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Jyrki Pusenius

Intraspecific Interactions, Space Use
and Reproductive Success
in the Field Vole



UNIVERSITY OF JYVÄSKYLÄ

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ABSTRACT

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Intraspecific interactions, space use and reproductive success in the field vole

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Diss.

The role of intraspecific interactions - e.g. competition and kin interactions - in the regulation of vole populations has recently been under intensive scientific debate. The aim of this thesis was to study space use and reproductive success in relation to each other and quantity and quality of interacting individuals in the field vole *Microtus agrestis*. The methods used were intensive live trapping of natural populations, follow up of individuals of known relatedness in large outdoor enclosures and experimental manipulation of familiarity and relatedness in enclosed populations.

The study of natural populations revealed that space use of breeding voles varied between sexes, among age classes and habitats, in time and with population density. Home range overlap between breeding females increased with increasing population density. Among females studied in the enclosures number of breeding sons and number of weaned young correlated positively with the distance to the nearest breeding female. Age, survival and bodyweight were other factors related to reproductive success. Females that lived with close kin seemed to be more successful at weaning young than those that lived separately. Weaning success of nonphilopatric young females correlated positively with distance to the nearest unrelated older female whereas that of philopatric young females did not. Mothers and their philopatric breeding daughters lived closer to each other than other breeding females. Philopatry of young maturing females was common only in the early part of the study. Later on kin clusters were rare. This result contradicts somewhat with the general assumption of philopatry among young female voles. Experimental manipulation of familiarity did not have any remarkable effects on space use and reproductive success of breeding field vole females.

I conclude that the flexible space use of breeding female field voles seems to be a means to adapt to prevailing conditions. However, the way the space use react on density and relatedness between breeding females makes it incapable to regulate breeding density.

Key words: Field vole; breeding female; space use; reproductive success; philopatry; kin interactions; familiarity.

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Contents

1	Introduction	9
2	Methods	12
2.1	Study areas	12
2.2	Trapping procedure	13
2.3	Basic variables	13
2.4	Familiarity experiment	14
3	Results	15
3.1	Demography, regulation of breeding density and space use in natural populations (I, II)	15
3.2	Associations between age class, space use and reproductive success (III)	16
3.3	Kin clusters and their effect on space use and reproductive success (IV)	17
3.4	Familiarity, space use and reproductive success (V)	17
4	Discussion	18
4.1	Space use and breeding density	18
4.2	Space use and reproductive success	19
4.3	Philopatry and kin effects	20
5	Conclusions	22
	Acknowledgements	23
	Yhteenveto	24
	References	26

List of original publications

This thesis is based on the following papers, which are referred to by their Roman numerals in the text:

- I Pusenius, J. & Viitala, J. 1993: Demography and regulation of breeding density in the field vole, *Microtus agrestis*. - *Ann. Zool. Fennici* 30: 133-142.
- II Pusenius, J. & Viitala, J. 1993: Varying spacing behaviour of breeding field voles, *Microtus agrestis*. - *Ann. Zool. Fennici* 30: 143-152.
- III Pusenius, J.: Variation in reproductive success in female field voles, *Microtus agrestis*. - Manuscript.
- IV Pusenius, J., Viitala, J., Marienberg, T. & Ritvanen, S.: Matrilineal kinclusters and their effect on reproductive success in the field vole *Microtus agrestis*. - Manuscript.
- V Pusenius, J. & Viitala, J. 1995: Familiarity of breeding field vole (*Microtus agrestis*) females does not affect their space use and demography of the population. - *Ann. Zool. Fennici* 32: 217-223.

1 INTRODUCTION

Dramatic cyclic population fluctuations of voles in the northern latitudes of Eurasia and North America have provoked much ecological research on the mechanisms of population regulation. Both extrinsic (weather, food, predators, parasites) and intrinsic factors (interactions between individuals in a population) have been suggested to be the cause of these fluctuations. The intrinsic factors may involve changes in stress and spacing behavior (e.g. aggressive behaviour, dispersal and territoriality) with changing population density. These behavioural changes should further feedback to population density.

Various hypotheses concerning the mechanisms by which the intrinsic factors may operate has been formulated. Christian (1980) suggested that crowding affects the endocrine system altering hormone balance and leading to reproductive failure. Chitty (1967) argued that crowding affected spacing behavior and aggressiveness through natural selection of different behavioural phenotypes during different density conditions. The most recent of these hypotheses are based on the model of social interactions by Hamilton (1964, 1970), which states that individuals should tolerate their relatives more than unrelated individuals and a high degree of relatedness between interacting individuals may enhance their fitness. Two somewhat contradictory models have been presented based on the assumption that voles behave amicably towards kin, but aggressively towards nonkin. The model of Charnov & Finerty (1980) states that during low population density kin associations will be frequent leading to high reproductive success and an increase in the population density. This increases dispersal, which leads to low relatedness between neighboring individuals, low reproductive success and low population density. The model of Lambin & Krebs (1991a) is based on a further assumption that females are philopatric and thus kin clusters of breeding females are formed as density increases and new individuals are recruiting into the breeding population. The kin clusters enhance reproductive success further. Depending on the mortality during the subsequent winter these kin clusters may persist or

break down and the reproductive performance during the next breeding season depends on the relatedness of breeding females in the beginning of the breeding season. However, there is also some evidence that familiarity between interacting individuals rather than the coefficient of kinship as such plays a more important role in mediating the nature of social interactions (Bekoff 1981, Ferkin 1988).

There is no evidence that intrinsic factors could produce cyclic population fluctuations. Recent studies have concluded that intrinsic features such as spacing behaviour would rather have a stabilizing effect on population dynamics (Heske & Bondrup-Nielsen 1990, Ostfeld et al. 1993). Although it seems that some within population processes may also be destabilizing (Ostfeld & Canham 1995), there is growing evidence that the delayed density dependence necessary for population cycles seems to be a result of specialist predators (Hanski et al. 1993). Especially spacing behaviour of breeding female voles has been demonstrated to regulate breeding density (Bujalska 1973, Saitoh 1981, Boonstra & Rodd 1983, Bondrup-Nielsen 1986) and influence immigration and recruitment (Redfield et al. 1978, Bondrup-Nielsen 1986). Whether spacing behaviour of breeding females stabilizes population density depends on how the behaviour relates to prevailing conditions. If individuals have mutually exclusive home ranges of constant size and with a constant proportion of overlap among home ranges independent of density, then the number of animals that can breed on a given area should be fixed and spacing behaviour should have a stabilizing effect on population dynamics. However, if territoriality breaks down with growing density (Bondrup-Nielsen 1985) or if e.g. relatedness between neighboring individuals loosens territoriality, the stabilizing effect may be weak or absent (Heske & Bondrup-Nielsen 1990).

In this research project my aim was to study space use and reproductive success and how they relate to each other and quantity and quality of individuals in the field vole *Microtus agrestis* (L). In Finland field vole inhabits separately situated often relatively unpredictable small patches such as flooding meadows, pastures, hayfields, abandoned fields and clearcuts. These environments are productive, but field vole maybe forced to change its habitat during its lifetime because of flooding, seasonal changes of vegetation and human activities (Myllymäki 1977a). Field vole populations undergo at least 'semi-cyclic' density fluctuations throughout the area of Finland (Hansson & Henttonen 1988).

In the first two papers I studied demography and space use of natural populations of field voles in different habitats. The space use among different age classes at different times during the breeding season and thus under different density conditions was examined as well as regulation of breeding density. The third paper deals with the relationship between space use, survival and different measures of reproductive success among different age classes of breeding females. In the fourth paper I studied how the assumptions of kin effects on reproductive success (Charnov & Finerty 1980, Lambin & Krebs 1991a) and the forming of matrilineal kin clusters of breeding females (Lambin & Krebs 1991a) hold in the field vole. Radionuclides were used to determine matrilineal kinship between the individuals in the studies III and IV

(see Tamarin et al 1983). In the fifth paper I examined experimentally whether familiarity between breeding females affect their space use and reproductive output. The last three studies were conducted in large outdoor enclosures.

2 METHODS

2.1 Study areas

The study areas of all studies situated in Konnevesi Central Finland (62°37'N, 26°20'E). The first two studies (I, II) were carried out during summer 1985 on two live-trapping grids founded on an abandoned field (0.7 ha) and in a thinned moist coniferous forest (1 ha). These study areas were closely juxtaposed so that dispersal between the areas was possible. The three later studies were conducted in 0.25 ha outdoor enclosures during the summers 1992 (III, IV) and 1993 (V). The third study (III) was carried out in six enclosures, the fourth study (IV) in five enclosures and the fifth study (V) in four enclosures. In fact the third and the fourth studies are based on the same data. The sixth enclosure was omitted from the fourth study as no kin clusters were observed in it. The enclosures were situated next to each other on an abandoned field. The enclosures were used to be able to control the movements of the radionuclide-labelled animals, to restrict the assortment of radionuclides needed for labelling (III, IV) and also to preserve the social relations formed during the manipulation of familiarity (V). The lack of opportunity to disperse undermines the generality of the results of the studies conducted in enclosures. Thus, in the studies III and IV we equipped each enclosure with four 5 m long one-way dispersal tubes (Gaines et al. 1979, Viitala et al. 1994), one tube on each side of the four-square enclosure. Vegetation was mown in a 1 m wide strip along the fence inside each enclosure to reduce the chance that the voles entered the tubes accidentally during their normal foraging activities. Dispersal tubes ended in a chamber that was provided with food and nesting material.

The vegetation of both the 0.7 ha open study plot and the enclosures was dominated by grasses (e.g. *Alopecurus pratensis*, *Phleum pratense*, *Elymus repens*, *Deschampsia caespitosa*, *Poa* spp.) interspersed by herbs (e.g. *Ranunculus acris*, *Hypericum maculatum*, *Geum rivale*, *Alchemilla* spp., *Trifolium* spp.). *Epilobium angustifolium*, *Rubus idaeus* and *Filipendula ulmaria* formed patches of pure stand on the 0.7 ha open study plot. 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*. Thus with respect to the habitat requirements of field vole the abandoned field habitats correspond to optimal habitat and the thinned forest correspond to suboptimal-marginal habitat as defined by Stenseth et al. (1977).

2.2 Trapping procedure

The animals used in the studies I and II were the field voles occurring naturally in the study areas. In the studies III, IV, V the founder animals introduced to the enclosures were caught from the Konnevesi area. In the studies III and IV eight sexually mature females and three sexually mature males were introduced to each enclosure. The procedure of the fifth study will be described later. The first two studies began in early May whereas the enclosure studies started in June. All studies lasted until the end of the breeding season i.e. September-October. In all studies the basic monitoring method was the CMR-method using Ugglan Special multiple capture traps arranged in a grid with 10 m intervals. The traps were baited with potato and oats and were checked two or three times a day at four to eight hour intervals. In the first two studies 8 to 10 trap checks were performed during a five day trapping period every other week. These studies consisted a total of 10 trapping periods. In the studies III and IV 15 trap checks were done during a three week period with one week pause between the three trapping periods. In the fifth study 10 trap checks were performed during a two week period and a two week pause was kept between the three trapping periods. At each capture the following data were recorded for the individual vole: identity, trap location, weight and sexual status. The animals were individually marked by toeclipping.

2.3 Basic variables

The number of individuals present during a given trapping period was estimated by the minimum number alive (MNA) method (Krebs 1966). The age of the animals was estimated from its body weight during the first capture using the growth curves in Myllymäki (1977b) and those constructed from the data of the study in question. Trappability of the animals was calculated as probability of an animal to be captured during one inspection of the traps in the study II. In the studies III, IV and V trappability was calculated as the mean number of captures of the individuals present during a given trapping period. Home range size was calculated as the number of traps visited during a trapping period (II) or as the greatest distance between capture points during a trapping period (II, III, IV, V). Inter-individual spacing was measured as the weighted proportion of traps used by two or more individuals of the total number of traps used and by the clumping index of David & Moore (1954) in the study II. In the studies III, IV and V the distance to the nearest neighbor was used (e.g. Krebs 1989). Persistence probability between given trapping periods was estimated as the proportion of recaptured animals (I, III, IV, V). Maturation rate was determined as the proportion of matured females out of all females

probably capable of maturing during the time considered (I). In study V the number of newly matured animals was used. The timing of parturition was estimated on the basis of weight changes of a breeding female (I, III). Reproductive success of breeding females during a trapping period T was estimated as follows (I, V): The number of new recruits during a trapping period one month later (T+1) was divided by the number of breeding females during the trapping period T. In the studies III and IV radionuclides were used to determine matrilineal kinship (Tamarin et al. 1983). Pregnant females were injected intraperitoneally with different gamma-emitting radionuclides or their combinations. As the radionuclides are transferred from mother to offspring via placenta and milk, they can be detected by whole body counts of the offspring. All new recruits were checked for radionuclide burden when caught for the first time.

2.4 Familiarity experiment

The experiment conducted to study the effects of familiarity between the breeding females (V) was designed as follows: Seven sexually mature females and three sexually mature males were introduced to each of the two replicate populations of either mutually familiar or unfamiliar breeding individuals. The familiarity was manipulated by keeping the familiar females together in 1 x 2 m arenas for two months before the experiment. The unfamiliar females were raised separately although they lived with an other female in a small 0.5 x 0.5 m arena until the experiment. So the opportunities to social contacts and stress were approximately the same between the animals of the both treatments before the experiment. Some of the familiarized females were also kin: There were two sister-sister pairs and one mother-daughter pair in one familiar population and two mother-daughter pairs in the other. The members of the kin pairs had, however overwintered separately before the familiarizing period. In the unfamiliar treatment none of the males had former experience of each other, but in the familiar treatment two of the males in both populations had lived in the same arena and in one of the populations these two were brothers.

In addition to the follow up of demography, space use and reproductive success between the treatments we performed behavioural trials on 0.5 x 0.5 m arenas during the first trapping period to imitate the contacts between the voles within both treatments. The arena, with an open bottom, was placed on the home range (= used trap station) of the other participant and the other participant was a trapped animal from the same enclosure. The participants were released from tubes on the opposite corners of the arena after calming down for 1 minute. The trials lasted for 10 minutes during which the number of different behavioural acts (aggressive, amicable, approach) of the participants was recorded.

3 RESULTS

3.1 Demography, regulation of breeding density and space use in natural populations (I, II)

Maximal population density in the abandoned field was about 4 times higher than in the thinned forest. In the abandoned field the population density had two peaks during the summer. The population density in the forest started to grow during the density low in the abandoned field in midsummer. Persistence probability and total reproductive success measured as the number of young weaned per breeding female was greater in the field than in the forest. In the field persistence probability of young breeding females and reproductive success of all breeding females correlated negatively with population density. Reproductive success decreased from May to the end of June when it was similar to that in the forest. At that time the number of breeding females in the forest started to increase. More females than males matured during the study. The spring born males disappeared from the field in June-July when they were ready to become sexually mature. An excess of immature males of this age class was found in the forest. When the effect of season was standardized the proportion of matured females had a significant negative partial correlation with the density of breeding females.

A pronounced variation in the space use of breeding voles was found. There was variation between sexes, among habitats and age classes, in time and with population density. Breeding males were more territorial and had larger home ranges than breeding females. Breeding females in the forest had bigger home ranges and less home range overlap than those in the field. In the field home ranges were larger and home range overlap smaller among the oldest age class of breeding females (born in winter or during the previous breeding season) than among the spring and summer born breeding females. Home range size correlated positively with population density. Home range overlap of the oldest age class correlated positively with the density of that age class. In the younger age classes home range overlap correlated positively with the

density of these age classes as well as with population density. In the forest home range overlap between breeding females correlated positively with their density. In the field spacing of breeding females changed from aggregations in late spring to territoriality in mid summer and again to aggregations in the late summer. The change to territoriality was simultaneous with a decrease in the number of breeding females and a shift of home ranges from the edges of the abandoned field to its central parts.

3.2 Associations between age class, space use, survival and reproductive success (III)

Unsuccessful breeding females (no weaned young) had a shorter distance to their nearest breeding female than the successful (≥ 1 weaned young) ones. The unsuccessful ones were summer born females whereas none of the founder females (introduced to the enclosures in the beginning of the study) was unsuccessful. Founder females weaned more young per female during the study than did their daughters, the summer born females. During the time the latter were in breeding condition there was no difference between these groups. The number of weaned young was highest in litters born in June-July, but decreased in time and was very low in August-September. Among the founder females the weaning success showed repeatability indicating differences in the phenotypic quality between individuals. The weaning success in the beginning of the study predicted the weaning success of the second litter, even though the former weaning success did not predict the weaning success of the third litter. Distance to the nearest breeding female in June-July correlated positively with the weaning success during the same time period. No correlations between space use and reproductive success were found among the later litters. However, the number of breeding sons was positively related to the mean distance to the nearest founder female during the study. Especially the distance to the nearest founder female in June-July (i.e. the time the breeding sons were born) correlated with the number of breeding sons. In addition the number of breeding sons had a great standardized variation indicating potential for selection.

Age, survival, body weight and mean distance moved between the trapping periods explained 38% of the variation in the number of young weaned by the founder females during the study. The same variables excluding body weight explained 50% of the variation in the number of matrilineal descendants alive in the end of the study. The associations between these variables maybe summarized using a concept of an ideal female, which should have the following characteristics: big, winter born, breeding far a way from the other females, moving long distances between trapping periods and surviving until the end of the study.

3.3 Kin clusters and their effect on space use and reproductive success (IV)

In pooled data from five enclosures 55% of young breeding females were philopatric in July-August, but 82% of the mother-daughter associations broke down by August-September. Of the young females that started to breed in August-September only 15% were philopatric. Thus the kin clusters found were short lived and few in number during the late breeding season. Population density increased simultaneously with the decrease in the prevalence of kin clusters. Nearest neighbor distance between all breeding females decreased somewhat at the same time. Relatedness seemed to affect inter-individual spacing. In July-August the nearest neighbor distance between a mother and her breeding philopatric daughter was smaller than that between founder females. The distance between a nonphilopatric young breeding female and its nearest founder female did not differ from that between founder females.

The mean reproductive success of females breeding in kin clusters in July-August was better than that of those breeding separately. In addition among the nonphilopatric females there was a positive significant correlation between reproductive success and the distance to the nearest unrelated founder female. Such correlation was not found among the philopatric females.

3.4 Familiarity, space use and reproductive success (V)

Population density, home range size, maturation rate and behaviour towards other breeding females was similar between the treatments. Nearest neighbor distances seemed to be smaller among the familiar females during the trapping period in August ($P < 0.1$). The persistence probabilities were somewhat greater ($P < 0.1$) among the familiar females in the beginning of the study. However the number of recruits produced seemed ($P < 0.1$) to be even larger among the unfamiliar females in the latter part of the study. The results suggest that familiarity between breeding females had no important effects in *Microtus agrestis*.

4 DISCUSSION

4.1 Space use and breeding density

Territoriality among breeding males seemed to regulate the number of breeding males in the free-ranging study population as indicated by the low persistence probability of spring born males and their excess in the suboptimal forest habitat (I, II). Myllymäki (1977b, c) came to the same conclusion in his studies with southern Finnish field voles. Nelson (1994), however suggested that female density had a significant effect on dispersal movements of juvenile and subadult males in a southern Swedish field vole population. It may be that inability to become established as a breeding male due to male territoriality was the ultimate reason for the dispersal of the young males although the proximate reason may have included aggression by females, which had to compete for food with the surplus males.

The situation among the females was different (I, II). Maturation rate of young females seemed to depend on the density of breeding females but not on the degree of their territoriality: The territorial phase among breeding females in midsummer did not affect maturation rate. Although the breeding females of the oldest age class seemed to be territorial towards each other they tolerated breeding females of the younger age classes. Data of the study IV shows that the young breeding females most closely associated with the old breeding females were likely to be their daughters. Besides maturation rate reproductive success of breeding females and persistence probability of the young breeding females seemed to be density dependent. Colonization of the suboptimal forest habitat during the time reproductive success decreased in the optimal habitat (I) also suggest some kind of density dependent reaction. Thus, there seemed to be density dependent stabilizing phenomena in the field vole population, but the territorial behaviour of breeding females could not act as a stabilizing factor: Home range overlap between breeding females correlated positively with density (II) and at least breeding daughters were tolerated by the old breeding females (IV). The simultaneous decrease in the number of breeding

females and the increase in their home range exclusiveness found in study II, could have involved some kind of social conflict as the females of separate groups along the edges of the abandoned field came into contact when the central parts of the field were inhabited. The tendency of the breeding females in the 'familiar' treatment to have shorter inter-individual distances than those of the 'unfamiliar' treatment in August (V) seems to be in accordance with this interpretation. However, half of the breeding females in August were recently matured young females, who should not have been affected by the familiarity treatment. Thus the effect of familiarity could not be confirmed.

The finding of this study, that female territorial behaviour is not an important regulator of breeding density is in accordance with previous studies with the same species (Viitala 1977, Myllymäki 1977c, Agrell 1995). However the effect of relatedness on space use has not been confirmed before. Agrell (1995) found that relatedness between neighboring breeding field vole females had no effect on inter-individual spacing. The related females in that study were sisters whereas my results are from mother-daughter pairs. The latter may be more prevalent in the field vole as I found no cases where sisters were the nearest neighbors (IV). The observed phenomena among breeding female field voles are also generally in accordance with the scheme suggested by Bondrup-Nielsen (1985) for this species: increasing home range overlap with increasing density and density dependent dispersal (persistence) among breeding females. The positive relationship between home range size and density (II) contradicts with a negative one suggested by Bondrup-Nielsen (1985) and reported in studies reviewed by Madison (1985). Large home ranges during high densities probably ensured enough food for the breeding females. The quality and quantity of food can change with season and - at least with a delay - with density (Agrell 1995).

4.2 Space use and reproductive success

Space use of breeding females was related to their reproductive success (III). Although it seemed that distance to the nearest breeding female was smaller among the females that failed to wean young than among the successful ones, this relationship was very likely connected to differences among the age classes: The unsuccessful females were all summer born. However the positive correlation between weaning success and nearest neighbor distance found among the founder females in the beginning of the study suggests that living far from the others was beneficial for breeding females. Probably access to resources is maximized and the probability of infanticide (Wolff 1993) is minimized in this way. Ostfeld et al. (1988) found a tendency - although not statistically significant - for successful *M. pennsylvanicus* females to have less intrasexual overlap than the unsuccessful ones. Mappes et al. (1995) found a positive correlation between weaning success and distance to the nearest breeding female among unrelated *Clethrionomys glareolus* females, but not among related ones suggesting that infanticide was the primary factor. A similar association was found in my fourth paper: the distance to the nearest unrelated founder female correlated positively with weaning success among

nonphilopatric young breeding females but not among the philopatric ones. The infanticide hypothesis was thus supported. However, the positive correlation between the number of breeding sons and distance to the nearest founder female found among founder females may also be interpreted by the exclusive access to resources hypothesis. Breeding sons are generally considered costly to produce especially among species with strongly female biased sex ratios (e.g. Trivers & Willard 1973). Thus females with exclusive access to resources should have a benefit. Furthermore the great standardized variance found in the number of breeding sons produced suggests that there was an opportunity for selection for the tendency to keep distance to the other breeding females in the study populations (see Clutton-Brock 1988).

Mean distance moved between the trapping periods was positively related with the number of young weaned among the founder females. Myllymäki (1977c) and Viitala (1977) have observed that field vole females shift their home range after they have weaned a litter. It may be that rearing a large litter leads to depletion of food resources in the nearest neighborhood of the nest. Thus it should be advantageous to move slightly between the litters. Sheridan & Tamarin (1988) found the opposite with *Microtus pennsylvanicus*. The females that failed to wean young moved longer distances between trapping periods than the successful ones. I suggest that this relationship maybe caused partly by nonestablished young individuals. The inclusion of them changed the direction of the relationship also in our data (see Table 1 in III).

4.3 Philopatry and kin effects

The model presented by Lambin & Krebs (1991a) to explain aspects of density fluctuations of voles is based on the assumption of philopatry of female voles. The results of the fourth study show that philopatry was common among maturing field vole females in midsummer. Kin associations however were short lived and philopatry was rare later in the breeding season. Thus relatedness between breeding field vole females was greater earlier in the breeding season at lower population density than later at higher density. These observations contradict with the assumption of Lambin & Krebs (1991a) stating that the average degree of genetic relatedness should increase among the neighboring breeding females as density increases during a breeding season. The pattern between relatedness and density was more like that assumed by Charnov & Finerty (1980) i.e. decreasing relatedness between neighboring voles with increasing density.

Lambin (1994) reported an increase in philopatry with increasing population density among *Microtus townsendii*. This was also found in a southern Swedish field vole population by Sandell et al. (1990, 1991). One reason for the differences between field vole populations from different geographic regions maybe differences in the habitat structure between these areas (see Bondrup-Nielsen 1985). In Finland the optimal habitats of field vole are mainly patches in more or less suboptimal environment. In southern Sweden field voles live in more contiguous agricultural habitats where the

increase in density may inhibit movements as it means that all inhabitable area is occupied. It could also be argued that my results are artefacts due to the confinement and the way these populations were founded. However it seems that the introduction of the animals to the enclosures may have been an event comparable to the colonization of the abandoned field by the naturally occurring field voles in the studies I and II. The timing of these events was the same and furthermore formerly unfamiliar individuals came into contact with each other in both events. The dispersal tubes of the enclosures further increased the natural character of the enclosure study. Thus I think there is no reason to believe that the results in the enclosure study would deviate markedly from the situation in the natural populations.

It is worth to note that although the spatial associations between philopatric breeding daughters and their mothers seemed to be closer than those between the unrelated breeding females, the nearest neighbor distances between breeding females decreased somewhat from July-August to August-September i.e. simultaneously with the decrease in the number of kin clusters (IV). The decrease in the distance to the nearest neighbor probably corresponds to the increase in home range overlap observed in late summer among some vole species (Myllymäki 1977c, Viitala 1977, Madison & McShea 1987, Lambin & Krebs 1991b, Agrell 1995). This increase is often interpreted to be caused by the forming of extended families (e.g. Lambin & Krebs 1991a), although the kinship between neighboring voles has not been assessed (for exceptions see Pugh & Tamarin 1990, Lambin 1994). In the light of our results we agree with Agrell (1995) that the reason for this shift in female social organization is not increasing relatedness between breeding females. The mechanism behind this shift is probably the mutual tolerance among the summer born breeding females which form the majority of the breeding females during this time, but the ultimate cause is unclear (Agrell 1995).

The assumption of the favourable effects of relatedness between neighboring individuals on their fitness included in the models of both Charnov & Finerty (1980) and Lambin & Krebs (1991a) was supported to some extent although no clear differences between individuals breeding next to related or unrelated females was found. The slight benefit possibly gained when breeding with kin was restricted to a short period of time. It is thus unlikely that the kin effects observed markedly affected population growth. The reproductive success of the introduced mutually unrelated females was high in the beginning of the study (III) suggesting that unrelatedness per se can not seriously inhibit reproduction. In addition the results of the last study (V) showed that the reproductive success was very similar in populations with mutually unfamiliar or mutually familiar founder females. Some of the females in the familiar treatment were also related. This experiment had only two replicates per treatment, but there was so much overlap between and variability within the treatments that it seems very unlikely that increasing the number of study populations would have changed the results.

5 CONCLUSIONS

The variable space use of breeding females of *Microtus agrestis* seemed to reflect prevailing social environment, but probably also food conditions. The observed associations between space use and reproductive success suggest that appropriate behaviour enhances fitness. However the way space use (territoriality) reacted to density and relatedness between breeding females makes it incapable to regulate breeding density (Heske & Bondrup-Nielsen 1990, Ostfeld & Canham 1994). The great within and between species variation in space use patterns observed among different vole species (e.g. Madison 1990) should be borne in mind when evaluating the population models assuming certain mode of behaviour. Although unlikely able to explain population cycles of voles the models like those of Charnov & Finerty (1980) and Lambin & Krebs (1991a) offer useful testable assumptions and predictions. However, the different statements of the models seem to be valid for different vole species and maybe also for the same species under different conditions as the differences between my study populations (IV) and those of Agrell (1995) suggest. According to Charnov & Finerty (1980) patchy distribution of habitats is decisive to their model. In more continuous habitats the relationship between density and relatedness may be more like that assumed by Lambin & Krebs (1991a). Thus the seemingly useless argument about the absolutely right models has still proved to be a useful mechanism to keep up the vast amount of research on the cycle puzzle.

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Yhteenveto

Lajin sisäiset vuorovaikutukset, tilakäyttäytyminen ja lisääntymismenestys peltomyyrällä

Myyrien dramaattiset sykliset kannanvaihtelut Euraasian ja Pohjois-Amerikan pohjoisilla leveysasteilla ovat olleet eräs populaatioiden säätelymekanismeihin kohdistuneen tutkimuksen keskeinen kohde. Kannanvaihteluiden syiksi on esitetty sekä populaation ulkoisia (sää, ravinto, saalistajat, loiset) että sisäisiä tekijöitä (populaation yksilöiden väliset vuorovaikutukset). Nykyisin ulkoisten tekijöiden uskotaan aiheuttavan syklit, mutta myös populaation sisäiset vuorovaikutukset näyttävän vaikuttavan populaation kokoon. Eräillä lajeilla sukulaiset tai keskenään tutut yksilöt suhtautuvat toisiinsa rauhanomaisemmin kuin keskenään vieraat yksilöt. Tämä voi näkyä edelleen tilakäyttäytymisessä (esim. reviirikäyttäytyminen) ja lisääntymismenestyksessä. Populaation tiheys voi vaikuttaa erilaisten vuorovaikutusten, kuten sukulaisvuorovaikutusten ja kilpailun yleisyyteen ja merkitykseen, sekä mm. reviirikäyttäytymisen ja lisääntymisen ehtoihin. Tämän tutkimuksen tarkoituksena on selvittää peltomyyrän tilakäyttäytymisen ja lisääntymismenestyksen välisiä suhteita ja riippuvuutta populaation tiheydestä ja yksilöiden välisestä sukulaisuudesta ja tuttuudesta.

Tutkimuksen tausta-aineisto hankittiin seuraamalla luonnonpopulaatioita elävänä pyytävillä loukuilla. Yksilöllisen lisääntymismenestyksen ja sukulaisuuden merkityksen selvittämiseksi radioaktiivisilla aineilla merkittyjä eläimiä ja niiden jälkeläisiä seurattiin tarhoissa. Tuttuuden vaikutusta tutkittiin vertaamalla tarhapopulaatioita, joiden yksilöt joko tunsivat tai eivät tunteneet toisiaan ennen koetta. Luonnonpopulaatioiden seurannan tulosten perusteella lisääntyvien myyrien tilakäyttäytyminen vaihteli sukupuolittain, ikäluokittain, elinympäristöittäin, ajassa ja populaatiotiheyden mukaan. Lisääntyvien naaraiden liikkuma-alojen päällekkäisyys lisääntyi populaatiotiheyden kasvaessa. Tämä oli tyypillistä erityisesti nuorilla naarailla. Tarhakokeiden perusteella tilakäyttäytyminen ja lisääntymismenestys riippuivat tutkimuksen alkupuolella toisistaan siten, että naaraiden lisääntymismenestys kasvoi etäisyyden toisiin lisääntyviin naaraihin kasvaessa. Myöhemmin nuorten kesällä syntyneiden naaraiden tullessa sukukypsiksi sukulaisryhmissä eläminen näytti parantavan lisääntymismenestystä. Emot näyttivät myös sietävän lisääntyviä tyttäriään lähellään paremmin kuin muita, erityisesti vanhempia lisääntyviä naaraita. Tästä huolimatta sukulaisryhmissä eläminen oli yleistä vain tutkimuksen alussa, mutta ei enää loppukesällä. Tämä tulos ei sovi yleiseen näkemykseen, jonka mukaan lisääntyvien naaraiden sukulaisryhmät yleistyvät lisääntymiskauden edistyessä nuorten kotipaikkauskollisten naaraiden tullessa lisääntymiskuntoon. Aikaisemmissa tutkimuksissa vierekkäin lisääntyvien naaraiden sukulaisuus on kuitenkin harvoin selvitetty luotettavasti. Naaraiden keskinäisellä tuttuudella ei näyttänyt olevan merkitystä käyttäytymisen tai lisääntymismenestyksen kannalta.

Saamieni tulosten perusteella peltomyyränaaraiden tilakäyttäminen näyttää heijastavan vallitsevaa sosiaalista ympäristöä, mutta ilmeisesti myös ravintotilannetta. Olosuhteisiin sopiva tilakäyttäytyminen mahdollistaa hyvän lisääntymismenestyksen. Reviirikäyttäytyminen ei kuitenkaan mahdollista lisääntyvän populaation koon säätelyä, koska populaatiotiheyden kasvu ja yksilöiden välinen sukulaisuus näyttävät vähentävän taipumusta reviirinpitoon.

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I

**DEMOGRAPHY AND REGULATION OF BREEDING
DENSITY IN THE FIELD VOLE, MICROTUS AGRESTIS**

by

Jyrki Pusenius & Jussi Viitala

Ann. Zool. Fennici 30: 133 - 142, 1993

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II

**VARYING SPACING BEHAVIOUR OF BREEDING FIELD
VOLES, MICROTUS AGRESTIS**

by

Jyrki Pusenius & Jussi Viitala

Ann. Zool. Fennici 30: 143 - 152, 1993

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III

**VARIATION IN REPRODUCTIVE SUCCESS IN FEMALE
FIELD VOLES, *MICROTUS AGRISTIS***

by

Jyrki Pusenius

Manuscript

VARIATION IN REPRODUCTIVE SUCCESS IN FEMALE FIELD VOLES *MICROTUS AGRISTIS*

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Abstract. Variation in reproductive success is a prerequisite for natural selection. Radionuclides were used to determine matrilineal kinship and reproductive success of field vole females in six 0.25 ha enclosures. Founder females introduced to the enclosures in June weaned more young per female during the study than did their daughters, the summer born females. During the time the latter were in breeding condition there was no difference between these groups. Number of weaned young was highest among litters born in June-July, decreased in time and was very low in August-September. The weaning success showed repeatability: The weaning success in the beginning of the study predicted the weaning success of the second litter, even though the former weaning success did not predict the weaning success of the third litter. No correlation was found between the reproductive success of mothers and their daughters. Distance to the nearest founder female in June-July correlated positively with the weaning success of the young born during the same time period. No correlations between space use and reproductive success were found among the later litters.

Among the founder females age, survival, body weight and mean distance moved between the trapping periods explained 38% of the variation in the number of young weaned during the study. The same variables excluding body weight explained 50% of the variation in the number of matrilineal descendants alive in the end of the study. Winter born females were bigger and weaned more young per female than the females of other age classes. Among the winter born females those that survived until the end of the study weaned more young than the non-survived. This relationship was reversed among the overwintered females as well as among the summer born females. Of the different measures of reproductive success the number of breeding sons, the number of breeding daughters and the number of daughters' offspring had the greatest standardized variance indicating the greatest opportunity for selection. The number of breeding sons was positively related to the distance to the nearest founder female, whereas the number of breeding daughters and the number of daughters' offspring were positively related to body weight.

Introduction

Variation in reproductive success is a prerequisite for natural selection. Depending on the definition of reproductive success and thus ultimately the objectives of the study, different components - e.g. longevity, mating success, fecundity, offspring survival - maybe involved. The extent the different components contribute to the total variation depends on the system studied. The amount of the total variation seems to depend much of the measure chosen. Based on a review on several taxons of both invertebrates and vertebrates Clutton-Brock (1988a) suggests that the

variation in reproductive success seem to increase when more advanced stages in life history (e.g. number of zygotes vs. number of breeding offspring) are used as its measure. Clutton-Brock predicts that the variation increases further if the subsequent generations are involved. In polygynous mammal species the variation of female reproductive success is thought to be relatively small especially compared to that of males. All estrous females are generally thought to be inseminated and the variation in litter size has been found to be relatively small (Clutton-Brock 1988a). However, differences in the survival of nestlings may increase the variation significantly. In a polygynous vole species *Microtus pennsylvanicus* the variation of female reproductive success - measured as the number of young produced to the trappable population - has been found to be even larger than that of males (Sheridan & Tamarin 1988).

Reproductive success and its components has been found to be related with factors like age, body size, dominance rank and traits of mate (Clutton-Brock 1988a). In voles reproductive success has also been found to be associated with space use (Sheridan & Tamarin 1988, Ostfeld et al. 1988, Koskela et al., unpublished). Another trait related to reproductive success is sex ratio of the young produced. Trivers & Willard (1973) suggested that parents could improve their reproductive success by investing more heavily on the sex which has the greater fitness variation. In a polygynous breeding system only mothers in good condition could produce males successfully competing with the established breeding males. Mothers in poorer condition should produce more female offspring.

In the present study my aim is to examine the amount and correlates of variation in reproductive success of female field voles during one breeding season. Thus I defined reproductive success as the number of young weaned during the study. To include different life history stages and the subsequent generation, I also determined the number of breeding offspring and the number of grand offspring. In addition to include the effect of offspring survival I determined the number of recruits alive in the end of the study. A more detailed description of the different measures of reproductive success follows in methods.

Kinship between individuals is difficult to determine in natural conditions for cryptic small animals like voles. By using radionuclide technique (see Tamarin et al. 1983) I could determine matrilineal kinship of field voles recruited into trappable population and thus, the number of young weaned by different breeding females. This method has been successfully applied in studies made with *Microtus pennsylvanicus*, which is a closely related to our study object, field vole *Microtus agrestis* (Anderson 1985). Mating structure of field vole may vary from polygynous (e.g. Myllymäki 1977a) to promiscuous (Nelson 1994). Older breeding females are usually mutually territorial, but younger females breed on home ranges overlapping more or less with those of other breeding females (Pusenius & Viitala 1993, Agrell 1995).

More specifically I seek answers to the following questions: 1) How wide is temporal variation in reproductive success, does tendency to be successful persist in time and does it even transfer to the next generation. 2) How are the different measures and components of reproductive success related to each other and individual characteristics such as age body size and space use. 3) What is the extent of variation among the different measures of reproductive success measured in different life history stages or generations and composed of different components.

Methods

The study was conducted in six adjacent 2500 m² outdoor enclosures at Konnevesi in central Finland (62° 35' N, 26° 20' E) during summer 1992. The enclosures were surrounded by a metal fence: 0.5 m below and 1 m above ground. An electric wire was laid about 10 cm over the fence to prevent predators to enter the enclosures. The habitat of each enclosure is mainly old field with bushes, which is the habitat preferred by field vole (e.g. Hansson 1977). Most abundant plants are grasses (e.g. *Alopecurus pratensis*, *Phleum pratense*, *Elymus repens*, *Deschampsia caespitosa*, *Poa* spp.) interspersed by herbs (e.g. *Ranunculus acris*, *Hypericum maculatum*, *Geum rivale*, *Alchemilla* spp., *Trifolium* spp.) and saplings of *Alnus incana* and *Salix* spp. The vegetation of the enclosures is fairly similar.

Lack of the opportunity for dispersal may reduce the generality of studies conducted in enclosures (Pusenius & Ylönen 1994). Thus each enclosure was equipped with four 5 m long one-way dispersal tubes (Gaines et al. 1979, Viitala et al. 1994), one tube on each side of the four-square enclosure. Vegetation was mown from a 1 m wide strip next to the fence inside each enclosure to reduce the chance that the voles entered the tubes accidentally during their normal foraging activities. Dispersal tubes ended in a chamber that was provided with food and nesting material.

In the beginning of the study on 18th of June, eight sexually mature females (later founder females) and three mature males were released simultaneously at the midpoint of each enclosure. These founder animals were trapped from different sites in Konnevesi area and were kept in a laboratory for at least one month before the study. The animals introduced to a given enclosure had no prior exposure to each other. After a one-week habituation period we started to monitor the populations by live-trapping. In each enclosure 25 Ugglan Special multiple-capture traps were set in a 5 × 5 grid 10 m apart. The traps were baited with potato and oats. We had three trapping periods: 29th of June - 17th of July, 27th of July - 14th of August and 24th of August - 11th of September, three weeks each. Fifteen trap checks were performed during each trapping period. Traps were checked twice a day: in the morning and in the evening. At each capture the following data were recorded for each individual vole: identity, trap location, weight and sexual status. The animals were individually marked by toe-clipping. The dispersal tubes were opened on 24th of July to allow dispersal since the time the young of the year recruited to the trappable population. All animals were removed from the enclosures immediately after the last trapping period using both livetraps and snaptraps. This removal trapping was done until the catch was zero and lasted for two weeks.

Number of individuals present during a given trapping period was estimated by the minimum number alive (MNA) method (Krebs 1966). The animals were classified to be disappeared if they were found from dispersal tubes or were not captured subsequently. Space use of breeding females was described using the greatest distance between capture points of an individual during a trapping period as an index of home range size and distance to the nearest breeding female (nearest neighbor distance, see e.g. Krebs 1989) as an index of territoriality. Nearest neighbor distances were calculated based on distances between activity centers of breeding females during a trapping period. The activity centers were calculated as weighed means of x- and y-coordinates of the capture points of an individual during a given

trapping period. A distance between activity centers on successive trapping periods was used as an index of movement.

Radionuclides were used to determine matrilineal kinship of the individuals (see Tamarin et al. 1983). Pregnant females were injected intraperitoneally with different gamma-emitting radionuclides or their combinations. The isotopes used (^{57}Co , ^{59}Fe , ^{54}Mn , ^{75}Se , ^{65}Zn) were selected because of their short half-lives, low toxicity, clearly separable spectral peaks and reasonable price. These isotopes and their combinations were sufficient for 17 clearly separable labels. In six different enclosures 80 breeding females were labelled so that a given isotope or a combination was used only once in a given enclosure. One female was omitted from the analysis because it had begun to reproduce before it was injected. The quantity injected was 0.5 ml isotonic NaCl solution, which contained 1 μCi activity. Booster injections (0.3 ml, 0.6 μCi) were given after the second and further pregnancies. As radionuclides are transferred from mother to offspring via placenta and in milk, they can be detected by whole body counts of the offspring. All new recruits were checked for radionuclide burden when caught for the first time (for more details see Pusenius et al., unpublished)

Age of an individual was estimated from its body weight during the first capture using the growth curves in Myllymäki (1977b) and those constructed from the data of this study. In addition to body weight we used characteristics of pelage (Viitala 1981) to determine the age of the founder females. Time of birth of litters was estimated on the basis of the weight curves of breeding females. Time between successive litters was approximately the same as the periodicity of our live-trapping. So the females produced generally one litter per trapping period. The weanlings were associated to a given litter according their labels and weight during the time of capture. Sex ratio was calculated as the ratio: number of weaned males + 1 / number of weaned females + 1. One was added because the number of weanlings of one or the another sex was zero in some cases.

I measured reproductive success as the number of young weaned during the study and during different trapping periods. Other measures calculated for founder females were the number of breeding daughters and sons produced during the study, the number of daughters' offspring, the number of offspring alive in the end of the study and the number of descendants - including daughters' offspring - alive in the end of the study. These measures are composed of different components as follows. The total number of young weaned during the study is a product of the reproductive life span - i.e. the number of litters produced - and the number of young weaned per litter. These components multiplied by survival of offspring until the end of the study gives the number of offspring alive in the end of the study. The number of matrilineal descendants in the end of the study is obtained when a term containing the number of breeding daughters multiplied with the number and survival of the young weaned by them is added to the number of offspring alive in the end of the study. Survival of offspring was determined as the fraction alive in the end of the study. The variability of the different measures of reproductive success was measured as the square of the coefficient of variation, which can be regarded as a measure of the opportunity for selection (Clutton-Brock 1988b).

Following phenotypic characteristics were measured to be tested for potential association with different measures of reproductive success and their components: body weight in the beginning of the study, mean of the minimum body weights during the different trapping periods, mean trappability, mean home range size,

mean distance to nearest breeding female, mean distance to nearest founder female, mean distance moved between trapping periods and survival until the end of the study. Minimum body weights during different trapping periods were used to minimize the effect of pregnancies on the estimates. These variables were mostly the same used by Sheridan & Tamarin (1988) and Ostfeld et al. (1988) when studying factors associated with reproductive success of *M. pennsylvanicus*.

I constructed statistical models to explain the variation in the measures of reproductive success among the founder females. The eight measures of phenotypic characteristics (see above) added with age class were used as independent variables. For normally distributed measures of reproductive success ANCOVA models were constructed with age class and survival until the end of the study as independent variables and the seven continuous measures of phenotypic characteristics (see above) as covariates. Reproductive measures not meeting the assumptions of parametric ANOVA, were classified into dichotomous variables and analysed with Logistic regression models using the same independent variables as in ANCOVA models. Both type of analyses were started with all independent variables and the nonsignificant ($P > 0.05$) ones were subsequently removed stepwise.

Statistical analyses were performed with *SPSS for windows* package (SPSS Inc. 1992). Normality of distributions of variables were tested with Kolmogorov-Smirnov goodness of fit test. Log-transformation was used to homogenize the variances if needed. Non-parametric methods were used if the validity of assumptions of parametric methods was violated. Tests are generally two-tailed. An exception was the test of the Trivers-Willard hypothesis, where only positive correlation between weight of the mother and sex ratio of offspring was expected. Values given are mean ± 1 SD. The data from different enclosures were combined to provide adequate sample sizes.

Results

Background

Population density was rather homogenous in the different enclosures until July-August, but since August-September there was some differentiation (Fig. 1). The density started to decline after August-September in all enclosures. The number of weaned young did not differ between the enclosures when all injected females are tested together ($F_{5,74} = 1.15$, $P = 0.34$). Neither did the different continuous measures of reproductive success, body weight and space use determined for the founder females (see methods) differ between the enclosures (MANOVA, Pillais' test, $P = 0.47$, $n = 33$). The 79 injected breeding females included to my analysis made up the great majority (81%) of the breeding females caught during the study. 10 out of the 39 (26%) injected breeding females that disappeared from the enclosures during the study were found from dispersal tubes and the rest 29 probably died. The mean number of young weaned by the injected females during the study was 4.32 ± 4.04 ($n = 79$). Successful females (weaned ≥ 1 young) had a longer presence in the study, were heavier and lived further away from each other than females that failed to wean young (Table 1). All 44 founder females were successful compared to 24 successful out of 35 (69%) summer born females ($\chi^2 = 16.07$, $df = 1$, $P = 0.000$).

Mean number of young weaned, mean number of litters produced and body size were smaller among the summer born females than among the founder females (Table 2). However, when comparing number of young weaned per litter (Table 2) the difference was only between winter born founder females and summer born females. The number of young weaned did not differ between the age classes during trapping periods when all age classes existed simultaneously (Fig. 2; July-August: ANOVA, $F_{3,63} = 0.51$, $P = 0.68$; August-September: Kruskal-Wallis ANOVA, $\chi^2 = 2.68$, $df = 3$, $P = 0.44$). Thus, the differences were due to longer reproductive life of the founder females during the study period.

Reproductive success and time

Various aspects of reproductive performance changed with time and some of them differently among the founder females and the summer born females. Pregnancy rate among the founder females was 100% until August-September when three out of 30 females still alive ceased their breeding. Nine out of 23 summer born females that started to breed in July-August ceased their breeding in August-September. Thus, the summer born females ceased their breeding more frequently than the founder females in August-September ($\chi^2 = 6.31$, $df = 1$, $P = 0.012$). However still 9 females started to breed not until August-September. The number of young weaned during a trapping period was greatest early in the reproductive season and declined subsequently (Fig. 2). Weaning success in August-September was very low in all age classes. The standardized variance of weaning success grew with time in all age classes and was highest among the spring born females in August-September. The standardized variance started to grow earlier among the overwintered females than among the other age classes (Fig 3). Among the founder females weaning success of the first litter correlated positively with that of the next litter ($r_p = 0.46$, $n = 40$, $P = 0.003$), but not with that of the latest litter ($r_p = 0.28$, $n = 26$, $P = 0.16$). Weaning success in June-July and July-August correlated positively with the total weaning success ($r_p = 0.87$, $n = 42$, $P = 0.000$; $r_p = 0.81$, $n = 42$, $P = 0.000$, respectively) and the number of matrilineal descendants alive in the end of the study ($r_p = 0.62$, $n = 35$, $P = 0.000$; $r_p = 0.59$, $n = 35$, $P = 0.000$, respectively). Among the summer born females the weaning success in July-August and August-September did not correlate ($r_s = -0.04$, $n = 13$, $P = 0.90$), although both correlated positively with the total weaning success (July-August: $r_p = 0.96$, $n = 25$, $P = 0.000$; August-September: $r_p = 0.42$, $n = 23$, $P = 0.047$). A correlation between reproductive success of mothers and their breeding daughters was determined using the number of young weaned per litter as a measure to remove the effect of different reproductive life span. The value used for the daughters was the mean of the breeding females of a same litter. A negative insignificant correlation was observed ($r_p = -0.21$, $n = 17$, $P = 0.42$).

When considering the trapping periods separately nearest neighbor distance between the founder females during the first trapping period correlated significantly with the number of young weaned during that time interval (Table 3). Among the summer born females no correlations were found between weaning success and the different measured characteristics. Neither were there any significant correlations among the spring born females considered separately from the other founder females (Table 4). Number of weaned males per number of weaned females (sex ratio) correlated positively with mother's bodyweight in the beginning of the study ($r_p = 0.30$, $n = 38$, 1-tailed $P = 0.035$). No such correlation was found later in the

season. Neither did the sex ratio or bodyweight in the beginning of the study correlate with the number of breeding sons produced ($r_s = 0.22$, $n = 42$, $P = 0.15$, $r_s = 0.16$, $n = 44$, $P = 0.30$, respectively).

Variation in the different measures of reproductive success among founder females

When comparing the standardized variance of the measures of reproductive success determined in successive life history stages of the progeny, it seemed that the number of breeding offspring had a greater standardized variance than the number of weaned young (Table 5). When including the next generation the standardized variance increased further: The number of daughters' offspring had a greater standardized variance than the number of breeding daughters. However, the number of breeding sons had the greatest standardized variance.

The most invariable measures of reproductive success were number of litters produced and offspring survival. Thus, their inclusion as components to the measures of reproductive success did not greatly increase the observed variation. E.g. the standardized variance of number of young weaned per litter and that of number of offspring alive in the end of the study was of the same magnitude (Table 5). The number of offspring alive in the end of the study had a high correlation with the number of weaned young per litter, a moderate one with survival of young and only a slight one with the number of litters produced (Table 6). In an analysis of covariance model the number of young weaned per litter accounted for 54%, offspring survival 14% and number of litters produced 9% of the observed variation in the number of offspring alive in the end of the study (ANCOVA, Model, $F_{4,39} = 39.4$, $P = 0.000$). 82 % of the variation in the number of matrilineal descendants alive in the end of the study was explained by the number of young weaned by the founder female itself and the number of young weaned by its daughter. When considering separately, these components explained 66% and 55% (respectively) of the observed variation (Linear regression, $F_{2,33} = 74.11$, $P = 0.000$).

Age class and the interaction between age class and survival until the end of the study as well as body weight in the beginning of the study and mean distance moved between the trapping periods each explained a significant amount of the variance in the number of young weaned and the number of young weaned per litter (Table 7). The observed interaction between age class and survival can be interpreted so that the difference in the reproductive performance between those that survived until the end of the study and those that did not was different among different age classes. Among the overwintered females the survived produced less offspring than the non-survived, the relationship was reversed among the winter born females and non-existent among the spring born females (Fig 4). For comparison it should be noted that among the summer born females those that survived until September seemed to wean less young than those that disappeared before (survived: 1.35 ± 1.50 , $n = 20$, non-survived: 2.67 ± 2.35 , $n = 15$; $t = 2.02$, $df = 33$, $P = 0.051$). When considering winter born females and summer born females together and omitting the females found from dispersal tubes (they are irrelevant when considering costs of reproduction) a significant effect of interaction between age class and survival was found (ANOVA, $n = 41$, age class by survival $F_{1,37} = 7.27$, $P = 0.01$) suggesting different relationship between reproductive success and survival in these age classes.

The model explaining the number of matrilineal descendants alive in the end of the study was very similar to those explaining the number of young weaned (Table

7, Fig 4). In addition to the main effect of age class and the effect of interaction between survival and age, survival had a main effect. Movement between the study periods was the only significant covariate. The variation in the number of offspring alive in the end of the study could be explained by age class (overwintered: 2.18 ± 1.66 , $n = 11$, winter born: 4.20 ± 2.78 , $n = 10$, spring born: 3.30 ± 2.14 , ANCOVA, $F_{2,39} = 4.90$, $P = 0.013$) as well as the covariates body weight in the beginning of the study (regression coefficient, $\beta = 0.60$, $t = 2.59$, $P = 0.017$) and mean trappability during the study ($\beta = 0.33$, $t = 2.40$, $P = 0.021$) constituting the regression term ($F_{2,39} = 5.23$, $P = 0.01$). The model was statistically significant ($F_{4,39} = 3.97$, $P = 0.009$) with the coefficient of determination $R^2 = 0.29$. For the variation in offspring survival I obtained a model including age class (overwintered: 0.38 ± 0.32 , winter born: 0.59 ± 0.24 , spring born: 0.60 ± 0.28 , ANCOVA, $F_{2,40} = 3.54$, $P = 0.38$) and mean distance to the nearest breeding female ($\beta = -0.34$, $F_{2,40} = 5.55$, $P = 0.024$). The model ($F_{3,40} = 3.66$, $P = 0.02$) had a coefficient of determination $R^2 = 0.22$. None of the independent variables used was associated with the survival of daughters' offspring.

Number of litters produced (classified to 1-2 and 3) was explained by survival until the end of the study (Logistic regression, $n = 40$, Wald-statistics, $W = 5.08$, $df = 1$, $P = 0.024$, Partial correlation between the variables $R = 0.25$). Number of breeding sons (classified to 0 and more or equal than 1) was associated by mean distance between founder females ($W = 6.64$, $df = 1$, $P = 0.010$, $R = 0.35$). Especially the distance to the nearest breeding female in the beginning of the study correlated with the number of breeding sons ($r_s = 0.37$, $n = 44$, $P = 0.014$). Number of breeding daughters and number of daughters' offspring (both classified to 0 and more or equal than 1) were associated with mean minimum weight during the study ($W = 7.16$, $df = 1$, $P = 0.007$, $R = 0.31$ and $W = 7.72$, $df = 1$, $P = 0.005$, $R = 0.33$, respectively). Age class appeared to be another factor affecting the number of breeding daughters (Table 2.). Survival until the end of the study was associated with age class ($W = 8.48$, $df = 1$, $P = 0.0036$, $R = 0.34$). 16 out of the 23 (70%) spring born females survived until the end of the study compared to 2 out of the 11 (18%) overwintered females ($W = 6.65$, $df = 1$, $P = 0.01$) and 2 out of the 10 (20%) winter born females ($W = 5.90$, $df = 1$, $P = 0.02$).

Discussion

Sheridan & Tamarin (1988) and Ostfeld et al. (1988) found that home range size, home range overlap, trappability, mobility between trapping periods, body size and survivorship differed between *M. pennsylvanicus* females that were either successful or unsuccessful at weaning young. When analysing the present data same way the authors above did, it appeared that of the variables above nearest neighbor distance (corresponding home range overlap), body weight and survivorship differed between successful and unsuccessful females (see Table 1). Thus the same kind of associations were found in these closely related species (e.g. Anderson 1985). However, as all the unsuccessful females in the present study were summer born, I suggest that most of the differences between successful and unsuccessful females were due to differences between founder females and summer born females. That is why I decided to analyse the founder females separately after the initial

comparisons. When interpreting the results of data like in the present study, one clearly need to be aware of the other sources of variation among individuals than those associated with phenotypic quality.

Repeatability and heritability of reproductive success

Weaning success decreased clearly as breeding season progressed. This means that the initial weaning success determined much of the total weaning success and the factors associated with the initial weaning success may be associated with the total weaning success. Weaning success exhibited also repeatability as the initial weaning success predicted the later weaning success. This indicates differences in the phenotypic quality between individuals. The third breeding attempt differed from the previous ones obviously due to season, which may have masked the effect of individual quality. Although the quality of an individual seemed to persist somewhat, the quality of mother did not simply transfer to the next generation. The used measure of heritability of reproductive success was crude, but indicated that a considerable similarity between mother and daughter was unlikely. This result is in accordance with the statement of Fisher (1930) that characteristics that explain a great proportion of variance in fitness have low heritabilities. The success of daughters might have been determined by slightly different factors than that of the mothers. Lack of experience and reproductive restraint may affect the reproductive success of females breeding for the first time (Clutton-Brock 1988a).

Space use and reproductive success

When considering the trapping periods separately, inter-individual spacing was associated with reproductive success of founder females in the beginning of the study. Those founder females living furthest away of the other individuals were most successful mothers. Mappes et al. (1995) found a similar correlation in the bank vole *Clethrionomys glareolus*. Probably the access to resources is maximized and the probability of infanticide (e.g. Wolff 1993) is minimized in this way. Later in the season the young of the year recruit into the breeding population and in many cases breed near their mother (Pusenius et al., unpublished). This may be one reason for the disappearance of the relationship between inter-individual spacing and reproductive success. The negative association between mean distance between breeding females and offspring survival may indicate potential positive effects of the mother-daughter breeding associations (Pusenius et al., unpublished). Among the summer born females none of the measures of space use correlated with reproductive success. However, a more detailed analysis (Pusenius et al., unpublished) revealed that spatial relationship to unrelated founder females was an important factor affecting reproductive success of these females. Among nonphilopatric summer born females the distance to the nearest unrelated founder female correlated positively with reproductive success. This relationship was not found among the philopatric ones living near their mother. These results suggest that infanticide may be an important factor in field vole populations. Agrell (1995) found that 30% of breeding field vole females (both overwintered and those born during the current year) showed infanticidal behaviour in experimental populations.

The number of breeding sons correlated positively with the mean distance between founder females during the study and with the distance to the nearest

breeding female in the beginning of the study. As sons maybe costly to rear (e.g. Trivers & Willard 1973) this result may indicate that spacing out of home ranges could primarily serve the need for exclusive use of food resources. Furthermore the great value of opportunity for selection in the number of breeding sons suggests that there is also potential for selection to favour spacing out of home ranges provided that it really is a mechanism to produce breeding sons.

Mean distance moved between the trapping periods was a significant covariate in all models constructed for the measures connected tightly to the number of weanlings produced. The females nursing large litters may deplete high quality food within their home range and thus maybe motivated to change their home range before the next litter. Dispersal between litters has been previously observed in *M. agrestis* by Myllymäki (1977b) and Viitala et al. (1994). However Sheridan & Tamarin (1988) found just the opposite in *M. pennsylvanicus*. Females that failed to wean young moved larger distances between trapping periods than successful ones. I suggest that this relationship maybe caused by non established young breeding females. Their inclusion changed the direction of the relationship between movements and reproductive success in our data (see Table 1).

Age, body size, survival and reproductive success

Age, body size and dominance rank are found to affect reproductive success in various taxa of invertebrates and vertebrates (Clutton-Brock 1988a). Age, size and parity of breeding females are the factors most often found to affect litter size of different vole species (Keller 1985, Cockburn 1988) including *M. agrestis* (Myllymäki 1977b). Thus these factors can be expected to affect also the number of young weaned. In the data including all age classes age alone explained 40% of the variation in the number of young weaned. The different performance between the founder females and summer born females seemed primarily to reflect the duration of reproductive life during the study. The founder females had more time to reproduce and the conditions may have been better in the beginning of the study: Population density was low and the production of the food items preferred by field voles was probably better than later in the season (Myllymäki 1977a). Deterioration of the habitat of the enclosures was also observable since August-September when the vegetation started to wither. Nelson et al (1991) found that the relationship between reproductive performance of different age classes changed between years in *M. agrestis*. These authors suggest that the reproductive performance of summer born age classes may increase considerably during years when food conditions are favorable in late summer and autumn.

Among the founder females age and body size explained much of the variation in the variables number of young weaned per litter, number of young weaned and number of offspring alive in the end of the study. Body size and age affected also the number of breeding daughters and body size affected the number of daughters' offspring. According to (Clutton-Brock 1988a) female body size has been found to correlate with milk yield and weight of offspring. The early development of an individual is further connected to its survival, probability of sexual maturation (Myllymäki 1977b) and breeding success (Clutton-Brock 1988a). A related observation was the positive correlation between body weight and sex ratio of the weaned young in the beginning of the study suggesting that larger females invested more heavily on male progeny than smaller females during that time. However, this

correlation was relatively low. In addition neither body weight of the mother nor the sex ratio of weaned offspring did correlate with the number of breeding sons. Thus the results are not clearly consistent with the hypothesis of Trivers & Willard (1973).

The effects of both age and body size were complicated by their relationship with each other and survival. The winter born females had the best reproductive success. This was probably connected to their big size. Especially among the overwintered age class the possible advantage gained by big size and former experience was probably counteracted by aging. The physiological old age may have affected the performance of the overwintered females already since July-August as indicated by the great variance in the number of weaned young (Fig. 3). Among the winter born females the superior quality of some individuals was evident as those that survived best were also the best at weaning young. Among the summer born females there seemed to be a negative relationship between number of weaned young and survival indicating cost of rearing many offspring. Although this kind of phenotypic correlations between different components of fitness should be interpreted carefully (Clutton-Brock 1988a), there were probably true differences between the different age groups. The young breeding females were less experienced and possibly more subordinate (e.g. Pusenius & Viitala 1993, Viitala 1977). Consequently it may have been more costly for them to provide enough food resources to nurse large litters. The more prevalent tendency to cease breeding in August-September among the summer born females than among founder females is in accordance with this view. In addition especially the age classes that start to breed late in the season have been found to abort whole litters (Myllymäki 1977b). As the winter mortality may be very high during some years (e.g. Pusenius 1992) the summer born females may have alternative strategies: Some females may put a maximal effort to their breeding during late summer with a risk dying young, some maybe sensitive to environmental conditions and allocate for next breeding season. The very high standardized variance of weaning success among the spring born females (see Fig. 3) may also indicate preparation to winter by some of the individuals. However, no differences in the survival during the subsequent winter was observed on this basis in a random small sample of this study population (Pusenius unpubl. data)

Extent of variation among different measures of reproductive success

The observed mean number of young weaned during the study and its variance were comparable to the values found by Sheridan & Tamarin (1988) with *M. pennsylvanicus* in a study using the same methods as those in the present study. The standardized variance value of the number of breeding offspring was greater than that of the number of young weaned. Both were quite near a median value observed in studies made with different bird and mammal species (Clutton-Brock 1988a). Furthermore the standardized variance in the number of daughters' offspring was greater than that in the number of breeding daughters produced. These findings are in accordance with the prediction of Clutton-Brock (1988a) stating that the variance in reproductive success increases from the slight variation in zygotes produced to great variation in the number of grand offspring. The greatest variation observed was in the number of breeding sons. The variation in the reproductive success of the offspring might have further increased if I had been able to measure the reproductive success of males (see however Sheridan & Tamarin 1988). It should be noted that my measures of reproductive success were not measures of lifetime

reproductive success. However, especially during the decrease phase of cyclic populations almost all individuals born before July have been found to die before the next breeding season (Myllymäki 1977b). Thus the number of weaned young during the study may be a close approximation for lifetime reproductive success especially for the non-overwintered founder females. During years of moderate winter survival many of the offspring may be able to become sexually mature during next breeding season (c.f. Boonstra 1989) and the number of breeding offspring produced during the lifetime could increase considerably. In this kind of situation the variance in offspring survival would account for much more of the variation in the reproductive success of a breeding female than found in the present study.

The associations found in this study maybe summarized using a concept of an ideal female, which should have the following characteristics: big, winter born, breeding far a way from the other females, moving long distances between trapping periods and surviving until the end of the study. If taking account the great opportunity of selection values obtained for the number of breeding sons and daughters and the number of grand offspring, it maybe concluded that especially tendency to keep distance to the other (unrelated) breeding females and big size are traits potentially under selection in these field vole populations. However even if the individuals equipped with these traits had a great reproductive success it seems that performace of their female descendants does not deviate from average. To get conclusive results heritability analyses should be done using lifetime reproductive success data unavailable for this study.

Finally, more than half of the observed variation remained unexplained by the measures derived from conventional live-trapping data. Some of the variation maybe due to chance. In addition changes in local environmental conditions unrelated to phenotype can have a major effect on reproductive success. These may include local differences in habitat quality and changes in population density (Clutton-Brock 1988a). Factors like microhabitat quality, dominance rank, levels of plasma steroids and parasite load (e.g. Haukisalmi et al. 1995) could be expected to explain some of the variation remaining unexplained in this study.

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Table 1. Differences in survivorship, mean body weight (g), trappability, mobility (m), home range size (m) and nearest neighbor distances (m) between successful (weaned ≥ 1 young) and unsuccessful breeding females. Survivorship is measured as the number of trapping periods an individual was present in the population, mobility was measured as the mean distance moved between trapping periods. Number of cases within brackets.

	Unsuccessful	Successful	t	P
Survivorship	1.82 \pm 0.41 (11)	2.54 \pm 1.10 (68)	-4.02	0.000
Mean body weight	28.06 \pm 6.79 (11)	34.90 \pm 8.33 (68)	-2.58	0.012
Trappability	4.12 \pm 2.18 (11)	5.40 \pm 3.12 (68)	-1.28	0.20
Mobility	13.5 \pm 9.7 (10)	11.2 \pm 6.2 (57)	0.74	0.48
Home range size	27.6 \pm 7.6 (11)	26.1 \pm 10.4 (66)	0.48	0.63
Nearest neighbor distance	6.2 \pm 4.1 (11)	8.4 \pm 2.8 (68)	-2.21	0.030

Table 2. Mean body weight, number of litters produced, number (N) of young weaned during the study, number of young weaned per litter, number of breeding daughters and the number of matrilineal descendants alive in the end of study in different age classes of breeding females.

	Age class				One-Way ANOVA		
	Overwintered	Winter born	Spring born	Summer born	Test-value	P	R ²
Mean body weight	41.6 ± 8.7 (11)	44.6 ± 5.8 (10)	33.4 ± 4.2 (13)	30.6 ± 5.9 (35)	F = 20.30	0.000 ¹	
Number of litters	2.45 ± 0.69 (11)	2.40 ± 0.70 (10)	2.70 ± 0.47 (23)	1.37 ± 0.49 (35)	$\chi^2 = 44.04$	0.000 ²	
N of weaned young	5.18 ± 5.29 (11)	7.70 ± 4.11 (10)	6.09 ± 3.75 (23)	1.91 ± 1.99 (35)	F = 16.49	0.000 ³	0.40
N of weaned young per litter	2.36 ± 2.25 (11)	3.22 ± 1.38 (10)	2.28 ± 1.33 (23)	1.59 ± 1.87 (35)	F = 2.57	0.060 ⁴	0.09
N of breeding daughters	0.91 ± 1.22 (11)	1.50 ± 0.53 (10)	0.43 ± 0.59 (23)		$\chi^2 = 13.30$	0.001	
Number of descendants in the end of the study	3.20 ± 3.08 (10)	5.50 ± 3.59 (8)	3.44 ± 2.26 (18)		F = 1.82	0.18	0.10

¹ The overwintered females and the winter born females were heavier than the spring born and summer born females (Tukey-type pairwise comparison $P < 0.05$).

² Differences between the summer born females and all classes of founder females (Tukey-type pairwise comparison $P < 0.05$).

³ Differences between the summer born females and all classes of founder females (Tukey's HSD, $P < 0.05$). F - value is based on log-transformed data.

⁴ Differences between summer born and winter born females (Tukey's HSD, $P < 0.05$).

Table 3. Correlations between reproductive success and measures of spacing behavior and weight obtained during the trapping period the weanlings were born. Data are from founder females.

	Total		June-July		July-August		August-September	
	n = 44		n = 42		n = 40		n = 26	
	r_p	P	r_p	P	r_p	P	r_s	P
Nearest neighbor distance between founder females	0.18	0.25	0.31	0.04	-0.02	0.91	0.08	0.71
Nearest neighbor distance between all breeding females	0.01	0.97	0.31	0.04	-0.21	0.19	0.05	0.80
Home range size	-0.00	0.99	0.18	0.26	-0.03	0.86	0.04	0.87
Trappability	0.08	0.59	0.24	0.12	0.20	0.23	-0.13	0.52
Body weight	0.08	0.61	0.10	0.52	0.04	0.80	0.28	0.17

Table 4. Correlations between reproductive success and measures of behavior and weight observed during the trapping period the weanlings were born. Data are from spring born founder females and summer born females.

	June-July		July-August		August-September					
	Spring		Spring		Summer		Spring		Summer	
	n = 23		n = 21		n = 25		n = 17		n = 23	
	r_p	P	r_p	P	r_p	P	r_s	P	r_s	P
Nearest neighbor distance between breeding females	0.34	0.13	-0.10	0.68	-0.05	0.80	0.06	0.83	-0.14	0.53
Home range size	0.32	0.16	-0.24	0.30	-0.03	0.89	-0.16	0.53	-0.05	0.82
Trappability	0.47	0.033	-0.04	0.85	0.04	0.85	-0.21	0.42	-0.13	0.55
Body weight	-0.21	0.37	-0.20	0.39	-0.06	0.78	0.28	0.28	0.03	0.90

Table 5. Means, standard deviations and standardized variances of different measures of reproductive performance among the founder females.

Measure	Mean	SD	Standardized variance (SD ² /Mean ²)
Total number or weaned young	6.23	4.25	0.47
Number of young weaned per litter	2.51	1.62	0.42
Number of litters	2.57	0.59	0.05
Number of breeding sons	0.18	0.45	6.25
Number of breeding daughters	0.80	0.88	1.21
Number of breeding offspring	0.98	1.09	1.24
Number of daughters' offspring	1.14	2.23	3.83
Offspring survival	0.54	0.29	0.29
Number of offspring alive in the end of the study	3.23	2.26	0.49
Number of matrilineal descendants alive in the end of the study	3.83	2.88	0.57

Table 6. Correlations between different measures of reproductive success and its components. Correlation coefficients are Pearson product moment correlation coefficients except in cases where variables number of litters, number of breeding daughters or number of daughters' offspring are involved. In these cases Spearman rank correlation coefficients are used. Number of cases is 44 except when variables survival of daughters' offspring or the number of matrilineal descendants alive in the end of the study are involved. In these cases number of cases are 14 and 36 respectively.

Measure	NWL	NL	NWY	OS	NOES	NBD	NDO	SDO
Number of young weaned per litter (NWL)	—							
Number of litters (NL)	-.18	—						
Number or weaned young (NWY)	.92***	.15	—					
Offspring survival (OS)	-.15	.04	-.15	—				
Number of offspring alive in the end of the study (NOES)	.70**	.19	.75**	.41**	—			
Number of breeding daughters (NBD)	.31*	.03	.31*	.20	.38*	—		
Number of daughters offspring (NDO)	.24	.12	.32*	.06	.25	.64***	—	
Survival of daughters offspring (SDO)	.25	.02	.32	-.04	.50°	-.35	-.11	—
Number of matrilineal descendants alive in the end of the study (NMDES)	.65***	.13	.71***	.41*	.88***	.57***	.68***	.52°

° P < 0.10, * P < 0.05, ** P < 0.01, ***P < 0.001

Table 7. Analysis of covariance table for the effects of age class and survival until the end of the study and covariates body weight in the beginning of the study and mean distance moved between trapping periods among the founder females. β denotes the regression coefficient. Analyses are based on data from the founder females. P-values of the covariates are based on t-tests.

Source of Variation	Number of young weaned per litter			Number of young weaned			Number of descendants alive in the end of the study		
	df	F	P	df	F	P	df	F	P
Regression	2	8.03	0.001	2	6.65	0.004	1	8.69	0.007
Body weight		($\beta = 0.72$)	0.007		($\beta = 0.68$)	0.013			
Mean distance moved		($\beta = 0.89$)	0.023		($\beta = 0.32$)	0.037		($\beta = 0.44$)	0.007
Age	2	8.26	0.001 ^a	2	7.58	0.002 ^b	2	8.16	0.002 ^c
Survival	1	0.04	0.834	1	0.31	0.583	1	7.88	0.009
Age by Survival	2	4.19	0.024 ^d	2	4.07	0.027 ^e	2	5.65	0.009 ^f
Model	7	3.41	0.008	7	2.85	0.020	7	4.26	0.004
Total	39			39			32		
		R ² = 0.43			R ² = 0.38			R ² = 0.50	

¹ The overwintered females weaned less young per litter than the winter born ($t = 3.86$, $P = 0.001$) and the spring born females ($t = 3.42$, $P = 0.002$).

² The effect of survival was different between the overwintered and the winter born females ($t = 2.71$, $P = 0.01$) and between the winter born and the spring born females ($t = -2.49$, $P = 0.02$).

³ The overwintered females weaned less young than the winter born females ($t = 3.78$, $P = 0.001$) and the spring born females ($t = 3.11$, $P = 0.004$).

⁴ The effect of survival was different between the overwintered and the winter born females ($t = 2.69$, $P = 0.01$) and between the winter born and the spring born females ($t = -2.42$, $P = 0.02$).

⁵ The winter born females had more matrilineal descendants in the end of the study than the overwintered females ($t = 3.59$, $P = 0.001$) and the spring born females ($t = 3.66$, $P = 0.001$).

⁶ The effect of survival was different between the overwintered and the winter born females ($t = 2.65$, $P = 0.01$) and between the winter born and the spring born females ($t = -3.24$, $P = 0.003$).

Legends of figures

Fig. 1. Mean population density (\pm SD) in the six enclosures during the different trapping periods.

Fig.2. Reproductive success of different age classes in June-July, July-August and August-September. Weaning success among the founder females decreased with time (Friedman ANOVA, $\chi^2 = 32.38$, $df = 2$, $P = 0.000$). Weaning success in June-July was greater than that in July-August which was greater than that in August-September (Wilcoxon Matched Pairs Test, $P < 0.002$ in all cases). Weaning success decreased from July-August to August-September also among the young of the year (Wilcoxon Matched Pairs Test, $Z = -2.10$, $P = 0.036$).

Fig. 3. Standardized variance in reproductive success (see methods) among different age classes during different trapping periods.

Fig. 4. Standardized residuals of the number of young weaned per litter (A), the number of young weaned during the study (B) and the number of matrilineal descendants alive in the end of the study (C) among the survived and non-survived females of different age classes of founder females. Survived were those that survived until the end of the study. The standardized residuals are obtained by subtracting the variation explained by the covariates in the table 7 from the variables considered. Age classes: 1 = Overwintered, 2 = Winter born, 3 = Spring born. Survival: 0 = non-survived, 1 = survived.

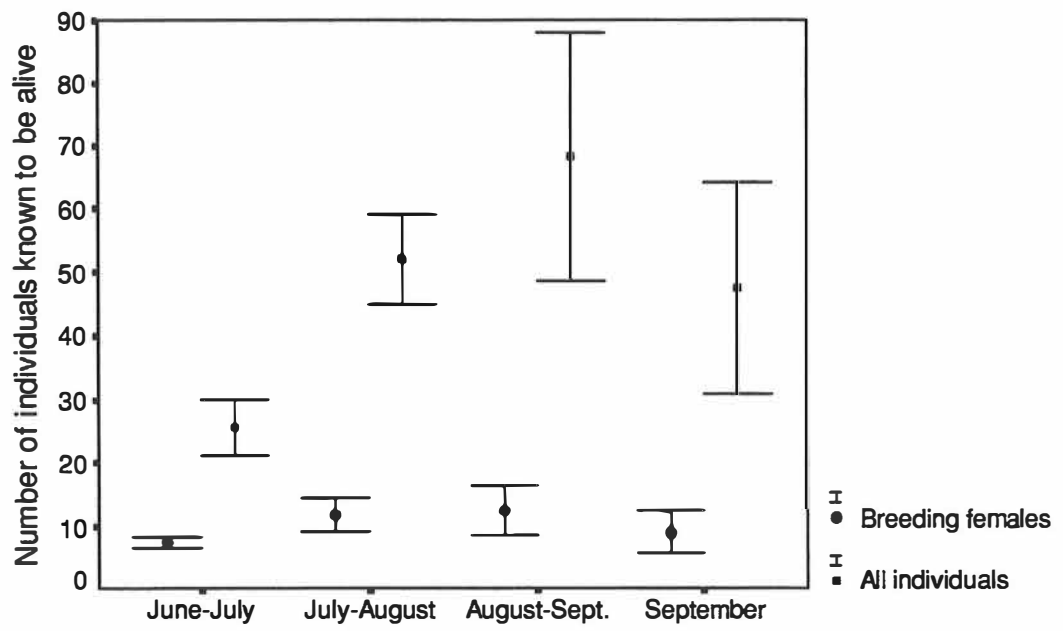


Fig. 1

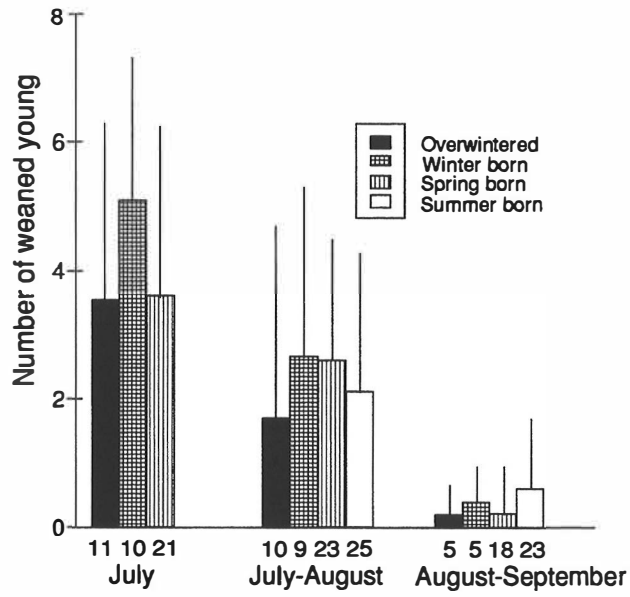


Fig. 2

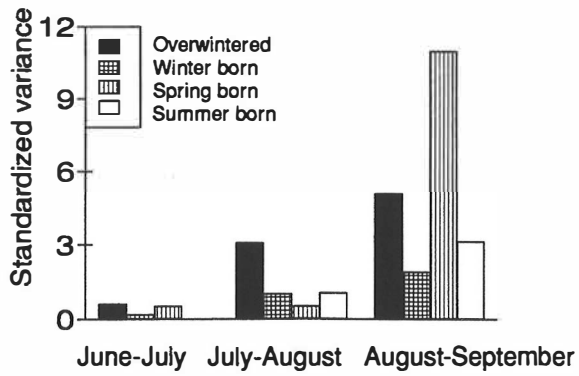


Fig. 3

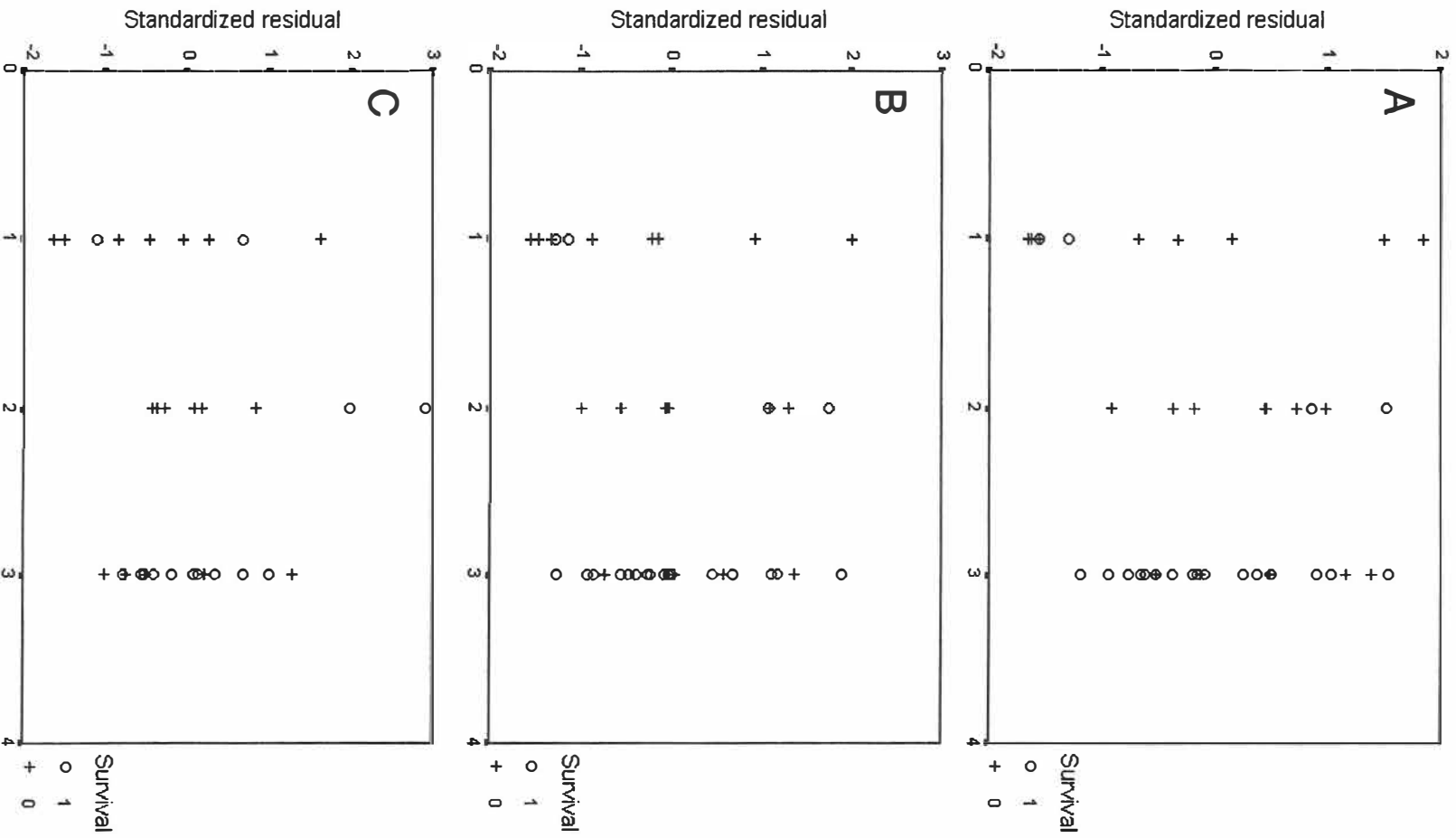


Fig. 4

IV

**MATRILINEAL KIN CLUSTERS AND THEIR EFFECT ON
REPRODUCTIVE SUCCESS IN THE FIELD VOLE, *MICROTUS
AGRESTIS***

by

Jyrki Pusenius, Jussi Viitala, Tuija Marienberg & Seppo Ritvanen

Manuscript

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V

**FAMILIARITY OF BREEDING FIELD VOLE (MICROTUS
AGRESTIS) FEMALES DOES NOT AFFECT THEIR SPACE USE
AND DEMOGRAPHY OF THE POPULATION**

by

Jyrki Pusenius & Jussi Viitala

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