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Special feature
Population Ecology of
Clethrionomys rufocanus

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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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).

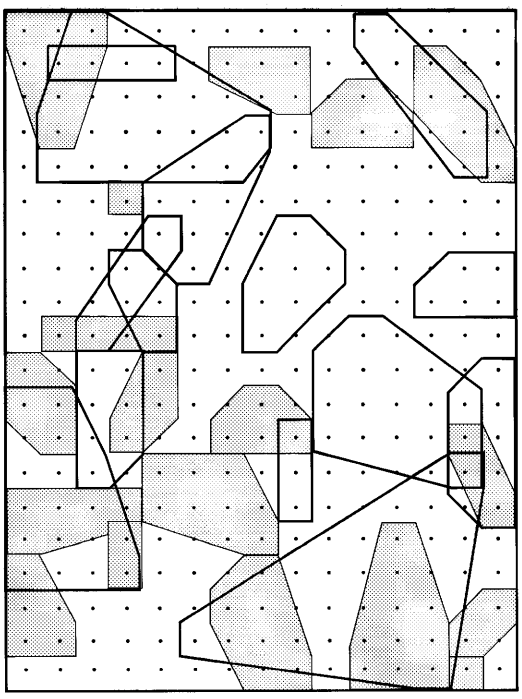

Fig. 1. Home range map on the fall breeding season (October 1992) in an experimental population of the gray-sided vole in Hokkaido. Home ranges are shown by the inclusive boundary strip method (Stickel 1954). Solid lines for males; shaded areas for females. Dots: trapping stations at 10-m interval.

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^2 to 600 m^2 (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^2–1300 m^2; 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^2, mature males 1,753 m^2; Bujalska and Grüm 1989).

Sexual maturation of young gray-sided vole females is inhibited when they fail to established 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 ranges 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

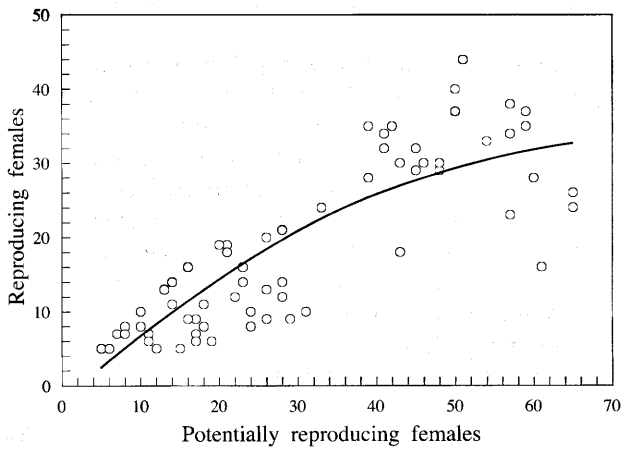

Fig. 2. The relationship between the number of actually reproducing females and that of potentially reproducing females (older than 40 days) observed in an experimental population of the gray-sided vole (modified from Fig. 5 in Saitoh 1991). The quadratic curve fits well for the relationship ($y=0.950\,x-0.006\,x^2-2.126$,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

1979; Bowen 1982; Plante et al. 1989; see Gaines and McClenaghan 1980; Lidicker 1985 for review), although it may be suppressed at extremely high density by social fence (Hestbeck 1982; Boonstra 1989; Lambin 1994; Ostfeld and Canham 1995). In a fenced population of gray-sided voles in Hokkaido, in which the 2.1-ha enclosure was divided into two parts and one of them received added food intensively during 2.5 years, Saitoh (1995) showed that the frequency of dispersal (>50 m) was greater in the food addition grid with high density than in the control grid with low density. In addition, dispersal from a high-density food addition grid to a lower-density control grid generally occurred more frequently than dispersal in the opposite direction (Saitoh 1989b).

Dispersers may affect the reproduction or growth of residents as well as being suppressed by residents. In *Clethrionomys* species, pregnancy interruption after exposure to an unfamiliar male or its odor has been demonstrated in the laboratory (*C. glareolus*, Clarke and Clulow 1973; *C. gapperi*, Clulow et al. 1982). Infanticide by unfamiliar females and/or males is also suggested in other small rodents (Wolff and Cicirello 1991; Lambin and Krebs 1993; Mappes et al. 1995; Wolff and Schauber 1996; Wolff 1997; Lambin and Yoccoz 1998). However, the influence of dispersers on the reproduction and survival of resident individuals is unknown in the gray-sided vole.

Sexual difference in dispersal patterns

Male gray-sided voles disperse further than females from the birth place to the location of the initial breeding attempt (Ims 1989; Saitoh 1995), similar to most other microtines (Bondrup-Nielsen and Karlsson 1985; Boonstra et al. 1987). Saitoh (1995) observed in a 2.1-ha enclosed experimental population that average dispersal distances (SD) from the natal site to the site of first reproduction were 64.9 m (51.1) and 35.3 m (45.6) for males and females, respectively (Fig. 3). These estimates are similar to those of *C. glareolus* (males 62.7 m, females 48.6 m; Mazurkiewicz and Rajska 1975). In the population, 51.2% of females settled within one home range length from the natal site, and 22.0% settled further than two range lengths, while only 24.8% of males settled within one home range length from the natal site, and 51.2% dispersed further than two range lengths (Saitoh 1995). Although dispersal distances may be more or less biased by enclosing (Steen 1994), male-biased dispersal seems to be real, since there is no reason that the enclosure gave different effects on dispersal behavior between males and females.

Timing and causes

Juvenile dispersal is associated with the presence of opposite sex parent within the natal home range and the timing of sexual maturity in most mammals, strongly supporting the idea that natal dispersal functions to avoid inbreeding (see Clutton-Brock 1989; Wolff 1993b; Pusey 1987; Pusey and Wolf 1996 for review). Many studies in mammals also infer that the adults must be forcing juvenile dispersal (Dobson 1982; Cockburn et al. 1985; Boonstra et al. 1987; see Cockburn 1988 for review), but no data is avaiable for supporting the inference (Wolff 1993b).

Most gray-sided voles of both sexes disperse at the beginning of reproduction (Ims 1989; Saitoh 1995; see also Kawata 1989). All females have just become sexually receptive (perforate vaginas) before they disperse, and at least some of them are mated (presence of copulatory plugs), and dispersing males are in the process of maturing or have just matured (Ims 1989). Male natal dispersal occurs in the absence of any obvious extrinsic factors such as the presence of parents or food limitation, and therefore intrinsic properties of the individuals seem to cause variation in both dispersal tendencies and space use characteristics (Ims 1990), although adult males may exclude young males near an estrous female (Kawata 1989).

Ims and Andreassen (1991) suggest that male-biased dispersal, predominant female territoriality and a promiscuous mating system are likely to be sufficient to keep inbreeding at a low level. Promiscuous mating is shown in a gray-sided vole population, in which parentage was established by genotyping at several microsatellite DNA loci (Ishibashi and Saitoh unpublished), as have been suggested previously (Kawata 1985a, 1988). In the population, a few incestuous mating between maternal full and half

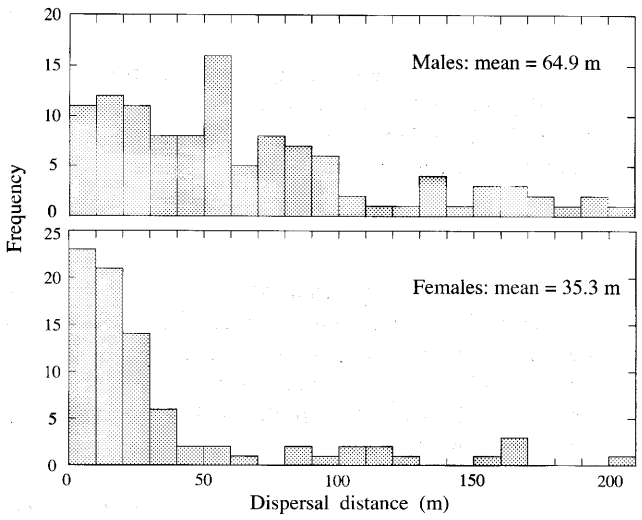

Fig. 3. Frequency distribution of dispersal distances from the natal sites for males (upper) and females (lower) in an experimental population of the gray-sided vole in Hokkaido (modified from Fig. 3 in Saitoh 1995).

siblings occurred only when the dispersal distances of the males were short and under low density just after the beginning of the breeding season. However, it remains unknown whether male gray-sided voles really disperse independent of the presence of their relatives or not. It is also unclear whether and how males would avoid inbreeding in microtine rodents, although several studies show suggestive results (e.g. Lambin 1994). To our knowledge, only a single field study, other than our study, using genetic markers reported relatively high frequency of incestuous mating in microtine rodents (*M. pennsylvanicus*; Pugh and Tamarin 1988). More studies on the frequency of inbreeding should be conducted with genetic markers to know the ultimate and proximate causes of male-biased dispersal.

Female philopatry

Formation of female kin-structure

Most female recruits stay near their mother's range during the breeding season in the gray-sided vole as mentioned above. Such philopatric females will have overlapping or adjacent home ranges among relatives, and are socially organized into maternal groups at high density, usually in late breeding season, as observed in many other microtines; a female kin cluster (e.g. Frank 1957; Boonstra et al. 1987; Ims 1989; Lambin and Krebs 1991a; Sera and Gaines 1994; Mappes et al. 1995; Salvioni and Lidicker 1995). Young female *Microtus* can breed within a home ranges shared with their mothers (Frank 1957; Lambin and Krebs 1991a), while *Clethrionomys* females are generally suppressed maturity in the territory of their mothers (Bondrup-Nielsen 1986; but see Gliwicz 1989 and Ims 1989). Thus, it is likely that philopatric *Microtus* females are tolerate by their mothers and can successfully breed near or at their birth site. *Clethrionomys* females can breed near the birth site if only they obtain an exclusive home range. On the other hand, very few dispersing females are able to establish themselves in breeding populations because of aggressive interaction with unfamiliar resident females (Boonstra and Rodd 1983; Ferkin 1988; Lambin and Krebs 1991a; Mappes et al. 1995). Consequently, female kin clusters may be prevalent at the end of the breeding season and the degree of kinship will become high on a small spatial scale (Pugh and Tamarin 1988, 1990; Ishibashi et al. 1998). Pugh and Tamarin (1990) did not find a consistent reduction or gain in the mean coefficient of relatedness among neighbors as density increased in the meadow vole *M. pennsylvanicus*. As population density become high, both related and unrelated females would distribute contiguously owing to female territoriality. In such a situation the average coefficients of relatedness among neighboring females might not differ considerably between populations of different densities.

Kawata (1985b) implied a clumped distribution of female relatives in a spring gray-sided vole population, since the genetic distribution is more heterogeneous in females than that in males. Ishibashi et al. (1997) examined highly variable microsatellite DNA loci and mitochondrial DNA (mtDNA) sequences in a spring free-ranging gray-sided vole population, and showed that several clusters of breeding female relatives without overlapping home ranges in the population (Ishibashi et al. 1997; Fig. 4). Ishibashi et al. (1998) also showed, in an enclosed population, that philopatric maternal relatives aggregated closely during winter, and that surviving females bred in close proximity to each other with less overlapping ranges in the following spring. These observations imply that the clumped distribution of close female relatives is common in spring gray-sided vole populations in Hokkaido.

Effects of female kin-structure

Substantial spring declines in density are well known in *Microtus* (Taitt and Krebs 1985); however, without the significant spring decline (particular in female numbers), a cyclic peak occurs. Yoccoz et al. (1998) suggested lower survival of reproducing adults during spring, and possibly summer, during low-density years in the gray-sided vole of Hokkaido. Lambin and Krebs (1991b) presented a model relating density fluctuations to changes in the degree of relatedness among neighboring females; vole populations with low relatedness will be subject to severe spring declines caused by exclusiveness, and will not reach high densities in that year. In contrast, populations with high relatedness will not experience a spring decline and will build up to peak numbers. Thus, spatial distribution of female relatives in early spring may affect population growth rate through the influence on the survival and/or reproduction of females, and thus peak number in the year.

The clumped distribution of female relatives may influence the survival rate of nestling and/or weaned juveniles in some microtines. Ylönen et al. (1990) found that in *C. glareolus* populations consisting of familiar and related females reached densities twice as high as the populations consisting of unfamiliar and unrelated females. Females in the "familiar" populations produced significantly more offspring per birth than females in the "stranger" populations. This was attributed to the infanticide towards unrelated nestlings and/or weaned juveniles by females (Mappes et al. 1995). Boonstra and Hogg (1988) found in the meadow vole *M. pennsylvanicus* that juvenile survival from birth to first capture in traps was substantially and significantly higher in the grid of high-

kinship treatment than the grid of low-kinship treatment. However, since there was no comparable difference in the number of recruits per litter produced, they concluded that kinship did not influence juvenile survival. Lambin and Krebs (1993) and Lambin and Yoccoz (1998) indicated that unrelated females and immigrants may influence survival of nestlings and weanlings in Townsend's vole *M. townsendii*. Furthermore, Lambin and Yoccoz (1998) examined the potential impact of changes in early juvenile survival and other demographic parameters to the population dynamics, and suggest that different degree of kin-structuring among females can provide difference in population growth rates. Kawata (1987) showed that female gray-sided voles are better able to acquire an exclusive home range when the neighboring females is a sister than when the neighbor is not a sister. But, the number of females that established home ranges and give birth to young do not differ significantly among the enclosures in his short-term experiment (Kawata 1987). Sera and Gaines (1994) also found no differences in indices of juvenile survival between treatments in the prairie vole *M. ochrogaster*, in which they released related and unrelated laboratory-born females into small enclosures in short-term experiments, despite an apparent effect of relatedness on home range size and overlap. Thus, conclusive results have not yet been obtained with regard to the effects of relatedness on population growth (see also Kawata 1990).

Familiarity is another important factor in microtine social organization. Encounters between familiar individuals may result in less agonistic behavior and more amicable acts than encounters between unfamiliar ones independent of relatedness/kinship (e.g. Ferkin 1988, 1990). Male strangers may kill infants that they have not sire to acquire reproductive access to the infant's mother (Wolff 1995). Female gray-sided voles respond to odor of strangers more intensely than that of neighboring females, whereas males do not show such a behavioral difference in response to odor of other males (Kawashima and Saitoh unpublished). Many studies suggest that microtines recognize relatives based on familiarity to the odor, which is learned during the continuous contact prior to weaning (Gavish et al. 1984; Boyd and Blaustein 1985; Berger et al. 1987; Ferkin and Rutka 1990; Lambin and Mathers 1997). Not only close relatives, but unrelated individuals would also become amicable to each other through continuous contacts. Since most studies on the relation between relatedness and population growth did not control familiarity among individuals for both sexes, such controversial results might have arisen as mentioned above (see also Ostfeld 1992; Wolff 1995).

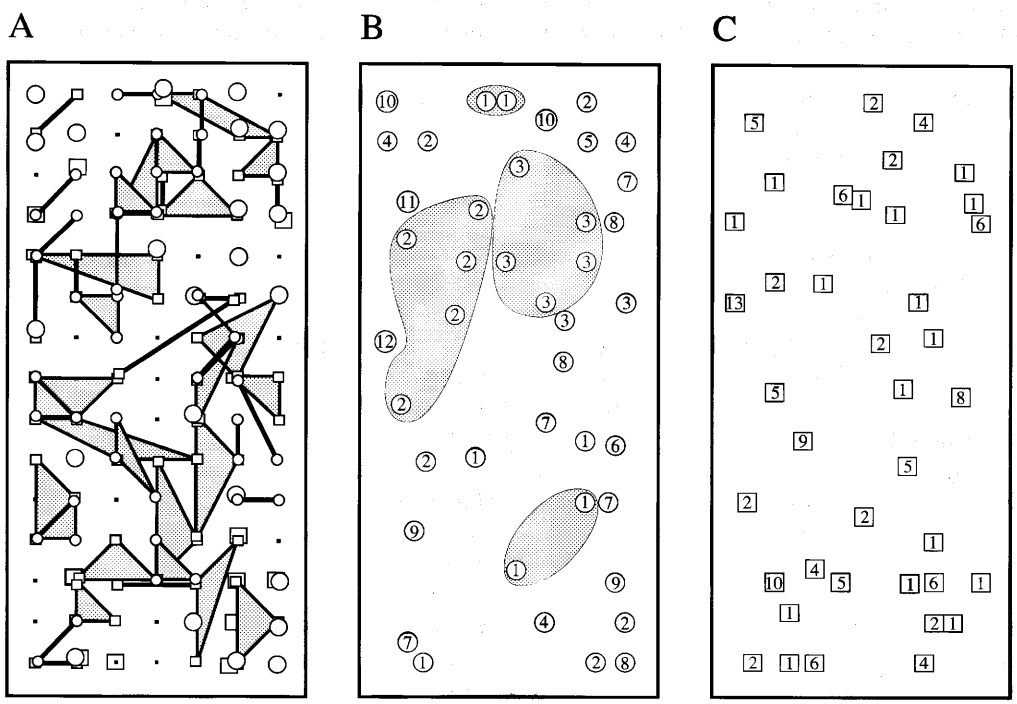

Fig. 4. Distributions of home ranges (A) and the centers of activity (B and C) in a spring population of the gray-sided vole in Hokkaido. A: Home ranges are shown by the minimum area method (Stickel 1954). A point at which a sexually matured male or female was trapped, is shown by open square or circle, respectively. Dots indicate trapping points set with 10-m interval. Activity centers for females (B) and for males (C). The number indicates the type of mitochondrial DNA for each individual. Neighboring matrilineal females with high relatedness (>0.45) are shown by shaded areas, while high relatedness was not found between neighboring males.

Although recent results of studies which focused on the effect of relatedness on population growth rates are not conclusive, relatedness and/or familiarity may have positive effects on survival and reproduction on the individual level (see Kawata 1990). Voles are unevenly distributed and individuals do not interact with all individuals in a local population. The range of individual interactions may be restricted to several neighbors. Kawata (1997) suggested on the basis of theoretical considerations that such scale influences density-dependency. Thus, in the studies which focus the effects of relatedness on population growth, the social structure at a small spatial scale, like female kin-clusters found in *C. rufocanus* (Ishibashi et al. 1997; Fig. 4) should be taken into consideration. In such studies, DNA markers are very useful to clarify population kin-structure.

Future studies

Spatial genetic organization

Many population studies in microtine rodents have focused on the issue of density fluctuations from a temporal perspective. However, several studies recently challenged the issue of synchrony of population fluctuation to estimate the geographic scale of vole populations from a spatio-temporal perspective. For example, Steen et al. (1996) estimated the spatial scale in synchrony of population fluctuation along a linear transect spanning 256 km in the Scandinavian population of the bank vole, *C. glareolus*. They demonstrated that synchrony of population fluctuation occurs on a scale of 30–40 km (see also Bjørnstad et al. 1998a for *C. rufocanus*).

Population structure should be recognized not only from an ecological aspect, but also from a genetic one (Hewitt and Butlin 1997). Although spatial genetic structure is mostly unknown in microtine rodents, the extent of a local population revealed genetically may be different from that revealed ecologically with regard to the scale. Stacy et al. (1997) observed geographic differentiation of mtDNA haplotypes along a linear transect in the Scandinavian population of *C. glareolus*, in which sampling was made at the same locations as in Steen et al. (1996). They conclude, based on the rapid decline of gene identity, that local populations extend over areas that are similar to, or less than 8.5 km. This scale may reflect the range of gene flow based on accumulated effects of female dispersal, since mtDNA is inherited maternally (Stacy et al. 1997). This scale is not consistent with the geographic scale (30–40 km) in synchrony of population fluctuation in the same region (Steen et al. 1996). Since long-distance dispersal among populations is unlikely, they thought that the synchrony in population fluctuation requires some external factors, e.g. mobile predators (Stacy et al. 1997).

Spatial genetic structure should also be clarified with regard to nuclear genes, because it is nuclear genes that chiefly organize and support an organism's life. In the root vole (*M. oeconomus*), geographic strains from north and south populations exhibit the difference in litter sex ratio (Ims 1994), signs of inbreeding depression (dos Santos et al. 1995), growth rate and reproductive efforts (Ims 1997) and dispersal responses to the habitat configurations (Bjørnstad et al. 1998b). These may result from the difference in the nuclear genome between the strains, which undergo different types of environments in the wild (see dos Santos et al. 1995). Most microtine rodents have a male-biased dispersal pattern. Besides, female dispersers are unlikely to establish themselves in a new habitat because of exclusiveness and nepotism of female residents. Thus, effective dispersal accompanied by acquisition of reproductive success should occur more frequently in males. This must make the range of local populations recognized in terms of nuclear genes larger than that for maternally inherited mtDNA.

Male-specific DNA markers, e.g. variable microsatellite DNA located on the Y chromosome, which would be comparable to mtDNA for females, are promising tools in order to clarify the role of male dispersal in organizing spatial genetic structure. In the gray-sided vole, genetic autocorrelation analyses using semivariogram (see Burrough 1995; Robertson 1987) on microsatellite genotype data demonstrated that only neighboring females within 20 m are genetically related, but that genotypes of males were rather randomly distributed in space (Kawata et al. unpublished; see also Ishibashi et al. 1997). Therefore, population structure revealed by using male-specific markers would be different from that revealed with mtDNA or autosomal gene markers in the vole, although male-specific markers are not available yet in microtines including the gray-sided vole. Empirical studies on the process in organizing local populations with the molecular markers, i.e. mtDNA, Y-chromosome DNA markers and autosomal DNA markers, will deepen our understanding of population structure.

Interspecific comparison may be useful to specify factors organizing population structure. Species with varied ecological properties might have different spatial scales even though they inhabit the same habitat. Bjørnstad et al. (1998a) demonstrated paradoxical results from the comparative analyses of spatio-temporal fluctuation patterns in the gray-sided vole and the wood mouse *Apodemus argenteus* in Hokkaido; the spatial scale of fluctuation pattern was 50–55 km for the vole and 20–30 km for the mouse, in spite of higher movement ability of the latter. They suggested that the spatial scale of the vole is regulated by predators, whereas the spatial scale of the wood mouse is related to food-resources dynamics. It would be interes-

ting to see whether an analysis using the molecular markers would provide contrasting results on spatial structure to those obtained by population dynamical properties. Following the explanation of Bjørnstad et al. (1998a), spatial genetic structure of the wood mouse would be closer to the structure based on population dynamical properties than would be the case for the vole. Such comparative studies in these rodents will be promising in the field of spatio-temporal analyses.

Effects of spatial genetic structure

Spatial genetic structure may influence evolution of social behavior. Since individuals interact mainly with neighbors, the fitness of individuals with a particular social behavior may be determined by the type of interactions they participate in. Thus, the frequencies of genes and phenotypes in the interaction neighborhood can be regarded as the environments within which individual fitness is determined. Furthermore, these frequencies might change as a consequence of reproduction, survival and movements of individuals. Understanding these complex relationships between individual interactions and change in local neighborhood environment will be an important subject for the study of evolutionary ecology.

For instance, females interact with related females more amicably than with unrelated ones, and so the relatedness between neighbors affect the fitness of individuals. Hamilton (1964) suggested that limited dispersal causes a population structure that promotes interaction among relatives, i.e. population viscosity, and thus, population viscosity has been considered to be a factor that facilitates the evolution of altruism by increasing the degree of relatedness among interacting individuals. However, Wilson et al. (1992) showed by a simulation that population viscosity with local regulation cannot promote kin selection or intrademic group selection, since limited dispersal leads to local density regulation that prevent an altruistic gene spreading into a whole population. In the gray-sided vole, sexual difference in dispersal patterns may increase the chance for the evolution of altruism in females, since altruistic behavior evolves among females and altruistic alleles are spread by male dispersal (Kawata submitted).

Inbreeding depression and mutation load are important subjects not only for evolutionary biology but for conservation biology. Although most vole species are not species to be conserved, examining the relationships between spatial genetic and social structure, population dynamics and deleterious genetic factors will provide important insight for conservation biology.

Inbreeding is likely to occur in any small population. Since inbreeding coefficient is affected by effective population size, which is influenced by spatial structure and dispersal distance, it is important to examine the relationship between inbreeding depression and spatial genetic structure. Inbreeding depression has, however, been hardly detected in natural populations of small rodents and other wild mammals (Shields 1993; Smith 1993; Lacy 1997). One possible method to detect inbreeding depression in the field is to use DNA markers to determine the degree of inbreeding of individuals and to compare the fitness of inbred individuals with outbred ones (e.g. Stockley et al. 1993). Another important subject is to compare the degree of inbreeding depression among populations with different spatial genetic structures due to difference in dispersal distance, habitat fragmentation and social structure, since the degree of accumulation of deleterious recessive alleles might be influenced by mating systems and effective population size (e.g. dos Santos et al. 1995). For this study, DNA markers also will be useful to detect mating systems and spatial genetic structure of populations. Since genetic structure may vary among populations owing to the variation in the cyclicity and amplitude of density fluctuation (e.g. Bowen 1982; Plante et al. 1989) and several potent DNA markers have already been developed (Ishibashi et al. 1995, 1997), the gray-sided vole is a suitable animal for unraveling these issues.

Deleterious mutation-accumulation is a significant source of extinction vulnerability in small sexual populations, although there are some controversy about how many individuals are required to prevent mutation meltdown (Charlesworth et al. 1993; Lande 1994; Lynch et al. 1995). Small effective population sizes increase the risk of accumulation of deleterious mutation and decrease the genetic variability. In the gray-sided vole, the density fluctuates and thus only a few individuals can be found in an area during the low density phase, which may result in small effective population size (Maruyama and Kimura 1980). In order to avoid the accumulation of deleterious genes, voles should move and mate within a large area. There might be some mechanisms that reduce the risk of mutation loads and maintain genetic variability, such as a balance among exclusion of deleterious mutations at very low density, small local population size to generate inter-populational differentiation and effective dispersal to maintain individual heterozygosity. To understand these mechanisms, spatial genetic structure and the degree of gene flows among local populations are needed to be surveyed in relation to density fluctuation on a large spatial scale.

Although effects of spatial genetic structure remain to be substantiated in wild vole populations, their evolutionary consequences have been inferred by recent genetic studies as reviewed above. Small rodents such as voles have rich background information about social organization and population dynamics by extensive field studies. In addition, recent molecular markers, e.g. microsatellite DNA, are particularly useful for genetic analysis. Both the field

and genetic works using small rodents will become an efficient battery of analyzing unsolved issues in population genetics and hence open new fields of population biology.

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