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Review

From population dynamics to experimental evolutionary ecology: causes and consequences of social processes in voles

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Cyclic population fluctuations of small rodents are characteristic in northern and central Fennoscandia. In Finland research addressing this problem was initiated in 1940s by professor Olavi Kalela, and the work is carried on by his co-workers and their students. One of the paramount questions is to what extent and by which ways social interactions among individuals contribute to the observed population dynamics. The focus at Konnevesi Research Station has — during its whole ten years of existence — been on social mechanisms of small rodents. This article is a review of our pending studies. It rather soon turned out that population cycles take place in spite of stabilising social mechanisms, not because of them. Our studies uncovered correlation between social organisation and quality of food and habitat. This led to comparisons between species and among populations, calling for experimental research both in large outdoor enclosures and in detailed laboratory tests. The questions studied were the effect of familiarity of interacting individuals on population growth and spacing behaviour, comparison of dispersal patterns between *Microtus* and *Clethrionomys,* and the effects of odours of conspecific and heterospecific rodents and of predators on the reproduction of individual voles. Quite recently we have focused on predator-prey interactions between rodents and their main predators, mustelids and raptors. Results of these studies imply that behaviour of voles exhibits great phenotypic plasticity as response to changing environment.

1. Introduction

Science is a growing tree. Every research project is built upon the experience of previous work and workers. This paper attempts to describe one line of research on social ecology of small rodents descending from the nordic "grand old man" of the mammal research of his time, the late Prof. Olavi Kalela. A good teacher can create new visions and both enthusiastic and critical attitude. Kalela´s message to his students was: be aware of the theoretical framework and of the biology of your study object, make the predictions with care, do not try to avoid hard work but avoid small sample sizes. He was also able to bring people together. It is a result of that spirit that the Kalela team in a way still exists after his death in 1974. Ten years after his death, a symposium on *Clethrionomys* biology at the new branch of Kalela-tree, The Konnevesi Research Station of the University of Jyväskylä, was dedicated to his tradition (Stenseth 1985).

The drastic population fluctuation of voles and lemmings in northern and central Finland was one of the main targets of Kalela's research and his 1957-paper "Regulation of reproduction in *Clethrionomys rufocanus...*" belongs to citation classics of papers on rodent population dynamics. According to Stenseth's (1985) statement "Kalela's scientific contribution is indeed a good example of the fact that good scientific work is noticed regardless of where it is published". He started the collection of the longest existing data set on vole and lemming population dynamics at Kilpisjärvi in the 1940s. That survey is still continuing. It has been a good basis and framework for all studies on small rodents and birds of prey. The lines of research on voles he started were: population dynamics and animal-plant interactions, ecology of animal movements, social organisations and spacing behaviour and how they are related to cyclicity. The research on small rodent population dynamics is continuing in Kilpisjärvi and Pallasjärvi. However, much of the research on social organisation and behaviour of small rodents nowadays takes place in Konnevesi Research Station established in 1983. It continues the work that began in Kilpisjärvi even though the methods have changed more and more from long term surveys to controlled experiments. Of course, new questions on causes and consequences of social behaviour have also arised. The main point concerning cyclicity, however, is that now we see it as a frame for all our studies — with all its consequences on individual vole's "quality" in behavioural trials, and the total lack of study material every third or fourth year, as was the case during last summer, 1993.

The present paper reviews some major aspects of Kalela's research in Kilpisjärvi. Then we draw together the main achievements of our own studies ca. 900 km south from Kilpisjärvi at Konnevesi Research Station during its first ten-years of existence. His long-term work on population dynamics, which tradition is maintained in the research of Heikki Henttonen and his group in and near Kalela's original study sites in Kilpisjärvi and Pallasjärvi, is outside the scope of the present paper.

2. Kalela and studies at Kilpisjärvi

Kalela was originally an ornithologist but as he was interested in population processes in general he started his work on lemmings in 1930s. In spring 1946 he got a message that lemmings are migrating around the lake Kilpisjärvi, in the North-Westernmost corner of Finland, where the country reaches the Scandinavian mountain range. That was the beginning of a research period which lasted for 27 years. The first research base was the "Mouse Cottage" — the former house of the forest warden Wiik. Kilpisjärvi Biological Station of the University of Helsinki was founded in 1964 and Kalela headed the station until his death in 1974.

The main interest of Kalela was the biology of the Norwegian lemming (*Lemmus lemmus*) and the famous lemming migrations (Kalela 1941, 1948, 1949, 1954, Aho & Kalela 1966, Kalela & Koponen 1971, Kalela et al. 1961 1971) that were confused with so many mythical opinions. He discarded the concept of suicide migrations as he uncovered the seasonal change of habitat and how it results in the long distance migrations as the numbers of lemmings increase. He also studied plant-herbivore interactions and the correlation between synchronous flowering rhythms of different plant species and the multiannual population cycles of rodents (Kalela 1962, Kalela & Koponen 1971, Tast & Kalela 1971). The hypothesis on plant-vole interactions regulating the cycles was probably a result of his studies on lemming as it seems to be the most food regulated species in Finland. Research on herbivory, in connection with his studies on the interactions between voles and their food resources as a cause of the cyclic fluctuations, brought him to co-operation with Prof. Eurola, a botanist in the University of Oulu, and his co-workers (Eurola et al. 1982, Laine & Henttonen 1983, 1987; see Federley 1972, too). Although no such relation was found, the research on plant cycles vs. vole cycles are fundamental for the understanding of the functioning of the sub-Arctic ecosystem.

The deep ecological understanding directed him to oppose the hypotheses on intrinsic causes of population cyclicity (Chitty 1952, 1960, 1967, Christian 1950, 1970, Christian & Davis 1955, Krebs et al. 1973). Even though his favourite hypothesis on plant-vole interactions generating cycles is no more valid as such, the approach of extrinsic factors he started has lead to better understanding of the ecological processes involving, besides plant production, especially predator-prey interactions, snow conditions, diseases and parasites, that seem to a great extent to generate cyclicity (Henttonen 1985, 1987, Hansson & Henttonen 1985a, 1985b, Henttonen & Hansson 1985, Henttonen et al. 1985, 1987, Hanski et al. 1993; for a review see Hansson & Henttonen 1988).

Together with his students Kalela established the Finnish school of behavioural ecology. He was mainly interested on behaviour and especially territorial behaviour as an ecological factor (Kalela 1954, 1956, 1957, Arvola et al. 1962). Spacing behaviour was an essential part of his classical study on the population regulation of the grey sided vole, *Clethrionomys rufocanus* (Kalela 1957). He was among the first to point out the stabilising effect of social behaviour on rodent population dynamics. After his encouragement to a comparative approach in microtine ecology Tast (1966) included spacing behaviour in his extensive study on root vole, *Microtus oeconomus* and Viitala (1975, 1977, 1980, 1984a, 1986, 1987) had the comparison of social organisations of free living *C. rufocanus*, *C. rutilus*, *M. agrestis* and *M. oeconomus* as his main topic. This approach evidenced for the first time, though on descriptive basis, the interspecific differences in the spacing behaviour of these two genera and gave the first insight into the adaptiveness of spacing behaviour and mating structure. Territorial regulation of puberty was evident in both *Clethrionomys* species but did not exist in *M. agrestis*. The correlation between social behaviour and habitat and food conditions became evident (Viitala 1977, 1986, Viitala & Hoffmeyer 1985, Ylönen et al. 1988). The breeding females of species living on scarcer food supply i.e. the generalist *Clethrionomys*, are distinctly territorial but those living on rich food supply in ephemeral habitat i.e. herbivorous *Microtus* are not. Breeding *Clethrionomys* males are non-territorial but *Microtus* males are territorial except for the short early phases of the breeding season.

The Kilpisjärvi studies also gave the first indications of plasticity of social behaviour. In private discussions Kalela was very worried about one of his study areas where the territorial *C. rufocanus* females behaved non-territorially (Kalela 1956, 1957). Studies on *M. oeconomus* revealed dependence of mating tactics on the habitat, density and the phase of breeding season (Tast 1966). There were overlapping home ranges of both males and females i.e. apparent promiscuity just after thaw, apparent polygynous groups later in the breeding season. Occasionally also male-female pairs were observed after mid summer during highest population densities in small patches of tolerable habitat surrounded by intolerable birch wood (Tast 1966, Viitala 1980 and in preparation). The first hints of age dependency and changes of the spacing behaviour during breeding season in *M. agrestis* were also discovered (Viitala 1977, 1986).

3. Studies in Konnevesi Research Station

3.1. Plasticity of spacing behaviour: *Clethrionomys* and *Microtus*

Comparative studies on the social ecology of voles started in Konnevesi in 1981 i.e. before the building of the Research Station. We tried to continue the studies with a familiar object from Kilpisjärvi, the grey-sided vole *Clethrionomys rufocanus*, but through an interesting observation of the lacking coevolution between the Nordic vole species and southern ticks, *Ixodes trianguliceps,* we were forced to change the study species, as the ticks killed all grey-sided voles introduced in a mainland enclosure (Viitala et. al. 1986). In islands of the Lake Konnevesi without tick infestation populations introduced during the next summer survived several years (Ylönen & Viitala 1987).

A comparative enclosure study on the flexibility of the social organisation of the bank vole *C. glareolus* was carried out 1982–87, by excluding the competitive *M. agrestis* from the 0.82 ha enclosure area (Ylönen et al. 1988). The first results of the great phenotypic flexibility of bank vole behaviour were presented in the *Clethrionomys*-Workshop during the 4th ITC in Edmonton 1985, and published for both the winter (Ylönen & Viitala 1985, 1991) and for the breeding season (Ylönen et al. 1988, Ylönen 1990, Viitala 1986). It appeared that from the two habitat enclosure system the abandoned field with some bushes was, surprisingly, more favoured habitat than the forest for the "forest vole" *C. glareolus*, when *M, agrestis* was lacking, and the greatest overlapping of home ranges of breeding females took place there (Ylönen et al. 1988). In a symposium volume of the following ITC in Rome 1989, the idea of the flexibility — but also the great variability — of social systems in several rodent species was commonly accepted and documented (Tamarin et al. 1990).

In central Fennoscandia winter is long and the overwintering voles have to face a long-lasting permanent snow cover and low temperatures. There exist only few studies dealing with behavioural adaptations of rodents during the winter (Merritt & Merritt 1978, Viitala 1984a). Therefore we started to follow the overwintering of the bank vole by means of long-term life-trapping (Ylönen & Viitala 1985, 1991, Ylönen 1990). It seems obvious that the basic social system during winter is a social aggregation. The size of the aggregation depends on the food resource; the richer the food patch the larger aggregations (Ylönen & Viitala 1991). The location of the aggregations is adjusted according to the depth of the snow cover. Of these two factors food is the more important one, however. In a two-habitat enclosure voles preferred to overwinter in open areas or forest edges with a thick snow cover (Ylönen & Viitala 1985) but the entire population lived in the forest with a poor snow cover when supplemental food was provided there (Ylönen unpubl.).

The aim of the comparison between *Clethrionomys* and *Microtus* has been to discover the ecological determinants of social behaviour: the roles of phenotypic plasticity and fixed behavioural patterns (Viitala & Hoffmeyer 1985, Viitala 1986, Viitala et al. 1993a). We studied both the herbivorous *M. agrestis* on two adjacent semi-isolated habitats: grassy coniferous forest and an abandoned field (Viitala & Pusenius 1990, Pusenius & Viitala 1993a, b) and the omnivorous *C. glareolus* on the same habitats (Pusenius & Ylönen unpubl.). The summer peak of green plant production offers much more food but of poorer quality for *M. agrestis* when compared to the food of *C. glareolus* that feeds on more concentrated but scarcer fruits, seeds and other storage organs of herbs, trees and dwarf scrubs (Hansson 1985). Even though these species on their typical habitats show distinctly different social organisations, there are considerable similarities in similar environments. For example, we have found occasional lack of territorial regulation of puberty in *C. glareolus* in meadow and territoriality of *M. agrestis* females in forest (Viitala et al. 1986, Pusenius & Viitala 1993b). The interspecific dissimilarities in dispersal patterns and the regulation of maturation seem to be mainly a consequence of differences in food preferences (Viitala et al. 1993a). *M. agrestis* females inhabit the environment according to the ideal free distribution (Fretwell & Lucas 1970): females begin to disperse into the suboptimal forest when breeding success in the field has decreased to the same level as that in the forest due to the increased population density and heavy exploitation of the food resource in the field. However, *C. glareolus* seems to exhibit a despotic distribution (Fretwell & Lucas 1970) in all situations. Bank voles' breeding success in optimal and suboptimal habitats remains different in spite of population density (Gliwicz 1990). One must notice that forest of any kind seems to be suboptimal environment to *M. agrestis* but meadow is an optimal habitat to normally forest dwelling *C. glareolus* when *M. agrestis*, a superior competitor, is lacking (Ylönen et al. 1988, Pusenius & Viitala 1993a, b).

We also carried out an intensive analysis on seasonality and age dependency of spacing behaviour of breeding *M. agrestis* (Pusenius & Viitala 1993b). In females territoriality, as measured by clumping of captures and by mutual overlapping of home ranges, and dominance, as measured by trappability (Gliwicz 1972), are both increasing by age. We have found out that old females and their breeding daughters tended to form short lived associations in July that were broken down by dispersal already in August (Pusenius, in preparation). The mid-summer crisis (Myllymäki 1977) is also characterised by distinct territoriality. This territorial phase does not prevent maturation of young females, however, as the biggest late summer cohort was sired at that time (Pusenius & Viitala 1993a, b). There was a significant aggregation of females in early June during the maturation of first summer born females and again in late August when the bulk of the breeding females were formed by mutually tolerant young animals. After the mid-summer crisis the breeding seem to be synchronous compared to asynchronous breeding in early summer. The late aggregation phase does not exist at Kilpisjärvi where the territorial phase of mid-summer crisis seem to continue to autumn depression of breeding (Viitala & Pusenius 1990).

In all of our studies we have had to face the still existing (Boonstra, pers. comm.) controversy about the role of social behaviour in explaining the multiannual cyclicity in voles (Chitty 1967, Krebs et al. 1973). With the comparative approach we were able to demonstrate the changing social system of the voles along the population cycle and the importance of food and habitat for the social system (see Ylönen 1990, Viitala et al. 1993a for reviews). However, we have not been able to manipulate the phase of the cycle, not even in enclosure experiments as we have been unable to keep out the mustelid predators from our enclosures. So the main conclusion is that the cycles take place in spite of variability of social system along the density fluctuation and not due to it. We see no evidence for the cyclicity theories based on some kind of intrinsic properties of individual voles living in different phases of the cycle. Dennis Chitty spoke out during the Fifth ITC in Rome, and stated that he is proud to have developed a hypothesis which has initiated as much empirical research on voles allover the world as it has done during the last two decades, but he must now accept that the hypothesis is not correct.

3.2. Kin interactions and demography

A short idea-paper by Charnov & Finerty (1980) on the impact of kin-selection on cyclic population fluctuations in rodents also initiated a lot of empirical vole research in the eighties. After the observations that the *Clethrionomys* voles overwinter in aggregations the next question was the cohesion of the aggregation. There exist no field data on the degree of relatedness in the winter aggregations, but one can speculate that it should be relatively high. Bank voles are philopatric and stay as close to their natal home range as possible (Ylönen et al. 1988). Mature daughters establish their home ranges in the vicinity of their mother's home range if there is space available. The last cohorts of the autumn remain immature and can stay in and around their natal home range. Thus the basis of an overwintering aggregation should be an old female — if she does not die in autumn — and her daughters which are either siblings or half-siblings (Ylönen 1990).

On the basis of these speculations we tested the assumption of the Charnov-Finerty hypothesis, that an increased degree of relatedness between individuals of a population causes an increased growth rate in the summer population. The result of our three-month enclosure experiment with known kinship and familiarity of the founder populations verified the assumption; "Friends" populations grew twice as high as the "Strangers" population during one breeding season (Ylönen et al. 1990). E.g. Ferkin (1990) has been able to demonstrate that phenotypic matching (familiarity) is the mechanism which rodents use for the kin-recognition. Therefore, we repeated the experiment with a known kinship vs. manipulated familiarity of the founder populations. We found out that both familiarity and relatedness between the founder individuals increase the population growth but that relatedness and familiarity together have a stronger effect than familiarity alone (Ylönen et al. 1993).

The Charnov-Finerty hypothesis has been shown to be insufficient to explain population cycles (e.g. Pugh & Tamarin 1990). Nobody has been able to show that decreasing degree of relatedness causes the population decline as stated by Stenseth & Lomnicki (1990). In our experiment unfamiliarity did not cause a population decline — just a slower growth rate (Ylönen et al. 1990, Ylönen et al. 1993). Lambin & Krebs (1991) have developed a new relatedness-model including the effects of winter mortality and decreasing degree of relatedness in the spring population. The assumptions of the Lambin-Krebs model are strongly criticised by Ostfeld (1992) and Ylönen et al. (1993). In *M. agrestis* the matrilineal associations found among breeding females did not last through the summer nor did they affect breeding success (Pusenius, in preparation). Again, we had to state that relatedness can affect population growth parameters and social system but they cannot produce the drastic declines necessary for cyclicity.

3.2. Predator-prey interactions

Small mustelids and vole behaviour

The "Fennoscadian school" of researchers in microtine cyclicity problematic represents an opinion that the cycles can be explained mainly with extrinsic factors, that now include snow cover, diseases, parasites and especially predation (Hansson & Henttonen 1988). The role of small mustelid predators is one of the main focusing points now a days (Hanski et al. 1991, Hanski et al. 1993). In the research on the impact of predators, the indirect effects have been neglected until recently. We started to seek reasons for mature females of a field population delaying breeding when there were numerous small mustelids in and around the study area (Ylönen 1989). In a series of experiments we have verified an assumption that besides direct changes in activity, feeding and spacing behaviour (e.g. Jędrzejewska & Jędrzejewski 1990a, b, Ylönen et al. 1992) also mating behaviour is affected by the presence of specialist predators (Ylönen 1989, Ylönen et al. 1992), especially small mustelids, the stoat and the weasel. The presence of generalist mammalian predators or avian predators does not affect the behaviour of voles as strongly as that of the mustelids (see Ylönen et al. 1992 for review). As the direct impact of mustelid predation becomes increasingly important towards the north, along the cyclicity gradient (Hansson & Henttonen 1985a, b) and the indirect impact of mustelids seems to delay breeding in some of the remaining individuals (Ylönen et al. 1992) — one is near the answer why the vole densities during the population crash are as low as they are.

Since predation of small mustelids can affect the populations very strongly during the winter after the peak year, it may well also affect the social behaviour of voles during the winter. According to Elgar (1989) increasing group size in prey is a common response under increased predation risk. Overwintering in social aggregations seems to be a common pattern in most microtines (Madison 1984). It is still unknown if this kind of social behaviour increases or decreases the risk of predation in the field. Small mustelids are able to hunt in the sub-nivean space and after finding a good food patch they can stay around as long as the reward remains higher than the cost of seeking a new — possibly distant — aggregation of food (voles) (Brown 1992). In this case staying in aggregation would increase the risk of predation. In enclosure experiments, however, Jędrzejewski et al. (1992) showed that staying in groups significantly improved the escape probabilities of individual voles during weasel attacks. If these short term experimental results are valid in field conditions where a weasel is in the trade-off situation of staying near a found aggregation and seeking a new one, is still unclear. We predict that in a patchy environment food resource is still a stronger adaptive force causing social, heat-saving aggregations in best overwintering patches. In a more even overwintering habitat — if such exists — it could be due to antipredatory abilities more profitable for an individual vole to stay territorial during the winter. The impact of small mustelids on the behaviour of voles during the breeding season is reviewed by Ylönen et al. (1992).

Microtines as preys for raptors

Microtines are the most important food items of several owls and raptors that reproduce well only during high population densities of their most favoured prey (Korpimäki 1985). Recent studies have revealed a very exotic feature in predator-prey interactions: the scent marks used as social signals in the prey species may offer a cue for hunting raptors to find prey. We found that the odour substances of *Microtus* voles absorb ultraviolet light (UV). As the eye structure of birds that have been studied allows detection of UV (Burkhardt 1982) the raptors seem to see the fresh vole trails. The female voles hide the urination but the fine trace urination marks of breeding males are spread allover the trail system (Hoffmeyer 1983).

To confirm the hypothesis presented above we carried out two experiments (Viitala et al. 1993b) using *M. epiroticus and M. agrestis* as prey. *M epiroticus* is more aggregative and also more vulnerable to kestrel predation (Hakkarainen et al. 1992).

In the first experiment we offered kestrels (*Falco tinnunculus*) a choice between two identical arenas with in a 5 × 4 × 2.5 m experimental room with black walls and ceiling. One of the arenas had been occupied by five individuals of *M. epiroticus* for 17 hours prior to the experiments. Both arenas were illuminated by visible light (VL) and UV. Nineteen out of 20 kestrels stayed above and scanned to the occupied arena.

In the second experiment we offered to the kestrels a choice between four arenas in the same room. Two of the arenas were inhabited by seven individuals of *M. agrestis* for 18 hours. The voles were removed before the arenas were exposed to the birds. Two control arenas were clean. One of both arenas was illuminated by UV (366±20 nm) and the other with VL (less than 1 per cent UV). The raptors were able to see the signs of voles in UV but not in VL. Thus social behaviour increases the predation risk to voles.

4. Conclusions

The comparative approach has shown that the social system found in a population of small rodents is related to the habitat stability and food conditions (greatly the result of food preferences) of the species in question. Instability of the environment increases the importance of the ability to rapid phenotypic chances of social behaviour. In fact there seems to be more phenotypic plasticity in the behaviour of *M. agrestis* — an inhabitant of ephemeral habitat — than in *Clethrionomys* species, inhabitants of more predictable environments (Viitala & Pusenius 1990). Thus study of vole social behaviour belongs to the field of evolutionary ecology. We feel that social behaviour together with morphological and physiological characteristics is an important aspect in the life history of small rodents facilitating adaptation to differences and rapid changes in the environment. That environment consists of resources, risks and social interactions. This approach is still a little ploughed field.

Krebs (1992) states in his review of the Tamarin et al. (1990) book "The social systems and population dynamics in voles", that "there is as yet little in the way of a coherent theory that ties together population dynamics and social organisation." and "That the theory is yet to come...". We agree with his opinion that the theory is yet to come. However, we feel that in the theory the social organisation does not belong to the causes-part but in the consequences one.

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