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For Tuomas and Susanne,
my two junior field assistants.

"Troz alledem!"
John Heartfield (1925)

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TEMPORAL VARIATION OF BEHAVIOURAL AND DEMOGRAPHICAL PROCESSES IN CYCLIC CLETHRIONOMYS POPULATIONS

Hannu Ylönen

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The social organization and behavioural ecology of *Clethrionomys* voles were studied in Konnevesi, Central Finland in the years 1982 - 88. The study consisted of long-term comparative work on an enclosed population of the bank vole *Clethrionomys glareolus* (Schreber) and island populations of the grey-sided vole *C. rufocanus* (Sund). Experimental studies, both in four enclosures and in the laboratory, were based on the experience of the dynamics of the local populations.

Previously in the literature described social organization of *Clethrionomys* voles, based on the territoriality of breeding females, could be observed in traditional *Clethrionomys* habitats with *Vaccinium* field layer. In more productive habitats, or with supplementary feeding, more flexible social systems could be observed or induced; home ranges of breeding females overlapped more and daughters could even maturate within their mothers' home range. During the breeding season, the mutual familiarity existing between the founders of the breeding population of *Clethrionomys glareolus* affected the growth of the population significantly; during the course of a three months' experiment the populations of founder individuals familiar with each other grew faster and had better survival of the young. This resulted in population densities twice as high at the end of the breeding season as in the populations founded by individuals strange to each other. Thus, kin selection could be of importance for the growth of breeding *Clethrionomys* populations at least during some phases of the cycle.

The activity pattern of the bank vole population, determined as the diel distribution of visits at the feeding station, was fairly uniform during the breeding season. This uniformity could be ascribed to the more flexible activity distribution of the young. On the whole, the activity pattern of a bank vole population seemed to be polyphasic and irregular.

The normal way of social overwintering in

Clethrionomys seems to be one of more or less tight social aggregation; in larger units or small groups consisting of a few females and at least one male. Territoriality during winter could not be induced, even with food distribution in the overwintering habitat, either. Habitat patchiness and food distribution, but especially the sufficiency of food seem to determine the social way of overwintering.

When overwintering together with harvest mice *Micromys minutus*, both voles and mice avoided each others' ranges. This avoidance persisted during the first half of the breeding season, having a demographical effect in the vole population, too.

The impact of the small mustelids on the study populations was observed throughout the local rodent cycles. Beside direct killing, delayed reproduction in the bank vole was observed during the winter and spring with numerous Mustelid predators. The suppressive impact of the presence of *Mustela nivalis* in the vicinity of breeding pairs of the bank vole on their breeding was positively shown in the laboratory, too.

On the basis of my studies, I can conclude, that the social organization and behaviour in *Clethrionomys* voles seem to be flexible, and to a great extent phenotypically determined. During different phases of the cycle and in different habitats one can observe different kinds of social organization in *Clethrionomys* females. Social factors are obviously of importance especially in increasing and possibly in the peak phases of the cycle. The cause of the crash - and the general causes of cyclicity - must be sought on the basis of more diversified hypotheses; with great attention to predation, parasites and diseases. The individual vole adapts its behaviour to circumstances determined by the habitat and the phase of the cycle.

Key words: *Clethrionomys*, social organization, behaviour, demography, temporal variability, cyclicity.

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The present thesis is based on the following publications, which are referred to in the text by their roman numerals:

I. Ylönen, Hannu, Kojola, Taina & Viitala, Jussi 1988: Changing female spacing behaviour and demography in an enclosed breeding population of *Clethrionomys glareolus*. - Holarct. Ecol. 11:286-292.

II. Ylönen, Hannu & Viitala, Jussi 1985: Social organization of an enclosed winter population of the bank vole *Clethrionomys glareolus.* Ann. Zool. Fennici 22:353-358.

III. Ylönen, Hannu & Viitala, Jussi 1989: Social overwintering and food distribution in the bank vole *Clethrionomys glareolus*. - Manuscript.

IV. Ylönen, Hannu 1988: Diel activity and demography in an enclosed population of the vole *Clethrionomys glareolus* (Schreb.). - Ann. Zool. Fennici 25:221-228.

V. Ylönen, Hannu, Mappes, Tapio & Viitala, Jussi 1989: Different demography in friends and strangers: an experiment on impact of familiarity in *Clethrionomys glareolus* (Schreb.). - Manuscript (submitted).

VI. Ylönen, Hannu: 1989: Weasels *Mustela nivalis* suppress reproduction in cyclic bank voles *Clethrionomys glareolus*. - Oikos 55: 138-140.

VII. Ylönen, Hannu 1989: Spatial avoidance between the bank vole *Clethrionomys glareolus* and the harvest mouse *Micromys minutus.* - Manuscript (submitted).

VIII. Ylönen, Hannu & Viitala, Jussi 1987: Social organization and habitat use of introduced populations of the grey-sided vole *Clethrionomys rufocanus* (Sund) in Central Finland. Zeitschr. Säugetierkd. 52:354-363.

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1. Introduction

One of the features observed in the ecological literature is the persistence of statements once made in a qualified forum. If Microtine populations are once described as showing cyclic fluctuations of population density (e.g. Elton 1942), or if female territoriality or male hierarchy has been shown to form a basic social structure in Microtine populations (Kalela 1957, Bujalska 1970, 1973, Viitala 1977), then most studies tend to confirm the prevailing paradigm. Every population should somehow be cyclic and Microtine species should show species-specific social organization.

However, recent studies have shown, that the patterns in population dynamics and social systems are much more diversified than previously thought; not by far all Microtine populations are cyclic (Henttonen et al. 1985, Hansson & Henttonen 1985) and the social organization also seems to show a great deal of flexibility due to e.g. habitat, resources and actual population density (I, see Ostfeld 1985, Viitala & Hoffmeyer 1985, Ims 1987 for review).

Clethrionomys species are mainly forest dwellers, the habitat being relatively predictable but not so productive. This environment seems to have favoured the evolution of relatively strong female territoriality, which may serve to prevent the overexploitation of the rather poor resources, by keeping even the peak population densities lower than those of the grassland dwelling *Microtus* (Kalela 1957, Bujalska 1970, 1973, Viitala 1977, see also Boonstra & Krebs 1977).

Because of their fairly stable original habitat and stable social system, the *Clethrionomys* species were found to be a good object to study phenotypical flexibility in various aspects of rodent ecology. Annual and possibly multiannual phenotypical variability in the social ecology of the bank vole *Clethrionomys glareolus* provides the framework of this study (I, II, III, IV, VIII). One main point in the present study is to examine the importance of the way of overwintering on the demography of the population during the following breeding season (II, III, VII, VIII). In addition, the aim of the present thesis is to study interspecific relations not between *Clethrionomys* and *Microtus* , which has become one model case of interspecific competition among rodents (e.g. Grant 1969, Henttonen and Hansson 1984, Viitala 1977), but between the bank vole and its small neighbour, the harvest mouse *Micromys minutus* (VII). The impact of probably the most important mammalian predator of forest dwelling rodents, the weasel *Mustela nivalis*, on the breeding behaviour of bank voles (VI), offering many new ideas for further research, finally closes the circle between behavioural adaptations and demographical events in the population.

The papers can in general be divided into comparative long-term studies (I, II, VIII and also IV) and experimental studies (III, V, VI, VII). Long-term studies monitor one or several populations over a number of years including preferably one "cycle". These kind of studies basing on the "Fennoscandian tradition" of ecological research are of fundamental importance for successful planning of experimental studies (see e.g. Haila 1988). The experimental studies in four enclosures or in the laboratory (III, V, VI, VII) are based on the findings of the long-term research of local microtine populations. The study deals with two out of three fennoscandian *Clethrionomys* species, the bank vole *Clethrionomys glareolus* and the grey-sided vole *C. rufocanus*. The red-backed vole *C. rutilus* was found to be an unsuitable object for experimental studies in enclosures or on small islands due to its large home ranges (Viitala 1988).

2. Methods

Study areas were situated around the Konnevesi Research Station of the University of Jyväskylä (62° N). Between the years 1982 - 86 an enclosure of 0.8 ha and several islands in the lake Konnevesi were used in the studies I, II, IV and VIII. The experimental studies of 1987-88 (III, VI, VII) were carried out in four enclosures 0.5 ha each. Study methods are described more exactly in each separate paper.

The main method in each study was the live-trapping of individually marked voles (CMR-method). The diel activity of an enclosed *Clethrionomys* population was monitored over almost two years by means of movie camera equipment set up at a feeding place (IV). Laboratory experiments were carried out in 1988 on the studies with *Mustela nivalis* and *Micromys minutus* (VI, VII).

3. Results and discussion

3.1. Social organization and habitat use of *Clethrionomys* populations during the breeding season

The populations in the enclosure and on islands during the study period (I, VIII) fluctuated syncronously in the same phase with free-living mainland populations (Ylönen 1989 and unpubl., J. Pusenius unpubl.) indicating common extrinsic factors for the synchrony (e.g. Oksanen & Oksanen 1981, Henttonen 1986, Hansson 1987, 1988). Mid-winter breeding was observed in the enclosure population in 1983/84, but there was a very early start to breeding during the next two years (I) and 1988 (VI), too. In 1986, with an early start to breeding, the population declined to zero until autumn, however (I).

In an enclosure it was possible to study a population of *Clethrionomys* with a known actual density and without competition with *Microtus agrestis* (Henttonen & Hansson 1984). In a case of unenclosed populations at the same study site, as in 1988, the field vole would have occupied the whole enclosure area (Fig. 1) consisting of abandoned field, brushwood and spruce forest. Without competition the bank vole also had the possibility to exploit the abandoned field areas of the enclosure, which had the highest densities of

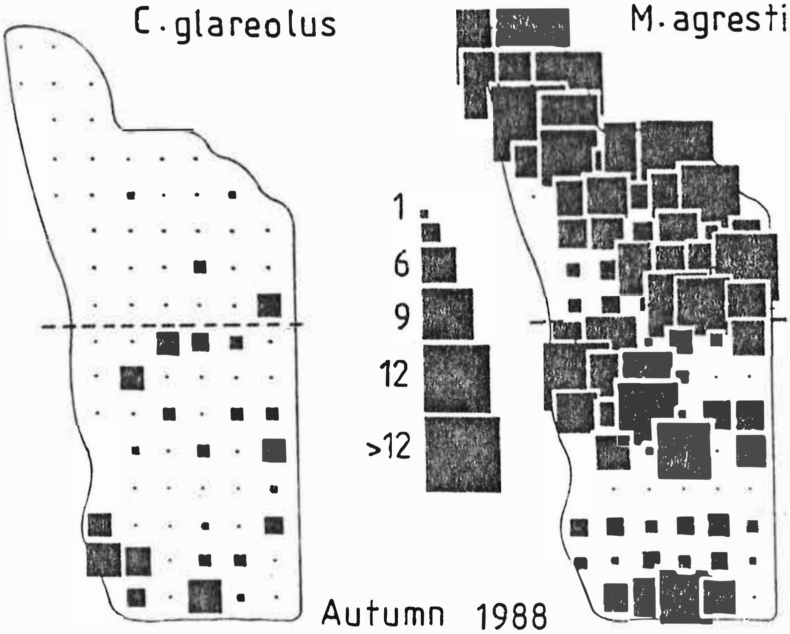

Fig. 1. The distribution of bank voles and field voles in the enclosure area in autumn 1988 during peak populations of microtines in the Konnevesi area. The fence had not been repaired for two years and so the situation resembles that of wild populations. The squares show how many times a vole of the each species was captured in a trap during the trapping period with eleven controls of traps. The dotted line shows the border between the abandoned field (upper part) and the forest (lower part).

voles, especially breeding females, in the peak year of 1984 (I). During the whole study period, the summer of 1985 excluded, the bank voles preferred the abandoned field or brushwood areas during the breeding season. In the summer of 1985 intruding *Microtus agrestis* were allowed to settle down in the field part of the enclosure a phenomenon which was immediately reflected in the the bank voles' habitat use (I, see also Fig. 1).

The highest densities observed in the enclosure were ca. 150 bank voles per hectare in 1984 and 1985 (I), which was about the same as the highest density (142 voles/ha) in the experiment on the effect of familiarity on the growth of the population density in 1988 (V). In the high density years 1984 and 1985, breeding stopped in the enclosure significantly earlier due to social reasons, as compared to the years with low or moderate densities (see also Bujalska 1970, Boonstra & Rodd 1983). The density of voles outside the enclosure in 1985 was also at the same level as that of the enclosure population (Pusenius et al., in prep.) , thus the enclosure population showed no overgrowth effect due to fencing observed in *Microtus* by Krebs et al. (1969) and Boonstra & Krebs (1977).

The social organization of the enclosure population formed by territorial breeding females was "orthodox" (Kalela 1957, Bujalska 1970) during the first two study years with moderate densities of about 50 voles per hectare (I). A similar situation was observed in the island population of *Clethrionomys rufocanus* in 1985 (VIII).

In 1984, after winterbreeding (II) the home range overlap of mature females by about 30 % was the highest observed during the study (I). The overlap was especially high in the *Microtus*-habitat: in the abandoned field area and in the brushwood. These were also preferred overwintering habitats. Obviously the familiarity between the individuals which had overwintered together in addition to the good food situation because of a good seed crop of coniferous trees and also *Alnus incana* in Konnevesi area (Suonenjoki Forest Res. Stn. Statistics, unpubl.) and productivity of old field areas permitted a high density of breeding females with overlapping territories. The same observation was made in the summer of 1988 after the experiment on the effect of food distribution on overwintering of the bank vole (III): due to habitat and familiarity, the daughters of females which had spent the winter in a large aggregation, dispersed from the mothers home range only shortly before the birth of their first litters. The movements from the natal home range to the breeding home range were short during the beginning of the breeding season; the daughters settled down as close to the mother as possible (I, III). This resulted in the formation of female kin groups with high philopatry (see Viitala 1977), which could be of great importance for the good survival of the young (Boonstra 1984) and rapid growth of the population in the beginning of the breeding season.

During the high population density of the breeding season also the time resource seems to be divided rather evenly among the members of the population; the activity pattern of the population measured at a feeding place showed uniform distribution of the visits over the whole 24-hour period (IV). During spring the adults vs. the subadults and juveniles born during the winter (II) showed the same kind of bimodal activity pattern. Until July the young individuals changed their activity to diurnal whilst the adults maintained the dusk/dawn activity pattern. Thus the young individuals seemed to be more flexible in their behaviour if the uniform total activity pattern of the breeding season could be seen as a result of different activity times of distinct social hierarchy groups (Chitty & Shorten 1946, Pearson 1962, Nygren 1978).

To summarize, the social organization of *Clethrionomys*, especially the spatial distribution and habitat use of the population as well as the activity patterns during the breeding season, seems to be a relatively variable, opportunistic system. It seems to react flexibly in accordance with environmental conditions in order to maximize the growth and survival of the population under limitations of available resources.

3. 2. The impact of kinship and familiarity on the demography of breeding populations of *Clethrionomys glareolus*

The effect of familiarity between individuals on the demography of the population, which was thought to have a great influence in the observations made in (I) and (III), was tested in four enclosures of 0.5 hectares each (V). The extent to which the rodents are able to distinguish between kin, neighbours and strangers has been a subject of several studies since the observation that strange males of the same species can cause a pregnancy block in rodents (Bruce 1960, Gavish et al. 1984, Porter et al. 1984, Ferkin 1988).

In the experiment with familiar vs. unfamiliar individuals in the founder populations of the bank vole the result was clear: during the three months experiment populations consisting of familiar parents grew to about twice the size of the populations with unfamiliar parents of the founder populations (V). This difference was due to significantly higher recruitment and better survival of the young in the populations with familiar founder individuals. The reason behind the better survival and recruitment of the young should be the lower level of aggression of adults towards the young among the "friend parents" (e.g. Boonstra 1984, Ferkin 1988, Rodd & Boonstra 1988). Familiarity, decreasing aggression between individuals, allows for a higher overlap of home ranges (I) and can even promote communal nesting (Wilkinson & Baker 1988). The question over whether the conflicting results from our familiarity experiment and those from Boonstra & Hogg (1988) are due to different behavioural strategies in *Clethrionomys* and *Microtus* as genera living in different environments is discussed in (V).

Kin-selection (Charnov & Finerty 1980) can promote rapid population growth in local populations (perhaps especially during the onset of breeding after the winter aggregations (II, III)). However, if different populations of the same area, even in enclosures and on islands (I, VIII) as well as different species (shrews included) show syncronous fluctuations in density (Kaikusalo & Hanski 1985, Henttonen 1986, Korpimäki 1986), kin-selection cannot be the reason for these fluctuations. During low populations phases with sufficient food resources and little or no predation pressure, familiarity can increase the speed of local population growth (V). However, with high densities over more than one peak year the amount of food and the number of predators, possibly together with other factors such as diseases and parasites limit the growth and survival of the populations and finally cause the decline of the populations (see Henttonen et al. 1987 for the effect of a lack of Mustelid-predators, Oksanen & Ericson 1987 and Hansson 1988 for the grazing impact of microtines, Hansson & Henttonen 1988 and Lidicker 1988 for general review).

3.3. Social organization and habitat use in *Clethrionomys* populations during the non-breeding season

The winters in the areas with strong cyclicity in microtine populations in Fennoscandia are characterized with long lasting permanent snow cover (Hansson & Henttonen 1985). The Konnevesi area belongs to the "category" of cyclic populations (I) on the basis of the stable snow circumstances, too. During the winter 1983/84 with a strong winter breeding there was also an exceptionally high snow cover. However, the reasons for the breeding were obviously nutritional rather than due to the high snow cover (see, however, Kaikusalo & Tast 1984, for winter breeding experiments with *Lemmus lemmus)*. According to Whitney & Feist (1984) 30 cm snow is enough to dampen the fluctuations of the subnivean temperature but the voles always prefere areas with the thickest snow cover (II, Hansson 1987). Besides the steady subnivean temperature the snow offers cover against generalist predators (e.g. Hansson 1987).

Of the two main social ways of overwintering, socially or solitarily (see Madison 1984, and West & Dublin 1984 for review) the *Clethrionomys* populations seemed to favour the social aggregation (II, VIII). As a measure of aggregation the strong overlap of capture points during each winter trapping was used. If, and to what extent, the aggregations include communal nesting could not be determined see Karlssons (1988) study with radiotelemetry.

The wintering enclosure population of *Clethrionomys glareolus* aggregated in areas with thick snow cover and a suitable microhabitat with hummocks and holes in the subnivean space. This was the case in the brushwood areas along the former ditches in the field site and forest edges with deciduous trees (II). Moreover, the bush pockets and an old ruin were preferred in the winter 1987/88 (III). The female aggregations were very stable during the whole winter, until as late as June; also the mature and even gravid daughters were allowed to remain in the aggregation area and its immediate surroundings until the birth of their first litters (II, III). The males exhibiting spring dispersal (or movements over large areas in search of possible mates) were attracted by the female aggregations. The reproduction in the aggregations began also earlier in the aggregations than in populations with even food distribution and small female groups (III).

Viitala (1977) reported strong indications of winter territoriality in the grey-sided vole in Finnish Lapland. However, when brought to Central Finland, the voles seemed to aggregate during winter (VIII) in the same way as did local bank vole populations. The obviously normal pattern of winter aggregations seems to be strongly dependent on the habitat.

In the food distribution experiment during the winter 1987/88 we could not induce winter territoriality in the bank vole by offering the voles a habitat with even food distribution (III). In the enclosures with even food distribution the females also established small overwintering groups including a male. The site for overwintering in these groups was chosen in the thickets along the ditches, the same way as in (II).

The pattern of life during winter seems to be very similar for females and males compared with the great differences in the spatial movements of the sexes during the breeding season. The home range size is almost identical during mid-winter until the maturation of males (III, Karlsson 1988). Although in the activity study (IV) the sexes could not be separated, according to trapping data (VII, Ylönen, unpubl.) it seems evident that both sexes living in the same small group or a larger aggregation are active at the same time of the day. Thus, inside the overwintering units the social system seems to be relatively "democratic", despite of potentially great weight differences between the overwintering individuals (II).

3.4. Coexistence of the bank vole *Clethrionomys glareolus* and the harvest mouse *Micromys minutus*

The ecology of the harvest mouse has been studied astonishingly little in areas with a permanent snow cover. However, this species may be the only one among central Finnish rodents - the eastern harvest mouse is lacking from other parts of Fennoscandia except southern and central Finland (e.g. Kaikusalo 1983) - which does not obligatorily take part in the synchrony of microtine fluctuations (own obs., Kaikusalo, pers. comm.). The reasons for this possible asyncrony are not yet clear, but one reason could be the strong ties of the local population outbreaks between the human activities, especially husbandry (Kaikusalo 1983). The harvest mice have to share preferred breeding habitats, old fields and forest edges, with field voles, in some cases also with bank voles, as well as overwintering habitats and barns with bank voles.

In autumn 1987, with high densities of both *Clethrionomys* and *Microtus*, I started an experiment on the coexistence of these species in enclosures over winter (VII). The enclosures had different food distribution (see also III). The small harvest mice were almost excluded from the single food patch by the bank voles, followed by a strong decline in the mouse population density during winter and spring, and a very low recovery during the breeding season. In the enclosure with even food distribution, the two species could coexist with exclusive overwintering areas. This spatial avoidance lasted also over the first half of the breeding season, which disturbed new experiments started in June (V) and the harvest mice had to be removed totally from the enclosures by the end of July.

The bank voles which had overwintered together in the same enclosure avoided the area inhabited by *Micromys* during the beginning of the breeding season. This spatial avoidance seemed to have demographical effects on the growth of the introduced vole population, too (V). The avoidance of the harvest mice traps by the bank vole was positively shown in laboratory experiments.

In North America the related species *Reithrodontomys megalotis* was found to avoid larger coexisting species (Heske & Rapp 1986). The finding that the larger species also would avoid harvest mice is new, and its mechanisms and ecological consequences should be the subject of further studies. Nevertheless, the harvest mice would profit from some kind of buffer against potential competitors, which could perhaps affect the breeding success of the mice during the early breeding season, with the first nests built on the surface of the ground. During the later breeding season *Micromys* build their nests above the ground and change to arboreal way of life, which minimizes the competition with other species during the highest densities of all species.

3. 5. The impact of weasels *Mustela nivalis* on the reproduction of bank voles

Winter breeding was observed in the enclosed bank vole population in 1983/84 and 1986/87 both years of increasing local microtine populations (II, Ylönen 1989) and lacking mustelid predators. In the winter experiment 1987/88 the voles also showed indications of breeding performance already in February but breeding was suppressed during the preceding ten weeks, with the first litters born in late April. The only observed difference for the previous two winters, with breeding during mid-winter, was the presence of weasels in the enclosure areas between January and March (VI).

The hypothesis that the risk of predation would influence the behaviour of prey (Ydenberg 1987), which has been supported by studies on insects and fishes (e.g. Endler 1987, Sih 1988), was tested in the laboratory in terms of the breeding behaviour of bank voles under stress from its main predator. The first experiments - further experiments could not be done because of early cessation of breeding during the peak year (I) - showed a significant influence of the presence of the weasel in the vicinity of the vole pairs on their breeding condition: none of the pairs with weasels present bred, compared with three out of four successful fertilizations in the group without a weasel. Also the weight of males was negatively affected due to the presence of a predator.

The findings support Ydenberg's (1987) hypothesis on the behavioural response of the prey on predation risk. The negative impact of weasels on the activity and spacing behaviour has been observed by Jedrzejewski and Jedrzejewska (1988, 1989), but the question, under which circumstances it would be of advantage for a female not to breed, is on the totally different evolutionary level. Further studies using more variable and less extreme methods are needed on the indirect influence of specialist predators on the behaviour of voles.

4. Conclusions

The social organization of *Clethrionomys* populations is flexible, reacting in accordance with changing environmental conditions. Individual voles react to the circumstances in which they live; habitat structure, food resources, predation pressure and possible outbreaks of diseases or parasites. Behind all this is hovering the ghost of cyclicity, of which the individual vole is of course unaware. If the voles face only some phases of the cycle during their life span, already this evidently leeds to a diversified system of population regulation of microtines (Hansson & Henttonen 1988). A single factor influencing the population dynamics and social organization during one phase does not have to have the same impact during another phase of cyclic fluctuation (Lidicker 1988).

On the basis of my research, I could summarize the main demographical and behavioural characteristics in a population of *Clethrionomys* voles against the background of cyclical fluctuations of microtines in my study area, as follows:

1) After the crash year the few remaining voles stay over the preceding winter in small groups in suitable habitat patches with as thick a snow cover as possible. The voles may be kin, but during winter they become familiar with each other. The survival rate is good and the onset of breeding can start early (depending on food situation).

2) Early breeding and good survival cause a rapid growth in the population and spreading out from the survival patches. Breeding females can build kin/familiarity clusters in the beginning of the breeding season, and females maturing late in the breeding season have moved further from their natal territory.

3) The next wintering of the voles occurs in aggregations or smaller groups; territorial overwintering could possibly take place on even but poor habitats. The survival rate is good and dispersing males, attracted by female groups, effect the early onset of breeding, if the food resources allow it.

4) A relatively high spring population and an early start of breeding causes an outbreak of the population density the following summer. Breeding females show exclusive territoriality of home ranges, which get smaller or exhibit increased overlap because of good food situation. Breeding stops relatively early due to social reasons. The survival of

the young decreases. Predation pressure increases.

5) The densities of the next overwintering populations are high. This is expressed in relatively even distribution of voles in optimal and suboptimal wintering habitats. However, territoriality is not commonly observed. The best habitat patches are overexploited. Predation pressure is high, which has a direct impact on density and possibly an indirect impact on the behaviour of individual voles. Strong winter decline could be caused by heavy predation, accompanied by parasites and diseases spreading throughout dense populations in subnivean space. During the decline of the spring 1989 I observed several trap deaths in both field and bank voles and some voles were too weak even to enter the trap and were found dead in front of it.

6) During the spring of the crash year, remaining females stay territorial. The survival of the young is poor obviously due to diseases and predation. The survival of the young could be selective; some litters die as a whole as some survive relatively well. This could promote the formation of small kin-groups. Summer decline is observed.

The described patterns, perhaps a little speculative, have to be verified in further studies, which have to be based on the knowledge of local population dynamics. One should pay attention on behavioural patterns against the background of cyclicity vs. non-cyclicity (cf. Hansson 1986) and the behavioural impact of predators. The role of dispersal which in the present study could not be determined - should also be a subject of further studies.

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Last but not least I would like to thank my family for support and understanding, my wife Sabine and my children. Tuomas, who is delighted about every single vole during our trappings together and show in great excitement with his sign language "A mouse, a mouse!". My daughter Susanne holds me in a healthy mass of generality, when calling from the living room by every natural history program in TV; "Dad, there's a nature program on the TV, it must be interesting!".

Selostus: Demografian ja käyttäytymisen ajallinen vaihtelu syklisissä *Clethrionomys*-populaatioissa

Tutkimukseni käsittelee *Clethrionomys*-suvun myyrien populaatioekologiaa ja käyttäytymistä. Tutkimus tehtiin Jyväskylän yliopiston Konneveden tutkimusasemalla vv. 1982 - 88, ja se koostui monivuotisesta vertailevasta metsämyyrän (*Clethrionomys glareolus*) tarhapopulaation ja harmaakuvemyyrän (*C. rufocanus*) saaripopulaatioiden seurannasta vv. 1982 - 86. Seuraavien vuosien kokeellinen tutkimus neljässä puolen hehtaarin tarhassa ja laboratoriossa perustui aikaisemmasta seurannasta saatuun paikallisen populaatiodynamiikan tuntemukseen.
Aiemmin kirjallisuudessa kuvattu lisääntyvien naaraiden territorialisuuteen perustuva *Clethrionomysten* sosiaalinen organisaatio tavattiin puhtaimmillaan metsäisten saarien populaatioissa ja suhteellisen alhaisen populaatiotiheyden aikana. Tuottavammalla habitaatilla havaittiin ja lisäruokinnalla saatiin aikaan tästä kaavasta poikkeava sosiaalinen organisaatio. Naaraiden liikkuma-alojen päällekkäisyys kasvoi ja tyttäret jopa saattoivat tulla lisääntymiskuntoon äitinsä liikkuma-alalla. Lisääntymiskauden alun perustajapopulaation yksilöiden toistensa tunteminen (tai sukulaisuus) vaikutti merkitsevästi populaation kasvuun; kolmikuukautisen kokeen aikana "tuttavapopulaatioiden" jälkeläistuotanto ja poikassäilyvyys olivat korkeampia kuin "outojen" populaatioissa. Tämän tuloksena edellisten populaatiotiheys oli kaksinkertainen kokeen lopussa jälkimmäisiin verrattuna. Havaitulla seikalla saattaa olla merkitystä *Clethrionomysten* demografiaan, ainakin jossakin syklin vaiheessa.
Metsämyyrän kesäaikainen aktiivisuus jakaantui suhteellisen tasaisesti koko vuorokauden ajalle. Tämä saattaa johtua juvenaalien vaihtelevammasta aktiivisuudesta. Yleensä metsämyyrän vuorokausiaktiivisuus näytti epäsäännöllisen polyfaasiselta.
Jonkin asteinen aggregaatio oli metsä- ja harmaakuvemyyrällä

yleisimmin havaittu sosiaalisen talvehtimisen muoto. Aggregoitumisen aste vaihteli suurehkosta myyräkeskittymästä pieniin ryhmiin, joihin kuului muutamia naaraita ja vähintään yksi koiras. Talviaikaista territoriaalisuutta ei pystytty kokeellisestikaan aikaansaamaan. Naaraiden ja koiraiden talvinen spatiaalinen jakautuminen oli hyvin samanlaista, toisin kuin lisääntymiskaudella. Habitaatin laikuttaisuus ja ravinnon jakautuminen, mutta varsinkin ravinnon määrä näyttävät määräävän *Clethrionomysten* sosiaalisen talvehtimisen tavan.

Talvehtiessaan pakettipellolla yhdessä, metsämyyrän ja vaivaishiiren (*Micromys minutus*) populaatiot välttelivät toistensa alueita. Välttely jatkui myös lisääntymiskauden alkupuoliskon ajan ja vaivaishiiren läsnäololla näytti olevan negatiivinen vaikutus metsämyyräpopulaation kasvuun. Lisääntymiskauden loppuvaiheessa vaivaishiiri muuttaa elinpiirinsä maanpinnan yläpuolelle, mikä lienee edullista kilpailutilanteessa muiden saman alueen jyrsijöiden kanssa.

Kärpän ja lumikon vaikutusta paikallisiin myyräpopulaatioihin seurattiin koko tutkimuksen ajan. Näiden näätäeläinten suoran saalistusvaikutuksen lisäksi havaittiin useiden lumikkojen (*Mustela nivalis*) esiintymisen koealueella viivästyttävän metsämyyrän lisääntymisen alkamista. Havainto pystyttiin todentamaan myös laboratoriokokeessa, jossa lumikon läsnäolo lisääntymiskuntoisten myyräparien läheisyydessä ehkäisi myyrien lisääntymisen.

Tutkimuksen perusteella voi todeta, että *Clethrionomysten* sosiaalinen organisaatio ja käyttäytyminen on joustavaa ja määräytyy suurelta osin fenotyyppisesti. Eri habitaateilla ja syklin eri vaiheessa myyränaaraiden sosiaalisessa organisaatiossa on eroavaisuuksia, millä lienee merkitystä varsinkin romahduksen jälkeisen nousun vuonna sekä mahdollisesti huippukantojen aikaan. Romahduksen aiheuttajaa - ja syklin syitä - tulee etsiä monimuotoisempien hypoteesien pohjalta, ottaen erityisesti huomioon petojen, loisten ja tautien vaikutus romahduksen aikana. Myyräyksilö sopeuttaa käyttäytymisensä kulloisiinkin elinolosuhteisiinsa, jotka suurimmalta osalta määräytyvät habitaatin laadusta ja syklin vaiheesta.

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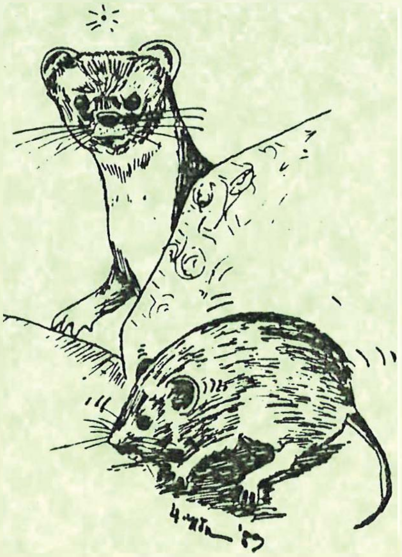

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APPENDIX:

Hannu Ylönen

POPULATION STABILIZING MECHANISMS IN CLETHRIONOMYS

POPULATION STABILIZING MECHANISMS IN CLETHRIONOMYS

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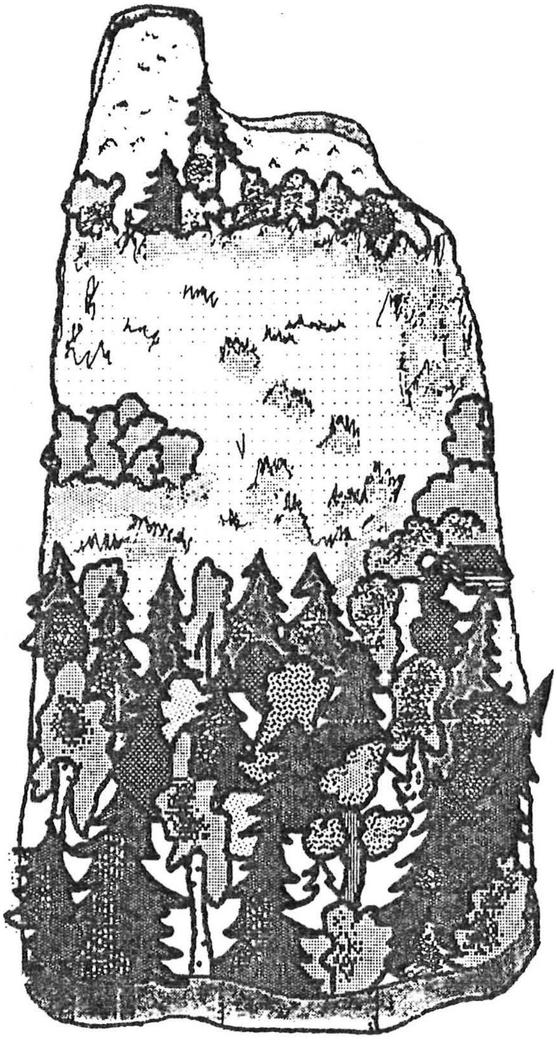
A well known feature in Clethrionomys is the "population regulation" by territoriality in breeding females. A prerequisite for breeding is normally the occupation of an own home range. The size and the overlap of the home range with neighbours seems to be dependent on the habitat and food resources. Among Clethrionomys aggressiveness between individuals is modest compared with e.g. Apodemus and Microtus. Thus there must exist a sophisticated mechanism for the maintenance of the territory. It can act through chemical, or other signals in contact situations.

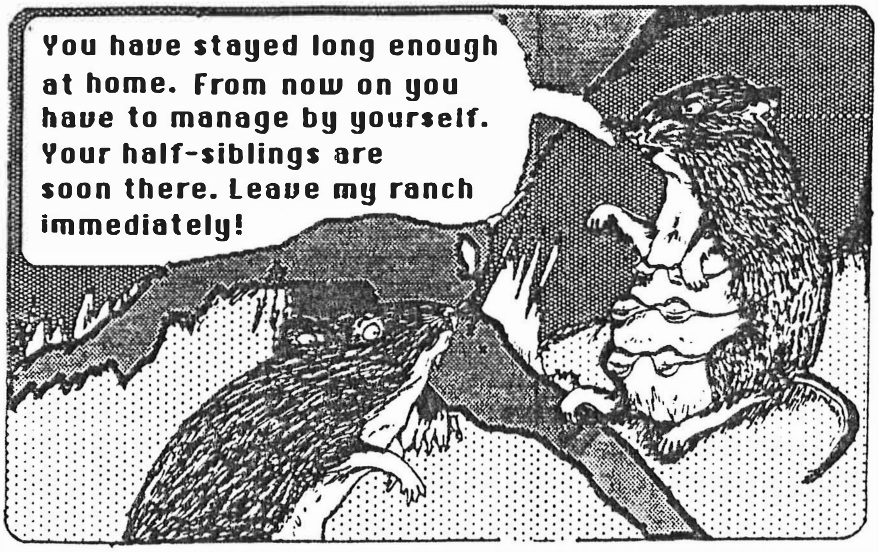
I studied social organization and behaviour of enclosed bank vole Clethrionomys glareolus populations in Konnevesi, Central Finland, between the years 1982 - 88. Central result of the study was e.g., that the social organization is flexible during the breeding and the non-breeding season. Behavioural trials made in the field in home ranges of females with known social position showed the dominance of the home range owner over the stranger already after the very first contacts. After that avoidance was the main feature of behaviour. Immature animals and mature neighbours, too, were tolerated by the females. Aggressiveness escalated against submature females apparently seeking for a free territory. The observations seem to support the hypothesis of importance of social odours in communication between Clethrionomys individuals, as already shown in laboratory studies with other genera. The aggressive behaviour in contact situations could gain in importance in very dense populations.

Once upon a time there lived a small isolated tribe of bank voles in central Finland. The tribe lived in an area surrounded not by the wall of China but by a fence of galvanized sheet.

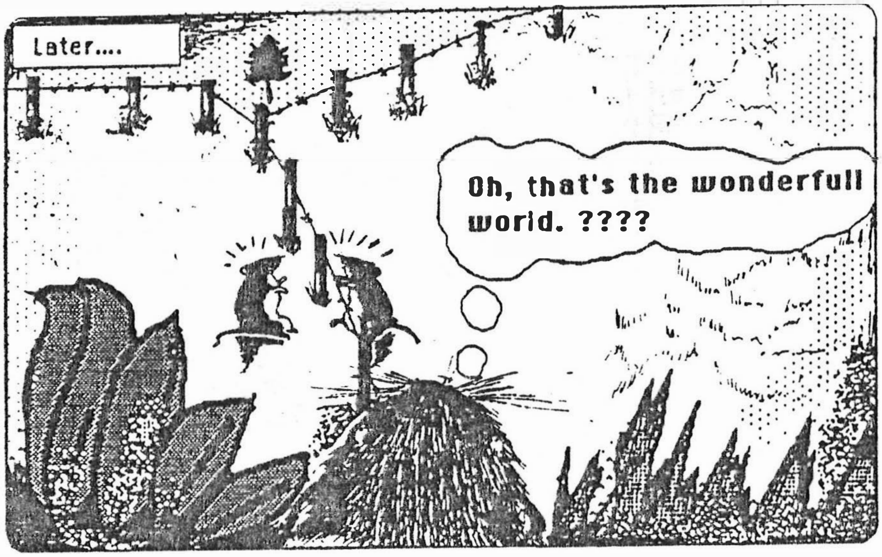
The tribe lived quite peacefully through the increase, peak as also crash years of the CYCLE. Matriarchat as social system existed in the tribe. During summertime the whole area was shared to "Home Ranches" owned by the women of the tribe. The men lived as merry vagabonds trying to enjoy the short moments by a mate or gambling with other men of the tribe.

One summerday our heroe (She), called 1-9-12, noticed strange vibrations in her soul and changes in her body. These changed also the behaviour of her previously so kind and loving mother. She was coming to puberty! And so ....

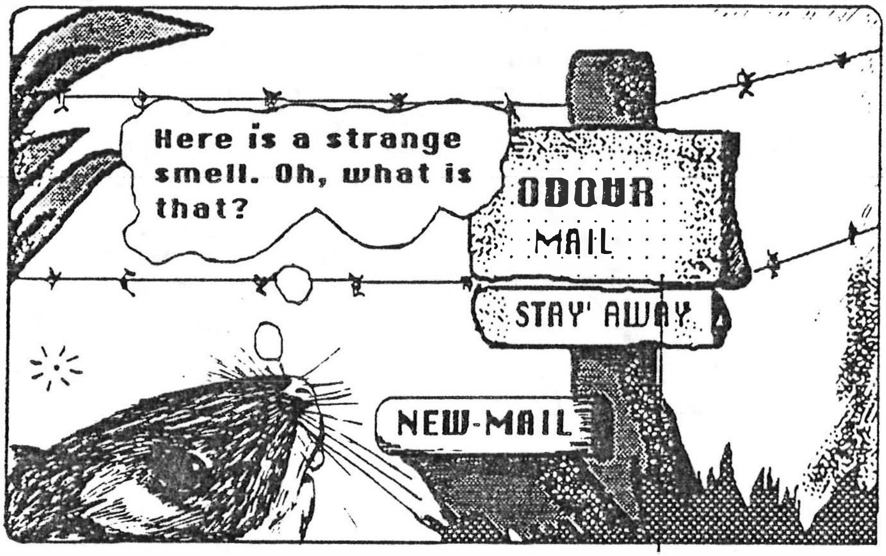




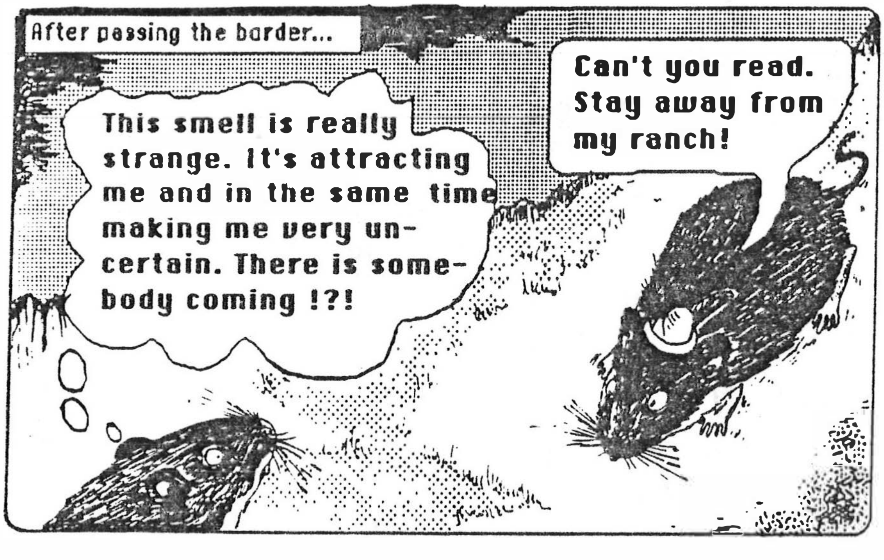
And so she had to leave the familiar ground and to face the new and exciting world, she never had seen before. She saw ranches with their owners babbling peacefully with each others.

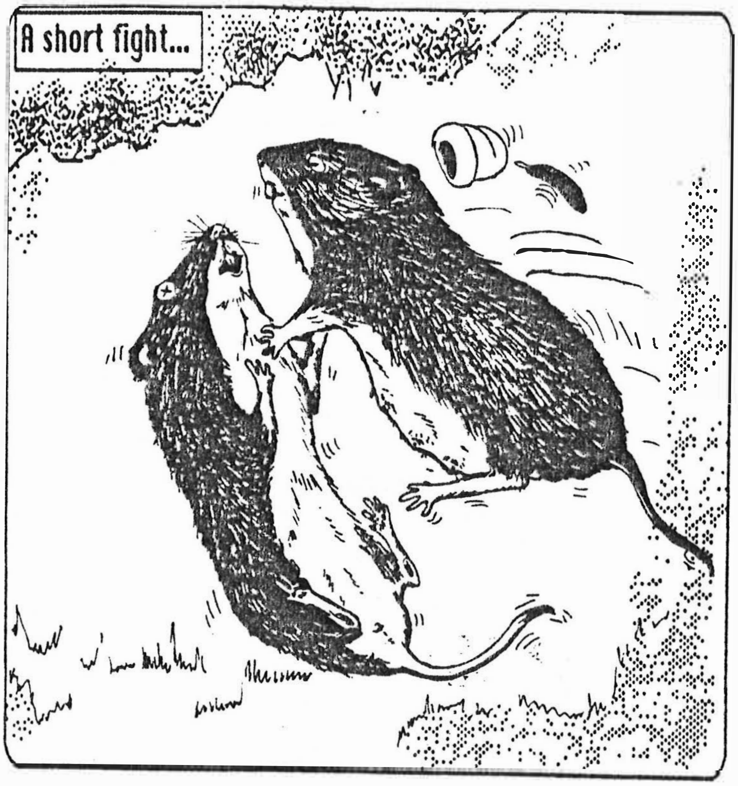


She came nearer to the fence of a ranch and...

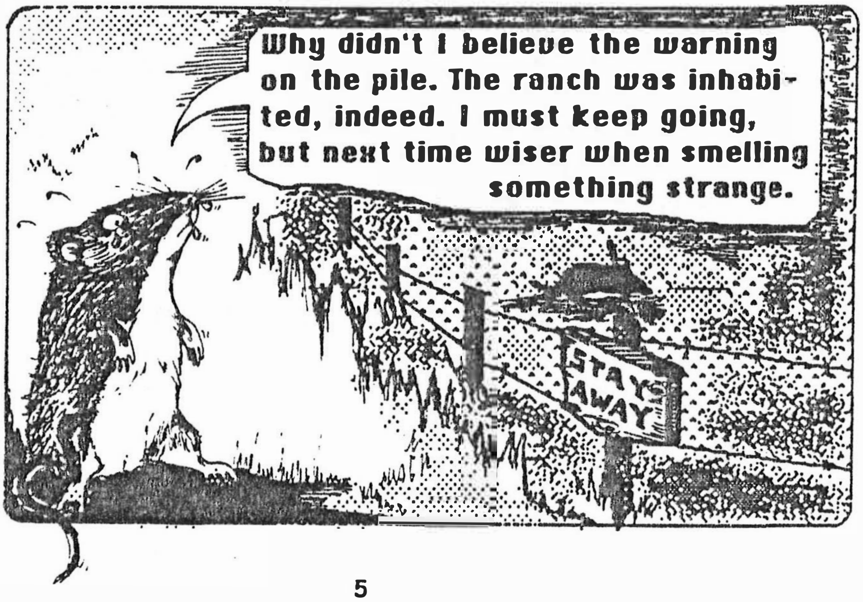


did not know the meening of the message on the post.

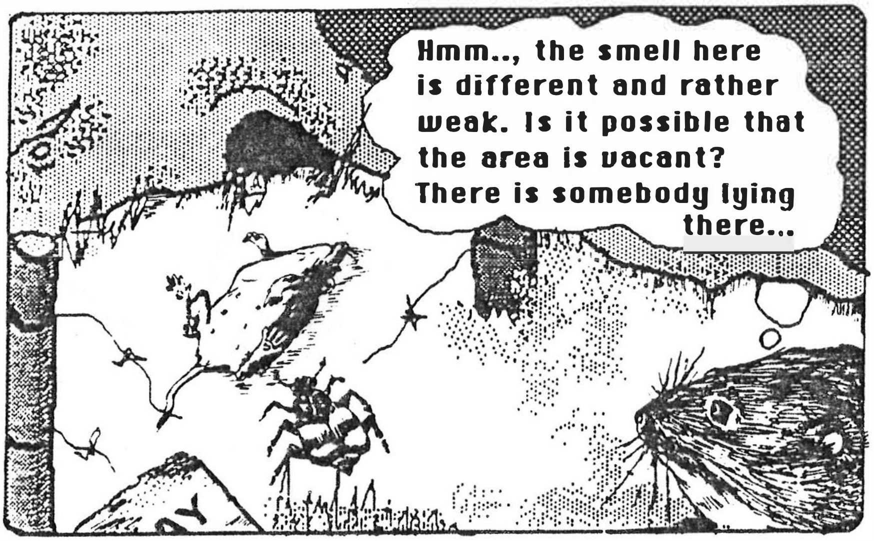


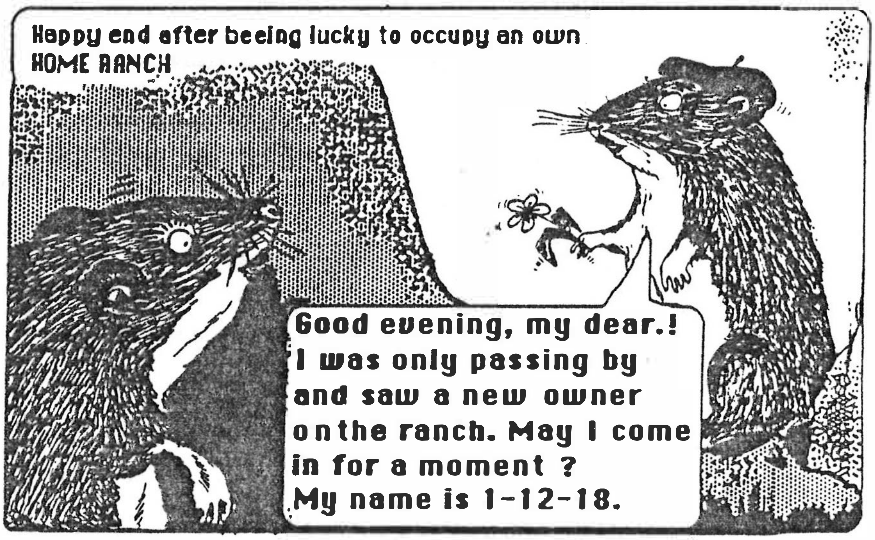


She was healthy and strong already. However, she had no chance against the furious mistress of the ranch.



After having learned a lot from the first meeting with ranch owner she moved on. Not far away from her mothers ranch she recognized an old ranch in a rather bad condition. The fence was unrepaired and it was too still around...





So she 1-9-12 learned the rules of living in the tribe. The meaning of the strange smells was evident to her now. During the maturation process her own body began to produce the same kind of odours which left her ranch in peace. With her neighbours she had good relations but she didn't like unknown female intruders. Only her siblings were tolerated. He, 1-12-18 left the ranch immediately after the CENSORED. She brought five first children to the world and again there was a charming man passing by ....

Regulation of the tribe size in a steady environment by means of odour signalling and by avoidance of too much aggression lays a basis for peaceful life of the tribe from cycle to cycle.

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