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Reviewed work(s):

Source: *Journal of Mammalogy*, Vol. 59, No. 1 (Feb., 1978), pp. 136-148

Published by: [American Society of Mammalogists](#)

Stable URL: <http://www.jstor.org/stable/1379883>

Accessed: 02/02/2012 22:26

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PITFALL TRAPPING OF *MICROTUS TOWNSENDII*

RUDY BOONSTRA AND CHARLES J. KREBS

ABSTRACT.—A field population of *Microtus townsendii* was trapped concurrently with live-traps and pitfall traps throughout the spring and summer of 1975. The population was at peak densities, with a maximum of 519 voles per acre. The number enumerated by pitfalls was up to two times larger than the number enumerated by live-traps. Capture of a large number of young in pitfalls indicated that mortality was higher among post-weanlings than among any other age group. Recruitment to live-traps was largely restricted to animals over 40 g, whereas in pitfalls animals were generally lighter. Over half of the 1,100 animals captured first by pitfalls were never caught by live-traps. Among those subsequently entering live-traps, many stayed away for 6 to 10 weeks, and some of the smaller ones stayed away even longer. Few animals dispersed to other nearby trapping grids. Pitfall trapping and live-trapping sample different subpopulations, young animals and transient adults being a large fraction of the individuals caught in pitfalls.

Population estimation techniques for small rodents either assume equal catchability of all members in the population (Jolly, 1965) or that virtually all the animals can be caught and enumerated (Krebs, 1966; Hilborn et al., 1976). The assumption of equal catchability can be tested by trapping with two or more different methods and comparing the populations captured by each type of trap. This was the first purpose for the present study.

The second purpose was to measure survival and dispersal rates of small juveniles between weaning and puberty. Juveniles are particularly difficult to capture by standard live-trapping techniques. However, changes in the rates of juvenile survival are of great importance in determining the rate of population growth in a number of *Microtus* species (Krebs and Myers, 1974).

The technique used to investigate juvenile survival and the efficiency of total enumeration trapping involved the use of pitfall traps concurrently with Longworth live-traps. Other workers (Kott, 1965; Andrzejewski and Rajska, 1972) have had success in trapping the younger segment of the population by the use of pitfalls that were continuously open. We modified the pitfall trap so that it could be prebaited when not in use.

METHODS

The study area was located on Westham Island in the Fraser River delta near Vancouver, British Columbia. The live-trapping grid used was Grid I, which served as the control in the experiment of LeDuc and Krebs (1975). This grid had been trapped continuously since July 1971. This study lasted from 6 May to 26 September 1975. The vegetation on the area was dominated by a grass community consisting of *Agrostis alba*, *Agropyron repens*, *Poa pratensis*, and *Holcus lanatus*. The grid was bordered on one side by a ditch filled with water for most of the summer and on the other three sides by grassland.

The trapping area had 100 trapping points arranged in a 10 by 10 pattern. Each trapping point was 7.6 m from the next. Because of high densities of voles, 150 Longworth traps were used throughout the study, with two traps at every other trap point. Traps were baited with oats; cotton stuffing was provided. In the summer, live-traps were set every second week on Monday afternoon, checked Tuesday morning, locked shut Tuesday afternoon because of the heat, set again Tuesday evening, and checked Wednesday morning, when they were then locked open. In the spring and autumn, when heat was not a problem, traps were left set Tuesday morning for an afternoon check.

The pitfall consisted of two five-pound coffee cans, one stacked on the other (Fig. 1). The end of the upper can was cut out and served as a platform to seal the pitfall trap when not in use. This

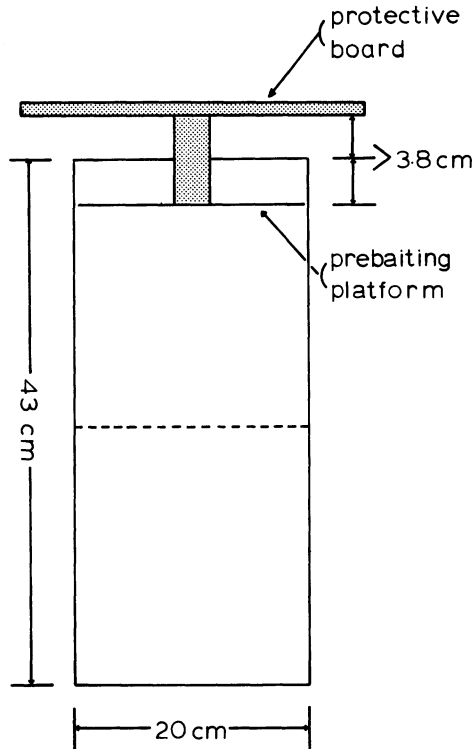


FIG. 1.—Diagram of the pitfall trap. See text for a description.

platform was attached to a short wooden rod fastened to a 25 by 30-cm board protecting the pitfall from rain and heat. This board stood about 3 cm above the top of the pitfall, and allowed voles to sit on the platform underneath the board and eat the bait. On the days that trapping was carried out, the platform was pulled out of the pitfall, the pitfall was cleaned and supplied with oats and cotton, and the board was inverted and placed above the pitfall. One pitfall was placed at every trap point at the intersection of two or three vole runways. These traps were set Wednesday afternoon, checked Thursday morning, Thursday afternoon, and Friday morning. The pitfall was then closed to voles by lowering the platform into it again. Heat never became a problem. Pitfall traps were set every week until mid-August, when we switched to a two-week interval because the number of new animals entering the population had tapered off. In late August, heavy rains flooded a number of the pitfalls, and in September brought the study to an end.

All voles were ear-tagged, and on capture, each animal's tag number, trap location, sex, weight, and sexual condition were recorded. On recapture in the same trapping session, only tag number and location were noted. Animals are classified as follows: adult (>42 g); subadult (30–42 g); juvenile (<30 g).

The total enumeration technique of Chitty and Phipps (1966) was used to draw comparisons between voles caught in live-traps and those caught in pitfalls. This type of demographic analysis requires that most of the individuals in the population be caught. The estimate of trappability used was the following for all N individuals:

$$\text{Trappability} = \frac{\sum_{i=1}^N \left(\frac{\text{number of actual captures for a given animal}}{\text{number of possible captures for that animal}} \right)}{N}$$

where N is the number of voles caught more than two times. In the number of actual and possible captures, the first and last times of capture are excluded from the calculation, because an animal is necessarily caught at these times.

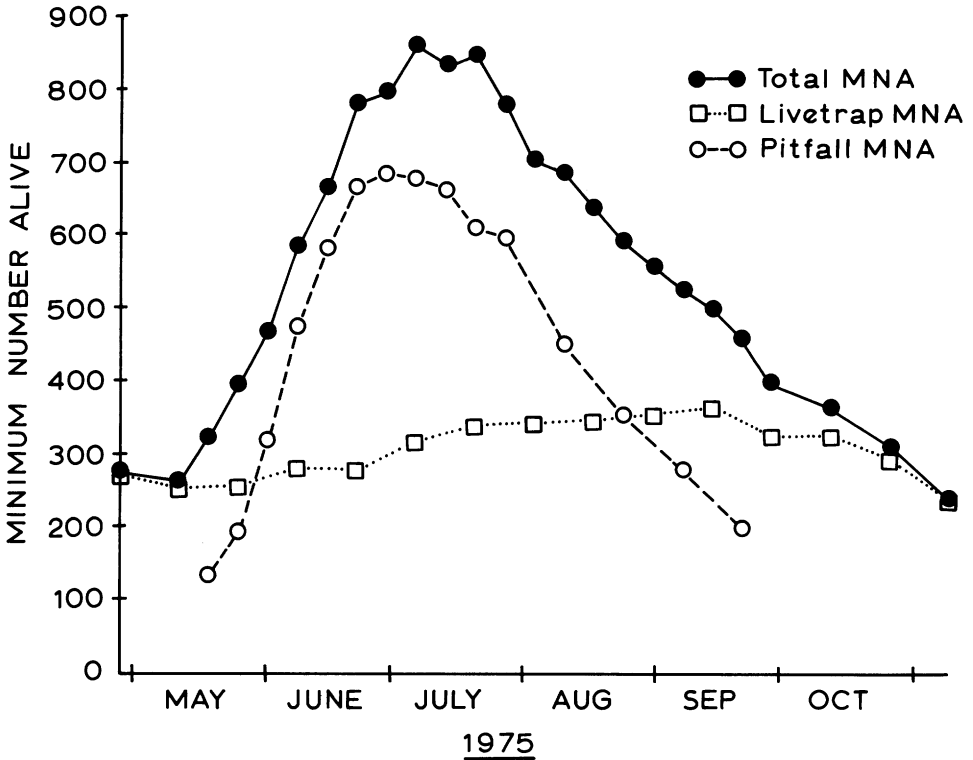


FIG. 2.—Population numbers of *M. townsendii* on Grid I. Minimum number alive (MNA) is given for the population known to have entered live-traps, for those known to have entered pitfalls, and for those known to have entered one or both trap types.

The index of survival of young that has been used in other *Microtus* population studies (Krebs 1966, and later papers) and will be used in this paper is the following:

$$\frac{\text{number of new voles less than 40 g at time } t}{\text{number of lactating females at } t - 4 \text{ weeks}}$$

RESULTS

Trappability

The trappability estimates for each of the two types of traps were calculated independent of information from capture in the other. Thus, animals known to be present from capture in pitfalls but not in live-traps were not included in the estimate of trappability of animals captured in live-traps. This also holds for the converse. During the first 4 years, densities in the summer were relatively low, and trappability in live-traps was always over 70% except in females in 1974. The mean trappability during this time was 78% (N = 531). In 1975 densities reached very high levels. Trappability in live-traps fell to 53% (N = 574), which was 15 to 40% less than it had been in previous years, when densities were lower.

Pitfall traps, because they are a multiple-capture trap, could theoretically catch all animals on the area. However, their success was only 27% (N = 840) about half that of the live-traps, which indicates that voles avoided repeated capture in pitfalls. Part of the reason for this lower success may be that the animals had learned to avoid capture

during the 11 consecutive weeks of pitfall trapping at the start of the study. Capture in pitfalls may have also been more traumatic than in live-traps because of the fall into the pitfall and the confinement with other voles (up to eight) caught at the same time. We concluded that, at these high densities, it is not possible to census the vole populations adequately with live-traps, and that pitfalls are even less effective.

Population Density

In 1975, *Microtus townsendii* numbers were extremely high compared with those in previous years. The minimum number alive in the live-trap population at the end of April 1975 was 272 animals compared with 41 in April 1974, 46 in April 1973, and 88 in April 1972. Throughout the study the number of voles caught on the area by live-traps remained between 250 and 370 animals.

Fig. 2 shows the minimum number of animals alive from those entering live-traps, pitfalls, and one or both trap types. Although breeding started in February, only a small proportion of the adult females (5%) was lactating during the first 8 weeks. In April, this proportion increased markedly, so that 20 to 65% of the adult females caught were lactating in each trapping session. Therefore, the majority of the young born would have been weaned when pitfall trapping was in progress. The population enumerated by pitfalls increased enormously in the first part of the study, owing to the capture of both voles tagged from previous capture in live-traps and untagged voles. From the beginning of the study until 1 July, this population increased at an average rate of about 33% per week compared with 3% per week increase in the live-trap population, so that the maximum number attained in July in pitfalls was 685 compared with 319 in live-traps. The rate of increase for the total population according to both trapping methods averaged about 17% per week. This increase stopped when reproduction tapered off in the beginning of July. The pitfall population then went into a steady decline averaging 10% per week compared with 0.1% decline per week in the live-trap population. The maximum number of animals known to be alive on the trapping area at one time was 860 voles. This was 2.7 times the number indicated by live-traps and 1.3 times the number indicated by pitfalls.

The stochastic model of Jolly (1965) assumes randomness of capture of all animals at risk of capture. The model gives an estimate of $1,140 \pm 75$ (2 SE) animals present on the area when the combined trap data were used for the trapping session in which the maximum number of animals was known to be alive on the area. This compares with an estimate of $1,163 \pm 127$ animals when only the pitfall data are used and 432 ± 48 animals when only the Longworth live-trap data are used. This suggests that the pitfall trapping method may more accurately sample actual population numbers.

By the time the rains came in September and we could no longer trap with pitfalls, these traps were enumerating a much smaller proportion of the animals known to be on the area. In the penultimate trapping session, pitfalls were enumerating only 53% of the animals known to be on the area while live-traps were now enumerating 64%. Even after trapping with pitfalls had stopped, the live-traps were still failing to catch all the tagged animals, as those caught previously only in pitfalls took a number of weeks to enter the live-trap population.

Survival

Changes in survival rates are important causes of population fluctuations in microtines (Krebs and Myers, 1974). In calculating these rates one assumes that the survival observed in the trappable population applies to the entire population of comparable age. These rates result from deaths on the grid and emigration from it.

Figure 3 shows the minimum survival rates for the trappable population of males and females caught in live-traps and in pitfalls. Poor survival is arbitrarily defined to be

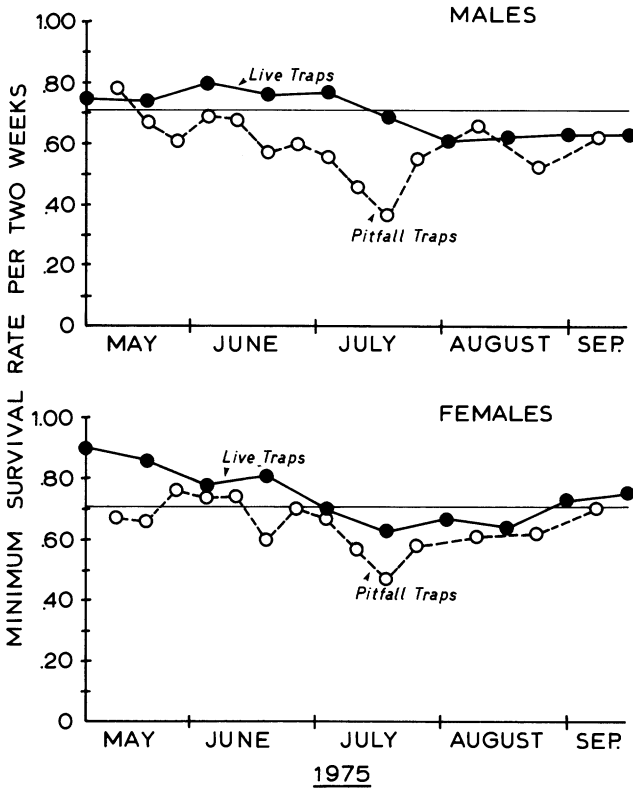


FIG. 3.—Mean minimum survival rate per 14 days for male and female *M. townsendii* caught in live-traps and in pitfalls on Grid I. The horizontal line is of a survival rate of 0.707, below which half the population disappears every 4 weeks.

any rate below .707 per 2 weeks (half of the population disappearing per 4 weeks). Both males and females in the live-trap population maintained good survival rates until the beginning of July. During the remainder of the summer both males and females had poor survival rates. This coincided with the start of infestations of botflies (*Cuterebra* sp.) and of the grey flesh fly (*Wohlfahrtia vigil*). Both of these were responsible for part of this poor survival (Boonstra, 1977; unpublished data). Male survival rates in live-traps showed a moderate correlation with female survival rates ($r = .56$,

TABLE 1.—Minimum survival rates per 14-day period for *M. townsendii* on Grid I in two types of traps. Sample sizes in parentheses.

Group	Live-traps		Pitfalls	
	Males	Females	Males	Females
Adults	.69 (713)	.76 (960)	.60 (843)	.70 (933)
Subadults	.66 (146)	.71 (269)	.61 (480)	.60 (933)
Juveniles	.50 (8)	.64 (11)	.48 (223)	.55 (279)
Total	.68 (867)	.75 (1,240)	.59 (1,546)	.66 (1,868)

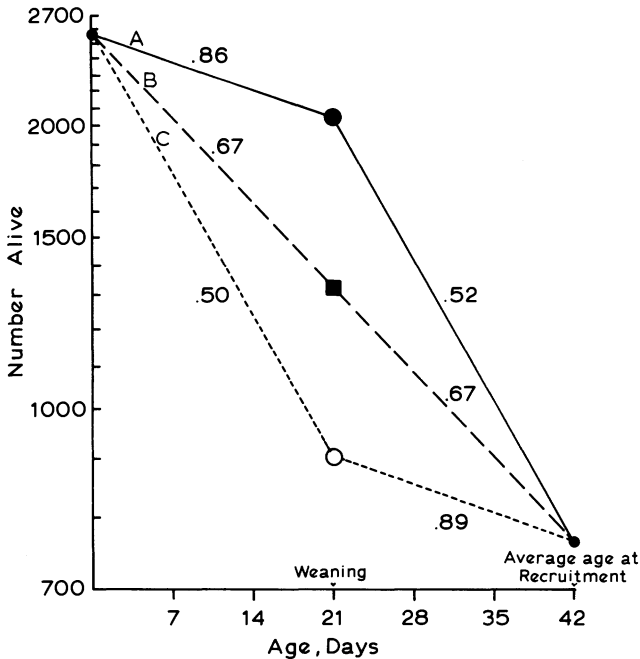


FIG. 4.—Survivorship curves for young voles between birth and recruitment. The number born (2,550) was estimated from the number of lactating females; the number of recruits was known. Three combinations of survival rates per 14 days are presented to account for a loss of two-thirds of the young from birth to average age at recruitment (42 days): A, high survival rate to weaning; B, uniform survival rate to recruitment; C, low survival rate to weaning.

$N = 9$). Over the entire study, females survived significantly better than males ($P < .001$, Table 1).

The population trapped in pitfalls had consistently poor survival rates throughout most of the study. Minimum survival rates of voles in pitfalls will necessarily be lower than in live-traps because of the lower trappability in pitfalls; therefore, the minimum survival rates of animals caught in the two trap types are not strictly comparable. Correlation between the survival rates of males and females in pitfalls was good ($r = .73$, $N = 14$). Females again survived significantly better than males ($P < .01$, Table 1). Survival was particularly poor in the first part of July in both males and females. The cause for this is unknown, because both types of parasitic flies were only just appearing, and reproduction was tapering off with the probable reduction in aggression associated with breeding. The periods of extremely poor survival in the pitfall population (mid-July) were not paralleled in the live-trap population. In males, where the difference between the minimum survival rate between live-traps and pitfalls was most pronounced, this difference was not restricted only to the young. In this period, adult males in pitfalls had a survival rate of .56 per 2 weeks compared with a survival rate of .73 in live-traps. This suggests that there may have been a real difference between the animals caught in the two trap types which was not simply related to differences in trappability. There was no correlation between the survival rates of males in live-traps and those in pitfalls ($r = .20$, $N = 9$). However, correlation between survival rates of females caught in pitfalls and those caught in live-traps was good ($r = .70$, $N = 9$).

There was no significant difference in mean survival rates between adult and sub-

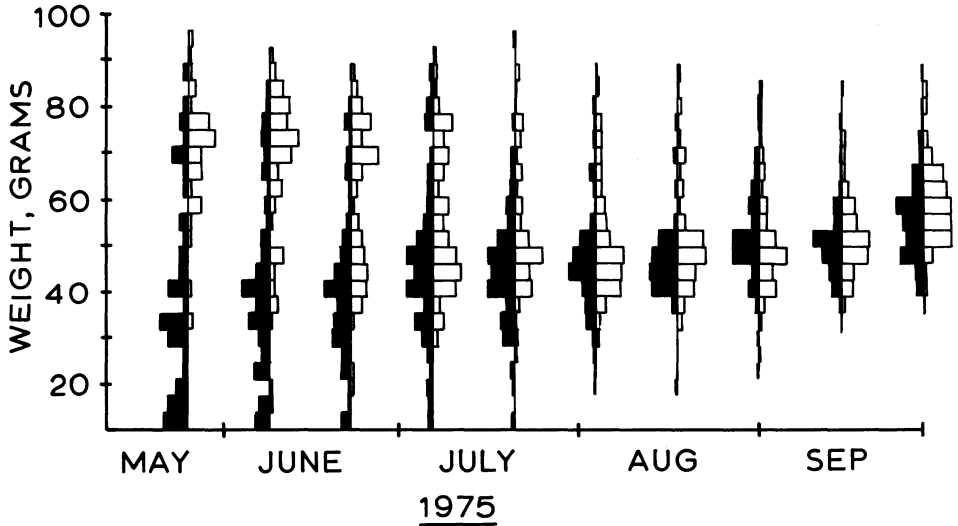


FIG. 5.—Weight distribution of males caught in pitfalls and in live-traps. Blacked-in histograms indicate voles caught in pitfalls.

adult classes within either sex for animals caught in live-traps (Table 1). In pitfalls, juvenile males had significantly lower survival rates than did adult or subadult males. Juvenile and subadult females have significantly lower survival rates than adult females. A number of the very young juveniles, which were not yet weaned, died in the pitfalls, so that capture in pitfalls may have depressed survival in this group. We have no evidence that survival of post-weanlings was detrimentally affected by capture in pitfalls, though it may have been.

The survival rate of voles between birth and weaning is particularly difficult to calculate, because of the long interval between weaning and capture in live-traps. For this particular population, the index for survival of young for live-traps only was very low (.34), because many of the young born on the area did not enter the live-trap population until they were adults. The index for both techniques combined was much higher (1.47). Therefore, changes in this index from year to year in live-traps may not necessarily indicate that survival is different, merely that trappability is different.

Because we were able to catch large numbers of the young soon after they left the nest, we made the following calculations to get a more accurate picture of survival between birth and weaning and between weaning and recruitment into the traps. The minimum number of females lactating during the breeding period was known (510). A female was assumed to be lactating separate litters if it was caught lactating at least 2 weeks apart. This is probably an overestimate because a female may be nursing the same litter in 2 consecutive weeks. Litter size was approximately five (281 pregnant females collected in 1973 and 1974 had a mean litter size of 5.05). The average weight at first capture of both males and females (<40 g) was calculated to be 27 g. This weight was converted to an age by the use of growth rate equations calculated for each month of the year and for each sex on all data obtained on *M. townsendii* from Westham Island. This weight was back-calculated to 20 g, at which the animal was assumed to be 4 weeks old. With this method, a 27-g male or female caught in either May or June, when the majority of breeding occurred, was calculated to be 6 weeks old. This may be an overestimate by up to a week if the young reach the 20-g weight earlier. However, this should not affect the general conclusions. Using this average age at first capture, we calculated three possible combinations of survival rates that could explain the

TABLE 2.—Numbers of animals first caught in pitfalls and later in live-traps, and those caught only in pitfalls.

Group	Males			Females			Total
	Adult	Subadult	Juvenile	Adult	Subadult	Juvenile	
Caught first in pitfalls and later in live-traps	118	112	58	61	113	74	536
Caught only in pitfalls	97	105	98	40	121	115	576
Totals	215	217	156	101	234	189	1,112

relationship between the number of young born and the number that eventually entered the trappable population (Fig. 4).

The minimum survival rate of a large sample of juvenile animals was known from the trapping data to be about 0.52 per 2 weeks (Table 1). In curve A, we assumed that this was the survival rate of all post-weanlings, in which case the preweanlings' survival rate would be very high (0.86). Curve A probably approximates the true situation most closely, with most of the losses occurring just after weaning. Curve B assumes constant survival from birth to recruitment. This constant survival is not likely to be the case because it implies a better survival rate than that observed among juveniles; for the same reason curve C, which assumes an even lower survival before weaning, is also unlikely. We conclude that survival was high before weaning and dropped drastically immediately after weaning.

Body Weight Differences

Animals subject to capture by live-traps and by pitfalls differ in body weight. Fig. 5 shows the corresponding weight distributions of males caught in pitfalls and in live-traps. From May to early July, large numbers of very small voles were caught in pitfalls, whereas live-traps caught only the heavier animals. Pitfalls during this time also caught fewer heavy voles than did live-traps. When breeding tapered off in early July, the weight distribution of the animals caught in both types of traps gradually became similar.

The mean body weight of males at the time of first capture in live-traps was $47.9 \pm .6$ g (SE) compared with $37.4 \pm .6$ g in pitfalls. Females caught in live-traps were also about 10 g heavier at first capture than females caught in pitfalls. Females in both pitfalls and live-traps were about 5 g lighter than males at time of first capture.

These results suggest that there is a considerable time lag between first capture in these two trap types. How long does it take for an animal first caught in a pitfall to enter a live-trap? Adults caught in pitfalls avoid capture in live-traps for an average of 5 to 6 weeks. Juveniles took 3 weeks longer to enter live-traps than did adults. Subadult females also took 3 weeks longer to enter live-traps than did adult females. There is a general trend indicating that the heavier an animal, the sooner it enters the live-trap population. Juveniles and subadults generally must attain larger body weights before entering the live-trap population. Of the 132 juveniles first caught in pitfalls and later caught in live-traps, 7% entered live-traps while still juveniles, 62% waited until they were subadults, and 31% waited until they were adults. Of the 225 subadults first caught in pitfalls and later caught in live-traps, 45% entered live-traps while still subadults, and 55% waited until they were adults. Young voles have the ability to trip the treadle mechanism if they enter a live-trap, so that their lack of capture at a relatively early age is not purely the result of a mechanical barrier.

Pitfall-trapped Voles

Over 1,100 voles were first caught in pitfalls. Table 2 shows that over half the animals first caught in pitfalls were never recaptured, that juveniles were the least

likely to be so recaptured, and adults the most likely. Thus, the larger a vole at first capture, the higher the probability of its entering the live-trap population. Males caught only in pitfalls had an average weight of $36.0 \pm .9$ g (SE) at first capture compared with $39.5 \pm .8$ g for males caught first in pitfalls and later in live-traps. Females showed the same 4 g difference. Generally, the younger an animal, the lower its chances of survival (Table 1), so that fewer of the low body weight individuals made it into the live-traps after capture in pitfalls.

It is possible that many of the voles appearing only in pitfalls were transients or voles living on the edge of the grid. If this is so, we would expect a higher number of these transients per trap in the outer than in the inner part of the grid. Grid I has three edges contiguous with adjacent grassland and one edge abutting a water-filled ditch. A significantly higher proportion of the voles was last caught in the outer rows of traps (Chi-square, $\chi^2 = 6.12$, $P < .025$; expected 28%, observed 35%), excluding the edge along the water. This indicates that some of the large number of voles which never entered live-traps were simply animals living on the edge of the grid, making occasional sallies into the trapped area.

There is still a large number of animals caught only in pitfalls that cannot be accounted for by this edge effect. Approximately 51% of these animals disappeared within one week. The other 49% were in the population for at least one week in which trapping with live-traps occurred, and a few were present in the population for 17 weeks without being caught by live-traps. These animals made up a substantial segment of the total population about which nothing could be known if one trapped only with live-traps. Most of these animals were either adults or subadults. Of the juveniles which were caught only in pitfalls, approximately 75% were caught only once, compared with 47% of the subadults and 41% of the adults.

How efficient were pitfalls at catching new animals that had come into the population either by birth or dispersal before they were caught by live-traps? Of all animals caught for the first time in live-traps, 77% ($N = 600$) had been previously caught in pitfalls. Trapping with pitfalls was, therefore, an efficient technique to trap animals before they were known to be in the live-trap population. During this entire period virtually no juveniles (1.7%) were caught by live-traps.

Dispersal

Some of the large number of voles never entering live-traps could have emigrated from the area. But of the 576 voles known to have disappeared before capture in live-traps, only nine are known to have dispersed to other areas. A total of 16 animals was known to have dispersed from Grid I during this time. This dispersal indicates that even at these high densities, a small number of individuals was leaving the population and settling on other areas, especially to low density sites such as the removal grids. The majority of these individuals (87.5%) was first caught in pitfalls, and over half of these were caught only in pitfalls before leaving. Most of the dispersing animals (62.5%) had already reached adult size before leaving. This was true of both sexes. Almost all the dispersing individuals were caught on the removal areas, even though an adjacent control grid was closer than two of the removal areas. Of all the individuals that disappeared during the study only a very small fraction could be accounted for by dispersal. Most animals which disappeared therefore probably died on the grid.

DISCUSSION

This study has indicated the difficulty of obtaining accurate information on population size and population processes in small mammals, especially at extremely high densities. Numerous workers have tried to elucidate the best methods of obtaining population information (for a review see Smith et al., 1975). Krebs and his co-workers (Krebs, 1966; Krebs et al., 1973; Krebs et al., 1976) have resorted to total enumeration

because rodent populations do not fit the assumptions of deterministic or stochastic models of population estimation (Leslie et al., 1953; Roff, 1973). The major assumption that is seldom met is that all marked and unmarked animals of equivalent age or weight in the population are equally catchable. The complete enumeration technique requires that the majority of the animals be counted. Through the use of a simulation model, Hilborn et al. (1976) have demonstrated that this technique may provide accurate population estimates when 80% or more of the voles are caught in each sampling period. When we entered our estimates of trappability in live-traps (50%) into this model, the model predicted an underestimate of the population size of 20%. The actual underestimate was 63% below the number known to be on the area in July. At this time the young were virtually untrappable in live-traps. In *M. californicus*, Krebs (1966) felt that he was able to enumerate 80 to 90% of the individuals in populations of up to 125 to 150 per acre. Above this density, only about 60 to 80% of the population could be enumerated. In Indiana, Krebs et al. (1969) had evidence that they could enumerate 90% of the *M. ochrogaster* and 75% of the *M. pennsylvanicus* (50% in summer). A trap-out of a number of enclosures suggested that, in Indiana, live-trapping was a fairly reliable technique for *M. ochrogaster*. In the present study, at peak densities, only 37% of the individuals known to be on the area were enumerated by live-traps, compared with 79% by pitfalls. Therefore, with the Longworth live-trapping setup used in this study, we did not succeed in getting accurate estimates of population density.

This *M. townsendii* population was in a peak phase during 1975. The maximum density reached was 519 voles per acre, which is considerably higher than has been enumerated for any other microtine population. Krebs (1966) reported a maximum density of 324 voles per acre for *M. californicus*. In Indiana, *M. pennsylvanicus* reached peak densities of 55 to 60 per acre and *M. ochrogaster* reached densities of 35 to 40 per acre (Krebs et al., 1969). In Britain, *M. agrestis* reached densities of about 300 per acre at Lake Vyrnwy (Chitty, 1952). In all of these studies, only live-traps were used. The above estimates may, therefore, be much lower than the actual population size.

In the present study there are at least two reasons for the inability of the live-trapping technique to give a good description of demographic events in this population. The first reason is that there were too few trap-nights available for all animals to be caught; animals were filling traps faster than they could be processed. Van Vleck (1968) found that the higher the population density the higher the number of traps necessary to catch a given percentage of the population. The second reason may be related to the behavior of dominant individuals, which may deter subordinates from coming near traps or entering them, especially in the reproductive season. Kikkawa (1964) witnessed a number of encounters at live-traps in *Clethrionomys glareolus*, where large dominant animals attacked and chased smaller subordinates away from traps. Gliwicz (1970) also found that the younger a vole, the lower its trappability, and suggested that this was related to its position in the social hierarchy. Andrzejewski et al. (1959) found a positive relationship in laboratory house mice between social dominance and the readiness to enter traps. Other workers have found similar evidence in other species (Davis and Emlen, 1956; Andrzejewski et al., 1967; Joule and Cameron, 1974). In the cotton rat (*Sigmodon hispidus*), Summerlin and Wolfe (1973) found that dominant, heavier animals were more trap-prone than subordinates. These subordinates tended to avoid traps contaminated with the odor of conspecifics, whereas dominant animals did not. Recognizing the odor of certain individuals in traps may be one of the ways young *M. townsendii* learn to avoid traps. However, it is known that the young still prefer to enter dirty traps, presumably because the traps are contaminated with the odor of conspecifics, than to enter clean traps (Boonstra and Krebs, 1976). In this study the young had to grow to a larger body size before they could enter the

live-trap population. Exactly what mechanism prevents young from entering live-traps at an earlier age is unknown, but it may be some form of aggression.

Andrzejewski and Rajska (1972) also trapped a vole population concurrently with pitfalls and live-traps. They found that as animals got older, they entered live-traps more readily and pitfalls less readily. New animals, when introduced into the population, were as hard to trap with live-traps as young residents. These individuals were thought to be low in the social hierarchy of the population. This may be part of the explanation for the long time interval between first capture of adult animals in pitfalls and subsequent capture in live-traps observed in *M. townsendii*. If these adult animals are individuals which have moved from their site of birth, it would presumably take them some time to establish themselves in the social structure of the population. The three animals, which dispersed from other trapping areas onto Grid I and were caught first in pitfalls, took up to 7 weeks to enter the live-trap population.

The two trapping methods sampled different segments of the vole population. Capture in pitfalls probably has two aspects—an accidental one in which animals unfamiliar with the area run down a runway and inadvertently fall into an open trap, and a deliberate one in which animals familiar with the area seek the pitfall as a source of food. Capture in live-traps involves mainly the deliberate aspect, for an animal must first encounter the trap and then enter it. Presumably for these reasons, pitfalls caught the young, inexperienced animals, the transients from surrounding areas, and some residents; live-traps caught mainly animals which had been on the area for some time. In the younger age classes, pitfalls caught animals randomly with respect to sex, whereas live-traps caught mainly young females. This suggests that the behavior of adults may be more effective in preventing young males from entering live-traps, than it is in preventing young females.

Microtines in general have an enormous potential for increase which is seldom realized. One of the reasons for this is the extremely poor rate of survival of the young (Krebs and Myers, 1974). These rates are particularly difficult to measure directly, and so are generally deduced from information on litter size, pregnancy rates, and subsequent capture of young. Immigration and emigration are assumed to cancel each other out. The assumption has been made that individuals caught on the area as young animals were born there and those caught as adult animals were born elsewhere (Hilborn and Krebs, 1976). This is clearly not the case for *M. townsendii* in this study. Young trapped as preweanlings were not trapped in live-traps for up to 6.5 months after their calculated dates of birth. Watts (1970) found similar evidence in *Clethrionomys gapperi*. On trapping areas from which he had removed the large adult males, juveniles entered traps at a younger age. These data suggested that in the unmanipulated population young had presumably avoided the traps. In a number of other studies on microtines, poor recruitment of juveniles has been found and interpreted to indicate poor survival (Getz, 1960; Golley, 1961; Krebs, 1964; Chitty and Phipps, 1966; Krebs, 1966; Krebs et al., 1969), but trap-avoidance until an older age may be part of the reason. This type of trap-response may occur in other cricetids.

Tanton (1965) found a large part of the population of wood mice (*Apodemus sylvaticus*) avoided capture during the summer, and suggested that their avoidance was due to an abundance of food. Sadleir (1965), Healey (1967), and Fairbairn (1976) working on a similar species, *Peromyscus maniculatus*, also found low numbers in the summer and increasing numbers in the autumn but suggest that the cause of this was poor juvenile survival during the breeding season, and good survival and recruitment at the end of the breeding season. However, it may be that juveniles avoid capture in the presence of reproductive adult animals, and enter the trappable population only when breeding stops. It is necessary, therefore, to look at other rodent populations at various densities with more than one trapping technique, to see if certain segments avoid traps.

There is very little information in the literature about the survival of preweanling and post-weanling mice. In *M. pennsylvanicus*, Getz (1960) estimated an average survival of 12% for the first month of life. If weaning occurs at about 21 days of age (Hamilton, 1941; Richmond and Conaway, 1969), this estimate would cover both the preweanling and post-weanling stage. Golley (1961) and Krebs et al. (1969) calculated similar poor survival rates for this species. This trend is also found in other species (Krebs, 1964, 1966; Krebs et al., 1969). In Britain, Godfrey (1955) found evidence that young *M. agrestis* suffered severe mortality after leaving the nest in a decline year. Hoffmann (1958) compared the number of active mammae of females to the number of placental scars in order to measure nestling mortality. His data showed a preweanling survival rate of 68% for *M. californicus* and 62% for *M. montanus*. This is comparable to our estimate of a preweanling survival rate of 74% (survival per 21 days). Hoffmann (1958) found that nestling survival in *M. montanus* actually increased during a decline, which suggested that nestling mortality was not contributing to the population decline. If the poor juvenile survival reported in peak and decline periods is not an artifact of trapping procedures (Chitty, 1952; Chitty and Phipps, 1966; Krebs, 1966; Krebs et al., 1969; this study), then the above data suggest that it occurs primarily in the post-weanling stage. It may be due to different social conditions the young experience during the various phases of a population cycle. Because changes in the rate of juvenile survival are an important driving force in population cycles (Krebs and Myers, 1974), experiments on young-adult interactions similar to those performed by Sadleir (1965) and Healey (1967) on *Peromyscus* would be useful.

The present study suggests several areas that should be explored further. Are the live-trapping techniques now used to study microtines as inefficient at low densities as they are at the high densities observed in this study? Populations of voles at different densities should be trapped concurrently with live-traps and pitfalls to examine this question. Because pitfalls capture the young at an early age, trapping with this technique throughout a cycle might give clues to the cause of the changes in juvenile survival that have been observed (Krebs and Myers, 1974). Finally, what prevents young and old animals from entering live-traps but not pitfalls? Observation of resident animals and introduced young and adults in small enclosures may indicate the role of aggression, odor, or other factors.

ACKNOWLEDGMENTS

This research was supported by grants from the National Research Council of Canada to D. H. Chitty and C. J. Krebs. We thank Jaroslav Picman, Donna Stace-Smith, and Mary Taitt for field assistance, and Dennis Chitty for criticism of the manuscript.

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