Efficiency of pitfalls versus live traps in enumeration of populations of *Microtus pennsylvanicus*

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Two populations of *Microtus pennsylvanicus* were trapped simultaneously with Longworth live traps and pitfall traps over a 3- and a 4-year period. The number of voles enumerated by live traps was usually between 2 and 4 times that enumerated by pitfalls. Of the 3671 new voles caught, 53.7% were first caught in live traps. Pitfalls captured more of the juveniles first (56%) and live traps captured more of the adults first (76%). Animals entering live traps for the first time were about 4 g heavier than those entering pitfalls for the first time. The time lag between entry first into pitfalls and then to live traps was 4–6 weeks; the time lag between entry first in live traps and then to pitfalls was 2–7 weeks. Approximately 18% of all voles never entered live traps. Live traps captured about 83% ($N = 747$) of all dispersers whereas pitfalls captured about 46%. We conclude that live traps were much more effective than pitfalls in capturing this species. These results are very different from those reported from studies on *Microtus townsendii*.

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Deux populations de *Microtus pennsylvanicus* ont été échantillonnées simultanément au moyen de pièges Longworth et de pièges à fosses, durant des périodes de 3 et 4 ans. Le nombre de campagnols capturés aux pièges Longworth est ordinairement entre deux et quatre fois supérieur au nombre d'animaux capturés dans les pièges à fosses. Des 3671 campagnols capturés, 53,7% ont d'abord été capturés au piège Longworth. Les pièges à fosses ont capturé plus d'immatures d'abord (56%), alors que les autres pièges ont d'abord capturé plus d'adultes (76%). Les animaux qui pénétraient dans les pièges Longworth la première fois étaient plus lourds d'environ 4 g que les campagnols qui entraient dans les pièges à fosses pour la première fois. L'intervalle entre la première entrée dans les pièges à fosses et l'entrée dans les pièges Longworth a été de 4–6 semaines; l'intervalle entre la première entrée dans les pièges Longworth et l'entrée dans les pièges à fosses a été de 2–7 semaines. Environ 18% de tous les campagnols n'ont jamais pénétré dans les pièges Longworth. Les pièges Longworth ont capturé environ 83% ($N = 747$) de tous les campagnols en dispersion, alors que les pièges à fosses n'en ont capturé que 46%. Il faut conclure que les pièges Longworth ont été beaucoup plus efficaces que les pièges à fosses dans la capture de cette espèce. Il semble en être tout autrement pour *Microtus townsendii* si on en juge par les résultats de la littérature.

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Introduction

In population studies involving different species of the same genus, it is simplest to assume that all members of the genus will respond in a similar manner to a given trap type. Thus, one can use techniques found to be successful in one species to trap another. Pitfall traps were used successfully in population studies of *Microtus townsendii* (Boonstra and Krebs 1978; Beacham and Krebs 1980). Pitfall traps captured different segments of the population and many of these animals dispersed before they could be caught in live traps (Beacham and Krebs 1980). The population estimation techniques currently used with small mammals either assume equal catchability of all members of the population (e.g., Jolly 1965) or that virtually all animals can be caught and enumerated (Krebs 1966; Hilborn et al. 1976). Therefore, knowledge of the efficiency of trapping methods is essential for accurate evaluation of numbers. The purpose of this study was to compare the effectiveness of pitfall traps and Longworth live traps in capturing fluctuating populations of *Microtus pennsylvanicus*.

Methods and materials

The study was carried out on two control grids at two sites near Toronto, Ontario. One site, at Aurora, 30 km north of Toronto, consisted of control grid A and four other grids. It was located on a 10-ha parcel of rolling grassland that had previously been pasture and mowed regularly prior to the start of this study. A second site, located adjacent to Toronto International Airport, consisted of control grid F and up to four other grids. It was located on a 10-ha parcel of flat ground dominated by an old-field community.

Each control grid had 100 trap stations with a 7.62-m trap interval and was arranged in a 10 by 10 pattern. Longworth live traps were

placed at every station and baited with oats; cotton was provided for warmth. Both grids always had at least 150 traps, and grid F had up to 200 during periods of high density. The live traps on grid A were protected from the elements by snow tunnels (Pruitt 1959) because this area experienced deep snowfalls; on grid F, lower snowfalls allowed the use of lower snow shelters (Iverson and Turner 1969). One pitfall, similar in design to that described by Boonstra and Krebs (1978), was placed at each station. The pitfall trap consisted of a watertight can (30 cm deep by 15 cm diameter) with a wooden cover.

During the main breeding season, live traps were set every 2nd week on Wednesday afternoon, checked Thursday morning and afternoon, and again on Friday morning, when they were locked open. In summer, live traps were set only in the evenings to avoid mortality during the heat of the day. Grid A was live trapped from 26 June 1978 to 28 May 1982 and grid F from 4 July 1978 to 21 May 1982, though only the information from grid F from the spring of 1979 onwards is presented as pitfall traps were not present until that time.

Pitfall traps were set at the same time as live traps. On grid A, they were used from July through November 1978, June through mid-November 1979, June through mid-December 1980, and late May through mid-November 1981. On grid F, they were used from late May through November 1979, late May through October 1980, and May through October 1981. Pitfalls were not trapped throughout the winter because few animals were caught when we did trap after a fresh snowfall and because snow made handling these traps very difficult. When the pitfalls were set, they were cleaned out and oats and cotton were supplied. When they were closed, the pitfalls were prebaited with oats.

All voles were ear-tagged, and on each capture the following were recorded: tag number, trap location, trap type, body weight, sex, and sexual condition. Animals were classified as follows (Boonstra and Rodd 1983): adults (>33 g), subadults (22–33 g), and juveniles (<22 g).

Population variables were determined by enumeration (Krebs 1966) to allow comparison with the work of Boonstra and Krebs (1978) and Beacham and Krebs (1980). This method requires that a large proportion of the individuals in the population be caught. To estimate trappability, we used the formula given in Boonstra and Krebs (1978). This formula provides a minimum estimate of trappability since it excludes the first and last captures of an animal. Thus, animals caught only once or twice in consecutive trapping sessions were excluded. The trappability estimates for each of the two types of traps were calculated independently. Thus, animals known to be present from capture in pitfalls but not live traps were not included in the estimate of trappability of animals captured in live traps. Trappability estimates were only calculated for the period when both trap types were operating.

Results

Trappability

Trappability of males in live traps was similar on both grids, averaging 52% ($N = 526$; range, 51–77%) on grid A over four summers and 59% ($N = 477$; range, 55–67%) on grid F over three summers. Trappability of males in pitfall traps was substantially lower, averaging 16% ($N = 74$; range, 7–20%) on grid A and 10% ($N = 107$; range, 5–16%) on grid F. Trappability of females in live traps was also similar on both grids, averaging 62% ($N = 688$; range, 55–64%) on grid A and 66% ($N = 557$; range, 64–74%) on grid F. Trappability of females in pitfall traps was substantially lower, averaging 18% ($N = 146$; range, 6–21%) on grid A and 12% ($N = 90$; range, 8–14%) on grid F. Thus animals were between 3 and 10 times less trappable in pitfall traps than in live traps.

Population density

We calculated the minimum number of animals known to be alive from live traps, from pitfall traps, or from both trap types combined. Pitfall traps on grid A usually enumerated between 20 and 40% of the total number of animals known to be alive (Fig. 1). However, there were periods, such as in the late fall of each year, when pitfalls only enumerated between 2 and 10% of the total population. In contrast, live traps usually enumerated between 80 and 90% of the total population. The lowest percent enumerated was 68% on 15 June 1979. The total population was followed more accurately by live traps ($r = 0.98$, $N = 52$) than by pitfall traps ($r = 0.66$).

Pitfall traps on grid F usually enumerated between 15 and 35% of the total number of animals known to be alive (Fig. 2). However, there were periods, such as in the spring of 1980 when the pitfall traps enumerated up to 48% of the total population. This coincided with the entry into the population of large numbers of young animals. Throughout the summer and fall of 1981, when few young entered the population, only between 6 and 18% of the total population was enumerated by pitfall traps. Live traps usually enumerated between 80 and 90% of the total population. The lowest percent enumerated was 68% on 6 June 1980. The total population was again followed more accurately by live traps ($r = 0.98$, $N = 39$) than by pitfall traps ($r = 0.61$). Thus, live traps on both grids gave a much better picture of population numbers and of population change than did pitfall traps.

First capture in live traps and pitfall traps

We compared the distribution of first captures in the two trap types. Only that time period when both trap types were operating was examined. However, an individual first caught in a pitfall trap could be subsequently caught in a live trap at any time during the study. Similarly, the converse could

occur. Of the 3671 new voles caught, 46.3% ($N = 1698$) were first caught in pitfall traps and 53.7% ($N = 1973$) were first caught in live traps. Of the voles first caught in pitfall traps, 38.8% did not enter live traps (35.6% ($N = 1108$) of the juveniles, 45.7% ($N = 481$) of the subadults, and 41.3% ($N = 109$) of the adults). Of the voles first caught in live traps, 72.3% did not enter pitfall traps (63.1% ($N = 866$) of the juveniles, 78.1% ($N = 754$) of the subadults, and 82.4% ($N = 353$) of the adults). Of the 1974 juveniles first caught, 56% were first caught by pitfalls. In contrast, pitfalls captured only 40% of the 1235 new subadults first and only 24% of the 462 new adults first ($\chi^2 = 199.4$, $df = 2$, $P < 0.001$). Thus, live traps have a higher probability of capturing an animal first and of subsequently capturing an animal after first capture in pitfall traps. Of all animals caught in either pitfalls or live traps, similar proportions of males and females in the three age-classes entered these traps ($\chi^2 = 3.2$, $df = 2$, NS (not significant) and $\chi^2 = 3.8$, $df = 2$, NS, respectively).

Body weights

We calculated the mean weight at first capture in each trap type, regardless of whether they had already been caught in the other trap type. For example, an animal would be included first when it was captured in a pitfall trap and again when it was captured in a live trap. Males were about 4 g heavier and females 3 g heavier when first captured in live traps than when first captured in pitfall traps (Table 1).

Time lags of entry into traps

The difference in first capture weight in the two trap types suggests that animals enter live traps at an older age. For all animals that entered both trap types, we calculated how long it took for voles first caught in one trap type to enter the other. Because both traps were being operated simultaneously, it was possible for an animal to be caught in both traps in one trapping session since there were three checks, and therefore the time lag would have been 0 weeks. For all classes of females and for all juvenile and subadult males, an average of about 4 weeks elapsed between first capture in pitfalls and subsequent capture in live traps (Table 2). Adult males averaged about 2 weeks longer to enter live traps. Over 70% of all classes entered live traps within 4 weeks and amongst juveniles this rose to 80%. Generally the heavier an animal was at first capture in a pitfall, the longer it took to enter a live trap (adult females were the exception). Over 40% of the juveniles, first caught in pitfalls, entered the live traps while still juveniles, whereas only about 10% waited until they were adults. Over 70% of the subadults, first caught in pitfalls, entered live traps while still subadults. There was no difference between the sexes in either the adult or juvenile class in the proportion that entered live traps at various stages. However, significantly fewer subadult males (45.6%, $N = 259$) entered live traps subsequently than did subadult females (64.4%, $N = 222$) ($\chi^2 = 16.4$, $df = 1$, $P < 0.001$). The maximum interval recorded between first capture in a pitfall and subsequent capture in a live trap was 38 weeks for a male first caught as a juvenile. Thus, in general there was not a long lag between first capture in pitfalls and then in live traps.

We also examined how long it took for voles first captured in live traps to enter pitfall traps (Table 3). Since pitfall traps were in operation for only part of the year, some voles captured in live traps in one season when both trap types were being used waited until the next year to be caught in pitfalls. Juvenile males took only 2 weeks to enter pitfalls and juvenile females

FIG. 1. Population density of *Microtus pennsylvanicus* on control grid A. Minimum number alive (MNA) is given for the population known to have entered live traps, for those known to have entered pitfalls, and for those known to have entered one or both trap types. Nonbreeding seasons are shaded.

took about 4 weeks. Adult males took 4 weeks and adult females took about 7 weeks. Over 70% of all classes, except adult females, entered pitfalls within 4 weeks and among juveniles this rose to 85%. Generally the heavier an animal was, the longer it took to enter a pitfall trap. About 60% of the juvenile males entered a pitfall while still a juvenile, whereas only 47% of the juvenile females did so. About 70% of the subadult males entered pitfalls as subadults, whereas only 46% of the subadult females did so. In general, of those voles that entered pitfalls, males did so sooner than females. The maximum interval between first capture in a live trap and subsequent capture in a pitfall was 64 weeks for a female first caught as a juvenile. Thus, in general voles first caught in live traps took as long to enter pitfalls as did voles first caught in pitfalls to enter live traps.

In this study, 659 voles were caught only in pitfall traps and over 90% of these were caught only once (Table 4). This number represents about 18% of all animals caught and thus was a substantial proportion of the population about which nothing would be known if enumeration had only been by live traps. Among the three size classes, 20.0% of the juveniles, 17.8% of the subadults, and 9.7% of the adults failed to enter

live traps. The maximum length of time an animal was known to be alive from captures only in pitfall traps was 12 weeks for a subadult male.

Dispersal

In both areas, other grids were being trapped at the same time as the grids with the two trap types. At Aurora, there was one total-removal grid, two partial-removal grids, and an intact grid, all of which were trapped until October 1980. Thereafter, only the total-removal grid was operating. At the airport, there were at times up to four partial-removal grids operating, and, except for the period from July to October 1981, at least two grids operating. Thus, we could identify some of the voles dispersing from the control populations and whether they had been caught in live traps, pitfall traps, or both. About 15% of all male dispersers and 22% of all female dispersers were caught only in pitfall traps before they dispersed (Table 5). In contrast, 57% of all male dispersers and about 50% of all female dispersers were caught only in live traps before they dispersed. If only pitfall traps had been used, they would have captured 46% of all dispersing voles. If only live traps had been used, they would have captured 83% of all dispersing voles.

FIG. 2. Population density of *Microtus pennsylvanicus* on control grid F. Minimum number alive (MNA) is given for the population known to have entered live traps, for those known to have entered pitfall traps, and for those known to have entered one or both types of traps. Nonbreeding seasons are shaded.

TABLE 1. Mean weight at first capture ($\pm$ SE) of *Microtus pennsylvanicus* in live traps and pitfall traps for two populations

Grid	Males		Females	
	Live traps	Pitfall traps	Live traps	Pitfall traps
A	24.4 $\pm$ 0.5 (978)	21.4 $\pm$ 0.6 (726)	24.9 $\pm$ 0.6 (915)	22.6 $\pm$ 0.7 (712)
F	26.8 $\pm$ 0.9 (570)	21.6 $\pm$ 0.9 (416)	25.0 $\pm$ 0.7 (576)	20.7 $\pm$ 0.8 (417)
Total	25.2 $\pm$ 0.7 (1548)	21.5 $\pm$ 0.7 (1142)	24.9 $\pm$ 0.6 (1491)	21.9 $\pm$ 0.7 (1129)

NOTE: Data for each grid are pooled over the entire study. Sample sizes are in parentheses.

Thus, live traps were effective at enumerating most animals before they dispersed elsewhere, whereas pitfall traps were only half as effective.

Discussion

Since three studies have now been carried out with the use of similar pitfall traps and Longworth live traps, two on

Microtus townsendii (Boonstra and Krebs 1978; Beacham and Krebs 1980) and one on *M. pennsylvanicus* (present study), it is useful to compare the efficiencies of these traps. Table 6 summarizes the major parameters. The response of *M. townsendii* is similar in both studies and that of *M. pennsylvanicus* is markedly different. In general, pitfalls were much less effective in capturing voles in our study: the trappability of *M. pennsylvanicus* in pitfalls was about half what it was in *M. townsendii*; pitfalls generally caught less than half of the total population in *M. pennsylvanicus* whereas in *M. townsendii* they caught over 70%; pitfalls caught about half as many new animals in *M. pennsylvanicus* as they did in *M. townsendii*; pitfalls caught about half as many of the animals that subsequently dispersed in *M. pennsylvanicus* than they did in *M. townsendii*. In contrast, although the overall trappability in live traps was much the same in the three studies, live traps tended to catch all segments of the *M. pennsylvanicus* population, to catch more of the new animals in the population, and to catch them at a younger age (lower weight differences and shorter time lags) than live traps had in studies on *M. townsendii*.

What were the reasons for these differences in the performance of the two traps in the two species? The first possible

TABLE 2. Percentage distribution by size class of intervals between first capture in pitfall traps and first capture in live traps for *Microtus pennsylvanicus*

	Males			Females		
	Juveniles	Subadults	Adults	Juveniles	Subadults	Adults
Duration (weeks)						
0-4	80.7	73.7	70.0	79.8	77.6	73.5
5-8	7.4	11.0	13.3	10.6	10.5	17.6
9-12	5.0	5.1	3.3	4.8	6.3	2.9
13-16	2.7	4.2	3.3	2.1	0.7	5.9
>16	4.2	5.9	10.1	2.7	4.9	0.0
Average interval ($\pm$ SE)	3.9 $\pm$ 0.3	4.7 $\pm$ 0.6	6.1 $\pm$ 1.6	3.8 $\pm$ 0.3	4.1 $\pm$ 0.5	3.6 $\pm$ 0.7
Sample size	337	118	30	377	143	34
% entering live traps as:						
Juveniles	44.5			41.9		
Subadults	45.4	76.3		48.3	72.0	
Adults	10.1	23.7	100.0	9.8	28.0	100.0

NOTE: Classification used is size at first capture in pitfall traps. Both grids and all years are combined.

TABLE 3. Percentage distribution by size class of intervals between first capture in live traps and first capture in pitfall traps for *Microtus pennsylvanicus*

	Males			Females		
	Juveniles	Subadults	Adults	Juveniles	Subadults	Adults
Duration (weeks)						
0-4	90.4	79.2	75.8	86.2	71.6	51.7
5-8	5.2	9.1	9.1	7.9	12.5	17.2
9-12	1.2	1.3	12.1	1.3	3.4	20.7
13-16	1.8	1.3	3.0	1.3	3.4	3.4
>16	1.2	9.1	0.0	3.3	9.1	6.9
Average interval ($\pm$ SE)	2.2 $\pm$ 0.3	4.9 $\pm$ 1.0	4.0 $\pm$ 0.7	3.8 $\pm$ 0.8	6.0 $\pm$ 1.1	7.4 $\pm$ 1.7
Sample size	167	77	33	152	88	29
% entering pitfall traps as:						
Juveniles	59.9			46.7		
Subadults	30.5	70.1		32.2	45.5	
Adults	9.6	29.9	100.0	21.1	54.5	100.0

NOTE: Classification used is size at first capture in live traps. Both grids and all years are combined.

TABLE 4. Percentage distribution by size class of interval between first and last pitfall captures of *Microtus pennsylvanicus* caught only in pitfall traps

Duration (weeks)	Males			Females		
	Juveniles	Subadults	Adults	Juveniles	Subadults	Adults
Grid A						
0	84.5	95.6	100.0	93.4	94.8	93.3
1-4	14.8	2.6	0.0	5.1	3.4	6.7
5-8	0.7	0.9	0.0	1.5	1.7	0.0
>8	0.0	0.9	0.0	0.0	0.0	0.0
Sample size	142	114	18	137	58	15
Grid F						
0	81.4	92.6	100.0	89.3	100.0	80.0
1-4	16.9	3.7	0.0	8.9	0.0	20.0
5-8	1.7	3.7	0.0	0.0	0.0	0.0
>8	0.0	0.0	0.0	1.8	0.0	0.0
Sample size	59	27	7	56	21	5

NOTE: Data from all years for each grid are combined.

reason was that the studies were not identical in the way trapping was conducted. In both the studies of Boonstra and Krebs (1978) and Beacham and Krebs (1980), trapping with pitfalls occurred every week while that with live traps occurred every 2nd week, and pitfalls and live traps were trapped con-

currently. In our study, trapping occurred only every 2nd week, and both traps were operated simultaneously. Thus, in our study the two traps were competing for the same pool of animals while this did not occur in the previous two studies. We trapped in this fashion both for logistic reasons (time and effort

TABLE 5. Comparison of the efficiency of live traps and pitfall traps in capturing *Microtus pennsylvanicus* before they disperse to other trapping grids

	Grid A		Grid F	
	Males	Females	Males	Females
Total no. of tagged dispersers caught	304	173	175	95
% caught only in pitfall traps	15.1	23.7	13.7	18.9
% caught only in live traps	55.6	53.8	58.3	44.2
% caught only in pitfall traps plus those caught in both trap types	44.4	46.2	41.7	55.8
% caught only in live traps plus those caught in both trap types	84.9	76.3	86.3	81.1

NOTE: Data are pooled over the entire study for grid A and from the spring of 1979 onwards for grid F.

TABLE 6. Comparison of the efficiency of capture of live traps and pitfall traps in *Microtus townsendii* from the studies of Boonstra and Krebs (1978) and Beacham and Krebs (1980) and in *M. pennsylvanicus* from the present study

Parameter	Study		
	Boonstra and Krebs (1978)	Beacham and Krebs (1980)	Present study
Trappability ^a in:			
Pitfalls	27	30 (28–35)	14 (5–21)
Live traps	53	64 (61–65)	60 (56–70)
% of total population enumerated at the height of the breeding season in:			
Pitfalls	80	70–100	6–48
Live traps	37	39–50	68–90
% of new animals caught in live traps that had previously been caught in pitfall traps	77	82	34
% of all new animals first caught in pitfall traps	89	89	46
% of new animals caught in pitfall traps failing to enter live traps	46	40	18
% of new pitfall animals caught only in pitfalls once	51	59	91
Weight difference (g) between entry into live traps and pitfall traps	10	12–15	4
Time lag (weeks) between entry first into pitfalls and then into live traps	5–9	5.1–9.3	3.6–6.1
% of juveniles first caught in pitfall traps that were still juveniles when caught in live traps	7	16	43
% of dispersers caught in:			
Pitfalls	—	90	46
Live traps	—	60	83

^aMean percentages, range in parentheses.

involved were more than halved) and because previous work had suggested that pitfalls captured primarily the young and subordinate animals which were not readily caught by live traps (Boonstra and Krebs 1978; Beacham and Krebs 1980). These two classes of animals had also been found by other workers in other species (Kikkawa 1964; Gliwicz 1970; Andrezjewski and Rajska 1972; Summerlin and Wolfe 1973; Joule and Cameron 1974). Thus, by using both traps at once, we believed that we would be sampling two segments of the population that did not overlap a great deal in their response to the two trap types.

However, this dichotomy in behavior between the younger and older animals was much less evident in *M. pennsylvanicus*. The younger animals (presumably the socially subordinate) entered the live traps much more readily than did young *M. townsendii*. This was indicated by the low weight difference between entry into the two trap types (Table 1), the large percentage of young juveniles and subadults that entered live traps while still in the same age category as when first caught in pitfalls (Table 2), and the short lag times between entry into the two trap types. Hence, some competition probably occurred between the two

trap types when animals were young. However, when the animals reached the adult class, this competition was of little importance: most entered only live traps. This was particularly obvious in the 1981 spring and summer on grid F (Fig. 2) when few juveniles were caught and only between 6 and 18% of the total population was known to be alive from captures in pitfalls.

The second possible reason was that our pitfall was only 30 cm deep compared with 43 cm deep in the studies of Boonstra and Krebs (1978) and Beacham and Krebs (1980). It is possible that some of the larger *M. pennsylvanicus*, which is about 10–15 g smaller than *M. townsendii*, were able to jump out of the pitfall. We do not think this was a serious problem because we never saw an animal jump out of a pitfall as we started to try to remove it.

Dispersal has been shown to play a major role in the regulation of microtine populations (see Gaines and McClenaghan (1980) for a review). The standard technique has been to measure emigration from intact populations into dispersal sinks (vacant areas) (Myers and Krebs 1971; Krebs et al. 1976; Tamarin 1977; Beacham 1980; Baird and Birney 1982). An alternate technique had been to measure immigration into a population by assuming that new young animals are born on the area, but that new adult animals are born elsewhere and are thus immigrants. Hilborn and Krebs (1976) and Redfield et al. (1978) made this assumption in *M. townsendii*, but Beacham and Krebs (1980) showed that this assumption was clearly violated as over half of the new voles caught in live traps in fenced populations were already adults. Dueser et al. (1981) made the assumption in *M. pennsylvanicus* that all new voles caught at <30 g were residents while all new voles ≥ 30 g were dispersers. We evaluated this assumption by calculating the percentage of new animals caught in pitfalls at <30 g that were ≥ 30 g when they first entered live traps. On grids A and F, 22.2 ($N = 568$) and 27.4% ($N = 372$), respectively, were in this category and their mean weights on entry into live traps were 34.6 (SE = 0.41) and 35.6 g (SE = 0.63), respectively. The maximum weight difference between entry into the two traps was 33 g for a 47-g male on grid A and 51 g for a 66-g male on grid F. Thus, approximately one-quarter of the animals entering live traps would have been classed as "dispersers" yet they were known to be present on the grid below the critical disperser weight. This result suggests that the zone of overlap between the size of residents and dispersers is larger than Dueser et al. (1981) proposed and thus their conclusions may be in error.

Through the use of a simulation model, Hilborn et al. (1976) demonstrated that the complete enumeration technique may provide accurate population estimates when trappability is high. We obtained trappabilities of approximately 60% in live traps during most summers and the model predicts an underestimate of the population of about 12–15%. For most of the study on both grids, this estimate is similar to the actual underestimate relative to the total population (Figs. 1 and 2). However, in some periods when large numbers of young were entering the population, the live traps underestimated by as much as 30%. We obtained trappabilities of about 10–15% in pitfalls in most summers and the model predicts an underestimate of 50–75%. Again, for most of the study, this estimate is similar to that obtained (Figs. 1 and 2). Thus, in comparison with the studies on *M. townsendii* (Boonstra and Krebs 1978; Beacham and Krebs 1980) in which the model performed poorly in predicting the underestimate of the true population

size, it performed much better in this study.

In conclusion, live traps were much more effective than pitfalls in enumerating *M. pennsylvanicus*. However, pitfalls did capture a large proportion of the total number of animals caught (18%) which were not captured by live traps and thus the use of pitfall traps did contribute to a more complete understanding of the population. The very pronounced difference in response by *M. pennsylvanicus* to the two trap types in comparison with *M. townsendii* suggests that each species, even within the same genus, must be studied separately to determine the most effective trapping scheme. The simplifying assumption that the same species in different geographical areas show similar responses to the same trap types may also be called into question. However, it is clear that populations of the same species near to each other geographically do respond similarly to the same trap types (e.g., two populations of *M. townsendii* (Boonstra and Krebs 1978; Beacham and Krebs 1980) and two populations of *M. pennsylvanicus* (our study)).

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