

## DENSITY ESTIMATION OF SMALL-MAMMAL POPULATIONS USING A TRAPPING WEB AND DISTANCE SAMPLING METHODS<sup>1</sup>

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**Abstract.** Distance sampling methodology is adapted to enable animal density (number per unit of area) to be estimated from capture-recapture and removal data. A trapping web design provides the link between capture data and distance sampling theory. The estimator of density is  $\hat{D} = M_{t+1} \hat{f}(0)$ , where  $M_{t+1}$  is the number of individuals captured and  $\hat{f}(0)$  is computed from the  $M_{t+1}$  distances from the web center to the traps in which those individuals were first captured. It is possible to check qualitatively the critical assumption on which the web design and the estimator are based. This is a conceptual paper outlining a new methodology, not a definitive investigation of the best specific way to implement this method. Several alternative sampling and analysis methods are possible within the general framework of distance sampling theory; a few alternatives are discussed and an example is given.

**Key words:** capture-recapture; density estimation; distance sampling; plotless sampling; removal sampling; small mammals; trapping; web design.

### INTRODUCTION

Models of capture-recapture and removal studies of small-mammal populations have been used in the estimation of population size for the past half century. These models cover a wide array of assumptions, estimation methods, and tests of model assumptions (see Otis et al. 1978, Cormack 1979, Nichols et al. 1981, Pollock 1981, and Seber 1982 for recent reviews).

In the traditional capture-recapture study, for each of a number of trapping occasions, animals are captured in live traps (often placed in a rectangular grid), marked, and released for subsequent recapture. Nearly all of the estimation methods produce estimates only of population size ( $N$ ). Often biologists are not interested in population size unless the geographic area ( $A$ ) relating to  $N$  is clearly known, in which case a meaningful parameter is density,  $D = N/A$ . However, most often this area is unknown and this represents a serious limitation of capture-recapture and removal studies (White et al. 1982:3–5). One could naively take  $\hat{N}$  divided by the area covered by the trapping grid as an estimator of  $D$ . Unfortunately, this procedure leads to

overestimation as a result of what has been called "edge effect," i.e., not all animals subject to capture have their entire home range within the trapping grid. Thus, the grid effectively traps a larger area than that defined by the grid boundary. Even though this problem has been known for decades (Dice 1938, 1941, Stickel 1954), existing methods still do not effectively handle the estimation of  $D$ .

Three types of methods designed to estimate density appear in the literature; two of them directly rely on Dice's (1938) concept of a boundary strip of width  $W$  around the trapping grid such that the "effective trapping area" is the grid area plus the area of this boundary strip. These two approaches attempt to estimate  $W$  from the capture-recapture data. The third approach involves a more complicated trapping design. The three approaches are (see Otis et al. 1978:67 for additional references):

1) Home range sizes, estimated from the capture locations of animals caught at least twice, are used to estimate the strip width  $W$ . A variety of approaches have been used; all are basically ad hoc and subject to numerous problems, e.g., results depend upon trap spacing and numbers of recaptures. The basic idea of estimating  $W$  based on movement data remains unsatisfactory (see, e.g., Jennrich and Turner 1969).

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2) The parameter  $W$  is directly estimated based on data from selected subgrids (Otis et al. 1978:67-74) using a weighted, nonlinear regression model. This method requires a large quantity of data in order to produce satisfactory estimates.

3) The use of "assessment" lines is the most complex approach to density estimation. It involves designing the study specifically to estimate the effective trapping area as well as the size of the population at risk of capture. There are numerous variants of this approach (Smith et al. 1971, 1972, 1975, Swift and Steinhorst 1976, O'Farrell et al. 1977), but often live-trapping is conducted for  $t$  occasions on a rectangular grid, followed by assessment lines of snap traps radiating from the grid to points well beyond the grid boundary. The effective size of the area trapped is computed using, essentially, ratios of marked to unmarked animals as a function of distance from the edge of the grid. The present analysis methods are ad hoc and the methods are valid only if very restrictive assumptions concerning the capture probabilities are made (i.e., Model  $M_0$  or, perhaps, Model  $M_t$ , see Otis et al. 1978:11).

Schroeder (1981) recently proposed a method that does not fall into any of the above three classes. It uses the relative trap success between inner and outer concentric rows in a square or hexagonal grid to estimate effective area trapped. A simulation study indicated that the method produced acceptable results if an appropriate trap interval was chosen and if the number of trapping occasions was large (on the order of 50). Schroeder's method has not yet been fully developed (the assumptions are not clear, there are no variance estimators, or goodness-of-fit tests). It does not, however, directly produce an estimate of small-mammal density.

Our purpose in this paper is to introduce a new field procedure for direct density estimation that we call a trapping web. Use of a trapping web design allows capture data to be considered as distance sampling data, which is a type of plotless sampling. Distance (plotless) sampling is useful in a variety of contexts. In particular, it includes line transects (see e.g., Burnham et al. 1980) and the special case of "point transects" (see e.g., Ramsey and Scott 1979). In plotless sampling the data are the distances  $d_1, d_2, \dots, d_n$  to the  $n$  entities detected, from either a random line or point. Estimation of density is based on the distribution of these distances. Unlike the traditional capture-recapture and removal methods, distance sampling can be used to estimate population density directly rather than separately estimating  $N$  and  $A$ . The basic theory of distance sampling can be adapted to estimate population size from capture data if a suitable sampling design is used. This trap design allows density of small mammals to be estimated under an entirely new analysis framework, one in which boundary strip width is not relevant, but distance from the web center is critical.

This is a conceptual paper outlining a new and general methodology; it is not a definitive investigation of a specific method. We begin with some review comments on capture-recapture and plotless sampling.

## APPROACHES TO ESTIMATION

### *Capture-recapture*

The theoretical basis underlying capture-recapture sampling has historically been the ball and urn model (Johnson and Kotz 1977) and its various extensions. This framework has the following disadvantages:

1) One must translate from a model based on a simple three-dimensional container to a two-dimensional field problem. This nearly always is done using a rectangular grid.

2) The statistical models for estimating  $N$  from the data are in a class of models whose properties are relatively poorly known.

3) All three approaches given above use  $\hat{D} = \hat{N}/\hat{A}$ ; therefore, if either  $\hat{N}$  or  $\hat{A}$  is biased, so is the estimator of  $D$ . Potential biases of various estimators of  $N$  have been well documented (Burnham and Overton 1969, Otis et al. 1978, Seber 1982). A strong bond exists between the estimators of population size ( $N$ ) and the capture probabilities ( $p$ ), which can take on a wide variety of structures over the population (cf. Otis et al. 1978). It is therefore essential to estimate these capture probabilities properly, which can be difficult, depending on the complexity of the structure of the probabilities. Unfortunately, estimators of  $N$  are often greatly biased because these probabilities are not properly estimated.

4) The sampling distribution of  $\hat{N}$  can be highly skewed even for fairly large samples. Also, there is a strong positive correlation between the estimates and their estimated standard errors. These facts result in poor confidence interval coverage.

## WEB DESIGN

Use of a trapping web enables density to be estimated using distance sampling analysis methods. The web design consists of  $L$  lines of equal length  $a_T$ , radiating from a single randomly chosen center point, each with  $T$  live traps (Fig. 1). Traps are located along each of the  $L$  lines at some distance interval  $\theta$ . Then traps are located at the following distances from the web center:  $a_1 = \theta/2$ ,  $a_2 = a_1 + \theta$ ,  $\dots$ ,  $a_i = a_{i-1} + \theta$ . In an equivalent way, we can define  $a_i = (i-1)\theta + (\theta/2)$  for  $i = 1, \dots, T$  (note that the length of each line is  $a_T$ ). Define points along each line, halfway between traps, as  $b_i$ ;  $i = 0, 1, \dots, T$ , where  $b_0$  is the center of the web ( $b_0 \equiv 0$ ) and  $b_T$  is the boundary of the web which lies beyond the last trap. Define  $b_i$  as  $a_i + \theta/2$  or as  $i\theta$  for  $i = 1, 2, \dots, T$ .

In the analogy to distance sampling methods, all captures by the  $i^{\text{th}}$  ring of traps are considered to be observations of animals at distance  $a_i$  from the center

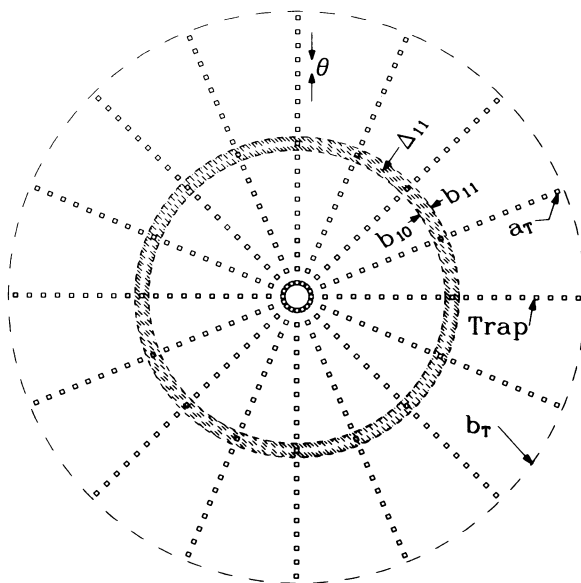


FIG. 1. Trapping web with 16 lines ( $L = 16$ ), each of equal length  $a_T$  and 20 live traps per line ( $T = 20$ ) for a total of 320 traps. The traps are equally spaced from the center of the web at distances  $a_1, a_2, \dots, a_T$ . The points along each line, halfway between traps, are denoted as  $b_i, i = 0, 1, \dots, T$ , where  $b_0 = 0$  is the center of the web and  $b_T$  is the boundary of the web and lies just beyond the last trap. Captures in the 11<sup>th</sup> ring of traps are assigned to the shaded ring  $\Delta_{11}$  which has area  $c_{11} - c_{10}$  where  $c_i = \pi(b_i)^2$ .

point. Because traps are at fixed, equally spaced intervals, these distance data should be treated as "grouped" data (see Burnham et al. 1980:48, 135). The captures in the  $i^{\text{th}}$  ring of traps should therefore be considered to arise from the ring defined by distances  $b_{i-1}$  to  $b_i$ . Heuristically, one can consider that this is the area being trapped by the  $i^{\text{th}}$  interval between traps. The total area of the web out to the  $i^{\text{th}}$  interval between traps is  $c_i = \pi(b_i)^2$ . The area trapped by the  $i^{\text{th}}$  ring of traps is then  $\Delta_i = c_i - c_{i-1} = \pi\theta^2(2i - 1)$  (see Fig. 1).

The trapping web design results in the density of traps being very high at the center of the web and dropping off as distance from the center increases. Typically, traps would be prebaited and placed by skilled technicians to minimize disturbance to the area being trapped. The purpose of the web design is to allow an assumption that all trappable animals at the center of the web are captured during the course of  $t$  days of trapping.

#### Assumptions

We can now state the assumptions needed to consider this web trapping design in a distance sampling framework:

1) Small mammals at the center of the web are captured with probability = 1 by the end of the  $t$  occasions. (It may be that all catchable animals within  $\approx 1/3$

$a_T$  of the center will be captured.) This assumption is analogous to the assumption in distance sampling that all animals on the centerline are detected with certainty.

2) Animal movement is "stable" with respect to the trapping web. This assumption is analogous to detecting individuals before they move from their original position.

3) Distances from the center of the web to each trap are measured accurately.

4) Animal captures are independent events.

Assumption 1 is the most critical for the validity of the general analysis method we propose. The validity of this assumption can be qualitatively verified by monitoring the number of new animals captured near the center of the web on subsequent trapping occasions. Assumption 2 implies that there is no directional movement of the population, toward, away from, or through the web during the study; animals move freely within their home range. We assume that animals are not attracted to the center of the trapping grid for any reason. Assumption 3 requires careful measurements to be made in the field. Assumption 4 is required for estimating the variance of the density estimator [ $\widehat{\text{var}}(\hat{D})$ ].

#### ESTIMATION OF DENSITY

The basic data ( $u_{ij}$ ) are the number of first captures in traps in ring  $i$  on trapping occasion  $j$ , where  $i = 1, 2, \dots, T$  and  $j = 1, 2, \dots, t$ . The standard removal data can be summarized as  $u_j$ , where

$$u_j = u_{1j} + u_{2j} + \dots + u_{Tj}.$$

The total number of different individuals captured in the  $i^{\text{th}}$  ring is denoted as  $n_i$  where

$$n_i = u_{i1} + u_{i2} + \dots + u_{it}.$$

Then, we have  $n = \sum n_i = \sum u_j \equiv M_{t+1}$ , which is similar to the notation used by Otis et al. (1978) except for the definition of  $n_i$ .

The data consist of  $M_{t+1} = \sum n_i$  animals captured and the area  $\Delta_i$  that is associated with each of these captures. In a trapping web, it is area that is being sampled; therefore,  $\Delta_i$  is the relevant statistic to be used. The estimator of density is (Patil et al. 1979 and Burnham et al. 1980:195).

$$\hat{D} = M_{t+1} \hat{f}(0)$$

where  $\hat{f}(0)$  is derived from a function estimated from the data and is then evaluated at zero. Specifically,  $f(c)$  is a probability density function (of area sampled) which can be estimated from the capture data. We recommend the Fourier series estimator based on grouped data as a first choice, although it may be that  $f(c)$  could be more accurately estimated in certain situations by using other estimation procedures developed for distance sampling (see Ramsey and Scott 1979, Burnham et al. 1980). These procedures allow both

TABLE 1. Capture data on *Peromyscus* spp. from a trapping web consisting of 320 live traps ( $L = 16$ ,  $T = 20$ ,  $\theta = 3$  m) near Los Alamos, New Mexico.

$i$	Distance (m)		Area (m <sup>2</sup> )		No. unmarked animals captured ( $u_{ij}$ )				Total $n_i$
	$a_i$	$b_i$	$c_i$	$\Delta_i$	Night 1	Night 2	Night 3	Night 4	
0	...	0	0	...	...	...	...	...	...
1	3	4.5	64	64	1	...	...	...	1
2	6	7.5	177	113	1	...	...	...	1
3	9	10.5	346	170	...	...	...	...	0
4	12	13.5	572	226	2	3	1	...	6
5	15	16.5	855	283	2	...	...	...	2
6	18	19.5	1195	340	...	1	1	...	2
7	21	22.5	1590	395	3	...	...	...	3
8	24	25.5	2043	453	1	...	...	1	2
9	27	28.5	2552	509	3	1	...	...	4
10	30	31.5	3116	564	5	2	...	...	7
11	33	34.5	3739	623	1	2	1	...	4
12	36	37.5	4418	679	5	...	...	...	5
13	39	40.5	5153	735	4	1	2	1	8
14	42	43.5	5945	792	4	2	...	...	6
15	45	46.5	6793	848	3	3	1	...	7
16	48	49.5	7698	905	3	2	1	...	6
17	51	52.5	8659	961	6	1	...	...	7
18	54	55.5	9677	1018	3	...	1	1	5
19	57	58.5	10 751	1074	5	1	2	1	9
20	60	61.5	11 882	1131	8	2	2	1	13
Total $u_j$					60	21	12	5	$m_5 = 98$

\*  $i$  = ring number,  $j$  = trapping night.

point and interval estimates of  $\hat{f}(0)$  to be made, as well as tests of model fit. The conditional variance of  $\hat{D}$  can be computed, for example, by

$$\widehat{\text{var}}(\hat{D}) = (\hat{D})^2 \left[ \frac{1}{n} - \frac{1}{\hat{N}} + \frac{\widehat{\text{var}}(\hat{f}(0))}{(\hat{f}(0))^2} \right]$$

where  $\hat{N} = \hat{D}c_T$ . This variance reflects only the uncertainty of the estimate  $\hat{D}$  of the given trapping web; it does not reflect any possible spatial variation in animal density. The procedure is difficult to compute without a computer; however, a program is documented and available (Laake et al. 1979) that can be used to calculate  $\hat{D}$  and  $\widehat{\text{SE}}(\hat{D})$ . Details on data analysis and use of this program are given in the Appendix.

#### AN EXAMPLE

A trapping web was placed in an area burned in 1977 4.8 km south of Los Alamos, New Mexico. Trapping was conducted for  $t = 4$  nights on a web with  $L = 16$  lines, with  $T = 20$  traps per line, giving 320 traps with  $\theta = 3$  m spacing. Here we will use the capture data for *Peromyscus* spp. summarized in Table 1 for each of the 20 rings. Note that in this example,  $a_1 = \theta$  rather than  $a_1 = \theta/2$  as we now recommend. Animals were marked using a monel metal fingerling tag placed in one ear.

No unmarked animals were captured in the innermost area (out to ring 7) on the fourth night, and only two new captures were made on the third night. This is taken as evidence that the probability of capture near the web center is one and thus satisfies the most critical assumption of the method.

It appears from the frequencies of capture in the two outer areas ( $\Delta_{19}$  and  $\Delta_{20}$ ) that animals outside of the web were attracted to the baited traps (Fig. 2). This is also common in grid trapping studies (a statistical test for this has been developed by Otis et al. 1978:70–71). In distance sampling these two rings can be truncated for analysis and this represents a significant advantage of the proposed method. The analysis is now based on the frequency for  $\Delta_1$  through  $\Delta_{18}$ .

The data ( $u_{ij}$ ) for each of the four trapping occasions ( $j = 1, \dots, 4$ ) are summed for each of the 18 rings ( $i = 1, \dots, 18$ ) to obtain  $n_1, n_2, \dots, n_{18}$  (see final column of Table 1) and these are summed to give  $n = M_{t+1} = 76$ . No recaptures are involved in the analysis; the data are "removal" data whereby animals captured are removed from the unmarked population of interest by marking.

Only the values of  $c_i$  and  $n_i$  are required as a basis for estimating  $f(0)$ ; details of the procedure used in this example are given in the Appendix. Only one Fourier coefficient was used ( $m = 1$ ) giving  $\hat{f}(0) = 0.00012$  and  $\hat{D} = 0.0092$  animals/m<sup>2</sup> or 92.56 animals/ha with a standard error of 13.4. This result seems reasonable as 76 animals were captured in the 18 rings and an estimated total of 90 were present ( $\hat{D} \cdot c_{18}$ ).

The Fourier series model fits the data ( $\chi^2 = 13.6$ ,  $df = 16$ ,  $P > .63$ ). The Fourier coefficient  $\hat{\alpha}_1$  is not significantly different from zero, probably due to the small value of  $\theta$ . The trap spacing  $\theta = 3$  is perhaps too small and, therefore, relatively few animals in the web were never captured. If a larger trap spacing were used, the function  $f(c)$  would probably drop more rap-

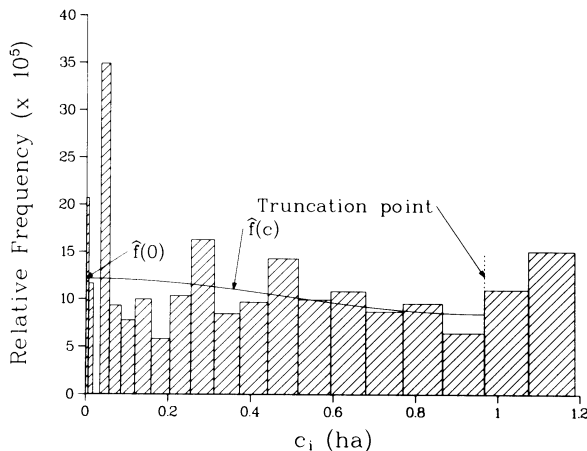


FIG. 2. Relative frequency histogram of capture data showing evidence of ingress on the outer two rings and a suggested truncation point at  $c_{18}$ . Also shown is the estimated probability density function of area sampled,  $\hat{f}(c) = (1/c_{18}) + \hat{\alpha}_1 \cos(\pi c/c_{18})$ , where  $c_{18} = 9677 \text{ m}^2$  and  $\hat{\alpha}_1 = 0.184 \times 10^{-4}$  ( $\text{SE}(\hat{\alpha}_1) = 0.166 \times 10^{-4}$ ). Each bar of the histogram has height  $n_i/(n\Delta_i)$ . Relative frequency scale values should be multiplied by  $10^{-5}$ .

idly and at least the first coefficient would be significant. If one believed that all the animals had been captured, density could be estimated as  $\hat{D} = M_{t+1}/c_{18}$ .

The estimated standard error of  $\hat{D}$  is a measure of conditional, or "within-plot," uncertainty of  $\hat{D}$  at the location of this trapping web (i.e.,  $[\text{var}(\hat{D}|D)]^{1/2}$ ). It is not valid to use it as a measure of spatial variation of the true population density. Hence, we cannot make inferences to a larger area based on this standard error (see Appendix for comments on using  $k$  webs).

The analysis might be improved by further grouping the data into, say, five large groups defined by rings  $b_0$ – $b_4$ ,  $b_4$ – $b_8$ ,  $b_8$ – $b_{12}$ ,  $b_{12}$ – $b_{16}$  and  $b_{16}$ – $b_{20}$  and then tabulating the corresponding new frequency counts,  $n_1, \dots, n_5$ , for analysis. Another possibility is to group the data into three intervals  $b_0$ – $b_6$ ,  $b_6$ – $b_{12}$ , and  $b_{12}$ – $b_{18}$ , and truncate the remaining areas if there is an edge effect due to animals whose home ranges lie largely outside the web being trapped.

#### DISCUSSION

A trapping web design enables data from capture-recapture and removal studies to be analyzed as plotless or distance sampling data. It is an attempt to estimate density directly by relaxing both the strong assumption of geographic closure (White et al. 1982: 120–131) in capture-type models and the need to know a model for the capture probabilities. Death during a 3-d period is frequently negligible, and very young animals can be ignored in the marking and data-recording program, thus making assumptions about demographic closure valid. Nothing is assumed about types of variation affecting the capture probabilities; essentially we

envision the population under Model  $M_{tbb}$ : capture probability varying by time, behavior, and individual heterogeneity. The method suggested is free from the concept of a boundary strip and associated estimation of a home range size. The concept of a web design can be thought of as an extension of assessment lines whereby, (1) the rectangular trapping grid is not employed, (2) trap density near the center is very high to allow all animals near the center to be captured with certainty, and (3) rigorous analysis methods are possible.

This paper was written for "small mammals" for convenience, but the application is perhaps much broader. There will be many variations in the field procedure. These are to be encouraged as long as the trapping assures that the capture probability = 1 in the center of the web. Trap spacing along each line should be determined with respect to the home range of the animal under study. The spacing should be such that there are perhaps 8–12 traps (or more) per home range in the center of the web.

Truncation of the distance data prior to analysis and estimation of  $f(c)$  lessens complications caused by animals being attracted to the baited web of traps. We suspect it will often be necessary to delete first captures from the outermost one or two rings of traps.

It appears that reasonably good estimates can be made from as few as 60 initial captures. An additional advantage of the trapping web design is the ease with which the web is laid out in the field. A stake driven at the center of the web, a light rope or cord marked at the  $a_i$  distances, and a compass are all that are needed to place the traps. Trapping can often be conducted for only three or four occasions and animals do not have to be uniquely marked. We tentatively recommend 16 lines in the web designs such that  $L \times T > 250$  (Fig. 1), and  $\theta \approx 4.5 \text{ m}$  for populations of mouse-sized mammals.

The proper analysis treats the data as grouped distance sampling data because the areas  $\Delta_i$  differ in size. We envision that many analyses would benefit from further grouping. Further grouping is done for testing purposes (both statistical and visual inspection of the relative frequency histogram), not estimation. The number of  $\Delta_i$  to be grouped need not be uniform, nor of equal area. The trap spacing  $\theta$  need not be equal for the validity of the analysis method proposed; however, we see no compelling reason to employ an uneven spacing of traps. It seems possible that the recapture data might be used, and thereby increase the efficiency of estimation. However, the use of these data may be possible only if more restrictive assumptions are allowed (e.g., no behavioral response to capture).

Other analysis methods are possible in this general framework. We suspect the exponential power series (Pollock 1978) and the exponential quadratic (Burnham et al. 1980:144–145) will also have good properties. These methods are also available in program

TRANSECT. Additional work is required to explore alternative approaches to variance estimation. In fact, the whole concept of using a trapping web design coupled with a distance sampling and analysis approach may be a fruitful research area for several years to come.

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#### APPENDIX

This section summarizes the estimation procedure using the Fourier series estimator on grouped data. Most of the following is a direct extension of the material from Burnham et al. (1980:195–196); also see Patil et al. (1979). The estimator of density from capture data gathered from a trapping web is

$$\hat{D} = M_{t+1} \hat{f}(0)$$

where  $M_{t+1}$  = the number of different individuals captured and  $\hat{f}(0)$  = the value of a function, evaluated at zero, that is estimated from the  $M_{t+1}$  distances from the web center to the trap in which individuals were first captured. The function  $f(c)$  represents the probability density function of capture during the study (all  $t$  occasions) based on the distance from the center of the web. Specifically,  $M_{t+1} = \sum_{j=1}^t u_j$  where  $u_j$  is the number of unmarked animals captured on the  $j^{\text{th}}$  occasion. Usually,  $t$  will be 3–4 occasions. The method does not require that animals be individually marked.

If  $n = M_{t+1}$  animals are captured over  $t$  occasions, the data are merely  $n_1, n_2, \dots, n_t$ , the number captured in area  $\Delta_i$  (see Fig. 1 and Table 1). The function  $f(c)$  can be estimated from these grouped data using a variety of methods. We suggest the use of the Fourier series because it has good properties for the estimation of  $f(c)$  in line transect sampling (Crain et al. 1979). A relative frequency histogram of the data can

be plotted using  $n_i/(n\Delta_i)$  for histogram heights. This gives a rough visual look at  $f(c)$  (see Fig. 2).

Although the capture data  $n_i$  are grouped, there still exists an underlying, continuous function  $f(c)$  to be estimated. Each captured animal occurs in one of the  $T$  mutually exclusive intervals  $\Delta_i$ . Under the assumption that these are independent events, the frequency counts  $n_i$  are multinomial random variables:

$$\Pr\{n_1, \dots, n_T\} = \left( \frac{n!}{(n_1)! \cdots (n_T)!} \right) \cdot \prod_{i=1}^T (p_i)^{n_i}$$

where  $p_i = \int_{c_{i-1}}^{c_i} f(c) dc$ . These probabilities are not the same as the capture probabilities in Otis et al. (1978).

The Fourier series model for  $f(c)$  is

$$f(c) \approx \frac{1}{c_T} + \sum_{k=1}^m \alpha_k \cos\left(\frac{k\pi c}{c_T}\right)$$

where the  $\alpha_k$  parameters are called Fourier coefficients and can be estimated from the grouped data. Using the Fourier series model the  $p_i$  become explicit functions of the unknown parameters  $\alpha_1, \alpha_2, \dots, \alpha_m$ :

$$p_i = \frac{c_i - c_{i-1}}{c_T} + \sum_{k=1}^m \alpha_k \left( \frac{c_T}{k\pi} \right) \left[ \sin\left(\frac{k\pi c_i}{c_T}\right) - \sin\left(\frac{k\pi c_{i-1}}{c_T}\right) \right]$$

This relates the unknown parameters  $\alpha_1, \dots, \alpha_m$  to the data through its multinomial distribution, hence these parameters can be estimated by the method of maximum likelihood (see Burnham et al. 1980:134–141). Finally, because  $\cos(0) = 1$ , we have

$$\hat{f}(0) \approx \frac{1}{c_T} + \sum_{k=1}^m \hat{\alpha}_k$$

where  $m$  is usually 1 or 2 and is selected using likelihood ratio tests (Burnham et al. 1980:70–73).

With slight modification of the input, computer program TRANSECT (Laake et al. 1979) can be used to compute  $\hat{\alpha}_1, \dots, \hat{\alpha}_m, \hat{f}(0), \hat{\text{var}}(\hat{f}(0))$  and  $\hat{D}$  easily using the Fourier series

method.<sup>2</sup> The frequency counts  $n_1, \dots, n_T$  are entered along with the cut points  $c_1, \dots, c_T$ . To allow for the program properly to estimate  $\hat{D}$  for capture data, the line length  $L$  must be set equal to 0.5 (program TRANSECT assumes the formula  $\hat{D} = n\hat{f}(0)/2L$ ).

The estimation of the (within web) sampling variance of  $\hat{D}$  will have to be computed by hand but this is easily done using the various results printed by program TRANSECT. The variance can be computed as

$$\widehat{\text{var}}(\hat{D}) = (\hat{D})^2 \left[ \frac{1}{n} - \frac{1}{\hat{N}} + \frac{\widehat{\text{var}}(\hat{f}(0))}{(\hat{f}(0))^2} \right]$$

where  $\hat{N} = \hat{D}c_T$  and the other quantities are given in the output from TRANSECT.

Finally, we mention that if a large area is to be sampled using  $k$  randomly placed webs, each trapped for  $t$  occasions, the same theory applies and the estimator for the average density for the entire area is

$$\hat{D} = \frac{M_{t+1}\hat{f}(0)}{k}$$

where  $M_{t+1}$  is the total number of initial captures on all trapping webs and  $f(0)$  is estimated from the pooled data. Because  $k$  will typically be small, the variance of this estimate of density might best be computed using the jackknife method (Burnham et al. 1980:53–54); however, other approaches are also possible (e.g., Burnham et al. 1980:51, Eq. 1.17) if  $k$  is larger. In fact, a referee suggested the use of

$$\hat{D} = \sum_{i=1}^k \hat{D}_i/k$$

and the corresponding empirical estimate of the sampling variance.

<sup>2</sup> A magnetic tape with the FORTRAN code is available from SHARE Program Library Agency, P.O. Box 12076, Research Triangle Park, North Carolina 27709 at a cost of ≈\$40.