Social organization in cyclic subarctic populations of the voles Clethrionomys rufocanus (Sund.) and Microtus agrestis (L.)

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Fluctuating populations of *C. rufocanus* and *M. agrestis* were studied by capture-marking-recapture trapping and snap-trapping at Kilpisjärvi, Finnish Lapland during several years.

All categories of *C. rufocanus* were nearly twice as trappable as those of *M. agrestis*, but differences in social status caused differences in trappability between individuals of the same category. Trappability was therefore used as a measure of the social status of the individual.

In both species the population had a group structure; each group consisted of many mature females with territories and some semi-territorial or non-territorial mature males. The immatures were non-territorial. In *M. agrestis* these groups, increased by immigrants, changed during the summer to harem-like structures defended by highly aggressive territorial males.

The numbers of reproducing females were controlled by territorial behaviour. In *C. rufocanus* maturation ceased when all habitable space was occupied, whereas in *M. agrestis* the young females emigrated to independent home ranges shortly before the birth of their first or second litter. In males of both species maturation was controlled by the aggressive behaviour of the highly mobile mature males. These formed a dominance hierarchy, and as a result some of the males that matured at a later stage were forced to emigrate.

During a population decline the oldest dominant age classes survived best, whereas during a population increase the young age groups survived somewhat better. In suboptimal habitats, changes in age structure always resembled those of a declining population.

In competition *M. agrestis* is superior to *C. rufocanus*, but the difference is slight, as indicated by the impact of *M. agrestis* upon the age structure of *C. rufocanus*.

Neither the early cessation of breeding observed in some years nor the population declines were directly correlated with population density, but other factors must be involved, possibly nutrition.

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1. Introduction

The aim of the present study was to examine the social structure and its ecological importance in two rodent species, *Clethrionomys rufocanus* and *Microtus agrestis*. Initially, the study was to have concerned the species *C. rufocanus* and *C. rutilus*, but the results for the latter species were too scanty. However, this was compensated by a heavy invasion of *M. agrestis*, which was thus available for study.

Small mammals which hide under the vegetation or are partly subterranean cannot be observed directly like larger species. Laboratory populations have been used for studies (e.g. STEINIGER 1950, FRANK 1954) on social behaviour and population structure, but the impossibility of emigration may cause abnormal behaviour. If the species to be studied is territorial, the space needed will cause the same difficulties as in the wild. Another method, but a laborious one, is live trapping. The disadvantages of this method will be discussed below.

In familiar language social is used in the same sense as sociable, i.e., animals are social if they live in groups. In the present study the term is used for all contacts or communications between individuals of the same or of different species. Thus even aggressive behaviour is included, although it may cause part of the population to emigrate.

KALELA (1956), who surveyed the older literature on social organization in mammalian populations, noted the similarity of structure in all mammalian orders studied. In all orders the ancestral form seems to have been a family with one male, one female and their immature litters. The next step in evolution was a polygamous or promiscuous colony or herd, and then these might be organized into supercolonies or superherds. These stages are still to be seen in ungulates, especially ruminants, in primates, in carnivores and in rodents. Further details of the social types in mammals were presented by BOURLIÈRE (1954) and for rodents only by EIBL-EIBESFELDT (1958) and ANDERSON (1970). Although knowledge has increased since the publication of KALELA's paper, the general view he put forward has remained unchanged.

Concerning the social structure of rodent populations there are still many unanswered questions. Interest has focused on the ecological functions of social behaviour. KALELA (1954,
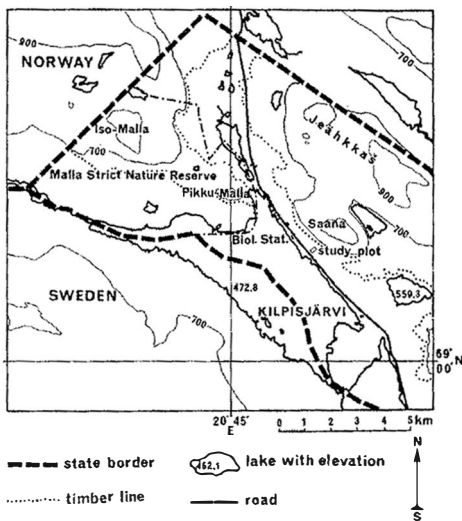

Fig. 1. The main study area around lake Kilpisjärvi.

1957) stressed the ecological significance of territorial behaviour, and the social groups have been regarded as tools of group selection (KALELA 1957, ANDERSON 1970). However, there is disagreement about this (BERRY & JACOBSON 1974). In all species studied so far (KALELA 1957, CROWCROFT & ROWE 1958, BUJALSKA 1970, 1971, VANDENBERGH 1971, METZGAR 1971) effective self-regulation of population increase has been based on social activities. These activities in *Clethrionomys rufocanus* and *Microtus agrestis* were the subject of the present study. The live-trapping experiments by KALELA (1956, 1957) on *C. rufocanus* and by REICHSTEIN (1959), MYLLYMÄKI (1970) and KOPONEN (1972) on *M. agrestis* afforded important data for comparison.

The impact of social activities upon survival and upon the age structure of the population was studied by live trapping, and age structure was also studied by snap-trapping. According to GLIWICZ (1970) and ANDRZEJEWSKI & RAJSKA (1972), there is a considerable correspondence between social classes and age classes.

The competition between rodent species is based not on differential ability to exploit natural resources, but on interference (for references, see MILLER 1967, GRANT 1972 and MORSE 1974). This interspecific competition is also considered here, because in the study area it can be observed at almost

all times owing to the simultaneous presence of four species (*C. rufocanus*, *C. rutilus*, *M. agrestis* and *M. oeconomus*), and in some years also *Lemmus lemmus*. The *Clethrionomys* species live mostly in birch woods on mineral soil (KALELA 1949, 1957, 1962; KALELA & PEIPONEN 1972), whilst the *Microtus* species are usually found on bogs and fens with sedges and grasses, in thickets growing on flood plains and in man-made habitats (meadows, road banks, etc.) (KALELA 1949; TAST 1966, 1968a, 1968b; KALELA *et al.* 1971). When the populations grow, both *Clethrionomys* and *Microtus* species extend their ranges and so come into competition in *korpi*-woods on peaty soil, in eutrophic woods, and in some years even in the richest mesotrophic woods. ECKE (1954) observed the competitive exclusion of *Rattus rattus* by R. *norvegicus* in the wild, whereas most students of this topic have used confined populations

(KOPLIN & HOFFMAN 1968; HILL 1969; GRANT 1970, 1972) or compared areas where two species occur together with those where one or other is absent (CAMERON 1965; KOPLIN & HOFFMAN 1968; MILLER 1964, 1967).

Intraspecific geographical variation may diminish the reliability of such comparisons (MAYR 1971).

In the Kilpisjärvi area, *C. rufocanus* is the most numerous rodent species almost every year, but it was also possible to study the social structure and its ecological significance in *M. agrestis*. Other species are dealt with only as far as is necessary.

II. Field investigations

1. Study area

The field work was conducted at Kilpisjärvi, Finnish Lapland (Fig. 1) in 1967—1970.

The basic data were collected on a study plot of 2—2.4 ha on the lower SW slope of Saana fell (Figs. 1 and 2). In summer 1967 counts were also made on a study plot of about 3 ha on the shore of the lake Kilpisjärvi. (Results from this plot were so scanty, however, that the following description refers only to the plot on Saana fell.)

Trap stations were set at intervals of 10 m (Fig. 2). Because two species were to be studied, a sampling area was chosen that had vegetation of mosaic type including plenty of eutrophic meadow forest. At every trap station every plant was counted and the coverages of the most numerous species were estimated (Table 1). The habitats are classified according to A. KALELA (1961) and HÄMET-AHTI (1963). To avoid too small subdivisions I have considered most types collectively.

The Kilpisjärvi area lies in the subarctic (subalpine) birch wood zone. The main tree species, *Betula pubescens* ssp. *tortuosa*, is dominant in the study plot. Other species appear as undershrubs only.

The following main habitat types could be distinguished on the study plot (Table 1):
— Oligo-mesotrophic heath woods. Empetrum-Myrtillus type coll. The driest oligotrophic woods, the Empetrum-Lichen type, did not occur on the study plot (Fig. 3A). 40 trap stations in 1969 and 1970.
— Mesotrophic heath woods. Geranium-Dryopteris-Myrtillus type coll. 60 trap stations in 1969 and 1970.
— Eutrophic meadow woods. Trollius-Geranium type. 75 trap stations in 1969 and 1970 (Fig. 3B).
— Mesotrophic and eutrophic patches of peaty *korpi*-woods not specified separately. 14 trap stations in 1969 and 1970.
— Small patches of open fens and bogs with very low field stratum. 11 trap stations in 1969 and 1970.

Study plot boundaries:
——— 1969-70
——- 1968
—·—·—1967-68
— — — 1967

Habitats:
eutrophic wood
mesotrophic wood
oligo-mesotrophic w.
korpi wood
open fens and bogs
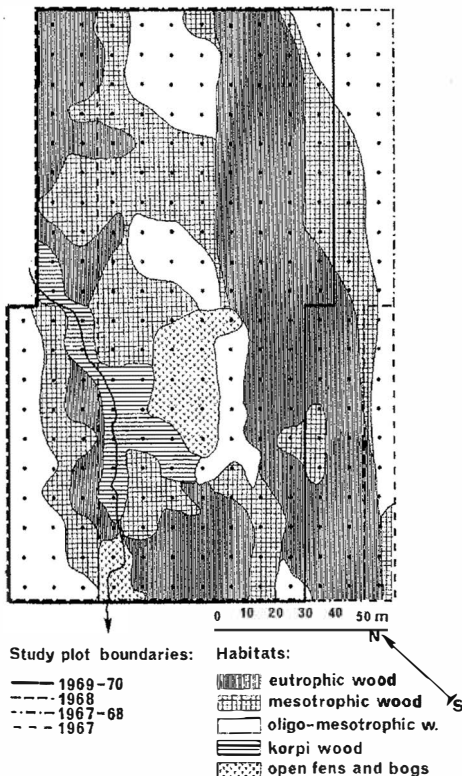
0 10 20 30 40 50 m

N

Fig. 2. Map of the main study plot showing the trap sites (dots) and the distribution of the different habitats. The curved line with arrowhead shows the position of a brook flowing through the study plot.

There were 200 trap stations in 1967, 1969 and 1970, but 240 in 1968.

A   B

Fig. 3. Habitats of the study plot. A is a typical oligomesotrophic wood, to which *C. rufocanus* was restricted during the cyclic peak of the two species in summer 1969. B is a typical eutrophic wood preferred by *Microtus* species during the cyclic peak.

The snap-trapping material was collected during Prof. Kalela's expeditions in 1964—1970, mostly below the timber line on Saana fell and Pikku-Malla fell, and at least 200 m from the study plot after the live trapping started. The team also collected a sizeable sample of *C. rufocanus* when trapping lemmings in the birch wood zone and in the alpine zone above the timber line up to 900 m on the Finnish fells Saana, Jeähkkaš and Malla as well as on the fells on the Swedish side of Kilpisjärvi (Fig. 1). There are also small samples from other fells of N. W. Finland.

The study area has been described in detail by KALELA (1949, 1957, 1961) and FEDERLEY (1972), for instance.

2. Material and methods

Samples of voles were collected by CMR trapping (capture-marking-recapture), carried out in 1967 and 1968 with single-catch live-traps measuring $6 \times 6 \times 18$ cm and in 1969 and 1970 with "Ugglan special" traps (HANSSON 1967) which can catch several individuals at a time.

Two equal parts of the study plot were trapped alter-

nately for 5-day trapping periods, except when the plot appeared totally empty, and in October 1967, when 4-day periods were used. The traps were set every day and inspected twice a day with an interval of 4—5 h. Trapping thus lasted 8—10 h daily. In August 1967 and 1968, when there were few animals, trapping was continued for 24 hours, and the traps were inspected morning and evening.

During the light arctic summer trapping was carried out in daylight. In early August, when the nights began to darken, the voles became night-active (PEARSON 1962, PEIPONEN 1962, ERKINARO 1969) and trapping was done at night, too. The traps were set at about 17.00, inspected at about 22.00 and opened at about 03.00. In October 1967 the traps were inspected every 2 hours, because the youngest individuals, which still have the juvenile pelage, cannot withstand exposure to cold.

The captured animals were marked individually by toe clipping. If possible, each animal was weighed at least once during every trapping period. The following observations were made every time an animal was caught: identity, sex, sexual status of males from size and position of testes (scrotal or abdominal) and of females from vaginal status (open or closed), size of nipples and milk glands, and visible pregnancy (vaginal

Table 1. The vegetation of the study plot. The coverage of vascular plants of the field layer (%) in the different habitats, as estimated for 1 m² squares at every trap station.

	Eutrophic wood	Mesotrophic wood	Oligomeso- trophic wood	Korpi- wood	Open bogs
No. of species	57	48	39	38	32
Coverage (%) of the field layer	124.8	95	88.1	65.2	65.8
Coverage of 12 meadow herbs	105.7	41.3	2.9	13.4	7.4
„ „ 7 dwarf shrubs	3.7	25.6	62.6	25.2	28.4

Table 2. The CMR sample. The number of captures and (in parentheses) the total number of live-trapped animals caught in 1967—1970. For the trapping periods in different years, see below. The *Microtus* individuals caught in 1967 were trapped on the Kilpisjärvi shore study plot. The first *Microtus* specimens on the main study plot appeared in autumn 1968. An asterisk indicates that some animals were caught in two consecutive years, but are included in the sum only once.

Year	C. rufocanus	M. agrestis	C. rutilus	M. oeconomus	Total
1967	131 (22)	12 (7)	32 (13)	17 (7)	192 (50)
1968	155 (28)	28 (6)	55 (12)	—— ——	238 (46)
1969	1116 (124)	710 (109)	293 (38)	54 (7)	2173 (278)
1970	375 (76)	86 (21)	53 (21)	19 (6)	533 (124)
Sum	1759 (234)*	836 (141)*	433 (82)*	90 (21)	3136 (478)*

Table 3. The snap-trapping samples of *Clethrionomys rufocanus*. The significantly different subsamples obtained from other areas or by other methods are treated separately. Line = line trapping, used mostly on Saana fell and samples identical with it, Malla = trapping on Pikku-Malla fell, Sets = trapping with sets of five traps placed in optimal vole habitats, Lemming = samples of lemming trapped by Prof. O. Kalela's expedition. The only samples available were of *C. rufocanus*. The values are numbers of individuals and (in parentheses) numbers of trap-nights.

Sample	1964	1965	1967	1968	1969	1970	Total
Line	820 (12280)	51 (4310)	119 (5595)	59 (2594)	416 (4933)	210 (6747)	1675
Malla	——	——	——	53 (3976)	——	——	53
Sets	146 (1000)	——	——	41 (1310)	——	——	187
Lemming	——	——	——	40 (2845)	279 (9366)	——	319
Total	966 (13280)	51 (4310)	119 (5595)	193 (10725)	695 (14299)	210 (6747)	2234 (54956)

smears were not taken), age according to pelage condition (KOPONEN 1964, 1970; MYLLYMÄKI 1970) to distinguish overwintered and summer-born voles if the weights overlapped, site and time of capture.

Altogether 478 individuals were trapped 3 115 times (Table 2) during the following periods:

1967: 15—19 June, 3 August — 15 September, 6—14 October;
1968: 9—19 June, 17—26 August, 16—25 September;
1969: 24—28 June, 3 July — 23 August;
1970: 6—15 June, 17 July — 3 August, 17—23 August.

Most of the snap-trapping samples used in age structure analyses were obtained by line-trapping with the trap stations 7 m apart along a line (KALELA 1957). At each station there were two traps less than 1.5 m apart, one baited with white bread, the other with apple. The line was usually about 350 m, so there were about 50 pairs of traps. The traps were inspected one day after they were set, and the line was then shifted about 5 m. The next day the traps were again inspected and a new line was laid about 25 m from the last. The line was then shifted alternately 5 m and 25 m per day, and continuous trapping in this way made it possible to cover a large area.

In spring and autumn, when trapping was hampered by snow, some voles were also caught with groups of five traps placed at likely sites.

Lemming were caught with unbaited traps, as in 1967—1970, either along lines in the way described above or with 7×7 pairs of traps at 7-m intervals in a grid. The pairs of traps consisted either of two big commercial rat traps, or a rat trap and a smaller mouse trap. Only the smaller traps were used in trapping voles. Of the samples of *C. rufocanus* only those were taken into account which were from the "normal" range of habitats of the species.

Samples collected from different areas and by different methods were tested for heterogeneity, and those that differed significantly in age structure or relative population density were excluded. For this reason the lemming samples (except those for 1970) will be treated separately and the Malla sample of 1968 has been wholly excluded, because interspecific competition strongly affected the rate of increase of the population.

The results of snap-trapping are presented in Table 3.

3. Trappability

When the CMR method is used, the results may be affected by the differential trappability of age categories within the species, and this point has to be taken into account when the relation between home range size and population density is examined. In accordance with GLIWICZ (1970) and ANDRZEJEWSKI & RAJSKA

(1972), the trappability of an individual has been used as an indicator of its social position. The problems caused in population estimates by the differential trappability of the different reproductive categories have been discussed by MYLLYMÄKI (1969a, 1969b, 1970).

Interspecific differences. Table 4 shows that all reproductive categories of *C. rufocanus* were significantly more trappable than the same categories of *M. agrestis*. A mature *C. rufocanus* individual was, on average, trapped more than five times per trapping period, whilst in *M. agrestis* this figure was only four. The trappability (Table 5) is a percentage expressing the number of times that members of a category were caught in relation to the number of opportunities the animals had to enter the traps. This percentage is obtained from the formula

$$ Tr = \frac{C \times 100}{I \times N} $$

where Tr = trappability, C = number of catches, I = number of inspections of the traps during trapping and N = number of individuals. The decreasing trappability of *C. rufocanus* in 1970 is probably due to the rapid decline of the population, several animals disappearing from the population during the trapping season.

Table 4. Trappability of *C. rufocanus* and *M. agrestis* on the main study plot in summer 1969. Only sedentary individuals are included, except for the immatures. Animals captured in successive trapping periods are included several times in the figures, so the totals do not tally with the numbers of individuals. $M = M.\ agrestis$, $C = C.\ rufocanus$. The juveniles and subadults described by MYLLYMÄKI (1969b, 1970) are included in the category of immatures. Some individuals were captured twice during one inspection of the traps, and so the numbers of captures may exceed the number of inspections, which was ten.

Number of captures	Males		Females		Immatures		Total	
	M	C	M	C	M	C	M	C
1	14	8	28	13	24	15	66	36
2	16	5	23	11	15	16	54	32
3	7	8	26	9	1	7	34	24
4	8	7	24	6	—	9	32	22
5	8	7	9	5	3	5	20	17
6	5	8	4	14	—	6	9	28
7	2	5	4	9	—	2	6	16
8	5	7	3	14	—	2	8	23
9	3	1	—	9	—	2	3	12
10	1	4	—	4	—	—	1	9
11	—	1	—	3	—	1	—	5
12	—	—	—	1	—	—	—	1
13	—	1	—	—	—	—	—	1
Total	69	62	121	98	43	65	233	226
Median test χ^2		5.843[1]		18.982[2]		15.773[2]		26.427[2]

[1] $P < 0.025$
[2] $P < 0.001$

Table 5. The trappability (%) of breeding *C. rufocanus* (*C*) and *M. agrestis* (*M*) in different years. (See also caption to Table 4).

Males

	1967		1968				1969				1970			
	C		C		M		C		M		C		M	
	%	N	%	N	%	N	%	N	%	N	%	N	%	N
June	0	0	0	0	0	0	—	—	—	—	47	(18)	35	(2)
July	—	—	—	—	—	—	53	(28)	35	(29)	37	(10)	47	(6)
Aug.	85	(4)	63	(4)	0	0	58	(21)	44	(23)	—	—	—	—
Sept.	50	(1)	36	(3)	40	(1)	—	—	—	—	—	—	—	—

Females

	1967		1968				1969				1970			
	C		C		M		C		M		C		M	
	%	n	%	n	%	n	%	n	%	n	%	n	%	n
June	0	0	0	0	0	0	—	—	—	—	63	(11)	36	(5)
July	—	—	—	—	—	—	52	(41)	29	(44)	57	(7)	43	(7)
Aug.	55	(2)	46	(6)	0	0	65	(34)	34	(50)	—	—	—	—
Sept.	85	(4)	30	(3)	80	(1)	—	—	—	—	—	—	—	—

Intraspecific differences. The following data are based chiefly upon observations on *C. rufocanus*, but similar differences were observed in *M. agrestis*. The trappability of summer-born breeding animals increases throughout the breeding season. GLIWICZ (1970) and ANDRZE-JEWSKI & RAJSKA (1972) also observed this in *Clethrionomys glareolus*. But when breeding ceases in autumn trappability seems to decrease (KALELA 1957). In autumn 1968 I could confirm this, but in other years trapping had to be discontinued when the animals were still breeding. In both species studied, the immatures were the least trappable category, the difference between immatures and reproducing animals being significant (*C. rufocanus*: $\chi^2 = 17.127$; P<0.001, *M. agrestis*: $\chi^2 = 32.434$; P<0.001. Table 4). But although maturation of young voles increased trappability (especially in summer 1969), animals with a lower social status remained less trappable than those that had overwintered. After a while, any males that were subordinate disappeared and the trappability of the summer-born breeding females rose to the level of overwintered animals.

In June 1970 the youngest mature females were about as trappable as the overwintered animals of the previous years, whilst the young mature males were clearly less so, apparently because of the large number of males. Few of them could stay on the study plot. Seven males,

with trappabilities of 60 % or more, were classed as dominants (cf. Fig. 14A), nine males with trappabilities of 20—40 % as subordinates, and ten males captured only once as occasional visitors (cf. MYERS & KREBS 1972). The number of visitors was greater than during any other trapping period.

In spring 1970 there were 14 overwintered sedentary *C. rufocanus* females living on the study plot. Their trappability averaged about 63 % (Table 5). Seven had been marked the previous summer, the other seven were immigrants. The trappabilities of these two categories were 81.4 % (57 catches) and 44.2 % (31 catches), respectively ($\chi^2 = 7.682$; P<0.01). Since all these females were overwintered matures with no obvious differences in their home ranges, the reason for the difference in trappability is presumably a difference in social status. This conclusion agrees with the observation of ANDRZEJEWSKI *et al.* (1963) that, irrespective of age, sex and earlier experience, new immigrants to populations of *Mus musculus* always had the lowest social status.

Trappability also differed from year to year. In *C. rufocanus* the values were highest in 1967, when population density was lowest, but since catches were very low during the first years of the study and the trap model was changed, no definite conclusions can be drawn.

III. Social organization of the populations

1. Home ranges

A. Site tenacity

Almost all mammalian species show some degree of site tenacity at some phase of the life cycle (BURT 1943). In *C. rufocanus* and *M.*

agrestis imprinting to the home range differed in strength both inter- and intraspecifically.

Clethrionomys rufocanus. The mature *C. rufocanus* females showed the strongest site tenacity. They were usually found within 20—30 m of the site where they were first captured but when

density was low (in 1967 and 1968) the distance was about 40—50 m during the time of observations, which for three voles was more than 12 months. Three females that matured in summer 1969 continued to breed on the same home range in summer 1970.

The breeding males were of two different categories, dominants with high (60—130 %) and subordinates with low (30—40 %) trappability. The dominants did not change their home ranges during the breeding season. In summer 1969 eight males remained dominant from early July to the end of the study period, and one more male attained dominance in early August. Each dominant moved over a large area, and between these ranges the subordinates had small ranges. The site tenacity of the latter was weak; some of them moved from one part of the study plot to another, and most of them probably left the plot during summer 1969.

During the low in 1967 and 1968 all the males behaved as the dominants did during the high. This may account for the somewhat higher trappability during the low (Table 5).

The site tenacity of the males may be restricted to the breeding season. Of four males marked when mature in 1969, only one was recorded in his former home range in summer 1970, and the three others (one dominant, two subordinates) and two that were marked when immature in August 1969 had moved to new home ranges. Thus, of the animals marked when immature in August 1969, only 2 out of 26 males but 7 out of 16 females survived to summer 1970. Only one of these females had changed her home range by more than 40 m. The sex ratio had not changed during the winter (cf. Fig. 19). This difference in site tenacity between the sexes is probably due to the greater tendency of the males to disperse (KALELA 1957). The frequent exchange of males between breeding colonies suggests that group selection may not play such a strong evolutionary role in *C. rufocanus* as was supposed by KALELA (1957) and ANDERSON (1970). Similar evidence against their view was presented by BERRY & JACOBSON (1974) for wild populations of *Mus musculus*.

During the breeding season, the immatures lived in small groups on the home range of a female, presumably their mother, but as some exchange was observed (Fig. 4), the members of a group were not necessarily all siblings.
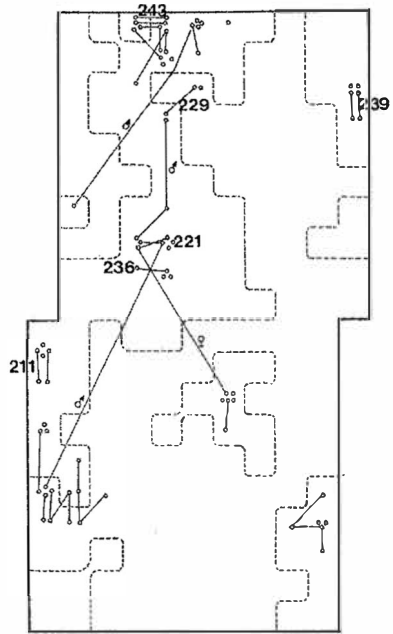

Fig. 4. Capture points (ring) of immature *C. rufocanus* in August 1969. The different sites where each individual was caught are connected with a continuous line. Numbered individuals are females captured again in June 1970. Areas inhabited by mature females are bounded with broken lines.

Microtus agrestis. On the whole, *M. agrestis* moved distinctly more than *C. rufocanus*. Most young females, when pregnant for the first or second time, changed their home ranges, often little by little, but sometimes as a true emigration, whilst the old (mostly overwintered) females seemed to have home ranges as fixed as the respective *C. rufocanus* females. Figs. 12 and 13 show the movements of one such female (no. 128) which had the same home range from July 1969 to late July 1970. Two other females which were caught in both June and July 1970 had changed their habitats (see p. 86). However, what appear to be changes of home range sites in these old territorial females may really be due to the small number of captures, if the animals use different parts of extensive home ranges at different times (cf. KAYE 1961).

The males appeared to follow the females in their movements. In July 1970, there were only four females on the study plot, with home ranges separated from each other by 20—40 m. The males then moved from one female range to another, presumably as the respective females came into oestrus (Figs. 13B and 14B).

Like the *C. rufocanus* males, the mature males were either dominants or subordinates. Although the hierarchy was not so stable as in *C. rufocanus*, it led to dispersal.

In the population founded by immigrants in August 1969 the males established individual territories. Many of them may have survived to the end of the breeding season, but none were recaptured the following summer.

Information on the immatures is scanty, because of their poor trappability. Like the immatures of *C. rufocanus*, they were observed to live in small groups. Of 17 immatures caught three or more times, 14 were residents and 4 (all males) wanderers which had moved more than 60 m between successive captures.

B. Movements outside the home range

In summer 1969 three *C. rufocanus* and five *M. agrestis* females had no fixed home range. One of these voles (no. 14 in Fig. 9A) was captured four times at successive sites separated by a mean distance of 60 m. Two of the *M. agrestis* females (Fig. 5) settled down later, and two of the wanderers were overwintered animals, which are usually strongly attached to their home ranges. The movements of such females may be caused by interspecific relations (cf. p. 86).

Sedentary *C. rufocanus* and *M. agrestis* females were now and then caught more than 100 m from their home ranges (Figs. 7—9, 11—13). This makes it difficult to decide which capture sites were within the normal range and which beyond it. At least some of these movements were oestrus runs (COLLET 1911—1912). *Sorex araneus* has a similar behaviour pattern during oestrus; in this way the female protects her sucklings from the males (CROWCROFT 1957). Such movements take the animals outside the areas they use in daily activities.

C. Home range size

For the following rodent species, at least, we know something about the factors regulating the size of the home range: *Microtus pennsylvanicus* (BLAIR 1940; GETZ 1961a), *Zapus hudsonicus* (QUIMBY 1951), *Peromyscus polionotus* (PEARSON 1953, STICKEL 1960), *C. rufocanus* (KALELA 1957) and *Apodemus sylvaticus* (MILLER 1958). In these species the size of the home range varies with several factors: amount of shelter afforded by the field layer, food available, season, reproductive status and population density.

The sizes of the home ranges of small mammals are calculated from live-trapping data. Several methods have been used. The results are affected by the distance between
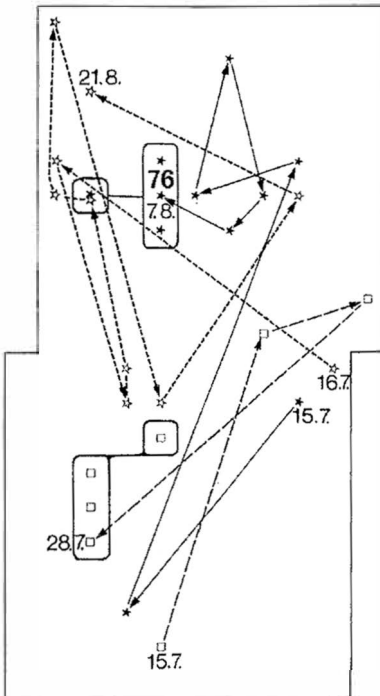

Fig. 5. Movements of three wandering *M. agrestis* females in summer 1969. The direction of movement is indicated with arrows. Two out of five such females settled down in August on the permanent home ranges outlined; 76 = serial no. of one of these two females.

traps, the number of inspections (HAYNE 1950, STICKEL 1954) and the size of the grid (FAUST et al. 1971).

According to BUJALSKA (1970, 1971), the most essential factor regulating the population is the number of breeding females per unit of inhabitable area. Therefore the area available for one female within the area inhabited by the population was taken to represent the "home range size". Because of overlapping, however, the true ranges are always larger. To estimate the "home range size" I devised the following formula:

$$A_{\overline{X}} = \frac{A_S}{N}$$

where $A_{\overline{X}}$ = mean area available for one female, N = number of females, and A_S = whole area where females or immatures were captured. Mature males were often captured apparently outside the range of the population; this occurred more often in *C. rufocanus* than in *M. agrestis*. The greater the number of observations, the nearer is $A_{\overline{X}}$ to the true home range size. Although the relatively small size of the study plot restricts the validity of the data obtained, those for the two species are regarded as comparable. Furthermore, the danger of an underestimate is greater during a population low than during a high.

Changes in home range size were very similar in the two species; they were strongly linked with population density (Fig. 6), but other factors may have been involved. In *C. rufocanus* during the lowest density (late summer 1967) "home range size" was 900 m² (= 9 trap stations). With increasing density it diminished to a certain level, and did not decrease further. In *C. rufocanus* this level was attained in late September 1968 when the juveniles dispersed to their winter territories and the number of territorial animals increased from 5 to 15. Then the "home range size" fell to 300 m².

After this the size remained about the same (290—330 m²) until June 1970. In fact, the decrease may have been still greater, because the size of the home range was underestimated when density was low. The slight apparent increase in home range size observed in *C. rufocanus* in summer 1969 is probably due to the increasing trappability of summer-born
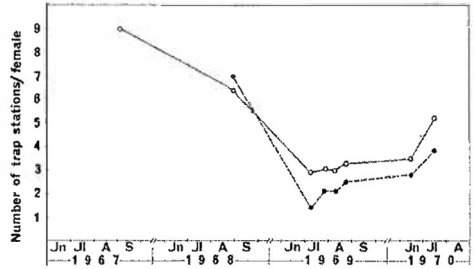

Fig. 6. Changes in female home range sizes during the population cycle from summer 1967 to summer 1970. Circles and solid line = *C. rufocanus*, dots and dashes = *M. agrestis*. The numbers of individuals are as in Figs. 19 and 20.

breeding females. If allowance is made for the occasional visitors, the size of the home range remained at 290 ± 1 m² from early July 1969 to June 1970.

In *M. agrestis* the home range size decreased from 700 m² in autumn 1968 to 140 m² in early July 1969, then, despite rising numbers, increased to 250 m². The change was not merely due to the increasing trappability of the young mature females. The lowest value appeared to be due to overlapping of the female ranges. As the young breeding females gradually matured, they moved to independent home ranges; the estimated value of the home range size then increased. The value of 250 m² in late August is therefore close to the true home range size of the species.

In *M. agrestis* the smallest possible home range size of the females was distinctly smaller than in *C. rufocanus*, partly owing to the lower trappability of the former, but also because of a true difference in behaviour.

In both species the home range size of the females reached the smallest possible value long before the whole available area was inhabited, i.e. all females could still have extended their home ranges. In spite of this they kept together in the smallest possible area.

The study plot was too small for a study of the trends in home range size among the males. In both species the males had distinctly larger ranges than the females. In territorial males of *M. agrestis* the value for late August 1969 was 770 m². In sedentary territorial *C. rufocanus* males it was 510 m² in spring 1970; if dominants only are considered it was 1 170

m^2; for semi- or non-territorial males the values may be much higher, but it is impossible to give exact values. Territorial behaviour seems to reduce the home range size of males more than density does.

DICE (1952) and many others after him attributed the decrease in home range size with increasing density to "general population pressure", i.e. agonistic behaviour. My observations, on the contrary, suggest that, up to a certain level, the diminution of home range with increasing density is due to group attraction, females seeking contact with conspecifics. This would mean that during high density the size of the home range is optimal. With the least possible expenditure of energy every breeding female can then maintain the optimal number of social contacts, while preserving a sufficient supply of food as well as nesting and hiding places.

Although determined by inherent factors, the smallest possible home range size of a species must be large enough to provide enough high-quality food. The less the amount of high-quality food available, the larger the home range and territory have to be. According to KOSHKINA (1957) and KALELA & PEIPONEN (1972), the food available to *Clethrionomys rutilus* is scarce compared with the species considered here. The smallest possible home range size of *C. rutilus* is about 18 times as large as that of *C. rufocanus* (own unpublished observations).

2. Social structure of the populations

A. Clethrionomys rufocanus

Overwintering colonies. According to ANDERSON (1970), breeding colonies of *Mus musculus* in granaries persisted longer than the life of an individual. KALELA (1957) observed that breeding units of *C. rufocanus* were formed in autumn before the breeding season, when the overwintering colonies were established. The establishment of winter colonies was studied in autumn 1968, a year when enough material was available. Figs. 8A and 8B show the capture sites and home ranges of mature breeding females and immatures of both sexes. The sites where immatures were caught in August 1969 are shown in Fig. 4, and the home ranges of mature females and immatures in early September 1967 in Fig. 7.
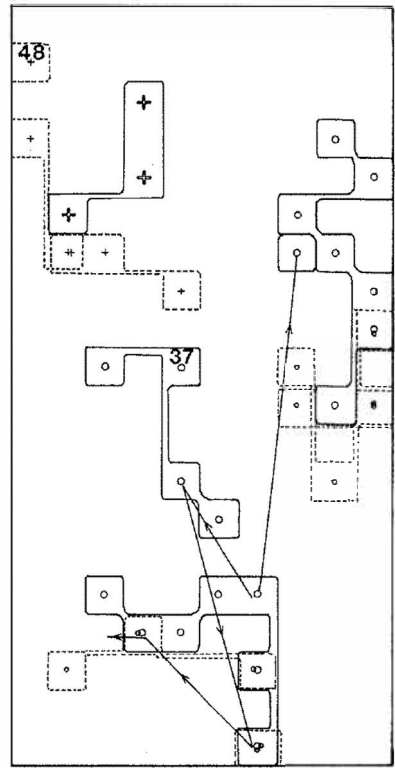

Fig. 7. Home ranges indicated by catch sites of *C. rufocanus* in autumn 1967. Small rings = breeding females, dots = immature animals and + = *C. rutilus*.

In late August 1968 and 1969 the animals that remained immature during their season of birth and would form the bulk of the overwintering stock (KALELA 1957:18) were still living in coherent groups in the home ranges of mature females, but by late September 1968 these groups had dispersed. Of 11 members of such late August groups seven were still on the study plot in late September 1968, and six new immatures had appeared on the plot. The area inhabited by post-breeding females and immatures covered 45 trap stations. Only one trap was visited by two individuals, i.e. territoriality was strictly observed, and at this time the home range size fell to the smallest possible value. In 1967 the immatures of early
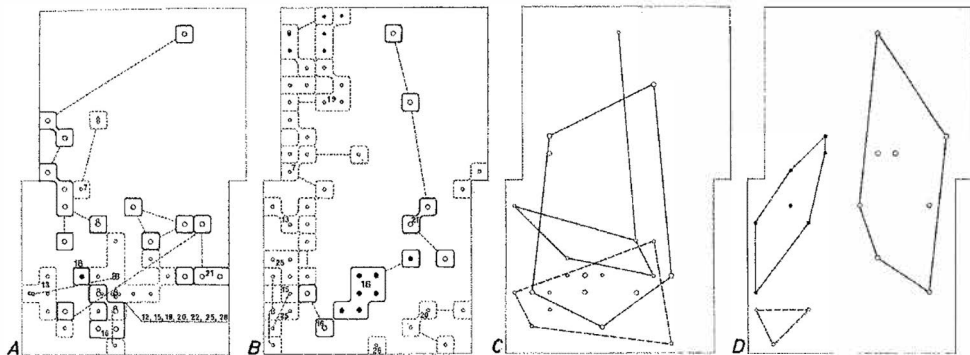
Fig. 8. Captures of *C. rufocanus* and *M. agrestis* in late August (A, C) and late September 1968 (B, D). Circle = *C. rufocanus*, dot = *M. agrestis*. In A and B small circles or dots indicate immatures. A and B refer to breeding females, and C and D to breeding males.

September appeared to be territorial to some extent, but the sample was too small for further conclusions.

When moving to a separate home range, which is possibly a real territory, an immature may travel many metres from its site of birth (e.g. no. 19 in Fig. 8). Of the animals marked as immature in late August 1969 and recaptured in June 1970, only two out of nine were captured in the same area as before; two had moved 20—40 m beyond the range and five more than 50 m. Most of these movements of immatures probably occurred during the shift to winter territories, but the males may also disperse in the spring, when attaining sexual maturity.

Despite the strict territoriality, the individual home ranges of the winter colony form a compact group surrounded by large areas of preferred habitat, so the group structures do not depend on differences in habitat.

An overwintering group differs from a breeding colony in two respects. In it, immatures of the previous breeding season and post-breeding individuals have the same status. Secondly, there is no difference in the behaviour of males and females, i.e. the home ranges are of roughly the same size and the animals behave territorially towards each other, irrespective of sex. The group observed in autumn 1968 comprised seven females and six males.

Breeding colonies. Before 1969 there were too few breeding individuals to permit detailed

observations on the breeding colonies. But the home ranges of the females were known to be in contact in some places (Figs. 7 and 8).

When a wintering colony becomes a breeding colony the greatest change is that the males extend their ranges (KALELA 1956, 1957). Even at this early stage they seem to become more aggressive towards each other. The change is difficult to study, because it occurs when the ground is still covered with snow. Snap-trapping data indicate that in most years the change takes place in late March — early April.

In spring 1969, most of the males of the first litters matured immediately. In July, when trapping became effective, there were 23 males on the study plot, 8 of them dominant and 15 subordinate. Some of the latter were presumably dominants with the main part of their home ranges outside the plot. Four of the males had overwintered. Two of these were clearly dominant; one was a subordinate (hind leg broken) and one was caught only in marginal sites (trappability only 40—50 %), presumably a dominant whose home range lay mainly outside the study plot.

Figs. 10A and 10B show the home ranges of four dominant males of the same breeding colony in summer 1969. In the middle of the study plot, which was presumably the centre of the breeding colony, the home ranges of the dominant males overlapped greatly. Around this centre every male defended his own sector as a territory. These territories remained in
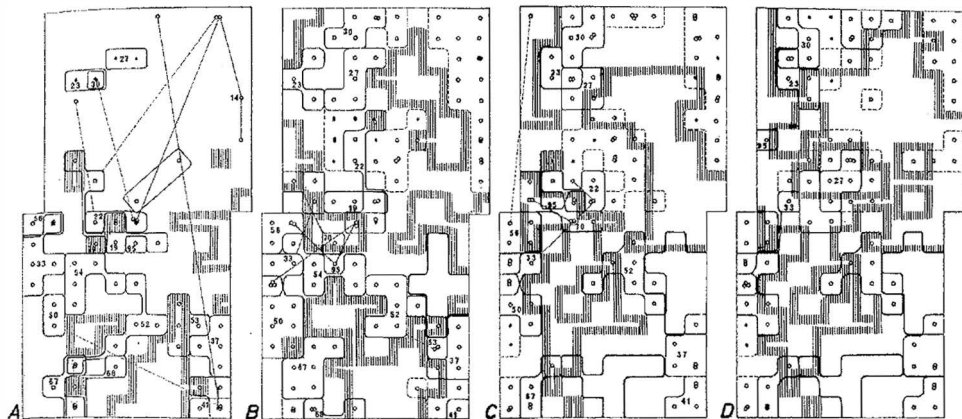
Fig. 9. Captures of breeding *C. rufocanus* females in early July (A), late July (B), early August (C) and late August (D) 1969. The home ranges are presented individually only for specimens marked in early July. The area inhabited by *M. agrestis* is surrounded by shading. Small dots in A are captures of four immature females which later matured.

nearly the same positions throughout the trapping season in 1969. The border where one breeding colony came in contact with another could easily be recognized from the movements of the dominant males, as there was almost no overlap.

To study the reasons for dominance hierarchies and partial territoriality, efforts were made to investigate the behaviour of the animals in the "Ugglan" traps, which can trap more than one individual (Table 6). When two animals were found in a trap simultaneously, their encounter was recorded as aggressive if fighting was seen, if one or both animals were bleeding, or if aggressive squeaking was heard. Otherwise, the encounter was classified as a peaceful contact. In aggressive encounters the loser was usually hiding under the flap door of the trap, and the winner patrolling in front of it. Every encounter between males was aggressive, and the same was true of the 10 further encounters in which one partner was *C. rutilus*. If two neighbouring females entered the trap (contacts between *C. rufocanus* with *C. rutilus* included), all contacts were peaceful. The traps used had become accepted as part of the normal environment of the animals, i.e. the traps were opened for 14—16 h per day, and the animals were then able to run through them. Individuals of *C. rufocanus* often used them as feeding shelters and left

heaps of *Vaccinium myrtillus* stems in them. Therefore the behaviour of the animals is believed to be comparable with their behaviour elsewhere in the area.
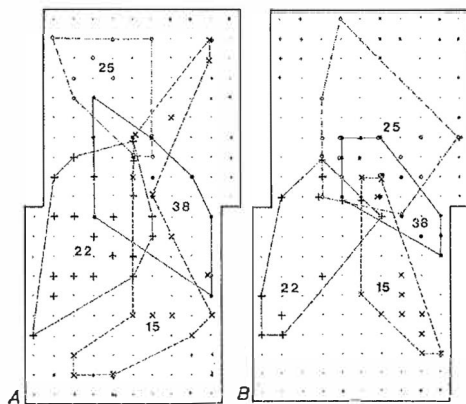

Fig. 10. Captures of dominant males of *C. rufocanus* in July (A) and August (B) 1969. The outlined areas belong to individuals (indicated by their serial numbers) of the same breeding colony. In addition, capture sites of other dominant males on the margins of the plot are indicated. Captures of sixteen subordinate males which lived on the study plot in July are excluded. The outlined avas belong to individuals (indicated by their serial numbers) of the same breeding colvny.

The aggressive behaviour of the males presumably explains their partial territoriality and the dominance hierarchies. It is not known whether the dominant males prevent the subordinates from mating. During oestrus runs two or three males were seen pursuing a female in oestrus, but none of the pursuers were ever identified.

The breeding colony of *C. rufocanus* is based on the territories of the breeding females. During the high densities of 1969 and 1970 mature females were far more numerous than mature dominant males, and in mid- and late summer they outnumbered all the mature males. In the breeding colony mentioned above, there were four dominant males throughout the trapping season in 1969, with 14 mature females in early July, 22 in late July and 16 in late August. These females were dominant to the males, which seemed incapable of retaliating when attacked by females (personal

Table 6. Double catches in "Ugglan special" traps in 1969 and 1970. m = males, f = females, i = immatures. *C.r.* = *C. rufocanus*, *M.* = *M. agrestis*, *C. rut.* = *C. rutilus*.

Species	ff	mf	mm	fi	mi	ii	Total
C.r. + C.r.	3	15	5[2]	21	6	38	84
C.r. + M.	0	0	0	0	0	0	0
C.r. + C.rut.	5	2	5[2]	5[1]	3[1]	0	20
M. + M.	1	7	2[2]	1	0	8	19
Total	9	23	12[2]	27[1]	9[1]	42	123

[1] = interindividual aggression occasionally observed,
[2] = fighting took place in every case.

Table 7. Overlapping of female home ranges in *C. rufocanus* and in *M. agrestis* in July and August 1969. Common = number of trap stations visited by two or more conspecific females, single = number of trap stations visited by only one female.

	Clethrionomys			*Microtus*			
	common	single	sum	common	single	sum	χ^2
July	20	86	106	23	31	54	10.246[1]
August	22	61	83	18	64	82	0.466
Sum	42	147	189	41	95	136	
χ^2		1.571			6.587[2]		

[1] P < 0.01 (near 0.001).
[2] P < 0.025

observations in 1974). This agrees with the behaviour seen by BUJALSKA & GLIWICZ (1972) in *Clethrionomys glareolus*.

The female territoriality and overlapping of home ranges in 1969 is presented in Table 7. The home range is the whole area in which an animal regularly moves and the territory is the area it "defends" against conspecifics of the same sex (BURT 1943). When examining the table one must keep in mind that the CMR method gives only a very rough picture of the movements of an individual. If a trap was on the borderline between two home ranges, these were recorded as "overlapping". The overlapping observed was concluded to be correlated with the actual overlapping. Table 7 and Fig. 9 suggest that in *C. rufocanus* females the home ranges are larger than the territories (cf. BURT 1943). The apparently increasing overlap of the home ranges during the trapping season in 1969 was not statistically significant; presumably it was due to the increasing trappability of the summer-born mature females.

If fighting does occur between females, it does not play the same role as in males. The factors involved in female territoriality will be discussed below (p. 71).

Immatures of *C. rufocanus* seem to move unchallenged over the whole area of the breeding colony and attach themselves to other litters. In the fighting sometimes observed between immature *C. rutilus* and mature *C. rufocanus* the former appeared to be the attacker.

B. Microtus agrestis

The promiscuous groups. It was not possible to study the establishment of the wintering colonies of *M. agrestis*. The bulk of the population of summer 1969 immigrated to the study plot just after the last trapping period in late September 1968. In 1968 only four individuals were caught, one male, one female and two immatures (Fig. 8). According to MYLLYMÄKI (1970), and to my unpublished observations, this species is characterized by winter migration. The capture sites and home ranges of *M. agrestis* individuals are shown in Figs. 11—14.

During summer 1969 a marked change took place in the social structure. In early July the population of *M. agrestis* on the study plot was a promiscuous group consisting of 9 mature males (2 of them overwinterers) and 11 breeding

females (4 of them overwinterers, the 7 others young primigravidae, Fig. 11).

The males seemed to move over the whole area inhabited by the females, without any sign of territorial behaviour. The area of the group lay partly outside the plot. Of the males, four were dominant (trappability 63 %) and five subordinate (30 %).

The home ranges of the overwintered females were in contact but did not overlap. The other four overwintered females living in the plot were also strictly territorial (Fig. 11).

The visibly pregnant young females moved freely, like the immatures, both on each other's home ranges and on those of the old territorial females. The non-territoriality of these young females was responsible for the value of 43 % for trap stations on areas simultaneously inhabited by two or more mature females.

Towards late July the group behaviour of the young mature females weakened, the range of the group expanded (Fig. 12), and the overlapping of the individual areas diminished. In late July two of these females had independent home ranges, whilst the others had their first litters on the home ranges where they were first caught. However, overlapping of female ranges was still seen throughout the breeding season, and was greatest in the females that matured latest.

Territorial males. Towards late July 1969 more immigrant females arrived, and many males extended their home ranges (Figs. 11 and 12). One of the dominant males (no. 48) already had a home range which later became a true territory (Fig. 12). This male attained dominant trappability on shifting to a separate home range. The dominant males on the group range
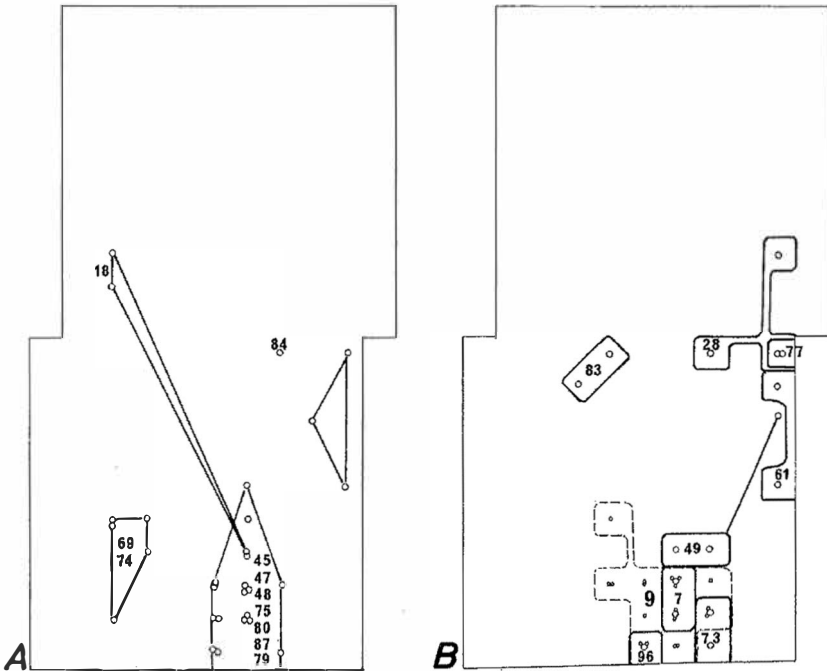

Fig. 11. Captures of male (A) and female (B) individuals of *M. agrestis* in early July 1969. Large circles in B denote old (mostly overwintered) females weighing at least 45 g, small circles young, newly matured females. The large numeral indicates the number of young females on a common home range. Erratum: In B, for 9 read 7, and for 7 read 9,
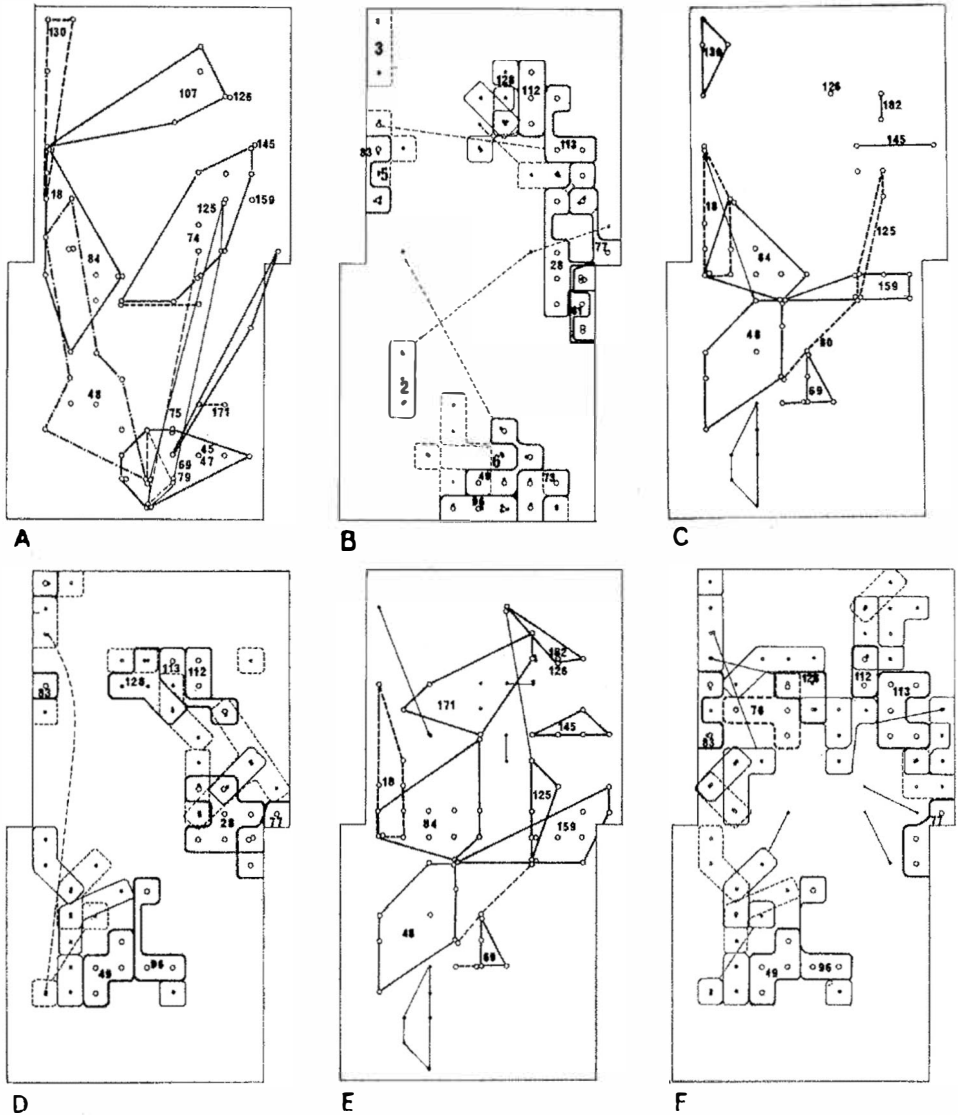
Fig. 12. Captures of male (A, C, E) and female (B, D, F) individuals of *M. agrestis* in late July (A, B), and early (C, D) and late (E, F) August 1969. Captures of two immature females (F) indicated with small dot sconnected by a line. Other symbols as in Fig. 11. Serial numbers of old females and breeding males captured in two or more consecutive trapping periods are indicated.
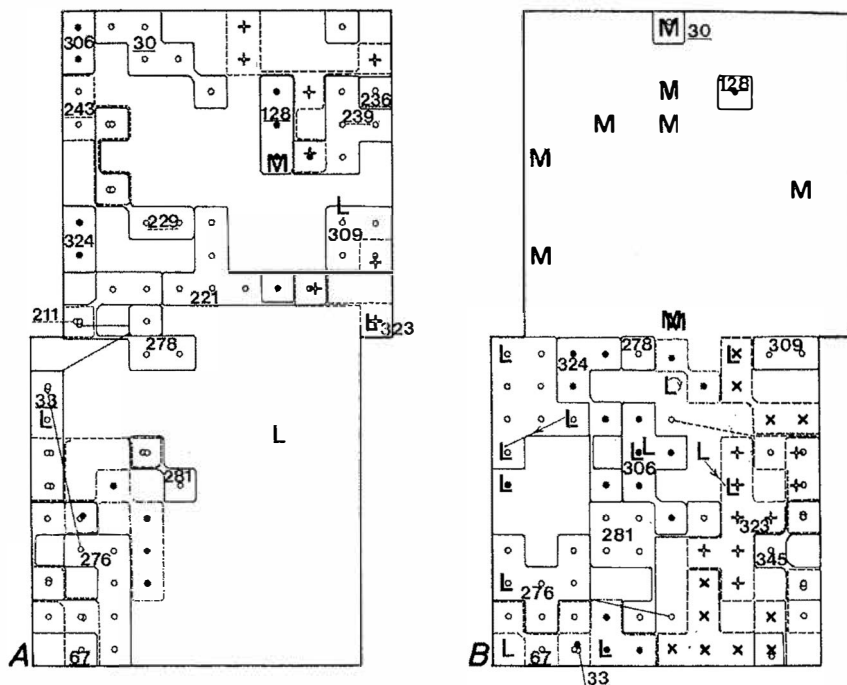
Fig. 13. Capture points of females of *C. rufocanus* and *M. agrestis* in June (A) and July (B) 1970. The capture points of *M. oeconomus* (×), *C. rutilus* (+), *Lemmus lemmus* (L) and *Mustela rixosa* (M) (removed) are included. Open circle = *C. rufocanus*, solid circle = *M. agrestis*.

were nos. 45, 69 and 75 (Figs. 11 and 12). Extensions of the home range presumably preceded the change from the group range to individual home ranges. Most of the immigrant males arriving in late July also established individual territories, but their home ranges overlapped to some extent (males nos. 18 and 84, and 125 and 159; cf. Fig. 12), partly because these were still unsettled. However, territorial behaviour increased as more immigrants arrived on the study plot. Ultimately, the breeding colony disintegrated and most individuals were forced to move away. This was due to an invasion of *M. oeconomus* to the meadow forest in the lower part of the plot in late July — early August. After this move the behaviour of the remaining males changed to strict territoriality (with the exceptions mentioned above) (Fig. 12). Partially territorial males

may exhibit a group formation comparable to that of *C. rufocanus* males.

The territoriality of the males obviously resulted from heightened aggressiveness. In early July only a few males had wounds and scars, whereas in August they all bore signs of fighting. In this respect they clearly differed from males of *C. rufocanus*. These fights show that in *M. agrestis* the dominance hierarchy is unstable, possibly because the males have to fight for territory.

The dispersal of the breeding colony did not greatly affect the behaviour of the females. In early August two groups of females could be distinguished, one with eight and the other with ten members (Fig. 12D); a third group extended into the plot. In August the area of the group in one portion of the study plot had nearly fused with that of the other groups
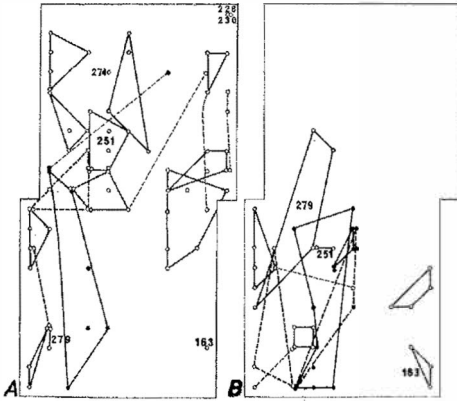
Fig. 14. Capture points of males of *C. rufocanus* and *M. agrestis* in June (A) and July 1970 (B).

(Fig. 12F). By then, in contrast to July, the males formed a system of separate territories.

Five female and three male *M. agrestis* in breeding condition were still living on the study plot in July 1970 (Figs. 13 and 14). The males moved from one female to another, showing no sign of territorial behaviour. Thus it appears that in mature *M. agrestis* males promiscuity is a common feature of behaviour in the study area.

3. Regulation of breeding

If an animal species has a high reproductive capacity, it is important that the reproduction and population density are regulated so that there is no overexploitation of resources (KALELA 1954, 1957). One regulatory mechanism maintaining the balance is territorial behaviour (KALELA 1954), and another is subadult behaviour leading to emigration (MYLLYMÄKI 1970). Such regulation was described in *C. glareolus* females by BUJALSKA (1970, 1971) and in *Mus musculus* males by VANDENBERGH (1971). The existence of such regulation in *C. rufocanus* was shown long ago by KALELA (1957).

A. Females

In 1967 and 1968, when density was low, the

only factor inhibiting breeding was the seasonal change in weather conditions, which acted either directly or indirectly by affecting nutrition (TAST & KALELA 1971). During the breeding season from mid-May to mid-September, young of both species were able to reach maturity.

C. rufocanus. In 1967 two young females of *C. rufocanus* became pregnant in late August — early September and each gave birth to its first and only litter in mid-September, and in 1968 one of two females that matured in late August littered in mid-September. Eleven females still immature in late August 1968 were newly weaned individuals weighing less than 20 g. A female may give birth to her first litter when only 40 days old. The high fecundity rate indicates great reproductive potential. In 1968 this caused almost exponential growth of the population, which increased by more than 15-fold. In 1969, when the population density was high, the increase was only 2.5-fold, although survival was good (cf. p. 88). In accordance with KALELA (1957), I believe this to be due to a regulatory system within the population. An endeavour is made here to demonstrate that this regulation is brought about by limitation of the number of breeding animals per unit area. One would expect territorial behaviour to play a significant role. But the mechanism appeared to be different
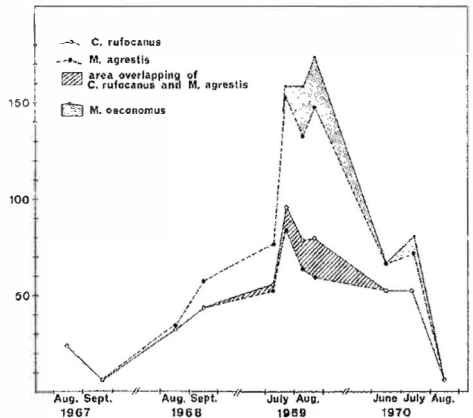

Fig. 15. Areas inhabited by *C. rufocanus*, *M. agrestis* and *M. oeconomus* on the study plot during the CMR trapping. Trap stations occupied by breeding females or immatures have been regarded as inhabited.

in *C. rufocanus* and *M. agrestis*. Breeding may also depend on other factors, which are at least partly independent of density, but these factors do not form part of the "self-regulatory system" of the population. For breeding *C. rufocanus* females the smallest possible home range size seems to be about 300 m², i.e. less than 35 individuals per ha. Most, if not all, of the study plot was inhabited in late July 1969 (Figs. 9B and 15); the part that appears to be uninhabited was used by *C. rutilus*, and probably by *C. rufocanus* too, but the trapping period was short. Although immature females usually mature straight after weaning, none of them were observed to attain sexual maturity after 20 July. The larger snap-trapping samples confirm this; the youngest pregnant females were about 20 days old. By early July most breeding females were summer-born.

An attempt was made to study the mechanism inhibiting maturation. In the lower right corner of Fig. 9A two capture points of an immature female are marked with small circles in contact. About a week later the same specimen (by then mature, possibly pregnant) visited the upper edge of the plot. The immature females nos. 23, 27 and 30 at first lived in a loose group (Fig. 9A), but dispersed to independent home ranges (presumably true territories) when they matured (Fig. 9B).

Since in both species studied aggression plays an insignificant part in the territorial behaviour of the females, I suppose that an avoidance reaction is involved, i.e. the animals avoid areas marked by conspecifics of the same sex. Maintenance of a territory thus seems to depend on a reaction exhibited by the intruding individual rather than on active defence.

This view is supported by the mutual attraction and group formation observed (p. 64), by the behaviour of young pregnant *M. agrestis* females (p. 67), and by some unpublished observations on *C. rutilus* which show that avoidance of other individuals and avoidance of their marked territories are not necessarily correlated. However, this view requires confirmation.

The territorial avoidance reaction implies the existence of pheromones (MUGFORD & NOWELL 1970, EISENBERG & KLEIMAN 1972). In *C. rufocanus* the reaction appears in prepuberty; this is important if it is to result in population regulation. When there is no space for new territories, maturation may be arrested

by a physiological mechanism (CHRISTIAN 1955, 1963, CHRISTIAN *et al.* 1965). When there is enough space, prepuberty is followed by maturation, with hardly any time gap, except in the winter territories. In late September 1968, for example, when density was low, such genital activation was observed in juvenile males; their testes descended to the scrotal position and grew to almost full size.

This phenomenon resembles the autumnal mating display and territorial behaviour of many species of birds (KALELA 1958, 1973). If no space is available for new territories at the time when the territorial avoidance reaction is developing, *C. rufocanus* females do not mature. However, they still try to establish individual home ranges. This subadult behaviour (MYLLYMÄKI 1970) makes them "landless and homeless" wanderers which disappear from the study plot (cf. p. 79). Fig. 9A shows that a female was successful in finding a range
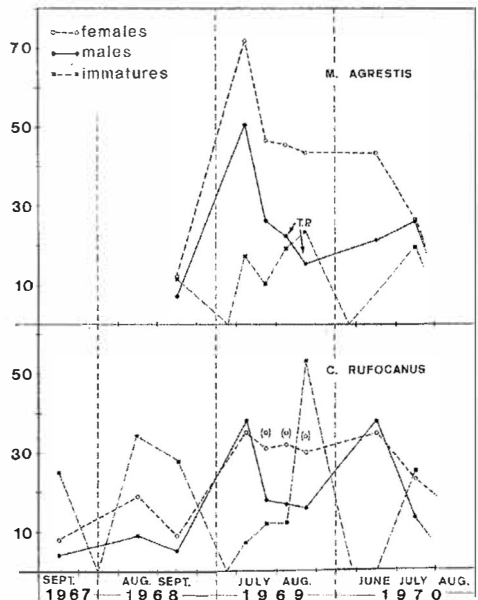

Fig. 16. Numbers in different reproductive categories within the areas inhabited (Fig. 15). T.P. = territorial phase. Circles in brackets = all females included; otherwise sedentary animals only. Edge effect was not taken into account, because the male home ranges could not be estimated.

when she moved more than 200 m from her first site. The trends in the home range size of the females (Fig. 6), the stability of the overlapping of these ranges (Table 7), and the densities of the different reproductive categories (Fig. 16) show beyond doubt that *C. rufocanus* females do exhibit territorial behaviour.

M. agrestis. In *M. agrestis* the young pregnant females did not behave territorially. In contrast to *C. rufocanus*, the young females attained sexual maturity even if the habitable area was crowded. In 1969, between 20 July and 10 August, 14 immature *M. agrestis* females attained maturity, but none of the immature *C. rufocanus* females did so (Tables 8 and 9).

In young *M. agrestis* females territorial behaviour developed in late July and in August (Table 7, Fig. 16), i.e. several weeks after maturation. If no space was available for individual home ranges, the females dispersed for considerable distances. Thus the density of breeding females in this species is mainly regulated not by a physiological mechanism, but by dispersal. However, it is also possible that, under certain conditions, physiological regulation induced by social factors is involved. In both 1967 and 1968 (years of low density) at least one female *M. agrestis* matured in late August — early September and had its first litter in mid-September. In 1969 (a peak year) the last summer-born females to mature were marked in early August and had their first litters at the end of August, i.e. more than 2 weeks earlier. These differences are correlated with the change in social structure, but the possibility is not ruled out that factors other than social may also be involved (cf. p. 75).

B. Males

In both species studied, the regulatory systems were similar to, but different from, those of the females. In the breeding males two phases were observed. The first was a probably hormonal mechanism blocking the attainment of maturity, as in *C. rufocanus* females, and probably released by aggression. The great mobility of the dominant males affects the juvenile males, which have much less opportunity to mature than the females. For this reason the proportion of immatures rose much earlier among the males than among the females

Table 8. *C. rufocanus* and *M. agrestis* males and females born in summer 1969 classed as immatures and individuals which attained sexual maturity during their season of birth. The table includes all animals born before the end of July. The data are based on the CMR sample.

	Clethrionomys				Microtus		
	♂	♀	sum	χ^2	♂	♀	sum
Matures	19	27	46	1.034	16	35	51
Immatures	32	25	57	4.678[1]	26	7	33
Total	51	52	103		42	42	84
χ^2		2.221				18.018[2]	

[1] $P < 0.05$
[2] $P < 0.001$

Table 9. Sex ratios of the samples in which the animals remained immature during their season of birth.

Date of marking	Clethrionomys			Microtus		
	♂	♀	sum	♂	♀	sum
3 July — 8 Aug.	11	4	15	13	0	13
12 — 23 Aug.	21	21	42	13	7	20
Total	32	25	57	26	7	33

(Kalela 1971). In 1969, the last maturing males of both species were recorded in very early July (Tables 8 and 9). In *M. agrestis* a significantly greater number of males than of females remained immature during their season of birth. Kalela (1957) observed the same difference in *C. rufocanus*, but in the present sample the difference was not significant.

In the *C. rufocanus* males born in late June 1969 the testes were already visible in living animals in late July (cf. Kalela 1957: 30), and at the same time trappability increased. This was the prepuberty phase, like that described for the females. At this stage the dominant males apparently recognised the young as males and attacked them. This may have caused a hormonal response which blocked the attainment of full maturity. In some males descensus occurred twice within a few days, but finally they remained immature and in most cases disappeared from the study plot as a result of subadult behaviour. This was confirmed by the snap-trapping sample (p. 80).

If such regulation came too late, i.e. if there were too few overwintered males in spring,

almost all the males of the first litters matured immediately after weaning. Then the population included more mature males than could attain dominant status. A dominance hierarchy was established, and subordinate males dispersed to unoccupied areas (cf. p. 80). In males of both species and in *M. agrestis* females similar trends were seen during the study period of 1969 (Fig. 16). The initially overdense population thinned out towards optimum level because of dispersal, brought about by aggressiveness in old males, but by a territorial avoidance reaction in young females.

M. agrestis males became territorial if mutually unfamiliar and intolerant males were forced to live as neighbours. Territoriality thinned their density more effectively than the dominance hierarchy (Fig. 16).

In June 1970 the study plot was occupied by 18 *C. rufocanus* males, 7 of them dominant. In this situation, when all the males were overwintered animals of about equal size, they exhibited territoriality but, in spite of this, some degree of group formation could be observed (Fig. 14A). None of the summer-born animals were seen to attain sexual maturity (cf. p. 82).

4. Discussion

Territorial behaviour. In the males of both species studied, territorial behaviour appears to be due to mutual aggression, as in many other rodent species. e.g. *Lemmus lemmus* (ARVOLA *et al.* 1962) *Microtus oeconomus* (TAST 1966) and *M. agrestis* (MYLLYMÄKI 1970, KOPONEN 1972). The existence of groups displaying little or no territorial behaviour may be due to individual differences in aggressiveness (cf. harmful versus harmless fighting; EIBL-EIBESFELDT 1958).

Females show specific differences in territorial mechanisms. *Lemmus lemmus* is aggressive after the establishment of territories in a pen (ARVOLA *et al.* 1962), but under similar conditions *Myopus schisticolor* females show no sign of aggressiveness, although they are strictly territorial (ILMÉN & LAHTI 1968). Correspondingly, HEALEY (1967) observed that in *Peromyscus maniculatus* territorial behaviour involved no aggression. Possibly, however, short-term experiments cannot explain all specific behaviour patterns; in *M. agrestis*, for example, the social structure of the population seems to be largely determined by mutual socializing processes

during immaturity (WILSON 1973). Both *Myopus* and *Peromyscus* show the behaviour pattern concluded to be present in the females of *C. rufocanus* and *M. agrestis*, i.e. strict territorial behaviour without mutual aggression.

Population structure. The clan structure characterizes the populations of many other rodents, e.g. *C. glareolus* (CORBET 1963), *Cryptomys hottentottus* (GENELLY 1965) and *Microtus californicus* (PEARSON 1960, BATZLI 1968). Information about the structure of such groups has been presented by FRANK (1953, 1954) on *M. arvalis*, by GODFREY (1954) and REICHSTEIN (1959) on *M. agrestis*, by KALELA (1956, 1957) on *C. rufocanus*, by GETZ (1961a, 1972) on *M. pennsylvanicus*, by TAST (1966) on *M. oeconomus* and by HEALEY (1967) on *Peromyscus maniculatus* (for Muridae see e.g. STEINIGER 1950, CALHOUN 1956, 1963a, ANDERSON 1964, 1965, 1970).

The group structure described for *C. rufocanus* and *M. agrestis* results from two opposing tendencies, territorial behaviour and group attraction (KALELA 1956). During the present study the latter was evident from the patchy distribution of individual home ranges in years of low or moderate density. In 1969 even the immigrant *M. agrestis* females settled down as near the former inhabitants of the study plot as possible. The same is true of several avian and mammalian species (KALELA 1954, 1956), i.e. even mutually unfamiliar individuals group together for reasons other than the structure of the habitat. The groups are to some extent true clans, i.e. partial or total lack of territorial behaviour and seeking of contacts with conspecifics is shown by individuals descended from the same female (CROWCROFT &. ROWE 1957, 1963, ROWE & REDFERN 1969). But in *C. rufocanus* it seems to be enough if the animals learn to know each other when immature. In *M. agrestis* females the development of sociability and territorial behaviour in a breeding colony showed that the sociability was a direct continuation of that acquired during the immature stage. WILSON (1973) showed that play is important in the development of social contacts between juveniles that learn to recognize each other as individuals. In this learning process, pheromones play an important role. According to ROPARZ (1966), colonies of *Mus musculus* have a special group odour which permits recognition of group mates. WILSON (1973), however, observed only

individual odours. According to FRANK (1954), juveniles of *M. arvalis* were attacked immediately and even killed when they entered the area of a foreign breeding colony, i.e. juveniles are accepted by their own colony because of the odour they share with their mother. On the whole, the groups of *M. arvalis* observed by FRANK (1953, 1954) resembled those of *M. agrestis* of the present study; however, groups of mature females with a common home range persisted longer in *M. arvalis* than in *M. agrestis*. Previous views on the social structure of the *M. agrestis* populations are apparently conflicting. GODFREY (1954) and REICHSTEIN (1959) described group structures like those observed in the present study. But MYLLYMÄKI (1970) found that the males were strictly territorial, while the females lived in loose groups with partially overlapping home ranges. KOPONEN (1972) observed that mature males and old females were both strictly territorial, whereas young breeding females were weakly territorial. Neither of the last-mentioned writers observed any sign of promiscuous groups.

During the present study, observations were made which seem to explain these contradictory results. During summer 1969 the structure of the *M. agrestis* population changed from a group to one composed of highly territorial males and females whose territorial behaviour may possibly have been strengthened by increased immigration which confused the former group structure (VIITALA 1975).

Thus, promiscuous groups of *M. agrestis* are formed in habitats and places where the population settles for at least one winter. The groups of immatures keep together then and, on attaining maturity in spring, continue to be mutually sociable. This population structure is characteristic of stable habitats (FENYUK 1937).

In a population established after or augmented by immigration the members are intolerant because they were not welded into a group by the mutually socializing process (WILSON 1973) when immature. Hence they are not accepted as members of the group; territoriality then increases and social groups cannot be formed. This population structure is characteristic of unstable habitats (FENYUK 1937). Habitat also affects social structure in populations of some desert rodents (EISENBERG 1967).

The absence or at least rarity of promiscuous groups in populations of *M. agrestis* in southern Finland may be due to the different type of environment, i.e. larger continuous meadow and field areas with nothing to prevent these groups from merging and so disappearing. It is not known, however, why groups of *C. rufocanus* on wide continuous habitats do not disperse. Another possible explanation would be an inherent racial difference in behaviour between populations of *M. agrestis*. Such differences are known in populations and races of *Mus musculus* (CALHOUN 1956, REIMOV *et al.* 1968). As a group structure has been observed in *M. agrestis* in forests, and a territorial structure on open grasslands, the first alternative seems to be more likely. TAST (1968b) observed that in Kilpisjärvi, Finnish Lapland, habitats suitable for *M. agrestis* were scattered, forming small patches in an otherwise unfavourable environment.

GEBCZYNSKI (1969) observed that immatures of *C. glareolus* had a common home range and rested in a common nest. Social heat conservation was suggested to be important in winter. In a wintering colony of *C. rufocanus* inspected in autumn 1968 such heat conservation was out of the question, because the animals were all territorial. Such different overwintering behaviour in these nearly related species may be an adaption to different environments. The winter food available after the short arctic summer is in short supply (KALELA 1962), but perhaps of better quality than at lower latitudes (RAATIKAINEN & RAATIKAINEN 1975). With this smaller supply of food the animals must survive through a winter twice as long as in Central Europe. Territorial behaviour may then prevent food shortage. Secondly, in the birch woods of the Kilpisjärvi region *C. rufocanus* lives under a thick permanent snow cover in winter, whereas in Central Europe the snow cover is thin and inconstant, and the need for social heat conservation may be greater. Another factor is that *C. rufocanus* is better adapted to cold than *C. glareolus* (PEARSON 1962).

Regulation of population growth. In many rodent species population size is regulated by increased dispersal. The migrants are usually young maturing animals (TAST 1966, WATTS 1969, MYERS & KREBS 1971, and this is the mechanism in *M. oeconomus*, even though the females produce every litter on a different home range, leaving the previous one to

the young (TAST 1966). In *C. rufocanus*, in contrast, maturation is regulated by a hormonal mechanism of the type described by CHRISTIAN (1955, 1963) and CHRISTIAN *et al.* (1965); a similar mechanism has been suggested for females of *C. glareolus* (BUJALSKA 1970, 1971), for *Peromyscus maniculatus* (TERMAN 1968) and for males of *Mus musculus* (VANDENBERGH 1971). ●nly the data for *C. rufocanus* and *C. glareolus* concern wild populations. A hormonal mechanism may also have been involved in the case reported by CROWCROFT & ROWE (1958), in which overcrowding caused cessation of breeding in a laboratory population of *Mus musculus*, for pheromones probably suppress oestrus (MUGFORD & NOWELL 1970). Territorial pheromones may have the same effect in *Clethrionomys*, but conclusive evidence is still lacking.

In males of *C. rufocanus* and *M. agrestis* numbers are regulated at two phases. The first step is physiological blocking of maturation, the next dispersal of subadults and subordinates caused by dominance hierarchies or territorial behaviour of mature males.

In females of *C. rufocanus* territorial behaviour developed in prepuberty, whereas in *M. agrestis* it appeared long after the first copulation. The frustration resulting from the territorial avoidance reaction with resultant blocking of maturation which is the system of regulation in *C. rufocanus* is replaced in *M. agrestis* by migration of mature individuals.

In *M. agrestis* maturation ceased in 1969 about 2 weeks earlier than in the two previous years. This occurred at a time when the group structure of the population was changing to a territorial, i.e. immigrant type, structure. FRANK's (1954) results on *M. arvalis* suggest that the factor evoking the hormonal response may be aggressive behaviour of mature females towards juveniles. This will ●ccur only in encounters between strangers. If such a mechanism exists in *M. agrestis*, the aggressive activity would be due to a change in the structure rather than in the density of the population.

The two-phase regulatory system of the males is highly effective. Hence, at high population density the number of breeding females was many times greater than that of mature males in both species. This significant phenomenon has been reported in other rodent species by STEIN (1952), FRANK (1953, 1954), KALELA (1957, 1971), ANDERSON (1965, 1970)

and MYLLYMÄKI (1969a and 1969b, 1970). In *Myopus schisticolor* the sex ratio is regulated by a genetic mechanism, i.e., when density is low or decreasing the sex ratio is almost balanced, but when density is high about three times as many females as males are born (SKARÉN 1963, KALELA & OKSALA 1966).

In his enclosure experiments on *Rattus norvegicus*, CALHOUN (1963a) observed that high-ranking rats formed breeding colonies with 2—3 males and a two- or three-fold number of females in breeding condition. The enclosures were also occupied by groups of mostly low-ranking males and a few females pushed away from their former groups and corresponding to the dispersing fraction in the wild (ANDERS●N 1970). In these low-ranking groups a female in oestrus had been forced into thousands of copulations with no time to rest or eat, the unbroken oestrus run causing a greatly decreased pregnancy rate. Only in the high-ranking groups with few males was breeding successful.

An uneven sex ratio during high density is thus advantageous, because a large number of mature males decreases the pregnancy and birth rates, and may increase the mortality of breeding females. As a by-product, more food is left for the surviving population. In the present study each breeding colony appeared to contain three or four dominant males in both species examined. In rats (CALHOUN 1963a) and mice (ANDERSON 1965, 1970) the colony consists of two or three males and about twice as many females.

In the peak year 1955 the breeding of *C. rufocanus* ceased in mid-August (KALELA 1957), and I observed the same during another peak year, 1964. During the peak year 1969 all habitable sites were occupied by late July, but breeding continued normally up to mid-September although the density had already reached the level of the previous peak years. Eleven out of 16 mature females were pregnant in late August. This means that all females were still breeding. Another difference is that in 1964 the density began to decline in late July — early August and continued until the population came near to extinction the following summer. The same was true in 1955 (KALELA 1957). In contrast, after the peak in summer 1969 density was still high in spring 1970 (cf. p. 88 and Fig. 24), the decline beginning early in summer 1970. KALELA (1962) and TAST & KALELA (1971) emphasized the relation between supplies of food and the densities of small rodent populations. They
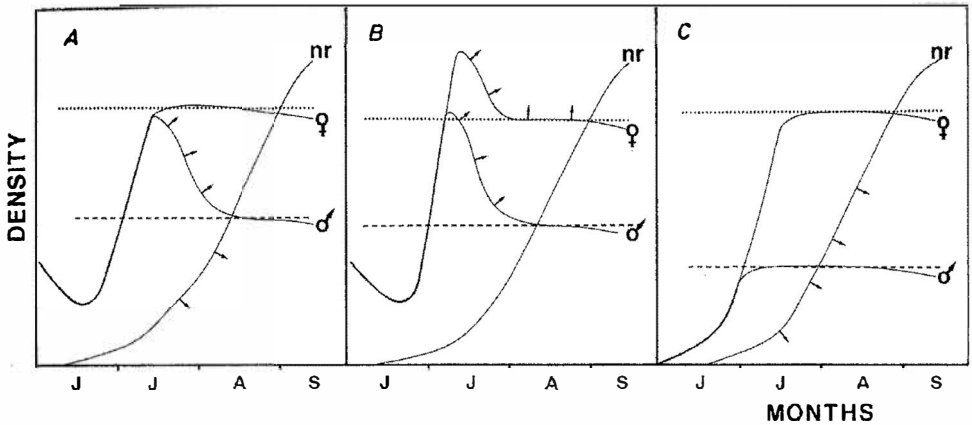
Jussi Viitala

Fig. 17, Population growth models in *C. rufocanus* and *M. agrestis*. The curves indicate relative numbers of the different reproductive categories. The horizontal lines indicate the maximum number of areas available for reproducing females (upper) and mature males (lower). The small arrows indicate the main migratory fractions. Further explanations in the text. (nr = nonreproductive immatures)

commented that 1969 was a year with abundant plant growth. Similar data were obtained by FLOWERDEW (1973) and ANDRZEJEWSKI (1975). The early cessation of breeding in some peak years may thus be only indirectly regulated by density, the basic factors probably being the joint effect of weather and population density upon the food resources. BUJALSKA (1970, 1971) observed that in late summer breeding decreased only in the youngest *C. glareolus* females, and thus the number of offspring remained fairly constant from year to year. Since young animals react more strongly to changing environmental conditions than older ones, this regulation may be only indirectly density-dependent (cf. p. 82).

My views on the self-regulation of the population are presented in Fig. 17, where only social factors are considered. Such a situation never exists in the wild, where other factors are always involved. The figure is restricted to the phase of population growth at which the self-regulatory mechanisms begin to operate, and it presents three different models.

Type A shows the situation in *C. rufocanus*. Density is assumed to be suboptimal at the beginning of the breeding season, i.e. space is available. Therefore all members of the first litters mature, and the result is a supraoptimal density of males. Immature males now begin

to accumulate in the population. Simultaneously, the dominance hierarchy reduces the male density. The self-regulatory mechanism prevents a supraoptimal density of breeding females. As soon as all the free space is inhabited, immature females begin to accumulate in the population. The time-lag between the cohorts that remain immature in males and females depends on the density at the start of the breeding season (KALELA 1957, 1971).

It is still uncertain whether a mechanism based on social factors alone could arrest or even slow down the breeding of *C. rufocanus* in the wild.

Type B in Fig. 17 shows the growth pattern of a sedentary population of *M. agrestis* established by individuals who have gone through the mutual socializing process (WILSON 1973); this process is involved in type A, too. In type B a group structure is established within the population, the density of breeding individuals becoming supraoptimal when the first litters attain sexual maturity. Migration caused by the developing dominance hierarchy (in males) or by the developing territorial avoidance reaction (in females) begins to reduce density towards the optimum. Males stop maturing immediately but, provided the group structure persists, females may continue to mature until breeding is prevented by shortage of food or

seasonal changes. Therefore immature females do not begin to accumulate in the population until very late in the breeding season. In a promiscuous group of *M. agrestis* the time-lag between the beginning of accumulation of immatures of different sexes is always longer than in *C. rufocanus*.

Type C shows the hypothetical growth pattern of an immigrant population of *M. agrestis*. Such a growth pattern was not observed; the type was reconstructed from observations made during a dense population phase. Only a small fraction of the males of the first litters attain sexual maturity, because the territorial males are highly aggressive. The maturation of the females may also be blocked early, because the whole area available is soon occupied; therefore immature females begin to accumulate as early as in *C. rufocanus*. This mechanism is produced by the aggressive behaviour pattern described by FRANK (1954) for *M. arvalis*.

Type B appears advantageous for species whose habitats are small patches surrounded by uninhabitable areas. A group produces many females in breeding condition, mostly pregnant when migrating to new home ranges.

Large size is an advantage to animals competing for space with other species, in this case with *C. rufocanus*. In the new area the first litters are born immediately after the establishment of the population, which is of type C. It may revert to type B, sending out mature emigrants, provided it survives through the winter.

According to TAST (1968b), the effective use of patchy habitats is vital for the survival of *M. agrestis* competing with the superior *M. oeconomus*, a species with almost identical habitat requirements. The significance of migration in *Lemmus lemmus* has been discussed by KALELA (1961), KALELA & KOPONEN (1971) and KALELA et al. (1971).

Types A and C are characteristic of dominant species occupying wide uniform habitats. The animals dispersing from such populations are small juveniles just attaining sexual maturity, as described by MYLLYMÄKI (1970) for *M. agrestis*. As most of the space around is habitable, there is no need for long-distance migration. But ultimately the separate groups must establish contact, and there will no longer be any free space. A regulatory system restricting the number of breeding individuals by a hormonal mechanism will then confer a definite advantage.

IV. Social organization and survival

Social status influences the survival of an individual and of a reproductive or social class (CHITTY & PHIPPS 1966, NEWSOME 1969a, 1968b, WILSON 1973). As the age structure corresponds roughly with the social structure of the population, the papers by ZEJDA (1961), GLIWICZ et al. (1968) and PETRUSEWICZ et al. (1971) illustrate the same point.

1. Methods

The CMR method. The results obtained with the aid of the calender of capture method (PETRUSEWICZ & ANDRZEJEWSKI 1962) are presented in Figs. 19 and 20 and in Tables 10, 11 and 14. As the study plot was not isolated by any barrier, losses caused by mortality and dispersion could not be distinguished. But in 1969 it was observed that the population may suffer significant losses by dispersion.

The lower trappability of immatures of *M. agrestis* caused difficulties. In a south-Finnish population of *M. agrestis* MYLLYMÄKI (1970) found that only about 50 % of the immatures could be trapped. Comparison

with data obtained for *C. rufocanus* suggests that a somewhat higher rate of trappability was possibly reached in the present study, perhaps owing to the different trap model. Members of all reproductive and social groups of *C. rufocanus* were captured satisfactorily by this method, except in early August 1969, when a spell of hot weather may have reduced trappability.

Age structure analysis. Age structure was analysed from snap-trapping samples taken in the Kilpisjärvi area in 196 1970 (Table 3). As these samples were collected from a large area and from different habitats, survival in all age groups may be assumed to depend mainly on mortality (for an exception, cf. p. 80). Therefore the differences between different social groups, years and seasons are taken to reflect differences in mortality.

The most reliable methods for age determination (DAPSON et al. 1968, OTERO & DAPSON 1972, DAPSON & IRLAND 1972) could not be employed. Age had to be determined from the growth and morphology of the second upper right molar or, if this had been destroyed, the left one. If both were lacking, the first lower molar was used. No significant differences were observed between the root lengths of the second upper and first lower molars (cf. TUPIKOVA et al. 1968, 1970).

The length of the entire tooth, the length of the cement layer in the tooth groove, and the length of the root
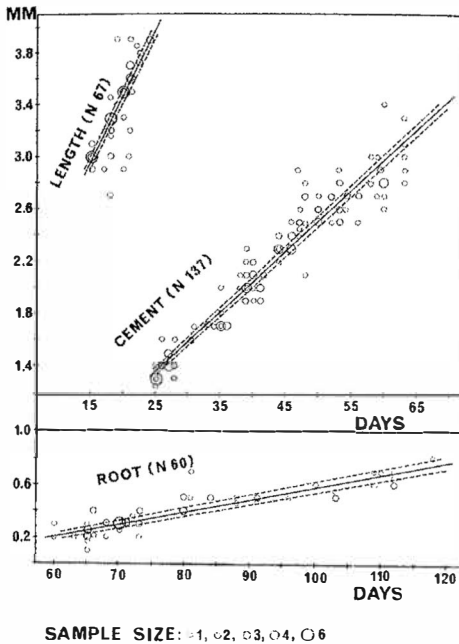
SAMPLE SIZE: ⊶1, ⊙2, ⊙3, ○4, ○6

Fig. 18. Growth of the second upper molar in individuals of *C. rufocanus* reared in captivity. Mean growth of entire tooth (in very young individuals), and that of the cement layer and root (with 5 % confidence limits) are presented. N = sample size.

were measured to the nearest 0.1 mm under a binocular fitted with an eyepiece micrometer. For measurement of the cement layer the tooth was cleft. The measurements made in this way were 0.2 mm longer than those presented previously (VIITALA 1971). Standard values were obtained from 318 reared specimens of known age. The age of 4 months was taken as the upper limit, because when the first cohort of summerborn animals reach this age the winter slows down tooth growth, and reduces the differences between cohorts.

In animals less than 25 days old the second upper molar grew from 2.96 mm at 15 days to 3.96 mm at 25 days (Fig. 18). In 87 % of the captive animals, age could be determined to within 2 days. The estimate could be confirmed by the slight wear and poor calcification of the tooth.

The cement layer grew from 1.55 mm at 25 days to 2.94 mm at 55 days. Neither the physiological condition of the animals nor external factors seemed to affect its growth. In 90 % of voles, age could be determined to the nearest ± 4 days. With this new method the cement layer gave useful information up to the age of 70 days.

In animals over 55 days old the most important criteria were the formation of the neck of the molar

and the growth of the root. At 50 days the tooth still had a thin layer of uncalcified bone at its base (VIITALA 1971, Fig. 4), but at 55 days even this layer was fully calcified, and the grooves in the tooth base were narrowing. When they closed early in the third month, growth of the root began. In the captive animals the mean growth of the second upper molar was 0.28 mm per month.

In 90 % of cases age could be determined to the nearest ± 10 days and in 97 % to the nearest ± 15 days.

No overwintering or overwintered specimens of *C. rufocanus* were available as standards. Nor could the mean growth of the root be estimated from the population means, because these were greatly affected by the different mortality of different age groups, and varied from 0.14 to 0.41 mm per month in different years. According to live trapping, the age structure did not change from August 1969 to mid-June 1970. Therefore the value calculated for early summer (0.26 mm per month) is the most reliable estimate for the mean growth of the molar root. It is the same as the mean calculated from the population means of different years (0.27 for males and 0.25 for females).

From mid-November 1969 to late March 1970 the mean increase in the length of the root was 0.11 mm per month. The value is reliable because during that time, according to live trapping, the age structure of the population did not change.

In different summers the differences between the extreme values remained about 1 mm all through the breeding season. Therefore individual variation is unlikely to have caused a major error in the age structure analysis. This agrees with LOWE's (1971) results obtained in *C. glareolus* with the aid of a vital colouring method. When age structure analysis was based on monthly mean values for molar root growth of 0.26 mm for summer and 0.11 mm for winter, the results corresponded well with those obtained by live trapping.

2. Survival of different age groups

As the CMR samples were too small to be reliable, supplementary information on age structure was obtained from line-trapping samples. However, the differences in the trappability of the social groups affected the results greatly; whereas breeding animals are trapped effectively throughout the season, the trappability of the immatures increases gradually until late autumn. Therefore the survival of immatures may be regarded as good if their numbers in the samples increase during the summer, and poor if they remain the same or diminish towards the winter. But this method cannot be used for quantitative comparisons.

The results obtained from the CMR samples are presented in Figs. 19 and 20 and in Tables 10, 13 and 14, and those from line trapping in Figs. 21 and 22 and in Tables 11 and 12. The data are examined in greater detail below.
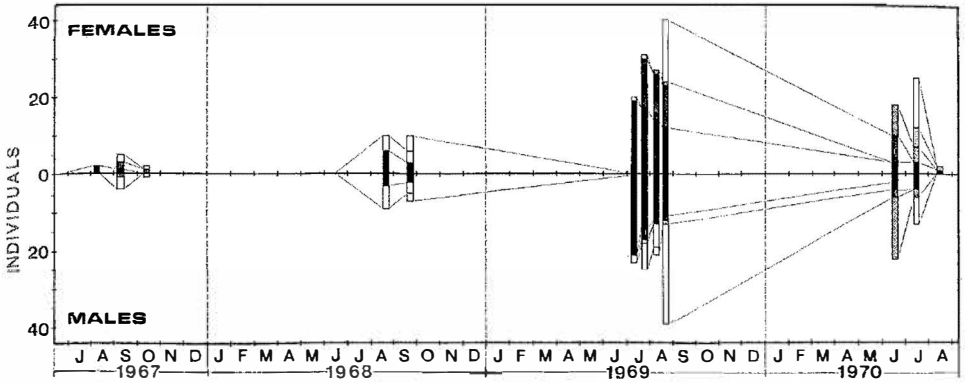
Fig. 19. Numbers and survival of *C. rufocanus* individuals marked at different times on the main study plot. Unshaded columnl denote immature specimens. Different types of shading denote animals in breeding condition marked at different times. Surviva of different groups is indicated by thin lines. Only sedentary animals are included.

A. Age structure in an increasing population

In 1968 and 1969, the numbers in the young age-groups increased (Fig. 21). In the CMR sample the survival of immatures marked in autumn 1968 was 64 % per month (Table 10), but in 1969 the value was only 13 %. Thus the results obtained with the two methods in 1969 appear inconsistent, but the low CMR value was due to dispersal of subadults in late July 1969. As the value for the survival of the immatures was always minimal, it was impossible to estimate whether or not they had a higher mortality than the breeding voles. In the latter, mortality appeared to be 20—25 % per month (Tables 10 and 11). The high apparent value
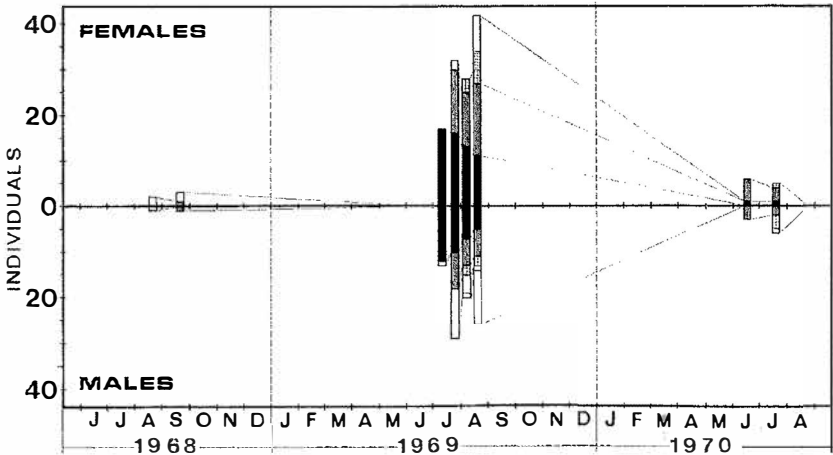

Fig. 20. Numbers and survival of *M. agrestis* individuals marked at different times on the main study plot. For explanations see Fig. 19.

Table 10. Mean monthly survival percentages of sedentary individuals on the main study plot in autumn 1967, in autumn 1968, in mid- and late summer 1969, in early summer 1970 (e), and in late summer 1970 (l). n = number of individuals marked.

C. rufocanus	1967		1968		1969		1970e		1970 l	
	n	%	n	%	n	%	n	%	n	%
Males	1	0	3	67	25	56	22	32	7	0
Females	4	50	6	50	31	78	18	40	8	25
Immatures	6	0	11	64	15	13	0	0	13	0
Total	11	18	20	60	58	69	40	35	28	7
M. agrestis	n	%	n	%	n	%	n	%	n	%
Males	0	0	1	100	20	65	6	67	5	0
Females	0	0	1	100	35	83	3	67	4	0
Immatures	0	0	1	0	12	0	0	0	1	0
Total	0	0	3	67	67	63	9	67	10	0

for males in 1969 (Table 10) was due to dispersal induced by the dominance hierarchy. In summer 1968 the value was low (Fig. 21), but as the population density was low, the sample was too small to be reliable.

During August 1969, when the population of *C. rufocanus* was still increasing, the survival pattern changed. In the overwintered animals survival was only 44 % per month (Table 11) and in those breeding in their season of birth only 29 % (Fig. 21). In the CMR sample the change was already visible in late July — early August, the monthly survival value for summer-born breeding animals being 66 % and for overwintered animals 87 %. From 3 July to 23 August only two out of nine overwintered animals disappeared; one of them was killed accidently during the trapping.

The change in the survival of the breeding age groups and the poor survival of all breeding animals in late summer 1969 were consequences of the heavy invasion of *M. agrestis* into the habitats formerly occupied by *C. rufocanus* (cf. p. 85).

In mature males, social status appeared to be more important than age or the dominance order of the species (p. 60). Of 15 *C. rufocanus* males marked in early July 1969 and classified as subordinates, only four were still on the study plot in late August. Three of them were captured in marginal traps only, and were thus probably really dominants living mainly outside the plot. The fourth was a heavy (50 g) overwintered male, with a broken leg which hampered its

movements and trappability. Thus in late August none of the remaining males could be classified as subordinate. Of the subordinates that disappeared two were recaptured on the plot in 1970. The importance of dispersal is revealed by the snap-trapping sample (Table 12), which shows that in August 1969 most of the mature June-born males were living in

Table 11. Mean monthly mortality percentages of overwintered individuals of *C. rufocanus* in three different years of high population density. The data are based on snap-trapping samples and are calculated from the density index values. n = total number of overwintered specimens captured.

	June	July	August	n
1964	26	68	76	249
1969	21	25	56	184
1970	70	60	78	172

Table 12. The sex ratios of summer-born individuals of *C. rufocanus* in August 1969 in optimal (vole trapping) and suboptimal (lemming trapping) habitats according to the snap-trapping data.

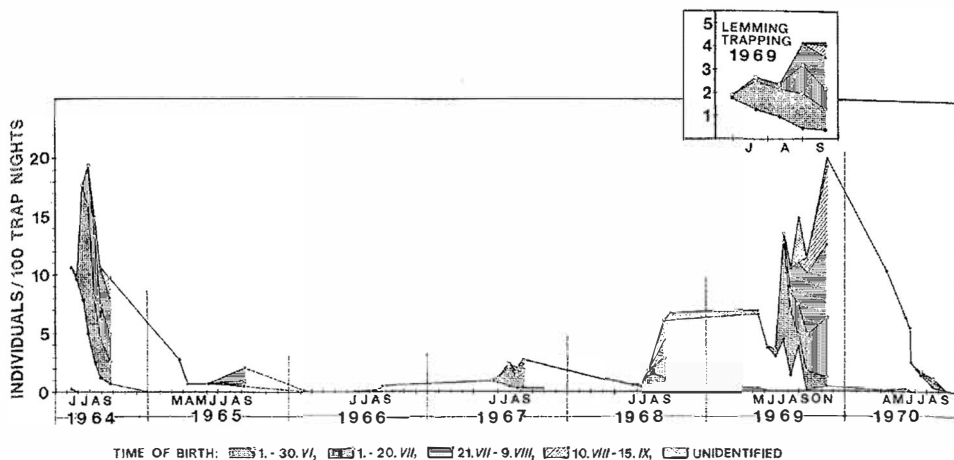| Habitat	No. of males	No. of females	Total
Optimal	5	18	23
Suboptimal	23	12	35
Total	28	30	58

$\chi^2 = 10.749$; $P < 0.01$ (near 0.001).

Fig. 21. Trends in age structure and population density of *C. rufocanus* in snap-trapping samples from 1964 to 1970. Different types of shading denote different cohorts of summer-born animals. Unshaded = overwintered specimens. Notice the different scale for the lemming trapping.

suboptimal habitats. This means that the youngest mature males are ousted from the habitats where they were born unless they achieve dominant status.

The mortality of sucklings may vary considerably during the breeding season (GLIWICZ *et al.* 1968, PETRUSEWICZ 1971) and also from year to year. The number of young born in a population can be calculated from a CMR sample (PETRUSEWICZ 1968). In 1969, survival was very high in *C. rufocanus* born in June, but not in those born in July (Table 13).

The value for young born in July may be too low, for trapping was discontinued early. The values for *M. agrestis* are certainly biased because of a heavy immigration into the plot

of mature animals born in June and because of the low trappability of the immatures born in July.

The survival of litters born in June could also be estimated from the snap-trapping sample. After maturation the trappability of these animals is high, so their numbers in the sample are comparable with those of overwintered animals. Assuming that by the end of June every overwintered female has borne one litter, the number of these old females at the end of June can be compared with the highest number of June-born animals observed in a July trapping period (Table 14). In 1967 the survival of the June cohort was almost as good as in the more favourable years 1968

Table 13. The survival of young from birth to trappable age (21 days) in summer 1969. The number of young born was calculated from the number of pregnant females, the duration of pregnancy and the mean litter size (PETRUSEWICZ 1968). Obs. = observed, % = percentage that survived.

	June			July			June + July		
	born	obs.	%	born	obs.	%	born	obs.	%
C. rufocanus	37	32	86.5	168	71	42.3	205	103	50.2
M. agrestis	37	33	89.2	171	51	29.9	208	84	42.4
Total	74	65	87.8	339	122	36.0	413	187	45.3

and 1969, and distinctly higher than in 1970. The value for 1964 is low because, in this year with high population density, many young did not attain sexual maturity during their season of birth and their trappability was consequently low.

The most characteristic feature of an increasing population was the rejuvenation, which could be seen even among the overwintered cohorts (Fig. 25). In samples snap-trapped in September 1968 and 1969 the proportion of animals born in July and August was more than 80 %. In 1964 this value was 73 %, in 1965 60 %, and in 1967 50 %. In 1970 it was not recorded owing to the rapid collapse of the population, but by November 1969 it had risen to 94 %. Because young animals are less easy to trap, the true values may be even higher. The November 1969 sample did not contain a single individual that was unquestionably born in September. Even in favourable years, the mortality of sucklings and weaned immatures seems to approach 100 % towards the end of the breeding season, so these litters have no effect on the population structure. The same conclusion is suggested by the age structure of overwintered *C. rufocanus*.

B. Age structure in a declining population

The age structure of a declining population is seen from the data for 1970, when numbers were decreasing more rapidly than in any other year of the present study. During this decline the age structure clearly reflected the great differences in survival between the different age groups.

Of the 113 young born on the study plot, only 13 attained trappable age, i.e. survival of sucklings was 11.5 %. None of the 13 juveniles survived a whole month. The snap-trapping sample also indicates a very high rate of juvenile mortality (Fig. 21). The snap-trapping value for suckling survival (8 %, Table 14) is biased, because none of the summer-born animals attained maturity. Therefore all through the breeding season the population consisted largely of overwintered specimens.

The mortality of the overwintered animals was about three times that of 1969 (Table 11), but great differences were observed between different cohorts. In June 1970 the study plot was occupied by 16 individuals of *C.*

Table 14. The survival of the sucklings of first litters of the year in *C. rufocanus*, according to the snap-trapping sample. Only the survival of cohorts attaining sexual maturity during the season of birth can be estimated (cf. text). n = mean number of young surviving to trappable age per female surviving to the end of June, % = percentage of the mean litter size (6.1, KALELA & OKSALA 1966).

Year	1964	1967	1968	1969	1970
n	2.1	4.8	5.4	5.0	0.5
%	34	78	89	82	8.0

rufocanus marked the previous summer. Nine of the animals, born in late July — early August 1969, had remained immature during their season of birth; these disappeared before mid-July 1970. Seven of the 16 specimens born earlier in summer 1969 had matured that summer and were still on the study plot in mid-July 1970 (Fig. 19).

The snap-trapping sample (Fig. 22) illustrates this difference in survival, and so do the data in Table 15. In both "young" and "old" groups summer mortality was higher in 1970 than in summer 1969, but in the "old" group the difference was not significant ($\chi^2 = 3.182$; $P < 0.1$), whereas in the "young" group it was highly significant ($\chi^2 = 32.867$; $P < 0.001$).; Thus the proportion of "old" voles in the overwintered population increased during summer 1970.

The age structure of the overwintered population followed a similar trend in all the years of the population decline (Fig. 22). The sample for 1965 was too small to be reliable, but the proportion of the youngest summer-born animals was low during this year, too.

Although the slopes of the curves for the population decline differed in different years, mortality was always negatively correlated with age, i.e. the proportion of the oldest animals increased. After the population decline during late summer 1967 and the following winter, the stock in early June 1968 consisted chiefly of individuals born in early summer 1967. In summer 1968 the population increased again, and in late summer 1968 some rejuvenation may have occurred (Fig. 22).

In 1964 the change towards older age in the overwintered stock was distinctly more rapid in the females (Fig. 22); the reason for this difference between the sexes is not known.

Table 15. Numbers of "old" and "young" (borderline birth date 20 July) overwintered individuals of *C. rufocanus* per 1778 trap-nights (the smallest number of trap-nights per subsample) in June and from July to August 1969 and 1970. For total number of individuals see Table 12. t-n = trap-nights.

	1969				1970			
	old[a]	young[a]	total	t-n	old[a]	young[a]	total	t-n
June	35.2	45.5	80.7	2620	28.0	93.0	121	1778
July — August	19.6	33.2	52.8	1816	6.2	6.2	12.4	3442
Sum	54.8	78.7	133.5		34.2	99.2	133.4	
χ^2		0.557				4.256[1]		

[1] $P < 0.05$.
[2] Born 1968
[3] Born 1969

C. Age structure in suboptimal habitats

The places where *C. rufocanus* was caught in traps set for lemming are not among the habitats preferred by this vole. The age structure of this sample in the breeding season of 1969 is shown in Fig. 21, and the combined data for overwintered animals in Fig. 22. In early September, animals born in July and August comprised only 65 %; the estimated suckling survival of the first litters was only 20 %. In spring the bulk of the overwintered individuals were old animals which had already bred the previous summer. This trend continued up to the autumn (Fig. 22). The age structure of the overwintered animals shows convincingly that this sample, although collected in a year of increasing density, has all the signs of a declining population. The trapping method may have biased the data about the younger animals.
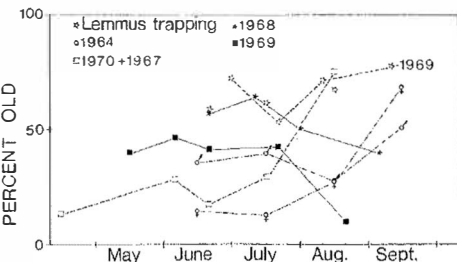

Fig. 22. The percentage of "old" overwintered *C. rufocanus* (born before 20 July the previous summer) in different samples. The sample trapped with lemming is from the years 1967--1969. Values are expressed as percentages of the total number of overwintered animals.

D. Winter survival

According to Petrusewicz *et al.* (1971), survival is normally higher in winter than in summer. In the present study the monthly survival values based on snap-trapping data varied between 84 and 88 for the whole population in the winters of 1968/69 and 1969/70. The effect of migration upon the November 1969/March 1970 sample was negligible. From late August 1969 to mid-June 1970 the monthly survival values of marked specimens averaged 85 %. The effect of migration is not known, but it may have been considerable among the males.

During the population decline in winter 1967/68 the monthly survival value obtained from snap-trapping data was near 80 %; this estimate, based on the relative density index, is too high. But in autumn 1967 the value was too low, because trapping ended too early.

In winter 1969/70, when survival was high, the age structure did not change (Figs. 19 and 21). After the population decline in winter 1967/68 the small sample showed a slight, although not significant, rise in the proportion of the oldest age groups born in summer 1967.

E. Survival in Microtus agrestis

Only a few observations on *M. agrestis* will be presented here, because there were no snap-trapping samples for age determination, and because the CMR sample of matures was adequate only in summer 1969.

That summer, the survival of mature females was good, as in *C. rufocanus* females (Figs. 19 and 20). In the males the effect of a dominant position was less distinct than in *C. rufocanus* males. Of seven males that were dominant in early July 1969 three disappeared before late August, as did five out of ten subordinate males. The reason for this may have been the instability of the male hierarchy, for these males lost their dominant positions before disappearing (cf. p. 69).

Data for the sedentary voles of both species on the study plot in August 1969 and June 1970 are presented in Table 16, which shows that in *M. agrestis* the population crash began in winter 1969/70. In contrast to *C. rufocanus*, however, one *M. agrestis* individual (female no. 128, Figs. 12 and 13) marked the previous summer was found after that winter decline. This was the last female captured on the study plot at the end of July 1970. She had already littered at least twice during her season of birth.

3. Discussion

The effect of social factors upon survival can be studied by two methods, (1) direct observation by live-trapping (GLIWICZ et al. 1968, PETRUSEWICZ et al. 1971), and (2) an age structure analysis based on snap-trapping (ZEJDA 1961). The trends in the "normal" dense population of *C. glareolus* examined by ZEJDA (1961) were very similar to those of the increasing population of the present study, i.e. the youngest age groups increased rapidly and remained proportionally high. ZEJDA's over-dense population exhibited the same characteristics of a declining population which were observed during the present study. According to ZEJDA, there are two reasons for these changes in the age structure of the population, (1) cessation of breeding and (2) intraspecific competition for food in the over-dense population, with resulting disappearance of the youngest and weakest animals. In the present study the intraspecific pressures were the most effective and, in some cases, the only factors responsible for the increase in the mean age of the *C. rufocanus* population during the decline.

NEWSOME (1968a, 1968b) examined populations of *Mus musculus* in Australia, where the

Table 16. Overwintering in 1969/70. Numbers of *C. rufocanus* (*C*) and *M. agrestis* (*M*) observed on the study plot in late August 1969 and June 1970.

	C	M	Total
August 1969	79	67	146
June 1970	40	9	49
Total	119	76	195

χ^2 11.698; P< 0.001

summer drought causes a population decline every year, as in populations of *Microtus californicus* in California (BATZLI & PITELKA 1971). Although NEWSOME did not study the social structure of the population, his conclusions about the role of social factors during a population decline are the same as those drawn from the present study. The socially high-ranking individuals are the oldest (GLIWICZ 1970, ANDRZEJEWSKI & RAJSKA 1972), but the social status of an animal also depends on whether it attains sexual maturity or not. This, in turn, is not always correlated with age. For instance, some of the *C. rufocanus* females born in mid-July 1964 became mature the same summer, probably because death of a breeding female left space for one immature female to attain maturity and the social status of a breeding female, although many older females remained immature for that season.

Another exception to the correlation between age and social position is that immigrants, regardless of age, always have a lower social status than established residents (cf. ANDRZEJEWSKI et al. 1963, GLIWICZ 1970, and ANDRZEJEWSKI & RAJSKA 1972), but these exceptions do not change the picture as whole. During periods of high density the survival of mature males was chiefly affected by the dominance hierarchy, which was quite distinct in *C. rufocanus*. Once a male had achieved a dominant position it was never ousted by other males, whereas in *M. agrestis* this occurred frequently. In both species the oldest males have the highest position.

GLIWICZ et al. (1968) and PETRUSEWICZ et al. (1971) investigated an island population of *C. glareolus* in Poland. In all years considered, the survival of overwintered animals was correlated with age, although still high in the oldest animals (77.3 % per month). The other

survival values also resembled those of increasing populations as found in the present study, except in the spring litters, in which the sucklings had a lower value (76.3 %) than in the Kilpisjärvi population (82—88.5 %). In Poland suckling survival decreased slowly to 47.5 % in the last autumn litters, whereas in Finland the value fell to near zero in autumn.

In both areas all age groups survived better in winter than in summer (PETRUSEWICZ et al. 1971, present study). Good winter survival is necessary for both *C. rufocanus* and *M. agrestis* at Kilpisjärvi, where the populations have to live for more than 8 months without compensating for the losses caused by mortality. Therefore very small changes in winter mortality may determine whether the population survives the winter well or poorly. When the survival values of *C. rufocanus* were 84 to 89 % per month, there were no changes in age structure (cf. PETRUSEWICZ et al. 1971). In winter 1967/68, although the monthly survival value may still have exceeded 70 %, numbers dropped greatly (Fig. 21).

According to KOSHKINA (1955), animals that breed in their season of birth die before the following breeding season. She based her conclusion on the observation that the

last females of *C. rufocanus*, *C. rutilus* and *C. glareolus* with placental scars from the previous breeding season were captured in early April. The same was observed by KAIKUSALO (1972) for *C. glareolus* in southern Finland. In the CMR sample from spring 1970, however, at least 16 % of the individuals of *C. rufocanus* permanently inhabiting the study plot had bred during the previous summer. In the snap-trap sample for that spring, however, the last female with visible placental scars was caught in early April. Thus, in *Clethrionomys* females, placental scars presumably disappear in late March or early April when the new breeding season begins and the uterus begins to thicken. Hence, baculum (ARTIMO 1964) and body length (KAIKUSALO 1972) might be better criteria for judging whether an overwintered animal has already bred.

When the population is increasing the animals with a second breeding season contribute little to its growth, but during a low it is these animals that carry the population through the critical period. During extreme lows such as that of spring 1966, when the population is near extinction, the next phase of increase may be brought about by the few animals that have survived two winters.

V. Interspecific relations

1. Areas inhabited by the species

Both *C. rufocanus* and *M. agrestis* increased in numbers during summer 1969. These species show interspecific territoriality, where the areas they inhabit overlap (Fig. 15). Such overlapping occurred to some extent at boundaries between different habitats, especially in narrow transition zones between eutrophic and dry oligomesotrophic woodland (Fig. 9). In such places the area visited by both species remained the same during the period of the study. But when overlapping occurred in uniform habitats, whether eutrophic or mesotrophic woods, then in the following trapping period the areas were usually occupied by *M. agrestis* only. In fact, interspecific territoriality was even more marked than appears from Fig. 15.

Up to late July 1969 both populations expanded their ranges, but in August the area

of *C. rufocanus* began to diminish as the area of *M. agrestis* (Fig. 15) increased. The population of the latter continued to expand until late August 1969.

2. Distribution in relation to habitat

Clethrionomys rufocanus. According to KALELA (1957) and KALELA et al. (1971), *C. rufocanus* prefers wooded habitats on mineral soil (including *korpi* woods, which form a mosaic on the present study plot). This preference can be seen from the distribution of its capture sites (Fig. 23) in 1967 and 1968. By early July 1969 *C. rufocanus* had expanded, probably into places where *M. agrestis* was absent, and by early July the difference had become statistically significant ($\chi^2 = 18.420$; $P < 0.001$). This difference from an even distribution on
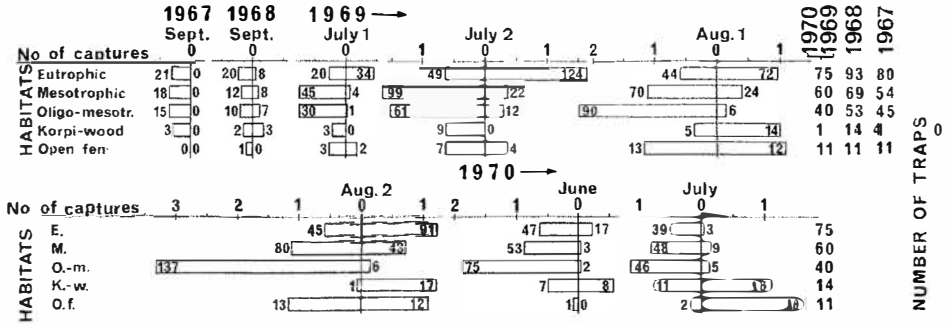
Fig. 23. Numbers of captures per trap station and the total number of captures of *C. rufocanus* (left of the zero line) and *M. agrestis* (right of the zero) in the different habitats. The numbers of traps are presented for different years.

the habitats on mineral soil was still more distinct in late August ($\chi^2 = 142.710$; P < 0.001). The distribution shows that the by then smaller range of the *C. rufocanus* population was mainly restricted to the most barren habitats, which *M. agrestis* does not tolerate. In other habitats *C. rufocanus* was mostly captured near the driest heath woods.

When the population of *M. agrestis* declined in winter 1969/70, the *C. rufocanus* population once again had the opportunity to disperse to the eutrophic habitats, but the process was hampered by its home tenacity, so in July 1970 the distribution was still almost the same as in the previous summer. Learning a new model of 'most favored habitat' (WECKER 1963) may also have retarded the dispersal. Although *M. agrestis* is superior to *C. rufocanus*, an increase in *M. agrestis* never threatens the survival of *C. rufocanus* because the ecological amplitude of the species overlap only partially. *C. rufocanus* survives and breeds successfully in drier heath woods that to *M. agrestis* are totally uninhabitable.

Microtus agrestis. When examining Fig. 23 one should bear in mind that *M. agrestis* is less trappable than *C. rufocanus*; no correction has been made to eliminate this source of error.

The first individuals of *M. agrestis* to invade the study plot were found in late summer and autumn 1968 on the narrow strip of paludified *korpi*-wood along the brook, but in summer 1969 the population increased

rapidly in the most eutrophic woods on mineral soil. In late July it was even more clearly restricted to these habitats than was *C. rufocanus* to dry heath forests a month later.

Although only four individuals of *M. oeconomus* moved to the study plot in late July and early August, they ousted all other rodent species from one-third of all the eutrophic meadow wood habitats, because of their large home ranges and interspecific territoriality (TAST 1966, 1968b). The increasing population of *M. agrestis* was gradually forced to retire to the mesotrophic and even oligo-mesotrophic woods where, in late August 1969, its numbers were significantly increased as compared with late July ($\chi^2 = 24.270$; P < 0.001). Since the habitats offered by these mesotrophic heath woods are close to the limits that *M. agrestis* can tolerate (KALELA 1949, TAST 1968b, KALELA *et al.* 1971), the rapid decrease in its numbers in winter 1969/70 may have been due, at least in part, to its having been driven to this unfavourable habitat.

After the winter decline the *M. agrestis* population returned to the paludified areas. In early summer 1970 two females made a real change of habitat from meadow wood to paludified *korpi*-wood (Fig. 13).

A basically similar relation existed between *M. oeconomus* and *M. agrestis*. *M. agrestis* occupied habitats that were not tolerated by the superior *M. oeconomus*, which was restricted to the most luxuriant parts of the meadow woods. In addition, *M. oeconomus* rarely reproduced in woods on mineral soil (cf. TAST

1968b). Possibly, real fighting occurred between members of the competing species.

3. Discussion

According to MILLER (1967) and GRANT (1972), competition between rodent species is always based on interference, i.e. on agonistic contacts between competing species instead of on unequal ability to exploit natural resources. CALDWELL (1964) had assumed that the competitive superiority of *Peromyscus polionotus* over *Mus musculus* was based on the better ability of the former to exploit seeds as food, but GENTRY (1966) and BRIESE & SMITH (1973) showed that in this case, too, competition is based mostly on pure interference.

As the amount of plant food is always limited, social competition and interspecific territoriality are of vital importance to the competing species. Competition involving over-exploitation would be fatal to both species, especially at Kilpisjärvi, where the voles have to live for 9 months on the storage organs produced by plants during 3 months. The territoriality of *C. rufocanus* in winter, a phenomenon not described in more southern rodent populations, was concluded to be an adaptation to make the the scanty stores last through the winter.

In competition, the superior species is usually larger than the inferior one (MILLER 1967, GRANT 1972 and MORSE 1974). In years of increase the weights of overwintered *C. rufocanus* ranged from 45 to 60 g, those of *M. agrestis* from 50 to 65 g; some of the pregnant females were heavier than this. The mean weight of *M. oeconomus* may exceed that of *M. agrestis* by more than 15 g (TAST 1966). The only exceptions I know are that the superior *M. arvalis* is smaller than the inferior *M. agrestis* (REICHSTEIN 1960) and, correspondingly, *Geomys bursarius* is smaller than *Cratogeomys castanops* (MILLER 1964, 1967).

Larger size is an obvious advantage in competition, if territoriality and ecological segregation are achieved by means of actual fighting and associated agonistic behaviour patterns, as in pocket gophers of the family Geomyidae (MILLER 1964, 1967), in North American *Microtus* species (KOPLIN & HOFFMAN 1968, MURIE 1971), in ground squirrels of the genus *Eutamias* (BROWN 1971, HELLER 1971, SHEPPARD

1971), in North American *Clethrionomys* species (MURIE & DICKINSON 1973) and in *Apodemus flavicollis* and *Clethrionomys glareolus* (ANDRZEJEWSKI & OLSZEWSKI 1963).

But interspecific territoriality and ecological segregation may be realized without any visible agonistic behaviour, as noted by MORRIS (1969), GRANT (1970) and MORRIS & GRANT (1972) in North American species of *Microtus*, *Clethrionomys* and *Peromyscus*. In these cases each species was dominant in its preferred habitat, but capable of inhabiting the area preferred by its competitor when the latter was absent.

CALHOUN (1963b) concluded that the species inhabiting a particular area have a dominance order. This was true in the area of the present study. The situation may be more complicated, however, as in the case reported by MORRIS & GRANT (1972), in which no true dominance order could be distinguished. STOECKER (1972) observed that in nature *Microtus pennsylvanicus* expanded its range at the expense of *M. montanus*, although in the laboratory *M. pennsylvanicus* is subordinate to *M. montanus* (KOPLIN & HOFFMAN 1968, MURIE 1971 and STOECKER 1972).

The data obtained in the present study resemble those for the Geomyidae and *Eutamias*. A similar relation was described by CAMERON (1971) between *Neotoma lepida* and *N. fuscipes*, which have similar food preferences. In a competitive situation *N. fuscipes* is always superior, but it does not threaten the existence of *N. lepida*, which has a wider habitat tolerance. In a competitive situation the inferior species must have a wider habitat tolerance than the superior one. The differences in tolerance may be only slight, as between *M. agrestis* and *M. oeconomus* (TAST 1968b).

Sympatric rodent species — whether closely related or not — do not always compete. Such situations were reported by GETZ (1961b) for *Microtus* and *Synaptomys*, and by FALL *et al.* (1971) for *Rattus rattus* and *R. exulans*, which avoid competition by adopting different feeding patterns. Such species do not react territorially towards each other. Interspecific territoriality may thus be an evolutionary result of similar feeding habits in two species. According to KALELA (1949, 1957, 1962), KOSHKINA (1957), TAST (1966, 1968a, 1968b), and KALELA & PEIPONEN (1972), such similarity exists between the *Microtus* species and *C. rufocanus*, but not to any appreciable extent between *Microtus* and *C. rutilus*.

Even non-territorial species may avoid direct contact with each other by occupying different parts of the common home range at any particular time, as do *C. rutilus* and *M. agrestis*. Such use of the home range was described by KAYE (1961) for marked specimens of *Reitrodontomys humilis* (cf. SINIFF & JESSEN 1969). Live trapping is too crude a method to detect such a system of mutual avoidance. These views are not in accord with the centre-of-activity concept suggested by CALHOUN & CASBY (1958), whose view has been opposed by WIERZBOWSKA & CHELKOWSKA (1970) and also by SMITH *et al.* (1973).

The difference in the competitive ability of two species may be slight, as in the case of *M. agrestis* and *C. rufocanus*. *M. agrestis* could oust young individuals of *C. rufocanus*, but had little effect on those that had overwintered. Evidently, some species are evenly matched, e.g. the American *Microtus* and *Peromyscus* (MORRIS & GRANT 1972).

VI. Population fluctuations

Although the causes of the population fluctuation were beyond the scope of this study, some remarks can be made in the light of the 1964—1970 snap-trapping samples of *C. rufocanus* (Fig. 24). The fluctuations of the other species were fairly synchronous (KALELA *et al.* 1971, TAST & KALELA 1971).

In the present study the term "population decline" is used only for a decrease of population density associated with characteristic changes in age structure (cf. p. 82). A decrease in density during overwintering without changes in age structure is thus not covered by this term. Density is expressed as the density index, number of individuals trapped per 100 trap-nights.

In spring 1964 the density index was already 10.6, and in late July it rose as high as 19.3. Then came a population decline, which continued all through summer 1965 and the following winter. In spring 1966 the population of *C. rufocanus* was near to extinction at Kilpisjärvi, but the breeding of the few survivors succeeded well, for in late summer 1966 the density index had reached about 1.0. The population survived the following winter well, for in spring 1967 the density index was 0.9, and a peak (2.3) was reached in late July. The subsequent decline was slow, and the density index reached 0.45 in spring 1968.

The most rapid population growth observed during the present study took place during summer 1968. In late September the density index reached 6.65. The increase must actually have been much higher, because trapping ceased before the youngest age groups reached their highest trappability. Therefore the ob-served density index was higher in spring 1969 than in autumn 1968. The increase in population was near the theoretical maximum, if we suppose a monthly survival of 80 %, and that all females born before early August reproduce.

After a short decrease at the time of the snow melt the density increased during summer 1969 to about fivefold by November; winter survival was good, and the age structure did not change. The population crash began in early summer 1970. During about 20 days in June the density dropped from 6.35 to 2.45, and not a single individual of *C. rufocanus* was captured after the end of August, in spite of intensive trapping. The data obtained from the CMR trapping agree fairly well with the results presented above.

During three breeding seasons (1966, 1968, 1969) the population of *C. rufocanus* increased, during two seasons (1965 and 1970) it decreased, and during the remaining two (1964 and 1967) it first increased and then decreased.

It is worth noticing that the population itself regulated only the intensity of the increase. It did not regulate the actual density whether the numbers were increasing or decreasing. In 1966 and 1967 the increase began from a low density and in 1964 and 1969 from a relatively high density. In 1965 and 1967 the decline took place during a low density, whereas in 1964 and 1970 it occurred during a high density. During the present study the highest densities (1964 and 1969) were considerably lower than the values observed by KALELA (1957) (50 individuals of *C. rufocanus* per 100 trap-nights). We may therefore con-

clude that density has never directly caused a population decline in the subarctic conditions so far examined.

According to NEGUS *et al.* (1961), KALELA (1962), WATTS (1969), TAST & KALELA (1971), TAST (1972) and LE LOUARN & SCHMITT (1972), there is ample evidence for the theory that fluctuations in rodent populations are related to the food available. Annual fluctuations in the quality and quantity of food depend on weather conditions and on the density of the foraging rodent population itself (BATZLI & PITELKA 1970).

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