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PITFALL VERSUS LIVE-TRAP ENUMERATION OF FLUCTUATING POPULATIONS OF *MICROTUS TOWNSENDII*

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ABSTRACT.—Four populations of *Microtus townsendii* were trapped concurrently with live-traps and pitfall traps from May 1976 until June 1978. The number of voles enumerated by pitfall traps in both increasing and peak populations was up to two times larger than the number enumerated by live-traps. Pitfall traps generally caught voles under 40 g, live-traps over 40 g. About 45% of 3,677 voles captured first by pitfall traps were never caught by live-traps. Among those voles subsequently entering live-traps, over 50% stayed away for more than 5 weeks, and 10% stayed away for more than 20 weeks. Pitfall traps previously caught more animals that dispersed than did live-traps. An index of juvenile survival based on data derived from live-traps may not be indicative of actual trends. Voles caught only in pitfall traps have faster growth rates than those first caught in pitfall traps and later in live-traps. Live-traps and pitfall traps sample different segments of the population with respect to size, wounding levels, and parasite loads.

Longworth live-traps and pitfall traps sample different segments of a microtine population (Boonstra and Krebs, 1978). Pitfall traps tend to catch younger animals than those caught in live-traps. Many individuals caught by pitfall traps fail to enter live-traps, whereas others may take several weeks to be recruited to live-traps (Boonstra and Krebs, 1978). Direct enumeration of microtine population size (Krebs, 1966; Hilborn et al., 1976) assumes that virtually all individuals are caught. The primary purpose of this study was to determine if live-traps enumerate all the individuals known to be present in the population at both high and low densities. A second purpose was to examine the characteristics of animals caught by both types of traps in order to determine why some individuals fail to be recruited to live-traps and to determine whether the two trap types sample different segments of the adult population.

MATERIALS AND METHODS

The study area was part of a Timothy hay field owned by the Canadian Wildlife Service on Reifel Island in the Fraser River delta near Vancouver, British Columbia. *Phleum pratense* was the dominant vegetation; *Agrostis alba*, *Lolium perenne*, and *Holcus lanatus* were also present.

Four populations of *Microtus townsendii* were live-trapped from May 1976 until June 1978. Populations B and C were enclosed by vole-proof fences, and populations A and D were unfenced controls. Each grid had 49 trap stations set 7.6 m apart in a 7 by 7 pattern. Each station had two Longworth live-traps and one pitfall trap similar to the type described by Boonstra and Krebs (1978). The live-traps, baited with oats and supplied with cotton, were set every second week on Monday afternoon, checked Tuesday morning and afternoon, and checked and locked open on Wednesday morning.

Pitfall traps, used from May through October 1976, April through September 1977, and April through June 1978, were set on Wednesday mornings, checked Wednesday afternoons and Thursday mornings, and closed on Thursday afternoons. During the months between these periods, the pitfall traps could not be used because of winter flooding. When traps of both types were set in one week, the pitfall traps were set after the live-traps had been locked open.

All voles were ear-tagged, and on each capture, tag number, weight, capture location, sex, reproductive condition, and number of wounds were recorded. All voles were released immediately after being processed. Voles were classified as follows: adult > 42 g; subadult 30–42 g, juvenile < 30 g (Boonstra, 1978; Boonstra and Krebs, 1977).

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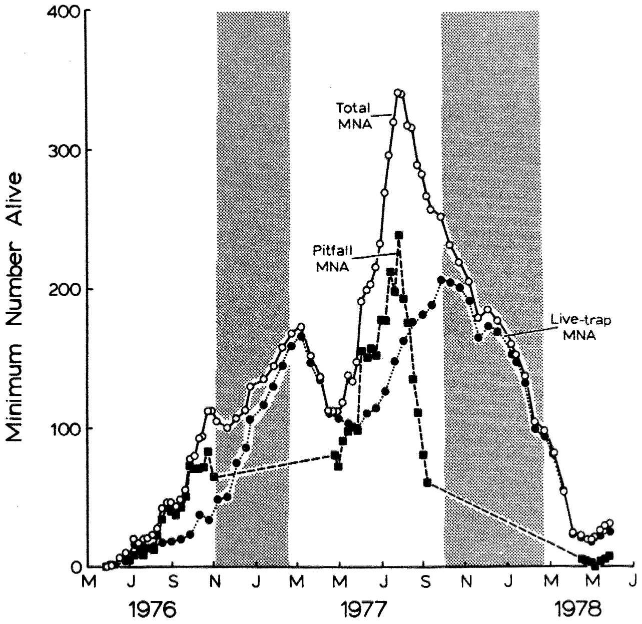

FIG. 1. Population density of *Microtus townsendii* on control grid A. Minimum number alive (MNA) is given for the population known to have entered live-traps, for those known to have entered pitfall traps, and for those known to have entered one or both types of traps. Nonbreeding periods are shaded.

Voles crossing a strip of mowed grass 18.3 m wide inside each enclosure were defined as dispersers. It was assumed that untagged voles caught in disperser traps inside an enclosure had been born on the grid and were therefore untagged dispersers. Dispersing voles were removed from the grids.

The total enumeration technique of Krebs (1966) was used in the determination of demographic data. The estimate of trappability used was:

$$\text{Trappability} = \sum^{N}\left(\frac{\dfrac{\text{number of captures for a vole}}{\text{number of possible captures for that vole}}}{N}\right)$$

where N is the number of voles caught more than twice. The first and last times of capture are excluded in the summation, because a vole is necessarily caught at these times.

RESULTS

Trappability.—Trappability estimates for live-traps and pitfall traps were calculated separately. For example, individuals known to be present from capture in pitfall traps but not in live-traps were not included in the trappability estimates for live-traps. Trappabilities of males and females in live-traps were similar and relatively constant from summer 1976 until spring 1978. In the summer of 1976, trappability was 61% for 324 animals. In the summer of 1977, it was 65% for 1,692 animals. During the low densities of spring 1978, male trappability increased to 95% for 96 animals and female trappability to 81% for 155 animals.

Males and females had similar trappabilities in pitfall traps. During summer 1976 it was 35% for 727 animals; in summer 1977 it was 28% for 1,726 animals. Trappability

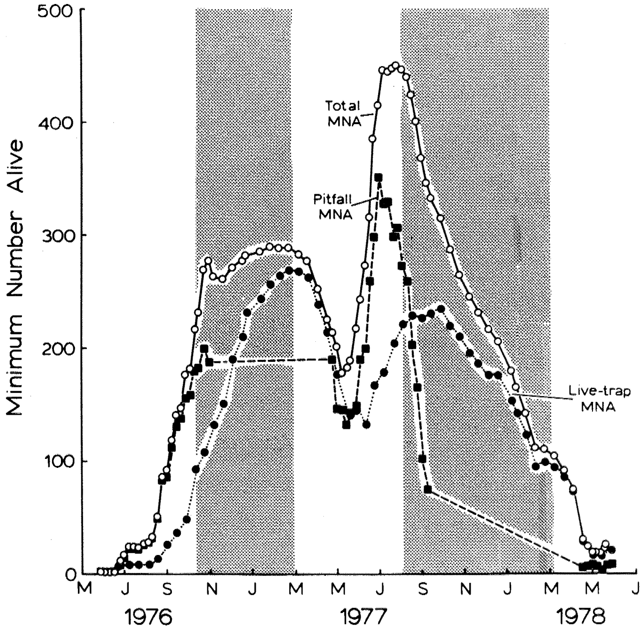

FIG. 2. Population density of *Microtus townsendii* on fenced grid B. Minimum number alive (MNA) is given for the population known to have entered live-traps, for those known to have entered pitfall traps, and for those known to have entered one or both types of traps. Nonbreeding periods are shaded.

could not be calculated for spring 1978 because no animal was captured more than twice. Pitfall traps were only about one-half as effective as live-traps in repeated captures of voles.

Population density.—Densities of the vole populations were low when trapping began in May 1976 but increased during the summer (Figs. 1 and 2). During this period the pitfall population estimates were similar to the combined live-trap and pitfall estimates, which indicates that the pitfall traps were capturing on both fenced and unfenced grids practically all of the voles known to be alive. The live-trap estimates were approximately one-half the magnitude of either the pitfall or combined live-trap and pitfall estimates. Live-trap population estimates steadily increased throughout the 1976 winter, when the populations were not breeding. Thus there was a considerable lag in recruitment of young voles to the live-traps during this time. Figs. 1 and 2 indicate that populations declined in the spring of 1977. By this time the live-trap population estimates were similar to the combined live-trap and pitfall estimates, which indicates that by spring 1977 live-traps were enumerating most of the voles known to be alive.

The pitfall population estimates increased rapidly during early summer 1977 at a rate of about 15% per week compared with a 4% per week increase in the live-trap populations. The pattern of 1976 repeated itself in the early summer of 1977. The pitfall population estimates were again similar to the combined live-trap and pitfall estimates, whereas live-traps enumerated approximately one-half of the voles known to be alive. With the tapering off of reproduction during the late summer of 1977, the pitfall population declined at about 20% per week while the live-trap population was relatively stable. There was again a considerable time lag in recruitment to live-traps,

TABLE 1.—*Mean weight (g) at first capture (±1 SE) of* Microtus townsendii *in live-traps and pitfall traps for four populations. Data for each grid are pooled over the entire study. Sample sizes are in parentheses.*

Grid	Live traps		Pitfall traps	
	Males	Females	Males	Females
A	48.8 ± 0.5 (378)	42.6 ± 0.4 (386)	35.1 ± 0.8 (426)	32.4 ± 0.7 (424)
B	46.7 ± 0.4 (480)	42.8 ± 0.3 (414)	29.1 ± 0.3 (661)	29.1 ± 0.4 (593)
C	45.2 ± 0.5 (391)	39.8 ± 0.3 (402)	29.1 ± 0.5 (530)	25.8 ± 0.4 (545)
D	49.0 ± 0.4 (459)	44.9 ± 0.4 (396)	36.1 ± 0.5 (568)	36.9 ± 0.7 (516)
Total	47.4 ± 0.5 (1,708)	42.5 ± 0.3 (1,598)	32.1 ± 0.6 (2,185)	30.8 ± 0.5 (2,078)

but by spring 1978 the live-traps were enumerating most of the animals known to be alive.

First capture of voles in live traps and pitfall traps.—We compared the distributions of initial vole captures in live-traps and pitfall traps. This comparison included only the time when traps of both types were used concurrently. Initial captures in live-traps during the winter when pitfall traps were not operating were excluded from this analysis. An individual first caught in pitfall traps could be recruited to live-traps at any time during the study.

Approximately 3,700 voles were first caught in pitfall traps and about 450 were first caught in live-traps. About 45% of the voles first caught in pitfall traps did not enter live-traps. In the unfenced control populations, into which immigration was possible, 50% of the adult males first caught in pitfall traps were not caught in live-traps, whereas 43% of adult females were not caught in live-traps. In the fenced populations 46%

TABLE 2.—*Percentage distribution by size class of interval between first capture in pitfall traps and first capture in live-traps for* Microtus townsendii. *Classification used is size at first capture in pitfall traps. All grids and years are combined.*

Parameters	Males			Females		
	Juvenile	Subadult	Adult	Juvenile	Subadult	Adult
Duration (weeks)						
1–5	43.3	47.5	54.8	44.5	48.1	71.3
6–10	22.7	20.9	25.4	24.6	23.7	18.2
11–15	15.0	16.3	10.2	11.6	13.4	7.0
16–20	9.1	6.0	3.4	7.0	5.3	2.1
>20	9.9	9.3	6.2	12.3	9.5	1.4
Average interval (±2 SE)	9.2 ± 1.3	8.6 ± 1.1	7.1 ± 1.2	9.3 ± 1.7	8.8 ± 3.7	5.1 ± 1.2
Sample size	559	282	177	588	283	144
Percent entering live-traps as:						
Juveniles	15.0			17.6		
Subadults	31.3	28.1		43.4	39.6	
Adults	53.7	71.9	100.0	39.0	60.4	100.0

TABLE 3.—*Percentage distribution by size class of interval between first and last pitfall captures of* Microtus townsendii *caught only in pitfall traps. Data from 1976 and 1977 are combined. Sample sizes are in parentheses.*

Duration (weeks)	Males			Females		
	Juvenile	Subadult	Adult	Juvenile	Subadult	Adult
			Control populations			
0	62.4	67.2	69.0	54.0	66.7	66.7
1–5	29.6	31.1	27.4	35.1	25.3	30.1
6–10	7.5	1.7	2.7	9.8	8.0	1.6
>10	0.5	0.0	0.9	1.1	0.0	1.6
	(199)	(119)	(113)	(174)	(99)	(63)
			Experimental populations			
0	47.6	55.5	62.4	56.1	68.8	71.4
1–5	43.1	34.3	30.4	33.8	23.9	23.8
6–10	7.8	7.3	5.4	8.4	7.3	0.0
>10	1.5	2.9	1.8	1.7	0.0	4.8
	(267)	(137)	(56)	(287)	(109)	(21)

of the adult males and 26% of the adult females were not caught in live-traps. When the data are pooled over all size and sex classes, a greater proportion of animals in the unfenced control populations failed to enter live-traps than in the fenced experimental populations ($\chi^2 = 12.78$, 1 d.f., $P < 0.01$).

Approximately 40% of 447 animals first caught in live-traps during the spring to fall period in each year were not trapped in pitfall traps. However, pitfall traps have a higher probability than live-traps of capturing a vole for the first time. Of 435 first-caught adult males, pitfall traps accounted for 80%, and of the 289 first-caught adult females, pitfalls accounted for 79%. The results were even more striking for the juvenile class, in which 94% of 2,213 first-caught individuals were captured in pitfall traps. After voles entered the trappable population, pitfall traps were able to catch them earlier than live-traps.

Body weight differences at first capture in live-traps and pitfall traps.—Table 1 shows the mean body weights of male and female *Microtus townsendii* at first capture in live-traps and pitfall traps. These means include weights of all individuals at first capture in one type of trap, regardless of whether or not they had already been caught

TABLE 4.—*Number of dispersing* Microtus townsendii *caught in live-traps and pitfall traps. Data are pooled over the entire study.*

Disperser category	Grid B		Grid C	
	Males	Females	Males	Females
Tagged dispersers caught previously by live-traps	120	84	61	40
Tagged dispersers not caught by live-traps	83	92	44	35
Tagged dispersers caught previously by pitfall traps	179	169	96	70
Tagged dispersers not caught by pitfall traps	24	7	9	5
Total tagged dispersers	203	176	105	75
Percent tagged dispersers caught by live-traps	59	48	58	53
Percent tagged dispersers caught by pitfall traps	88	96	91	93
Untagged dispersers	85	91	58	47
Total dispersers	288	267	163	122
Percent total dispersers caught by live-traps	42	31	27	33
Percent total dispersers caught by pitfall traps	62	63	59	57

TABLE 5.—*Juvenile minimum survival rates and index of juvenile survival of Krebs and DeLong (1965) for total populations and for live-trap populations of* Microtus townsendii. *Data are pooled over the entire breeding season in each year. The 1978 sample includes March to June only. The total population includes combined live-trap and pitfall populations.*

Year	Grid	Minimum survival per 2 weeks	Index total population	Index live-traps
1976	D	0.44	1.06	0.38
	A	0.58	1.16	0.46
	B	0.70	2.54	0.82
	C	0.66	2.55	0.77
1977	D	0.50	0.83	0.13
	A	0.58	1.07	0.21
	B	0.56	1.27	0.16
	C	0.63	0.60	0.13
1978	D	0.25	0.55	0.50
	A	0.25	0.40	0.40
	B	0.25	0.60	0.43
	C	0.00	0.50	0.00

in the other type of trap. For example, all individuals initially trapped in pitfall traps and which later entered live-traps were included in the calculation of mean weight at first capture in live-traps.

The mean body weight of males at first capture in live-traps was about 15 g more than in pitfall traps. Females were about 12 g heavier at first capture in live-traps than in pitfall traps. Males and females in the unfenced populations A and D were significantly heavier at first capture in pitfall traps compared with males and females in the enclosed populations (all t values = 4.40, all d.f. = 967, $P < 0.01$) (Table 1). Immigration of heavier animals into the unfenced populations may account for this difference.

Mean weight at first capture in live-traps was higher than in pitfall traps. Pitfall traps were more likely to capture juvenile voles, whereas live-traps were more likely to capture adults ($\chi^2 = 1753.06$, d.f. = 1, $P < 0.0001$). A higher proportion of females entered live-traps as juveniles or subadults than did males in both the control ($\chi^2 = 45.57$, $P < 0.0001$) and fenced populations ($\chi^2 = 60.46$, $P < 0.0001$). Young males were less likely than young females to enter live-traps.

These results suggest that there is a time lag between first capture in pitfall traps and first capture in live-traps. Table 2 shows that adult males first caught in pitfall traps were not caught in live-traps for about 7 weeks, whereas adult females were not caught in live-traps for 5 weeks. Juvenile males took 2 weeks and juvenile females 4 weeks longer than adults to enter live-traps. Over 50% of those juvenile males first caught in pitfall traps which did enter live-traps were adults by that time (Table 2). Juvenile females first caught in pitfall traps were more likely to enter live-traps for the first time as subadults. The heavier an individual at first capture in pitfall traps, the sooner it tended to enter the live-trap population. The maximum interval recorded in this study between first captures in pitfall traps and live-traps was 54 weeks for a subadult female.

In this study, 1,644 voles were caught only in pitfall traps. Table 3 indicates that over 50% of the individuals caught only in pitfall traps were trapped only once. The average time between first and last captures of these individuals was less than 2 weeks. These animals comprise a substantial portion of the population about which nothing would be known if enumeration had been by live-traps only. The maximum duration of life recorded for an individual caught only in pitfall traps was 38 weeks for a juvenile female.

TABLE 6.—*Demographic attributes of male* Microtus townsendii *caught during summer 1976 in pitfall traps and live-traps. All grids are combined. The time interval is the entire summer except for the botfly results when males in the botfly season (July through September) were scored. Sample sizes are in parentheses.*

Weight	% scrotal	Wounds/male	Wounds/scrotal male	Bots/male
		Pitfall captures of males		
40–49	23.5 (259)	0.53 (259)	0.98 (61)	0.38 (213)
50–59	62.3 (199)	1.28 (199)	1.34 (124)	0.33 (153)
60–69	76.0 (146)	0.82 (146)	0.96 (111)	0.68 (120)
70–79	92.8 (56)	0.68 (56)	0.65 (52)	0.63 (49)
≥80	91.7 (12)	0.50 (12)	0.45 (11)	0.18 (11)
Total	53.4 (672)	0.83 (672)	1.04 (359)	0.45 (546)
		Live-trap captures of males		
40–49	13.6 (88)	0.41 (88)	1.08 (12)	0.28 (72)
50–59	38.7 (111)	0.70 (111)	0.67 (43)	0.39 (92)
60–69	73.8 (107)	0.61 (107)	0.74 (79)	0.44 (86)
70–79	93.5 (46)	0.56 (46)	0.56 (43)	0.24 (29)
≥80	100.0 (6)	0.17 (6)	0.17 (6)	0.00 (2)
Total	51.1 (358)	0.58 (358)	0.69 (183)	0.37 (281)

Dispersal.—The experimental design used in this study identified dispersing voles. A dispersing vole could previously have been caught in live-traps, pitfall traps, both types of traps, or neither. Table 4 shows that live-traps enumerated about 30% of all dispersers and 60% of tagged dispersers. Pitfall traps, operating only part of the year, caught 60% of the total dispersers and 90% of the tagged dispersers. Pitfall traps were more effective than live-traps in capturing dispersers before they left the population.

Excluding juveniles, 193 males and 130 females in the fenced populations were caught only in pitfall traps. Table 4 indicates that there were 127 dispersing tagged males not enumerated by live-traps. Of these 127 individuals, 120 were either subadults or adults. Therefore, a maximum of 62% of the subadult and adult males caught only in pitfall traps dispersed. There were 122 known subadult and adult female dispersers that had been trapped in pitfall traps only. These dispersers accounted for a maximum of 94% of the 130 subadult and adult females in the experimental populations that failed to enter live-traps.

Juvenile Survival.—Juvenile survival is usually measured indirectly by means of an index (Krebs and DeLong, 1965), because direct estimation of survival is dependent upon capturing large numbers of juveniles. This condition was satisfied in this study, and a comparison between observed juvenile survival and the index of Krebs and DeLong (1965) can be made. Juvenile minimum survival rates per 2 weeks were highest in the 1976 increasing populations and lowest in the 1978 declining ones, as was the Krebs and DeLong (1965) index for the combined live-trap and pitfall population (Table 5), and both measures of juvenile survival were correlated ($r = 0.69$, $P < 0.02$). However, the data derived solely from live-trapping show that the index was lowest in the 1977 peak populations, and was not correlated with observed minimum survival rates ($r = 0.22$). In these high density populations of *M. townsendii*, the Krebs and DeLong (1965) index was too low.

A comparison of adult males caught in live-traps and pitfall traps.—It has already been demonstrated that pitfall traps tend to capture juvenile voles, whereas live-traps capture adults. However, adult voles can be caught in both types of traps. Are there any demographic differences between adult voles caught in pitfall traps and those caught in live-traps? Assuming that subordinate voles have more wounds, we inquired

TABLE 7.—*Demographic attributes of male* Microtus townsendii *caught during summer 1977 in pitfall traps and live-traps. All grids are combined. The time interval is the entire summer except for the botfly results, when males in the botfly season only were scored. Sample sizes are in parentheses.*

Weight	Percent scrotal	Wounds/male	Wounds/scrotal male	Bots/male
		Pitfall captures of males		
40–49	18.8 (768)	0.04 (768)	0.20 (145)	0.16 (681)
50–59	53.7 (296)	0.96 (296)	1.78 (159)	0.22 (197)
60–69	93.4 (274)	1.76 (274)	1.85 (256)	0.34 (82)
70–79	98.1 (267)	1.70 (267)	1.72 (262)	0.40 (42)
⩾80	99.0 (101)	1.21 (101)	1.19 (100)	0.16 (19)
Total	54.0 (1,706)	0.81 (1,706)	1.48 (922)	0.20 (1,021)
		Live-trap captures of males		
40–49	9.2 (489)	0.06 (489)	0.49 (45)	0.10 (459)
50–59	52.3 (386)	0.70 (386)	1.27 (202)	0.28 (265)
60–69	90.4 (468)	1.09 (468)	1.17 (423)	0.49 (172)
70–79	95.6 (434)	1.00 (434)	0.93 (415)	0.24 (127)
⩾80	100.0 (105)	1.15 (105)	1.15 (105)	0.08 (26)
Total	63.2 (1,882)	0.72 (1,882)	1.08 (1,190)	0.26 (1,049)

if live-traps and pitfall traps sampled different social segments of the population. In addition to reproductive maturity and wounding levels, we also examined degree of parasitic botfly infection in adult male voles. Females were excluded from the analysis because they were seldom wounded and their reproductive maturity was difficult to assess, because females in the early stage of pregnancy are not externally distinguishable from nonreproductive females. Males were organized into five 10-g weight classes from 40–90 g. We chose these weight groupings in order to examine demographic characteristics of adult voles, and further weight classes would have increased the unbalanced design in the analysis of variance of growth rates. Male reproductive maturity was externally judged by testes size and position. The number of wounds, number of parasitic botflies (*Cuterebra* sp.), and reproductive state were recorded for males captured in live-traps or pitfall traps. These data were recorded for each capture in each trap type, and the data were summed over the intervals in which both trap types were operated concurrently. Data on botfly parasitism were summed only in the periods of infestation (from July to September in each year). The average number of wounds per male and per reproductive male were calculated for each weight class in each trap-type population. A total of 20 comparisons was made in each year. When males caught in pitfall traps had more wounds than males caught in live-traps, the comparison was scored as a +; when the pitfall males had fewer wounds, the comparison was scored as a −. When no males were caught in one or both classes, the comparison was NC. A sign test analysis was used to analyze the data.

Table 6 indicates that in the summer of 1976, males of 40–59 g caught in pitfall traps were more often in reproductive condition than were similar-sized males caught in live-traps (40–49 g, $\chi^2 = 3.89$, $P < 0.05$; 50–59 g, $\chi^2 = 15.93$, $P < 0.01$). The males in these weight classes caught in pitfall traps attained reproductive maturity at lighter weights than did similar-sized males caught in live-traps. In 1976, reproductive males caught in pitfall traps had more wounds (12+, 3−, 5NC, $P < 0.05$) as did all males (13+, 3−, 4NC, $P < 0.05$). Males caught in pitfall traps also had higher levels of botfly infestation (12+, 3−, 1 tie, 4NC, $P < 0.05$).

Table 7 shows that males 40–49 g caught in pitfall traps during 1977 were more often in reproductive condition than were similar males caught in live-traps ($\chi^2 = 21.80$, $P < 0.001$). At this peak density males caught in pitfall traps had more wounds than did males caught in live-traps (17+, 3−, $P < 0.01$) as did reproductive males

TABLE 8.—*Demographic attributes of male* Microtus townsendii *first caught in pitfall traps in 1976 that were caught in live-traps and of those males that were not. All grids are combined. The time interval is the entire summer except for the botfly results, when males in the botfly season only were scored. Sample sizes are in parentheses.*

Weight	Percent scrotal	Wounds/male	Wounds/scrotal male	Bots/male
	Males first caught in pitfall traps but not in live-traps			
40–49	28.8 (90)	0.70 (90)	0.92 (64)	0.38 (76)
50–59	67.1 (64)	1.30 (64)	1.12 (43)	0.50 (48)
60–69	85.7 (28)	1.21 (28)	0.91 (24)	1.00 (15)
70–79	75.0 (8)	1.75 (8)	2.00 (6)	1.00 (7)
≥80	100.0 (1)	0.00 (1)	0.00 (1)	(0)
Total	52.4 (191)	1.01 (191)	1.06 (138)	0.51 (146)
	Males first caught in pitfall traps and later in live-traps			
40–49	20.7 (169)	0.44 (169)	0.94 (35)	0.38 (137)
50–59	60.0 (135)	1.27 (135)	1.30 (81)	0.25 (105)
60–69	73.0 (119)	0.72 (119)	0.89 (87)	0.63 (105)
70–79	95.8 (48)	0.50 (48)	0.52 (46)	0.57 (42)
≥80	90.9 (11)	0.54 (11)	0.50 (10)	0.18 (11)
Total	53.7 (482)	0.75 (482)	0.94 (259)	0.43 (400)

(18+, 2−, $P < 0.01$). Males caught in pitfall traps had fewer botflies (7+, 10−, 3 ties), but not significantly fewer.

In 1978 males caught in pitfall traps, whether or not they were reproductive, had more wounds (6+, 1−, 12NC), but there were not enough comparisons to indicate significance by the sign test. No botfly data are available from 1978 because the study ended before the botfly season began.

In summary, males caught in pitfall traps have higher levels of wounding and tend to have greater rates of botfly infestation. Males 40–49 g caught in pitfall traps were more often in reproductive condition than were males of the same size caught in live-traps. Rates of male reproductive maturity were the same in the heavier weight classes. Males 40–49 g and greater than 79 g tended to have lower woulding rates than did medium-sized adult males. Very large males had lower rates of wounding. Wounding rates were higher and botfly infestation lower in the peak 1977 populations than in the increasing 1976 populations.

Why are some males not caught in live-traps?—Some males first caught in pitfall traps later entered live-traps; some did not. An analysis similar to the one previously outlined was conducted on these two groups of individuals. Males caught only in pitfall traps are defined as PO males while those eventually caught in live-traps are PL males.

Table 8 indicates that in 1976 males 40–59 g caught in pitfall traps only were more often in reproductive condition than were males eventually caught in live-traps, but the difference was not significant. PO males had more wounds than their PL counterparts (10+, 6−, 4NC), as did PO reproductive males (8+, 6−, 2 ties, 4NC), but the differences were not significant. PO males had higher rates of botfly infestations than did PL males (10+, 4−, 6NC), but again this difference was not significant.

In 1977, males 40–49 g caught only in pitfall traps were more often in reproductive condition than were 40–49 g males entering live-traps ($\chi^2 = 22.55$, $P < 0.001$) (Table 9). PL males had more wounds (4+, 13−, 4NC, $P < 0.05$) as did PL reproductive males (3+, 14−, 3NC, $P < 0.05$) than their PO counterparts. PL males also had more botflies (3−, 14+, 3NC, $P < 0.05$). Under high density conditions, those males that eventually were recruited to live-traps had more wounds and more botflies than those males caught only in pitfall traps.

TABLE 9.—*Demographic attributes of male* Microtus townsendii *first caught in pitfall traps in 1977 that were caught in live-traps and of those males that were not. All grids are combined. The time interval is the entire summer except for the botfly results, when males in the botfly season only were scored. Sample sizes are in parentheses.*

Weight	Percent scrotal	Wounds/male	Wounds/scrotal male	Bots/male
	Males first caught in pitfall traps but not in live-traps			
40–49	13.8 (550)	0.05 (550)	0.34 (76)	0.16 (518)
50–59	52.5 (236)	1.02 (236)	1.92 (124)	0.22 (152)
60–69	93.1 (262)	1.80 (262)	1.89 (244)	0.35 (74)
70–79	98.6 (284)	1.61 (284)	1.62 (280)	0.43 (40)
⩾80	99.0 (95)	1.20 (95)	1.21 (94)	0.16 (19)
Total	57.3 (1,427)	0.92 (1,427)	1.58 (818)	0.20 (803)
	Males first caught in pitfall traps and later in live-traps			
40–49	28.1 (229)	0.08 (229)	0.15 (65)	0.18 (163)
50–59	58.2 (67)	0.54 (67)	0.92 (39)	0.20 (45)
60–69	100.0 (15)	0.66 (15)	0.66 (15)	0.25 (8)
70–79	100.0 (4)	1.00 (4)	1.00 (4)	0.00 (2)
⩾80	100.0 (4)	0.00 (4)	0.00 (4)	(0)
Total	39.5 (319)	0.21 (319)	0.47 (127)	0.19 (218)

Males 40 to 49 g and greater than 79 g again tended to have lower wounding rates than did medium-sized adult males. They also had lower rates of botfly infection. PL males had higher wounding rates in the peak 1977 population than did PL males in the 1976 increasing populations. Presumably there is heightened competition to enter the resident live-trap population in peak populations, and greater wounding levels are indicative of increased interactions among individuals. PO males in 1977 had lower wounding rates than did PO males in 1976. This low level of wounding in 1977 may be partially attributable to the dispersal of PO males before they accumulated many wounds.

Growth rates of voles caught in pitfall traps and live-traps and of those caught only in pitfall traps.—The analysis so far indicates that male voles failing to enter live-traps attained reproductive maturity at lighter weights than did males eventually entering live-traps. To investigate if growth rates in these two groups of voles were different, we examined instantaneous growth rates (Brody, 1945) as determined from pitfall-only captures. Growth rate data from both sexes were included. We performed a 5-way analysis of covariance with growth rate as a dependent variable, weight as a covariate, and sex, grid, group, weight class, and year as the five indices. The analysis indicated that there was a significant difference in growth rates between sexes ($F = 47.29$, d.f. = 1, 3,426, $P < 0.0001$), among grids ($F = 2.87$, $P < 0.05$), between groups ($F = 8.60$, $P < 0.01$), among weight classes ($F = 132.46$, $P < 0.0001$), and between years ($F = 13.47$, $P < 0.001$). The significance of the class index shows that there is additional variability in growth rates associated with body size that is not removed by the linear regression of growth rates on body weight.

The following comparisons of growth rates are based upon mean growth rates corrected for size effects by covariance analysis. Males grew about 24% faster per day than females. Voles on the unfenced control grids grew 8% faster per day than voles on the enclosed grids. PO voles grew 11% faster than did PL voles, whereas individuals in summer 1976 grew 8% faster than in summer 1977. The interaction between weight class and group was not significant, which indicates that there was about the same difference between groups within each weight class. The mean growth rates for each weight class of PO voles were always higher than for the same weight class for PL voles. This analysis clearly indicates that those voles first caught in pitfall traps but never caught in live-traps had higher instantaneous growth rates than did those voles first caught in pitfall traps and later in live-traps.

DISCUSSION

Size of small mammal populations can be estimated by stochastic statistical models (Jolly, 1965), deterministic models (Leslie et al., 1953), direct enumeration (Chitty and Phipps, 1966; Krebs, 1966) or other methods (Smith et al., 1975). Small rodent populations violate the major assumption of the statistical models that all marked and unmarked animals are equally catchable (Krebs, 1966). Therefore, Krebs (1966, later papers) used direct enumeration as an alternative method of estimating population size. The major assumption of this method is that live-traps catch all the adult animals in the population. It is known that juvenile voles do not readily enter live-traps, and Krebs and DeLong (1965) measured juvenile survival indirectly by means of an index. Failure of live-traps to catch all juveniles, but not all adults, is expected.

Krebs (1966) suggested that he was able to enumerate 80 to 90% of *Microtus californicus* in densities up to 150 per acre. There was no method of confirming this estimate. Above this density Krebs estimated that 60 to 80% of the population was enumerated. Krebs et al. (1969) believed that they enumerated 90% of *M. ochrogaster* and 75% (50% in summer) of *M. pennsylvanicus* populations. A trap-out of enclosures suggested that live-trapping enumerated most of the individuals (Krebs et al., 1969). It was assumed that voles did not avoid snap-traps used in the trap-out. Boonstra and Krebs (1978) found that of 213 adult *M. townsendii* first caught in pitfall traps, only 62% were eventually caught in live-traps. In the present study, of 574 adults first caught in pitfall traps, 56% were eventually caught in live-traps. In *M. townsendii* populations, the assumption that live-traps enumerate all adults is clearly violated.

Live-traps do not succeed in completely enumerating any age class of *M. townsendii*. Studies typically use only live-traps, and the determination of demographic characteristics is based upon data from enumerated voles only. This study demonstrated that voles never caught in live-traps had faster growth rates than those entering live-traps. Thus, growth rates derived solely from live-trap data underestimate the average growth rate. Smaller adult males caught only in pitfall traps were more often in reproductive condition than those that were recruited to live-traps. It appears that males which attained sexual maturity earlier tended to disperse without being caught in live-traps. Median weights at sexual maturity derived solely from live-trap data overestimate the actual values for the population. The loss through dispersal of voles attaining sexual maturity before entering live-traps reduces the apparent proportion of reproductive individuals in the population. The loss of these individuals also affects minimum finite survival rates. The assumption is made that survival of a particular age and sex class obtained by live-trap enumeration is a representative estimate of the minimum survival of that class. Disappearance has both a death and dispersal component. The actual minimum survival of an age group will be lower than that estimated by live-traps because they fail to catch all early maturing, dispersing individuals.

The present study indicates that live-traps did not totally enumerate any segment of the *Microtus townsendii* populations, and may produce biased demographic data for both increasing and peak populations, and likely for declining populations as well. However, although the absolute estimates of many parameters may be in error, we suggest that the relative magnitude of the parameters is accurately determined. For example, although median weight at sexual maturity will be biased if only live-trap data are used in its determination, these data will still demonstrate that increasing populations have the lowest median weight at sexual maturity and peak ones the highest.

This study demonstrates that live-traps did not accurately enumerate *Microtus townsendii* populations. One explanation could be that there were too few live-traps available to catch all individuals likely to enter them. In this study the density of live-traps used was greater than or equal to densities used by other workers (Krebs, 1966; Krebs et al., 1969; Tamarin, 1977). However, because trappabilities were about 65% in increasing and peak populations and over 80% in the low density 1978 spring populations, there were indications of competition among voles for the live-traps. Van Vleck (1968) found a positive relation between population density and the number of traps necessary to capture a constant proportion of the population.

Individual behavior is important in determining which voles are caught in live-traps. There are indications that live-traps sample mainly the larger, dominant individuals. Kikkawa (1964) observed encounters of *Clethrionomys glareolus* at live-traps and noted that larger, dominant individuals chased away smaller, subordinate voles. Summerlin and Wolfe (1973) also found that heavier, dominant *Sigmodon hispidus* were more likely to be trapped than were smaller, subordinate rats. Gliwicz (1970) reported that young voles have low trappability in live-traps, and suggested that individuals low in the social heirarchy, such as juveniles, have low trappability. A positive relationship between social dominance and trappability has been demonstrated in several species (Davis and Emlen, 1956; Andrzejewski and Rajska, 1972; Joule and Cameron, 1974). It appears that some form of behavior deters subordinate voles from entering live-traps.

Immigration rates are difficult to measure. New voles caught in unfenced open populations may be immigrants or native to the study area. Some workers have assumed that new small voles are born on the area, but that new adult voles are immigrants (Hilborn et al., 1976; Redfield et al., 1978). In the fenced populations, 52% of the voles were in the adult weight class at first capture in live-traps, although none was an immigrant. The assumption that new adult animals in unfenced populations are all immigrants is thus wrong.

Hilborn et al. (1976) developed a simulation model to show that when trappability is above 65%, the minimum number alive estimate derived from enumeration underestimated the actual population size by about 10%. Therefore, in this study, when trappability in live-traps during summer was about 65%, the model predicts an underestimate of actual population size by 10%. In October 1976, live-traps underestimated the actual population by 55 to 70%, and in July 1977 the underestimate was between 50 and 60%. This discrepancy is a direct result of the absence of a large class of voles from live-traps.

These *M. townsendii* populations were in a peak phase during the 1977 summer. The maximum densities recorded varied between 401 and 530 voles per acre, among the highest ever enumerated for microtine populations. Only the results of Boonstra and Krebs (1978) are similar, because both pitfall traps and live-traps were used concurrently in their study. They recorded a maximum of 519 voles per acre for a population of *M. townsendii.* Other students have used only live-traps to enumerate vole populations. Chitty (1952) recorded a density of 300 voles per acre in a population of *M. agrestis.* Krebs (1966) reported a maximum density of 324 *M. californicus* per acre. Krebs et al. (1969) estimated maximum densities of *M. pennsylvanicus* at 60 voles per acre and *M. ochrogaster* at 40 voles per acre. Densities of *M. breweri* and *M. pennsylvanicus* were recorded at 50 voles per acre each by Tamarin (1977). The actual population sizes in the latter studies may have been much higher than recorded as a result of the failure of live-traps to enumerate substantial portions of the populations.

Pitfall traps and live-traps, when operated concurrently, sample different segments of the population. Adult males caught in pitfall traps have more wounds and higher rates of parasite infestations than do similar-sized males caught in live-traps. Although some of the wounds accumulated by males caught in pitfall traps may be a result of confinement with other voles in the pitfall, we suggest that these wounds constitute a minor portion of the total wounding load. If one assumes that subordinate voles have more wounds, then it appears that pitfall traps sample the subordinate individuals in the population. Andrzejewski and Rajska (1972), by trapping a vole population concurrently with live-traps and pitfall traps, found that as individuals became older, they were more trappable in live-traps and less so in pitfall traps. Thus it appears that as individuals ascend in the social heirarchy, they are more likely to enter live-traps.

The present study demonstrates that live-traps fail to capture a large portion of the vole populations, and that trapping with pitfall traps is a necessity if one is interested in obtaining a comprehensive demographic analysis. This study also suggests some areas that should be explored further. The social factors that prevent smaller, subordinate voles from entering live-traps could be investigated by examining the role of aggression, odor, or other factors.

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