



## Social Organization of the Vole *Clethrionomys rufocanus* and its Demographic and Genetic Consequences: a Review

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**Abstract.** Recent findings on the relationship between social interaction and demographic process in the gray-sided vole *Clethrionomys rufocanus* are reviewed with reference to the findings in other microtine rodents. Social behavior was particularly focused on spacing and dispersal, and their effects on population dynamics are discussed. Female territoriality can limit a population abundance as a density-dependent factor, although its regulatory effect is controversial. Female philopatry and male-biased dispersal should bring about the clumped distribution of female relatives and genetically random distribution of males during the breeding season. The sexual difference in dispersal patterns can contribute to the mating behavior of the vole; promiscuous mating and low frequency of incestuous mating. However, effects of social structure, including kinship, on reproduction and survival of individuals still remains to be clarified. Molecular markers may help to solve these issues and provide new field of population ecology in microtine rodents.

**Key words:** dispersal behavior, kin cluster, philopatry, spatial genetic structure, territoriality, the gray-sided vole.

### Introduction

Multiannual or cyclic fluctuations have been widely reported in many microtine populations (Stenseth and Ims 1993; Krebs 1996). The cyclic fluctuations seem to be produced by the integrated effects of intrinsic (i.e. social interaction) and extrinsic factors (i.e. predation, food supply, climate and others). Controversy exists on the relative importance and the way of interaction among these factors (Taitt and Krebs 1985; Stenseth et al. 1996a).

Social interaction affects reproduction, survival and dispersal of individuals (Trivers 1985; Krebs and Davies 1987; Chepko-Sade and Halpin 1987), thus, influencing demographic processes fundamentally. Among social interactions, territoriality may be the most important component affecting population dynamics through direct density-dependence in microtine populations (Bjørnstad et al. 1996, 1998a; Stenseth et al. 1996a; Saitoh et al. 1997, 1998a).

Recent studies in microtine rodents suggest the possibility that kinship among individuals affects the contents of interactions, such as amicable or aggressive (see Kawata 1990 for review). Dispersal behavior should be involved as a factor affecting population dynamics since population kin-structure is formed under the influence of individual dispersal.

The gray-sided vole *Clethrionomys rufocanus* (Sundevall, 1849) exhibits both multiannual and seasonal density fluctuations in Hokkaido, Japan, and these fluctuating populations can be characterized by both direct and delayed density-dependence in the time series data of population abundance (Bjørnstad et al. 1996, 1998a; Stenseth et al. 1996b, 1998; Saitoh et al. 1997, 1998a, b). The direct density-dependence is prevailing in all populations, and the delayed density-dependence is restricted to the cyclic fluctuation (see Stenseth et al. 1996b; Saitoh et al. 1997, 1998a, b; Bjørnstad et al. 1998a).

Here, we review recent findings on the relationship between social behaviors and demographic processes in the gray-sided vole. In the last part of this paper, we also present the possible studies on genetic issues in this

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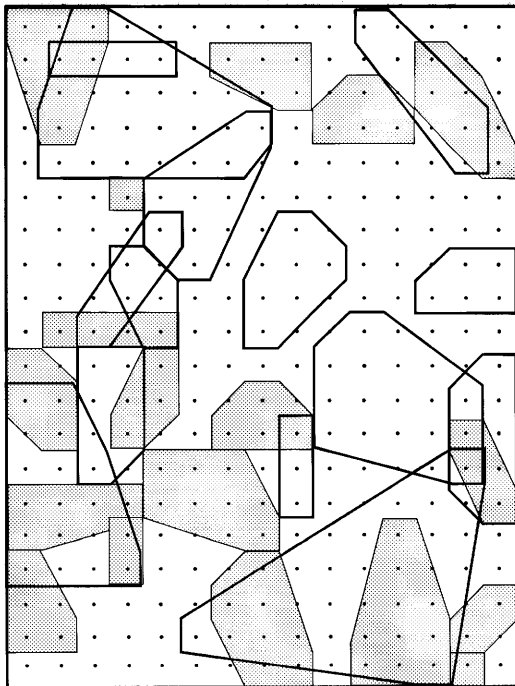
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small rodent. This species is widely distributed from Fennoscandia to East Asia (Stenseth 1985a; Kaneko et al. 1998), but our ecological knowledge of this rodent mainly comes from Hokkaido and Fennoscandia.

## Spatial social structure

### Breeding season

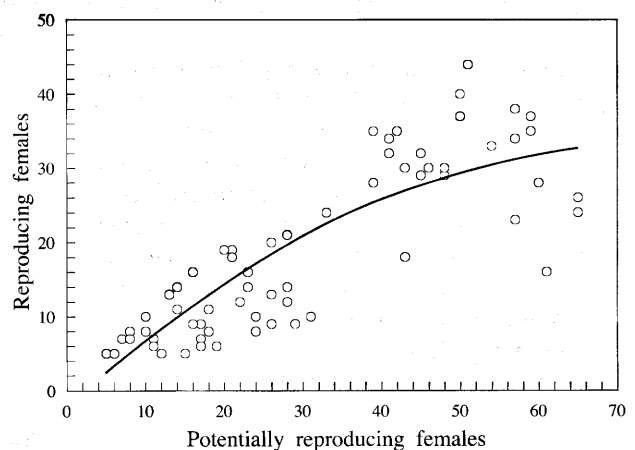
Territoriality is a prevalent component of animal social systems (Cockburn 1988) and also frequently observed during the breeding season in small rodents (Madison 1985; Ostfeld 1985). Here, we regard an exclusive home range as a territory, although the function of exclusive spacing is controversial in microtines (Ostfeld 1985; Saitoh 1985; Ostfeld and Klosterman 1990; Wolff 1993a). *Clethrionomys* is one of the typical taxon which is territorial. Female territoriality is observed during the breeding season in all species of this genus having been investigated (for reviews, Bondrup-Nielsen and Karlsson 1985; Viitala and Hoffmeyer 1985; Ostfeld 1990; and see also Kalela 1957; Bujalska 1970, 1973, 1985; Abe 1976; Saitoh 1985, 1991; Bondrup-Nielsen 1986; Gilbert et al. 1986; Nakata 1989).



**Fig. 1.** Home range map on the fall breeding season (October 1992) in an experimental population of the gray-sided vole in Hokkaido. Home ranges are shown by the inclusive boundary strip method (Stickel 1954). Solid lines for males; shaded areas for females. Dots: trapping stations at 10-m interval.

The main breeding season of the gray-sided vole in Hokkaido is from April to November (Ota 1984; Kaneko et al. 1998). Female gray-sided voles hold breeding territories (Tanaka 1953; Saitoh 1985) with a size ranging from 200 m<sup>2</sup> to 600 m<sup>2</sup> (Saitoh 1991; Fig. 1). The size of female home range changes depending on habitat (i.e. food condition) and reproductive state (Koskela et al. 1997). Breeding females maintain a territory within which nesting, courtship, mating and most foraging take place (in sensu Hinde 1956; Wilson 1975; Itô 1978; Morse 1980). Males have larger home ranges covering several females' territories (400 m<sup>2</sup>–1300 m<sup>2</sup>; Ota 1984), and their home ranges frequently overlap with each other (Fig. 1; Saitoh 1985). These territory sizes are slightly smaller than those of the bank vole *C. glareolus* (mature females 897 m<sup>2</sup>, mature males 1,753 m<sup>2</sup>; Bujalska and Grüm 1989).

Sexual maturation of young gray-sided vole females is inhibited when they fail to establish a territory, even though they have reproductive potential (Saitoh 1981, 1990). Females whose home ranges overlap with other females fail to become pregnant (Kawata 1987). Consequently, the number of breeding females per unit area is limited as observed in *C. glareolus* (Fig. 2; Nakata 1989; Saitoh 1991; see Bujalska 1985, 1995a for *C. glareolus*), although the reduction of home range (territory) size has been observed at high density (Saitoh 1991). *Clethrionomys* females have been thought to have more rigid territoriality than *Microtus* females: while young female *Microtus* can breed in a home range shared with their mothers, *Clethrionomys* females do normally not reach maturity in the territory of their mothers (e.g. Bondrup-Nielsen 1986). However, some exceptions were



**Fig. 2.** The relationship between the number of actually reproducing females and that of potentially reproducing females (older than 40 days) observed in an experimental population of the gray-sided vole (modified from Fig. 5 in Saitoh 1991). The quadratic curve fits well for the relationship ( $y = 0.950x - 0.006x^2 - 2.126$ , adjusted  $R^2 = 0.724$ ,  $P < 0.001$ ).

recently reported between relatives; female gray-sided voles can reproduce with overlapping home range with their mothers (Ims 1989) and littermate sisters with overlapping home ranges wean juveniles successfully (Ishibashi and Saitoh unpublished; see also Gliwicz 1989 and Mappes et al. 1995 for *C. glareolus*).

Ostfeld (1985) emphasized that female territoriality should be food-based, whereas for males it should be female-based (see also Ims 1987a). Ims (1987b) showed experimentally that the spatial organization of breeding *C. rufocanus* females is determined by the distribution and abundance of food, and that exclusive use of space by females seems to be maintained by site-specific dominance when food is limiting. The position of female home ranges is unaffected by males, whereas the spatial distribution of males reflects that of estrous females (Ims 1988).

Limitation of breeding individuals by territoriality could function as a density-dependent factor in population dynamics. Watson and Moss (1970) regard the presence of non-breeding members, which are produced by social interaction, to lower the reproductive output of the population. On the other hand, Krebs (1971) considers territoriality only to have a weak density-dependent effect since territory size is so variable from year to year in the great tit. Heske and Bondrup-Nielsen (1990) also suspect its effects as a stabilizing factor because territory holders can breed repeatedly. In fact, most breeding females of the gray-sided vole have more than two litters in a breeding season (Saitoh and Ishibashi unpublished). However, it is generally expected that through seasonality of reproduction, territoriality may function as a stabilizing factor (Stenseth 1985b, c).

### *Non-breeding season*

The gray-sided vole aggregates with common use of shelters during cold non-breeding season (Kalela 1957; Ylönen and Viitala 1987; Saitoh 1989a). Such huddling, or communal nesting, is commonly seen in microtine rodents (e.g. Webster and Brooks 1981; Wolff and Lidicker 1981; Madison et al. 1984; Karlsson 1988; see Madison 1984 for review). The potential cost of sharing a space (thus resources) could be compensated for by other advantages. Survival rates are usually higher during winter than during the breeding season, despite limited or at least unrenewable food supply in winter (Petrušewicz et al. 1971; Bujalska 1975; Dewa 1975; Viitala 1977; see Ostfeld and Canham 1995 for *M. pennsylvanicus*). The relatively low mortality in winter has been thought to be related to the huddling and the change in social system from being territorial during the breeding season to aggregation during winter (Kalela 1957; Madison 1984; West and Dublin 1984). Such a change in the social organization may help to lower the energy expenditure (Petrušewicz et al.

1983; Hayes et al. 1992) as well as may result in the cessation of social conflicts (McShea 1990; Bujalska 1995b). However, prairie voles *M. ochrogaster* form communal groups throughout the year (Getz et al. 1993; McGuire and Getz 1995). Recently, Berteaux et al. (1996) showed experimentally in *M. pennsylvanicus* that group size had no effect on field metabolic rate, water turnover, body mass changes, body composition and survival. The physical benefit hypothesis for explaining winter aggregation thus needs reevaluation.

Kinship among nest-sharing members has been known only in a few *Microtus* species (*M. ochrogaster*, McGuire and Getz 1995; *M. pennsylvanicus*, Madison et al. 1984; Madison and McShea 1987; *M. xanthognathus*, Wolff and Lidicker 1981). In the gray-sided vole, kin-based overwintering groups seem to be common. Within an enclosed gray-sided vole population in Hokkaido, in which parentage was established for all weaned juveniles by using microsatellite DNA markers and thus kinship is known among individuals, all but one individuals aggregated and seemed to nest communally in March (Ishibashi et al. 1998). Most wintering groups consisted of voles which had neighboring home ranges at the end of the breeding season. Since most juveniles were philopatric in fall, the winter groups consisted of maternal relatives, i.e. mother and offspring or siblings from the same and/or different litters, forming a maternal family. Several maternal families included an unrelated vole (an adult male, a young female or a young male); a few included a father. Dispersers, which were apart from the relatives, also aggregated into a group independent of their sex and kinship, forming a mixed lineage group. Most voles who survived the winter stayed in the same group during wintering. After the onset of the breeding season, these wintering groups were dissolved quickly, and then female relatives showed a clumped distribution because of female philopatry.

Since lower survival during winters following high fall densities seems to be the case in the gray-sided vole in Hokkaido (Yoccoz et al. 1998), the relationship between fall density and winter group formation should be clarified. Most previous studies on the relation between social organization and demographic process were focused on the phenomena during the breeding season. Further observational and experimental studies are needed to address the wintering process.

### **Dispersal**

#### *Density and dispersal*

Dispersal occurs more frequently at high population density than low density in microtine rodents (Gaines et al.