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Demography and regulation of breeding density in the field vole, *Microtus agrestis*

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Demography of field vole (*Microtus agrestis*) was studied by live-trapping wild populations in an abandoned field and a grassy spruce forest in Konnevesi, Central Finland. Population density had two peaks in the field during the summer. The intervening low coincided with colonization of the suboptimal forest. Reproductive success of females in the field correlated negatively with population density. Reproductive females were distributed among the habitats according to ideal free distribution as the forest was inhabited when reproductive success in the field lowered to the same level as in the forest. 28% of females and 3% of males matured during the year of their birth. Maturation rate of females correlated negatively with density of reproductive females. Most males born in late spring disappeared from the field resulting in an excess of spring born males in the forest. The different life histories of the sexes are due to their different social organizational modes.

1. Introduction

Environment is heterogenous in space and time regarding the possibility to reproduce succesfully. According to the density-dependent habitat selection theory (see e.g. Morris 1989), reproductive success should decline with increased population density. If individuals are free to move among habitats they should assort themselves so that fitness in different habitats would be similar (ideal free distribution, Fretwell & Lucas 1970). If individuals are constrained in their habitat selection by e.g. territorial behaviour, fitness should differ between habitats.

In addition to the habitat selection of already mature individuals or those at puberty, breeding density is affected by the maturation of young individuals. Whether an individual matures or not depends on 1) its “decision”, which should be sensitive to prevailing conditions (e.g. food availability, population density, season) and/or 2) constraints set by dominant individuals.

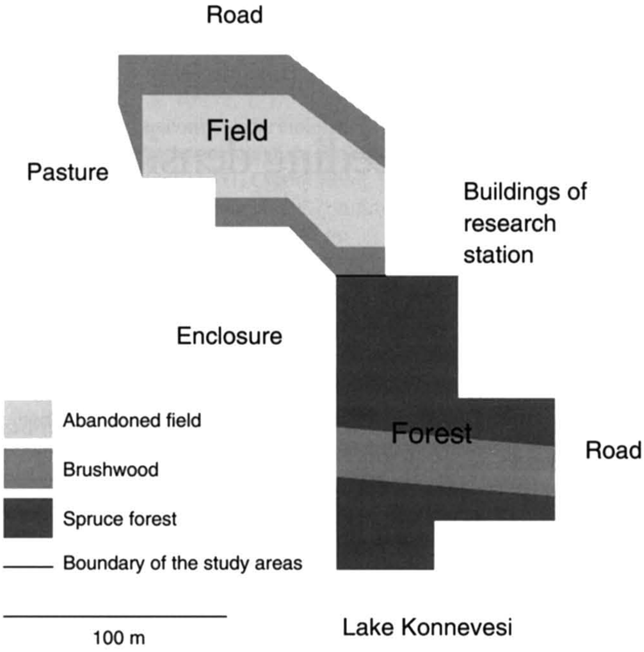

Fig. 1. The study area and its habitats.

Viitala & Hoffmeyer (1985) distinguish two fundamental types of social organization of voles in respect to maturation (for other classifications see e.g. Cockburn 1988). In the first type the young females can mature only if they manage to obtain a territory of their own. These "regulators" live in wide uniform and predictable habitats with high quality but sparse food. All *Clethrionomys*-species belong to this group. The "non-regulators" live in ephemeral patchy habitats with abundant but low quality food. Young females can mature on the home range of their mothers. Maturing males obviously have to have a territory. The number of young produced by the population is not strictly restricted by density. The North-European *Microtus*-species belong to this group.

The first aim of the present study is to describe and compare the demography of field vole (*Microtus agrestis*) in two different habitats during a breeding season. The habitats were an abandoned field, an optimal habitat, and a grassy spruce forest, a suboptimal-marginal habitat (Stenseth et al. 1977).

The second aim is to examine the regulation of breeding density based on data of spacing behaviour (see Pusenius & Viitala 1993).

2. Study area and methods

The study was carried out in Konnevesi (62°35′N, 26°20′E) Central Finland in summer 1985. The study areas, an abandoned field (0.7 ha) and a thinned moist grassy coniferous forest (1 ha) are situated close to each other (Fig. 1). The study areas were surrounded by an enclosure, heavily grazed pasture, buildings of the Research Station and roads. Despite this relative isolation, dispersal was not prohibited.

The main plant species in the old field were in order of abundance, *Alopecurus pratensis, Elytrigia repens, Urtica dioica, Cirsium arvense, Deschampsia caespitosa, Anthriscus silvestris* and *Epilobium angustifolium. E. angustifolium* as well as *Rubus idaeus* and *Filipendula ulmaria* formed patches of pure stand. The tree and field layer in the marginal parts and under an electrical power

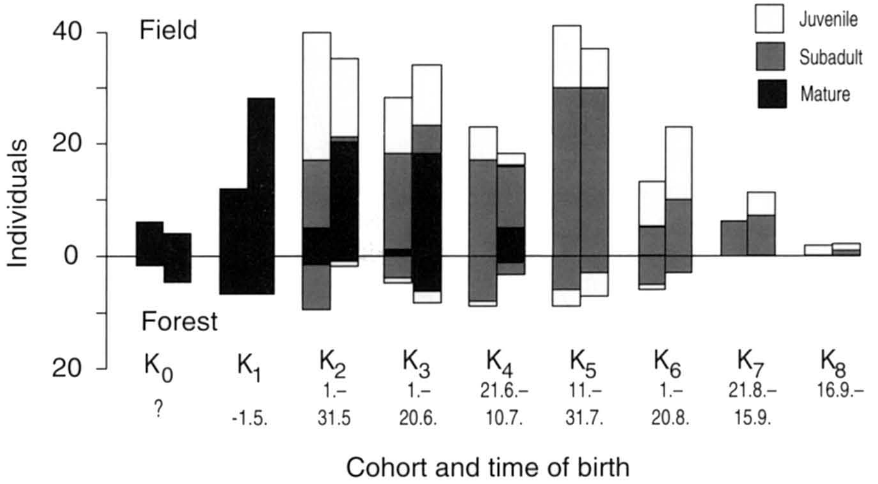

Fig. 2. Material of the study: The cohorts, sex ratios, maturation and estimated time of birth. Left column = males, right column = females. Sex ratio differs between habitats in cohort K_2 ($\chi^2 = 4.78$, $df = 1$, $P < 0.05$). The proportion of mature animals differs between sexes in cohorts K_2 ($\chi^2 = 19.54$, $df = 1$, $P < 0.01$), K_3 ($\chi^2 = 25.40$, $df = 1$, $P < 0.01$) and K_4 ($\chi^2 = 7.92$, $df = 1$, $P < 0.01$).

line were dominated by *Alnus incana, Rubus idaeus, Epilobium angustifolium, Gymnocarpium dryopteris, Deschampsia caespitosa, Vaccinium myrtillus* and *Equisetum sylvaticum*. In the thinned forest the dominating plants in the field layer were *Deschampsia caespitosa, Calamagrostis arundinacea, Vaccinium myrtillus, Gymnocarpium dryopteris, Oxalis acetosella* and *Maianthemum bifolium.*

Voles were monitored by live-trapping (CMR-method) using Ugglan Special multiplecapture traps arranged in a grid with 10 m intervals (71 traps in the field and 97 traps in the forest). The traps were baited with oats and potato. Each part of the study area was checked for 5 days every second week. In September and October the study areas were checked for one week only. One trapping period consisted of 8 to 10 trap checks. In the field the trapping periods in mid June and August had 8 trap checks and the trapping period in October had 9 checks. In the forest the trapping period in the end of June had 9 checks and the trapping periods in the end of July, early August and in the end of August had 8 checks. All other trapping periods had 10 trap checks. The traps were checked two or three times a day at four to five hour intervals. The trapping was done in day time except for one night during every trapping period. In May, September and October there were three night trappings during every trapping period.

The animals were marked individually by toe-clipping. For each capture the following information was checked: identity, time, trap station, weight, sex, sexual status and the status of milk glands. Females that were visibly pregnant, lactating or had a perforated vagina and males with scrotal testes were considered sexually mature. The term immature includes juveniles i.e. newly weaned individuals in juvenile pelage and subadults i.e. nonreproductive individuals in postjuvenal or preadult pelage (see Viitala 1981).

The time of birth i.e. the cohort of an individual was estimated when first captured on the basis of weight curves calculated by Myllymäki (1977a) for southern Finnish field voles. The material was divided in eight age cohorts (Fig. 2). Out of the 421 individuals captured during the study 405 could be reliably assigned to cohort.

The number of animals caught during a given trapping period was used as the estimate of population numbers. Possible occasional visitors are thus included. There are, however good reasons to assume that the numbers are not seriously

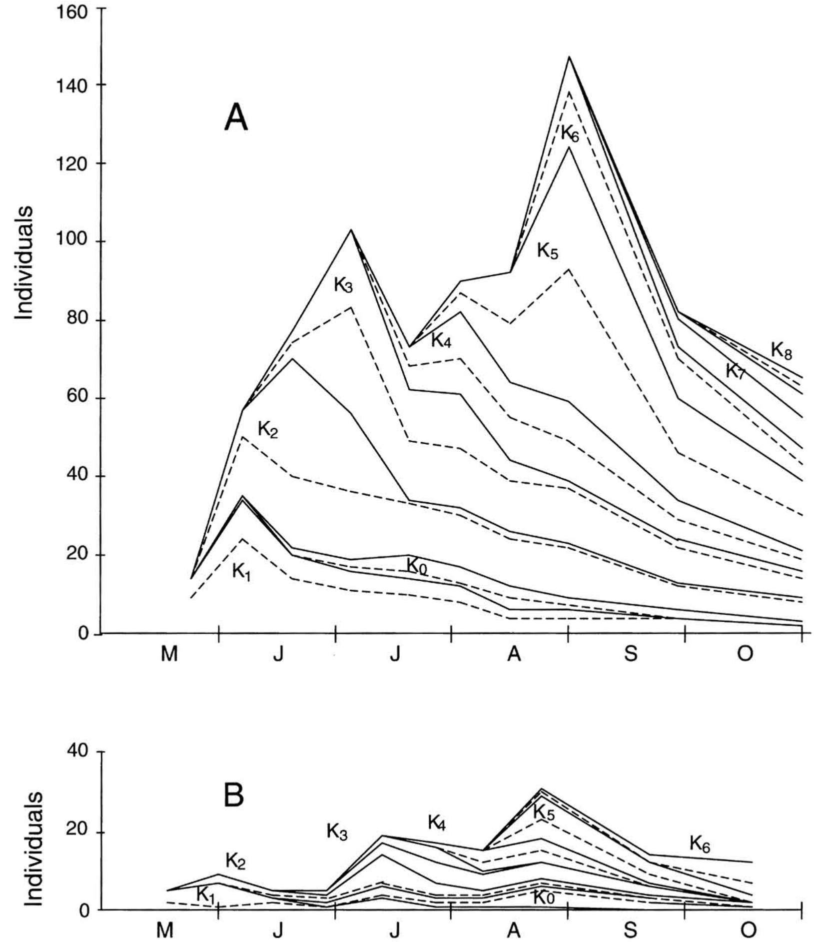

Fig. 3. Population density given as the number of captured animals during a trapping period and the proportion of different cohorts in the field (A) and in the forest (B). Females are below and males above the dashed line.

overestimated. Firstly, according to our experience from an enclosure study with *M. agrestis*, (J. Pusenius, unpublished), there are individuals that do not enter livetraps. Secondly, trappability may be considered as an indication of dominance (Gliwicz 1970) and the occasional visitors are without an exception subdominant (see e.g. Petrusewicz & Anrzejewski 1962, Viitala 1977). Consequently, as the trappability in our study was low (see Pusenius & Viitala 1993), it may be that occasional visitors were rarely caught. The variation in the number of trap-checks per trapping period may have affected the estimates of numbers in the least trappable categories i.e immatures (see Pusenius & Viitala 1993), although the effect is hardly considerable.

The persistence probability (see Ostfeld et al. 1985) was calculated as the proportion of the individuals captured during trapping period *t*, in the catch during the trapping period *t*+1. Dispersal and mortality cannot be separated in this kind of study. However, when the persistence of a given category was low in the field but its numbers increased simultaneously in the forest, a considerable proportion of the loss from the field is assumed to be due to dispersal. That was confirmed also by direct observations of dispersing individuals.

The reproductive success of breeding females was calculated from the formula

$$J_{t+2} / (F_t + J_{t+2}),$$

where J_{t+2} = the number of juvenile recruits weighing ≤18g and caught for the first time during trapping period t+2, and F_t = the number of resident (caught at least twice) reproductive females during trapping period t. Taking into the account the length of the gestation period (20 d) (Clarke 1977), the nestling period (two weeks), the juvenile behaviour (Myllymäki 1977b) and the growth rate (Myllymäki 1977a) of the field vole, the weanlings of the given size (≤18 g) during the trapping period t+2 are most probably born at the study site during the trapping period t.

The maturation rate of young females from trapping period t to t+1, was determined as the proportion of females having matured until the end of t+1, out of all females potentially capable of maturing during t.

3. Results

3.1. Density, survival and reproductive success

The population density had two peaks in the field (Fig. 3A). The density increased rapidly in the early summer when the large K_2 cohort recruited to the trappable population. In mid June the number of reproductive females decreased: 40 percent of the reproductive females disappeared between two consecutive trapping periods, but in spite of this, the total population density increased (Figs. 3A, 4A). In the beginning of July males of the cohort K_2 survived poorly (Fig. 4B) and the recruiting cohort K_4 was small, thus the total population decreased. The number of mature females started to increase in the end of June as the females of the year started to mature (Fig. 4A). The second peak of population density (147 individuals or 200 ind./ha) occured in late August after the recruitment of cohorts K_5 and K_6.

In the forest the population began to grow in July (Fig. 3B). Immigration of especially K_2 males contributed to the increase. Out of the 19 individuals captured in the forest in mid July, 10 (53%) had emigrated from the field. Four of these immigrants were K_2 males, but there was also one reproductive K_1 female and one K_3 female, both of which settled in the forest as breeding residents. The peak population density (30 individuals/ha) occured in late August due to the recruitment of cohort K_5 borne by the resident females.

The biweekly persistence was higher in the field than in the forest (Table 1). The difference was significant for old reproductive animals and in the youngest cohorts. In the field the persistence of females was higher than that of males. The difference was significant in cohorts K_2 and K_3. Attainment of puberty lowered markedly the

Table 1. Mean biweekly persistence probabilities (p) in different cohorts and habitats. m = males, f = females, N = number of animals in the beginning of a trapping period (summed over trapping periods), FE = Fisher's exact test. Significant male/female or habitat differences: *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$.

Cohort	Field					Forest					Habitat difference	
	Male		Female			Male		Female		χ2 or	Male	Female
	p	*N*	*p*	*N*	χ2	*p*	*N*	*p*	*N*	FE	χ2 or FE	χ2 or FE
K_1	0.67	39	0.73	92	0.50	0.33	10	0.42	12	FE	4.43*	4.84*
K_{-1}	0.75	20	0.56	9	1.10	0.83	6	0.56	9	FE	0.18	FE
K_2	0.37	65	0.76	120	27.14***	0.50	14	0.67	6	FE	0.83	0.26
K_3	0.58	72	0.74	104	4.19*	0.29	7	0.60	20	2.05	2.29	1.39
K_4	0.55	44	0.65	43	1.01	0.00	8	0.40	5	FE	8.10***	1.21
K_5	0.50	62	0.60	72	1.27	0.22	9	0.00	7	FE	2.44	9.17***
All	0.54	302	0.70	440	21.87***	0.35	54	0.47	59	1.75	6.24*	12.59***

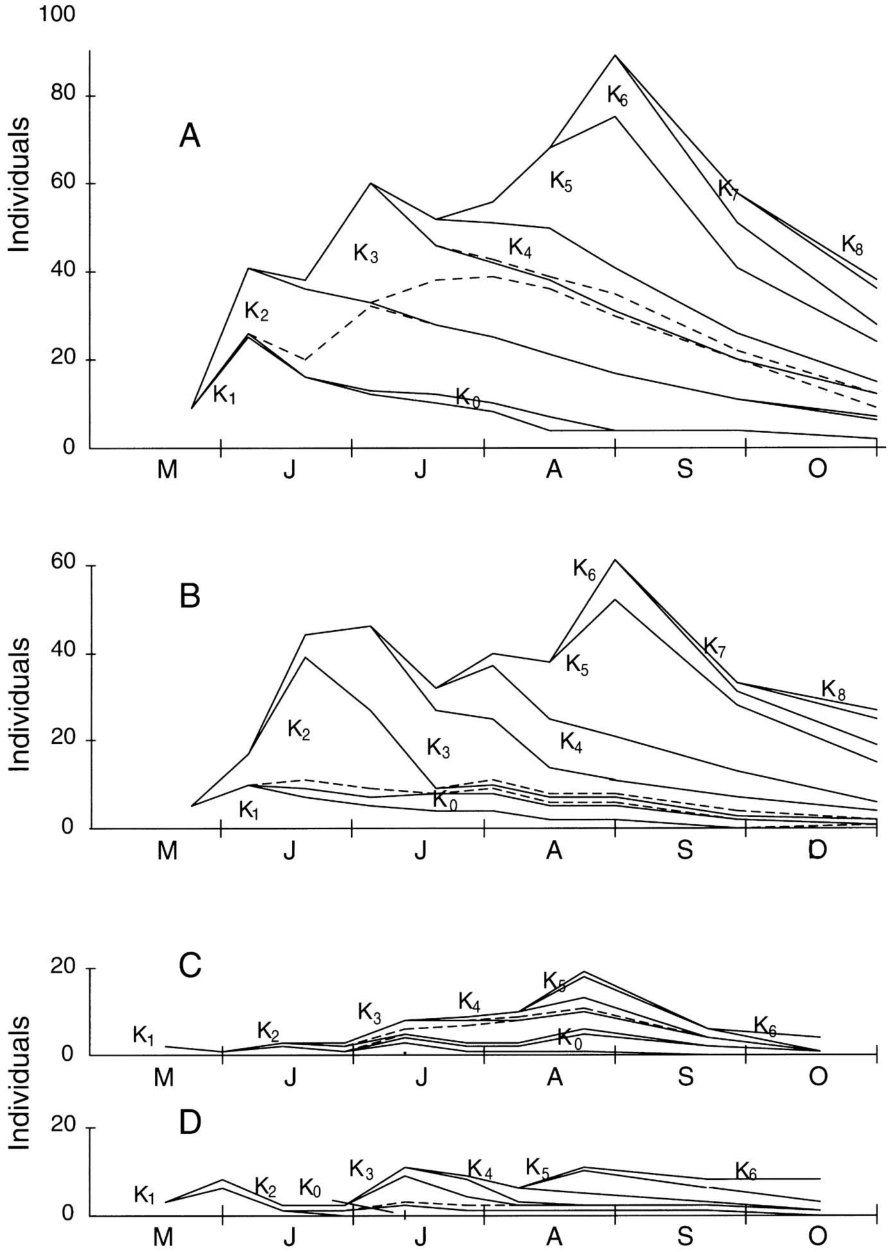

Fig. 4. Structural variation of the populations of different sexes during the breeding season. A = field females, B = field males, C = forest females, D = forest males. Mature animals are below and immature above the dashed lines.

persistence of males in these cohorts (Fig. 4). The young mature females had the highest probability to persist to next trapping period in both habitats. The combined persistence probability of the young mature females of cohorts K_2 and K_3 in the field, correlated negatively with population density from the beginning of July until the end of September ($r = -0.97$, $df = 3$, $P < 0.01$).

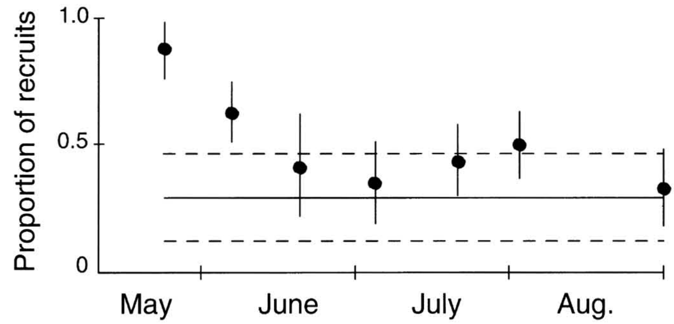

Fig. 5. Reproductive success of breeding females (see methods). Dots denote reproductive success in the field. Vertical lines denote the 95% confidence limits. The continuous horizontal line denote pooled mean reproductive success over trapping periods in the forest and the dashed lines denote its 95% confidence limits.

In the data pooled over the breeding season, the total number of juvenile recruits (<18 g) per total number of resident mature females (caught at least twice, and only on either stydy area) was greater in the field than in the forest (field: 175 recruits, 54 females, forest: 8 recruits, 10 females, $\chi^2 = 8.89$, $df = 1$, $P = 0.003$). Following a peak in late May the reproductive success in the field decreased until late June (Fig. 5). Thereafter it was similar to that of the pooled mean in the forest. The pooled mean was used because of the small sample size especially in the early summer. The difference in the total reproductive success between the habitats was due to the extensive reproduction in the field in the early summer: if the first two trapping periods are ignored the difference between the habitats disappears (field: 90 recruits, 45 females, forest: 6 recruits, 8 females, $\chi^2 = 3.14$, $df = 1$, $P = 0.08$). The reproductive success during the different trapping periods correlated negatively with population density in the field ($r = -0.89$, $df = 5$, $P < 0.01$).

3.2. Sex ratio and maturation

The overall sex ratio did not deviate from 1:1, nor did it within different cohorts. It differed, however between the habitats. In cohort K_2 the proportion of males was higher in the forest (Fig. 2). The operational sex ratio (the number of reproductive females per a reproductive male) was greater in the field (field: 72 females, 19 males, forest: 16 females, 11 males, $\chi^2 = 4.33$, $df = 1$, $P < 0.05$). It increased during the summer in both habitats and was significantly female biased in the field from early July (Fig. 4).

Overall, the maturation rate of females was greater than that of males: 50 out of the 177 (28.2%) recruiting females and 6 out of the 183 (3.3%) males matured during the study ($\chi^2 = 42.71$, $df = 1$, $P < 0.001$). The difference between sexes was evident in all maturing cohorts (Fig. 2). In the forest there were no subadult females until the cohort K_4. The proportion of the females having matured from period t to $t+1$ in the field, correlated negatively with the number of reproductive females during the trapping period t (partial correlation, season standardized: $r = -0.76$, $df = 7$, $P = 0.04$).

4. Discussion

4.1. Demography

The variation in the number of trap checks may have slightly modified the curves describing the density variation in different population categories. The density lows do not, however coincide with the trapping periods with less than 10 checks. An exception is the decrease in the number of breeding females in the field in mid June. The decrease is real also in this case, because the animals that disappeared before that period were never caught again.

The results support the general view of the habitat selection of field vole (see e.g. Hansson 1977, 1982). The population density in the spruce forest was very low during the whole breeding season. According to our observations the abandoned field was uninhabitable in spring after the snow melt. There was no cover nor food, and the forest edges and brushwoods were used as a refuge. The field was colonized as soon as the vegetation began to flourish there. Similar habitat shift in the beginning of breeding season has been documented by Tast (1966) for *M. oeconomus* and by Pokki (1981) for *M. agrestis*. From the beginning of June until midsummer the forest was inhabited by only few individuals. The great proportion of young immature males with low persistence lowered the overall persistence in the forest.

The better reproductive success of females in the field than in the forest was probably related to the differences in the food availability between the habitats. Food quality and quantity has been found to be a very important determinant of reproductive success in microtines (e.g. Batzli 1986). The difference between the habitats, however, disappeared after the early summer. The negative correlation between reproductive success and population density in the field may suggest a decrease in food availability as the density increases (Boonstra & Krebs 1977, Myllymäki 1977a, b) or less likely some kind of stress effect (e.g. Madison 1978). The increase in the proportion of the young females of the reproductive females, may also have decreased the female reproductive success. The litter size of young females is usually smaller than that of old females (Myllymäki 1977a). The importance of food is indicated by the fact that the decrease in reproductive success coincided with nutritional "midsummer crisis" described in *Microtus agrestis* in Southern Finland by Myllymäki (1977a, b) and Pokki (1981). The phenomenon might be caused by the termination of growth of the grasses when they begin to flower. The decrease of population density in the field in midsummer is another indication of the crisis. Besides *M. agrestis* (see also Pokki 1981) the midsummer crisis occurs in *M. pennsylvanicus* in North America (Mihok 1984). In our study the disappearance of reproductive females in early June and young males in early July clearly contributed to the population low. It is likely that the disappearance of the latter group was mediated by social factors (Myllymäki 1977b, Sandell et al. 1990, Pusenius & Viitala 1993) although food may have been the ultimate cause (Sandell et al. 1990).

4.2. Regulation of breeding density

The extensive home range overlap of young mature females with their mothers in our study population (Pusenius & Viitala 1993) indicates, that female maturation was not regulated by territoriality as it is in *Clethrionomys* (Bujalska 1970, Viitala 1977, Saitoh 1981, Gilbert et al. 1986). The degree of territoriality increased in midsummer (Pusenius & Viitala 1993), but that did not prevent maturation either. The negative correlation between the density of reproductive females and intensity of maturation indicates that the density of reproductive females per se may have affected maturation. Density-dependent maturation of females has also been reported in *M. pennsylvanicus* (Boonstra 1989). The most intensive period of maturation coincided with the decline in the density of reproductive females in the early summer. Probably other factors like photoperiodism (Lepri 1985) and a change in food availability (Myllymäki 1977a, b) contemporaneously had an effect on maturation. These factors were probably most important late in the breeding season, because not a single K_5 female attained puberty. Subadult K_4 and K_5 females accumulated also in the forest in late August.

Another aspect in the regulation of the breeding density is the dispersal of mature animals. The disappearance of many reproductive females from the field in June coincided with the decrease in the reproductive success in the field to the level of the suboptimal surroundings. There is one direct observation of habitat shift connected to that situation. Social factors (see Pusenius & Viitala 1993) and death due to old age may also have affected the number of females. However, soon after the reproductive success was equalized between the habitats, the breeding population in forest started to grow. These results indicate that the females distributed between the habitats according to the ideal free distribution (Fretwell & Lucas 1970). The persistence of young mature females seemed to be inversely dependent on the population density in the field. That may indicate sensitivity to search for a more profitable breeding place during crowded conditions. Dispersal of young mature females was not very common, however, as their high persistence values indicate. The probability to find vacant places in the suboptimal surroundings obviously decreased after the midsummer.

The males had much worse chances to recruit to the breeding population in the year of birth than the females. That was due to the mating system, which was polygynous with male territoriality (Pusenius & Viitala 1993). Koponen (1972), Myllymäki (1977b) and Viitala (1977) suggest that field vole males in puberty are forced to disperse by the old reproductive males. Sandell et al. (1990), on the other hand, propose that the reproductive females are responsible. The fate to be driven away applies especially to the males of early cohorts. That is indicated by their poor survival in the field and the accumulation of subadult males in the forest resulting in male surplus. In cohorts later than K_3 survival increased because factors other than social ones may have prevented puberty. It may also be possible that the decision to disperse is done by the young male himself: Aggressive encounters with old males would be too costly. The young males have a possibility to recruit to the breeding population of a suboptimal habitat: one K_2 male managed to do so in the forest. However, the chances of these males to breed in the next year may be better (see Boonstra 1989).

The delayed maturation of the later cohorts is obviously adaptive in both sexes. According to our preliminary results (J. Pusenius, unpublished) winter survival of these subadult animals was better than that of the postbreeding animals or juveniles born late in the breeding season. In addition, the reproductive success seems to be in its maximum early in the breeding season during the low density, and the genetic contribution of the few reproducers then should be considerable.

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