

Understanding the boundaries between chromosome races of common shrews in terms of restricted movement by individual shrews

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ABSTRACT. Data on population density, dispersal and homing in common shrews of the Moscow chromosome race are discussed. A population of common shrews is regarded as a set of “independent populations” with each such independent population characterised by their distinctive dynamics in population density. These distinctive dynamics result from the restricted exchange of individuals between the independent populations. The movement of individuals that belong to an independent population is hypothesised to be driven by a network of signals resulting from common activity (tunnels, nest places, pathways etc.) and direct or indirect social interactions (aggression, acoustic communication, scent marks and so on), i.e. Naumov’s “signals field”. Data on year to year fluctuations of population density in two closely located sampling sites were used to reveal independent populations of this sort. Homing experiments were conducted to establish areas through which shrews are most likely to travel. Surveys of micromycetes on the fur support the idea of discontinuity between independent populations. The boundaries between different chromosome races in continuous forests may be explained in terms of the low probability of dispersal of shrews beyond the area of an independent population.

KEY WORDS: *Sorex araneus*, chromosome race, independent population, dispersal.

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Границы между хромосомными расами обыкновенной бурозубки как следствие ограничения подвижности особей

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РЕЗЮМЕ. Обсуждаются данные по плотности, расселению и хомингу обыкновенных бурозубок хромосомной расы Москва. Население обыкновенной бурозубки рассматривается как набор независимых популяций, т.е. группировок, поддерживающих свою численность независимо от таких же соседних группировок. Такая группировка может быть выделена на основе независимой динамики численности. Независимость динамики является следствием ограниченного обмена особями между двумя независимыми популяциями. Предполагается, что расселение управляется сигнальным полем в понимании Наумова. Данные по межгодовым колебаниям численности на двух участках использованы для выявления «независимых популяций». Эксперименты по изучению хоминга были проведены для выявления территорий с различной вероятностью успешных перемещений. Данные по составу микромицетов на шерсти зверьков использованы для подтверждения представления о прерывистости расселения. Образование границ между хромосомными расами в монотонных лесах объясняется различной вероятностью расселения землероек внутри территории независимой популяции и за ее границы.

КЛЮЧЕВЫЕ СЛОВА: *Sorex araneus*, хромосомная раса, независимые популяции, расселение.

Introduction

Hausser *et al.* (1994) gave the following definition for a chromosome race: “a group of geographically contiguous or recently separated populations which share the same set of metacentrics and acrocentrics by descent”. The common shrew (*Sorex araneus* L.) is characterised by at least 68 such chromosome races (Wójcik *et al.*, 2003) which are parapatric but they can hybridise where they meet. In 14 cases of parapatric contact, the course and the width of the hybrid zones has been established reasonably well (Searle & Wójcik, 1998). For these hybrid zones the main focus of study has been

genetical. The ecology of racial interactions in the common shrew, which is of the great interest as well, is not so clear. In particular there is little understanding of why individuals of one race fail to invade the area inhabited by another race. Sometimes two races make contact at a physical barrier. Thus, the Aberdeen and Oxford races and the Uppsala and Hällefors races meet at rivers (Mercer & Searle, 1991; Narain & Fredga, 1996). This situation is not general: not all races meet at a geographic barrier. New data on the distribution of Neroosa, Serov and Sok chromosome races shows that these races have traversed great rivers and meet with neighbouring races in continuous forests (Bystrakova *et al.*, 2007).

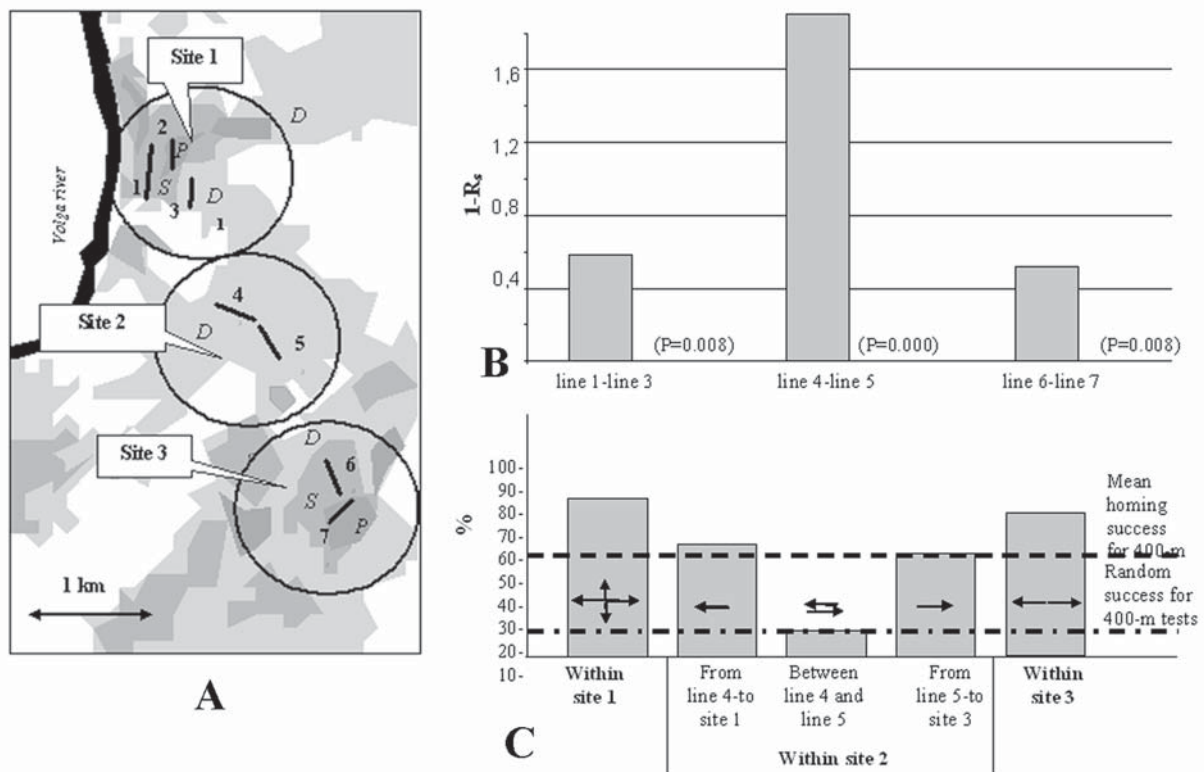


Figure 1. Some characteristics of common shrews in the study area.

A — study area. Forested area is shaded: light shading “D” — deciduous habitats; medium shading “S” — spruce, and dark shading “P” — pine. Solid lines show the location of the transects.

B — the difference between the micromycete spores on the fur of common shrews from various localities (see text for details).

C — homing success in different areas. Small arrows indicate the direction of release of shrews relative to their home ranges.

The failure of one race to spread into the range of another could result from different habitat preferences. The sibling species *Sorex coronatus* and *Sorex araneus* inhabit areas with different climatic characteristics (Neet & Hausser, 1990). Different habitat preferences have also been found for the parapatric Tomsk and Novosibirsk races. The Novosibirsk race prefers steppe-forest habitats while the Tomsk race prefers taiga habitats. The 200 m isocline separates these types of habitats and so the Novosibirsk race inhabits altitudes below 200 m and the Tomsk race above 200 m (Polyakov *et al.*, 2003). The latter situation is unusual for the common shrew. Polyakov and colleagues wrote “this is the first case where two parapatric chromosome races show clear environmental differences in where they live”. Many parapatric chromosome races of the common shrew inhabit ranges with a similar set of habitats without any clear environmental differences. In the most studied hybrid zone between the Oxford and the Hermitage races, the course of zone does not entirely follows a physical barrier or a climatic factor (Jones & Searle, 2003).

In relation to the ecological factors that determine the position of chromosomal hybrid zones in the common shrew, it is pertinent to consider our data on spatial dynamics of populations of the Moscow race (Shchipanov, 2003; Shchipanov *et al.*, 2006). In particular, in our study locality we have found areas with indepen-

dent fluctuations in population density. These areas are localised 4 km apart from each other and are not separated by any physical barrier. Both areas have a similar set of habitats. Following Beklemishev (1960), I treat the distinctive population dynamics in terms of restricted exchange of individuals deriving from “independent populations”. Naumov (1973) suggested that movements of individuals within an area could be driven by a network of signals from other individuals resulting from common activity (tunnels, nest places, pathways etc.) and direct or indirect social interactions (aggression, acoustic communication, scent marks and so on). He called this network a “biological signal field”. I hypothesise that the restricted exchange between independent populations results from intrinsic informational processes within such units: individuals move within some area using signals from conspecifics of a “native” population to orientate within the bounds of the area. This paper presents published and new data on various issues of the ecology of populations of the common shrew that could support this idea and the idea is applied to hybrid zones between chromosome races.

Material and methods

The studies were carried out in the Upper Volga River region, on the Russian Plains (N 56°, E 35°)

where common shrews belong to the Moscow chromosome race (Bulatova *et al.*, 2000). Forests (mainly coniferous or mixed) fragmented by grasslands cover the area. Mature coniferous forests with damp mossy floors were dominated either by spruce (*Picea abies*) or pine (*Pinus sylvestris*) and birch (*Betula pendula* and *B. pubescens*). Following logging, the latter is replaced by deciduous or mixed forests, dominated by alder (*Alnus incana*), birch (*Betula pendula*) and aspen (*Populus tremula*), with herbaceous plants covering the forest floor. Older mixed deciduous forests contain spruce undergrowth, which later becomes dominant. Three sites were monitored (Fig. 1A). Spruce forests with patches of pine or deciduous (post-logging) habitats are present in sites 1 and 3. Site 2 occurs in between the other two sites and is covered by continuous deciduous forest (similar to deciduous forest in sites 1 and 3).

Populations of small mammals have been monitored since 1995 (site 1) and since 1997 (site 3). Site 2 has been studied since 2002. The methodology used has been an approach of capture-mark-recapture (CMR) applied to lines of live-traps. The use of lines instead of grids has enhanced productivity of the trapping effort greatly (Shchipanov *et al.*, 2000). All lines were 375 m in length and contained 50 traps (except for the spruce habitat, where the line contained 100 traps and was 750 m in length). The traps were only operative for three hours (and were checked every 1.5 hours) each day. Animals could move during most of the day without limitation. We clipped one or two toes per foot (three feet when necessary) using a binary code. It gives 9999 numbers. In fact we use several hundred numbers per year. The mortality of individually marked common shrews was less than one percent. Some marked individuals were monitored for 14 months (the maximum life span). Data on population density fluctuation at two of the sites have been published, covering the period 1995–2001 (Shchipanov *et al.*, 2006). Now I have more data and I can analyse variation in population dynamics between various habitats using correlation analysis. Here I analyse data on 2238 *S. araneus* individually marked by toe clipping (8509 recaptures).

For this analysis individuals recaptured at least once over a two week trapping session were considered resident. The probability of recapture of an individual after long-distance movement is very low. About 65% of individually marked shrews were not recaptured near the place of first capture but we found only 21 individuals at distances greater than 500 metres, and only seven of them at distances over 1 km (the maximum recorded distance was 1579 metres). Such data on long distance movements are evidently insufficient for statistical analyses. Therefore I was forced to look for a group marker in order to assess the probability of movement between areas. Fortunately we have found that micromycete spores attach to the fur of small mammals (Shchipanov *et al.*, 2003). We analysed occurrence of micromycete spores on the hair of four species of small mammal sampled from different habitats in different sites (Shchipanov *et al.*, 2006). Here I only use data for

the common shrew. Hairs from 143 common shrews were collected and used to grow up micromycetes on agar media. The sporiferous forms of the micromycetes were used for identification. The quantity of spores of a species was estimated as the number of Petri dishes where the micromycete was present, i.e. the number of positive tests. The fur from 10 individuals was used to characterise the composition of micromycetes at a given locality and comparisons were made between localities using correlation analysis.

Another technique that can be used to study the mobility of non-resident shrews is homing. We used homing experiments to test whether immature shrews are willing to travel through a given area (Kuptsov & Shchipanov, 2004). Resident individuals were transferred in opaque boxes at 150-m, 400-m, and 900-m distances from the centre of their home ranges. The areas were surveyed for 2–3 weeks after removal. Here I analyse homing success of the common shrew using data from 109 tests.

Results

Fluctuation of population density. Common shrews in the area under study inhabited various habitats. To use Beklemishev's criterion for independent populations one should compare fluctuations of population densities between various habitats in the same site and between the same habitats from different sites. I made such comparisons between sites 1 and 3 (Fig. 1A).

In site 1 the Spearman rank correlation (R_s) in year to year fluctuations of numbers of resident yearling common shrews between spruce and pine habitats was 0.67 ($p=0.03$), it equalled 0.89 ($p<0.001$) between pine and alder and 0.87 ($p<0.001$) between alder and spruce. Though the correlations between various habitats within the trapping area were high, no correlation was found between populations living in the spruce habitats of sites 1 and 3 ($R_s=0.13$; $p=0.76$). As a result, year to year fluctuations of the mean population density for sites 1 and 3 were independent ($R_s=-0.04$; $p=0.92$). This is the reason to regard populations at site 1 and site 3 as Beklemishev's "independent populations".

The discontinuity in composition of micromycete spores on the fur as evidence of interruption to movements. Previous studies on a variety of small mammals (Shchipanov *et al.*, 2006) demonstrated 108 species of micromycetes on the fur of the common shrews (846 positive tests). There was turn-over in the composition of spores within a month. Therefore the set of spores on the fur could mark an individual in a given locality for a short time. The spore compositions on the fur of small mammals from habitats located closer to each other differed less than the spore compositions from more remote habitats (Shchipanov *et al.*, 2006). I calculated Spearman rank correlations (R_s) for common shrews from various habitats using data collected simultaneously within a week. The correlation (R_s) between micromycete spore composition on the fur of common shrews from spruce and pine habitats in site 3 (lines 6 and 7) was 0.47 ($p=0.003$), but this correlation

between spruce habitats of sites 1 and 3 (lines 1 and 6) was -0.16 ($p=0.33$), and between spruce habitat of site 1 (line 1) and pine habitat of site 3 (line 7) $R_s=-0.05$ ($p=0.65$). The correlation between neighbouring spruce and alder habitats in site 1 (lines 1 and 3) was 0.42 ($p=0.008$), but there was no correlation between alder habitat in site 1 and spruce habitat in site 3 ($R_s=0.02$; $p=0.81$). I propose that the similarity of spore compositions on the fur of common shrews from neighbouring habitats within a site can be explained by the mobility of individuals between those habitats. Thus, the exchange of individuals could be assessed by the similarity of the micromycete compositions on the fur. I calculated the correlation for common shrews sampled from neighbouring trap-lines of the different sites. Though the correlation between neighbouring lines within site 1 and within site 3 was significantly positive, this correlation within site 2 between lines 4 and 5 was negative and significant. The latter district is overgrown by continuous alder herbaceous forest, and the high difference in composition of spores on the fur of common shrews from these lines likely resulted from the lack of exchange of individuals. To illustrate the difference I use $1-R_s$ as a measure of dissimilarity (Fig. 1B).

Homing in the areas studied. Studying homing in shrews, Kuptsov & Shchipanov (2004) found that all common shrews that had been transferred at a 150-m distance returned to their localities of capture ($n=20$). Mean homing success for the 400-m distance was 63% ($n=78$), and it was 64% ($n=11$) for the 900-m distance.

One may expect that an individual could find its home range by a compass or due to knowledge of the surrounding area. In both cases its way home will be as short as possible and the period of absence minimal. Therefore, an important measure for the present study is the time of absence (delay in homing) of individuals that have been transferred. Here I give new data on the delays. An individual could cover at least a 400-m distance in 1.5 hours (the interval between the periodic checks of live-traps). However, even at the minimal distance we found two shrews showing significant delays in homing (4 and 7 days). The mean delay for 400-m tests was 7.5 ± 1.9 days and for 900-m tests it was 8.6 ± 2.1 days. To assess the delay accurately, the average period of recapture for each individual was calculated and a delay was scored only when the term of absence was greater than this period + sd. As a result delays were found in 10% of 150-m experiments and in 53% of 400-m experiments and all individuals returned with a delay from 900 meters. In this study I assume that 150-m distance represents the mean radius of a familiar area, and 300-m as the mean diameter and I use 400-m homing tests to estimate the probability that a shrew will move through a given area.

The occurrence of long-term delays from a distance which a shrew should be able to cover quickly suggests that shrews do not use a compass for homing. Being removed from their home range and released at some distance an individual has a chance to find its way back by moving a random direction. The individual can return moving within a triangle made by the release point and

the extreme points of a familiar area. The mean percent of successful homing from random movements can be assessed as a ratio of the top angle of the triangle to the whole ring – 360° . The random homing success for the 400-m distance and 300-m diameter of a familiar area averaged 19%. The observed homing success was significantly greater and was on average 55.5% ($n=103$).

As shown by Kuptsov & Shchipanov (2004) homing success in common shrews within site 1 was similar for various directions and averaged 88% ($n=25$). Within site 3 this success was also similar for various directions and was 68% ($n=28$). In site 2 homing success varied depending on the direction and location of tests. Five individuals (56%) returned to their localities from the edges of the site ($n=9$), but only three individuals out of 16 (19%) found their way home when they had been transferred across the central area of site 2.

Here I have generalised our published data with respect to homing success at the three sites within our study area. I found that homing success was significantly higher than random in sites 1 and 3 and at the edges of site 2. Homing success in the central part of site 2 was significantly lower than the average observed over all sites ($p<0.01$). The level of successful homing for this area coincided with the expectation from random movements (Fig. 1C).

Discussion

Analysing survival of species in heterogeneous environments, Levins (1968) proposed that populations persist in an area through re-colonisation of depopulated sites by dispersal from nearby areas. Local populations occupy various habitats and therefore a segment of a population has a chance to escape extinction. A number of local populations make a “metapopulation”. The metapopulation concept remains one of the most attractive in population ecology. The concept elucidates various issues of interaction of local populations but it provides no insight into the basis for discontinuity in a population.

The idea of discontinuity of natural populations has been suggested by V.N. Beklemishev (1960). He showed that the control of pests could cause a long-term population depression in one area, and the same type and magnitude of control in another area (of the same size) could cause a short-term effect. Beklemishev suggested that the numbers of individuals in some local populations depend on the birth – mortality ratio rather than immigration. He called these groups “independent populations”. Other local populations are conversely supported particularly by immigration. An “independent population” is detached from another “independent population” by the restricted exchange of individuals and it could be operationally distinguished under pest control. Is it possible to find independent populations of this sort in nature?

Analysing impacts of pest control and natural disasters on small mammal populations I found three different responses among species: a change in demographic pattern from a low rate of dispersal to a high rate (type 1), maintenance of a high rate of dispersal (type 2), and

maintenance of a low rate of dispersal (type 3). Species showing the first type of response can be subdivided into those that change demographic pattern following an external impact (type 1a) and species that change demographic pattern following intrinsic population fluctuations (type 1b). Only type 1b species can display independent fluctuations in population density (Shchipanov, 2000, 2002). Regarding various aspects of the population ecology of the common shrew we consider this species as the 1b type (Shchipanov *et al.*, 2006). The independent fluctuation of population density in common shrews reported in this paper can be regarded as evidence of independence in population function. This is an unusual situation and we were apparently lucky to find neighbouring populations of common shrews in our study area with a lack of synchronicity in population dynamics.

Lidicker (1994) wrote that a "population" in ecological studies "can be distinguished operationally from other similar groups by partial or complete discontinuities in space or time or both". An independence in population dynamics implies the lack of exchange of individuals. Therefore a limitation of mobility (i.e. "discontinuity in space") would occur where two populations meet. In my study the restricted exchange of individuals from sites 1 and 3 is supported by data on the distribution of microcycete spores in the fur of common shrews (Fig. 1C).

I should emphasise that the discontinuity in dispersal needs not be complete. Independence in population dynamics could result from a level of mobility between "independent populations" which is insufficient to support synchronicity, i.e. from some (but not a complete) restriction of the exchange of individuals.

Does such a population discontinuity necessarily need some geographical barrier?

To discuss this issue I will turn to Naumov's (1973, 1977) studies. He supposed that a complex of long-term and current signals generated by conspecifics within the network of their pathways and tunnels could direct travelling individuals. He called this complex of signals a "biological signal field". I have previously suggested that these fields could amalgamate local populations into an "independent population" (Shchipanov, 2003). How could this field operate? Here I suggest a "pan model". I hypothesise that there are signals that operate for individuals of one "independent population" and not for individuals of a different "independent population". Those signals could mark the edge of an independent population. The majority of dispersing individuals would turn back at the edge of the area. A trajectory of a travelling individual will look like the trajectory of a piece of butter on a hot pan. It moves in a random direction to the edge, and afterwards it moves in another random direction inside the pan. This assumption was verified by homing.

Homing success could result from a random choice of the correct direction, from the knowledge of surrounding space or from use of a compass. Our data show that homing success was significantly greater than random. The distance that individuals were transferred could be covered in 1.5 hours. In fact it takes several days (a week on average) for many individuals to find

their home ranges. Such great delays argue against knowledge of surrounding space or use of a compass. In particular the "pan model" predicts that the homing success of an individual outside a "signal field" will be close to the random value. This effect was in fact found for the central part of site 2 where the discontinuity in "signal fields" of the "independent populations" is proposed.

Studying the network of tunnels of small mammals, Bykov (2005) found that they tend to be centred on burrows of *Microtus* in forest glades. Later, when the glades become covered by forest again, these burrows become connected into the forest network of tunnels due to the digging activity of forest species. I assume that such a network can be at a different density in different locations. It could be complicated by activities of a given species and can become specific to different species. This network of tunnels may reflect the history of a particular habitat and it could be denser in some areas and less dense at the periphery of an inhabited area. The denser parts can become the core of a population territory. As a result an "independent population" can shape its area and establish a boundary. The course of this boundary may not follow any current physical barrier.

The metapopulation concept assumes that populations inhabit a heterogeneous environment. There are some habitats favourable all year round and some only seasonally. The population in the first type of habitat is constant, and in the second it is temporal. Though "independent populations" cannot share an area, a zone of intergradation is possible in temporally favourable habitats. Seasonal population density in the zone of intergradation could be even greater than the densities in each of the contacting population when the rate of dispersal is high, similar to Lidicker's (1985) sink habitats. Taking into account that individuals disperse from the zone of intergradation area in a random direction one could expect gene flow between the "independent populations" under high population density. A severe glacial climate could diminish population numbers, and, consequently, reduce emigration in a zone of intergradation. The latter could lead to isolation of "independent populations" without any additional factors. Therefore there is no need to look for geographical barriers to explain the distribution of chromosomal races in the common shrew. An "independent population" could accumulate chromosomal rearrangements in a relatively short period of time. It is important to note that the boundary of a chromosome race is composed of the boundaries of "independent populations". And so one could find effects similar to those described above at the hybrid zones. All these considerations allow a hypothesis to be formulated: "The movement of individuals out of the area of an independent population is limited by intrinsic informational processes within the population."

This hypothesis predicts that:

- A species could show a discontinuity in genetics, morphology or biochemistry without any geographical barrier.
- Hybrid zones between chromosome races could represent such a discontinuity.

In the common shrew it is of particular interest to map the precise distribution of different races in hybrid zones, to establish whether they can lie in a location without a geographical barrier. This may be the case for the hybrid zone between the Moscow and Seliger races (Bulatova *et al.*, 2007).

Obviously the data discussed above are not sufficient to make final conclusions. One needs more accurate and detailed studies to understand the nature and the location of signals that could limit movements of individuals. Here I want to show that there are good reasons to study intrinsic as well as extrinsic factors influencing dispersal of individuals.

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