**Rarity and Coexistence of a Small Hibernator, *Zapus hudsonius*, with
Fluctuating Populations of *Microtus pennsylvanicus* in the Grasslands of
Southern Ontario**

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RARITY AND COEXISTENCE OF A SMALL HIBERNATOR, *ZAPUS HUDSONIUS*, WITH FLUCTUATING POPULATIONS OF *MICROTUS PENNSYLVANICUS* IN THE GRASSLANDS OF SOUTHERN ONTARIO

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SUMMARY

(1) The meadow jumping mouse (*Zapus hudsonius*) and the meadow vole (*Microtus pennsylvanicus*) are sympatric over most of the northern half of North America and occur in the same habitats. We tested the hypothesis that these species compete directly for space by examining the response of the *Zapus* to experimental manipulations of *Microtus* numbers from 1978 to 1982.

(2) *Zapus* populations reached maximum densities (28.6–37.1 per ha) after a 2-year time-lag on a grid where all resident *Microtus* were removed, intermediate densities (11.4–20.0 per ha) on grids where either male or female *Microtus* were removed and low densities (1.4–5.7 per ha) on control grids.

(3) *Zapus* used the same habitats on the grids as *Microtus* but avoided traps visited by *Microtus*. Thus, avoidance was temporal rather than spatial.

(4) Because of low trappability of *Zapus*, clear differences among grids in most other demographic variables were not found. Transiency rate was highest on the control grids and lowest on the grids with lowest *Microtus* density. Most between-grid movements of *Zapus* (68%) were towards the *Microtus* removal grid.

(5) These results indicate that in southern Ontario, *Zapus* populations compete with, and are perennially low because of *Microtus* populations. We suggest that this is the case throughout the range of *Zapus* because of the lag times caused by peculiarities of *Zapus* life-history traits (hibernation and one or two litters per year) and because of short periods when *Microtus* populations are declining or low.

INTRODUCTION

The importance of competition in structuring animal communities has recently come under a great deal of criticism (Simberloff 1983; Strong 1983; Strong *et al.* 1983). Many of these criticisms, though not all (Connell 1983), are directed at studies on multi-species communities where inference rather than experiment has been used to assess the role of interspecific competition. Some of the strongest evidence for the importance of interspecific competition comes from experimental studies on small mammals (M'Closkey 1976; Redfield, Krebs & Taitt 1977; Brown 1978; Grant 1978). Microtines, because of their population fluctuations, can potentially have major effects on populations of sympatric species (Blaustein 1980; Linzey 1984).

The meadow jumping mouse (*Zapus hudsonius* Zimmerman) has a wide distribution throughout North America, occurring from the Atlantic coast to the Aleutian Islands in Alaska and from northern Georgia to the arctic tree-line (Hall 1981). The meadow vole

(*Microtus pennsylvanicus* Ord) has an even greater distribution, which is almost completely sympatric with that of the jumping mouse (Hall 1981). In general, the meadow jumping mouse is rare (Whitaker 1963, 1972; Nichols & Conley 1982; Alder, Reich & Tamarin 1984) and the meadow vole is common (see Krebs & Myers 1974 for numerous references). Both species typically prefer moist meadow habitat (Getz 1961; see Whitaker 1972 and Reich 1981 for reviews of the mouse and the vole, respectively), but whereas the mouse is primarily a granivore/insectivore, the vole is primarily a herbivore. The mouse typically weighs 16–20 g and hibernates for 8 months per year; the vole typically weighs 35–45 g and is active all year.

There is no experimental evidence that competition occurs between these two species, though there is limited evidence that traps capturing *Microtus* may be avoided by *Zapus* (Alder, Reich & Tamarin 1984) and that in the presence of *Microtus*, *Zapus* may choose other habitats (Porter & Dueser 1982; Morris 1983). From an experimental study of *Microtus* we present evidence that *Zapus* abundance is directly limited by *Microtus* abundance and that suggests that the life-history traits of *Zapus* predispose it to perennial rarity throughout the grasslands of North America.

STUDY AREA

This study was carried out on a 10-ha parcel of rolling grassland that had been abandoned for at least 5 years. It was located 30 km north of Toronto, Ontario (43°41'N, 79°38'W), near the town of Aurora (Fig. 1). The area was surrounded on three sides by roads, but only two were heavily used, and thus small mammals could disperse from or onto the area. The dominant plants on the live-trapping grids are shown in Table 1. The percentage cover was determined by the use of 1 × 1 m plots (25 each on A, B, C, and E; 14 on D) systematically placed throughout the grids. On all grids, approximately 60% of the cover consisted of various grasses with *Agropyron repens* (L.) Beauv. dominating. Grids A and E were very similar (Table 1 and Fig. 1), with a dark band of vegetation occurring on about half of each grid and a drainage stream, flowing mainly in spring, going through the middle of both. It appeared that half of each of these two grids had been planted prior to the study to *Lotus corniculatus* L. (birdsfoot trefoil) and *Phleum pratense* L. but that this was changing with an invasion of creeping thistle (*Cirsium arvense* (L.) Scop.) and other grasses. Though the grass was not cut during our study, it had previously been cut annually.

TABLE 1. Percentage cover of the major species of grasses and herbs on the trapping grids

	Grids				
	A	B	C	D	E
<i>Agropyron repens</i> (L.) Beauv.	60	44	46	45	41
<i>Dactylus glomerata</i> L.	10	5	14	2	9
<i>Phleum pratense</i> L.	1	7	11	4	7
<i>Poa pratensis</i> L.	4	2	1	10	11
<i>Cirsium arvense</i> (L.) Scop.	6	4	1	3	10
<i>Lotus corniculatus</i> L.	7	0	4	0	5
<i>Potentilla</i> spp.	0	1	1	3	1
<i>Solidago</i> spp.	0	8	0	5	3
<i>Taraxacum officinale</i> Weber	3	4	6	1	2
<i>Vicia cracca</i> L.	4	17	14	9	3

FIG. 1. Photograph of the study area near Aurora, Ontario. The locations of the trapping grids are indicated with hatched borders.

METHODS

The study area contained five live-trapping grids. Each grid was covered by a checkerboard of points spaced 7.6 m apart. Three of the grids were square (A, B, E) and two were irregular (C, D); four contained 100 trap points (A, B, C, E) and one contained 98 (D) (Fig. 1). One Longworth live-trap was placed at each trap point and baited with whole oats; cotton nesting material was provided for warmth. Fifty extra traps were placed on grid A as densities increased. Traps were left permanently on the grids and covered with a board or a snow shelter (Pruitt 1959; Iverson & Turner 1969). We set all grids every second week in the afternoon, and checked traps the following morning, the next afternoon, and again on the second morning, when the traps were locked open. During the summer, traps were set only in the evenings to avoid trap mortality during the heat of the day. Grids A and B were also trapped with pitfall traps (Boonstra & Rodd 1984) during the spring, summer, and autumn, but since *Zapus* were never caught in these, we will not deal with these data here.

Five other small mammal species were caught on the grids and are listed in order of decreasing abundance: *Microtus pennsylvanicus*, *Blarina brevicauda* (Say), *Peromyscus leucopus* (Rafinesque), *Mus musculus* L., and *Sorex cinereus* Kerr. As part of a simultaneous study into the causes of poor juvenile survival, *Microtus* populations were manipulated in the following manner: grids A and B were live-trapped, grid C was a

female-removal grid, from which all breeding females were continuously removed; grid D was a male-removal grid, from which all breeding males were continuously removed; and grid E was a total removal grid. Onto grids B, C, D, and E during the summers of 1978, 1979, and 1980, small cohorts of young *Microtus* (approximately 20 animals each) were periodically introduced and later removed. Grid A was trapped throughout the spring, summer and autumn from 26 June 1978 to May 1982, and in winter, weather permitting. Grid B was trapped from 26 June 1978 to 2 November 1979 and from 28 May to 31 October 1980. Grids C and D were trapped from 26 June 1978 to 6 October 1978, from 28 May to 2 November 1979, and from 28 May to 31 October 1980. Grid E was trapped from June to 17 November 1978, from 18 April to 14 December 1979, from 16 April to 12 December 1980, from 4 March to 27 November 1981, and from 31 March to 28 May 1982. Thus, trapping on grids A and E always occurred throughout the complete active season of *Zapus* in 1979, 1980, and 1981.

To examine how the presence of *Zapus* was affected by *Microtus*, we utilized two measures of spatial overlap. The coefficient of interspecific association of Cole (1949, as modified by Ratliff 1982) was calculated for grids C, D, and E for all years. Too few *Zapus* were caught on grids A and B to make the calculations meaningful. Within a trapping session, we noted the number of trap stations that caught only one, both, or neither of the species. Weeks in which no *Zapus* were caught were eliminated from the analysis. Cole's coefficient varies from +1, indicating maximum positive association, to -1, indicating maximum negative association; a value of 0 indicates random association. The index of overlap of Koplin & Hoffmann (1968) was also calculated for grids C, D, and E. It measures the degree of habitat separation of these two species on each grid. Over the entire study, each trap station was categorized as having caught *Zapus* only, *Microtus* only, both species, or neither species. This index varies from 0 for complete habitat separation to 100 for complete habitat overlap.

All *Zapus* were ear-tagged, and on each capture the following data were recorded: tag number, trap location, body weight, sex, and sexual condition. We attempted to determine sexual condition in males by testes position, but were not confident in this measure, and in females by the presence of lactational tissue (present or absent) and by obvious pregnancy. We estimated population parameters by enumeration, because our poor trappability did not permit use of Jolly-Seber estimators. Trappability was calculated by means of the minimum trappability estimate given in Krebs & Boonstra (1984).

RESULTS

Trappability

We calculated trappability for the 3 years in which trapping had occurred throughout the active season of *Zapus* for grids C, D, and E (numbers on A and B were too low). The mean unweighted trappability was $6.8\% \pm 3.46$ (1 SE) for males (range: 0.0% ($N = 3$, grid C 1979) to 20.9% ($N = 12$, grid E 1980)) and $19.5\% \pm 5.04$ for females (range: 0.0% ($N = 2$, grid D 1979) to 35.9% ($N = 8$, grid C 1980)). None of these trappability estimates was based on sample sizes greater than twelve and this was the result of the elimination of animals caught only once or twice in adjacent trapping sessions in the calculation of the minimum trappability estimate. Of the 208 individuals caught over the entire study on all grids, 132 were caught only once. Another indication of the poor trappability was that animals known to be alive in successive years were often caught only once or twice per year. For example, eighteen animals were caught once in each of two

successive years and, not including the first and last capture times, they were present for an average of 7.4 trapping periods when they could have been caught during the active season. A particularly graphic example illustrating the difficulties in capturing this species is female number 5136, which was caught a total of six times: 23 August and 6 September 1979, 29 May and 21 August 1980, and 11 June and 20 August 1981.

Density

When the study started in 1978, both *Microtus* and *Zapus* were at low densities (Fig. 2). However, while *Microtus* increased rapidly on control grid A to reach numbers that never dropped below fifty after the first year, *Zapus* numbers always hovered around one or two individuals, except for one instance in 1980, when four were caught. Grid B showed the similar low numbers of *Zapus* throughout the study. In contrast, *Zapus* numbers increased on the total removal grid E from a maximum of three in 1978, to sixteen in 1979, and finally stabilized at between fifteen and twenty-six individuals in the next 3 years. Thus, *Zapus* showed a pronounced increase in numbers when a resident population of *Microtus* was absent, but there appeared to be a time-lag of about 2 years before densities stabilized.

Since we had also created two grids (C and D) with densities intermediate between the control and the removal grid, we examined whether the negative effect of *Microtus* on *Zapus* was related to the density of *Microtus*. We investigated this relationship for 1979 and 1980, when complete trapping data were available for all five grids. The index used for *Zapus* was the total number of different individuals caught on a grid throughout the active season and for *Microtus* it was the average minimum number of resident animals caught on a grid throughout the active season of *Zapus*. Residents were defined as those voles caught more than once on a grid. The new animals continually removed from grids C, D,

FIG. 2. Minimum number alive of *M. pennsylvanicus* and *Z. hudsonius* on Control Grid A and on Removal Grid E (where all *Microtus* were removed).

FIG. 3. The relationship between the total number of *Z. hudsonius* caught in an active season and the average minimum number of resident *M. pennsylvanicus* alive on all trapping grids in 1979 and 1980.

and E were probably mainly immigrants and are less likely to have had an effect on the *Zapus* populations than the more permanent residents. Figure 3 shows that there is a similar inverse relationship between numbers of the two species in both 1979 ($P < 0.01$) and 1980 ($0.05 < P < 0.10$). We conclude that at high densities of resident *Microtus*, few *Zapus* are caught.

Spatial overlap

Table 2 shows that in every year and on all three grids, Cole's coefficient of interspecific association was negative, though it was not always equally strong or significant. For all three grids pooled for all years, the coefficient was -0.44 ($P < 0.001$). Thus, within a

TABLE 2. Number of trap stations with various combinations of species presence or absence. All trapping periods within a year are pooled and only those weeks in which *Zapus hudsonius* were caught are included. Cole's Coefficient of Interspecific Association (C7) was calculated for each year and for the total of each grid. Abbreviations are as follows: B, both species caught in a trap; Z, only *Zapus* caught; M, only *Microtus* caught; N, neither species caught

		Grid C				Grid D				Grid E			
		B	Z	M	N	B	Z	M	N	B	Z	M	N
1978		0	2	21	77	1	6	92	97	1	5	51	243
	C7		-1.0				-0.70				-0.04		
1979		7	7	401	185	5	10	365	110	12	33	210	345
	C7		-0.26				-0.56***				-0.28		
1980		27	22	554	96	11	8	471	95	28	69	478	288
	C7		-0.34***				-0.24**				-0.51***		
1981										16	47	391	569
	C7										-0.36*		
1982										1	26	32	141
	C7										-0.76		
Total		34	31	976	358	17	24	928	302	58	180	1162	1586
	C7		-0.28***				-0.44***				-0.40***		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

trapping session, *Zapus* avoids traps capturing *Microtus*. Even when the density of *Microtus* is high, such as on grids C and D in 1980, and the majority of traps were visited by *Microtus* (as indicated by the low sample size in the 'neither' category, Table 2), *Zapus* selected traps not visited by *Microtus*.

On grids C, D, and E over the entire study, *Microtus* was caught at all trap stations. However, on grid C, *Zapus* was caught only at 42 trap stations, on grid D at 34, and on grid E at 80. Koplin & Hoffmann's index of overlap was 71 for grid C, 67 for grid D, and 90 for grid E. We conclude that there was no indication that *Microtus* selected certain parts of the grids over others. There was also no indication that *Zapus* selected habitats that were different from those selected by *Microtus*. Figure 4 shows a typical example of the overlap in trap positions where both species were caught over four trapping sessions in May and June 1980. Thus, avoidance of *Microtus* by *Zapus* appears to be temporal rather than spatial.

FIG. 4. Spatial relationships of *M. pennsylvanicus* and *Z. hudsonius* caught on Removal Grid E (100 trap points: 10 × 10 pattern) during the period May–June 1980. Circles indicate trap points where rodents were captured. Numbers within circles indicate the number of captures.

Demographic responses to *Microtus* presence

If *Microtus* presence has negative effects on *Zapus*, we predict that this should be reflected in poorer survival, lower reproductive rates, and restricted movements of *Zapus*. However, variances of the demographic traits was high because samples were small and animals hard to trap. Hence, we limit ourselves to a discussion of three traits.

Transients are defined to be *Zapus* that were only caught once, while residents are defined as *Zapus* caught more than once. To allow comparison among all grids, we examined only the data from 1978 to 1980. Both sexes were pooled. The transiency rate ((number caught only once/total number caught) × 100) was 100% ($N = 10$) on grid A, 84% ($N = 32$) on D, 80% ($N = 10$) on B, 63% ($N = 87$) on E, and 62% ($N = 40$) on C and there was significant heterogeneity among them $\chi^2 = 10.85$, d.f. 4, $P < 0.05$. Thus, on grids with higher *Microtus* densities (Fig. 2), most *Zapus* were transient.

For those animals defined as residents, we calculated their expectation of life (Leslie *et al.* 1955). Table 3 shows that the expectation of life is generally above 15 weeks on grids B, C, D, and E, but the variation is so high that no definite pattern emerges.

TABLE 3. Expectation of life (weeks $\pm$ 1 SE) for all *Zapus hudsonius* caught more than once from 1978 to 1980 and defined as residents. Grid A is not included as no residents were caught. Sample sizes in parentheses

Grid	Males	Females
B	55.0 (1)	11.0 (1)
C	25.3 $\pm$ 6.6 (7)	24.0 $\pm$ 6.9 (8)
D	42.0 (1)	28.5 $\pm$ 10.6 (4)
E	18.3 $\pm$ 5.2 (15)	14.4 $\pm$ 3.8 (17)

Finally, we examined movements of *Zapus* within and between grids. Again, high variation within grids and low sample size resulted in no obvious within-grid movement patterns. However, of the twenty-five between-grid movements, seventeen were towards total-removal grid E and five were away from it. Grid E thus appeared to operate as a dispersal sink.

DISCUSSION

Any study attempting to assess the importance of competition in structuring small mammal communities with live-trapping methods presumes high trappability of all species. Unfortunately, for *Zapus hudsonius*, this criterion is usually not met. Blair (1940) found that individual *Z. hudsonius* disappeared from his trapping area and then reappeared. He attributed this to movement from the area. Quimby (1951) suggested a similar explanation for disappearances. Adler, Reich & Tamarin (1984), from a 5-year study in Massachusetts, reported a trappability of 84.5%, but this included all animals caught only once (44 of 55 mice) and is clearly a very pronounced overestimate (Krebs & Boonstra 1984). Morris (1984), from a 2-year study in southern Ontario, also caught most mice only once (a total of 30 captures of 26 mice). We also found most mice were caught only once (a total of 372 captures of 208 mice). Only Nichols & Conley (1982), from a 1-year study in Michigan, had higher trappabilities (a total of 372 captures of 88 mice), often exceeding 50%. However, even in their study trappability fluctuated enormously. For example, in the third week of May, sixteen mice were caught; one week later, only three were caught; and one week later, eleven were caught. We conclude that *Zapus hudsonius* is generally an untrappable species and that this poor trappability, not movement from the trapping area (we found only twenty-five between-grid movements), probably accounts for the 'disappearance' (Blair 1940) of individuals. However, some doubt does still remain which can ultimately only be resolved by techniques such as radiotelemetry.

Is the convincing evidence of competition between *Zapus hudsonius* and *Microtus* (Figs 2, 3) thus simply an artefact of poor trappability of *Zapus* and high trap occupancy by *Microtus*? We believe that this is not so. Even on control grid A, in virtually all checks within a trapping session, between 25 and 50 traps were empty, and *Zapus*, if present, could have entered these. In addition, numbers of *Microtus* on grid A were low at times (Fig. 2: midsummer 1979 and spring 1981) when there was no sudden increase in *Zapus* numbers, even though moderately high *Zapus* densities were present 60 m away on grid E. Over the entire 5-year study, only 10 different *Zapus hudsonius* were caught on A in comparison with 111 on E.

The other possible explanation for our results is that it is an artefact caused by habitat differences among grids. We reject this explanation as well. Grids A and E were most similar in habitat (Fig. 1), yet showed the greatest differences in *Zapus* densities (Figs 2,

3). Grid E did have trees in one corner, while A did not, but *Zapus* were seldom caught in this habitat. Grid C had no trees on or near it and was on the top of a slight hill and thus was drier than A or E, which both straddled the same seasonal stream, yet C had the second highest *Zapus* densities on the area. Thus, though habitat differences did occur among the grids, this was not a sufficient explanation to account for differences in *Zapus* densities.

Although the distribution of *Zapus* may not be limited by other species such as *Microtus* (Getz 1961; Whitaker 1963) our evidence indicates that abundance of *Zapus* is reduced by abundance of *Microtus*. The maximum densities of *Zapus* caught on total-removal grid E in spring (37.1 per ha in 1980 and 28.6 per ha in 1981) were substantially higher than those recorded in all other studies, except that of Nichols & Conley (1982) (24 per ha), whereas the maximum densities recorded on grids A and B (1.4–5.7 per ha) are similar to those reported in other studies (Blair (1940) 9.6 per ha; Quimby (1951) 6.9 per ha; Adler, Reich & Tamarin (1984) 3.1–7.5 per ha). Why Nichols & Conley (1982) found such high *Zapus* densities is not clear to us but they do report presence, though not the abundance, of *Microtus* on the grid. Porter & Dueser (1982), from an island study involving the capture of six small mammal species in different habitats, found a significant negative partial correlation coefficient (-0.19) between *Microtus pennsylvanicus* and *Zapus*. Adler, Reich & Tamarin (1984), from a live-trapping study, found that the two species tend to avoid one another in traps. In contrast, Morris (1983), from a live-trapping study in which he correlated species presence to micro- and macro-habitat differences, concludes that habitat, not species interactions, is probably the explanation for the distribution of any given species. We reject this conclusion. The crucial question is not how are the species distributed when other species are present, but how are they distributed in absence of the presumed competitor? Grant (1978) reviewed the experimental evidence for the role of competition in structuring small mammal communities, and it is clear that it plays a central role.

Although it is easy to understand why *Zapus* may compete with *Peromyscus* spp. (Nichols & Conley 1981) or with *Napeozapus insignis* (Miller) (Brower & Cade 1966) because of similar food and habitats, it is less obvious why *Zapus* competes with *Microtus*, since the former is essentially a granivore/insectivore and the latter is an herbivore. Perhaps direct interference competition may occur between them in the same manner as may occur between *M. townsendii* (Bachman) and *P. maniculatus* (Wagner) in grassland (Redfield, Krebs & Taitt 1977) or between *M. californicus* (Peale) and both *Mus musculus* and *Reithrodontomys megalotis* (Baird) (Blaustein 1980; Heske, Ostfeld & Lidicker 1984). In addition, by cropping the grasses and herbs, *Microtus* reduces the potential seedfall. Batzli & Pitelka (1970) found that high densities of *M. californicus* reduced seed-fall by 70%. Cranford (1978) reported that the prehibernation weight gain in *Z. princeps* (J. A. Allen) is directly tied to the presence of seeds in the diet and that an insufficient weight gain at this time may reduce over-winter survival, especially in juveniles (Cranford 1983). The crucial time for *Zapus* populations may therefore occur just prior to hibernation. Thus, *Microtus* may compete with *Zapus* directly by interference competition and indirectly by resource competition.

If interference competition is occurring, it should be as evident on grid E in 1980, when *Microtus* numbers ranged from 50 to 150, as it was on grid A, when numbers ranged from 200 to 300 (Fig. 2). We suggest that it is not evident because the important segment of the *Microtus* population is the resident segment, and on grid E there were virtually no residents (Fig. 3). We had hoped to be able to distinguish between the relative importance of male

and female resident *Microtus* from the selective removals from grids C and D. However, if such sex-specific effects do occur, they were too subtle to be detected by our design. The mechanism of this possible interference competition is unclear. It may operate primarily by direct behavioural aggression of the larger species towards the smaller, and perhaps secondarily by infanticide by *Microtus* when *Zapus* nestlings are found. However, infanticide by *Microtus* towards conspecifics appears uncommon (Caley & Boutin 1985; McShea 1985; I. T. M. Craine, personal communication) and thus this probably plays a very minor role.

Since *Zapus* is obviously the inferior competitor in comparison to *Microtus*, why does it not go extinct? Blaustein (1981), in a review of the theory of the non-equilibrium maintenance of two ecologically similar species, concludes that local extinctions of the superior competitor and asynchrony of extinctions on a regional scale may allow for the maintenance of the fugitive species through spatio-temporal heterogeneity. Blaustein (1980, 1981) found good evidence for this in California grasslands, with the distribution and abundance of *M. musculus* and *R. megalotis* being inversely related to that of *M. californicus*. Though *Microtus pennsylvanicus* does show 2- to 4-year cycles in population numbers (Krebs & Myers 1974; Tamarin 1977; Boonstra 1985), it is unclear how asynchronous these cycles are on a regional basis nor whether *Zapus* are mobile enough to detect and exploit pockets of low *Microtus* abundance. Because of its life-history traits (8-month hibernation, one or two litters per year (Whitaker 1972; Nichols & Conley 1982; Hoyle & Boonstra 1986), *Zapus* may be unable to respond numerically to massive declines in *Microtus*. The time-lags caused by *Zapus* life-history traits may be greater than the time it takes for *Microtus* to start increasing again. In our study, maximum spring densities were not reached on grid E until spring 1980, 2 years after the study started. The low initial densities of both species were probably the result of the regular mowing of the grass in the years prior to our study. We suggest that in more natural situations, since *Microtus* are seldom low for long after a decline, *Zapus* may be restricted to perennially low populations. The conclusions of our study could have been strengthened if we had stopped removing *Microtus* from grid E and monitored the response of *Zapus* to increasing vole densities. We were not permitted to because the landowners required the land. However, we suggest that if such an experiment were to be successful, a lag-time of up to a year might be required to verify the effect of the recolonization by voles.

Connell (1983) points out that few studies on interspecific competition try to tease out the importance of intraspecific competition. We also have not directly tried to assess the importance of intraspecific mechanisms in the population regulation of *Zapus*. However, it is clear that *Zapus* is able to exist at much higher densities in the absence of resident *Microtus* populations than in their presence (Fig. 2). Thus, intraspecific regulatory mechanisms are likely to play a minor role in the population ecology of this species. However, since virtually nothing is known of the social system of this rare but widespread species, a great deal more work needs to be done here.

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