# Trappability estimates for mark–recapture data

CHARLES J. KREBS
Department of Zoology, University of British Columbia, Vancouver, B.C., Canada V6T 2A9

AND

RUDY BOONSTRA
Division of Life Sciences, Scarborough College, University of Toronto, West Hill, Ont., Canada M1C 1A4

Received March 21, 1984

KREBS, C. J., and R. BOONSTRA. 1984. Trappability estimates for mark–recapture data. Can. J. Zool. **62**: 2440–2444.

Mark–recapture methods produce more accurate estimates when a high fraction of the population is trapped. Three estimates of trappability are used in the literature, and we compare them for four species of *Microtus* livetrapped in Longworth traps. The trappable population is defined by the weight at first capture and varies greatly in different species. Jolly trappability is the best estimate of trappability and is on average 4% above minimum trappability and 8% below maximum trappability. Trappability in *Microtus* varies seasonally, is lowest in summer, and may be reduced at high densities. Females are, on the average, 2% more trappable than males. Trappability is the same in fenced and unfenced populations and is highly consistent in different populations of the same species. Comparisons between different population studies or trapping techniques should utilize the Jolly trappability measure and recognize that it will usually have a positive bias if capture probabilities are heterogeneous. Minimum trappability is a good second choice.

KREBS, C. J., et R. BOONSTRA. 1984. Trappability estimates for mark–recapture data. Can. J. Zool. **62**: 2440–2444.

Les techniques de marquage et de recapture produisent des résultats plus exacts lorsqu'une fraction élevée de la population est capturée. Trois indices relevés dans la littérature permettent de mesurer la susceptibilité à la capture et ils sont appliqués ici à quatre espèces de *Microtus* capturés dans des pièges Longworth. La population "capturable" est estimée en termes de masse à la première capture et elle varie fortement chez les différentes espèces. L'indice de Jolly est la meilleure estimation et il est en moyenne de 4% plus élevé que l'indice minimum et 8% plus faible que l'indice maximum. Chez *Microtus*, la susceptibilité à la capture varie en fonction de la saison, est plus faible en été et peut diminuer à des densités élevées. Les femelles sont en moyenne de 2% plus "capturables" que les mâles. La susceptibilité à la capture est la même chez les populations libres ou les populations contenues dans une enceinte et elle est constante chez les différentes populations d'une même espèce. L'indice Jolly est donc recommandé dans les comparaisons entre différentes études de population ou différentes techniques de piégeage; il faut toutefois tenir compte du fait qu'il entraîne une surestimation lorsque les probabilités de capture sont hétérogènes. L'indice minimum constitue un bon second choix.

[Traduit par le journal]

## Introduction

The accuracy of population parameters estimated by mark–recapture techniques is strongly determined by the fraction of the population trapped (Hilborn et al. 1976). For many small mammals trappability exceeds 50%, and many authors have abandoned mark–recapture models in favor of enumeration techniques, but this has recently been criticized (Jolly and Dickson 1983; Nichols and Pollock 1983). The inferences that may be drawn from mark–recapture data are strongly affected by trappability, and we thus require a measure of trappability for field studies.

A difficulty in comparing trappability arises because several different measures of trappability are used in the literature. The purpose of this paper is to summarize methods of measuring trappability, to determine which method is most accurate, and to investigate how trappability varies in the two sexes at different seasons of the year and under varying population density and different trapping schedules for several species of small mammals.

## Methods

We define three measures of trappability. *Maximum trappability* was defined by Krebs et al. (1969) as follows:

maximum trappability (%) =

$$100 \sum_{i=1}^{n} \left(\frac{\text{no. caught in sample } i}{\text{no. known to be alive in sample } i}\right)$$

where $n$ = number of sampling periods. Table 1 illustrates how it is calculated. Maximum trappability is known to be an upper limit on trappability. It is biased by including individuals caught only once and never caught again, and it weights individuals that are long lived more heavily than those that are short lived.

*Minimum trappability* was defined by Hilborn et al. (1976) as an average over individuals in the population:

minimum trappability (%) =

$$100 \frac{\sum_{i=1}^{N} \left(\frac{\text{no. of actual captures for an individual} - 2}{\text{no. of possible captures for that individual} - 2}\right)}{N}$$

where $N$ = number of individuals potentially caught more than two times. To calculate minimum trappability the first and last times of capture are excluded from the calculations, since by definition an individual must be caught at these times. Thus all individuals caught only once are excluded from these calculations, as are all individuals caught only twice in succession. Table 1 illustrates these points and illustrates how different maximum and minimum trappability can be for a set of data.

*Jolly trappability* was defined implicitly by Jolly (1965) and Jolly and Dickson (1983):

Jolly trappability (%) =

$$\frac{\sum_{i=1}^{S} \left(\frac{\text{total no. of marked individuals caught at time } i}{\text{estimated marked population size at time } i}\right)(100)}{S}$$

where $S$ = number of sampling times and marked population size is estimated by the Jolly–Seber model (Jolly and Dickson 1983). Table 1 illustrates how these calculations are done.

Trapping data analyzed in this paper were all collected in the same

TABLE 1. Hypothetical data to illustrate the three measures of trappability estimation used for mark–recapture data. For each individual the capture record is indicated as 1 = captured, 0 = not captured but known to be alive

| Individual | Sampling time 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Maximum trappability | Minimum trappability |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | | 6 of 8 | 4 of 6 (66.7%) |
| B | | | 1 | 0 | 0 | 1 | | | | | 2 of 4 | 0 of 2 (0.0%) |
| C | | | | 1 | | | | | | | 1 of 1 | No data |
| D | | | | 1 | 1 | | | | | | 2 of 2 | No data |
| E | | 1 | 1 | 0 | 1 | | | | | | 3 of 4 | 1 of 2 (50.0%) |
| F | | | | | 1 | 0 | 0 | 1 | 1 | | 3 of 5 | 1 of 3 (33.3%) |
| | | | | | | | | | | | Total: 17 of 24 (70.8%) ($n$=6) | Total ($n$=4): 150.0% Average: 37.5% |
| Jolly estimate of $\hat{M}_i$ (formula in Jolly (1965)) | | 3.1 | 4.4 | 8.2 | 7.9 | 5.2 | 4.0 | 3.1 | 2.6 | | | |
| Jolly trappability | | $\frac{2}{3.1}$ | $\frac{3}{4.4}$ | $\frac{2}{8.2}$ | $\frac{4}{7.9}$ | $\frac{2}{5.2}$ | $\frac{1}{4.0}$ | $\frac{1}{3.1}$ | $\frac{2}{2.6}$ | | | |
| | | 65% | 68% | 24% | 51% | 38% | 25% | 32% | 77% | | | |

Average Jolly trappability for 8 samples = 47.6%

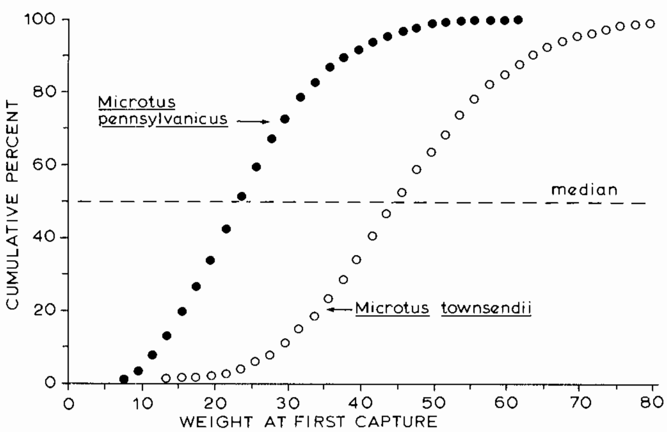


FIG. 1. Cumulative frequency distribution for weight at first capture in Longworth traps for two populations: *Microtus pennsylvanicus*, grid A, Aurora, Ontario; *Microtus townsendii*, grid I, Vancouver, B.C.

manner, described in detail in Krebs (1966). For voles, prebaited Longworth live traps were set for 2 days every 2nd week throughout the year, except for a few cases where snow prevented trapping. The data we analyze here were obtained from the following sources: *Microtus californicus*, Krebs (1966); *M. ochrogaster*, Krebs et al. (1969); *M. pennsylvanicus* in Indiana, Krebs et al. (1969); *M. pennsylvanicus* in Ontario, Boonstra and Rodd (1984); *M. townsendii*, Krebs (1979) and unpublished data.

Trapping data have been summarized over four seasons where possible. We defined *spring* (March to May) as the season when breeding starts until young animals begin to appear in traps. *Fall* (September to November) is typically the opposite time, when breeding is ending. There is some variation among sites in these seasons but we decided to define seasons on the basis of calendar months for simplicity.

## Results

*Weight at first capture*

All population estimates refer to the trappable population, which is poorly defined in most small mammal studies. Figure 1 illustrates the differences that can occur between vole species in size at capture and the variation in weight at which individuals are first trapped. Table 2 provides two quantitative measures of first capture size for four species of *Microtus*. Weights at first capture in Longworth traps form a positively skewed distribution, so the median is always less than the mean weight at first capture.

*Trappability estimates*

Table 3 summarizes for four species of voles the average of the three measures of trappability used in the literature. Maximum trappability exceeds minimum trappability by about 12% on the average, but this difference varies from 8% in *M. ochrogaster* to 19% in *M. californicus*. Jolly trappability is almost invariably above minimum trappability but only by a small amount on average: 4%, ranging from −2 to 12%. Maximum trappability is on average 8% above Jolly trappability for these four species. There is no detectable difference among these species in these patterns. Trappability appears to be the same in fenced and open populations of voles (Table 4).

Females may be more trappable than males in *Microtus*, but the differences are slight. From Table 3, Jolly and minimum trappabilities are 2% higher in females than in males, but these differences are not quite statistically significant ($p$ = 0.07).

*Seasonal variation*

Table 4 summarizes Jolly trappability estimates for the four *Microtus* species over the four seasons. The mean pattern is invariant: trappability is always least in summer. These differences are large. Trappability is depressed in summer 24% in *M. pennsylvanicus*, 21% in *M. californicus*, 16% in *M. townsendii*, and 10% in *M. ochrogaster*. The simplest interpretation of this depression is that it is a result of trapping techniques. Longworth livetrapping can be carried out only at night during the hot summer months, which reduces trapping intensity. In all these studies we checked the traps only once each night. This is probably not a sufficient explanation in all cases, however. At least in *M. townsendii* trappability is also lower in autumn after normal day and night livetrapping has been resumed.

There are three other possible mechanisms for low summer trappability. Food is more abundant in summer, and voles may not enter traps as frequently to get bait. In addition, voles often stuff Longworth traps full of cut grass and dirt so that the trap does not operate properly. We do not know why voles act this

TABLE 2. Median capture weight and average weight at first capture for populations of several vole species. By definition, 50% of all individuals are caught at or below the median capture weight

| | Median capture weight (g) | Average weight at first capture (g) | | Total sample size |
|---|---|---|---|---|
| | | Males | Females | |
| *Microtus californicus* | | | | |
| Parr field | 33 | 35.9 | 32.7 | 1115 |
| Tilden control | 34 | 36.6 | 32.9 | 2022 |
| RFS 6 | 30 | 31.1 | 30.9 | 302 |
| *Microtus ochrogaster* | | | | |
| Grid A | 27 | 28.6 | 27.2 | 398 |
| Grid H | 25 | 25.3 | 24.9 | 321 |
| Carlson's | 26 | 26.5 | 25.6 | 333 |
| Grid B* | 26 | 26.4 | 27.2 | 297 |
| Grid D* | 29 | 30.0 | 28.8 | 723 |
| *Microtus pennsylvanicus* | | | | |
| Indiana Grid A | 25 | 28.7 | 26.2 | 1099 |
| Grid I | 29 | 32.3 | 29.6 | 544 |
| Grid B* | 25 | 27.7 | 25.5 | 758 |
| Ontario Grid A | 23 | 25.7 | 25.1 | 2534 |
| Grid F | 27 | 29.8 | 28.1 | 2239 |
| *Microtus townsendii* | | | | |
| Grid C | 35 | 39.2 | 35.4 | 1562 |
| Grid E | 35 | 41.4 | 34.9 | 1582 |
| Grid I | 46 | 49.6 | 43.2 | 2996 |
| Beacham A | 45 | 48.8 | 42.6 | 764 |
| Beacham B* | 45 | 46.7 | 42.8 | 894 |

*Fenced grid.

TABLE 3. Average overall trappability for the three measures of trappability defined in the text. All trapping data are from Longworth live trapping only

| Species | Maximum trappability | | Minimum trappability | | Jolly trappability | | Total no. of individuals | | No. of individuals present in >2 trap sessions | |
|---|---|---|---|---|---|---|---|---|---|---|
| | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| *Microtus californicus* | | | | | | | | | | |
| Parr field | 80.4 | 83.2 | 54.2 | 66.4 | 55.0 | 69.9 | 546 | 569 | 182 | 282 |
| Tilden control | 79.1 | 76.9 | 60.2 | 59.6 | 67.2 | 71.6 | 1105 | 917 | 517 | 533 |
| RFS 6 | 88.6 | 89.2 | 70.4 | 70.6 | 63.0 | 67.4 | 147 | 155 | 44 | 52 |
| *Microtus ochrogaster* | | | | | | | | | | |
| Grid A | 93.1 | 91.3 | 82.3 | 81.2 | 89.3 | 86.8 | 224 | 174 | 98 | 103 |
| Grid H | 88.5 | 89.2 | 78.0 | 84.6 | 80.3 | 81.3 | 173 | 148 | 84 | 89 |
| Carlson's | 92.8 | 90.7 | 83.6 | 81.4 | 86.3 | 87.6 | 162 | 171 | 79 | 93 |
| Grid B* | 90.5 | 86.6 | 82.7 | 79.0 | 90.0 | 80.6 | 158 | 139 | 112 | 103 |
| Grid D* | 88.1 | 87.9 | 81.9 | 81.5 | 88.8 | 88.6 | 372 | 351 | 329 | 297 |
| *Microtus pennsylvanicus* | | | | | | | | | | |
| Indiana Grid A | 70.8 | 73.4 | 60.8 | 65.3 | 61.9 | 66.2 | 599 | 500 | 369 | 349 |
| Grid I | 71.2 | 73.1 | 59.3 | 64.2 | 61.5 | 63.5 | 295 | 249 | 159 | 157 |
| Grid B* | 69.1 | 66.8 | 53.1 | 54.0 | 64.9 | 59.2 | 368 | 390 | 264 | 295 |
| Ontario Grid A | 73.3 | 76.8 | 57.9 | 67.8 | 59.1 | 68.7 | 1314 | 1220 | 631 | 718 |
| Grid F | 69.8 | 73.7 | 59.7 | 65.4 | 59.2 | 66.8 | 1159 | 1080 | 719 | 747 |
| *Microtus townsendii* | | | | | | | | | | |
| Grid C | 81.9 | 84.2 | 71.6 | 77.2 | 75.0 | 80.2 | 831 | 731 | 442 | 441 |
| Grid E | 82.9 | 81.3 | 75.0 | 73.0 | 81.8 | 80.9 | 833 | 749 | 548 | 518 |
| Grid I | 81.1 | 78.1 | 70.5 | 67.4 | 77.8 | 76.8 | 1460 | 1536 | 912 | 1055 |
| Beacham A | 72.4 | 71.5 | 61.7 | 59.9 | 60.1 | 63.2 | 378 | 386 | 241 | 267 |
| Beacham B* | 70.3 | 70.3 | 59.3 | 61.0 | 64.5 | 62.6 | 480 | 414 | 350 | 295 |

*Fenced grid.

TABLE 4. Mean Jolly trappability estimates for the two sexes over four seasons* (data grouped over years)

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | Spring* | Summer | Autumn | Winter | Spring | Summer | Autumn | Winter |
| *Microtus californicus* | | | | | | | | |
| Parr field | 51.3 | 43.7 | 74.4 | 56.1 | 64.6 | 65.7 | 75.3 | 74.8 |
| Tilden control | 72.6 | 57.5 | 68.4 | 67.4 | 80.0 | 57.4 | 67.1 | 74.5 |
| RFS 6 | 68.3 | 44.1 | 43.6 | 75.3 | 76.3 | 35.8 | 51.4 | 81.3 |
| Mean | 64.1 | 48.4 | 62.1 | 66.3 | 73.6 | 53.0 | 64.6 | 76.9 |
| *Microtus ochrogaster* | | | | | | | | |
| Grid A | 94.0 | 76.9 | 95.9 | 91.1 | 94.0 | 75.6 | 95.1 | 84.3 |
| Grid H | 77.2 | 72.8 | 86.7 | 82.4 | 60.8 | 76.8 | 88.5 | 88.4 |
| Carlson's | 84.1 | 81.3 | 98.5 | 89.0 | 84.3 | 88.0 | 92.7 | 86.9 |
| Grid B† | 94.7 | 84.5 | 88.2 | 92.8 | 87.3 | 69.9 | 81.0 | 84.6 |
| Grid D† | 95.6 | 83.1 | 84.0 | 90.3 | 97.5 | 81.8 | 83.2 | 88.6 |
| Mean | 89.1 | 79.7 | 90.7 | 89.1 | 84.8 | 78.4 | 88.1 | 86.6 |
| *Microtus pennsylvanicus* | | | | | | | | |
| Indiana Grid A | 68.0 | 34.6 | 64.2 | 62.3 | 76.9 | 32.0 | 70.7 | 69.9 |
| Grid I | 72.1 | 48.8 | 56.6 | 67.4 | 69.7 | 43.0 | 67.3 | 70.4 |
| Grid B† | 79.6 | 52.1 | 59.4 | 58.7 | 65.2 | 46.5 | 65.5 | 51.7 |
| Ontario Grid A | 71.8 | 51.0 | 58.3 | 62.1 | 77.9 | 66.7 | 70.0 | 69.8 |
| Grid F | 70.0 | 54.8 | 59.9 | 62.6 | 79.6 | 63.4 | 68.0 | 67.3 |
| Mean | 72.3 | 48.3 | 59.7 | 62.6 | 73.9 | 50.3 | 68.3 | 65.8 |
| *Microtus townsendii* | | | | | | | | |
| Grid C | 86.4 | 64.1 | 69.5 | 80.1 | 89.1 | 72.0 | 79.4 | 80.3 |
| Grid E | 88.5 | 74.8 | 80.2 | 85.5 | 87.1 | 79.8 | 77.6 | 80.1 |
| Grid I | 86.7 | 68.9 | 73.4 | 80.0 | 85.2 | 68.9 | 73.7 | 76.7 |
| Beacham A | 85.0 | 52.1 | 39.4 | 62.8 | 79.5 | 61.6 | 55.2 | 55.9 |
| Beacham B† | 83.1 | 44.4 | 54.7 | 65.8 | 78.4 | 55.5 | 54.7 | 60.7 |
| Mean | 86.5 | 66.4 | 69.1 | 78.0 | 83.9 | 71.1 | 72.0 | 70.7 |

*Seasons are defined as 3-month blocks: spring = March to May, etc.
†Fenced grid.

way, and no one has yet measured the seasonality of this trap-stuffing to see if it is more frequent during summer. There are also more young voles in summer, and young may be less trappable than adults.

*Population density*

Trappability may tend to fall with increasing population density if there is some competition for traps. There is good evidence for this effect in some species such as *Microtus townsendii* (Fig. 2). The same density effect occurs in *M. californicus* ($r = -0.67$). But we could detect no density effect in either *Microtus ochrogaster* or *M. pennsylvanicus*. Seasonal variability in trappability is so large in *M. pennsylvanicus* that it may swamp any density effects.

*Interval between trapping*

Not all small mammal trapping can be done on a 2-week trapping schedule, and we ask how Jolly trappability estimates may change on a 4-week schedule. We attempted to estimate this by discarding trapping data from every other sample and then analyzing the same trapping grid for 4-week trappabilities. This is not exactly equivalent to a 4-week trapping schedule (c.f. Renzulli et al. 1980). We did this for six grids of the four *Microtus* species and got a consistent pattern. Four-week Jolly trappability estmates were 3.3% above those of 2-week trapping. There is apparently a slight gain in trappability at the longer trapping interval. This apparent rise in trappability also occurred for maximum trappability (6%) and for minimum trappability (4.9%).

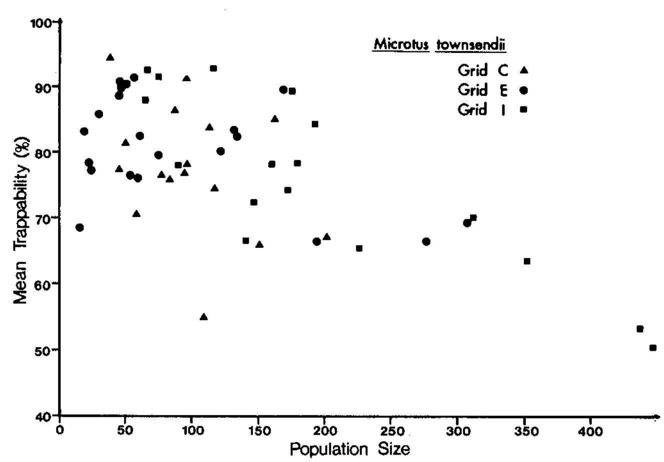


FIG. 2. Average Jolly trappability for the two sexes of *Microtus townsendii* in relation to estimated population size (Jolly model). Data grouped for summer and winter periods for three areas near Vancouver, B.C. ($r = -0.64$).

This apparent rise in trappability occurs because estimates of population size have a larger negative bias when a 4-week trapping interval is used. Renzulli *et al.* (1980) showed that population estimates in *M. pennsylvanicus* were depressed about 13% on average in 4-week trapping schedule compared

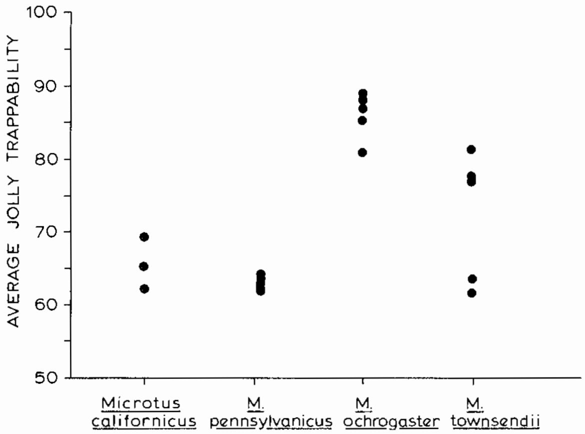


FIG. 3. Average Jolly trappability estimates for three populations of *Microtus californicus* and five each of *M. pennsylvanicus*, *M. ochrogaster*, and *M. townsendii*. All years and both sexes pooled.

with a 2-week schedule. The comparison of trappability estimates is difficult for populations trapped at different time intervals.

## Discussion

The equal catchability assumption underlies all of this analysis in the same way that it is a key assumption of mark–recapture models (Nichols and Pollock 1983). When this assumption does not hold, both Jolly trappability and minimum trappability overestimate true trappability, since in both cases the data are weighted in favour of the individuals that are more easily caught. Another assumption implicit in calculating a measure of trappability is that trappability is the same on each sampling occasion. For the sampling reported here this assumption is probably valid, but it may not be in all mark–recapture studies.

Of the three measure of trappability, we suggest that the Jolly measure is most appropriate, in agreement with the recommendations of Nichols and Pollock (1983). Because randomness of capture is rare with small mammals, the Jolly measure will usually have a positive bias. Minimum trappability is very similar to Jolly trappability, and because it is usually lower than Jolly trappability, it may often be closer to true trappability. In some cases, particularly at low population sizes, the Jolly model of population estimation cannot be applied because too few marked individuals are caught. In these cases minimum trappability should be a good estimate to use. Maximum trappability is the worst estimate and should not be used.

The four *Microtus* species analyzed here have remarkably similar trappabilities within each species (Fig. 3). Within the constraints of the trapping protocol we employed, we can rank them by overall Jolly trappability as folows: *M. ochrogaster* > *M. townsendii* > *M. californicus* > *M. pennsylvanicus*. Trappability may thus be a species-specific trait modified seasonally and by the exact trapping regime.

We had originally hoped to use trappability estimates to screen the population estimates produced by Jolly's (1965) stochastic model. Often in a series of population estimates one estimate is greatly out of line and biologically unreasonable. For example, a Jolly population estimate for midwinter may rise dramatically at a time of year when recruitment or immigration is unlikely. But unfortunately in all situations we have analyzed all three trappability estimates fall at the same time and provide no objective criterion for questioning the Jolly population estimate.

There is one important caveat in all this discussion. We know from pitfall trapping (Beacham and Krebs 1980; Boonstra and Rodd 1984) that Longworth live traps do not sample the entire adult vole population. At high densities in *M. townsendii*, 40–50% of the adults present were not caught in Longworth traps (Beacham and Krebs 1980). In these high density situations we must emphasize that we measure trappability of only part of the population, and true trappabilities may be only one-half those estimated from Longworth livetrapping.

## Acknowledgements

We thank Robert Tamarin, Barry Keller, Mike Gaines, Judy Myers, Mary Taitt, Jim Redfield, Terry Beacham, Janice Leduc, Helen Rodd, and all those who have helped in the gathering of the data analyzed here. The Natural Sciences and Engineering Research Council of Canada provided financial support for which we are grateful. We thank Dennis Chitty, Mary Taitt, and two referees for their helpful reviews of this paper.

BEACHAM, T. D., and C. J. KREBS. 1980. Pitfall versus live-trap enumeration of fluctuating populations of *Microtus townsendii*. J. Mammal. **61**: 486–499.

BOONSTRA, R., and F. H. RODD. 1984. Efficiency of pitfall versus live traps in enumeration of populations of *Microtus pennsylvanicus*. Can. J. Zool. **62**: 758–765.

HILBORN, R., J. A. REDFIELD, and C. J. KREBS. 1976. On the reliability of enumeration for mark and recapture census of voles. Can. J. Zool. **54**: 1019–1024.

JOLLY, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. Biometrika, **52**: 225–247.

JOLLY, G. M., and J. M. DICKSON. 1983. The problem of unequal catchability in mark–recapture estimation of small mammal populations. Can. J. Zool. **61**: 922–927.

KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. **36**: 239–273.

——— 1979. Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. Fortschr. Zool. **25**: 61–77.

KREBS, C. J., B. L. KELLER, and R. H. TAMARIN. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology, **50**: 587–607.

NICHOLS, J. D., and K. H. POLLOCK. 1983. Estimation methodology in contemporary small mammal capture–recapture studies. J. Mammal. **64**: 253–260.

RENZULLI, C. B., J. F. FLOWERS, and R. H. TAMARIN. 1980. The effects of trapping design on demographic estimates in the meadow vole, *Microtus pennsylvanicus*. Am. Midl. Nat. **104**: 397–401.