Ann. Zool. Fennici 40: 27–34 ISSN 0003-455X
Helsinki 26 February 2003

Population dynamics and foraging of *Sorex cinereus* (masked shrew) in the boreal forest of eastern Canada

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Received 1 Mar. 2002, revised version received 9 Oct. 2002, accepted 9 Oct. 2002

Bellocq, M. I. & Smith, S. M. 2003: Population dynamics and foraging of *Sorex cinereus* (masked shrew) in the boreal forest of eastern Canada. — *Ann. Zool. Fennici* 40: 27–34.

The ecology of shrews is better understood in the boreal forest of Eurasia than in similar regions of North America. In this study, the abundance, reproduction, population structure, and diet of *Sorex cinereus* (Masked shrew) were analyzed in jack pine plantations in the southern boreal forest of eastern Canada over two years. Abundance of *S. cinereus* showed variations between years. The seasonal pattern of capture was unimodal with the peak occurring at the end of the summer. Breeding began in May or earlier with litter sizes averaging 6.7 ± 0.3 (mean ± SE) embryos per pregnant female. The breeding season was at least six months long (May–October). Two distinctive cohorts were identified. The spring cohort, primarily produced by overwintering shrews, had a higher reproductive value than the summer cohort because they may have reproduced in the year of birth. The summer cohort was produced by both overwintering individuals and shrews of the first generation in that year. Lepidopteran larvae (moth) were the primary food type in stomach contents of immature shrews, followed by coleopterans (beetles) and arachnida (spiders). The mean percentage volume of lepidopteran larvae in shrew stomach contents was similar between years, months, and sites. The patterns identified for *S. cinereus* are compared with those of the most common Eurasian shrew (*Sorex araneus*).

Introduction

Community and population ecology of shrews are better understood in the boreal forest and taiga of Eurasia than in similar regions of North America. Patterns of community organization (Shvarts & Demin 1994), interspecific interactions (Churchfield 1984, Henttonen 1985), population dynamics (Sheftel 1989), and foraging ecology (Saarikko 1989, Churchfield 1994) were already identified for several species and assemblages of Palearctic shrews. In North America, a few studies were conducted on shrew ecology in deciduous forests (e.g., Merritt *et al*. 1994), and occasional contributions were made for the boreal forest (e.g., de Vos 1957, Innes *et al*. 1990, Bellocq *et al*. 1994). Some of the identified patterns are similar and others differ between boreal assemblages in the Palearctic and Nearctic regions (Hanski 1989). For instance, shrews show interspecific differences in body size in both regions; in contrast, the most abundant species in Palearctic assemblage is a large-size shrew (*Sorex araneus*) whereas in the Neoarctic is a small-size shrew (*Sorex cinereus*).

In a similar way, population biology of the most abundant shrew species in Eurasia is better understood than that of the North American most common shrew. Thus, latitudinal variations in life histories (Kaikusalo & Tast 1994), population dynamics (Churchfield 1980, Henttonen *et al*. 1989), inter- and intraspecific interactions (Michelsen 1966, Moraleva 1989), social behaviour and dispersal (Moraleva & Telitzina 1994), and foraging behaviour (Barnard & Brown 1981, Pierce 1987) of *S. araneus* are relatively well known compared to *S. cinereus* in North America. Although some studies have identified general patterns of life history (Innes 1994) and latitudinal variations in morphology (Huggins & Kennedy 1989) for *S. cinereus*, most short- and long-term patterns of population biology have yet to be determined.

In this study, short-term patterns of abundance, reproduction and diet of *S. cinereus* are identified and described for the southern boreal forest of eastern Canada. The abundance, reproduction, population structure, and foraging are analyzed based on shrews captured in jack pine (*Pinus banksiana*) plantations in northern Ontario over a two-year period. Patterns are identified by contrasting the results with information previously published on shrew ecology in the Canadian boreal forest. Additionally, the identified patterns are compared with those of the most common Eurasian shrew.

Materials and methods

Study area

The study area was located in an extensive sand-flat region of the southern boreal forest, approximately 30 km south of Gogama, Ontario, Canada (47°31´N, 81°44´W). Extensive monospecific and mixed coniferous-deciduous forests of jack pine, ranging in age from 1 to over 60 years, dominate the area, many of which were artificially regenerated after clearcutting or wildfire. The work was conducted in jack pine stands planted during 1988. In addition to jack pine, the stands were dominated by trembling aspen (*Populus tremuloides*) and specked alder (*Alnus rugosa*) in the overstory, and blueberries (*Vaccinium* spp.), sheep laurel (*Kalmia angustifolia*) and mosses in the understory.

Sampling of shrews

Shrews were captured in dry and wet pitfall traps, arranged in four grids of dry (Grids 5 to 8) and four of wet (Grids 1 to 4) traps, during June–October 1993 and May–November 1994. Grids 1, 2, 5, and 6 were separated approximately 45 km from Grids 3, 4, 7, and 8, and were established in different stands, at least 300 m apart from each other. Dry pitfall traps were used to capture shrews and wet traps for arthropods. Unfortunately, many shrews were also captured in the wet traps and, rather than discarding them, were included to augment our sample size.

Dry pitfall traps consisted of plastic containers (30 cm deep, 20 cm diameter) containing approximately 4 cm of pine needles and inserted flush with the ground. A square, slender piece of wood was placed over the top as a roof to avoid flooding, and whitefish was used as bait. Grids consisted of 22 traps, 25.8 m apart, arranged in four parallel lines of 6, 5, 6, and 5 traps, covering 0.5 ha. Dry traps operated for two consecutive days every 2 to 3 weeks (total effort 44 trap-nights per sampling period), and were checked twice a day in the morning and evening. Captured shrews were toe-clipped and released at the site of capture.

Wet pitfall traps consisted of plastic containers (12 cm deep, 15 cm diameter) filled 1/3 with water and inserted flush with the ground. Each grid consisted of 25 traps (12.5 m apart) placed in a 5 × 5 pattern in 1993, and of 49 traps arranged in a 7 × 7 pattern in 1994. Traps operated during 6 consecutive days every 2 to 3 weeks for a total effort of 150 trap-nights per sampling period in 1993 and 294 trap-nights in 1994, with the exception of two sampling periods (20–28 September 1994: 392 trap-nights, and 6 October–4 November: 1421 trap-nights). Dead shrews captured in these traps were placed in labelled plastic bags and frozen for later dissection.

Body mass (± 0.01 g), after the liquid had been absorbed by paper towels, and total body length (± 0.1 mm) were recorded for all shrews. Males with testes ≥ 3 mm in length and females pregnant, lactating, or with thick and vascularized uterus were considered reproductively active (e.g., Innes *et al.* 1990, Bellocq *et al.* 1992, Teferi *et al.* 1992). Litter size was determined by counting the number of embryos. Stomachs were removed and the contents preserved in a solution of 50% alcohol and water. Skins and internal organs were also removed and skeletons cleaned by dermestid larvae. The age class of shrews was determined on the basis of tooth wear following Rudd's (1955) method, and individuals were identified as young of the year (age class < 6) and overwintering adults (age class ≥ 6) following Teferi *et al.* (1992).

Diet analysis

The content of 60 stomachs was analyzed to determine the diet of shrews in Grid 1 during August 1993 and 1994 and during September 1993, and in Grid 2 during September 1994. Thus, comparisons were made between years (August 1993 and 1994 in Grid 1) and grids (September 1993 in Grids 1 and 2). Only sexually inactive shrews were considered in these comparisons because previous studies showed adult and juvenile *S. cinereus* consumed different proportions of food types (Bellocq *et al.* 1992, 1994). Stomach contents were analyzed following the general procedure described by Whitaker and French (1984). The cumulative frequency of new items appearing in stomachs, as a function of the number of stomachs analyzed (Churchfield 1982), indicated that a sample size of 10 stomachs was sufficient to provide a good representation of the diet. Most food items were identified to order. Diet was quantified as percentage volume of each food type in each stomach content, and summarized as average percentage volume. The frequency of occurrence of each food type was estimated as the number of stomach contents containing the food type divided by the total number of stomach contents analyzed.

Statistical analysis

An heterogeneity chi-square and a *t*-test for unequal variances were used to test for differences in shrew abundance between years and grids. We used two tail *t*-test for unequal variances to test for differences in the consumption of main food types between years, months and grids. Means are presented ± one standard error (SE). SAS/STAT™ was used to perform most statistics tests.

Results

Pattern of abundance

Overall, 27 shrews were caught 28 times in the dry pitfall traps during 1993 and 25 shrews 26 times during 1994 (Table 1). The number of shrews caught in the four Grids was similar in 1993 and 1994 ($\chi^2 = 2.364$, $P > 0.5$). Mortality in dry traps accounted for 41% and 38% of the captured shrews in 1993 and 1994, respectively. Consequently, the number of surviving shrews was insufficient to analyze population parameters and trends. Those shrews that survived, however, provided valuable information on microhabitat selection (Bellocq & Smith 1995).

Overall abundance of shrews showed year-to-year variation with a total of 478 *S. cinereus* caught in wet pitfall traps during 1993–1994. The mean number of captured shrews per 100 trap-nights was higher in 1993 (3.90 ± 0.88) than in 1994 (1.67 ± 0.07) ($t = 2.531$, $P < 0.04$).

The seasonal pattern of capture was unimodal, as the abundance increased smoothly through spring-summer reaching a peak by the

Table 1. Number of shrews caught in dry (live) pitfall traps in four grids in young jack pine plantations in northern Ontario during the summer of 1993 and 1994.

	1993	1994
Grid 5	9	6
Grid 6	5	2
Grid 7	8	10
Grid 8	5	7
Total	27	25
Trapping effort (trap nights)	308	352

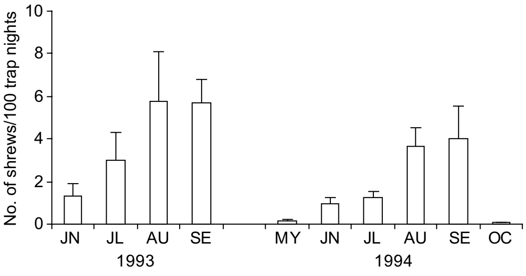

Fig. 1. Seasonal variation in numbers of *Sorex cireneus* collected by pitfall traps from the southern boreal forest of eastern Canada over two years.

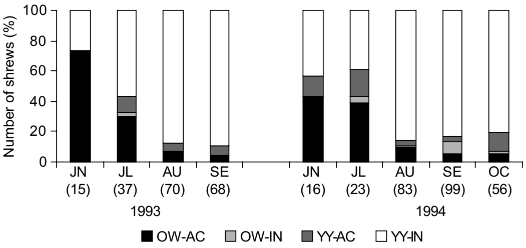

Fig. 3. Seasonal variation in age structure (overwintering individuals, OW, or current-year young, YY) and reproductive condition (sexually-active, AC, or inactive, IN) of *Sorex cinereus* in the southern boreal forest of eastern Canada over two years. Numbers into brackets are sample sizes for the month.

end of the summer and then declining suddenly (Fig. 1). The pattern of capture in individual grids revealed that peaks of abundance might occur at different times in different locations. The earliest peak occurred in Grid 1 by mid-August 1993 and the latest was recorded in Grid 3 in September 1993 (Fig. 2). Total number of shrews caught differed among grids in 1993 ($\chi^2 = 28.379$, $P < 0.001$) but not in 1994 ($\chi^2 = 0.797$, $P > 0.9$). With months as replicates, however, there was no significant difference in the abundance of shrews among grids in 1993 ($F = 1.12$, $P > 0.4$).

Mean body length and body weight of shrews was 90.9 ± 0.3 mm (range 64.7–115.9 mm) and 3.17 ± 0.04 g (range 1.41–9.58 g), respectively.

Population structure and reproduction

A total of 96 males and 91 females were captured in 1993 and 157 males and 134 females in 1994.

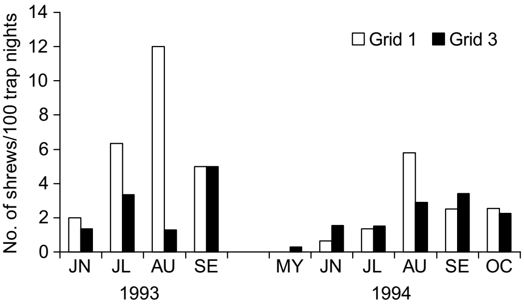

Fig. 2. Abundance of *Sorex cinereus* from two different young jack pine stands (Grids 1 and 3) in the southern boreal forest of eastern Canada over two years.

Sex ratio of the overall captured population was consistent with a 1:1 hypothesis in both 1993 ($\chi^2 = 0.139$, $P > 0.25$) and 1994 ($\chi^2 = 0.139$, $P > 0.25$). In 1994, however, sex ratio was biased towards males in June–August (June: $\chi^2 = 2.941$, $0.05 < P < 0.1$; July: $\chi^2 = 6.800$, $P < 0.01$; August: $\chi^2 = 9.012$, $P < 0.005$), and towards females during September-October, although differences were not significant (September: $\chi^2 = 1.318$, $P > 0.5$; October: $\chi^2 = 2.500$, $P < 0.25$).

Even though most of the population captured in June were overwintering, sexually active shrews, the presence of current-year young in this month indicates that breeding started in May or earlier both years. The proportion of the population that were current-year young in June was higher in 1994 than in 1993 (Fig. 3) with more sexually-active current-year young caught during June in 1994 than in 1993, suggesting that reproduction and recruitment of juveniles started earlier in 1994 than in 1993. The capture of sexually-active males and females from June to October and the presence of current-year young in June indicate that the length of the breeding season was at least six months (May–October). Litter size was 6.7 ± 0.3 embryos per pregnant female.

Most of the captured overwintering shrews were sexually active along the whole breeding season, except for September 1994, whereas the proportion of sexually-active, current-year young declined from June to September (with a slight recovery in October 1994) as recruitment of juveniles increased (Fig. 3). The earliest capture of current-year young, pregnant females occurred in early July 1993 and mid-June 1994; prior to that, all captured pregnant or lactating females were overwintering shrews. Of the sexually-active females, 57% were current-year young in July and 77% in August–October. In 1993, no current-year young males were sexually active whereas in 1994, the first sexually-active male was captured in July. Of the sexually-active males, 9% were current-year young in July and 7% in August–October.

Most of the shrews caught during June were sexually-active individuals that successfully survived the winter (Fig. 3). The abundance of overwintering shrews decreased whereas that of current-year young increased from June to October, showing that the peak of abundance (Fig. 1) was due to recruitment of juveniles by natality and/or immigration.

Diet

Analysis of the stomach contents revealed that shrews fed on a variety of arthropods. Lepidoptera larvae represented the majority of food found in the stomach contents, followed by adult beetles (Coleoptera) and spiders (Aranea) (Table 2). Crickets and grasshoppers (Orthoptera) were also present in the diet but only during September. The mean percentage volume of Lepidoptera larvae in the stomach contents was similar between years ($t = 1.590$, $P > 0.1$), months ($t = 0.720$, $P > 0.1$), and plots ($t = 1.824$, $P > 0.05$).

Discussion

Trapping technique

Trapping techniques that continuously remove animals have weaknesses compared to mark-and-recapture techniques to study population dynamics. We were unable to describe population dynamics based on mark-and-recapture data because masked shrews avoid life traps such as Sherman traps and dry pitfall traps lead to high mortality (which is common in captive masked shrews). Most studies describing shrew populations in Eurasia and North America are based on snap or pitfall trapping (e.g. Naylor & Bendell 1983, Henttonen *et al.* 1989, Sheftel 1989, Innes *et al.* 1990) which allows for valid general comparisons. When trapping efficiency is high, pitfall traps take resident animals at the beginning of the trapping period, and then shrews that disperse into the grid. Consequently, the patterns described here refer to the trapped population, knowing that pitfalls are biased towards dispersing shrews (Sheftel 1989).

Table 2. Mean percent volume (% Vol.) and percent frequency (% Freq.) of food types in stomach contents of young of the year, sexually inactive, *Sorex cinereus* comparing the diet in time (year-to-year and month-to-month) and space (Grids 5 and 6).

	Grid 1						Grid 2	
	August 1993 (n = 24)		September 1993 (n = 11)		August 1994 (n = 11)		September 1993 (n = 14)	
Food types	% Vol.	% Freq.	% Vol.	% Freq.	% Vol.	% Freq.	% Vol.	% Freq.
Insect larvae								
Lepidoptera	81.1	100.0	84.2	100.0	66.6	100.0	70.2	92.9
Undetermined	0	0	0.4	0.1	0	0	3.0	14.3
Adult insects								
Coleoptera	6.3	3.3	0	0	3.4	81.8	11.2	42.9
Hymenoptera	< 0.1	4.2	1.6	36.4	3.6	27.3	1.2	14.3
Diptera	3.1	4.2	0	0	5.5	27.3	0.4	7.1
Orthoptera	0	0	0.4	45.4	0	0	4.4	7.1
Undetermined	1.3	16.7	6.1	27.3	11.1	63.6	0.7	0.7
Aranea	7.7	16.7	8.0	0.1	0.6	14.3	8.9	28.6

Patterns of abundance

Abundance of *S. cinereus* showed variations between years in the southern boreal forest of eastern Canada. De Vos (1957) presented evidence for a widespread peak in *S. cinereus* populations during the late summer of 1955 in Ontario. Similarly, previous pitfall trapping conducted in the same general area as our study showed that shrew populations were higher during 1985 (Innes *et al.* 1990) than in previous (Naylor & Bendell 1983) and later (Bellocq *et al.* 1992) years. In similar zones of the Palearctic region, populations of the most common shrew (*S. araneus*) also showed year-to-year variations, with erratic fluctuations rather than regular multiannual population cycles (Henttonen *et al.* 1989 and references therein). In northern Ontario, the population peak of *S. cinereus* recorded during 1985 coincided with an unusually high abundance (outbreak) of Lepidoptera larvae (Innes *et al.* 1990). In Eurasia, food supply during the summer seems to act as a density-dependent factor affecting population dynamics of *S. araneus* (Kaikusalo & Hanski 1985).

Seasonal dynamics of *S. cinereus* showed increasing abundance during the spring-summer, reaching a peak by late summer-early fall and then a sudden decline. This pattern was also observed in mature mixed-wood forests of jack pine-white spruce (de Vos 1957) and black spruce (K. Frego, pers. comm.) in northern Ontario. Such annual population peaks will vary in time and space, depending on seasonal trends. The seasonal dynamics of *S. araneus* (and other Palearctic shrews) also shows higher abundance in late summer–early fall than during other months, with peaks occurring at different times in different years (Henttonen *et al.* 1989, Sheftel 1989). These seasonal changes in abundance were attributed to the variable effect of rainfall on species-poor assemblages and to interspecific interactions in richer communities. In Canada, rainfall is a major factor influencing *S. cinereus* activity (Vickery & Bider 1978), and thus it is expected to affect trapping indices. In our study, a unimodal seasonal pattern of abundance was found, but bimodal patterns were occasionally described in both *S. cinereus* (Innes *et al.* 1990) and *S. araneus* (Sheftel 1989).

In the eastern boreal forest, abundance of *S. cinereus* varies among different types and age of forests. Mid-age pure jack pine stands seem to support higher numbers of *S. cinereus* than either younger pure jack pine or mixed conifereous-desciduous forests in northeastern Ontario (Naylor & Bendell 1983). In pure jack pine forests, abundance of *S. cinereus* seems to increase with increasing stand age until the plantation is about 40 years of age (Sims & Buckner 1973, Naylor & Bendell 1983, Innes *et al.* 1990). Our study showed that maximum abundance of *S. cinereus* populations may occur at different times even in sites with similar habitat and age of plantation. In contrast, Innes *et al.* (1990) found that the pattern of capture through the summer was different between 20- and 40-year old jack pine stands but alike among stands of similar age.

Patterns of reproduction

The reproductive activity of *S. cinereus* in eastern Canada started in early spring, varying slightly in time and space. The capture of current-year young in June indicates that reproduction must have begun during May or even earlier. Differences in the proportion of current-year young between June 1993 and 1994 suggested that reproductive activities started earlier in 1994 than in 1993. Similar early spring reproductive activity was shown by Teferi *et al.* (1992) for an insular population in eastern Canada, where young recorded in May indicated a reproductive start during March or April. Differences in clime between localities and year-to-year variation in local weather conditions might explain the observed spatial and temporal differences in the actual start-point of reproductive activities.

The sex ratio of the captured shrew population showed month-to-month variation, although overall it averaged 1:1 in both 1993 and 1994. In 1994, month-to-month variations in sex ratio were male-biased during the spring and summer and female-biased during the fall, in agreement with observations by Teferi *et al.* (1992). Month-to-month variations in sex ratio of the captured population, however, unlikely reflect true variation in the overall population sex ratio. The probability of being captured by pitfall traps depends, among other factors, on the degree of locomotion activity, and females tend to spend time near the nest during lactation. This may explain why sex ratio of the captured population was male-biased during the spring and summer. In fact, sex ratio of current-year young was approximately 1:1 whereas sex ratio of overwintering shrews was male-biased during the spring and summer of 1994.

Two distinctive cohorts may be identified, considering the month-to-month variation in population structure, weaning age (20 days, Innes 1994), and gestation length (probably about 20–25 days given the values for other *Sorex* species, Innes 1994). The spring cohort, recruited in May–July, was essentially produced by shrews that successfully survived the winter. The summer cohort, recruited in August–October, was primarily produced by overwintering males and by both overwintering and current-year females. Age of sexual maturation seemed to be higher in males than in females. Previous studies also found that most of the overwintering shrews were sexually active (with activity declining in the fall), and that most current-year young were sexually inactive (with activity starting in June–July) in tamarack bogs of southeastern Manitoba (Buckner 1966) and in Nova Scotia (Teferi *et al.* 1992). We found that the proportion of sexually-active current-year shrews was higher in females than in males. In contrast, Teferi *et al.* (1992) found that the proportion of sexually-active current-year shrews was similar in males and females.

The spring and summer cohorts appeared to differ in their reproductive value. The spring cohort presumably has the highest reproductive value, because individuals born early in the breeding season may reach sexual maturation and reproduce in the year of birth. In contrast, reproductive value of the summer cohort is low due to low life span given that individuals must survive the winter to reproduce in the following year. Overall litter size was 6.7 ± 0.3 and it was similar to the 6.5 ± 0.3 reported by Innes (1994) based on 31 populations. Although we could not analyze month-to-month variation in litter size, previous work in jack pine forests of northeastern Ontario has shown litter size to be the highest during June (Innes *et al.* 1990). The probability of juvenile survival is relatively high when food supply is high (spring) and weather conditions are relatively benign during the months following birth. Litter size decreased as food availability decreased and weather conditions become harsher through the summer-fall. Presumably, neonate body mass increases with decreasing litter size, but further research is required to compare neonate body mass between cohorts.

Foraging

Lepidoptera larvae were the primary food found in stomach contents of shrews. Previous research conducted in older forests, in the same general area as our study, showed similar results (Bellocq *et al.* 1992, 1994). Studies conducted in other localities, however, suggest that *S. cinereus* is a generalist insectivore, with its diet depending on the availability of alternate prey. Whitaker and French (1984) reported a higher proportion of Coleoptera than Lepidoptera larvae in the diet of shrews from New Brunswick, and Steward *et al.* (1989) showed that differences in the frequency of occurrence of prey items in the diet of shrews was related to prey availability over a gradient. We only considered the diet of juvenile shrews in our study because diet is known to differ with sexual activity, and adult *S. cinereus* have a more diverse diet and consume lower proportions of Lepidoptera larvae than juveniles (Bellocq *et al.* 1992, 1994). Thus, our work on *S. cinereus* likely overestimates the percentage volume of Lepidoptera larvae in stomach contents and underestimates dietary diversity when compared to studies where all individuals were included, regardless of maturity status.

Acknowledgements

We greatly appreciate the field and laboratory assistance of A. Applejohn, A. Breau, C. Desabrais, M. Doka, J. Farnworth, K. Fernie, and N. Maheswaran. An anonymous reviewer made insightful comments that improved the manuscript. The Royal Ontario Museum kindly allowed access to the dermestid room for cleaning skeletons. The logistic field support of E. B. Eddy Forest Products was invaluable. This research was funded by the Northern Ontario Development Agreement and the Forestry Canada Green Plan. Preparation of this manuscript was supported by the Ontario Ministry of Natural Resources and the Consejo Nacional de Investigaciones Científicas y Técnicas of Argentina.

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