

The fence effect reconsidered

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Ostfeld, R. S. 1994. The fence effect reconsidered. – *Oikos* 70: 340–348.

The fence effect consists of two related observations: (1) enclosed populations of small mammals grow to abnormally high densities; (2) they then overexploit resources, destroy their habitat, and decline precipitously. The fence effect is widely considered strong evidence for the critical role of emigration in regulating population size, and for ultimate limitation of populations of small-mammal herbivores by resource exhaustion. I reexamine published evidence for the fence effect and conclude that studies in small, artificial pens are unreliable in addressing the fence effect. Studies in large, natural enclosures are mixed in their support of the fence effect. Only two unreplicated studies show evidence for “abnormally” high densities of microtines inside enclosures, whereas several others do not. No studies confirm that habitat destruction and starvation cause the decline from high density inside enclosures. Fences tend to eliminate small predators like shrews that probably have a constant effect on vole populations, but are permeable to larger predators, such as carnivores and raptors, whose response may incorporate time lags. Therefore, it is possible that the fence effect is due largely to predator-prey interactions. My own data from three enclosed meadow vole (*Microtus pennsylvanicus*) populations support the notion that a fence contributes to rapid population increases; however, the populations showed widely divergent patterns of growth and decline. Although these populations reduced aboveground plant biomass relative to lower density vole populations, the plants rapidly compensated, and there was no evidence for overgrazing causing the declines. I suggest that a fence effect is most likely to occur in moderately productive habitats, in which herbivore populations are net producers of dispersers, but in which compensation by plants is slow. But it should be unlikely to occur in either highly productive or unproductive habitats.

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The most critical demonstration of the importance of emigration in regulating population size of small mammals is the “fence effect”. This term was coined by Krebs et al. (1969), and later was called the “Krebs Effect” by MacArthur (1972). The fence effect consists of two related observations: (1) Enclosed populations of small mammals grow to abnormally high densities; (2) they then overexploit resources, destroy their habitat, and decline precipitously (“crash”) due to starvation.

The fence effect has been an extraordinarily influential notion in small-mammal ecology. The fence effect concept has led to models of microtine population cycles that invoke social barriers to dispersal causing population buildups, local resource exhaustion, and population crash

(e.g., the social fence hypothesis: Hestbeck 1982). Other models of microtine cycles that invoke strong herbivore-plant interactions (Freeland 1974, Stenseth 1986, Stenseth and Oksanen 1987, Heske et al. 1988) appear to have been influenced by the assertion that habitat destruction and a consequent population crash are caused by high consumer densities within enclosures (Krebs et al. 1969). Further, the fence effect notion has led to a proliferation of field enclosure designs, such as creating “dispersal sinks” and “exit tubes”, specifically to prevent an expected fence effect (e.g., Gaines et al. 1979, Tamarin et al. 1984, Desy and Batzli 1989).

More generally, the fence effect concept has kept alive the belief that emigration is critical in regulating pop-

Accepted 4 February 1994

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ISSN 0030-1299

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Table 1. Influential early studies of voles in small pens.

Species	Pen size (m ²)	Location: indoors (in) outdoors (out)	Substrate:		Supplemental food:		Source
			artificial (a)	natural (n)	yes (y)	no (n)	
<i>Microtus agrestis</i>	67	out	a		y		Clarke (1955)
<i>M. arvalis</i>	70	out	a		y		Frank (1954)
<i>M. arvalis</i>	100	out	n		y		van Winjngaarden (1960)
<i>M. californicus</i>	111	out	n		y		Houlihan (1963)
<i>M. pennsylvanicus</i>	14	in	a		y		Louch (1956)
<i>M. pennsylvanicus</i>	28	out	n		n		Hatt (1930)

ulation size, despite repeated observations that emigration rates of small mammals are not density dependent (Gaines and McClenaghan 1980, Lidicker 1985). Without emigration rates (proportion of individuals emigrating) that increase with population density, emigration should not be a key process regulating population size (Stenseth and Lidicker 1992). Finally, acceptance of the fence effect concept has contributed to views of population regu-

lation exemplified by the following: "All animal populations are regulated ultimately by a limiting resource (s), such as food, and proximally by their social behavior and organization". (Tamarin 1983: 700). The implication is that once social spacing mediated by dispersal is disrupted or prevented, animal populations will grow to a level set by food limitation, but that predation, parasitism, and disease play unimportant roles in regulation.

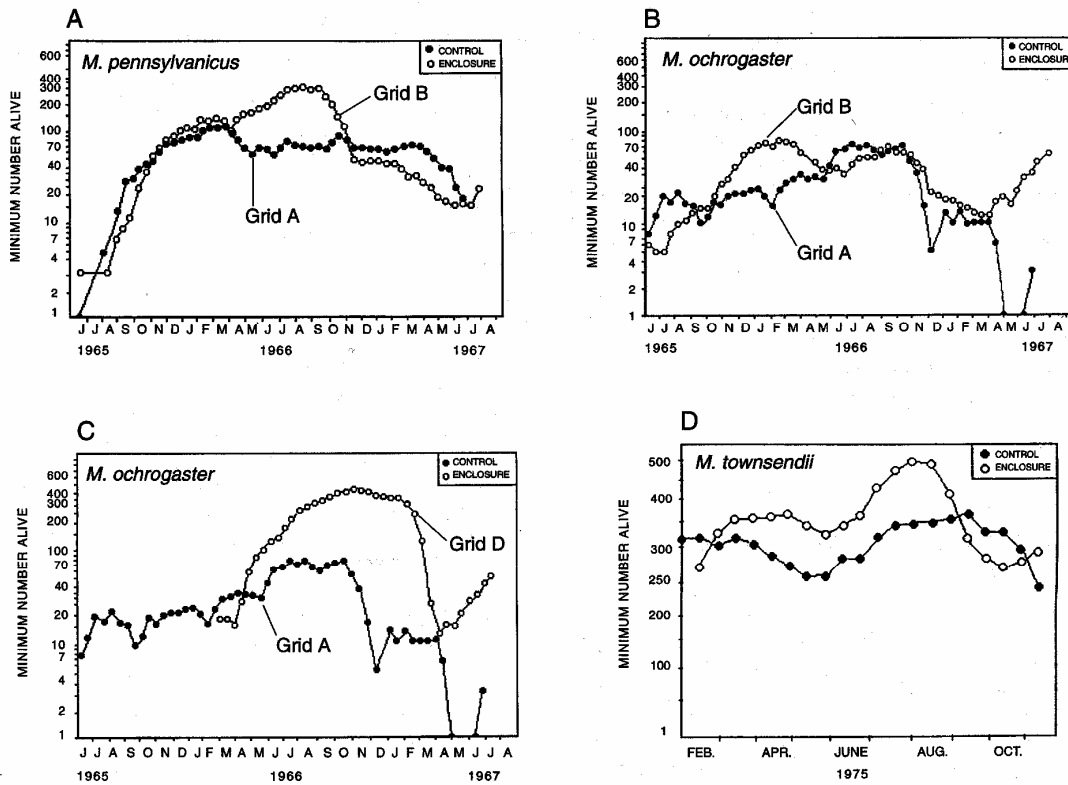


Fig. 1. Comparisons of enclosed and control (unenclosed) populations of three species of *Microtus*. A. shows *M. pennsylvanicus* populations in a 0.8-ha enclosure that also contained a population of *M. ochrogaster*, the dynamics of which are shown in B. C. shows dynamics of *M. ochrogaster* populations in an enclosed site in the absence of other small mammal species; the control is the same as in part B. D. shows dynamics of a *M. townsendii* population in a 0.44-ha enclosure. A–C were redrawn from Krebs et al. (1969), and D was redrawn from Boonstra and Krebs (1977).

My purpose here is to reexamine the evidence for the fence effect. I shall briefly review early studies of enclosed rodent populations that helped lay the foundations for the fence effect concept. I shall then reconsider the data sets that led directly to the development of the fence effect notion, and review other studies that do not show a fence effect. Finally, I shall describe my recent studies of enclosed populations of the meadow vole, and evaluate them in light of the fence effect.

Early studies

Elements of the fence effect were described in a series of early studies of enclosed small mammal populations (Table 1). The growth of several small mammal populations to densities 10 to 100 times greater than those observed under natural conditions was indeed impressive evidence that confinement influences regulatory processes (Lidicker 1985, Krebs 1992). Later studies in both indoor and outdoor pens showed similar results (Lidicker 1979, Semb-Johansson et al. 1979). These studies made important contributions to our knowledge of physiological and behavioral responses of individual animals to crowding, but their relevance to processes that regulate population size of rodents under natural conditions is questionable. In each study in Table 1, the enclosures used to house populations of animals were a fraction the size of an individual home range. Moreover, these confined populations subsisted on ad lib artificial food and were not subjected to natural rates of predation. Because of compression of entire populations in an area insufficient to support a single individual, ad lib food, and lack of predators, few reliable conclusions can be drawn from these studies regarding the role of confinement on regulatory processes within small mammal populations.

The fence effect in large outdoor enclosures

The fence effect has been described for three species of vole (*M. ochrogaster*, *M. pennsylvanicus*, and *M. townsendii*) confined in large outdoor enclosures (Krebs et al. 1969, Boonstra and Krebs 1977). For example, after 11 months of population growth similar to that of an unenclosed control population, a fenced population of *M. pennsylvanicus* in a 0.8 ha enclosure in Indiana grew to a density approximately four times that of the control (Fig. 1A). The enclosed population then declined rapidly and persisted for six months at levels well below that of the control population. This pattern was interpreted as follows: the fence prevented emigration, thereby disrupting

normal regulatory processes mediated by social behavior and dispersal. The population then grew to an unsustainable density and severely overgrazed its habitat, leading to massive mortality due to starvation (Krebs et al. 1969, 1973, Krebs and Myers 1974).

On the same sites as the fenced and control populations of *M. pennsylvanicus* were populations of *M. ochrogaster* (Krebs et al. 1969). The *M. ochrogaster* populations showed somewhat different patterns of density fluctuations (Fig. 1B). The fenced *M. ochrogaster* population began to exceed the density of the unfenced population within six months after the initiation of the experiment, at a time when the two (fenced and control) *M. pennsylvanicus* populations were at equal density (Fig. 1A). The fenced *M. ochrogaster* population remained for about six months at a level approximately four times that of the control population, and then declined gradually to a level quite similar to that of the control. The two populations then remained at similar densities for about 1 yr.

For both species the presence of a fence appeared to cause "abnormally" high densities to be reached. However, several factors confound interpretation of the population dynamic patterns demonstrating the fence effect. The study was unreplicated. Two species of vole were present simultaneously on both experimental and control plots, but the effects of their interactions are unknown. The two species were out of phase with respect to periods when the fenced population exceeded the control in density, indicating that competitive interactions might have been occurring. The enclosed *M. ochrogaster* population was declining (winter-spring 1966) when the enclosed *M. pennsylvanicus* population was increasing. If overgrazing and consequent starvation are responsible for declines in fenced vole populations, both of these species (which show extensive dietary overlap: Batzli 1985, Ostfeld 1985) should have declined synchronously.

An additional experiment was performed by Krebs et al. (1969) with only one species (*M. ochrogaster*) inside an enclosure (Fig. 1C). This population showed a dramatic increase to levels about five times higher than the control and declined rapidly after about 1 yr. Nevertheless, the fenced population declined to a level no lower than that of the control, and it immediately began increasing at a time when the control population declined. If the enclosed vole population had destroyed its habitat, one would expect a crash to a lower level than that occurring on an unenclosed site where no habitat destruction took place. This pattern does not support the notion that overgrazing and habitat destruction by the fenced population caused the crash.

Similar results were obtained for *M. townsendii* (Boonstra and Krebs 1977; Fig. 1D). The population in a 0.44-ha enclosure exceeded that of an unfenced control by a factor of about 1.5, then declined more rapidly than the control population. But again, the fenced population showed signs of immediate recovery at the same time that the control population continued to decline, indicating that the fenced population's impact on the habitat may

Table 2. Enclosure studies that do not show a fence effect^{1,2}.

Species	Enclosure size (ha)	Replication		Unfenced control		Source
		yes (y)	no (n)	yes (y)	no (n)	
<i>Clethrionomys glareolus</i>	0.8	n		n		Ylönen et al. (1988)
<i>Microtus californicus</i>	0.13	y		y		Ford and Pitelka (1984)
<i>M. pennsylvanicus</i>	0.1	y		n		Barrett (1988)
<i>M. pennsylvanicus</i> ³	0.4	n		n		Wiegert (1972)
<i>M. pinetorum</i>	0.8	y		n		Gentry (1968)

¹ Studies in which enclosures were permeable, or were supplied with exit gates, dispersal sinks, or supplemental food were excluded.

² Lack of a Fence Effect was concluded when populations grew slowly and reached maximum densities well below peak densities known to occur for that species.

³ Enclosures used were outside the geographic range of this species.

not have been as severe as claimed. As with the Krebs et al. (1969) study, the Boonstra and Krebs (1977) experiment was unreplicated. In both Krebs et al.'s (1969) and Boonstra and Krebs' (1977) studies, alternative causes of declines within fences, e.g., intense predation pressure on a locally dense prey population (the pantry effect; Desy and Batzli 1989), or outbreaks of disease, were not ruled out.

Lack of a fence effect in large outdoor enclosures

Most fencing studies of small mammal populations are unable to address the fence effect simply because they have been designed to avoid it. For instance, in several enclosure studies, areas of suboptimal or poor habitat ("dispersal sinks") were included or created, and individuals entering these dispersal sinks were removed (e.g., Tamarin et al. 1984, Desy and Batzli 1989). In other enclosure studies (e.g., Gaines et al. 1979, Verner and Getz 1985, Hestbeck 1986, Erlinge 1987, Heske 1987), permeable fences were used, causing uncertainty in the rate of emigration from enclosures. Other fencing studies have included supplemental feeding of enclosed populations (e.g., Beacham 1981, Kawata 1989, Saitoh 1989, Ylönen and Viitala 1991), which prevents the effect of the fence itself on population growth from being determined. Finally, some enclosure studies (e.g., Porter and Dueser 1986, Bergeron and Jodoin 1993) were too brief for the existence of a fence effect to be detected.

A few fencing studies have been performed in large (here defined as at least several times the size of an average individual home range) outdoor enclosures in which there were no dispersal sinks, fences were impermeable, and no supplemental food was added, but in which no fence effect was observed (Table 2). However, the evidence against a fence effect in these studies is not strong, due to infrequent use of replication or controls.

Field studies of *Microtus pennsylvanicus*

I established nine fenced enclosures in a hayfield in Millbrook, SE New York, U.S.A., in June 1990. Fences consisted of 1.27-cm mesh galvanized hardware cloth extending 0.3 m below ground and 1.0 m above ground. Materials and depth of fences were comparable to Krebs et al. (1969) and Boonstra and Krebs (1977). Each enclosure was 0.16 ha (40 m by 40 m), which is approximately 8–16 times the size of an average meadow vole home range (Madison 1980). All existing populations of voles were cropped after the initial trapping session to 2–3 pairs per enclosure. Thereafter, the populations were allowed to grow to either low, medium, or high population density. Designated low and medium density enclosures were managed at target densities by removing subadult voles as needed throughout the study (Ostfeld and Canham 1993), and designated high density grids were unmanipulated. Low and medium density enclosures averaged 75 and 180 voles · ha⁻¹, respectively. Dynamics of all three density treatments are shown in Ostfeld et al. 1993. Enclosures were arranged in a randomized block design, with three blocks and three enclosures per block (one at each density level). Blocks 1 and 2 were dominated by the grasses *Bromus inermis*, *Poa pratensis*, and *Arrhenatherum elatius*, and bedstraw (*Galium mollugo*). Block 3 contained these species, but also had numerous goldenrods (especially *Solidago rugosa*), thistles (*Cirsium arvense*), and milkweeds (*Asclepias syriaca*).

Two 0.16-ha unenclosed (control) trapping grids were established in August 1991. In addition, traps were set occasionally in a ring around the outside of the enclosures to detect rate of escape via climbing or burrowing. On all trapping grids, I used standard mark-recapture techniques to enumerate population size biweekly from establishment (June 1990 [enclosures] or August 1991 [controls]) until April 1992. In addition, to measure the gross impact of vole population density on food abundance, four times in 1991–92 I took vegetation biomass samples from five randomly located 30 cm by 30 cm quadrats per grid (15 per density level). All plant material was clipped at ground level, sorted, dried and weighed. In April, 1991

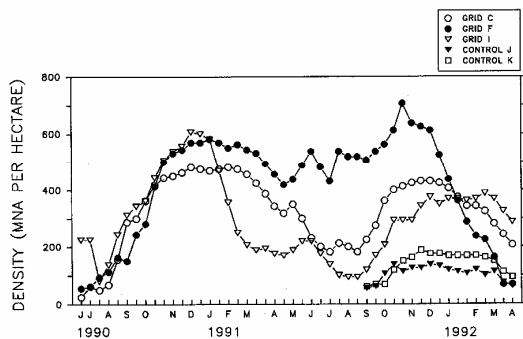


Fig. 2. Dynamics of three enclosed, but otherwise unmanipulated, populations of *Microtus pennsylvanicus* in Southeastern New York, U.S.A., together with two control (unenclosed) populations. Density is expressed as minimum number alive (MNA) per ha.

and 1992, all green biomass was herbaceous and potentially edible by voles. In June and September 1991, large saturated plants, such as thistle, milkweed, and goldenrod, were excluded because they are avoided by voles (Batzli 1985).

Four percent of the 3094 voles marked in enclosures moved between grids or were captured outside the fences, a figure comparable to that of Boonstra and Krebs (6.5%). Voles probably accomplished these movements by climbing, since holes beneath fences were quite rare and immediately destroyed. Thus, although the fences were not completely vole-proof, clearly they were effective barriers to dispersal.

The three high density grids showed diverse patterns of

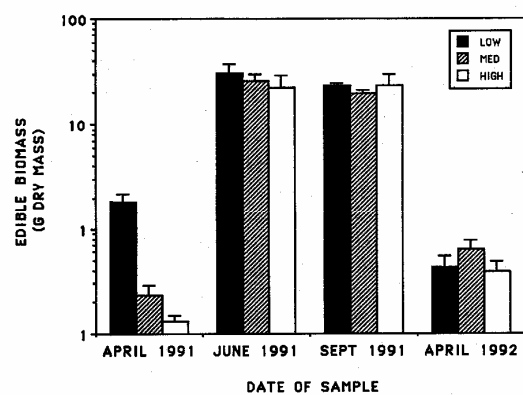


Fig. 3. Comparison of aboveground green (living) biomass in vole enclosures subjected to either high, medium, or low vole density. Means (± 1 SE) of 15 30 cm by 30 cm quadrats per density level are presented. In June and September, 1991, large saturated, "woody" plants that are known to be avoided by voles (e.g., thistle, milkweed, goldenrod) were excluded to obtain an estimate of "edible" biomass.

population dynamics (Fig. 2). All populations grew rapidly after the initial culling, but subsequently their behavior differed substantially. Grid I, which had the highest vole density when the fences were established, showed the most rapid early growth to the highest 1990 peak (606 voles \cdot ha $^{-1}$ [= 97 voles known to be alive on the grid]). The Grid I population then declined rapidly in winter 1990–91 to a plateau of about 200 voles \cdot ha $^{-1}$ (comparable to peak densities of unenclosed populations of this species: Taitt and Krebs 1985). During an unusual summer drought in May–June 1991, that population declined further to 94 voles \cdot ha $^{-1}$, after which it grew to 388 \cdot ha $^{-1}$.

Grid C showed roughly sigmoidal growth to a peak of 481 voles \cdot ha $^{-1}$ in 1990, then declined gradually for 8 months (trough = 181 voles \cdot ha $^{-1}$). The population grew to another peak (431 \cdot ha $^{-1}$) in autumn 1991 and again declined gradually until the end of the study. In contrast, Grid F showed the slowest initial growth, but reached a peak of 580 voles \cdot ha $^{-1}$, which it maintained for about 14 months before declining fairly rapidly in winter-spring 1992.

Early in the 1991 growing season (April), the effect of high vole density on aboveground plant biomass was extreme compared to medium (average = 180 voles \cdot ha $^{-1}$) and low density (average = 75 voles \cdot ha $^{-1}$) enclosures (Fig. 3). By the middle of the 1991 growing season (June) the three density treatments showed more similar aboveground biomass, and by September 1991 there was no detectable difference among density treatments. This lack of a density effect persisted until the end of the study (April 1992; Fig 3). Two-way analysis of variance revealed that density had no statistically significant effect on biomass ($F_{2,26} = 0.62$, $P = 0.55$), but that biomass varied significantly with date of sample ($F_{2,26} = 36.48$, $P < 0.001$). There was no significant interaction between density and date ($F_{4,26} = 0.30$, $P = 0.87$).

If overgrazing and consequent starvation cause declines in enclosed populations, I expected biomass to be lowest within those enclosures that recently had experienced sharp declines: Grid I in spring and summer 1991, and Grid F in spring 1992. In no case was this expectation met. For the April 1991 biomass sample, Grid I had biomass levels intermediate between the two other grids. In June 1991, Grid I had the highest edible biomass, > 100% higher than either Grid C or Grid F. For the April 1992 sample, Grid F had biomass levels > 100% higher than either of the other high-density grids (Table 3). Moreover, vole populations performed relatively well in April 1991, when plant biomass was most strongly depleted.

Discussion

Testing for the existence or generality of the fence effect requires two questions to be answered: Does the curtail-

Table 3. Means (SD) of edible plant biomass (g·900 cm⁻²) taken near the times of population crashes.

Month	Year	Grid		
		C	F	I
April	1991	0.102 (0.06)	0.164 (0.18)	0.118 (0.12)
June	1991	17.3 (4.96)	13.7 (7.96)	36.0 (23.55)
April	1992	0.164 (0.08)	0.732 (0.37)	0.284 (0.22)

ment of emigration caused by fencing result in “abnormally” high population density? Is the decline from high density inside enclosures due to overgrazing, habitat destruction, and ensuing starvation?

Some studies provide strong evidence for abnormally high densities occurring inside enclosures (Krebs et al. 1969, Boonstra and Krebs 1977), whereas others do not (Table 2). In the present study, fenced populations grew to extremely high levels compared to unfenced control grids (Fig. 2). Unfortunately, I did not establish the controls until part way through the study, by which time populations on experimental and control areas were at different levels. Nevertheless, all populations were growing at the time of establishment of controls, and those that were enclosed reached much higher peaks. I tentatively interpret my data as supporting the role of fences in contributing to population growth at my study site.

The observed differences in population response to fencing may reflect differences among populations in the importance of emigration in regulating population size, which may in turn vary among habitat types. In the current study, there was pronounced variation in population dynamics even among enclosures 50 to 150 m apart in the same field (Fig. 3). Variable responses to fencing may also result from species-specific social systems or variable enclosure size.

Studies in which fences cause abnormally high densities have been interpreted as supporting a key role for emigration in regulating population size, despite numerous other studies that show emigration rates are not density dependent (Gaines et al. 1979, Gaines and Mc Clenaghan 1980), or are dependent on density in complex ways (Lidicker 1985). Enclosure studies in which fences were designed to avoid an expected fence effect are particularly illuminating in this context. Tamarin et al. (1984) used enclosures that incorporated poor habitat for meadow voles (forest), and classified voles captured in forest as dispersers. They found that meadow vole populations inside enclosures behaved nearly identically to an unenclosed control. This similarity apparently was due to low numbers of dispersers, suggesting that dispersal rate plays only a minor role in the population dynamics of this species. Similarly, Verner and Getz (1985) used permeable enclosures and drift fences to detect emigration by both *M. pennsylvanicus* and *M. ochrogaster*, and found losses via dispersal to be low and uncorrelated with either density or rate of increase. These studies indicate that the

absolute prevention of emigration would not by itself have caused abnormal rates of population growth.

Note that fences prevent both emigration and immigration (Krebs 1992). In habitats in which populations typically produce surplus individuals, but which receive few immigrants (“source” or “optimal” habitat types: Pulliam 1988, Ostfeld 1992a), prevention of bidirectional dispersal movements is likely to stimulate population growth because of the curtailment of emigration. But in habitats in which populations require immigration to be sustained (“sink” or “suboptimal” habitat types), a fence is likely to cause declines in numbers and possible local extinction. In those sites where emigration and immigration are roughly equivalent, a fence should have minimal effect on density. Because small-mammal ecologists tend to select sites for study in which population density is high and growth rapid, there may be an inherent bias toward finding a fence effect. Therefore it is surprising that so few examples of rapid growth after fencing a population exist. Enclosures should be useful in delineating habitat types (source or sink) based on whether there is growth or decline after dispersal is prevented.

There are two other possible mechanisms by which fences may contribute to rapid population growth of voles: exclusion of predators, and exclusion of competitors. These factors have received relatively little attention by small-mammal ecologists (Desy and Batzli 1989). At Boonstra and Krebs' (1977) and my study sites, no other small vertebrates at the study site compete with voles for food or other known resources, and therefore it is doubtful that exclusion of competitors is an important consideration. In the present study, capture records and direct observations revealed that predators such as weasels (*Mustela erminea*), foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*) and red-tailed hawks (*Buteo jamaicensis*) were not excluded by the fences. However, fences appear to be effective barriers to immigration by short-tailed shrews (*Blarina brevicauda*), which may be important predators on juvenile voles (Getz et al. 1992).

Potentially, both the rapid growth and sharp decline phases that characterize the fence effect may be due to the fence's impact on predation. Shrews typically experience high mortality rates under trapping protocols designed for rodents (pers. obs.); therefore, shrew populations inside enclosures may become depleted with little opportunity for replenishment. By preventing immigration by shrews, fences may allow vole population growth through relaxa-

tion of predation. However, the resulting high local densities of voles may later attract larger predators, for which the fence is not a barrier, and which may be responsible for the decline.

No studies provide strong evidence that abnormally high densities inside enclosures cause habitat destruction leading directly to a crash. Habitat destruction was described but not quantified by Boonstra and Krebs (1977) and Krebs et al. (1969). In nearly all the populations studied by Boonstra and Krebs (1977) and Krebs et al. (1969), fenced populations declined to levels no lower than controls, and began growing immediately after the decline. It seems likely that either the habitat's ability to support vole populations was only weakly affected by high vole density (and the decline was due to predation or disease), or that habitat quality was affected only temporarily.

Bergeron and Jodoin (1993) showed that *M. pennsylvanicus* densities of ≥ 1000 voles \cdot ha $^{-1}$ caused a decrease in quantity, but not nutritional quality, of plant biomass. But because they removed all voles after one growing season, effects of biomass reduction on vole populations were not determined. Similarly, Pokki (1981) found that on Finnish islands, depletion of vegetation became apparent only after *M. agrestis* populations exceeded 1000 voles \cdot ha $^{-1}$, a highly unusual situation on the mainland. Moen et al. (1993) found that vole densities equivalent to 1480 individuals \cdot ha $^{-1}$ caused a sharp decline in aboveground plant biomass compared to no-vole controls. However, for two species, *M. agrestis* and *Clethrionomys glareolus*, individuals maintained body mass well even after the depletion of vegetation, subsisting adequately on an apparently poor food supply.

A strong reduction in aboveground biomass was demonstrated in the present study (Fig. 3), but it was ephemeral; the plant community recovered within a few months despite continuing to sustain high vole density. The initial decline on Grid C (Fig. 2) coincided with increasing plant standing crop (Fig. 3). Moreover, the grids experiencing the sharpest declines did not exhibit the lowest biomass at or near the time of decline (Table 3). In a follow-up study, vole populations introduced into the enclosures that had experienced chronically high vole density performed as well as those introduced into previously medium- and low-vole-density enclosures (Ostfeld et al. 1993). Similarly, *C. rufocanus* introduced to islands that had previously experienced high vole density and heavy exploitation of their food supply (*Vaccinium myrtillus*) showed high rates of survival, reproduction, and population growth (Oksanen et al. 1987). In the study by Moen et al. (1993), even abnormally high vole densities did not reduce aboveground biomass of grasses one growing season after vole removal, although biomass of some dicots was reduced.

To summarize, no studies to date have demonstrated that starvation causes declines from high density. Although extremely high vole densities often reduce plant biomass, voles appear to be resilient to reduced food

quantities. In addition, the effects of food depletion on subsequent population dynamics of herbivores are not well understood. The steepness and length of any habitat-related decline in vole density will be affected by the ability of plant communities to resist or rebound from overexploitation. Because plant biomass provides both food and cover for voles, declines in vole density that coincide with reduced plant standing crop may result from predation rather than starvation.

I predict that the fence effect is not likely to occur in either highly productive or unproductive habitats. In the former, emigration rates normally will exceed immigration rates, and so growth of enclosed populations is expected to be high, but the plant community is expected to recover rapidly from exploitation by consumers. Population declines that occur in highly productive habitats are more likely to be caused by predation and disease than by starvation (Oksanen et al. 1981, Oksanen 1990). In unproductive habitats, emigration rates are likely to be low due to low herbivore productivity, and immigration may be necessary to achieve population growth. Thus, fencing will have a negative effect on population size, and these populations will be unlikely to increase to the point where they depress food availability.

In contrast, in moderately productive habitats, emigration may often exceed immigration, but plant communities will be less resilient than highly productive communities are to grazing pressure by small herbivores. Under this scenario, enclosed populations will be likely to increase dramatically to the point where they significantly reduce food availability or protective cover and undergo a crash.

The effects of habitat productivity on dispersal patterns will also depend on the nature of other patches in the landscape. Patches of high or moderate productivity should experience high emigration rates when they are surrounded by habitats of poor quality (Ostfeld 1992a, b). Therefore, perhaps *relative* habitat quality, rather than absolute quality, is most important in determining whether a particular patch is vulnerable to a fence effect.

Conclusions and future directions

Enclosing a small mammal population appears to give rise to variable and unpredictable results, often inconsistent with the notion of the fence effect. One element of the fence effect, namely that abnormally high densities result from enclosing a field population of rodents, has been demonstrated in only three studies, only one of which was replicated (Figs 1, 2). The other element, that abnormally high densities produced by enclosing a population results in habitat destruction perpetrating a crash due to starvation, has not been demonstrated.

Models of microtine cycles that depend on the generality of one or both of the above elements must be reconsidered. For instance, the social fence hypothesis (Hestbeck

1982, 1986) assumes that social groups of voles surrounding a central group act as a barrier to dispersal. It further assumes that this barrier will result in extreme density build-up in the central group, which grows to the point of resource exhaustion and then crashes. In an experimental test, Hestbeck (1986) failed to demonstrate resource exhaustion in socially "fenced" California vole (*M. californicus*) populations. Models of plant-herbivore limit cycles similarly rely on assumptions of habitat destruction by herbivores during density peaks and a subsequent lag in habitat recovery (Freeland 1974, Stenseth 1986, Stenseth and Oksanen 1987, Hansson 1988, Heske et al. 1988), which have not been well validated (Ostfeld et al. 1993). The model of Oksanen et al. (1981) predicts that the impact of herbivores on plants will be highest in regions of low primary productivity (e.g., tundra), and lower in areas of greater primary productivity (e.g., temperate grasslands). In the latter habitat, in which the fence effect was initially described, herbivore biomass is predicted to be regulated by predation, but not by resource availability (Oksanen et al. 1981). This prediction remains to be tested for microtine rodents.

Future explorations of the existence and generality of the fence effect will require that several questions be addressed. What is the role of reduced standing crop of food in herbivore declines? To what extent does the enhancement of primary productivity by grazing (Mc Naughton 1979, Oksanen et al. 1987) counteract reduced standing crop? Is there a gradient from low-productivity to high-productivity habitats in the extent to which plant communities compensate for high consumption rates, and hence ameliorate the effects of grazing? Does recovery by plant communities entail a significant time lag? Finally, is the fence effect unique to moderately productive "source" habitats, or to patches surrounded by poor quality habitat?

Acknowledgements – I am grateful to C. Borg, D. Braun, J. Jimenez, K. Kinder, P. Nielson-Murphy, S. Plambeck, and J. Schnurr for able assistance in the field; to R. Boonstra, C. Canham, and J. Wolff for illuminating discussions; to L. Oksanen for insightful comments; and to A.-O. Wilhelm and G. Capreol for helping draw the figures. This research was supported by the Central Hudson Gas and Electric Corporation and the Mary Flagler Cary Charitable Trust. This is a contribution to the program of the Inst. of Ecosystem Studies.

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