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Intraspecific interactions in the common shrew *Sorex araneus* in Central Siberia

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This paper describes interactions between individuals belonging to different functional groups of the common shrew (juveniles, adult males and adult females). The competitive ability of members of the functional groups was studied using field observations and laboratory experiments in relation to season and population density in a cyclic population of the common shrew in Central Siberia. The results support Croin Michielsen's (1966) hypothesis about the social dominance of juveniles over adults. Adult males in particular appear to experience a high level of social pressure, and it is suggested that they may be forced to occupy marginal habitats in summer and have an increased rate of mortality due to frequent aggression.

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1. Introduction

Relatively little is known about the social factors that affect the rates of dispersal and mortality in shrews (Crowcroft 1956, 1957, Pernetta 1977, Churchfield 1980). Here I report field observations and laboratory experiments on interactions between members of different functional groups of the common shrew *Sorex araneus* L., one of the numerically dominant species of small mammal in Central Siberia. I shall also compare the competitive performance of individuals during the prepeak and peak years of the synchronous 4-year cycle of small mammals, characteristic to the study area (Sheftel 1989). This study is a part of the research programme on the ecology of shrews in the Middle Yenisei taiga in Central Siberia.

2. Methods

The studies reported here were carried out at the Northern Ecological Station Mirnoe of the A. N. Severtsov Institute of Evolutionary Morphology and Ecology of Animals, USSR Academy of Sciences (Sheftel 1989). The station is located on the eastern bank of the Yenisei, at the eastern edge of the West Siberian plain. The study area has a typical taiga landscape and is characterized by a continental climate (Sheftel 1989).

2.1. Trapping

To monitor changes in population density in the study region, shrews were trapped with trapping ditches from 20 June to 3 September in 1976–1985. Each ditch was 20 m long and 15 cm deep, and it had two large pitfall traps located 5 m from the two ends of the ditch. Some 20 permanent ditches were operated in different types of habitats. The results are expressed as shrews caught per 100 trap-nights. The trapping ditches were operated in cooperation with B. Sheftel (Sheftel 1989).

Shrews were live-trapped in an area of 2.25 ha on the eastern bank of the Yenisei, about 1.5 km from the river. The live-trapping area has mixed forest with *Pinus sibirica*, *Picea obovata* and *Populus tremula* as the dominant tree species. The field layer is dominated by *Vaccinium myrtillus*, *Equisetum sylvaticum* and *Equisetum pratense*. Mosses cover 40–50% of the area and consist mainly of *Pleurozium schreberi* and *Hylocomium splendens*.

Live-trapping was carried out with self-made, box-type live-traps and pitfall traps with food and moss provided to increase the survival of shrews in the traps. A piece of porous spongy material (Porolon) was laid on the bottom of the pitfall to absorp extra moisture. The pitfalls were covered to prevent rain water entering the trap.

Within the study area, 100 live-traps were arranged in a grid of 15×15 m, and additionally 60 pitfall traps were placed in seemingly favourable spots about 30 m apart on average. The livetraps and pitfalls were examined every 6 to 8 hours, and the shrews caught were marked. In 1984 the live-trapping periods were: 23 June to 3 July, 6–15 August, 31 August to 4 September and 14–19 September. In 1985 the trapping periods were: 10–20 June, 7–17 July, 1–12 August and 14–19 September. The date, time and point of capture of each shrew were recorded. Shrews were classified either as juveniles (sexually immature current-year animals) or adults (sexually mature overwintered animals; Dehnel 1949), and adult shrews were sexed. Juveniles could not be sexed. The shrews were marked by toe-clipping. Dead shrews were autopsied.

Trapping with both box-type live-traps and pitfalls in the same area should provide the most reliable results on the structure of the population. Extended movements and frequent captures by pitfalls provide evidence that an individual is unfamiliar with the area (Moraleva 1983). In contrast, resident shrews are mostly caught in live-traps (Moraleva 1983). Similar results have been obtained by Beacham & Krebs (1989) for *Microtus townsendii* (but see Boonstra & Rodd 1984 for *M. pennsylvanicus*). The trapping techniques and determination of home ranges are described in detail in Moraleva (1983).

2.2. Laboratory experiments

A series of neutral arena tests were conducted to make detailed observations on the behaviour of the common shrew. Wild-caught animals, which had been settled in captivity for at least 3 days, were introduced in pairs into plastic cages measuring 80×80×50 in size and divided into two parts by a removable partition. The floor of the cage was covered with a thin layer of clean sawdust. Before each experiment the cage was cleaned with a piece of cotton dampened in alcohol. Both individuals were first kept in their parts of the cage for 10 minutes, then the partition was removed and the behaviour of the shrews was observed for 30 minutes.

The behaviour of an individual in an encounter between two shrews can be classified as either aggressive or nonaggressive. Aggressive behaviour can be described as follows: one individual rears up on its hind legs; both rear up; one throws itself on its back; one bites the tail of the other; the two seize each other's tails and spin around, etc. (Crowcroft 1957). Behaviour without these features was considered to be nonaggressive. The numbers of encounters between individuals belonging to different functional groups are given in Table 2.

3. Results

3.1. Spatial distribution of shrews and their seasonal dynamics

Fig. 1 shows the distribution of the different functional groups in 6 different habitats in the years 1978–1981, covering one 4-year cycle of population

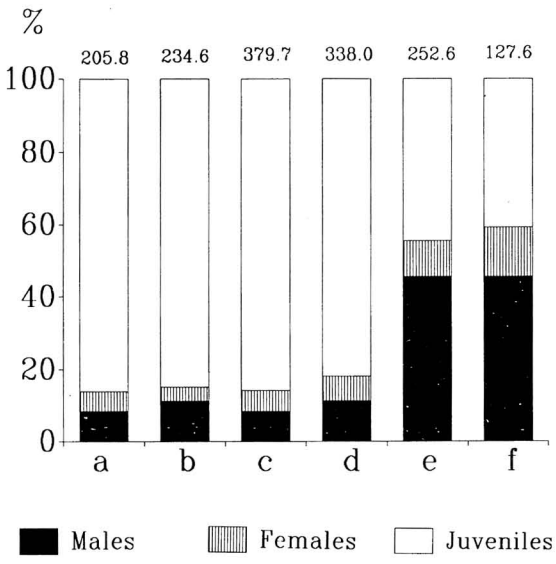

Fig. 1. Percentage distribution of the 3 functional groups in 6 different habitats. The habitat types are: a, mixed forest dominated by conifers; b, mixed forest dominated by deciduous trees; c, forest edges and cleared areas; d, riparian fir-tree forest; e, flood plain forest and meadows; and f, cultivated meadows. The figures above the columns give the average number of shrews per trapping ditch in 1978–1981.

density. Two types of habitats can be distinguished on the basis of the frequency of adult males (Fig. 1):

1) taiga forests including riparian fir-tree forest, forest edges and cleared areas (adult males 4 to 18%), and
2) flood plain forests and meadows and cultivated meadows (30 to 55%).

The proportions of the functional groups differ highly significantly between these two kinds of habitat (t=10.8, P<0.001). These results are consistent with long-term trapping data demonstrating that the majority of adult males settle in the flood plain habitats, the majority of juveniles stay above the flood plain area (in the taiga forest), while the adult females have an intermediate spatial distribution (Sheftel 1989).

Seasonal changes in the numbers of the different functional groups, as revealed by pitfall trapping, are shown in Fig. 2. As the numbers of adult shrews cannot increase during the summer, an increase in their number in the trapping results must be due to increased activity and mobility. The gradual increase in the activity of adult females coincides with the decrease in their breeding activity towards the end of

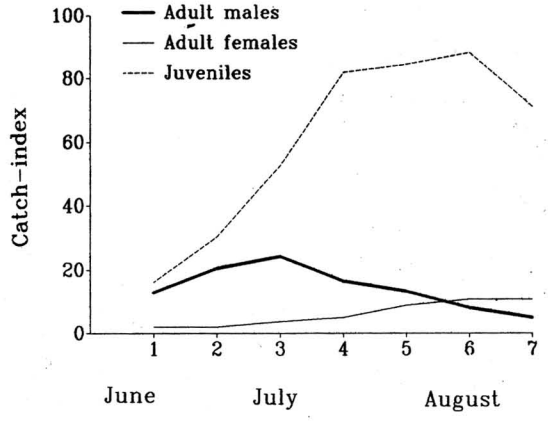

Fig. 2. Seasonal changes in the numbers of the different functional groups in the years 1976–1983 (average result, trapping ditches). The vertical axis gives the numbers of individuals per 100 trap-nights.

July and the beginning of August (Fig. 2). Adult males are much more active than adult females in the beginning of the trapping period, towards the end of June. A decrease in the numbers of adult males in the second half of the summer is probably due to mortality (Fig. 2).

Changes in the numbers of adult males and juveniles in the taiga forest and flood plain habitats are shown in Fig. 3. The numbers of adult males are significantly higher in the flood plain habitats than in the taiga (Figs. 1 and 3), suggesting active dispersal from the taiga to the flood plain habitats early in the season. In June and at the beginning of July adult males dominate in the flood plain habitats, but from the second half of July onwards, with increasing numbers of juveniles in the taiga, they also start to appear in larger numbers in the flood plain habitats. At this time the numbers of adult males decrease.

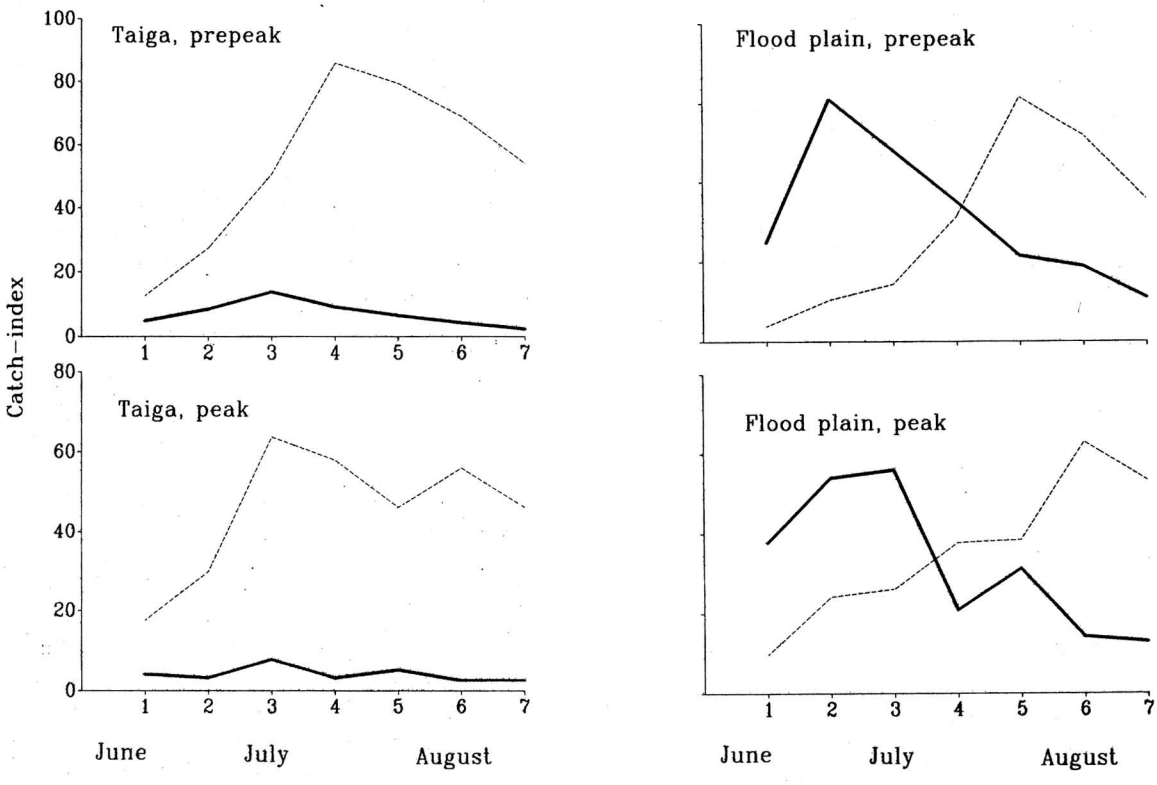

Fig. 3. Seasonal changes in the numbers of adult males (continuous line) and juveniles (broken line) in taiga forest and flood plain habitats (average result for the 1976, 1980 and 1984 prepeak years and 1977, 1981 and 1985 peak years). The vertical axis gives the numbers of individuals per 100 trap-nights.

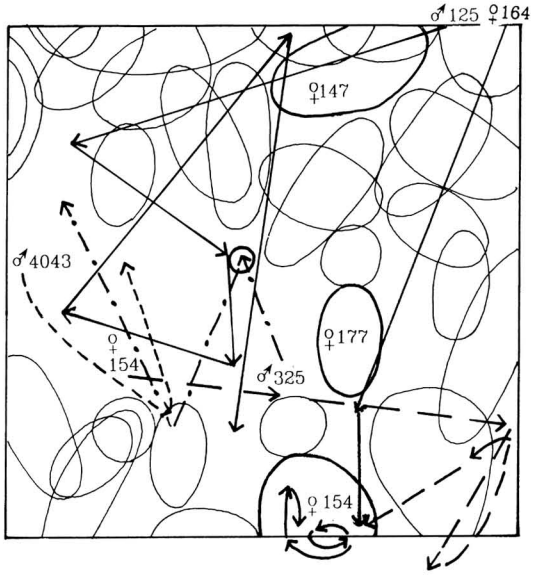

Fig. 4. Movements of adult shrews (arrows) and the home ranges of resident juveniles (thin line) and adult females (thick line) in the study area in August 1984.

Table 1. Distribution of the captures of juvenile common shrews in the study area. The first column gives the average number of captures per 15×15 m square in different parts of the trapping area. The parts occupied by adult males and adult females are compared with the trapping area as a whole (χ^2), and the significance of the test result is given in the table.

	Captures	Significance
The study area as a whole (2.25 ha)	4.1	
Part of the area occupied by adult males (0.32 ha)	2.1	$P < 0.01$
Part of the area occupied by adult females (0.16 ha)	1.9	$P < 0.05$

3.2. Spatial distribution of the functional groups within the live-trapping area

In June and July adult shrews were only rarely captured in the live-trapping area. It will be shown below that resident adults can remain within their home range for some time without being captured more than occasionally. Therefore, in 1984, when there had been no previous live-trapping in the study area, it is not known which of the adult shrews were residents and which had dispersed to the study area. In 1985, even a single capture of a previously marked adult individual conclusively proved that it was a resident.

Situation in the prepeak year

In June 1984, a prepeak year, three adult individuals were caught in the live-trapping area. A pregnant female was captured twice and then died. One of two males also died, while the second one was not recaptured.

In August 1984, 25 adults were marked in the study area. Seven of them stayed in the area for some time and were recaptured several times. Their movements are shown in Fig. 4. The home ranges of resident young shrews are also plotted in this figure although individual movements outside the home ranges are not shown. During that time, the study area was used by three adult males, nos 125, 352 and 4043. On August 4, male no. 4043 was found at a distance of 70 m from the study area. Five days later he appeared within the study area and stayed there until the end of trapping in August. After moving around, female no. 154 settled down temporarily within a small area. Female no. 164 crossed the study area and left it. Females nos 154 and 164 completed breeding and lactating and started to disperse. Females nos 147 and 177 may be assumed to have lived in the study area before the trapping started, because they were caught within small areas and only in box-type traps. Comparing the locations of the home ranges of resident young shrews with the home ranges of adult shrews reveals relatively little overlap. Table 1 shows that juvenile shrews were rarely caught in places actively used by adult shrews, whereas the home ranges of juveniles overlapped significantly with each other (Fig. 4). Overall, these results indicate that adult males and females that are moving around seem to stay in areas with low density of resident juveniles, and that dispersing juveniles do not establish territories in places occupied by resident breeding females.

The remaining 18 shrews (12 males, 6 females) marked in August 1984 either died in their first recapture (3 individuals) or were not caught later on. As resident adults are seldom captured, we cannot be sure that there were no residents amongst these animals. However, as the captures of these individuals were concentrated near the borders of the study area,

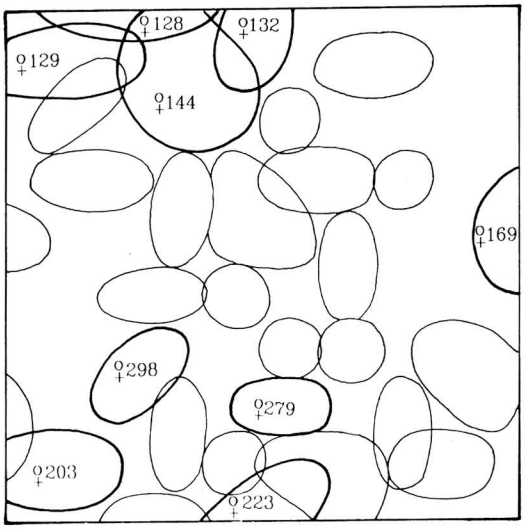

Fig. 5. Position of the home ranges of adult females that were marked in 1984 and were recaptured in 1985 (thick line), and the home ranges of resident juveniles in 1985 (thin line).

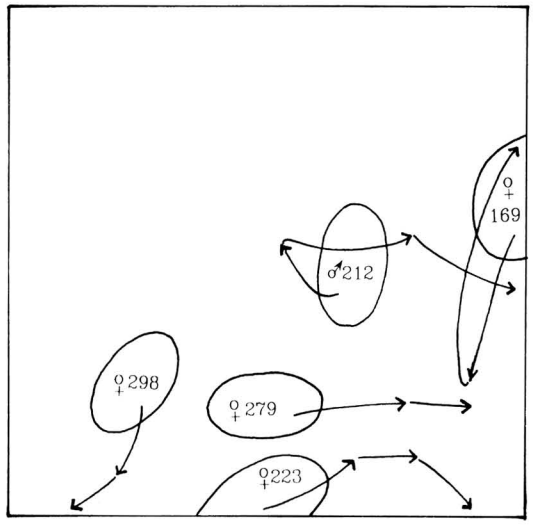

Fig. 6. Movements of adult shrews away from their home ranges in August 1985.

and they were mostly caught in pitfalls (10 of the 15 animals caught alive), it seems more probable that the majority of these individuals were dispersers.

After September 1 in 1984, adult males were not observed in the study area. At the end of August and the beginning of September, five unmarked adult females were captured, three of which left without being recaptured, while the two others were caught within small home ranges and stayed until the end of September. The home ranges of these females and the home ranges of juveniles did not overlap. The females did not breed in September.

Situation in the peak year

During 10 days of trapping in the middle of June in 1985, only four adult shrews marked in the previous year were captured. Female no. 259 and male no. 81 were captured within their previous home ranges in 1984. The two other males, nos 16 and 186, had been captured only once in 1984. These males are likely to have resided beyond the study area in 1984; their captures in the outer trapping lines in June 1985 suggest an expansion of their home ranges at the beginning of the breeding season.

More shrews (5 females and 1 male) marked in the previous summer were captured in July and at the beginning of August in 1985, suggesting that not all residents had been recorded in June. All these individuals were caught within or not far from their previous home ranges (Fig. 5). With the exception of female no. 223 recorded for the second time in August, all these shrews were trapped only once. Apart from these individuals, eight unmarked adult shrews (5 females and 3 males) were recorded in July. The types and locations of the traps in which they were caught suggest that most of them were dispersers, not familiar with the study area.

In the next trapping period in August, shrews marked in 1984 but not recaptured in June or July 1985 kept appearing within the study area. Five such adult shrews appeared to be leaving their home ranges (Fig. 6), while 4 other individuals marked in 1984 were captured near the borders of the study area. It is noteworthy that four adult males, recaptured in August 1985, the peak year, had not moved far from the territories which they had occupied in the previous year.

At the beginning of August, a set of young individuals established their home ranges in the study area. Fig. 5 shows only the home ranges of those juveniles which had inhabited the study area in June and July and had divided the area amongst themselves by August. In addition to these individuals, there were

Table 2. Numbers of encounters and proportions of aggressive encounters in neutral arena tests between members of different functional groups of the common shrew.

Type of encounter	Number of encounters	Proportion of aggressive encounters	Interactions per 30 mins
Two adult males	32	0.94	20.8
Adult male vs juvenile	46	0.89	19.3
Adult female vs juvenile	30	0.76	21.3
Two juveniles	59	0.60	18.4

Table 3. Average numbers (±*SD*) of different behaviour types per 30 minutes.

Interaction	Encounter: Initiated by:	Adult male & juvenile: Male	Juvenile	Adult female & juvenile: Female	Juvenile
Primary contact		7.2±1.1	8.5±1.0	6.9±2.0	7.6±1.4
Aggressive behaviour		3.9±0.6	11.8±1.4	7.8±1.4	6.1±1.2
Retirement		11.5±1.5	4.4±0.6	4.3±0.8	9.4±1.4

significant numbers of other juveniles trying to establish a territory in August 1985 (their movements and captures are not plotted in Fig. 5). Comparing the locations of the territories of the young resident shrews and the home ranges of adult females living in the area since the previous summer reveals that the juveniles tended to occupy home ranges not overlapping with those of adult females. In late summer, the adult shrews gradually disperse or die, and their territories are taken over by young individuals.

In August 1984, the prepeak year, the density of young shrews was 1.5 times lower than in August 1985, the peak year (Moraleva 1988). In 1984, dispersing adults could settle in places within the study area with low density of young individuals (Fig. 4). In August 1985, the entire study area became occupied by the territories of young shrews, and adult individuals did not stay there. In September 1985, no adult shrews were recorded within the study area.

3.3. Experimental results on a neutral arena

The field observations pointed to an important role of antagonistic interactions between members of the different functional groups of the common shrew in establishing and maintaining the social structure in the population. Further studies of individual interactions were conducted on a neutral arena.

During encounters of all types, the average number of interactions is approximately the same (Table 2). The highest percentage of aggressive interactions is found amongst adult males and between adult males and juveniles (Table 2).

The interactions between juveniles and adult males were asymmetric (Table 3). Juveniles tended to initiate contacts and aggressions more often than adult males, although the difference was statistically significant only in the case of aggressions ($P<0.01$). Adult males run away significantly more often than juveniles (Table 3; $P<0.01$), while the latter continue to follow and attack adult males. At the end of the encounter, adult males hide themselves in a corner of the experimental arena, apparently trying not to attract attention.

The percentage of aggressive interactions between juveniles and adult females was significantly lower ($P<0.01$) than between juveniles and adult males (Table 2). Juveniles less frequently initiated aggressions towards adult females than towards males, and juveniles retired from a contact more frequently than adult females (Table 3). During three encounters, signs of friendly behaviour were observed: animals climbed under and over one another, smelling each other for a long period of time and sitting side by side. Interactions of females and their young are similar (Moraleva & Pavlova 1983).

Juveniles were the most tolerant of each other (Table 2). The percentage of nonaggressive interac-

tions between young shrews is significantly higher than either between juveniles and adult males ($P<0.001$) or between juveniles and adult females ($P<0.05$). During some encounters (17%), juveniles were observed to be friendly and climbed under and over each other. In contrast, in some encounters between adult males and females the latter were so aggressive towards males that the experiment had to be stopped.

These experimental results clearly indicate that in encounters on a neutral arena, young shrews socially dominate adult males but not adult females.

4. Discussion and conclusions

Croin Michielsen (1966) described how several adult males were observed within the home range of one female. The breeding males undoubtedly compete for females and are aggressive towards each other. The experimental results obtained here showed that the interactions between adult males were the most aggressive. Aggressive behaviour of pregnant females towards adult males is also intensive but was not studied in the present experiments. The experiments conducted on neutral arenas indicated that the juveniles are also aggressive towards adult males and are usually the "victors" over them. Thus adult males experience the most intensive social pressure of all the functional groups in the population.

Perhaps to avoid intraspecific competition, some adult males range widely through the forest and concentrate in habitats unoccupied by other individuals of the species. Such habitats include the flood plain, which is vacant of small mammals after the spring flood, and cultivated meadows. Accumulation of low ranking males in particular areas has been reported for winter aggregations of the bank vole *Clethrionomys glareolus* (Karlsson 1986). In the middle of the summer, young shrews start to disperse to all habitats, including the flood plain. With the appearance of these juveniles the numbers of adult males decrease, most of them probably dying.

More complicated relationships exist between adult females and juveniles. The neutral arena tests did not indicate any advantage of juveniles over adult females. In spring and at the beginning of summer, most females reside within their territories, and the juveniles of the first litter occupy vacant areas not overlapping with the territories of adult females. Some females, after weaning their first litter, may leave their previous home range (Pucek 1959) and move to another area. A substantial increase in the numbers of dispersing adult females is recorded at the beginning of August, when the dispersal of juveniles is also highest.

It is of interest to correlate yearly variation in the mobility and apparent death rate of shrews to variation in population density during the 4-year cycle. The data obtained so far are not sufficient for a comprehensive analysis but they suggest a number of working hypotheses.

The mobility of adult males during the breeding season is likely to depend on the number of females within the area. In the years of low population density males may be expected to move longer distances while searching for females than in the years of higher density. In support of this suggestion, in the peak year some males were found to have stayed within the limits of their home ranges in the previous summer until the beginning of August, apparently competing for the females in the close neighbourhood.

The rate of mortality in old shrews may be related to the density of young shrews. In the prepeak year adults moving through the taiga may discover areas unoccupied by resident young shrews. In the peak year, practically all the space available is divided amongst the juveniles by the beginning of August, and free dispersal within the population is strongly restricted. These circumstances appear to lead to a higher rate of mortality of adults in the peak year than in the prepeak year.

It is well known that in captivity shrews live for much longer than in their natural environments (Pearson 1945, Pucek 1964). The possible reasons for the autumnal mortality of adult shrews include lack of a regular autumn moult (Stein 1954, Dokuchaev 1980), tooth wear (Pernetta 1977, Pankakoski 1989) and heavy infestation by parasites (Borowski & Dehnel 1959). Croin Michielsen (1966) suggested that autumnal mortality of adult shrews might result from the struggle between members of the population for living space, at the time when the juveniles become socially dominant over the old ones. The data obtained here support the hypothesis of social dominance of old shrews by young ones. Particularly the adult males appear to suffer from frequent interactions with other individuals.

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