 cal/gram of energy. The data was evaluated only if the larvae were devoured without pausing and immediately following seizure i.e., there was no intervening interval due to the shrew taking the meal-worm under cover to eat. When undisturbed, the shrews usually ate their prey immediately.

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Results and Discussion
The raking of the measured handling times corresponded

with the ranking of the body mass (and jaw size) of the shrew species (data shown as X±SE): *N. fodiens* ate faster (23.73±5.93 sec; n = 54) than *N. anomalus* (30.22±5.45 sec; n = 15), followed by *S. araneus* (33.36±6.53 sec; n = 25), *C. suaveolens* (36.05±7.65 sec; n = 15) and *S. minutes* (57.56±13.08 sec; n = 16). Minima ranged from 10.56 sec (*N. fodiens*) to 37.30 sec (*S. minutes*). Comparative data on “Non-starved” *S. araneus* (according to occasional measurements during normal feeding in the home terraria) did not differ significantly (36.19±10.02 sec; n = 45).

In many cases the larvae were not eaten completely, a phenomenon known as partial prey consumption (Sih, 1980). In the course of keeping shrews in captivity from spring to late autumn in 1988 and 1989. I collected 4581 leftovers which I evaluated according to remaining segments in order to supplement the data provided by Hutterer (1976) for *S. araneus* and *S. minutes*.

Polling the data for all five shrew species reveals the following distribution of feeding patterns (n = 4581): 52.7% of the larvae were eaten from the anterior end, leaving abdomen or abdomen and thorax (only the head missing). Anterior leftovers (head, head and thorax) comprised 29.4%. 16.1% were eaten from at both ends. This procedure, however has not been observed directly and the pattern could well be a result of eating an already partially consumed larva after some time, regarding it as a new prey item. Only 1.7% constituted whole meal-worms, merely showing bites in the thoracic or anterior abdominal region. This distribution differs significantly ($p<0.01$) from expected random values. The trend shows only little intraspecific deviations, although it is most distinct in *S. minutes* (71.4% posterior leftovers.)

The arrangement of the cuticular plates or the position of the extremities could provide tactile sensory clues for directing the first bite to the head region, which would be of benefit in immobilizing the larvae for storage. In small mammal caresses for instance, directive cues are probably constituted by the direction of the hair-stroke and by the position of a distinct “head”, as has been demonstrated in experiments using dummies (Haberl, 1993).

The phenomenon of partial prey consumption in shrews is not yet understood. Food surplus may not be the answer, as even starved shrews behave in this manner. The conclusion that the size of the meal-worms exceeds the size of the shrews natural prey items (Hutterer, 1976) also does not seem to explain this behavior, since *N. fodiens* has been shown to often partially consume *Tenebrio* larvae irrespective of the size of the larvae. It is well possible that on encountering a profitable patch of food this behavior ensures obtaining the required energy quickly while simultaneously securing a food supply before moving on to the next patch which has uncertain profitability. My observation of captive water shrews returning to their leftovers to feed after some tome would support this assumption. Still, it has to be considered that the handling times and patterns are not necessarily fixed, but may be dependent on previous experience.

The preliminary result presented in this paper would need to be ascertained in free-living shrews. In future studies it would be essential to take a closer look at interspecific differences. Further experiments should also consider different prey items, age dependent and individual differences in larger samples as well as the effects of deprivation time, which seems likely to be highly variable between species.

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