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Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus*: Social odours, chemistry and biological effects

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This paper reviews social mechanisms of vole species belonging to the genus *Clethrionomys* and compares them with those of some *Microtus* and *Apodemus* species living on similar and different habitats.

All *Clethrionomys* species living in large predictable habitats seem to have mechanisms to regulate the numbers of mature animals in high density situations by territorial behaviour in females and by hierarchy formation in males.

The *Microtus* species living in predictable environments seem to have similar mechanisms to restrict maturation during high population density whereas those species living in unpredictable succession habitats do not restrict maturation.

The site tenacity and stability seem to be high in species of predictable environments but they seem to be low in species living in unpredictable habitats.

The "regulators" of the predictable habitats have specific marking behaviours usually not found in "non-regulators" of the unpredictable places. The chemistry of the agents involved are still largely unknown except for the hexadecylacetate of preputial gland in male *C. glareolus* used to signal social dominance. Other agents of that gland affect female attraction and female choice of mate.

The two *Apodemus* species dealt with here are specialized granivores. They often exhibit seasonal change of habitat. They show low juvenal survival and maturation rate during high numbers of overwintered non-tolerant adults.

Predictions on social mechanisms in these species on the bases of habitat, food and way of life (e.g. arboreal vs. ground dwelling) have been discussed.

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1. Introduction

A considerable number of reports have appeared on the social behaviours and population structures of different small rodent species. An understanding is emerging as to how these social processes make animals cope with a variety of ecological conditions. We expect that different environmental conditions will favour the evolution of different social systems.

Since all *Clethrionomys* species are predominantly inhabitants of woody climax vegetation (Kalela et al. 1971, Mihok 1979) in contrast to, for example, the Scandinavian *Microtus* species (e.g., Frank 1953, Reichstein 1959, 1960, Myllymäki 1970) one may expect to find great similarity in the behavioural adaptations of *Clethrionomys* and quite different adaptations in those species inhabiting different types of environment.

These social processes are very little known, however. This is particularly so for social scent marking and the associated behaviours except for laboratory data on rats and mice. There exist studies on olfactory cues, urinary marking and responses to cues in urinary marking and preputial glands of *Clethrionomys glareolus* males (Godrey 1958, Johnson 1975, Christiansen et al. 1978, Gustafsson et al.1980a, Christiansen 1980, Hoffmeyer 1982, 1983, Brinck & Hoffmeyer 1984) and on the marking behaviours of some North American *Microtus* species (e.g., Wolff & Johnson 1979). But, similar studies on females, expected to be so important from the point of view of social regulation are largely lacking.

The aim of the present paper is to show, on the basis of a review, how *Clethrionomys* social organization is adapted to the predictable habitat and how it differs from species living on similar and different habitats. Some *Microtus* species are used as examples of species living in unpredictable habitats. The comparison with the two *Apodemus* species attempts to show that taxonomically far related species use different mechanisms for the same goal. Most of the literature forming the basis for this review is summarized in Table 1.

The territory concept has been used for "defended" areas. Home range is used for areas shared with other individuals of the same kind.

2. Social organization of *Clethrionomys*

2.1. *Clethrionomys rufocanus*

C. rufocanus is a typical forest dweller. In the Kilpisjärvi area in Finnish Lappland, it is, for example, the dominant species of the climax arctic-alpine birch forest (Kalela et al. 1971). It is also frequently captured in all kinds of forests on mineral soil except in the dryest lichen woods. Thus, the species lives largely in a fairly predictable environment.

The species shows very distinct 4-5 years cyclic density fluctuations with typical summer declines, sometimes resulting in almost zero density (Kalela 1957, Lahti et al. 1976, Viitala 1977). When the population density increases the distribution of animals is typically clumped (Viitala 1977). The female descendants of one particular female move on to territories as close to the place of birth as possible (Viitala 1977). This results in a kind of family clan system. After different groups have expanded so as to come in contact with each other, such a family clan system is no longer discernible. Then the social environment of a female is formed by its near neighbours, which are much better tolerated than unfamiliar individuals. Towards strangers, a breeding female behaves very aggressively (Viitala 1977). Thus, familiarity may be an important ecological factor. The territorial behaviour of females being familiar with each other does not seem to involve severe agonistic behaviour (Viitala 1977, 1985). The females in multiple captures sometimes observed in boundaries of two ranges do not show aggression toward each other nor do the females often have scars (Viitala 1985, Henttonen unpubl. data). There exist evidence that territorial females do not avoid individuals but intensively use areas of other females (Viitala 1985). Thus, we may suppose chemical and auditory communication to be used in the maintenance of territorial boundaries. The cues used are still unknown, however. The preputial gland which is well developed in males is very small in females (Christiansen et al. 1978); and female urinary marking is different from and less frequent than that of males.

Territorial females seem to form the basis of the population. Males and juveniles direct their movements on the basis of how females are distributed (Viitala 1977). In social encounters females seem to be dominant over males (Viitala 1977) as also found in *C. gapperi* (Mihok 1976).

It has been shown that territorial behaviour may restrict the maturation of young females in high density situations (Kalela 1957, Viitala 1977, Saitoh 1981). A young female in the process of maturation disperses in order to find available space. Pregnancy seems to be possible only for individuals holding territories (Viitala 1977, Saitoh 1981). Thus the young animals constitute the main dispersing fraction of the population. When all available space is occupied, maturation of young females seems only to occur so as to compensate for the deaths of older females. Thus, the regulation of female maturation slows down the population growth rate (Viitala 1977).

The territory size seems to be negatively correlated with population density (Viitala 1977). This may be correlated with the need of social stimulation during low density (Viitala 1977) but there is strong evidence that food is the most important factor determining territory size (Henttonen, unpubl. data).

The males have much larger home ranges than females. Often there exist groupings of three or four males with greatly overlapping ranges isolated from other males (Viitala 1977). There may also be some tendency for territorial behaviour between these male groups.

The site tenacity and survival of territorial females and male groups are high during increase and peak years. The male groups usually survive throughout the breeding season. In multiple captures mature males are seen to behave much more aggressively than females and juveniles (Viitala 1977 and in

Table 1. Social structures of some microtine and murine small rodents. Explanations: *regulation* denotes regulation of puberty, ? denotes information not found, + denotes yes or good, - denotes no or poor, +/- denotes sometimes observed.

	male dominance	promiscuity	polygyny	male/female pairs	site tenacity	female territories	female regulation	male territories	male regulation	colonizing	juvenal dispersal	adult dispersal	source
Clethrionomys:													
glareolus	(+)	+	-	-	+	+	+	+/-	?	-	+	-	1)
rufocanus	-	+	-	-	+	+	+	+/-	+	-	+	-	2)
rutilus	-	+	-	-	+/-	+	+	+/-	+	-	+	-/+	3)
gapperi													
(subarctic)	?	+	-	-	+	+	-	-	?	?	?	?	4)
(temperate)	-	+	-	-	+	+	+	+/-	?	-	+	-	5)
Microtus:													
agrestis	-	+/-	+/-	-	-	+/-	-	+	+	+	+	+	6)
arvalis	?	+	+	-	-	-	-	+	+	+	?	?	7)
pennsylvanicus	?	+	-	-	-	+/-	-	-	-	+	+	+	8)
oeconomus	-	+/-	+/-	+/-	+/-	+	?	+/-	?	+	+	+	9)
ochrogaster	?	-	-	+	+	+	+	+	+	-	+	-	10)
montanus	?	-	+	-	+	+	+	+	+	-	-	-	11)
xanthognathus	?	-	+.	?	+/-	-	+	+	+	+	+	-	12)
Apodemus:													
speciosus	+	+	-	-	+	+	+	-	-	?	+	?	13)
sylvaticus	+	+	+/-	-	+	+/-	+	+/-	+	+	+	+	14)

Sources: 1) Bujalska (1970, 1971), Hoffmeyer (1983) — 2) Viitala (1977), Saitoh (1981) — 3) Viitala (1980, 1985) — 4) Mihok (1979), Fuller (1979) — 5) Bondrup-Nielsen (1985) — 6) Reichstein (1959), Myllymäki (1970), Viitala (1977), Stoddart (1982), Hoffmeyer (unpubl.) — 7) Frank (1953), Reichstein (1960) — 8) Getz (1978), Madison (1980) — 9) Tast (1966), Viitala (1980) — 10) Getz (1978), Getz et al. (1981, 1983) — 11) Jannett (1978, 1980, 1981a,b) — 12) Wolff & Johnson (1979), Wolff (1980), Wolff & Lidicker (1980) — 13) Kondo (1977, 1981) —14) Brown (1966), Watts (1969), Flowerdew (1974), Gurnell (1978), Green (1979), Montgomery (1980), Hoffmeyer (1983).

prep.). In particular the overwintered males of the peak year are far less tolerated by females and other overwintered males than the summerborn mature males of the increase year are (Viitala 1985). Males always show more scars than females but never as frequently as territorial males of *Microtus agrestis* (Viitala 1977). Familiarity seems to be important in reducing male aggression and in forming male groups.

The mating system of *C. rufocanus* is promiscuous (Kalela 1957). In every oestrus run there are several males running after the female in heat (Collett 1911-12), Viitala 1977). Fighting between males may then have been caused by strange males trying to pursue the same female in heat (Kalela 1957).

2.2. *Clethrionomys rutilus*

The basic social structure of *C. rutilus* populations is very similar to that of *C. rufocanus*. In the Kilpisjärvi area they live in the same habitat types most commonly found in eutrophic meadow forests. In other parts of their geographical range they are restricted to mossy coniferous forests (Kalela et al. 1971, Viitala 1985). Thus the similar social systems may be adaptations to the very similar predictable environments. Some differences exist, however. Henttonen (unpubl. data) found autumn dispersal in *C. rutilus* during an increase year in Pallasjärvi but not during a peak year. Viitala (1984) found, consistently with Henttonen's observation, that both females and males changed their home ranges during the winter after the increase year but remained on their former territories during the peak year. Thus *C. rutilus* sometimes seems less attached to its territory than females of *C. rufocanus* do.

Another difference between *C. rutilus* and several other rodents in the Kilpisjärvi area is the extremely large home ranges and territories of *C. rutilus*. While *C. rufocanus* and *M.*

agrestis females need territories of 3-4 ares during high density situation, *C. rutilus* needs more than 0.4 ha. The home ranges of *C. rutilus* males could not be measured on a study area of 6.7 ha since the grid was too small.

Combined with a system regulating maturation of the young animals similar to that of *C. rufocanus*, the large territories of *C. rutilus* result in very strict limitation of population density (Viitala 1985). When brought into an enclosure with unlimited food supply in Middle Finland, a female vole was able to breed successfully on a territory of 5 ares. Hence, territory size may be phenotypically determined so that the population density and reproductive output may be determined by food availability. In other parts of its geographic range in Finland, *C. rutilus* have smaller territories and higher population densities in peak years than in the Kilpisjärvi area (Henttonen unpubl. data). Because territory size can be affected by the food supply, it seems possible that phenotypic adjustment of reproductive output may be common in voles regulated by maturation rate.

2.3. Other *Clethrionomys* species

The other *Clethrionomys* species so far studied (i.e., *C. glareolus* and *C. gapperi*) show the same territorial mechanisms. However, Mihok (1979) and Fuller (1979) did not find evidence for the regulation of maturation in subarctic populations of *C. gapperi* probably, as suggested by Mihok (1979), due to the low density of breeding animals. In more southern populations of this species Bondrup-Nielsen (1985) did, however, find such a mechanism.

The female territoriality and the inhibition of maturation in an island population of *C. glareolus* are studied in great detail by Bujalska (1970, 1971, 1985). Her results are in good agreement with those on other species of this genus. She has further suggested that the reproduction of already mature females may be socially inhibited.

2.4. Social odours in *Clethrionomys*

The high social stability of most *Clethrionomys* populations and the regulatory mechanisms imply effective signalling systems, which most probably are based on odours. The comparative study on *Clethrionomys* and *Microtus* (Viitala 1977) indicated that fighting in general occurs less in *Clethrionomys* than in *Microtus*. This difference was supposedly due to a better developed system of communication in *Clethrionomys*.

Olfaction is the most important modality for intraspecific communication in rodents. Experiments mainly on laboratory mice and rats have shown that odours may be used to transmit information about individual identity (species, race, kin and even individual) about sex and reproductive condition, social status and about motivational states (aggressiveness, alarm). Scent signals from an individual may in accordance with their information contents cause short-term or long-term changes in the physiology and behaviour of conspecifics. Among so-called "releaser"-effects are changes in alertness, aggressiveness, sexual behaviour (including marking responses). Among "primer"-effects are acceleration or inhibition of sexual maturation, estrus-induction and interruption of pregnancy. Scent signals may be transmitted by products in urine, feces, saliva, and by secretions from specialized glands. The position of such scent clands on the animal's body is generally adapted to the species living habits. Thus, for example, flank glands are most highly developed in small rodents which travel in tunnel systems (*Microtus, Arvicola*), whereas a climber like *Apodemus*, which often uses the tail for support, has a gland on the tail (the subcaudal gland). Scents from different glands may have different functions; and different small rodent species may use different scents (and glands) for the same purpose (such as, e.g., the regulation of numbers of reproducing animals). It is therefore important to examine the behavioural context in which secretions are deposited, as well as the animals' responses to the secretions, before going into more detailed studies about their chemical nature.

The influence of specific odours has been studied in very few species of microtine rodents; hence, there is a general lack of data which makes comparisons difficult. However, as far as possible we will attempt such comparisons below.

Social odours in Clethrionomys glareolus

Odours may be used in mate choice to discriminate between races (Godfrey 1958). Differences in urinary marking between two races of bank voles, and between males and females were described by Johnson (1975). The urinary marking pattern characteristic of male bank voles ("fine trace" urinations) was further found to vary with season and sexual maturation (Christiansen 1980): Christiansen suggested that trace marking serves the purpose of depositing secretion from the preputial glands (see review by Brown & Williams 1972) with either sexually attractive or socially repulsant signals (or both). In laboratory mice such effects of male urine had earlier been attributed to secretions from the preputial glands (Bronson & Caroom 1971, Brown & Williams 1972). The development of the preputial glands of the bank vole was found to be associated with sexual maturation, and mature males have much larger glands than females (Christiansen et al. 1978). The size of male preputial glands is correlated with social status — dominant males having larger glands than subordinates (Gustafsson et al. 1980). Subsequent studies have strongly supported the view that the urine marking of males plays a role in defining the male dominance hierarchy and mate competition (Hoffmeyer 1982, 1983b): estrus female bank voles were more attracted by cues from dominant males; and the males marking behaviour and reactions to marking components depended on their social status and age. In these studies, the dominant male of a group had previous to testing been identified through its aggressiveness toward an unfamiliar male intruder (subordinate) and toward its own group mates, and through its characteristic behaviour patterns, e.g., flank scratching with hind foot, and "displacement digging" described by Sørensen (1981).

The dominance relations of male bank voles were correlated with clear differences in scent marking frequency and pattern (Hoffmeyer 1983), behavioural reactions to chemical components and chemical constitution of the marking substances (Brinck & Hoffmeyer 1984): Dominant males marked significantly more frequently than subordinates, and the specific type of "fine trace"-urination marking was more numerous in dominants. The marking frequency of the subordinate males was lower both in the presence of a strange male intruder, and in the presence of females. Reduced marking by subordinates was found even in the absence of the dominant male; i.e., when the subordinate was alone in its home range. As the females responded positively to male marking substances, and as the subordinate males did not show any increase in amounts of marking in the presence of females (even when the dominant male was absent), the difference in marking behaviour was supposed to be of significance in males' competition for mates. A positive correlation was also found in a subsequent experiment, between the marking frequency of individual males (of unknown social status) and the mating success of these males (Hoffmeyer 1983).

Female bank voles were more attracted by dominant males than by subordinates, and they were also more attracted by the odours from dominant males (Hoffmeyer 1982). The female-attractant effect was enhanced by using male "marking urine" (=extracts from urinary markings) instead of the urine collected in metabolic cages; or by adding preputial gland secretion to the urine in simulation of urine marking. Chemical analyses showed that preputial gland secretion was deposited with the males' urinary marking (Brinck & Hoffmeyer 1984); thus, gas chromatography (GC) and mass spectrometry (MS) showed that hexadecyl acetate, a component of preputial gland secretion, was present in marking urine but not in metabolic urine (Brinck & Hoffmeyer 1984). The synthesis of this acetate is androgen-dependent, and may therefore be suppressed in subordinate (and immature) male bank voles (Brinck et al. 1983).

Young post-weanling subadult males (age 18 days) and subordinate adult males avoided traps with the odour of hexadecyl acetate, whereas dominant males and maturing non-subordinate males (age 32–36 days) were attracted to such traps; females were indifferent, however (Hoffmeyer 1983, Brinck & Hoffmeyer 1984). Thus, hexadecyl acetate seems to play a role in male dominance interactions rather than in sexual relations. The positive reactions of females (i.e., attraction) to the urine and preputial secretion of dominant males must therefore be due to other cues.

Other forms of marking were also observed in male bank voles. These are flank scratching with hind foot, and defecation which probably involves the deposition of anal gland secretion. Flank scratching was performed most frequently by dominant individuals, and then mostly in agonistic situations (Hoffmeyer & Sørensen, unpubl.). Supposedly this behaviour is connected with deposition of secretion from the flank region (Quay 1968). Although the formation of distinct latrine sites seems to be much less clear in *Clethrionomys* than in, for example, short-tailed voles, water voles, or rabbits, *Clethrionomys* often defecate in response to novelty, or during interactions with conspecifics (Hoffmeyer, unpubl); *Clethrionomys* have large anal glands. In *Microtus agrestis*, secretion from anal glands coat expelled faecal pellets (Khan & Stoddart, pers. comm). If defecation in *Clethrionomys* is a kind of scent marking, which has significance in communication with conspecifics, it is likely to have a meaning in agonistic rather than sexual relations. Thus, this behaviour was shown by dominant males in agonistic interactions with other males, but rarely in connection with sexual encounters with females (Hoffmeyer 1983).

In view of the important role of territoriality in breeding female *Clethrionomys*, the scent marking mechanisms are important from the point of view of the whole population. The territorial behaviour of females does not, however, seem to involve severe agonistic behaviour except toward strangers (Viitala 1985, Henttonen unpubl. data). A female's scent marking may make territory familiar to herself; in fact, familiarity with the olfactory environment could be a requisite for the initiation of reproduction. Further, females' scent markings may also attract males; and the presence of a male is important for the induction of estrus in several microtine rodents (e.g., Richmond & Stehn 1976). Scent marking may also function as a form of indirect territorial defence by increasing the female's self-confidence and her ability to win aggressive encounters, and thereby helping her to keep intruders out from her territory. Scent marking may also help a resident female distinguish between familiar females from neighbour territories and unfamiliar females, i.e., immigrants. So far, we only know that female bank voles do not show "fine trace markings" like mature males do (Johnson 1975), and that their preputial glands are very small (Christiansen et al. 1978). But females show flank scratching with hind foot and defecations during agonistic situations. Probably therefore, anal gland secretion and flank gland secretion as well as urinary factors may be important in territorial defence. Auditory signals may, however, also be involved in territorial defence: *Clethrionomys*, like most other microtines, are in fact very "vocal".

Conclusion

Mainly the chemical communication of male bank voles has been investigated. Their urinary marking, including deposition of preputial gland secretion, may signal social dominance status, and facilitate approaches to females. The rank- and age-dependent urinary marking and reactions of the males show the role in male dominance relations, and are in good agreement with the often found social hierarchy system of male *Clethrionomys* (Viitala 1977, 1985, Sørensen 1981). If urinary marking contributes to the territoriality of males, the found indifference of female bank voles to hexadecyl acetate (to which the males reacted according to rank and age) may help explain the fact that male home ranges and territories do not restrict females' movements. The changed tolerance of females to overwintered males, during peak years, could well be the consequence of a change in male odour signals (e.g., lack of preputial gland secretion due to social suppression in the high density situation) and unfamiliarity: males disperse in winter.

Unfortunately, nothing is known about the signals involved in female-female relations. Familiarity/kinship is supposed to play a great role for the lack of aggression between females occupying neighbouring territories. Therefore, one would expect some kind of scent marking in females providing information about individual identity, and at the same time possibly having aversive effects on potential intruders.

The role of social odours in reproductive inhibition constitutes a main subject for future investigations. Exposing young male bank voles for a long time to urine odours from dominant males caused some suppression of growth and maturation: body weight and preputial glands were smaller in the males exposed to urine odours between age 18–42 days than in the controls; but there was no difference in testes or seminal vesicles; Hoffmeyer unpubl.). However, a similar experiment using hexadecyl acetate, found in males' preputial gland secretion gave opposite effects (Hoffmeyer unpubl.); this might, however, have been due to the application of too low doses. In fact, low concentration of marking odours might correspond to the message "absence of the dominant (territory owner)", or "low population density"; and in both cases stimulation instead of suppression of reproduction should be adaptive.

There has been no investigation of the role of olfaction in reproductive inhibition of young female bank voles. It is likely that adult territorial females may cause such effects in young females which do not disperse (see, e.g., Bujalska 1985). In laboratory studies maturation of young male bank voles was found to be suppressed by adult females (Gustafsson 1983). However, here the animals were in direct contact with each other; hence, the importance of olfactory stimuli *per se* could not be assessed.

3. Social organization in other genera

3.1. *Microtus*

Most *Microtus* species are grassland dwellers. However, as noted by Getz (1978) some of them are inhabitants of fairly stable climax grasslands: their environment is quite predictable. The majority of *Microtus* species are, however, inhabitants of flooded shore meadows, marshes and early successional grassland stages changing into forests by time. Thus their environments are mostly made up of unpredictable patches (see, e.g., Viitala 1977). Their strategy is that of a typical *r*-strategist.

The types of social organization within the genus *Microtus* are much more variable than in *Clethrionomys*. From an ecological point of view we may divide the social mechanisms into two groups. First, those characterized by low social stability, lack of a status signalling system, lack of puberty regulation and high adult dispersal rate making the species good colonizers. Species like *M. agrestis* (Viitala 1977), *P. pennsylvanicus* (Getz 1978) and most probably *M. oeconomus* (Tast 1966) and *M. arvalis* (Frank 1953, Reichstein 1960) belong to this group which we call "non-regulators" because they do not restrict maturation of young. The other group is, in general, much more like *Clethrionomys*: this group is characterized by high social stability and site tenacity at least during high population density, by puberty regulation, low colonizing ability due to lack of adult dispersal, and by possessing specific marking behaviours usually not found in the first mentioned *Microtus* group (Getz 1978). Species like *M. ochrogaster* (Getz 1978), *M. montanus* (Jannett 1978, 1980, Thomas & Birney 1979), *M. xanthognathus* (Wolff 1980, Wolff & Lidicker 1980) belong to this group: this group we will call "regulators" because they regulate maturation of young socially.

M. agrestis is a good example of such a colonizer species or "non-regulator". It has a promiscuous or mostly polygynous system, where male territories do not restrict female movements (Viitala 1977). In the Kilpisjärvi area in Finnish Lappland, females become pregnant when still living on the territories of their mothers; they become territorial during their adult life, and, as a consequence, are large adults, mostly pregnant, when dispersing to their individual territories. Therefore, dispersal of adult females is common at all population densities (Viitala 1977). Hierarchical structures among adult males may be formed in spring of high density years; under such conditions subordinates soon disperse. Only territorial males have been found later in the summer (Myllymäki 1970, Viitala 1977). Unlike *Clethrionomys*, the rank and the ability to hold a territory depend entirely on the ability to fight in *M. agrestis*. Hence, the individual males on a certain area change all the time.

M. montanus is a good example of a "regulator" (Jannett 1978, 1980, 1981a). Mostly it exhibits a polygynous territorial system. Both male and female puberty is strictly regulated during high population density. The species is an extremely poor colonizer since even juvenile dispersal rate may be very low in high density situation. Both male and female territories are stable; males have a specific territory marking behaviour (Jannett 1980). The "regulators" show features of a *K*-strategist. When their local habitat is crowded, all other more reasonably distant habitats are likely to be crowded, too. Thus they need some signalling system which could help slow down reproduction and unnecessary dispersal during high density situations.

3.2. *Apodemus*

The two *Apodemus* dealt with in Table 1 (Brown 1966, Watts 1969, Flowerdew 1974, Randolph 1977, Kondo 1977, 1981, Gurnell

1978, Green 1979 and Hoffmeyer 1983) have each developed a different method of regulating the maturation of young animals. Males and females seem to belong to the same regulatory unit. Because of dominance of the old overwintered males, maturation of young may be restricted whereas the mortality and dispersal of juveniles may be high. Rapid population growth may therefore begin just in late summer after the disappearance of most overwintered animals (Flowerdew 1974). The higher mutual tolerance of summerborn animals may then result in high survival and rapid maturation of younger animals. Thus, the number and survival of old animals greatly determine the autumn density of these populations (Flowerdew 1974). This kind of regulation seems to result in a rather stable density from year to year. The interspecific differences in *Apodemus* social organization have been discussed by, for example Hoffmeyer (1983).

These species are greatly depending on seeds of broad-leaved trees as food. They are able to hoard (Hoffmeyer 1983). Their environment is three-dimensional because of their arboreal way of life. Whether this is the ultimate cause of their social structure being different from that of microtines, is not known. However, there might be shortage of food before the growing of new crop of seeds in early summer. The old individual may then be most capable to obtain food in this phase. Thus their food situation may be better already in early summer.

One way to cope with the poor food situation could be seasonal change of habitat. In fact this is several times reported in *Apodemus* (e.g., Bergstedt 1965, Flowerdew 1974, Ylönen et al. unpublished). Thus the population may contain mutually unfamiliar and therefore untolerant individuals. This may increase the aggressive behaviour of old animals.

4. Discussion

4.1. General

As mentioned, there is a general lack of comparative data concerning chemical communication in microtine rodents. For instance it would be interesting to compare the marking behaviours and odour substances used by those with *climbing* vs *non-climbing* habits, and of those being more *granivorous* vs those being more *folivorous*. Possibly, the more distinct use of latrine sites by, for example, the short-tailed voles and water voles as compared to the bank voles and wood mice has to do with such differences. Conversely, the special urinary "fine trace" marking pattern shown by male bank voles could constitute an adaptation to marking on narrow branches (see Schilling 1980), where formation of latrine sites is impossible.

It would be of interest to compare the chemical communication of so-called *"regulators"* and *"non-regulators"*. Although they may use different glands and scents for the same purpose (territoriality and regulation of the number of reproducing animals) there are regulators within both climbers and non-climbers, and within granivores as well as folivores.

A main feature separating "regulators" and "non-regulators" is the relative importance of site tenacity vs dispersal; this difference is likely to have implications for the nature of social relations and communication in the population.

The "regulators" generally have the stronger site tenacity, which enables more stable social relations, based on well developed communication: males may, for example, have stable dominance relation based on chemical signals of status. Females maintain separate territories with little aggression between neighbours; the factors responsible for such a system are not known, but cues allowing individual recognition or at least the distinction between familiar/kin vs unfamiliar are likely to be important.

In the other type, "non-regulators" (with *Microtus agrestis* as an example), the social organization is much less stable and rank and territory holding depend more on direct fighting. Generally, this could be so because it is more advantageous for an animal which must settle in a new area to use the more primitive type of overt aggression than the more subtle signals of, for example, social status, individual identity etc. The difficulty of maintaining long-time stable social relations in these groups of species may also explain why specific scent glands, for example, the preputial glands are less developed in *Microtus agrestis* than in *Clethrionomys glareolus*. On the other hand, such kinds of odours which in general cause aversiveness, could help maintaining territory borders in an area with many strangers. One would further expect the colonizers to have means of acquiring quick information about changes in food conditions and population density. In *Microtus agrestis* the latrine sites could possibly constitute centers of such information exchange: the nature of the waste products may give information about the feeding conditions, and urine and anal gland secretion may have aversive effects on subordinates and strangers, and furthermore give information about the levels of aggression in the population. In rabbits, for example, the frequency of visits to latrines was found to increase in close relation with aggression toward a strange intruder (Bell 1980). In *Microtus agrestis* social odours may also cause aversion to conspecifics (Stoddart 1982). A poorly developed scent communication system for signalling dominance and subordination, combined with strong reactivity to smells from strange conspecifics, may explain the violence and persistence of agonistic interactions seen in, for example, *Microtus agrestis* and *Lemmus lemmus* when exposed to unfamiliar immigrants of the same sex (Viitala 1977, Hoffmeyer, unpubl. obs.). This violent aggression from resident animals toward a stranger may contribute to social instability during high population densities with an associated high immigration pressure. However, kin recognition seems to be the basis of breeding colonies in *M. arvalis* (Frank 1953) and the same may be true for the overlapping of home ranges of breeding *M. agrestis* females (Viitala 1977).

4.2. Regulation of sexual maturation

It appears that in the "regulators", young maturating animals disperse during the increase phase, but may stay within the area of adults during peak population densities. From the point of view of chemical communication, this involves the following possibilities:

1) Odours, which develop in the young in connection with sexual maturation, release aggression and chasing behaviour by the adult residents of the same sex.

2) Sexual development of the young is accompanied by increased reactivity of these young to the scent markings of adult residents and this may contribute to initiate dispersal.

3) At high population densities, the cost of dispersal may be too high. It is then more advantageous for a young animal to stay within the range of a familiar adult; and the best way of being allowed to stay together with such an adult individual would be to avoid emitting odours, which may release aggression from adults. "Olfactory concealment" could be the "purpose" of inhibited urinary marking shown by subordinate males in the presence of a dominant (e.g., the results with bank voles; Hoffmeyer 1983, for *Mus musculus* see Mugford & Nowell 1970). An alternative strategy would be to mask one's own odour by getting impregnated with the odours of the adult resident by visiting communal scent marking sites.

It seems quite obvious that the great similarity in social mechanisms of different species of *Clethrionomys* is a result of their close relatedness and most of all of their common adaptation to climax vegetation communities. In the closely related genus *Microtus*, those species which are adapted to stable climax vegetations show social mechanisms similar to those of *Clethrionomys* species but very different from those of the *Microtus* species which live in unpredictable successional communities. The two *Apodemus* species reviewed in an earlier section inhabit fairly predictable climax vegetations. The unpredictable yearly yield of seeds may be the reason why *Apodemus* is not as site tenacious during the non-breeding season as most *Clethrionomys* populations. However, *Apodemus* exhibit clear puberty regulation of young animals during times with high densities of overwintered animals, even though the actual mechanism seems to be unlike that found in *Clethrionomys*. That is, inhabitants of predictable environments seem to exhibit regulation of puberty and lack of adult dispersal at least in the breeding season during high density conditions but the similarity of the actual mechanisms used by the various species depends on their taxonomic relatedness.

4.3. Predictions about scent communication in microtines

Background for predictions about scent communication in microtines

1) The main differences between mice (*Apodemus*) and microtines (*Clethrionomys* and

Microtus) are the differences in *food* and *reproductive* characteristics.

Microtines are more specialized on a folivore/grass-diet and they are generally less agile than mice. This may make the reproductive female microtines relatively more territorial than female mice. The female microtine has to keep an area, where the young can find food and be safe during the first time after leaving the nest. Female mice are better able to hoard food for the young, into the nest.

Female microtines also have another characteristic, which presumably constitutes a further adaptation to their more unstable food conditions. Their reproductive activity is dependent on male stimuli. Thus, female microtines have male-induced estrus, male-induced ovulation, and male facilitation of pregnancy. The presence of the male in combination with specific male odour signals are mostly required (see e.g. Richmond & Stehn 1976, Carter et al. 1980).

This implies that a male microtine must invest more in mating, and therefore should show a stronger tendency to get rid of male competitors in advance of mating by, for example, territorial exclusion (e.g., the *Microtus agrestis* pattern) or by social suppression (e.g., the *Clethrionomys glareolus* pattern). Consequently male-male competition in microtines should generally be stronger than in mice.

2) The main differences between *Clethrionomys* and *Microtus* species seem to be habitat and food specializations, which determine differences in the degrees of site tenacity (*Clethrionomys* more site-attached than *Microtus*), and in the number of adult males covering the ranges of breeding females. Breeding female *Clethrionomys* are reported to be more long-term site-tenacious than female *Microtus* (Myllymäki 1977, Viitala 1977), which is attributed to the more heterogeneous habitat of *Clethrionomys*; and more males overlap their ranges, which may be a consequence of a more energy-rich food and of the more heterogeneous environment.

Predictions for scent communication

The above main differences are supposed to reflect on the communication system in the following ways.

1) Comparing mice and microtines:

a) *Female* microtines should have effective signals for site tenacity and territoriality; i.e., for own familiarization with area and for exclusion of other females. Female microtines should also have strong male attractants.

b) *Male* microtines should have more effective cues for male-male competition, and to have strong responsiveness to female attractants.

c) *Male* microtines should have more effective cues for female-stimulation (estrus-induction, sexual maturation, ovulation, and pregnancy facilitation or disruption).

2) Comparing *Clethrionomys* and *Microtus* species

a) *Female Clethrionomys* should have stronger cues for site tenacity, and for exclusion of other females.

b) *Male Clethrionomys* are likely to have a mechanism for the maintenance of social hierarchy among males; i.e., for the communication of social status, while male *Microtus* should have better means of territorial exclusion of other males. Male *Microtus* should have effective aggression eliciting cues while dominant male *Clethrionomys* should have submission eliciting cues.

c) *Female Clethrionomys* should have a mechanism for mate choice since several males may be present within their range at the time of mating. Even though only one territorial male overlaps the territories of breeding of female *Microtus* a similar mechanism of female choice might exist for females that disperse.

d) *Clethrionomys* may generally, owing to stronger site tenacity, with ensuing close association between relatives and more stable social relations, have mechanisms for kin recognition, incest avoidance, and social hierarchy. Possibly also, for individual recognition. Furthermore, *Clethrionomys* may, because of their climbing habits, have more specialized urine marking and less extensive latrine sites, than ground dwelling *Microtus* species.

Conclusion

The results reviewed in earlier sections on bank voles appear to agree with the above predictions.

Male bank voles have mechanisms for male-male competition and the maintenance of social dominance relations (see 2b). Female bank voles have a mechanism for mate choice (see 2c). Furthermore, bank voles have a specialized urinary marking pattern probably adapted to their climbing habits (see Schilling 1980; see also 2d).

4.4. Suggestions for future studies

In view of the apparently central role of female territoriality in the regulation of *Clethrionomys* populations, future investigations should be concentrated on the possible territorial scent marking of reproductive females, and on the effects of such markings on other females (aversiveness, delay of estrus and delay of sexual maturation).

The question of mechanisms in estrus induction or delay of female bank voles is of great interest as it determines the operational sex ratio. Furthermore, the chemosignals involved in female scent marking and regulation are not known. Apart from the urinary compounds — as found in *Microtus ochrogaster* — secretions from flank and anal glands may be involved (see above).

Also, the existence of a mechanism for kin and/or individual recognition should be subject to future studies. According to the predictions this should be better evolved in *Clethrionomys glareolus* than in *Microtus agrestis.*

Concerning *M. agrestis,* main subjects suggested for future studies are the role of scent marking and overt aggression by a dominant male in territorial exclusion of other males, and olfactory mechanisms involved in female regulation and dispersal.

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