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Estimation of Small Mammal Using Recapture Methods: Partitioning of Estimator Variables [1]

[With 1 Fig.]

A model was developed to estimate small mammal densities when capture-recapture methods are used to gather the data. The model includes a grid design surrounded by a dense line of traps to detect movement of animals into and out of the grid. If movement is detected into or out of the grid, dispersal behavior, death rate, trap avoidance, and animal-trap relationships are determined and partitioned to provide the most reliable density estimates. If there is no movement or it is not detected, the density estimates would likely be less reliable. Both the field design and the estimator are coordinated to provide a reliable estimate without home range data. This model seems most useful in studies where permanent or semi-permanent grids are established in populations that cannot be disturbed by removal or kill trapping.

I. INTRODUCTION

Estimating densities of small mammals and other animals in their natural environments is complicated with population variables such as dispersal, death rates, trap avoidance, and animal-trap relationships, which themselves are variously confounded. This confounding stimulates numerous questions concerning the validity of existing estimators and probably includes the reasons why results of work using these estimators have not been satisfactorily duplicated or predicted. It is likely that partitioning of these variables will be required before precise estimators can be developed. This is particularly true when one has to use capture--recapture methods to avoid reducing the population.

Several recent attempts (Calhoun & Casby, 1958; Janion, Ryszkowski & Wierzbowska, 1968; Jolly, 1963, 1965; Leslie, 1952; Tanaka, 1963; Tanaka & Kanamori, 1967; Tanton, 1965, 1969) have been made to generate raliable estimators, but none have taken full advantage of the benefits inherent in coordinating the estimator with the field design. Past attempts have been restricted largely to developing mathematical rationale and procedure that can be used with recapture data, however they are obtained.

This study provides a proposed field design and subsequent analyses that complement each other so that the confounding of variables is greatly reduced and appropriately partitioned. This method should be particularly helpful in studies where permanent or semi-permanent study plots must be maintained.

II. FIELD DESIGN

The basic field design is a 12×12 grid completely surrounded by a dense line[2] (Fig. 1). The grid size and the number of stations may vary to accommodate the species to be studied, providing each station on the grid contains two traps.

Dispersal into and of the grid is estimated with the dense line, which can detect which animals move. A perimeter line[3] is established between the border of the grid and the dense line. The perimeter line is used to determine precisely which of the animals trapped in the grid and/or the dense line should be counted as residents of the grid; thus, becoming a part of the density estimate.

The rationale for the dense line is easier to understand after the methods have been defined for determining how far the dense line should be from the grid border. Line X of the dense line is established a units from the grid border; where a is determined by using the recapture radii for all animal classes of interest. The estimates for recapture radii with .95 confidence are determined by methods proposed by Burge & Jorgensen (1970). Where recapture radii (r) are not known or are known to differ among the classes, a would be expected to be unknown or different for each class. Fortunately, it is not necessary to know the precise values for r since the field design can be adjusted

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[2] The dense line (Fig. 1) is actually three lines (X, Y, Z) of traps that completely surround the grid. The two inner-most (X and Y) maintain trap spacing and number (2 per station) comparable to the grid, but the outer-most (Z) may have one trap per station and the stations are much closer together. The distance between Y and Z is arbitrary, providing it is less than b.

[3] The perimeter line is imaginary since it cantains no traps and is situated mid-way between the border of the grid and the dense line (specifically X).

during sampling to compensate for any error that might have been made. The limitations imposed by a are rather broad, so that several classes can be sampled simultaneously, unless the differences in their respective r values are extreme. If b is the distance between trapping stations in the grid, and r_l and r_h represent the classes with estimates of the lowest and highest recapture radii (r), respectively; then a is chosen so that $(r_h-b)<a/2<r_l$. When a is chosen with these specifications, the area actually trapped by the grid can be accurately determined since animals
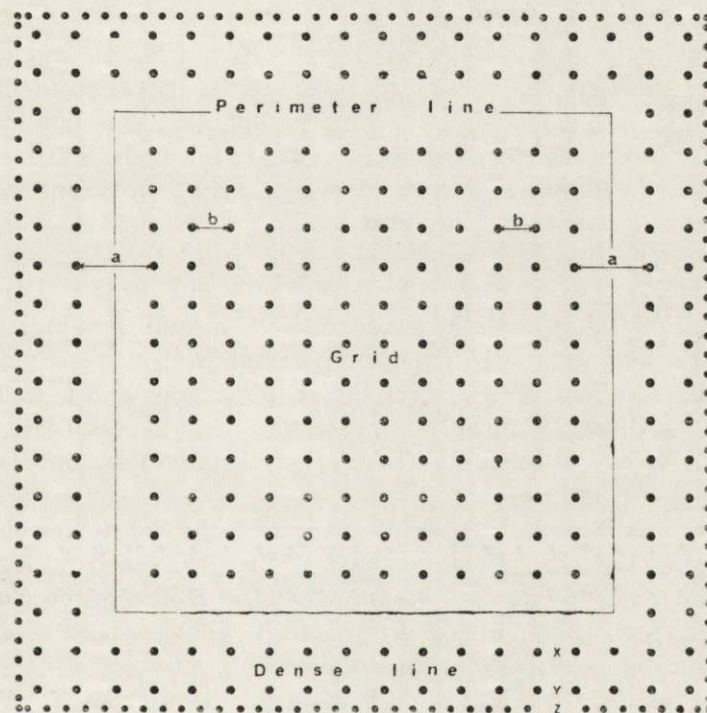

Fig. 1. Schematic diagram of the grid and dense line design. The dense line is made up three (3) lines — X, Y, and Z from the innermost to the outermost. The perimeter line is imaginary and contains no traps.

with the recapture radius r_l will be trapped on the grid — their centers of activity are inside the perimeter line; and animals with the recapture radius r_h are not likely to move from the Z line area to the grid in their normal movement. Whenever possible, a should be a multiple of b since this will simplify establishing the dense line around the grid. This can be done by adjusting the spacing (b) of traps on the grid and/or by adjusting a.

The advantages of this design in estimating densities are evident. It is not necessary to obtain home range data since only those animals whose centers of activity are truly on or inside the perimeter line are counted among the residents of the grid. Thus, it is not necessary to expand the grid by some factor estimated as a function of the home range. Assuming that an animal moves randomly, if its center of activity is right on the perimeter line, one would expect that 50% of its captures would be on the dense line and 50% on the grid. It is unlikely (because of the method for determining a) that an animal will be captured more than two trap--lines from its center of activity.

According to the laws of probability, if an animal is caught at least 60% of the time on the dense line, one can be 95% confident that its activity center is outside of the perimeter line and it is not included in density estimates even on those days when it is caught on the grid. All animals that are caught less than 60% of the time on the dense line are considered to be residents of the grid.

The perimeter line is basically independent of the activity radii for the different classes under consideration, but if one must use an a which is excessive, grid densities for classes with very small r values may have to be determined with grid expansion techniques, since a may be too large for these animals to reach the dense line or the grid if their centers of activity are directly on the perimeter line. It is necessary to use r_h in estimating a if one is interested in that particular class; otherwise, data concerning it are not useful.

When animals that are frequently caught on the Z line are also caught periodically within the boundary traps of the grid (with no signs of directional movement), one may assume that the Z line is too close to the grid and a is too small. This condition can be corrected by re-estimating a and expanding it or by placing another line between X and Y which has spacing identical to X and is b distance away from X. The latter method provides for a wider dense line with more traps, but also provides density estimates for classes with rather small r values.

III. ANALYTICAL METHODS

With confidence established in the area being sampled, one must now estimate the population size within that area, and this can be done while taking full advantage of the information from the dense line. Previous estimators that included mortality L e s l i e, 1952; J o l l y, 1963; 1965) have several behavioral and population characteristics confounded in this one function. This study will attempt to partition mortality, dispersal, and trap avoidance from this confounding. It must be kept in mind that

this partitioning is based on stochastic procedures and should not be considered absolute for any given animal.

The primary function of population estimators is to estimate the number of animals (N_i) at time i, and since a proportional index procedure is used with capture-recapture data, this index must be established first. If Ψ_i is the proportion of marked to unmarked animals in the grid population at time i, then Ψ_i can be estimated with

$$\Psi_i = \frac{m_i}{n_i} \tag{1}$$

where: $m_i =$ the number of animals caught at time i that were previously marked, and

$n_i =$ the number of animals caught in the sample at time i, from data provided by animals caught on the grid, or if data from the dense line are available with

$$\Psi_i = \frac{M_{i-1} - \delta_i(l_i + d_i) + s_{i-1}}{N_{i-1} + k_i - (l_i + d_i)} \tag{2}$$

where: $M_i =$ the number of marked animals in the population at the beginning of trapping time i,

$l_i =$ the number of animals leaving the grid between time $i{-}1$ and i,

$d_i =$ the number of animals that died on the grid between time $i{-}1$ and i,

$s_i =$ the number of n_i animals that were newly marked and released at time i, and

$k_i =$ the number of animals coming onto the grid between time $i{-}1$ and i.

The proportion of animals marked at the beginning of the nest trapping day is provided with

$$\delta_{i+1} = \Psi_i + \frac{s_i}{N_i} \tag{3}$$

It is assumed that animals will respond similarly to traps on the grid and on the dense line. This response (expressed as a probability) may vary from $i \ldots i_n$, but it cannot change substantially between the dense line and the grid on any given day. Since this probability (Φ_i) is essentially what provides the basis for estimating N_i when $N_{i+1} = n_{i+1}/\Phi_{i+1}$, it must be solved for.

The proportion of marked to unmarked animals in the population at time i can now be shown equivalent to

$$\Psi_i = \frac{l_{ti}}{P_{toti} - pk_i} \tag{4}$$

where: l_{ti} = the number of animals caught for the first time on the dense line at time i, that had previously been caught on the grid, and that subsequently disappeared,

P_{toti} = the number of animals caught on the dense line at time i, that are not residents of the dense line or do not remain residents of the dense line, and

pk_i = the number of animals moving onto the grid that were marked on the dense line at time i.

One can conveniently solve for pk_i with

$$pk_i = \frac{\Psi_i P_{toti} - l_{ti}}{\Psi_i} \tag{5}$$

Now that pk_i is solved, and k_{ti} is defined as the number of animals moving onto the grid that were trapped on the dense line at time i and then on the grid at time $i+1$, one can obtain k_{ti} as the product of Φ_i and pk_i. Consequently Φ_i can be obtained with

$$\Phi_i = \frac{k_{ti}}{pk_i} \tag{6}$$

N_{i+1} can now be obtained since $N_{i+1} = n_{i+1}/\Phi_{i+1}$, and an estimate of the population on the grid is available.

This population estimate may (and often will) change among the trapping days necessary to obtain a reliable estimate with confidence. The number of trapping days depends to some extent on the animal-trap behavior and how long it takes to obtain useful data for the species of concern. It would appear that a minimum of 10 days are required, particularly if one requires maximum partitioning of the variables mentioned earlier. The change in the population size (ΔN_i) from time $i-1$ to i is simply the difference between the two days.

$$\Delta N_i = N_i - N_{i-1} = \frac{n_i}{\Phi_i} - \frac{n_{i-1}}{\Phi_{i-1}} \tag{7}$$

and assuming the young animals just entering the trappable population can be identiffied, the change may be attributed to the numbers of trappable animals coming onto, leaving, and dying from on the grid. Thus, ΔN_i may be redefined as $\Delta N_i = k_i - d_i - l_i$.

This partitioning of ΔN_i must be solved if one wants to know the reason for the estimated changes. It might also be recalled that the solution to this equation will provide an estimate of mortality rate and dispersal rate within classes of trappable animals. Assuming the young animals just entering the trappable population can be determined, it is possible to assess further what is providing for k_i since $d_i + l_i = k_i - \Delta N_i$. Substituting this statement in equation 2, one obtains

$$\Psi_i = \frac{M_{i-1} - \delta_i(k_i - \Delta N_i) + s_{i-1}}{N_{i-1} + k_i - (k_i - \Delta N_i)} \tag{8}$$

Since the ratio M_i/N_i is equivalent to m_i/n_i, M_i can be solved and substituted into equation 8 to provide the solution for k_i

$$k_i = \frac{-\Psi_i N_{i-1} - \Delta N_i \Psi_i + s_{i-1} + M_{i-1} + \delta_i \Delta N_i}{\delta_i} \tag{9}$$

Once k_i has been solved, one can solve for the probability of an animal being caught on the dense line during time $i(p_i)$ with $p_i = pk_i/k_i$, which can be used to solve for the total movement onto and off from the grid. The total movement is estimated with $P_{tot i} = P_i l_i + pk_i$, and l_i is conveniently provided as

$$l_i = \frac{P_{tot i} - pk_i}{p_i} \tag{10}$$

Mortality rates are then obtained by simply solving $d_i = k_i - \Delta N_i - l_i$.

Basically, if movement is detected, estimates for N_i and ΔN_i can be conveniently obtained. Also, ΔN_i can be partitioned into d_i (mortality rate), l_i (number of animals leaving the grid), and k_i (number of animals coming onto the grid). It is possible to partition d_i further to estimate trap avoidance (a_i) and separate this from the pooled likelihood that an animal died, estivated, etc. If an animal is caught at time i and was not recaptured before the sampling period (time t) ended, it either died, left the grid undetected by the dense line, or avoided recapture for $t-i$ days.

The probability that it left the grid undetected may be estimated with:

$$q_i = \sum_{j=i+1}^{t} (1-p) \frac{l_j}{N_{j-1}} \tag{11}$$

Now the probability that it stayed on the grid, but simply avoided the traps (a_i) may be estimated as the product of the probability that it was not trapped and the probability that it stayed on the grid. This is obtained with:

$$a_i = \prod_{j=i+1}^{t} (1-\varPhi_j)\, q_i \tag{12}$$

When q_i and a_i are estimated, a new probability of mortality (d'_i) may be obtained with $(1 - a_i - q_i)$. This estimate may then be used to estimate mortality rates in the naturally existing population during the trapping period. This estimate is obviously separate from trap kills. One must always consider that d'_i also includes animals that are not at risk because of estivation.

When movement is not detected on the dense line, except for only one day, J o l l y's (1965) estimate of $\varPhi_i$ ($= p_i$ of J o l l y, 1965) can be used to provide an estimate of N_i if m_i does not vary appreciably. For days when movement is detected in either direction on the dense line, one can estimate p_i, l_i, k_i, d_i, and d'_i. If one can assume a constant relative efficiency of the grid to the dense line, it may be defined with $C = \varPhi_i/p_i$, and used to provide an estimate of $p_i = \varPhi_i/C$ for days where movement data are not available. Again, this uses J o l l y's (1965) estimate of $\varPhi_i$. With p_i solved on days of undetected movement, it follows that $1 - p_i$ is the probability of having the maximum l_i animals move through the dense line undetected is provided with $(1 - p_i)l_i > .05$ at the .95 confidence interval. By using J o l l y's (1965) B_i, which is the number of animals dispersed, a .95 confidence interval can also be placed on the minimum $d_{i(min)} = B_i - l_{i(max)}$, and since $k_{i(max)}$ equals $l_{i(max)}$, $l_{i(max)}$ can also be solved.

An estimate of population number should be accompanied by an appropriate confidence statement. Since the estimates of N_i inside the grid are based on a simple binomial model with parameter $\varPhi_i$, one can use a normal approximation of a confidence interval around the real parameter estimated by $\varPhi_i$. This relationship is readily obtained with:

$$N(0,1) = \frac{\hat{\varPhi}_i - \varPhi_i}{\sqrt{\dfrac{\hat{\varPhi}_i\,(1-\hat{\varPhi}_i)}{pk_{i-1}}}} \tag{13}$$

This is further expressed as a confidence on N_i with:

$$p\left[-Z_{\alpha/2} < \frac{\hat{\varPhi}_i - \varPhi_i}{\sqrt{\dfrac{\hat{\varPhi}_i\,(1-\hat{\varPhi}_i)}{pk_{i-1}}}} \right] = 1 - \alpha \tag{14}$$

or:

$$p\left[\hat{\Phi}_i - Z_{\alpha/2}\left(\sqrt{\frac{\hat{\Phi}_i(1-\hat{\Phi}_i)}{pk_{i-1}}}\right) < \Phi_i < \hat{\Phi}_i - Z_{\alpha/2}\left(\sqrt{\frac{\hat{\Phi}_i(1-\hat{\Phi}_i)}{pk_{i-1}}}\right)\right] = 1 - \alpha \quad (15)$$

By inverting and multiplying by n_i, since $N_i = n_i(1/\Phi_i)$, a confidence on N_i may be obtained with:

$$p\left(\frac{n_i}{\hat{\Phi}_i + Z_{\alpha/2}\sqrt{\frac{\hat{\Phi}_i(1-\hat{\Phi}_i)}{pk_{i-1}}}} < N_i < \frac{n_i}{\hat{\Phi}_i + Z_{\alpha/2}\sqrt{\frac{\hat{\Phi}_i(1-\hat{\Phi}_i)}{pk_{i-1}}}}\right) = 1 - \alpha \quad (16)$$

In cases where pk_i is high, this confidence expression is good, but if pk_i is small (resulting from no detectable movement), J o l l y' s (1965) variance estimate should be used since his approximates a maximum likelihood estimate. Consider the following two cases:

	Case 1	Case 2
pk_7	5	10
k_7	4	8
n_8	40	40
$\hat{\Phi}=k_7/pk_7$	.80	.80
N_8	50	50

In case 1:

$$p\left(\frac{40}{.80+1.96\sqrt{\frac{(.80)(.20)}{5}}} < N_8 < \frac{40}{.80-1.96\sqrt{\frac{(.80)(.20)}{5}}}\right) = .95$$

or $p(35<50<85)$. In case 2, $p(39<50<69)$ is a much improved statement. The confidence in case 1 is too broad to be particularly useful and probably should have used J o l l y' s (1965) variance estimate. The skewed confidence interval is due to $\Phi_i=.80$, thus it might be better to use the actual binomial since the normal approximation is best at $\Phi_i \approx .50$.

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OCENA LICZEBNOŚCI MAŁYCH SSAKÓW METODĄ POWTÓRNYCH ZŁOWIEŃ:
PODZIAŁ ESTYMATORA

Streszczenie

Ocena zagęszczenia małych ssaków jest skomplikowana z uwagi na trudności uzyskania dokładnych informacji odnośnie takich zmiennych populacji jak struktura przestrzenna, tempo wymierania, unikanie pułapki i stosunki zwierzę—pułapka. Największe trudności istnieją w ocenie śmiertelności, zmiennej ważnej dla oceny zagęszczenia, a często obejmującej również inne parametry.

Charakterystyki populacji, zostały w tej pracy usystematyzowane pod kątem uzyskania ocen: prawdopodobieństwa złowienia (*Φ*), ilości zwierząt w terenie (*N*), ilości zwierząt, które opuściły powierzchnię w czasie połowów (*l*), ilości zwierząt, które naszły na powierzchnię w czasie połowów (*k*), ilości zwierząt, które padły na powierzchni w czasie połowów (*d*) i ilości zwierząt na powierzchni a unikających pułapki (*a*).

Powierzchnie odłowne (Ryc. 1) winne być otoczone trzema rzędami pułapek (»dense line«). Jeżeli stwierdzi się migracje zwierząt przez tę strefę zagęszczonych pułapek, to możliwe jest ocenienie wyżej opisanych parametrów oraz wielkości populacji. Jeżeli jednak nie wykryje się takich migracji to oceny zawierać będą mylne charakterystyki i będą mniej realne.

Omawiana metoda może być odpowiednio modyfikowana i stosowana odnośnie wszystkich małych ssaków, które mogą być schwytane w pułapki żywołowne. Bardzo wskazanym jest, by w badaniach ciągłych powierzchnia badawcza była czynna w tym samym miejscu raczej dłuższy okres czasu i by populacja nie była zakłócana przez usuwanie lub zabijanie zwierząt.