Ann. Zool. Fennici 26:335–338. 1989

Population biology of Eurasian shrews: Introduction

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Recent ecological, physiological and population genetic studies on small mammals have greatly enlarged our understanding of the biology of microtine rodents in Finland and elsewhere, while shrews, the family Soricidae of the Insectivora, have remained those relatively little known creatures that tend to die in live-traps. A wide-spread misconception about shrews is that they are difficult to trap and study alive. Another obvious reason for the scarcity of ecological studies on shrews, in comparison with the profusion of investigations on rodents, is the economical significance of the latter and the apparent insignificance of shrews. Shrews may, however, play an important role in the control of many forest insects, such as pine sawflies, in temperate forests (Holling 1958, Hanski 1987, 1990). On the other hand, shrews may hinder reforestation programmes by consuming large numbers of seeds of coniferous trees (Myllymäki & Paasikallio 1976).

Regardless of their importance or insignificance to humans, shrews comprise a key guild of insectivores in northern coniferous forests, and a group of mammals with much potential for ecological and biological studies. Shrews are small, and include some of the smallest extant mammals, of which *Sorex minutissimus* and *Sorex hoyi* have transcontinental distributions in northern temperate regions in Eurasia and North America, respectively. The small size of shrews poses intriguing biological problems about the physiological, behavioural and ecological adaptations that allow them to survive in temporally changing environments in spite of their exceptionally short starvation times (Crowcroft 1957, Hanski 1985).

This issue of Annales Zoologici Fennici is based on the second workshop of Finnish "soricologists", held at the Lammi Biological Station on 3 to 5 March 1989; the idea for this compilation of papers was conceived already in the first such workshop on 7 to 8 March 1987. The aim of this issue is twofold. We wished to review and summarize our current knowledge about the occurrence, numbers and dynamics of shrews in Finland, but we also wanted to cover the ecology and biology of northern temperate shrews more generally. To aid the latter purpose, we have included three papers dealing with the ecology and behaviour of shrews in Siberia. The Siberian fauna of soricine shrews is exceptionally rich in species, with a mixture of eastern and western species overlapping widely in Central Siberia.

A brief history of biological studies on shrews in Finland

Finland is located in the transition zone of three faunal regions in the Palaearctic, the European, Siberian and Arctic regions (Siivonen 1972). As a consequence of its zoogeographical position, Finland has a relatively rich mammalian fauna with six species of shrew. The common shrew *Sorex araneus* L. and the pygmy shrew *S. minutus* L. belong to the European faunal type, while the black shrew *S. isodon* Turov, the masked shrew *S. caecutiens* Laxm. and the least shrew *S. minutissimus* Zimm. are representatives of the Siberian faunal type. Arctic shrew species are absent in Finland, but the widely distributed water shrew *Neomys fodiens* (Penn.) is present.

As little as forty years ago the Finnish fauna was considered to have only three species of shrew, *S. araneus*, *S. minutus* and *N. fodiens* (Kivirikko 1940). At the beginning of the 1950s, observations of exceptionally small common shrews were published (Komonen 1952, Nuorteva 1953), and Siivonen (1954) soon demonstrated that these small-sized common shrews were *S. caecutiens*, though he used the name *S. macropygmaeus* Mill. In his handbook published in 1956 Siivonen also includes *S. minutissimus*, called *S. hawkeri* Thomas, in the Finnish fauna (see also Kaikusalo & Skarén 1958). The biology of this rare species has thereafter been studied in laboratory experiments (Skarén & Kaikusalo 1966, Kaikusalo 1967, Skarén 1978, Hanski 1984). The latest faunistic discovery was the black shrew, which was reported from Finland by Skarén (1963, 1964) as *S. unguiculatus* Dobson, but which was later shown to be *S. isodon* (Siivonen 1965, see also Skarén 1979b). Siivonen

(1969) confirmed that the Finnish black shrew is not *S. centralis* Thomas, the name used for *S. isodon* by Dolgov (1964).

Our knowledge about the distribution of the six shrew species in Finland has been greatly increased due to the increased use of pitfall traps in small mammal studies (Skarén & Kaikusalo 1966, Pankakoski 1979a, Henttonen 1982). The trapping techniques most suitable for shrews have been developed by Myllymäki et al. (1971), Pankakoski (1979a) and Jäderholm (1982).

There are numerous studies dealing with the *ecology* of shrews in Finland, and covering population dynamics (Skarén 1972, Kaikusalo & Hanski 1985, Pankakoski 1985), the relationships between shrews and their predators (Henttonen 1985, Korpimäki 1986) and parasites (Erkinaro & Heikura 1977), and breeding and moulting (Skarén 1973, 1979b). Dispersal to and dynamics of shrews on small islands have been studied in the 1980s by Hanski and his co-workers (Hanski 1986, Hanski & Peltonen 1988). Diel activity and the effect of weather on this have been studied by Kaikusalo (1967, *S. minutissimus*) and Pankakoski (1979b, *S. araneus*). Studies on *morphological variation* have been conducted to clarify the taxonomy of Soricidae (above) but also to further our understanding of the ecology of the species; the latter type of studies include Skarén (1979b) and Hanski & Kuitunen (1986). Chromosomal polymorphism and racial evolution of *S. araneus* have been studied by Liisa Halkka and her co-workers (Halkka & Skarén 1964, Halkka et al. 1974, Halkka & Söderlund 1987, Halkka et al. 1987). Mating behaviour and postnatal development of *S. isodon* have been studied by Skarén (1979a, 1982).

The foraging behaviour of shrews is of particular interest because of their small body size, short starvation time and the consequent need to consume up to twice their body weight of food in 24 hours (Hanski 1984). Laboratory studies have been conducted on the responses of small and large species of shrew to temporal (Hanski 1985) and spatial change in food availability (Hanski 1989). Field studies have examined the behaviour of shrews as pupal predators of forest insects (Hanski & Parviainen 1987).

Investigations on the *physiology* of shrews have been conducted in Finland for over twenty years, much of the work being focused on their winter adaptations. The metabolism of the Brown Adipose Tissue plays an important role in the wintering strategy of shrews (Hyvärinen 1968b, 1969a, Hyvärinen et al. 1971, Hissa & Tarkkonen 1969, Pasanen 1969, 1971, Pasanen & Hyvärinen 1970). The physiological mechanisms underlying the shrinking of the skull and the reduction of the body weight, which reduce the metabolic demands during the unfavourable season, have been studied by Hyvärinen (1968a, 1969b), and the functions of the endocrinal glands have been examined by Hyvärinen (1967, 1969c, d, 1972), Saure et al. (1972) and Pankakoski & Tähkä (1982).

Contents of this issue

The 13 papers comprising this special issue of Annales Zoologici Fennici can be divided into four sections, dealing with the ecology, morphometrics, behaviour and genetics of Eurasian shrews.

The first paper by Hanski & Kaikusalo gives an overview of the distribution and habitat selection of shrews in Finland: what species do we have, where do they occur, and why? The unique research opportunities presented by the great abundance of islands on lakes and in the Baltic have been used by several ecologists working on shrews in recent years. Peltonen, Peltonen, Vilpas & Beloff summarize the occurrence and numbers of shrews on different sorts of islands from the Baltic up to Lapland.

Population dynamics of shrews in Finland are described by Henttonen and others, who demonstrate how the year-to-year changes in the numbers of shrews are related to respective changes in the populations of other species of small mammals. This connection is of special interest because it may relate to the still largely unknown mechanisms driving the regular multiannual cycle of microtine rodents in northern Fennoscandia. Two papers from central and north-eastern Siberia, by Sheftel and by Dokuchaev, add a transcontinental perspective to the population ecology of Eurasian shrews. The study locality in Central Siberia where Sheftel has conducted his long-term studies has a record number of 9 species of soricine shrews, which show a strikingly regular 4-year cycle. Dokuchaev's study areas in north-eastern Siberia have an exceptionally severe climate, with temperatures falling to –60°C and below, and the shrews to a large extent depend on a particular food source, larch seeds. One species, *Sorex caecutiens*, is common throughout the vast northern part of the Eurasian continent, and the three papers on population dynamics allow some interesting comparisons (Hanski, concluding paper).

The remaining two papers in the ecology section deal with the natural enemies of shrews, their preda-

tors (Korpimäki & Norrdahl) and parasites (Haukisalmi). Both papers include information from elsewhere in Europe, and provide the most up-to-date reviews of their respective topics from western Europe. Korpimäki & Norrdahl report how most predators of shrews only turn to them when the preferred prey of microtine rodents is scarce, thereby increasing the synchrony of the shrew and rodent dynamics. Haukisalmi finds surprisingly little geographical variation in the intestinal helminths of shrews, and the parasites appear not to discriminate between the different shrew species. The latter observation is consistent with the notion of different shrew species showing little variation in the selection of their prey species, the intermediate hosts of the parasite.

Many ecological and biological investigations on shrews have employed morphometrical techniques. Pankakoski & Hanski describe in detail the traits and the techniques that have been found most useful in such studies. Pankakoski's paper on tooth wear in *Sorex araneus* and *S. minutus* is another demonstration of how morphometrical studies may help answer some ecological questions.

Two papers deal with the behaviour of shrews. Saarikko reviews studies on the foraging behaviour of soricine shrews in the light of the optimal foraging theory. Much of the work done in Finland has focused on shrews' responses to temporally and spatially varying food availability, an important consideration in view of the short starvation time of shrews. Moraleva's paper describes social interactions in *Sorex araneus* in Central Siberia, in the same locality where Sheftel has conducted his extensive studies on population ecology.

The final paper by Heikkilä reviews genetic variation in and differentiation of shrew populations and species in Europe as revealed by enzyme electrophoresis studies.

Acknowledgements. Lammi biological station, the Department of Zoology of the University of Helsinki and the Academy of Finland supported in various ways the meeting on which this issue of Annales Zoologici Fennici is based. We thank Risto A. Väisänen for editing one of the articles and the numerous individuals who reviewed the manuscripts. Samuel Panelius did most of the technical editing of the papers. Dick Forsman drew the frontispiece and cover illustration.

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Received 6.XI.1989
Printed 22.XII.1989