Chapter 15 Social Behavior and Self-Regulation in Murid Rodents

Charles J. Krebs, Xavier Lambin, and Jerry O. Wolff

MURID RODENTS have been a favorite group for studies of both ecological and behavioral questions, and the broad outlines of both social behavior and population dynamics are now available for many species. What is lacking is the bridge between rodent social organization and rodent population dynamics. Two polar views can be recognized. The first view is that social behavior is interesting and important to study but has nothing to do with population dynamics. Population changes are believed to be driven by predators, disease agents, and food supplies, without any need to consider how social behavior might be involved as a destabilizing influence. At most, this first view considers that social factors may contribute as a stabilizing agent to setting some notional carrying capacity. This view can be traced back to many authors like David Lack (1954) and is widely supported in the current literature (e.g., Turchin 2003). We will refer to it as the dominant current view. The alternate view is that social behavior is an important component of population dynamics because of its potential impacts on variation in birth and death rates and dispersal. This view arose from the early work of John Christian, David E. Davis, and Dennis Chitty in the 1950s. The paradox of this polarization is that in spite of excellent evidence in many rodents about the impact of social behavior on birth, death, and dispersal rates, almost no one believes that these impacts translate into population dynamics beyond contributing to seasonal dynamics.

Social behavior, including territoriality, dispersal, reproductive suppression, and infanticide has been studied extensively in the laboratory and field in many species of rodents. In this chapter, we consider the current theory regarding social behaviors and then show how they are altered by changes in density that could affect rates of population growth. We draw heavily on examples from *Microtus* and *Peromyscus* in North America and Europe because of the extent of experimental work involving hypothesis testing in field and laboratory studies. We will not review all aspects of social behavior; rather, we limit our discussion to behaviors that show the greatest potential for self-regulation of fluctuating populations.

Avian ecologists had already suggested in the 1920s and 1930s that territorial behavior could limit population density (Howard 1920; Nice 1937; Hensley and Cope 1951). Mammal ecologists were slower to accept that social behavior might impact population dynamics, and the first approach was through physiology. Hans Selye in 1937 suggested that crowding in rodents could lead to physiological stress mediated through the adrenal gland, and that stress could reduce reproductive output as well as increase death rates. David E. Davis and John Christian (1956) did the first field experiments to show that aggressive social interactions could reduce Norway rat population size, and since these early experiments, many authors have contributed studies that evaluate the role of social behavior in affecting population events. How might social processes affect rodent population dynamics?

Mechanisms of Population Regulation via Social Behavior

Social behavior can affect population dynamics via five different mechanisms: limiting the size of the breeding population, control of the timing of sexual maturation, infanticide, control of dispersal, and direct aggression (= interference competition). Wolff (2003) has reviewed these aspects of the social ecology of rodents and has concluded that social interactions play little role in regulating or stabilizing rodent populations. We will not review the detailed aspects of these social interactions, which are covered well in Wolff, but we wish to review here the dominant current view that social interactions are rarely relevant to population dynamics.

The self-regulation hypothesis proposes that individual differences in spacing behavior influence reproductive performance and subsequent population trends either through genetic or maternal effects (Krebs 1978, 1996; Oli and Dobson 2001). Wolff (1997) provided an evolutionary argument for how various aspects of social behavior could lead to intrinsic population regulation. For social behavior to limit the growth rate of a population, it must decrease fecundity, or at least juvenile recruitment, or decrease survival rates. Decreased juvenile recruitment could result from decreased litter size, decreased juvenile survival, fewer females breeding, or a delay in time to sexual maturation of young females. There is little or no evidence that litter size is affected by social interactions other than might be affected by decreased nutritional state of females due to limited food resources. However, social stress at high density can delay the onset of sexual maturation, which slows population growth (Oli and Dobson 1999). A decrease in number of females breeding also could be affected by territoriality or some form of reproductive suppression. In the following we follow the basic conceptual arguments of Wolff (1997) and review the major determinants of social behavior that could regulate populations.

Female territoriality

The key behaviors in rodents that might impact on population density can be broadly classed as spacing behavior. If individual rodents maintain a personal or group space, then clearly the density of that population will reflect this spacing. Spacing is most readily thought of as resulting from direct physical aggression, but this mental image must be broadened to include spacing by avoidance behavior as well as spacing by direct physical interactions. We first ask if spacing behavior could limit population density (Watson and Moss 1970).

Social systems of rodents are variable and flexible and appear to depend to a great extent on the distribution of females. In most rodents, individuals or groups of related females defend territorial space against unrelated females. Territories vary considerably in size, from as little as 25 m^2 in high-density populations of microtines to several hectares in larger species and/or at lower densities (Wolff 1985a). For most grassland rodents that weigh less than 100 g, territories are typically 50 to 150 m^2, whereas forest-dwelling species often occupy territories of several hundred square meters (Wolff 1985a, 1989). During the breeding season, territories are relatively exclusive with respect to unrelated females, but often overlap and are shared with daughters or sisters (e.g., *M. townsendii, M. canicaudus, P. leucopus*). Home range size and daily movements often are related to resource availability; however, territoriality in female rodents may not be solely based on defense of a food resource as proposed by Ostfeld (1985). According to the food-defense hypothesis, the distribution, abundance, renewability, and type of food should determine whether females defend territories or share space with other adult females (Ostfeld 1985). An alternative, but not exclusive, hypothesis is that females defend territories to protect their offspring against infanticide from conspecific females (Wolff 1993b). Species of rodents that hoard food such as seeds in a central larder seem to defend this food source; however, green vegetation, perishable, or nonstorable and other widely scattered food may not be defensible (Wolff and Peterson 1998), and whether they are limiting during the breeding season is equivocal (Taitt and Krebs 1981; Ostfeld 1985; Lambin and Krebs 1993; Wolff 1993b).

Infanticide is common among female rodents and is hypothesized to be a form of reproductive competition, in which perpetrating females kill offspring to eliminate competitors and gain access to breeding sites (Sherman 1981b; Wolff and Peterson 1998). The fact that female aggression that leads to territoriality is associated with lactation and the breeding season (Maestripieri 1992; Wolff 1993b) and does not occur in the middle of the nonbreeding seasons supports this latter hypothesis (Wolff and Peterson 1998). However, considering that territories become established when vegetation greens up, several weeks before the first litter of the year is conceived, is consistent with a dual influence of the need to secure access to food resources and social space. The infanticide hypothesis is also applicable to other taxa of mammals and is associated with altricial young that require a burrow, tunnel system, or protected den site for successful rearing of offspring. In that rodents fit these needs, females compete for this limited offspring-rearing space. Competition for breeding space contributes to territoriality in female rodents (Solomon and Keane, chap. 4, this volume).

If breeding male or female rodents defend a territory, the potential exists for spacing behavior to limit population density. The larger a territory that is defended, the lower the population density, and the immediate question arises as to what determines territory size. There has been an ongoing argument in the bird literature between those who interpret territory size as a consequence of population density and those who interpret it as a cause:

territory size → population density
population density → territory size

The only way to test these two views is to experimentally manipulate territory size, typically by manipulating aggression (e.g., Watson and Jenkins 1968; Moss et al. 1994; Mougeot, Redpath, Leckie, and Hudson 2003; Mougeot, Redpath, Moss, Matthiopoulos, and Hudson 2003), but few of these kinds of experiments have been done on wild rodents (Gipps et al. 1981; Taitt and Krebs 1982), in part because they are technically difficult.

Experiments that demonstrated the role of spacing behavior in herbivorous *Microtus*, (*townsendii, agrestis, pennsylvanicus*) have been performed near the onset of spring reproduction, when the greening of the vegetation triggers the transition from reproductive quiescence to the breeding season. Defense of space during that seasonal bottleneck in food availability is necessary for early reproduction and also secures space where offspring may later become established when vegetation availability no longer limits access to reproduction, but social space is at a premium. In *Microtus agrestis* for instance, over-wintered females defend exclusive territories, but spring-born females breeding in the year of their birth are more tolerant (Agrell 1995; Pusenius et al. 1998).

If spacing behavior limits spring *Microtus* population size, a paradox is that in the absence of any notable interannual variation of food availability that characterizes seed-eating murids (e.g., *Peromyscus* and *Apodemus*), *Microtus* outbreaks occur and are preceded by much higher densities of breeding females in spring than occurs in most years. In these years of high density, either spacing behavior is unable to reduce population size to the normal value, or individuals in high-density populations adopt an alternative spacing behavior, and their reproductive potential is not too adversely affected (since the population continues to grow to outbreak densities). The possibility that kinship among overwintered females, and hence the risk of infanticide, differs in those years, and hence allows a different mode of spacing behavior, is considered in the following.

Does territoriality limit population size?

If females defend breeding spaces (territories) and these are limited, then potentially territoriality could limit the size of the breeding population. One view is that territory size is not fixed; rather, it shrinks and expands like an elastic disk, with changes in density and intruder pressure (Wolff 1989; Wolff and Schauber 1996). If this is the case, territoriality would only limit populations when territories have shrunk to their minimum size. How small can a territory become? Studies with voles in enclosures show that without dispersal, territory size shrinks to only a few square meters, with considerable overlap with neighboring females (e.g., Boonstra and Krebs 1977; Wolff and Schauber 1996; fig. 15.1). The fact that rodent populations in enclosures reach exceedingly high densities suggests that territoriality in itself (in the absence of potential dispersal) is insufficient to stop population growth (Boonstra and Krebs 1977; Wolff and Schauber 1996; fig. 15.2). The real question is, does territoriality create surplus individuals that are not breeding? An alternative is that factors other than intruder pressure contribute to setting territory size, as shown experimentally with red grouse (Moss et al. 1994; Mougeot, Redpath, Leckie, and Hudson 2003).

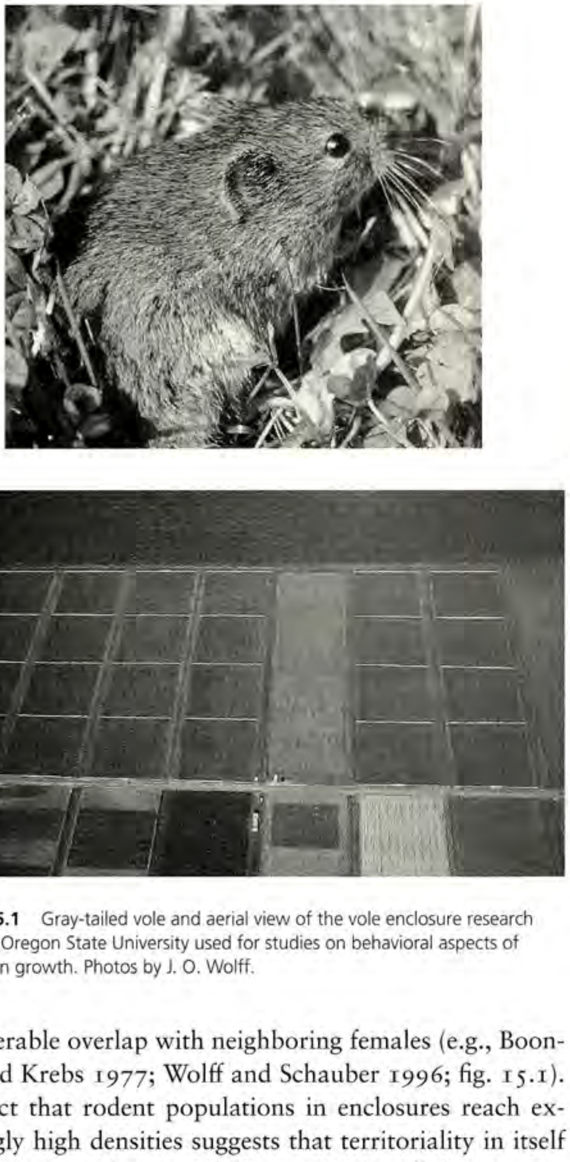

Figure 15.1 Gray-tailed vole and aerial view of the vole enclosure research facility at Oregon State University used for studies on behavioral aspects of population growth. Photos by J. O. Wolff.

Does territoriality create surplus individuals?

We define *surplus* animals as those that are of reproductive age, but are not breeding. Following the lead of early experiments on songbirds (Hensley and Cope 1951), rodent ecologists used removal experiments to measure the number of surplus rodents. Krebs (1966) reports one early experiment on *Microtus californicus* in California. These and many other removal experiments have shown that when

Figure 15.2 The Fence Effect demonstrated here with Townsend's voles indicates that without dispersal, voles reach very high densities (left side) and do not intrinsically stop population growth, compared to unenclosed populations (right side), where dispersal is not deterred by a fence. Photo by C. J. Krebs.

you remove breeding adult rodents from an area, a flood of surplus individuals colonize the removal site, and in many cases bring the population density of the removal site back to the control density (e.g., Krebs et al. 1978). These removal experiments raise many issues that are relevant to rodent pest control. Where do these surplus animals come from? What is their fate if a removal experiment is not taking place? Do the surplus animals differ in age, sex, or size from resident animals? Many of these questions have been discussed by Anderson (1989) and Cockburn (1988). Clearly, if we accept the standard Darwinian principles, each of these individuals is attempting to maximize its own fitness, and our explanations of these results must fit in with contemporary evolutionary theory. Removal experiments to assess surplus individuals have been criticized in some species, since adjacent territory owners may shift their home ranges into the evacuated area (Schieck and Millar 1987). This criticism will affect the quantitative measurement of surplus animals, but it does not eliminate them. Schieck and Millar (1987) and Clinchy et al. (2001) have shown that surplus animals immigrate into unmanipulated areas as well as local residents shifting their home ranges into the evacuated area. A limitation of these field studies is that we do not know what the reproductive fate of immigrants into removal areas would have been if they had not moved. The assumption is apparently made that if they remained as residents they would become animals of low or zero fitness.

Given that we have surplus individuals, the second question is whether these individuals can breed when given the opportunity either in their home site or in the colonization area. The assumption is typically made that they would not achieve reproductive maturity in their home site, but this has not been tested adequately on individuals. Our results with removal experiments on *Microtus* voles have shown that there is no impediment to breeding in surplus voles that colonize removal areas, once the residents have been artificially removed from the area (Krebs et al. 1978; Myers and Krebs 1971). The impact of adult females on the suppression of maturation of young females has been studied particularly well in *Clethrionomys* voles (Bujalska 1970; Gilbert et al. 1986; Kawata 1987). The conclusion to date is that if there are surplus individuals in a rodent population, they are capable of breeding if social controls of maturation are relaxed, either in a resident population or in a newly colonized site.

Does territoriality affect recruitment?

A key question in rodent population dynamics is what controls recruitment into the trappable population. Rodents are model systems of species with very high reproductive rates coupled with high death rates, and the question we need to answer is what happens to all the young produced in a rodent population. A second question is whether that loss rate is constant or is influenced by prevailing or past density. The general finding in rodent-trapping studies is that a low fraction of the young produced ever recruit into the breeding population (Adler et al. 1987). The assumption is usually made that predators, diseases, bad weather, and other environmental factors control the survival of juveniles in their first few weeks of life.

Adult rodents can limit the recruitment of juveniles, and this can be another critical bridge between social behavior and population dynamics. If adults can limit recruitment

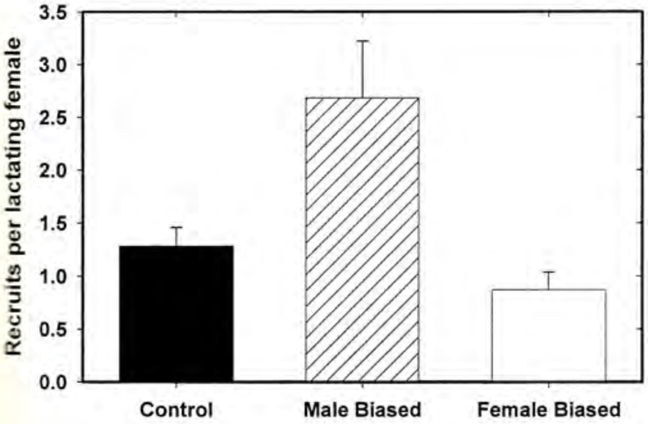

Figure 15.3 The average recruitment of juvenile *Microtus townsendii* for the summer breeding seasons of 1972 and 1973 on control (unmanipulated), male-biased (80% adult females removed) and female-biased (80% adult males removed) areas. Recruitment in this population is clearly controlled by adult females. Recruitment measured as the number of juveniles live-trapped at 2–5 weeks of age per pregnancy. Error bars are 95% confidence limits. (Data from Redfield et al. 1978, table 6).

of juveniles, we must ask if both sexes are involved or only one. Redfield et al. (1978) carried out biweekly sex-specific removal experiments on *Microtus townsendii* and *M. oregoni* for two years. The results are summarized in figure 15.3 which shows that adult females were the key to understanding why recruitment is restricted. Recruitment was 109% higher on the area with a more male-biased sex ratio, compared with a control area, and 32% lower on the area with a more female-biased sex ratio. The same pattern was found in a more carefully controlled experiment with the same basic design with *Microtus canicaudus* by Wolff et al. (2002). Boonstra (1978) showed with a weaned juvenile introduction experiment that young juvenile *Microtus townsendii* would survive well if introduced at 3 weeks of age into a field from which all the adults had been removed, but few survived introduction into a field with only adult females present or both adult sexes present. The implication is that adult females directly kill strange juveniles or drive them out of the area, thereby limiting recruitment locally.

At the present we do not have a good quantitative analysis of the rate of loss during the first few weeks of life of nestling rodents. For *Microtus* voles, a few estimates of neonate survival are available. McShea and Madison (1989) found an average survival to recruitment of 31% in *Microtus pennsylvanicus* from 132 litters of radio-collared females. Boonstra and Hogg (1988) by contrast found an average 57% survival of neonates from 43 litters of the same species in an enclosure study. Lambin and Yoccoz (1998) found a neonate weekly survival of 70–75% over the first two weeks of life in 325 litters of *Microtus townsendii,* which translates into 0.42 to 0.54 survival to the usual trappable age of three weeks (fig. 15.4). In *Microtus canicaudus* only 1–3 juveniles are caught per pregnancy, which represents 17–50% of a modal litter size of 6 (Wolff and Schauber 1996; unpublished). Given the life history of murids, even small differences in neonate survival have profound implication for predicted population growth rate.

What happens to all these neonates? We do not know whether most of these young die in the nest or just after they leave the nest. It seems unlikely that dispersal is a primary cause of loss in the first three weeks of life (since dispersal

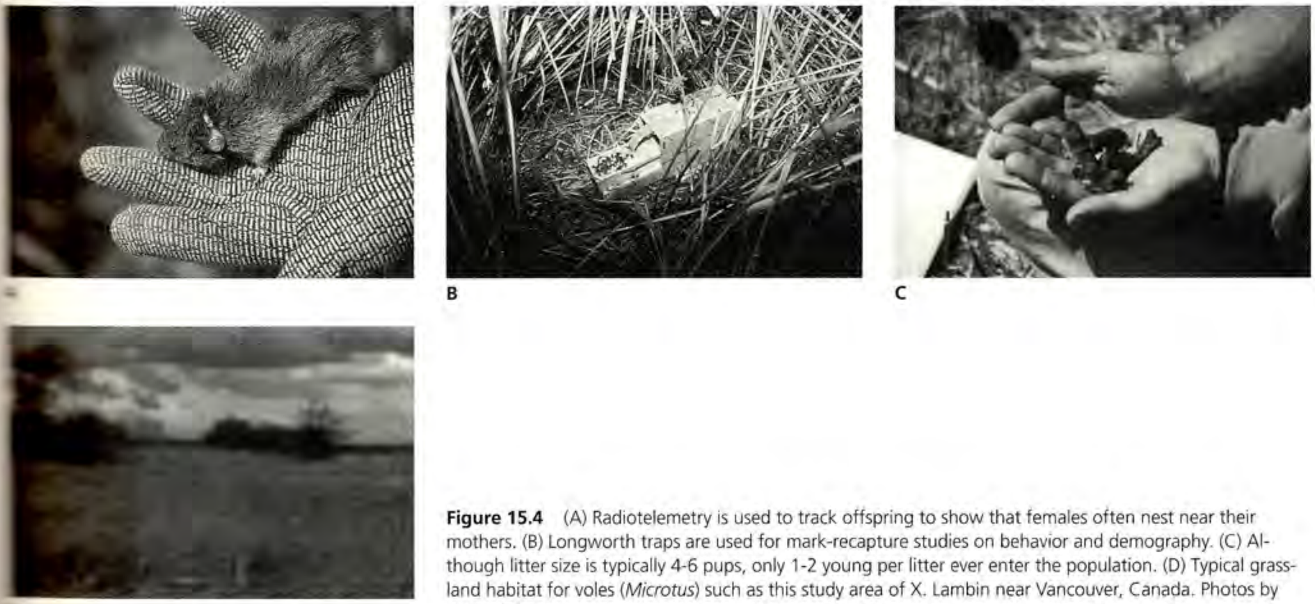

Figure 15.4 (A) Radiotelemetry is used to track offspring to show that females often nest near their mothers. (B) Longworth traps are used for mark-recapture studies on behavior and demography. (C) Although litter size is typically 4-6 pups, only 1-2 young per litter ever enter the population. (D) Typical grassland habitat for voles (*Microtus*) such as this study area of X. Lambin near Vancouver, Canada. Photos by X. Lambin.

usually occurs at a later age); there seem to be only three possible agents of loss: predation in the nest, infanticide, and bad weather (e.g., flooding). Considering that survival from birth to recruitment is usually inversely density dependent (Wolff et al. 2002; Krebs 2003) the limiting factors appear to be intrinsic rather than extrinsic. It is clear from a demographic perspective that variation in the nestling survival rate could account for a large portion of the variation in the per-capita rate of increase of rodent populations. One observation that has gained prominence in recent years is that infanticide is prevalent in rodent societies (Ebensperger and Blumstein, chap. 23, this volume), and could account for considerable neonate mortality.

Infanticide

Infanticide is common among male and female rodents and has been studied extensively in the laboratory and less so in the field (Agrell et al. 1998). Infanticide is committed by females to gain breeding space and by males to provide a breeding opportunity. Theoretically, the incidence of infanticide should change with density, but differ for the two sexes (Wolff 1995; table 15.1). At low densities, males move over large areas and will be more likely to commit infanticide in areas where they have not mated and have low confidence of paternity. At high densities, however, males are confined to smaller areas, have many females with which to mate, and should be less likely to commit infanticide within their resident home ranges or territories. One could speculate that females, on the other hand, should not commit infanticide at low densities, because breeding space would not be limited and thus competition is sufficiently low that all females can acquire breeding space. At high densities, however, breeding space should be limited, competition intense, and the rate of infanticide high as females compete for limited offspring-rearing space. Thus infanticide is likely to occur at high and low densities, but differ for the two sexes (Wolff 1995); however, this has not been tested experimentally. The problem is that infanticide is most difficult to study in field populations, and we badly need information on its frequency in relation to population increases and declines.

Table 15.1 Predicted density-dependent effects on various aspects of the social behavior of rodents (after Wolff 2003)

	Low density	High density
Territoriality	Large, widely spaced, mutual avoidance, low aggression, vacant space available	Territories small, considerable overlap, aggression high
Dispersal and philopatry	All males disperse relatively far, females disperse close to natal site, dams might bequeath maternal site to daughters	Delayed emigration, sons and daughters remain on natal site, extended families, cooperative and communal breeding of females
Age at sexual maturity	Sons and daughters mature at young age	Delayed sexual maturation for both sexes, cooperative and communal breeding for some species (see text)
Infanticide	High for males, low for females	Low for males, high for females

The Bruce effect

Another factor that could decrease the rate of population growth is pregnancy disruption, commonly referred to as the Bruce effect. The Bruce effect is a form of pregnancy disruption in mammals in which exposure of a female to an unknown male results in pre- or postimplantation failure. If a female's pregnancy is disrupted following exposure to unfamiliar males intruding into her territory, this potentially could affect the rate of juvenile recruitment, especially when populations are high and many males are moving through female territories. Some form of pregnancy disruption has been reported in the laboratory for at least 12 species of rodents, including seven of the genus *Microtus* (reviewed in Mahady and Wolff 2002). However, two field studies have failed to support the relevance of this phenomenon. In field experiments with gray-tailed voles (de la Maza et al. 1999) and prairie voles (Mahady and Wolff 2002), 100% turnover of resident males and exposure to strange males every 10 days failed to detect any significant pregnancy disruption. In gray-tailed voles, no differences occurred in pregnancy rates, interbirth intervals, or juvenile recruitment between treatment and control populations. In prairie voles, nulliparous females took slightly longer to initiate first breeding in treatment populations and experienced poorer juvenile recruitment, but this effect was minimal and did not occur in parous females. The decreased juvenile recruitment in prairie voles could have been due to infanticide when young pups were exposed to strange males. In wild populations of voles and other rodents, females are commonly exposed to strange males, and it is questionable whether selection would favor any form of pregnancy termination following this exposure. Also, in most species of rodents females mate promiscuously and mated males are inhibited from committing infanticide (Agrell et al. 1998). Thus females should not need to sacrifice current pregnancies. The high rates of pregnancy and births at predictable intervals in most rodent populations make it seem unlikely that the Bruce effect has a marked effect on population growth or demography.

Reproductive suppression

The high intrinsic rate of growth of rodent populations is due to a great extent to high fecundity and early breeding of young females. In most species of rodents, young females become sexually mature and can breed shortly after weaning, as young as 20 days of age. Females exhibit postpartum estrus and breed at regular intervals as short at 21 days. Life expectancy is short, often less than 4 months; however, a given female can be expected to produce about 20 offspring in an average lifetime, so that under ideal conditions the population could double every 5 weeks.

A major factor that determines the size of the breeding population is the rate at which young females become sexually mature and experience their first pregnancy. In some species of rodents, such as *Clethrionomys,* each female needs its own individual territory to breed; that is, young females do not breed on their mothers' territories, and sexual maturation is retarded at high population densities (Gilbert et al. 1986). It is not known how common this pattern is because we have relatively few data on the relatedness of females in wild populations and position of nests within territories for most species of rodents (see kinship following). However, it is well documented for several species of *Microtus* and *Peromyscus* that daughters at times breed on their maternal site, often communally and cooperatively with other female relatives (e.g., Lambin 1994b; Wolff 1994b, Wolff et al. 1988). In *Clethrionomys* and other species in which females require individual territories, territoriality can limit the size of the breeding population and consequent rate of population growth. Females that do remain on their natal site beyond the time of normal reproductive maturity would be reproductively inhibited until they obtain a territory of their own. However, for species in which daughters are not reproductively inhibited by their mothers, and breed on shared maternal territories or even in the same nest, such as most *Microtus* and *Peromyscus,* territoriality would have a minimal effect on the size of the breeding population. The key question is what factors permit related females to breed in shared territories, and in particular whether the prevalence of these communal breeding groups is density dependent.

Resource or reproductive competition within family groups appears to be minimal for much of the breeding season but may be critical at the start of breeding in spring (Lambin and Krebs 1993; Andreassen and Ims 2001). Unrelated females are expected to commit infanticide as a form of competition for breeding territories (Wolff 1997; Wolff and Peterson 1998). At high densities, pregnancy rates typically remain high; however, juvenile recruitment declines with an increase in density (Wolff et al. 2002; Krebs 2003). The mechanism for reproductive suppression of young females is difficult to detect in the field, but field observations with other mammals and laboratory experiments with rodents demonstrate that unrelated adult females typically inhibit young females from breeding (Drickamer 1984e; Wolff 1997; Krebs 2003).

Dispersal and philopatry

Dispersal has been studied extensively in rodents, primarily from a population regulation point of view. Most dispersal involves juveniles or young adults emigrating from the natal site and immigrating to a territory or home range area that will be the adult breeding site. The general dispersal pattern for rodents, as it is in most mammals, is for young males to disperse from their natal site and for daughters to be philopatric and remain on or near their natal site (Boonstra et al. 1987; Wolff 1993a, 1994b). Young males leave the natal site to find vacant space and unrelated breeding-age females. However, dispersal distance of young males is highly variable and dependent in part on the degree of habitat saturation and the availability of vacant territories or mating partners (Lambin et al. 2001). Since inbreeding avoidance appears to be an important function of emigration of young males from their natal site, dispersal distances are probably determined in part by the proximity of related females around the natal area, encounter rates with unrelated females, and competitive interactions of resident males (Wolff 1993a, 1994b; Andreassen and Ims 2001; Lambin 1994b; Lambin et al. 2001).

Young females typically attempt to establish breeding space close to their natal site. At low densities when adjacent space is available, young females establish individual home ranges or territories in close access to the natal site. In some cases, mothers appear to bequeath their natal site to daughters and move a short distance and establish a new territory or nesting site that overlaps the previous natal site (Wolff and Lundy 1985; Lambin and Krebs 1991a, 1993; but see Lambin 1997); however, the spatial pattern of mothers and daughters is not well understood for most species. At very high densities, mothers and daughters often nest within meters of each other or sometimes communally and cooperatively in the same nest (e.g., Wolff 1994b; Lambin and Yoccoz 1998; Solomon and Getz 1997).

If resident adults cause new recruits to disperse, and dispersal is costly in terms of survival in unfamiliar habitats, dispersal could be a process that is involved in population regulation. The most striking experimental argument for the role of dispersal in population regulation has been the fence effect (Krebs et al. 1969; Boonstra and Krebs 1977; Wolff and Schauber 1996; fig. 15.2. Ostfeld (1994) suggested that the fence effect was an artifact of predator exclusion, but this conclusion is incorrect, particularly since Boonstra's site was on an island with no mammalian predators that might be restricted by a fence.

Two general problems have plagued efforts to evaluate the role of dispersal in population limitation. First, estimates of dispersal rate and distance are difficult to obtain. Removal areas measure some components of dispersal but may bias the quantitative results (Schieck and Millar 1987). Radiotelemetry studies of dispersal are more promising, but sample size problems and scale issues complicate interpretations (Beacham 1980; Gillis and Krebs 1999). A new combined approach of direct capture-mark-recapture with microsatellite genotyping to identify parents and offspring in different populations and hence infer who disperses and how far shows considerable promise when a large proportion of putative parents can be sampled genetically (Telfer et al. 2003). When applied to water voles (*Arvicola terrestris*), dispersal rates were more than two times greater for females and three times greater for males relative to estimates based on capture recapture. Second, if dispersal is to contribute to population regulation, it must somehow be related to population density. Many studies have suggested that dispersal rate is inversely density dependent, with maximum rates at low density and minimal rates at high density (Gaines and McClenaghan 1980; Wolff 1997; Andreassen and Ims 2001). The low dispersal rates at high density are supposedly due to a social fence of territorial neighbors that deter immigration, resulting in philopatry of sons and daughters remaining in their natal site (Wolff 1997). If this generalization that dispersal rate is inversely density dependent continues to hold, any dispersal impacts on population regulation or limitation will have to be achieved by indirect means. One way to achieve this would be for dispersal to be selective for certain phenotypes that have different types of spacing behavior (Krebs 1985). Whether or not this occurs in rodents is unclear at present.

Does dispersal regulate population growth?

The characteristic dispersal pattern in rodents is for males to disperse relatively long distances and for females to settle in territories near their natal site. However, in continuous habitats at high densities when all breeding space is occupied by territorial males or females, young juveniles are deterred from emigrating from their natal site by a social fence of aggressive territorial owners inhibiting immigration (Wolff 1994b; Lambin et al. 2001). This social fence acts as a negative density-dependent factor, reducing the rate of dispersal (Andreassen and Ims 2001). Thus the rate of dispersal in territorial species is inversely density dependent (Wolff 1997; Lambin et al. 2001). As density increases, the rate of dispersal decreases, resulting in extended families as sons and daughters remain on their natal sites past the time of normal dispersal and sexual maturation. This delayed emigration from the natal site can inhibit sexual maturation of young females by direct competition with their mothers (Gundersen and Andreassen 1998), or act as a mechanism to avoid inbreeding with male relatives (Wolff 1997; Lambin et al. 2001). In patchy environments, or those in which individual movements are not deterred by neighbors, dispersal should not be delayed and may, in fact, help to stabilize or regulate density within the patch.

Alternatively, philopatry in female rodents may cause a delay in density dependence that would destabilize density. Female small mammals are highly philopatric, and breeding females may therefore be surrounded by their philopatric relatives under some circumstances. If female voles depress the survival of offspring of nonkin females only, and do not influence the survival of offspring of their female kin, time-delayed density dependence in the regulation of vole numbers by social behavior would be the result (Lambin and Krebs 1991a). The time delay occurs because the previous pattern of recruitment and mortality in a population gives rise to female kin-clusters. Kin-clusters are formed following successful reproduction, philopatric recruitment of females, and high survival; they decay with mortality and immigration. If juvenile survival and recruitment are less affected by female density in kin-structured populations, such populations could temporarily escape the social consequences of high density (Lambin and Krebs 1991a, 1993; Lambin and Yoccoz 1998).

Kinship effects

If spacing behavior can affect population size at the onset of the breeding season and the recruitment rate of young animals, as well as their rate of sexual maturation, we need to find out more information about the rules that govern spacing behavior in rodents. Darwinian arguments about inclusive fitness would suggest that for a start relatives should respond differently to one another than they should to strangers. This simple idea spawns several questions about how relatives might recognize one another, and how familiarity might substitute for genetic relatedness (see Holmes and Mateo, chap. 19, this volume), but the first question we need to answer is whether or not there is a genetic structure of relatives in field populations. The formation of kin groups, cooperation among kin, and having kin for neighbors should be beneficial for group defense and reduce the incidence of infanticide by neighboring females (Charnov and Finerty 1980; Wolff 1995). Lambin and Krebs (1991a) suggested that, since females controlled recruitment in voles, changes in female relatedness might have a significant impact on population dynamics. Specifically, they pointed out

Table 15.2 Impact of kinship on reproduction and nestling survival and summer population growth rates in seven studies

Study	Reproduction and nestling survival	Summer population growth rate (λ) per month			Parous females used?	Experimental area (ha)
		Observed	Predicted for kin	Predicted for non-kin		
Kawata 1987	No data	Spring only, unequal numbers			Yes	0.50
Boonstra and Hogg 1988	3.5 vs 2.2 young per litter	Unequal numbers	1.43	1.28	Mixed	0.15
Lambin et al. 1993, 1998	3.15 vs. 2.54 young per litter	No data	1.72	1.48	Yes	0.50
Sera and Gaines 1994	No effect	No data			No	0.09
Mappes et al. 1995	3.0 vs. 1.7	2.73 vs 1.61	1.69	1.10	Yes	0.50
Pusenius et al. 1998	2.96 vs. 0.93 young in July and August	No data	1.35	1.04	Yes	0.25
Dalton 2000	No effect	Unequal numbers			No	0.20

NOTES: For this analysis we used simple standard age-based Leslie matrices (c.f. Lambin and Yoccoz 1998) to explore the potential impact of changes in demographic parameters associated to changes in female relatedness on the dynamics of these vole populations.

that any impact of prevailing kinship on present demographic rate ought to generate a positive feedback on population growth as present kin-clusters are formed following past successful reproduction, philopatric recruitment of females, and high survival. Table 15.2 lists 7 partial tests of this idea that kinship affects population growth rates in voles by manipulating the size of matrilineal kinship groups in fenced or open populations. In four of seven studies there was higher reproductive output and juvenile survival, leading to the prediction of higher population growth rates in kin groups. For example, Lambin and Yoccoz (1998) found that relatives nested closer to one another than did unrelated females in *Microtus townsendii*, and pup survival in the nest was improved in the first two weeks of life when relatives were nearby (fig. 15.4). In addition, adult female survival at the start of the breeding season was higher for kin group females than for unrelated females. All experiments that failed to detect any effect of kinship on juvenile survival used nulliparous females, suggesting securing space for their offspring may contribute to the infanticidal behavior of female voles. If these kinds of kinship effects are significant, populations with matrilines should grow faster than those with only unrelated females. These kinds of studies need to be repeated and carried out on other rodent species before we will know how general this kinship model is in natural populations.

Summary and Conclusions

Rodent social behavior has been studied extensively, but whether it impacts population dynamics has been questioned. Social behavior is affected significantly by population density, and the question is whether this is a circular causal system. Infanticide, dispersal, sexual maturation, and direct aggression are all potential processes that are a part of spacing behavior in rodents that may cause large changes in survival, reproduction, and movements. There are several mechanisms by which social behavior can affect birth, death, and dispersal rates and thereby changes in population density. In any natural population of rodents, social behavior will operate in a matrix of extrinsic mechanisms like predation, and disentangling the relative contribution of specific factors can be done only with carefully designed experiments. We need to know both the frequency and strength of these processes in rodents, and how they change with population abundance. Recruitment in rodent populations may be limited by the presence of breeding adults, and the kin structure of populations may affect the potential rate of population growth. Further experimentation with more species is needed to uncouple the potential interaction of social behavior and extrinsic processes like predation and food supplies in limiting population abundance in natural populations of murid rodents.