

## 6.5. Social Organization

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### 6.5.1. Methods of study

The study of the social structure, e. g. of interactions among population members, in rodent populations is methodologically difficult. The best method, successfully used by workers dealing with primates, large predators and ungulates, is direct observation. But the application of this method to the studies of small, generally non-colonial rodents which are mostly nocturnal is very limited. In fact, it can successfully be used only in laboratory populations, but in that case we study social relations among individuals living in densities that differ from natural ones. This is true of spatial structure, food availability, etc., and all these factors may substantially modify social organization. For this reason the most reliable results on social organization in rodents have been obtained for laboratory populations of rats and house mice (e. g. Calhoun, 1952, 1956; Petruszewicz, 1957, 1960, 1966b; Crowcroft, 1966), since for these animals, laboratory conditions deviate little from natural conditions. All these studies have shown that social organization in rodent populations has an important effect on many population processes such as birth rate, death rate, or migrations. Consequently, the knowledge of the social organization in the population is necessary for understanding the mechanisms of population functioning.

Direct observation allows recognition of the type of encounters among individual animals. These encounters may be tolerant or aggressive, resulting in a fight or an escape of attacked animal; escape of both or mixed variants of these behaviours. Thus, to get a general picture of social organization in the population through direct observations, it is necessary to develop a system of classification that would allow a transition from subjective statements to numerical estimates for the entire group. Nearly every investigator applies a different classification of the encounters observed. The direct laboratory observations of the social structure for the genus *Clethrionomys* were conducted by Johst (1967), Mihok (1976) and Skirrow (1969).

As such observations are labour-consuming and somewhat subjective, it is interesting to note Kock & Rohn's (1971) finding that in laboratory populations of *C. glareolus* and *Lemmus lemmus* there is a close inverse relationship between the rank in the social hierarchy and the intensity of activity wheel running by individuals.

The method of direct observation of individual interactions in free-living population has been used on very rare occasions. The best results were obtained by means of a noctovisor (Andrzejewski & Olszewski, 1963b), but only a small part of the population can be observed in this way.

The largest number of data on the social organization of free-living populations has been obtained by persistent live-trapping. This method allows only indirect conclusions concerning individual interactions, on the basis of differences in the parameters that can be determined as a result of frequent trapping. For example, it has been found that the trappability of individual voles indicates their social rank (Gliwicz, 1970; Watts, 1970a; Andrzejewski & Rajska, 1972), and that there is a close relationship between the trappability of individual voles and the size of their home ranges, occupancy of better microhabitats, and sometimes the rhythm of activity (Andrzejewski, Petruszewicz & Waszkiewicz-Gliwicz, 1967). Thus, each of these characteristics is also closely correlated with the social rank of an individual.

The most recent method for recording intraspecific contacts in the field is the application of two-compartment traps, which allows the observation of the sequence of capture of two animals. Frequently, this method is modified in such a way that an animal of known characteristics is put to one of the two compartments, and the animal caught afterwards is noted (Kalinowska, 1971); Kołodziej *et. al.*, 1972). This method is based on the assumption that since some individuals enter the trap and other do not, is a result of their mutual tolerance, avoidance, or attraction.

#### 6.5.2. General Characteristics of Social Organization

Intraspecific contacts in the bank vole populations are much more frequent than in populations of co-occurring species, e.g. *Apodemus flavicollis* (Turček, 1960; Andrzejewski & Olszewski, 1963a; Kalinowska, 1971). For example, Kalinowska (1971) has found that the traps already containing one bank vole are more frequently visited by another bank vole than are empty traps or traps containing *A. flavicollis*. At the same time, traps with *A. flavicollis* were much less often visited by individuals of both the same and other species than indicated by a random distribution of events. Similarly, Rajska-Jurgiel (1976) recorded many more visits to the traps with bank voles than to empty traps. This suggests that social bonds are strongly developed in these rodents, thus intraspecific relationships should have a significant effect on demographic processes in the population. Additionally, studies on

bank vole populations inhabiting a large forest site and a 4-ha island showed that social organization is more pronounced and that avoidance or attraction is stronger in the isolated island population than in the open population (Rajska-Jurgiel, 1976).

The development of social organization arranges contacts among population members by establishing the norms of response to each other (Rajska-Jurgiel, 1976). The rank of an individual in a social organization depends on its physiological features such as age, sex, etc., thus it is based on the primary differentiation of individuals, which accounts for more or less permanent secondary differentiation among population members (Łomnicki, 1978).

### 6.5.3. Social Rank in Relation to Age

Social rank of individual animals in bank vole populations largely depends on age. The subordinate position of young individuals in relation to the adults was noticed by all authors studying social organization. Andrzejewski & Olszewski (1963a), who observed individual interactions at feeders, have noticed that adults were feeding long enough to become satisfied (chasing or tolerating other individuals), while young individuals spent little time at the feeders, each time taking a few grains and running away to the nearest shelter to eat them. They were frequently harassed by adults.

Rajska-Jurgiel (1976) pointed out that young individuals were caught in traps with adults less frequently than by chance, especially when a male was in the double trap first. The subordinate position of the young is reflected in their low trappability in baited live-traps. Such a trap is an attractive requisite, and for this reason it is quickly occupied by the dominant, older individuals (Gliwicz, 1970; Andrzejewski & Rajska, 1972). This thesis is consistent with the results of experiments carried out by Watts (1970a), in which the trappability of young individuals increased after the removal of adult males from the population; similarly the age of voles trapped for the first time was lower in the experimental population, as compared with the control.

In the island population of the bank vole, different population indices were estimated separately for each cohort. It has been shown that members of successive cohorts established home ranges of decreasing mean sizes (Mazurkiewicz, 1971) and in deteriorating microhabitats (Bock, 1972). These are features that, as noted above, are correlated with rank in the social hierarchy. This provides a basis for an hypothesis that the rank of individuals in the social hierarchy is determined by their age or, strictly speaking, by the sequence of their recruitment

into the breeding population (Gliwicz, 1979). By mid-summer, the overwintered animals ( $K_0$ ) are dominants, and the young born early in spring ( $K_1$ ) are co-dominants, to become dominants when the overwintered animals die out. The members of the two last cohorts ( $K_3$  and  $K_4$ ) have the lowest rank in the population. When recruited into the population, they occupy the smallest home ranges and are forced to the poorest (driest) microhabitats. This pattern of social hierarchy is maintained to the end of the breeding season.

It is possible that this relationship between social rank and age is particularly clear in isolated populations, where migration is not possible. In open populations the social rank of an individual depends on the time of its residence in the population.

#### 6.5.4. Social Rank in Relation to Maturity

Young, immature individuals of both sexes, form aggregations in the population (their home ranges have clumped distribution), and they are often caught together in two-compartment traps, suggesting that they are mutually tolerant (Naumov, 1951; Bujalska, 1970; Mazurkiewicz, 1971; Rajska-Jurgiel, 1976). In a dense population of the common vole (*Microtus arvalis*), young individuals can establish a common, group home range during the breeding season, which shows that they are not aggressive (Chełkowska, 1978). It is possible that a similar phenomenon also occurs in the bank vole population before sexual maturity is reached and dispersal takes place.

The time when males reach sexual maturity seems to depend only on their age, thus older males, with a high social rank, are also mature individuals, while subdominant males are younger and immature. Contrastingly attainment of maturity by females depends not only on their age but also on the establishment of exclusive or nearly exclusive home ranges (Kalela, 1957; Koshkina, 1965; Bujalska, 1970; Mihok, 1976). As Bujalska (1970) has shown, a young female which has contacts with too many mature females cannot reach maturity. As a result, home ranges of mature females have a character of territories, and they tend to be evenly dispersed. Interactions among mature females kept under laboratory conditions are aggressive (Mihok, 1976), but we may expect that in the wild encounters between mature females are rare because of behavioural mechanisms isolating mature females in space. Rajska-Jurgiel (1976) found that mature females are less frequently captured in two-compartment traps with other mature females already present in them than indicated by the random distribution of capture. In a free-living bank vole population experimentally supplied with additional

food, where population members probably became more tolerant of their conspecifics (this can be inferred from a significant increase in the overlap of their home ranges), mature females continued to maintain evenly spaced and only slightly overlapping home ranges (Bujalska, 1975b; Andrzejewski & Mazurkiewicz, 1976).

Territorial mature females have a higher social rank than immature females. This is indicated by both, direct observations (Kock & Rohn, 1971; Mihok, 1976) and indirect indices such as a higher trappability of mature females. But the maturity-related social hierarchy in females is also strongly correlated with their age structure, since females born in early spring and in summer, when the population density is low, have a greater chance of establishing a home range (a prerequisite of maturity) than do females born in late summer and autumn, when the density of the population is high. As a result, in an island population under study, most of the mature females were represented by overwintered animals and by members of the first spring cohort, while females born in late summer and in autumn did not reach maturity in the year of their birth (Bujalska *et al.*, 1968).

#### 6.5.5 Social Rank of Migrants

According to many ecologists, individuals of a low social rank in their native populations become migrants\* (Andrzejewski & Wroclawek, 1962; Lidicker, 1975 — saturation dispersal; Lomnicki, 1978). Thus, these are likely to be subdominant mature and maturing males, also females that reached the age of maturity but failed to establish a home range-territory, etc.

Therefore, an experiment was done to get information on the social position that can be reached by immigrants in an established population. Alien individuals were released into organized laboratory and free-living populations, and their fates were followed either by direct observations or by means of some indices of social rank, such as trappability or running in an exercise wheel. Classic studies of this type were carried out on laboratory populations of white mice (Andrzejewski *et al.*, 1963; Walkowa, 1964). Similar experiments with laboratory populations of the bank vole were conducted by Kock & Rohn (1971), and with free-living bank vole populations by Kołodziej *et al.* (1972) and Rajska-Jurgiel (1976). The conclusions were the same in all cases. Independent of their age, sex, and breeding condition, all individuals entering an organized po-

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\* This mostly concerns emigration stimulated by social organization and not emigration forced by a drastic deterioration of habitat conditions (e.g. flood) or seasonal migrations; the fates of emigrants, however, is the same in all cases.

pulation had the lowest rank in the social hierarchy, corresponding to the rank of the youngest independent individuals in this population. They lost fights, occupied the worst nest boxes, had low trappability avoided two-compartment traps with individuals of the local population inside, and frequently ran the wheel. It has also been shown that the introduced individuals readily occurred together (they entered the two-compartment traps with individuals of the same category), which is similar to the already noted clumping of young, subordinate individuals, noted previously.

These results show that the social rank of immigrants is low, and this concurs with theoretical predictions based on classic papers concerning the development of social organization in the population (see a review in Allee *et al.*, 1958). According to these predictions (1) residents holding an area for a long time and defending it against intruders easily win, and (2) the outcome of fight for dominance heavily depends on the earlier experience of animals. Immigrants are always intruders in established populations, and, in addition, they held a very low social rank in their own population. The immigrant's chance of surviving and establishing a home-range and of its possible rise in social hierarchy depends, according to the authors quoted above, on the density of the local population (in relation to resources available), on social relations in this population (the level of aggregation), and on the number of immigrants. Also the phenological time of immigration can be important.

#### 6.5.6. Social Organization in the Annual Cycle

The differentiation of population members discussed so far concerns the breeding season. In most of the free-living populations under study, trapping was carried out from early spring (March, April) to late autumn (October, November). It has also been stated that the clear differentiation in trappability, size and shape of home ranges, and in spatial distribution of individuals occurred only in spring and summer while disappearing almost completely in autumn, independent of the age of maturity of individual animals (Gliwicz, 1970; Mazurkiewicz, 1971; Andrzejewski & Rajska, 1972; Rajska-Jurgiel, 1976). This is related to the termination of breeding, and probably implies that at the beginning of winter, social organization of the population changes, individual interactions are less severe, mechanisms that isolate individuals crumble, and the aggression level in the population declines. A conspicuous effect of this situation may be the formation of large winter aggregations of the bank vole (Naumov, 1951; West, 1977), which may account for

a reduction in energy expenditures and mortality of the population, particularly in the areas and years characterized by severe winters.

In early spring, when reproductive activity is resumed, social hierarchy is re-established. This process is accompanied by an increase in aggression. At least in this way Chitty & Phipps (1966) explain the increased mortality of overwintered animals observed during March in *Microtus agrestis* populations, and also occurring in the bank vole. The increase in the level of aggression can reflect the fact that animals which were largely differentiated in the preceding breeding season, become similar to each other in winter. As a result, all overwintered animals are of similar body weight (Bujalska & Gliwicz, 1968, 1972) and all are mature. Development of social hierarchy among similar individuals is a very difficult process (Shilov *et al.*, 1974; Gliwicz, 1975, 1979).

#### 6.5.7. Conclusions: the Effect of Social Organization on Demographic Processes

**Reproduction.** As was shown in the section dealing with the reproduction, avoidance among mature and maturing females gives rise to competition for space among them and to the limitation of the number of females that can reproduce.

**Survival.** Disturbances in social hierarchy of the population account for an increased mortality. This has been confirmed in many laboratory studies (Petruszewicz, 1966b, 1978) and also in the studies on free-living bank vole populations (Chitty & Phipps, 1966; Gliwicz, 1975). It is unclear, however, to what extent the length of life depends on the social rank of individual animals. It seems that in the case of a drastic deterioration of environmental conditions, the chance of surviving will depend on the social rank, thus on the size of home ranges, on the quality of the microhabitat occupied, etc. Such a relationship between social rank and survival under extreme environmental conditions was obtained by Warnock (1965) for a laboratory population of *Microtus pennsylvanicus*, deprived of water and shelters. But in open populations, a decline in numbers under such conditions is likely to be achieved through an increased emigration.

**Migrations.** Social organization in rodent populations plays an important part in number regulation through migrations. It stimulates emigration and also accounts for difficulties in the establishing of homes by immigrants. This has been confirmed for the bank vole in many field studies (Andrzejewski & Wrocławek, 1961, 1962; Pielowski, 1962; Adameczyk & Ryszkowski, 1965; Rajska-Jurgiel, 1976).