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CENSUSING MOUSE POPULATIONS BY MEANS OF TRACKING¹

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Abstract. A new approach based on mark-and-sample tracking is presented that may substantially reduce errors in censusing small mammals. A test is included to check the underlying assumption of equal tracking from marked and unmarked mice. A procedure for applying the tracking approach to estimating births and deaths between samples is also presented.

The tracking approach was demonstrated on a population of *Peromyscus maniculatus*. The number of tracks left nightly by males was significantly greater than by females. However, the tracking rate was about the same each night for all individuals of the same sex, even though tracking fluctuated from night to night. The test revealed no strong difference in the tracking rates of marked and unmarked mice. It is concluded that population estimates based on tracking can be highly precise and are far superior to estimates based on trapping alone.

Methods for censusing small-mammal populations by trapping have received continuing attention in the literature, yet trapping methods remain less than satisfactory. This paper presents a new approach that combines tracking with the usual trapping, thereby compensating for several limitations of trapping alone. Mice are trapped and marked by clipping their toes, and the total population is estimated from the proportion of mouse tracks that have appropriately missing toes. This "mark-and-sample" censusing is a non-capture variation on mark-recapture, as there are no captures during the sampling.

Tracking using smoothed sand (Blair 1951, Falls 1953, Bider 1968), smoked paper (Justice 1961, Batzli 1965, Sheppe 1965), and metal plates coated with "liquid talc" (Brown 1969) has been used to study home ranges and activity patterns of mice. It does not seem to have been used for censusing small mammals until recently, when Marten (1970c) developed the approach reported here and Lord et al. (1970) independently used the incidence of mouse tracks as an indicator of relative abundance.

The treatment below concerns mouse populations, but the principles can be applied to censusing many other kinds of animals as well. Further details on many aspects of the non-capture approach to censusing may be found in Marten (1970a).

ADVANTAGES OF TRACKING

Tracking, or any other non-capture sampling technique, has a number of advantages over trapping. With trapping, a small sample size due to small population size or low catchability can generate an enormous standard error. Tracking has the advantage that each individual in the population may be sampled

many times, instead of just once as in a single trapping, and with minimal disturbance to the population. This generates large sample sizes and therefore a more precise estimate of the ratio of unmarked to marked mice used to estimate population size. Fig. 1 contrasts the standard errors for trapping and tracking with an unknown population $U = 100$, a typical population size in ecological research. It is necessary in trapping to recapture more than 60% of the total population to attain an error of less than 10% in estimating the unmarked portion. With tracking, the error is less than 10% if the number of marked tracks exceeds the number of mice in the population.

Another advantage is that tracking is more independent of marking than is trapping, thereby conforming to the equal catchability assumption of mark-and-sample estimates. Tanaka (1963), Tanton (1965), and Marten (1970b) have reviewed the ways in which unequal catchabilities of marked and unmarked mice can inject a severe bias into mark-recapture estimates.

Whether some mice track more than others is irrelevant as long as this is not correlated with their marked/unmarked status. It may be expected that the less similar the sampling stations (e.g., tracking boards) are to the traps used to capture and mark mice, the less likely is a differential response from marked and unmarked mice. Even if bias is present in non-capture sampling, it is more likely than in trapping to be correctable; for example, the sampling rates of marked and unmarked mice, though not equal, may conform to the constant-ratio assumption of the regression method employed by Marten (1970b) to correct for bias.

Tracking also allows a direct conversion from estimated population number to population density in an unenclosed census area. This circumvents a problem of trapping, that mice from outside the trapped area may also be captured, which introduces a ques-

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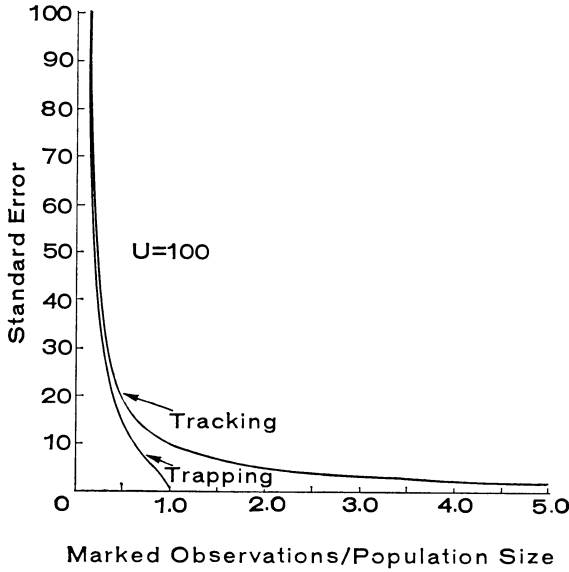


FIG. 1. The standard errors of trapping and tracking mark-and-sample estimates as they depend upon the number of recaptures or marked tracks relative to population size (i.e., $(m + m^*)/N$). The standard errors are based upon $s_{\hat{c}}$, eq. (A-2), applied to a population of 100 mice which remain unmarked before sampling. Further explanation of standard errors may be found in the appendix.

tion of the area occupied by the censused mice. The usual solution has been to compute a boundary strip around the trapped area (reviewed by Pelikan 1967), but this requires information on home-range size which is not easily obtained and is generally lacking in precision. If, on the other hand, a fraction of a mouse is defined to inhabit the census area according to the fraction of its activity (or its tracks) that falls in the area, population density is simply the number of "mouse-equivalents" in the census area.

Finally, a tracking estimate of population density has high resolution in space and time. The census sample can be on any spatial scale and follow any spatial pattern, directly surveying the density of occupancy at the sample locations; and occupancy can be averaged over any time period, from hours to months.

ESTIMATION PROCEDURE

To apply the tracking approach, it is necessary to sample a "census area" for the tracks of all mice, marked and unmarked, whose activities fall wholly or partly within it.

m = the number of tracks of marked mice in the census area.

u = the number of tracks of unmarked mice in the census area.

In addition, sampling must extend over a "calibration area," which includes entirely the home ranges of a known number of marked mice (M), in order

to infer the average number of tracks per "whole" mouse for a particular sample (henceforth called the tracking rate K).

$$\left. \begin{aligned} \hat{K} &= \frac{m + m^*}{M} \\ s_{\hat{K}} &= \hat{K} \sqrt{\frac{1}{m + m^*}} \end{aligned} \right\} (1)$$

where m^* = the number of tracks of marked mice outside the census area.

The calibration area may be identical to the census area, it may contain the census area as in Fig. 3, or it may be entirely separate. It is only necessary that the tracking rate in the calibration area is the same as that in the census area. It is furthermore important that a significant portion of the activity of marked mice does not extend beyond the calibration area, as serious errors may otherwise result.

Once the tracking rate is known, tracks from the census area provide sufficient information to estimate the number of marked mice, $M(c)$, and unmarked mice, $U(c)$, in mouse-equivalents, inhabiting the census area:

$$\left. \begin{aligned} \hat{M}(c) &= \frac{m}{\hat{K}} \\ \hat{U}(c) &= \frac{u}{\hat{K}} \\ \hat{N}(c) &= \hat{M}(c) + \hat{U}(c) \end{aligned} \right\} (2)$$

Standard errors of the population estimates are based upon the inherent variability in tracking counts, the procedure for deriving standard errors being given in the appendix.

$$\left. \begin{aligned} s_{\hat{M}(c)} &= \hat{M}(c) \sqrt{\frac{m^*}{m(m + m^*)}} \\ s_{\hat{U}(c)} &= \hat{U}(c) \sqrt{\frac{1}{u} + \frac{1}{m + m^*}} \\ s_{\hat{N}(c)} &= \sqrt{s_{\hat{M}(c)}^2 + s_{\hat{U}(c)}^2} \end{aligned} \right\} (3)$$

(All estimates are henceforth understood to apply to the census area, and the c in parentheses will usually be omitted for the sake of notational brevity.)

Actually m , m^* , and u must be the number of independent visits to the tracking stations for the standard error estimates to be correct. Number of "tracks" is understood to mean the number of such visits.

Normally the error in \hat{N} (eq. 3) depends primarily upon the error in the estimate of the unmarked population (\hat{U}), which is the portion of the population not directly known and therefore remaining to be estimated. One way to reduce the error is to mark

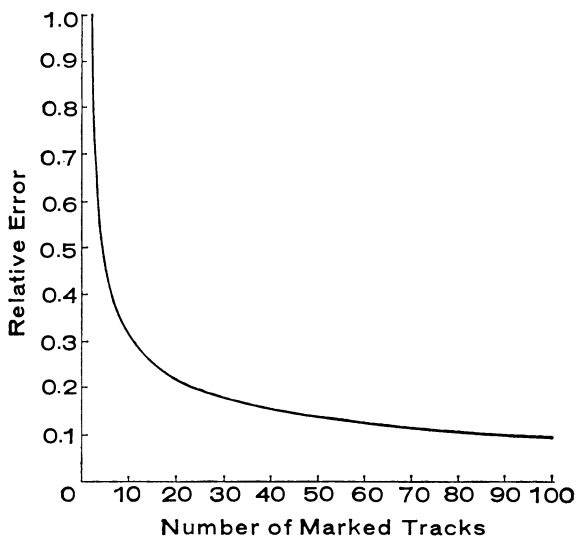


FIG. 2. The relative error of the tracking estimate of the unmarked population ($s_{\hat{U}}/U$), from eq. (3), as it depends upon the number of marked tracks ($m + m^*$). Graphed above is the case where the number of unmarked tracks is large enough to contribute little to the error. If unmarked tracks were few compared to marked ones, the error would depend upon the number of unmarked tracks in exactly the same way as graphed above.

as much of the population within the census area as possible.

The main source of error in estimating the unmarked population is often an insufficient number of marked tracks, $m + m^*$. As seen in Fig. 2, the relative error in estimating the unmarked population becomes quite large when $m + m^*$ is less than 10 and diminishes slowly once $m + m^*$ extends beyond 50.

A REMOVAL TEST

The validity of the assumption of equal tracking of unmarked and marked mice should be checked whenever a mark-and-sample method is employed. One approach is to combine removal with mark-and-sample, where the removal of mice from the unmarked population is accomplished by trapping and marking them between successive tracking samples. Even if equal tracking of unmarked and marked mice does not pertain, N may be estimated under a less-restrictive assumption: the average tracking rates of unmarked and marked mice are in a constant ratio (b) to one another through at least two samples on a closed population. N and b are then estimated from a linear regression equation, with the mark-and-sample estimate of the unmarked population as the dependent variable and the cumulative number of marked mice in the census area as the independent variable (Marten 1970b):

$$\hat{U}_t = b(N - \hat{M}(c)_t) \tag{4}$$

$$\text{where } \hat{U}_t = \left[\frac{u_t}{m_t + m^*_t} \right] M_t \tag{5}$$

and M_t = the cumulative number of marked mice at sample t

$\hat{M}(c)_t$ = the cumulative number of marked mouse-equivalents estimated to be in the census area at sample t .

If $b = 1$ (i.e., the tracking rates of unmarked and marked mice are equal), the simple mark-and-sample estimate (eq. 2) may be applied. If $b \neq 1$, it is advisable to use the regression method to estimate N only with three samples or more, since severe errors can result if the constant-ratio assumption of the regression method is not satisfied. Three or more samples allow the validity of the constant-ratio assumption to be checked by observing whether the points ($\hat{M}(c)_t, \hat{U}_t$) fall on a straight line.

In some situations it may be desirable to trap the population only once, in which case only two tracking samples are possible—before the trapping and after. Although two samples are not sufficient to estimate N safely with the regression method when $b \neq 1$, they suffice to check whether $b = 1$, for applying the simple mark-and-sample estimate. With two samples, the estimation of b from eq. (4) reduces to

$$\hat{b} = \frac{\hat{U}_1 - \hat{U}_2}{\Delta \hat{M}(c)} \tag{6}$$

where $\Delta \hat{M}(c)$ = the estimated number of mouse-equivalents marked in the census area between the first and second samples.

Assuming no birth, death, immigration, or emigration between the two samples, the increase in marked mice in the census area means a corresponding removal from the unmarked population. Equation (6) simply checks whether the estimated decrease between two samples in the unmarked population inhabiting the census area is the same as the actual known decrease.

The procedure in the field is to combine removal with mark-and-sample tracking. The census area is first tracked to obtain information on the unknown numbers of marked mice (M_1) and unmarked mice (U_1) already within it:

- m_1 = the number of tracks from the M_1 mice in the census area during the first tracking
- u_1 = the number of tracks from the U_1 mice in the census area during the first tracking.

If no marked mice are present on the census area from previous censusing, some must be trapped and marked before the first tracking.

Trapping and marking M_2 new mice between the first and second trackings then effects their removal

from the unmarked population. (The newly marked mice should be released immediately to discourage the immigration of any new mice to take their place.) M_{12} of the original M_1 marked mice may also be captured and given a new mark, leaving M'_1 of the original M_1 marked mice uncaptured.

The second tracking includes the census area and any additional area which may be occupied by the known number of mice ($M_2 + M_{12}$) just captured and marked. The number of mouse-equivalents occupying the census area during the second sample may then be estimated from eq. (2), using

$$\left. \begin{aligned} M &= M_{12} + M_2 \\ m &= m_{12} + m_2 \\ m^* &= m^*_{12} + m^*_2 \\ u &= m'_1 + u_2 \end{aligned} \right\} (7)$$

where

- m_{12} = the numbers of tracks from M_{12} in the census area during the second tracking
- m_2 = the number of tracks from M_2 in the census area during the second tracking
- m^*_{12} = the number of tracks from M_{12} outside the census area during the second tracking
- m^*_2 = the number of tracks from M_2 outside the census area during the second tracking
- m'_1 = the number of tracks from M'_1 in the census area during the second tracking
- u_2 = the number of tracks from unmarked mice in the census area during the second tracking.

Note that in estimating the population size the mice in the M'_1 class are treated computationally as if they were unmarked during the second tracking, because even though they are marked, their numbers are not precisely known, as are the M_2 and M_{12} mice.

Turning to the estimation of b , the quantities in eq. (6) follow from eq. (2):

$$\left. \begin{aligned} \hat{U}_1 &= \frac{u_1 \hat{M}_1(c)}{m_1} & \hat{U}_2 &= \frac{u_2}{\hat{K}} \\ \Delta \hat{M}(c) &= \frac{m_2}{\hat{K}} \\ \hat{M}_1(c) &= \frac{m'_1 + m_{12}}{\hat{K}} \end{aligned} \right\} (8)$$

where $M_1(c)$ is the number of marked mice estimated to be in the census area during the first track-

ing and \hat{K} is the tracking rate during the second tracking.

Substituting eq. (8) in (6),

$$\hat{b} = \frac{(m'_1 + m_{12}) u_1 - m_1 u_2}{m_1 m_2}$$

$$s_{\hat{b}} = \sqrt{a_1^2 \left[\frac{1}{m'_1 + m_{12}} + \frac{1}{m_1} + \frac{1}{u_1} \right] + \frac{a_2^2}{u_2} + \frac{\hat{b}^2}{m_2}} \quad (9)$$

where

$$a_1 = \frac{(m'_1 + m_{12}) u_1}{m_1 m_2}$$

$$a_2 = \frac{u_2}{m_2}$$

If \hat{b} were a regression coefficient from eq. (4), based on more than two samples, then $s_{\hat{b}}$ would be the usual standard error, given by Marten (1970b), based upon the scatter of points about the fitted regression line. However, as \hat{b} in eq. (9) is based upon only two samples, $s_{\hat{b}}$ is estimated from the inherent variability in tracking counts (derivation in appendix). If it is desired to check for bias with a precision of at least 10% (i.e., $s_{\hat{b}} < .1$), then $m'_1 + m_{12}$, m_1 , u_1 , u_2 , and m_2 should all exceed 100.

The above estimates assume the M_2 and M_{12} marked mice track at the same rate during the second tracking. The validity of this assumption may be checked by computing \hat{K}_2 , K_{12} , and their standard errors from eq. (1) and noting whether \hat{K}_2 and \hat{K}_{12} differ significantly from each other. If they do differ significantly, all estimates should be based only on \hat{K}_2 or \hat{K}_{12} , whichever generates a value of \hat{b} closest to 1.

REPEATED CENSUSES

It may be desired to census a population periodically, e.g., once a month, trapping only once at each census. The procedure just described—two tracking samples separated by a trapping—can be used at each census to estimate population size and check the assumption of equal tracking rates in marked and unmarked mice. The marked mice for the first tracking in each census are supplied from the marking of previous censuses.

In addition, the birth rate (B) and death rate (D) during the interval between censuses may be estimated by assuming marked mice experience the same death rate as all mice in the population (following Jolly 1965: 233–234). The death rate is the proportion of marked mice present at the end of the previous census but missing at the beginning of the present census.

$$\hat{D} = \frac{\hat{M}_2(t-1) - \hat{M}_1(t)}{\hat{M}_2(t-1)} \quad (10)$$

where

$$\hat{M}_2(t-1) = \frac{m'_1(t-1) + m_{12}(t-1) + m_2(t-1)}{\hat{K}(t-1)}$$

$$\hat{M}_1(t) = \frac{m'_1(t) + m_{12}(t)}{\hat{K}(t)},$$

computing \hat{K} from eq. (1) and (7). $\hat{M}_2(t-1)$ is the number of marked mice estimated to be in the census area after the trapping and marking of the previous census. $\hat{M}_1(t)$ is the number of those $\hat{M}_2(t-1)$ mice estimated to have survived the interval, i.e., the number of marked mice in the census area before the trapping and marking of the current census.

The birth rate is the change in population that is not accounted for by deaths:

$$\hat{B} = \frac{\hat{N}(t) - \hat{N}(t-1)}{\hat{N}(t-1)} + \hat{D}. \quad (11)$$

The reader may use the procedure outlined in the appendix to generate standard error formulas for the above estimates, or for different estimates that he may tailor to his own sampling scheme.

A FIELD EXAMPLE

A population of *Peromyscus maniculatus* was censused in August 1969 to examine the effectiveness of smoked-paper tracking for non-capture sampling. The census area was located in a postburn study plot of the University of California's Sagehen Creek Research Station in the Sierra Nevada Mountains near Truckee, California. *Arctostaphylos*, *Ribes*, and *Wyethia* were the dominant forms of vegetation, and the layout was as shown in Fig. 3. *Citellus*, *Eutamias*, *Perognathus*, and *Sorex* were also present and leaving tracks, but their tracks were easily distinguishable from those of *Peromyscus* and from each other. It is interesting that *Perognathus* tracks were common in the area although only a few *Perognathus* had been captured over 5 years of regular trapping.

Technique

The procedure was to alternate trapping with tracking, marking additional mice at each trapping in order to apply the removal test. A central square in the census area (Fig. 3) was trapped for one night with 140 Sherman and Longworth traps, and M_1 mice were captured, toe-clipped, and released. The census area was then tracked for three nights (the first tracking). The central square was trapped again,

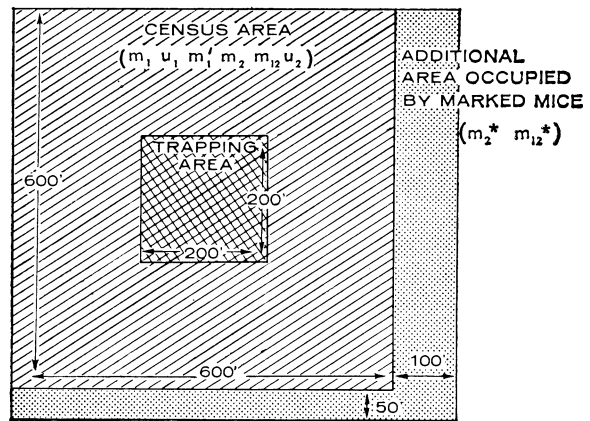


FIG. 3. Layout of the tracking area at Sagehen Creek Station. The figure shows which symbols in eq. (7) apply to the census area and which apply to the additional area occupied by marked mice. The total area is the calibration area.

all M_1 mice were recaptured, but three were accidentally killed, leaving M_{12} mice (Table 1); M_2 new mice were toe-clipped and released. Finally, the census area and a boundary extending beyond it on two sides (Fig. 3) were tracked for three nights (the second tracking).

One night was allowed after each trapping before tracking began, to diminish any immediate effect of previous capture upon tracking. The observation of Sheppe (1967) that the tracking rate of *Peromyscus* increased immediately after trapping suggests this stabilization period may be important.

Tracks were obtained with 8-inch smoked-paper discs purchased from the Bristol Co. (Waterbury, Connecticut) and placed on a 50-ft grid (169 discs in the census area). No shelters were used; each disc was simply held down with a few small stones. Tracks were fixed in the field each morning with Bristol fixative spray, which was found to be more satisfactory than the charcoal fixative spray supplied by art dealers. Whenever a disc was tracked, it was removed the next morning and replaced by another disc placed at least 10 ft away. The discs were placed in locations judged favorable for mice, such as under shrubs or next to logs.

The far right toe on each foot was removed from males in the first trapping, and the next toe from the females. The other two toes were removed from new males and females, respectively, in the second trapping. Even though some of the discs were heavily tracked, reading errors were minimized because each foot carried the same code. This was particularly useful when discs were visited by more than one mouse.

Tracking response

Before proceeding to population estimates, some observations on how tracking rate changed with

tracking technique are in order. No bait was used the first night of the first tracking and 20% of the discs were tracked by *Peromyscus*. Only 7% were tracked the second night. The third night half the discs were baited with a dab of peanut butter in the center and half with a grain of oatmeal in the center and several grains just outside the edge; tracking increased to 28%. In the second tracking peanut butter was discontinued because a visited disc was so heavily tracked that it was difficult to read. The first night of the second tracking the discs were baited only with oatmeal and 81% were tracked. The next night no bait was used and 10% of the discs were tracked. The third night a single grain of oatmeal was placed on each disc (none next to it), and 23% were tracked.

These observations indicated the behavior of the mice toward the paper discs is far from random. If mice stepped on the discs only by chance, there would be few tracks, since the discs occupied only a fraction, 1.5×10^{-4} , of the census area. Initially when no bait was used the mice tracked out of curiosity; each disc was tracked very lightly, indicating a brief inspection. Curiosity waned after a few days, but tracking revived when bait was introduced. The greater the amount of bait, the heavier was the tracking of each disc visited, making some discs difficult to read. It will probably be necessary in each situation to work out the baiting technique that results in a large number of discs being tracked, but not too heavily tracked to be read.

Observations on unbaited smoked-paper discs in a 10-m-square enclosure revealed no conspicuous orientation of resident *Peromyscus* to the discs, but the time pattern of tracking indicated a subtle response. When unbaited discs were new to the mice, they were tracked within a few minutes of being placed in the enclosure. A mouse would pass over the disc so quickly its passage was hardly noticed. Unbaited discs were tracked a few more times in the course of their first night but received few additional tracks on subsequent nights.

Census estimates

Tracking results for adult *Peromyscus* are given in Table 1. The first two nights of the first tracking are pooled to form sample A for m_1 and u_1 ; the third night, when bait was used, forms sample B. The first night of the second tracking forms sample A for m_{12} , m^*_{12} , m_2 , m^*_2 , and u_2 ; the second and third nights are pooled to form sample B. The spatial distribution of adult *Peromyscus* tracks in the census area is given in Fig. 4.

Table 2 summarizes the tracking rate (K) for the several distinct groups of marked mice during the second tracking and shows that tracking rate was consistently about 60% higher for males than for

TABLE 1. Numbers of smoked-paper discs tracked by adult *Peromyscus*

	Tracks	Sample	Males	Females
First Tracking	m_1	A	10	10
		B	8	14
	u_1	A		28
		B		26
Second Tracking	m_{12}	A	17	18
		B	6	5
	m^*_{12}	A	0	0
		B	0	0
	m_2	A	32	17
		B	12	8
	m^*_2	A	6	1
		B	4	1
u_2	A		33	
	B		15	

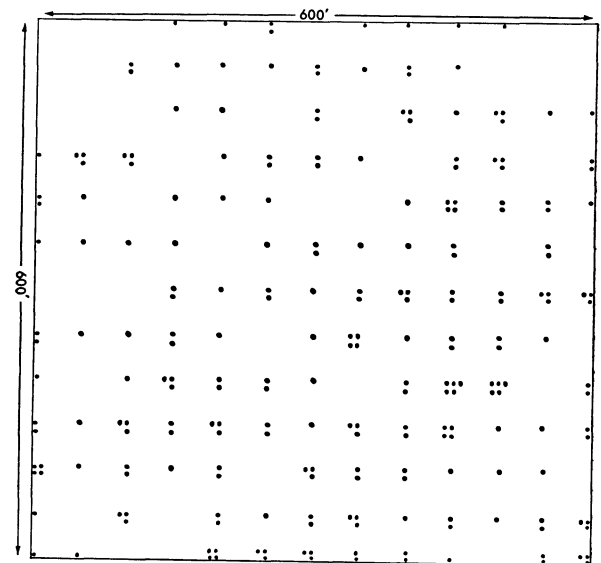


FIG. 4. Occurrence of adult *Peromyscus* tracks in the census area. A location received a dot if any tracks appeared during the night. There was a total of six nights.

females. The tracking rates of the two groups of marked mice, M_2 and M_{12} , were consistently the same when males and females were considered separately, even though the overall tracking rates of samples A and B (i.e., successive nights) were quite different. Estimates (Table 3) can therefore proceed on the assumption that the M_2 and M_{12} marked mice tracked at the same rate.

DISCUSSION

Heterogeneity of tracking rates

Equation (2) is correct when all mice in the population track at the same rate during any particular

TABLE 2. Tracking rates (with one standard error) for the several groups of marked mice at the second tracking, based upon Table 1, using eq. (1)

$$\hat{K}_{12} = \frac{m_{12} + m^*_{12}}{M_{12}} \quad \hat{K}_2 = \frac{m_2 + m^*_2}{M_2}$$

	Males	Females	Males	Females
Sample A	8.5±2.0	6.0±1.4	7.6±1.2	4.5±1.1
Sample B	3.0±2.4	1.7±0.8	3.2±0.8	2.3±0.7
Total	11.5±2.4	7.7±1.6	10.8±1.5	6.8±1.3

TABLE 3. Estimates (with one standard error), based on samples A and B pooled from Table 1, using eq. (2), (3), (7), and (9)

Observations	
$M_{12} = 5$	$M_2 = 9$
$m_{12} = 46$	$m_2 = 69$
$m^*_{12} = 0$	$m^*_2 = 12$
$m_1 = 42$	$m'_1 = 0$
$u_1 = 54$	$u_2 = 48$
Estimates	
$\hat{N} = 17.96 \pm .97$	
$\hat{b} = .68^a \pm .34$	

^aCorrected for the loss of three mice from M_1 between the first and second trackings by substituting for m_{12} in the formula for \hat{b} , eq. (9): m_{12} (corrected) = $m_{12} (M_{12} + 3) / M_{12}$.

sample. Equation (2) is also correct when different mice track at different rates, provided mice of different tracking rates are marked in proportion to the occurrence of that tracking rate in the population. Otherwise, heterogeneity of tracking rates within the population leads to an underestimate of N . This error is primarily one of estimating the unmarked portion of the population and will be smallest when the unmarked population is as small as possible as a consequence of marking.

If the sexes track at different rates, as in Table 2, the best way to deal with the problem is to compute \hat{N} separately for each sex, as though the two sexes were two separate populations. Unfortunately this cannot be done with tracks alone because unmarked tracks cannot be distinguished as to sex. Genital markings, which accompanied some of the *Peromyscus* tracks, could provide a basis for separate computation of \hat{N} , but a sufficient number was not obtained in this study.

Separate computations should be applied to any other groups that track differently from one another, such as juveniles and adults, whose unmarked tracks can be distinguished. Accordingly, the tabulations and computations of Tables 1-3 apply to adults only, though the few juveniles that were marked seemed to track at the same rate as adults.

Marten (1972) has outlined another approach to

estimating different segments of a population separately, based upon a distinct time pattern of activity in each segment. For example, males and females may concentrate their tracking activities in different portions of the night—which can be ascertained from the tracks of marked mice of known sex. Marten (1972) continuously recorded the time pattern of *Peromyscus* activity with long, electronic detection cables on the ground, which registered whenever a mouse passed over.

Estimation of b

The fact that \hat{b} is significantly less than 1 (Table 3) indicates a possible underestimate of U due to pooling the sexes or to a higher tracking rate in marked mice. It is also possible that marked and unmarked mice actually tracked at the same rate, but that there was a slight bias in reading the smoked-paper discs. It is desirable to score the number of visits of marked and unmarked mice, respectively, as a reflection of their proportions in the population. However, different visits are difficult to distinguish on a heavily tracked disc; and counting all the marked and unmarked tracks does not help because the number of tracks left by each visit is highly variable.

This source of error is small as long as multiple visits are rare. The fact that marked male and female tracks sometimes appeared together repeatedly suggests *Peromyscus* sometimes travel in pairs, which could cause multiple visits to occur more frequently than expected by chance. If this seems a problem, bias may be avoided by selecting at random only one track from each disc for scoring.

It is quite likely that \hat{b} was less than 1 in this instance not because marked mice tracked at a higher rate than unmarked ones, but rather because a basic assumption of the removal test itself was violated. It is assumed that known marking between the first and second trackings accounts entirely for any change in the unmarked population. In this instance the two trackings were a week apart because of technique experimentation, but when done properly, no more than a few days should elapse between trackings, to minimize the opportunity for unknown changes to occur. It was observed that juvenile tracks appeared in the "holes" left by the accidental killing of several resident mice, and unmarked mice with adult tracks could have immigrated as well. $\Delta \hat{M}(c)$ in eq. (6) would then indicate the decrement in U to be greater than actually occurred, and \hat{b} would underestimate b .

Additional errors

In small populations there could also be random errors due to departures from sampling assumptions—random errors not taken into account by the

standard error equations presented above. For example, the marked population may consist by chance of individuals tracking at a different rate, on the average, from unmarked ones. Furthermore, even if marked and unmarked mice track the same on the average, their activities (and therefore their expected numbers of tracks) may differ by chance on any particular night. The uniformity of tracking rates observed within the *Peromyscus* population (Table 2) indicates this kind of error may not generally be large.

Nonetheless, it is possible that some species of mice are as heterogeneous (within the population) for tracking as they are for trapping, perhaps because of social dominance. Particularly when the smoked paper is baited, trapping and tracking could be correlated, leading to bias.

Tracking technique

It would be helpful for populations under continuous study if footprints could be marked in a way that does not require the removal of toes (e.g., attachment of a removable wax ring to a toe). This would allow mice to be re-marked at each census without cumulative injury.

Tracking strips traversing the census area, which are coated while laid down, should provide better samples than single smoked cards. A mouse can avoid individual tracking stations, but it must cross strips if it travels about its home range at all. In addition, alternative coatings to smoke might be applied more conveniently in the field or might be more resistant to rain. The ink and mineral oil coating employed by Lord et al. (1970) appears most promising in this regard.

CONCLUSIONS

Tracking permitted the estimation of a small population (Table 3) with a standard error of 5% and a bias (reflected in \hat{b}) that was probably equally small. In contrast, trapping was too erratic to give any precise idea of the total population actually inhabiting the census area.

With sufficient sample sizes of m_1, u_1, m_2 , etc., it should be possible to arrive at tracking techniques in each particular situation that both bring \hat{b} sufficiently close to 1 and make $s_{\hat{b}}$ sufficiently small. Tracking censuses should be satisfactory for many purposes even when some errors persist.

Intensive ecological research aimed at computing birth and death rates to explain population fluctuation and control is less tolerant of error. Complete enumeration seems the best approach to intensive research, not only because there is no error, but because additional information on age, reproductive condition, and so forth is needed anyway. Tracking

and other non-capture sampling techniques can be of service to intensive research in population ecology by checking whether the entire population has in fact been enumerated and, if it has not, by providing an estimate of the hopefully small portion that remains unknown.

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APPENDIX

Standard errors in the text are first-order approximations, derived as outlined by Bennett and Franklin (1954: sec. 3.34). As an illustration, the variance of \hat{b} , from eq. (9) is

$$\begin{aligned} \text{Var}(\hat{b}) &= \left[\frac{\partial \hat{b}}{\partial m'_1} \right]^2 \text{Var}(m'_1) + \left[\frac{\partial \hat{b}}{\partial m_{12}} \right]^2 \times \\ &\quad \text{Var}(m_{12}) + \left[\frac{\partial \hat{b}}{\partial m_1} \right]^2 \text{Var}(m_1) \quad (\text{A-1}) \\ &\quad + \left[\frac{\partial \hat{b}}{\partial u_1} \right]^2 \text{Var}(u_1) + \left[\frac{\partial \hat{b}}{\partial u_2} \right]^2 \times \\ &\quad \text{Var}(u_2) + \left[\frac{\partial \hat{b}}{\partial m_2} \right]^2 \text{Var}(m_2). \end{aligned}$$

$m'_1, m_{12}, m_1, u_1, u_2,$ and m_2 are assumed to be independent Poisson variables: $\text{Var}(m'_1) = m'_1, \text{Var}(m_{12}) = m_{12},$ etc.

Substituting derivatives and variances in eq. (A-1),

$$\begin{aligned} \text{Var}(\hat{b}) &= \left[\frac{u_1}{m_1 m_2} \right]^2 m'_1 + \left[\frac{u_1}{m_1 m_2} \right]^2 m_{12} \\ &\quad + \left[\frac{-(m'_1 + m_{12})u_1}{m_1^2 m_2} \right]^2 m_1 \\ &\quad + \left[\frac{m'_1 + m_{12}}{m_1 m_2} \right]^2 u_1 + \left[\frac{-1}{m_2} \right]^2 u_2 \\ &\quad + \left[\frac{-(m'_1 + m_{12})u_1 + m_1 u_2}{m_1 m_2^2} \right]^2 m_2. \\ \text{Var}(\hat{b}) &= \left[\frac{(m'_1 + m_{12})u_1}{m_1 m_2} \right]^2 \left[\frac{1}{m'_1 + m_{12}} \right. \end{aligned}$$

$$\begin{aligned} &\quad + \frac{1}{m_1} + \frac{1}{u_1} \left. \right] + \left[\frac{u_2}{m_2} \right]^2 \left[\frac{1}{u_2} \right] \\ &\quad + \left[\frac{(m'_1 + m_{12})u_1 - m_1 u_2}{m_1 m_2} \right]^2 \left[\frac{1}{m_2} \right], \end{aligned}$$

the square root of which is $s_{\hat{b}}$, eq. (9).

The standard errors for trapping and tracking graphed in Fig. 1 are based upon the estimate \hat{U} in eq. (2), where in the case of trapping u and m are the number of unmarked and marked captures, respectively, and m^* does not apply. It is assumed for trapping that u and m are independent binomial random variables:

$$\begin{aligned} \text{Var}(u) &= u \left[1 - \frac{u+m}{N} \right] \\ \text{Var}(m) &= m \left[1 - \frac{u+m}{N} \right]. \end{aligned}$$

This corresponds to the fully stochastic case of Darroch (1968), where the exact sample size ($u + m$) is not predetermined. Applying the same procedure as illustrated above for $s_{\hat{b}}$, the standard error of the estimate of the population which was unmarked before sampling is (for both trapping and tracking):

$$s_{\hat{U}} = \sqrt{\frac{X}{w}} \quad (\text{A-2})$$

where X = the number of mice never captured (i.e., $U - u$ for trapping and U for tracking), $w = (m + m^*)/N$.

In trapping, w is the proportion of the population that is recaptured. In tracking, w is the number of marked tracks relative to population size, and eq. (A-2) is an alternative way of stating eq. (3).