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# Population biology of Eurasian shrews: Towards a synthesis

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Boreal assemblages of soricine shrews consist of species with a strikingly similar body shape but of distinctly different sizes. Eurasia and North America have morphologically parallel but phylogenetically distinct series of species in two different subgenera. This paper reviews related issues in the behavioural, population and community ecology of boreal shrews, including the reproductive biology of male shrews, body size and extinction probability in sympatric species, synchrony of population dynamics of sympatric shrews and microtine rodents, and the possible role of dispersal behaviour in population dynamics. Central Siberian populations of *Sorex caecutiens*, one of the three transcontinental Eurasian species, are characterized by large individuals, small litters and predictably cyclic dynamics, while populations at both the western and the eastern ends of the species' range have smaller individuals, larger litters and more irregular dynamics.

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## 1. Introduction

The boreal and arctic regions of Eurasia, the biogeographical zones that are characterized by coniferous forests and tundra, and which extend from Fennoscandia to Siberia and the Pacific coast, have some 14 species of soricine shrews. Apart from the water shrew *Neomys fodiens*, all these species belong to *Sorex* (Corbet & Hill 1980). Until the 1950s, taxonomic knowledge on shrews was fragmentary, and for instance in Finland only three of the six species were correctly identified (Hanski & Pankakoski 1989). Today, in most areas in the Palearctic region, identification of shrew species in local assemblages is relatively straightforward, though it requires experience. Some taxonomic uncertainties still remain about the species in the *Sorex araneus* complex, which are characterized by the sex chromosome mechanism $XX/XY_1Y_2$ (Hausser et al. 1984), and about some relatively little-studied taxa restricted to eastern Siberia (Corbet & Hill 1980, Okhotina 1977, Dokuchaev 1989). Heikkilä (1989) reviews much of the data on genetic differences amongst the Eurasian shrews.

Boreal assemblages of shrews typically consist of species with a strikingly similar body shape but of distinctly different sizes (see Frontispiece). As an example, Fig. 1 compares the Finnish *Sorex* with the assemblage of species found in Alberta, western North America. In the skull measurements, one may identify pairs of morphologically similar species, such as *isodon-arcticus*, *caecutiens-monticolus* and *minutus-cinereus* (Fig. 1). Interestingly, the North American species appear to deviate in skull shape from the Eurasian species, as indicated by the position of the species along the second principal component in Fig. 1. Such systematic differences may reflect a phylogenetic divergence, most of the species on the two continents belonging to two different subgenera (George 1988). In post-cranial skeletal measurements interspecific differences in body size are more dominating, and in both assemblages species adjacent in a size-ranking exhibit almost equal size ratios, or "community-wide character displacement" (Strong et al. 1979). There is little doubt that the size differences facilitate coexistence of many shrew species, in the same manner as size differences are known to play a significant role in the coexistence of many granivo-

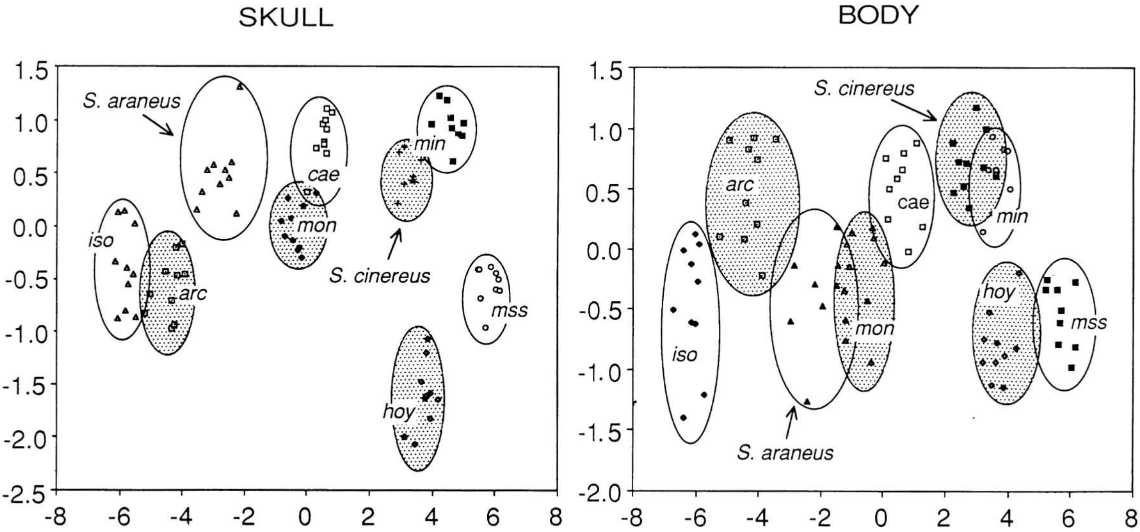

Fig. 1. Principal component analysis of skull and post-cranial skeletal measurements of *Sorex* shrews from comparable regions of coniferous forest in Finland and Alberta, western North America. The first principal component (horizontal axis) reflects the general size of the species. The Finnish species are (from the largest species on the left to the smallest species on the right) *isodon*, *araneus*, *caecutiens*, *minutus* and *minutissimus*; the North American species have been shaded, and they are *arcticus*, *monticolus*, *cinereus* and *hoyi* (H. Virtanen & I. Hanski unpubl.).

rous, desert-dwelling rodents (Bowers & Brown 1982, Hopf & Brown 1986, Brown 1987) and in mustelids (Dayan et al. 1989), though exactly why and how size makes a difference in shrews is not entirely understood (Hanski 1990, Hanski & Kaikusalo 1989).

My aim in this concluding paper is to draw attention to the many interesting results reported in this special issue of *Annales Zoologici Fennici*, based on a meeting of shrew ecologists held at Lammi Biological Station, Finland, on 3–5 March 1989. I have seized the opportunity to present my own interpretation of some of the results, I have attempted to relate one set of observations to another, and I have added some extra analyses and ideas where this has seemed appropriate.

## 2. Behavioural ecology of soricine shrews

Moraleva (1989) reported field observations and neutral arena tests on interactions between members of three functional groups of the common shrew *Sorex araneus* in Central Siberia: adult males, adult females and juveniles (immature males and females cannot be reliably sexed alive). The thesis advocated by Moraleva is that adult males have a low social position in the population, as they are harassed by other adult males (competition for oestrus females), by breeding females (defence of breeding territory and nest), and by juveniles (competition for space and for food resources). Moraleva suggested that many adult males are forced to move, during the summer, to marginal habitats with a low density of conspecifics, and that the rate of mortality in adult males is positively related to population density, and especially to the density of juveniles. Although the data available are not sufficient to prove these suggestions conclusively, Moraleva's results raise interesting questions about the life history of male shrews and about the role of seasonally flooded (marginal) habitats in the population dynamics of small mammals.

Adult males of shrews invest heavily in reproduction, in other words in locating oestrus females and in copulations. The weight of the testes and the accessory sexual organs amount to nearly 10% of the body weight of adult *Sorex araneus* (Brambell 1935)! Heavy investment in reproduction might correlate with vulnerability to social and other biotic and abiotic pressures. An extreme parallel is the recently

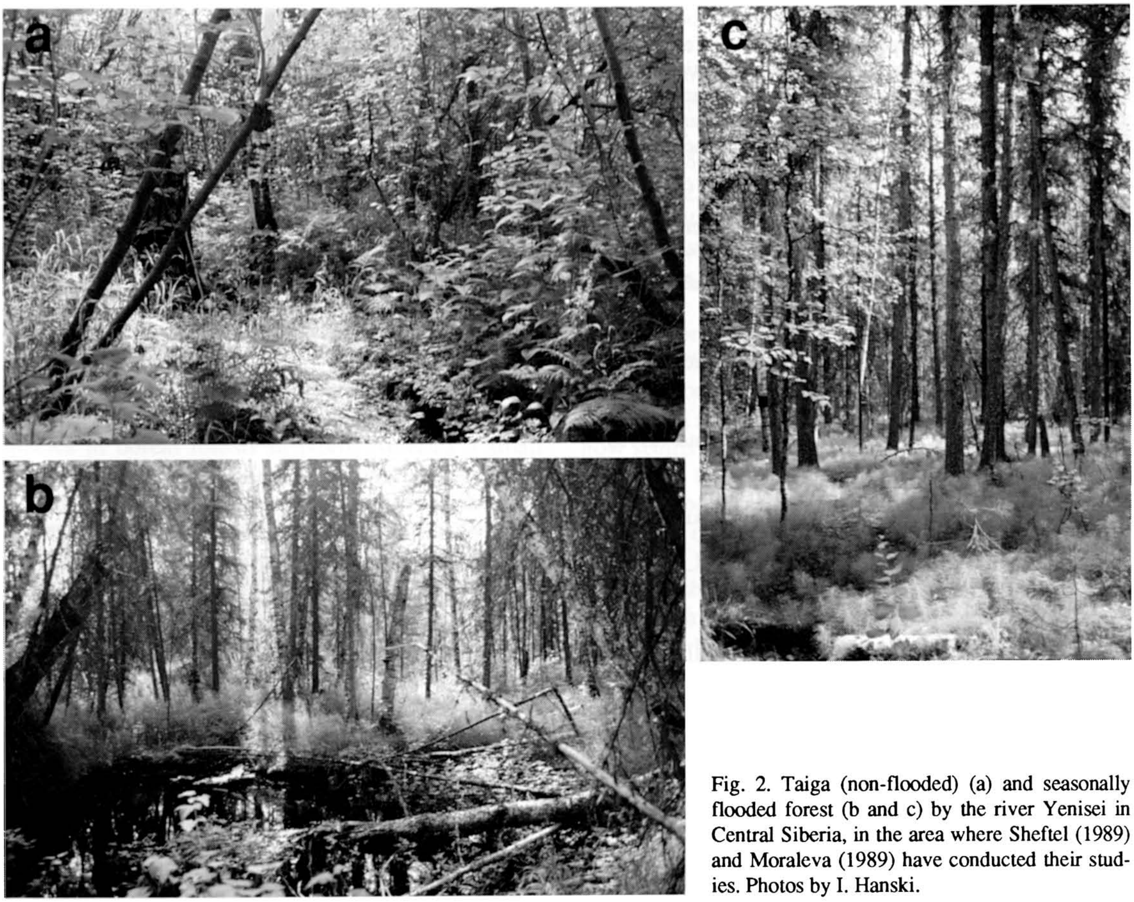

Fig. 2. Taiga (non-flooded) (a) and seasonally flooded forest (b and c) by the river Yenisei in Central Siberia, in the area where Sheftel (1989) and Moraleva (1989) have conducted their studies. Photos by I. Hanski.

discovered dramatic and complete post-mating male mortality in some species of *Antechinus* (Dasyuridae), insectivorous marsupials in Australia. In *Antechinus* males, an intensive breeding effort leads to a general stress response, including suppression of the immune and inflammatory responses (Lee et al. 1977, Braithwaite & Lee 1979, Lee & Cockburn 1985), which inevitably end in the death of the individual. Such an extreme strategy is not likely in *Sorex*, because female shrews produce several litters during the summer, but one may ask exactly how heavy is the breeding effort in *Sorex* males, and at what cost? The answers are not known.

Another question raised by Moraleva's (1989) observations is the role of the flood plain habitats, to which the adult males are suggested to "escape", in the population dynamics of shrews and other small mammals. Vast areas of the boreal regions are covered by relatively barren coniferous forests, which contrast sharply with the often luxuriant, seasonally flooded forest and meadow habitats by rivers (Fig. 2). The spring flood may penetrate many kilometres from large rivers, such as the Yenisei in Central Siberia.

Moraleva's results indicate that adult males of *Sorex araneus* are overrepresented in the flooded forests in early summer. Do the adult males disperse to the flooded forest in early summer, soon after the spring flood has receded, as suggested by Moraleva? This would be unexpected if most females remain in the unflooded forest. Or have many males and females overwintered in the flooded forest, where food availability must be higher than in the more barren, unflooded forest, and do many females disperse in early summer to breed in the surrounding taiga? If so, how do shrews survive the spring flood, which varies in depth and duration from one year to another? That the flooded forest is a superior habitat for shrews in

Table 1. Temporal fluctuations in the numbers of coexisting populations of *Sorex araneus* and *S. caecutiens* in four localities in northern Europe. The level of population fluctuations is measured by the coefficient of variation, *CV* (100 × standard deviation divided by the mean). The mean is the number of individuals caught per 100 trap-nights, and n is the number of years over which *CV* and mean were calculated.

| Locality | Species | *CV* | Mean | *n* | Reference |
|---|---|---|---|---|---|
| East Finland | *araneus* | 48 | 12.9 | 5 | Hanski (unpubl.) |
| | *caecutiens* | 168 | 14.2 | | |
| East Finland | *araneus* | 34 | 17.2 | 8 | Skarén (1972) |
| | *caecutiens* | 131 | 6.2 | | |
| Soviet Karelia | *araneus* | 87 | 14.6 | 16 | Ivanter (1976a) |
| | *caecutiens* | 139 | 0.5 | | |
| Finnish Lapland | *araneus* | 100 | 8.5 | 18 | Kaikusalo (1980) |
| | *caecutiens* | 120 | 2.0 | | |

summer is evidenced by the result that all the eight species of *Sorex* that occur in the area studied by Moraleva (1989) and Sheftel (1989) may be found together in a patch of flooded forest.

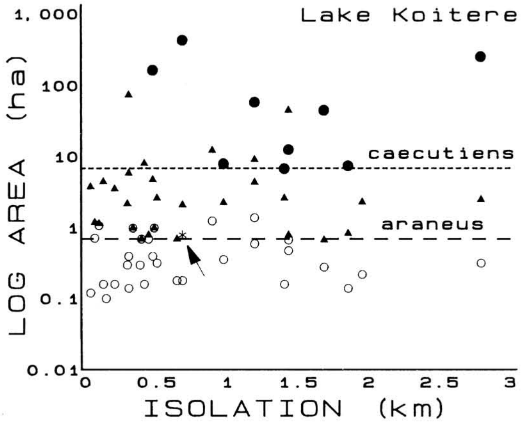

Fig. 3. Occurrences of *Sorex araneus* and *S. caecutiens* on islands in two lakes in eastern Finland (lakes Koitere and Sysmä). The horizontal axis gives the isolation of the island from the mainland, while the vertical axis gives the logarithm of island size. Symbols: black dots = islands occupied by both *araneus* and *caecutiens*, triangles = islands occupied by *araneus* alone, asterisk = one island occupied by *caecutiens* alone, and open circles = unoccupied islands. Note that the minimum island size of *araneus* is by an order of magnitude smaller than the minimum island size of *caecutiens* (the broken lines; partly based on A. Peltonen & I. Hanski unpubl.).

## 3. Effect of food shortages on population dynamics

Shrews, because of their high mass-specific metabolic rate and small body reserves, have starvation times of only a few hours. Saarikko (1989) reviewed the behavioural consequences of short starvation times, but short starvation times also have critical population dynamics implications.

The numerically dominant species of shrew in northern Europe is *Sorex araneus*, a relatively large species (juveniles 5 to 8 g), while the two other common species, *Sorex caecutiens* (3.5 to 5 g) and *Sorex minutus* (2 to 4 g), are substantially smaller and have even shorter starvation times than *S. araneus*. The shorter starvation times of the smaller species make them more sensitive to temporal variation in food availability, a form of environmental stochasticity. Sensitivity to environmental stochasticity, in turn, should be reflected in increased temporal variance in population size. Comparing the two common species, *S. araneus* and *S. caecutiens*, the smaller and generally less abundant *caecutiens* has indeed higher temporal variance than *araneus* in population size (Table 1).

To develop this argument further, let us recall that high temporal variance in population size in relation to average density increases the probability of extinction of a local population (Leigh 1981). Extinctions of local populations are easiest to study on islands, which have the advantage for population ecological studies that they come in many sizes and degrees of isolation, providing research opportunities that have been exploited in the studies reviewed by Peltonen et al. (1989).

Peltonen et al. found that *Sorex caecutiens* had a relatively large minimum island size, around 15 ha, in Lake Inari in Finnish Lapland. In a previous study conducted in eastern Finland, Hanski (1986) found that the larger *S. araneus* had a much smaller minimum island size of around 1 ha. Fig. 3 presents previously unpublished, comparative data for *araneus* and *caecutiens* on the same set of islands in eastern Finland. It is clear that there is indeed an order of magnitude difference in the minimum island sizes of the two species. The difference is not likely to be due to interspecific competition and the probable competitive superiority of *araneus*, not to any great extent at least, because the minimum island size for *caecutiens* was the same on islands with *araneus* (Fig. 3) as on islands without this species (Fig. 1 in Peltonen et al. 1989), and because Peltonen & Hanski (unpubl.) found no higher rate of extinction of *minutus* and *caecutiens* on islands with *araneus* than on islands without it. A more likely explanation of the difference in Fig. 3, and an explanation in accordance with the population dynamic theory, is the demonstrated greater sensitivity to environmental stochasticity of *caecutiens* compared to *araneus* (Table 1). The above chain of arguments, substantiated by the results of Saarikko (1989) and Peltonen et al. (1989), demonstrates the value of interspecific comparisons in the study of population dynamics.

It is likely that the numerical dominance of *S. araneus* in western Eurasia is to some extent based on its relatively small sensitivity to environmental stochasticity. But why then is the numerically dominant species in boreal forests in North America a small species, *S. cinereus*? My guess is that the main reason is the lower food availability for shrews in most North American coniferous forests in comparison to western Eurasia, shifting the balance towards smaller species with smaller per capita food requirements (Hanski 1990). In accordance with this hypothesis, in Europe the smaller species are relatively more abundant in the more barren habitats (Hanski & Kaikusalo 1989). Thus the feeding biology of shrews and the dependence of metabolic rate on body size (Hanski 1984) provide an explanation linking habitat selection with a major pattern in the geographical distribution of shrews.

## 4. The microtine rodent connection

Sheftel's (1989) results from Central Siberia present convincing evidence for a regular 4-year cycle in the pooled density of shrews (the cycle has retained its 4-year periodicity for the past 4 cycles, up to 1989). Different species of shrew have tended to peak in different years of the cycle in pooled density, which variation Sheftel attributes to interspecific differences in population growth rates and competitive abilities. Similar conclusions have been drawn about interspecific differences amongst the 8 species of rodents that are involved in the multiannual cycle in Finnish Lapland (Henttonen et al. 1984) and about the coexistence of weasels and stoats (King 1989). Such differences may contribute to the coexistence of many competitors (Chesson & Case 1986).

In Central Siberia, the synchrony in the cyclic dynamics extends to rodents (Sheftel pers. comm.), and it seems likely that there as in north-western Europe the rodent populations play the leading role in the small mammal cycle. But why are the dynamics of herbivorous and omnivorous rodents and insectivorous shrews synchronized? Several authors have suggested that the synchronizing factor is shared predators, which switch to shrews when microtine rodents, the preferred prey, become scarce (Hansson 1984, Henttonen 1985, Kaikusalo & Hanski 1985, Korpimäki 1986, Hanski 1987, Sonerud 1988, Henttonen et al. 1989). Korpimäki & Norrdahl (1989) demonstrated that the rate of shrew predation by the Tengmalm's owl is not related to the density of shrews themselves but depends on the density of microtine rodents, a result consistent with the prediction of optimal foraging theories (Stephens & Krebs 1986, Saarikko 1989).

It is worth stressing that even if the synchrony in rodent and shrew dynamics were due to predation, as now seems likely, this observation in itself does not prove that the cyclic dynamics are driven by predators. It is possible that the rodent cycle is driven by something other than predators, which in this scenario would just follow, numerically, the rodent cycle, and switch to shrews when the rodents crash (the alternative prey hypothesis; Angelstam et al. 1984, Hörnfeldt et al. 1986).

There is some disagreement about the kinds of predators that are most likely to have the greatest impact on shrews. The synchronous low years of rodents and shrews in Lapland have been attributed to specialist mammalian predators, the weasel and the stoat (Hansson 1984, Henttonen 1985, Hanski 1987, Henttonen et al. 1989), but Korpimäki & Norrdahl (1989) suggested that the key predators in their study region in western Finland are some birds of prey, such as Tengmalm's owl, short-eared owl, long-eared owl and kestrel, while small mustelids consume very few shrews, if any. However, there are hardly any data on the diet of small mustelids from Lapland, and there may be important geographical differences in the feeding habits of these predators (King 1989). For instance, mustelids seem to use more shrews in North America than in Europe (Korpimäki & Norrdahl 1989).

One final puzzle is the apparently much better synchrony of rodent and shrew dynamics in Sheftel's study area in Central Siberia compared with Fennoscandia (for the latter area see especially Sonerud 1988). I can make three suggestions, of which the first is a methodological one. Sheftel has used pitfall traps set in trapping ditches to collect his material. In comparison with other trapping techniques, Sheftel's method most probably yields results biased towards dispersers (Moraleva 1989), hence his results are affected by possible changes in dispersal rate during the multiannual cycle. It is possible that the rate of dispersal of shrews increases with the density of small mammals (next section), in which case Sheftel's method would give a misleading picture of exceptionally high peak densities. Nonetheless, it is hardly possible to explain the cyclic changes in shrew densities in Central Siberia by this factor alone.

Secondly, there is one important mammalian predator in Sheftel's study area that might improve the synchrony in rodent and shrew dynamics, and this is the sable *Martes zibellina*, which is known to consume shrews readily (Sheftel pers. comm.). And thirdly, the continental climate in Central Siberia, by providing a predictable environment for ecological interactions, may tend to result in more predictable patterns of population dynamics than is the case with the more marine climate in Fennoscandia. If relatively little is yet known about the role of predators in the dynamics of shrews, even less is known about the role of parasites. Haukisalmi (1989) reported that sympatric shrew species tend to have the same intestinal helminth parasites, notwithstanding that the larger and more abundant species, and the species with the most generalized diets, have higher incidences of parasites than the other species. An interesting question is whether the smaller and less abundant species with probably somewhat more specialized diets obtain any relative advantage from the greater parasite loads of the larger congeners and potentially superior competitors (Saarikko 1989).

Unfortunately, no general argument can be advanced one way or another. The smaller species may have the advantage of fewer parasites, in the same manner as they appear to suffer less mortality owing to predation than the larger species (Korpimäki & Norrdahl 1989). Positively frequency-dependent parasitism could facilitate coexistence of competing shrew species. But one may also make a case for the opposite argument, according to which the large and abundant shrew species maintain a rich and abundant community of parasites that may readily infect any individuals of the smaller species, which themselves would not sustain all these parasite species — the apparent competition hypothesis (Holt 1977). Thus whether the intestinal and other parasites facilitate coexistence of competing shrew species or make it more difficult cannot be decided by any a priori arguments; and no empirical results are yet available.

## 5. Stress, dispersal and population crashes

Sheftel (1989) suggested that the crash of shrew populations in Central Siberia every fourth year is due to increased mortality owing to increased stress in dense populations. The evidence for high densities is good (Sheftel 1989, Moraleva 1989). The evidence for increased "stress" is twofold, decreased frequency of lactating females in the peak years (Sheftel 1989), indicating a high rate of termination of reproduction (common in mammals under unfavourable conditions; Millar 1988); and increased level of fluctuating asymmetry of bilateral morphological traits in the surviving offspring (Zakharov et al. unpubl.), suggesting a lowered level of developmental stability, apparently due to the poor physiological condition of breeding females. Unfortunately, the crucial question about the causes of mortality in the crash winters still remains open.

Sheftel (pers. comm.) has suggested that the rate of dispersal of shrews and other small mammals is highly elevated in the late summer-early autumn of the peak years, due to a high level of mutual disturbance. Hanski & Peltonen (unpubl.) found that natal dispersers of *S. araneus* from low density populations were smaller in skeletal measurements than residents, whereas there was no such difference in high-density years. This observation is contrary to what one might expect from Lidicker's (1975) saturation-presaturation dispersal hypothesis, but the observation suggests that there are at least two proximate causes of natal dispersal. In low-density years, some individuals (smaller skeletal measurements, hence probably social subordinates) are forced out from the population, whereas in high-density years most or all individuals have a high tendency to disperse (hence no morphological differences between the dispersers and the residents). These observations are consistent with Sheftel's suggestion about elevated dispersal rates in peak years. Assuming that the rate of mortality is high amongst the dispersers, as often seems to be the case (Stenseth 1983 and references therein), exceptionally high densities inducing a high rate of dispersal could even lead to a population crash. This possibility may be demonstrated with a simple model.

Assume that individuals belong to one of three classes, floaters, residents and dispersers. All individuals start as floaters searching for a territory, as juvenile shrews do after weaning (Croin Michielsen 1966, Moraleva 1989). If a floater succeeds in establishing a territory, it becomes a resident. If it does not succeed in establishing a territory, due to a high density of residents, it remains a floater or becomes a disperser. Residents may also become dispersers if much harassed by floaters and dispersers. For simplicity, let us ignore the possibility of a disperser

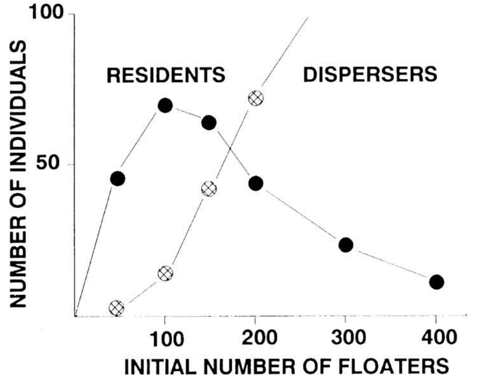

Fig. 4. Results of numerical iteration of the model of Eqs. (1). The horizontal axis gives the initial population size (floaters, $F$), while the vertical axis gives the numbers of residents ($R$) and dispersers ($D$) after a certain constant length of time. The parameter values are: $K=100$, $c_1=100$, $c_2=0.1$, $c_3=0.01$ and $c_4=1$.

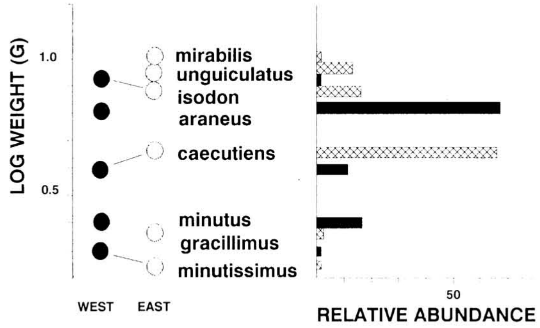

Fig. 5. Body sizes (fresh weight) and relative abundances of *Sorex* shrews in the Soviet Karelia (shaded) and Soviet Far East (unshaded), on the western and eastern edges of the Eurasian coniferous forest, respectively. Data for Karelia are from Ivanter (1976b, 1981) and for the Far East from Okhotina (1974).

becoming a resident within the period of time of interest.

The following model gives the rates of change in the numbers of floaters ($F$), residents ($R$) and dispersers ($D$):

$$dF/dt = -c_1F(1-R/K) - c_2F(F+R+D) \qquad (1a)$$
$$dR/dt = c_1F(1-R/K) - c_3R(F+D) \qquad (1b)$$
$$dD/dt = c_2F(F+R+D) + c_3T(F+D) - c_4D. \qquad (1c)$$

In this model, $K$ is the environmental carrying capacity (the maximum number of residents), and $c_1$, $c_2$, $c_3$ and $c_4$ are four parameters determining the rates of change from floaters to residents, from floaters to dispersers, from residents to dispersers, and the rate of mortality of dispersers. Fig. 4 gives an example of the predicted changes in $R$ and $D$ for one set of (supposedly reasonable) parameter values. The point is this: if the initial density of juveniles (floaters) much exceeds $K$, as may happen in the peak years, then most individuals may become dispersers with high rate of mortality, and the numbers of individuals surviving until the following breeding season may be much less than $K$ (Fig. 4). An important proximate cause of death amongst the dispersers may be predation, and predators may prevent the population from recovering in the following summer. For a comprehensive discussion of dispersal and population cycles in small mammals see Stenseth (1983).

## 6. Geographical variation in the transcontinental shrew *Sorex caecutiens*

Three species of *Sorex* have a transcontinental distribution in Eurasia, *S. minutissimus*, the very smallest *Sorex*, *S. isodon*, one of the largest species, and *S. caecutiens*, a middle-sized species (Fig. 5). It may be recollected that another middle-sized species, *S. cinereus*, is the dominant one in the coniferous forests in North America (Fig. 1). Throughout its range in Eurasia, *S. caecutiens* coexists with 4 to 7 other congeners, but its position in the shrew assemblage varies greatly. In western Europe, the assemblage is always dominated by *S. araneus*, and *S. caecutiens* is relatively more abundant in barren habitats (Hanski & Kaikusalo 1989). In Central Siberia, the situation is much the same, but because barren coniferous forests, too unproductive to sustain a high density of *S. araneus*, are widespread, *S. caecutiens* is regionally abundant. *Sorex araneus* is absent in East Siberia, where *S. caecutiens* is the numerically dominant species (Fig. 5; Dokuchaev 1989, Okhotina 1974).

Fig. 5 shows the body weights of the *Sorex* species at the western and the eastern edges of the Eurasian taiga region.

The "community-wide character displacement" hypothesis (Strong et al. 1979), alluded to above on the basis of the relatively constant size ratios in Fig. 1, would predict that the three transcontinental species

Table 2. Multiple regression models of the condylobasal length (CL) of the skull of *Sorex caecutiens* throughout its range in Eurasia. The data includes 28 localities. For further explanation see the text.

| Model | Independent variables | Coeff. | $t$ | $P$ | $R^2$ |
|---|---|---|---|---|---|
| Model I | latitude | –7.36 | –3.58 | 0.0015 | |
| | precipitation | –0.16 | –3.21 | 0.0036 | 0.37 |
| Model II | longitude | 4.77 | 3.73 | 0.0010 | |
| | longitude$^2$ | –0.02 | –3.95 | 0.0006 | 0.34 |
| Model IIb | longitude | 3.94 | 2.67 | 0.0133 | |
| | longitude$^2$ | –0.02 | –2.95 | 0.0070 | |
| | latitude | –2.60 | –1.13 | 0.2708 | 0.35 |

show shifts in their body weights according to which other species are present in local communities. And such changes are indeed evident in Fig. 5. Although these observations alone are insufficient to prove the significance of interspecific competition in structuring shrew communities, they certainly suggest that more comprehensive analyses along these lines are warranted.

Dolgov's (1985) recent compilation of skull measurements in Eurasian *Sorex* allows one to examine geographical variation in *S. caecutiens* throughout its range. I found climatic data for 28 of the localities for which Dolgov (1985) gave skull measurements. Table 2 gives the results of multiple regression models for the condylobasal length (CL) of the skull. With these data, one cannot distinguish between two models which both explain 35% of the variance in CL. In the first model, CL decreases with increasing latitude, contrary to Bergmann's rule and the general pattern in mammals (Zeveloff & Boyce 1984), and decreases with increasing precipitation. The second model involves a second-order polynomial of the longitude, the largest individuals being found in Central Siberia, from where CL decreases towards both the east and the west. If latitude is included in the second model, it has a negative but nonsignificant coefficient (Table 2).

The shrinking of the skull and the decrease in the body weight of boreal shrews in winter have frequently been interpreted as adaptations to decreased food availability during the adverse season (Saarikko 1989). In the same way one could argue that decreasing body size with increasing latitude is an adaptation to increasingly poor environments. The frequent consumption of larch seeds by *S. caecutiens* during the severe winter of North-East Siberia (Dokuchaev 1989) supports the argument about scarcity of insect food in the north. The interesting linkages here are between foraging ecology, physiology and morphology, and geographical variation. It would be most interesting to compare seasonal changes in body measurements in different parts of the geographical range of *S. caecutiens.*

Turning to reproduction, comparative data on uterine litter size shows substantial geographical variation in *S. caecutiens*, from 5.9 in Central Siberia (Sheftel 1989) to 8.6 in East Siberia (Dokuchaev 1989) and 8.9 in northern Finland (Table 3). Generally, litter size appears to be smallest in Central Siberia (Table 3), where the body size is largest (Table 2). The general pattern in mammals is a negative rela-

Table 3. Geographical variation in litter size (mean±*SE*) in *Sorex caecutiens* throughout its transcontinental range in Eurasia.

| Locality | Litter size | $n$ | Reference |
|---|---|---|---|
| North-East Siberia | | | |
| Omolon | 8.6 ± 0.30 | 54 | Dokuchaev (1989) |
| Tchelomdza | 7.5 ± 0.28 | 44 | Dokuchaev (1989) |
| West and Central Siberia | | | |
| West Siberia | 7.0 ± 0.30 | 25 | Judin (1962) |
| Altai | 6.0 ± 0.24 | 21 | Judin et al. (1979) |
| Central Siberia | 5.9 ± 0.17 | 137 | Sheftel (1989) |
| Europe | | | |
| Soviet Karelia | 7.5 | ? | Ivanter (1975) |
| Finnish Lapland[1] | 8.9 ± 0.36 | 22 | Henttonen (pers. comm.) |

[1] Average litter size was 9.8 in 14 overwintered females and 7.3 in 8 young ones.

tionship between litter size and body size (Eisenberg 1981, May & Rubenstein 1984), but in small mammals (less than 1 kg) the relationship may be positive (Tuomi 1980), and in *Sorex* in particular there is no clear interspecific relationship between litter size and body size (regression coefficient –1.00, NS; data on litter size from Table 6 in Sheftel 1989, body sizes from unpublished Finnish material; see also Genoud 1988). The result for *Sorex* much depends on the smallest species, *S. minutissimus*. Sheftel (1989) reports a single observation of 9, while according to Judin (1962) *S. minutissimus* has a small litter of 4–5. I have speculated previously that the very small *minutissimus* females might have difficulty in lactating litters of 6 to 8, characteristic of *Sorex* in general (Hanski 1984). There exists a great deal of scope for detailed studies on the reproductive biology of *Sorex*.

The population dynamics of *S. caecutiens* are distinctly different in western Europe, Central Siberia and North-East Siberia, as reported by Henttonen et al. 1989, Sheftel 1989 and Dokuchaev 1989. In Finland, shrew dynamics is not very closely related to rodent dynamics, although in the areas where rodents have distinctly cyclic dynamics (northern Fennoscandia), shrew populations tend to be small and do not generally increase in the summers when the rodents are scarce (Sonerud 1988, Henttonen et al. 1989). In contrast, in Central Siberia the shrew dynamics are closely synchronized with rodent dynamics, possibly for the reasons discussed in the previous section, whereas in North-East Siberia the dynamics of *S. caecutiens* are dominated by the supply of larch seeds, which greatly enhance winter survival in the very uncharitable climate (Dokuchaev 1989).

This brief summary of geographical variation in the population biology of *Sorex caecutiens* suggests one pattern: the Central Siberian populations are characterized by large individuals, small litters and predictably cyclic dynamics, while populations in both the western and the eastern ends of the species' range have smaller individuals, larger litters and more irregular dynamics, though irregular in different ways and for different reasons.

The association between large body size and small litter size, though the standard result in interspecific comparisons (May & Rubenstein 1984), has not been previously reported for any one species of mammal (Boyce 1988). Large litter size itself is often associated with seasonal environments (Boyce 1988), but it seems difficult to attribute the observed geographical variation in the litter size of *S. caecutiens* to seasonality, as all the populations live in highly seasonal environments. Stenseth & Framstad (1980) suggested that litter size in small mammals is positively correlated with the magnitude of population fluctuations, but this does not appear to be the case in *S. caecutiens*, with all populations showing much variation in density. However, one may speculate that the regularity of population fluctuations is important: litter size increases with the level of irregularity in population dynamics, which create every now and then situations when rapid population growth is possible. In the cyclic populations, predation is likely to be heavy in the crash years (see Sonerud 1988 and Henttonen et al. 1989 for *S. araneus*), and selection may not operate to increase reproductive effort via large litters, even if population density is low. The regularity and causes of population fluctuations may thus affect litter size as much or more than just the magnitude of fluctuations.

I have attempted to indicate in this paper how behavioural, physiological and ecological observations on boreal shrews contribute towards an enriched understanding of major population biological issues, such as evolution of life histories, stability of populations, and interactive structuring of communities. If I have given the impression that shrews are exceptionally attractive creatures to study, I am satisfied.

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