ECOLOGICAL APPLICATIONS OF ELEMENTAL LABELING: ANALYSIS OF DISPERSAL, DENSITY, MORTALITY, AND FEEDING

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ABSTRACT

Trace elements show promise as labels for mark-recapture studies on dispersal, density, mortality, and feeding of insect populations. I review how each of these variables can be estimated, illustrating the use of trace element labels with examples from mark-recapture studies on *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae), a larval endoparasitoid of *Heliothis* and *Helicoverpa* spp. (Lepidoptera: Noctuidae). Criteria for distinguishing labeled from unlabeled insects should include the risk of misidentifying labeled insects. A maximum of 7 to 63 distinct marks are possible, depending on the detection techniques used. In absolute measures of dispersal distances, one must account for dilution of recaptures in estimating the probability of dispersal to a given distance. Dispersal must be accounted for in estimates of mortality in open populations, and a method for doing this is suggested. Trace elements can be used in estimates of population density and mortality involving single mark-releases with single or multiple samples after release. In analyzing trophic relationships, trace elements are best used for positive identification of trophic links. Although the promise of trace element labels has yet to be fully realized, perhaps because of the labor involved in mark-recapture studies, increased use of trace element labels and mark-recapture in the future seems likely given the importance of the variables which they can be used to estimate.

INTRODUCTION

Trace elements, like rubidium (Rb), cesium (Cs), and strontium (Sr), which are physiological analogues of metabolically active elements such as potassium and calcium, show promise as labels in mark-recapture studies (Richardson et al. 1969, Berry et al. 1972, Stimmann et al. 1973, Shepard and Wadill 1976, Graham and Wolfenbarger 1977, Graham et al. 1978b, van Steenwyk et al. 1978a, Wolfenbarger et al. 1982, Burns et al. 1983, Moss and van Steenwyk 1984, Legg and Chiang 1984, Hayes and Hopper 1987; although see Chamberlain et al.1977 and Mitchell et al. 1982 for less successful applications of trace element labels). Several crucial ecological variables can be measured with mark-recapture techniques, including dispersal, population size, mortality, and trophic relationships. Measurement of these variables is a large and complex problem. Fortunately, mark-recapture studies using trace element labels are in many ways no different than such studies with other sorts of labels, and general mark-recapture techniques and data analysis have been thoroughly treated elsewhere (e.g., Seber 1982 and Southwood 1978). Here, I limit myself to a brief review of how dispersal, population size, mortality, and trophic relationships can be measured using trace element labels. I will illustrate methods of analysis with examples from my own work on the population ecology of *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae), a larval endoparasitoid of *Helicoverpa zea* (Boddie) and *H. virescens* (F.) (Lepidoptera: Noctuidae). In this research, I labeled adult parasitoids by rearing them as larvae on hosts fed artificial diet labeled with Rb, Sr, or Rb and Sr (Hopper and Woolson 1991).

DISTINGUISHING MARKED FROM UNMARKED INSECTS

Levy and Cromroy (1973) found in a survey of elemental composition of insects that potassium concentrations ranged from 464 to 31709 ppm, depending on insect species, although concentrations were mostly from 5000 to 15000 ppm. If all of this potassium were replaced with rubidium, a very strong and unmistakeable signal would result because of the rareness of rubidium in the environment. Complete replacement is not possible because of the dynamics of uptake and elimination (Fairbanks and Burch 1968, Webster and Crossley 1978), toxicity of some trace elements at very high concentrations (Moss and van Steenwyk 1984), and cost. Also, background concentrations of some trace elements are high in some systems (Hayes and Hopper 1987). Thus, unambiguous criteria are needed for distinguishing labeled from unlabeled insects. Criteria that could be used include (1) trace element concentration is beyond the upper limit of maximum concentration in unlabeled insects, (2) trace element concentration is beyond the 95% or 99% confidence interval of mean concentration in unlabeled insects, and (3) trace element concentration is beyond three standard deviations of the mean concentration in unlabeled insects. The first criterion can be very sensitive to the number of insects examined to determine the maximum unlabeled concentration. The second criterion is unsuitable for classifying insects as labeled or unlabeled because a confidence interval for mean concentration describes the likely values for the mean, not for individual observations. The third criterion, first suggested by Stimmann (1974), is the most reasonable currently in use.

If the concentrations in unlabeled insects are normally distributed, the probability of an unlabeled insect having a trace element concentration three standard deviations above the mean is 0.0013. Thus, with this criterion, the probability of incorrectly identifying an unlabeled insect as labeled (p) is very low. Unfortunately, elemental concentrations are often not normally distributed (Hopper and Woolson 1991) so that p could be greater or less than 0.0013, depending on the exact distribution of concentrations. If enough unlabeled insects are analyzed to allow calculation of an accurate probability density function, it would be better to use this empirical distribution rather than to assume a normal distribution. Furthermore, the Stimmann criterion addresses the probability of misidentifying unlabeled insects, but not of misidentifying labeled insects. When only one element is used in an insect and the objective is to measure dispersal, misidentifying labeled insects just loses data. However, in dispersal studies where more than one element is used per insect or in studies on population size or mortality, misidentifying labeled insects could seriously affect the results. In these cases, it would be useful to have a criterion which minimizes the risks of misidentifying both labeled and unlabeled insects. Such a criterion would depend on the actual distributions of concentrations in unlabeled insects and in insects labeled with each trace element.

THE NUMBER OF DISTINCT MARKS

A general constraint with using trace element labels is that there are few suitable elements and thus few distinct marks. If one assumes that insects are either labeled or not labeled with each element, the number of marks possible is 2^u-1, where u is the number of elements. Three elements, Rb, Sr, and Cs, are reported in the literature as useful when atomic absorption spectrophotometry (AAS) or atomic emission spectrophotometry (AES) are used for detection (Berry et al. 1972, Burns et al. 1983, Moss and van Steenwyk 1984). This means seven distinct marks are possible. Adding neutron activation analysis for detection could increase the number of elements to around six (Monro 1968, Richardson et al. 1969), which means 63 marks. However, the lathanoid elements made available by neutron activation analysis are extremely expensive and not feasible for use in the large quantities often needed in mark-recapture studies.

Another way to increase the number of marks would be to use several concentrations of each element. Here, the number of marks is L^u-1, where L is the number of levels of concentration of each element. With three elements and three concentrations (including 0), this means 26 distinct marks, a decided improvement over the seven available with only two concentrations. Unfortunately, element concentration often declines after insects cease eating

labeled food (Fairbanks and Burch 1968, Webster and Crossley 1978, van Steenwyk et al. 1978a, Fleischer et al. 1986), so the use of more than two concentrations (background and labeled) would require knowing the time since cessation of feeding on labeled food. Furthermore, the variance in elemental concentration is often high, even in insects that ceased feeding on labeled food at the same time, which hampers the use of more levels than labeled versus unlabeled.

DISPERSAL

One of the prime reasons for the original use of trace element labels was the desire to measure insect dispersal in the field (Richardson et al. 1969, Berry et al. 1972), and measurement of dispersal remains the only published use of trace element labels in studies of insect populations. The principal advantage of trace element labels is that they allow labeling of large numbers of insects with little disturbance to their behavior. Berry et al. (1972) found they could label insects with rubidium by treating host plants with an aqueous solution of rubidium chloride, so that populations could be labeled in the field without handling the insects.

Once insects are labeled, data can be collected in several ways, depending on the question addressed, and a few examples illustrate this. To answer the question 'What is the the effect of host density on female parasitoid dispersal?', I released labeled female *M. croceipes* in field plots with various densities of host larvae and recorded the spatial distribution of recaptured females. I compared the proportion of recaptures in release plots with that in other plots as a function of host density in release plots (Fig. 1). To get a qualitative picture of the spatial and temporal pattern of dispersal of *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae), Van Steenwyk et al. (1978a) labeled a field population by treating cotton, *Gossypium hirsutum* L., with RbCl. To estimate dispersal, they used the percentage of marked moths among moths captured in light and pheromone traps at various distances from the labeled field plot. Wolfenbarger et al. (1982) used a similar approach to estimate dispersal of the boll weevil.

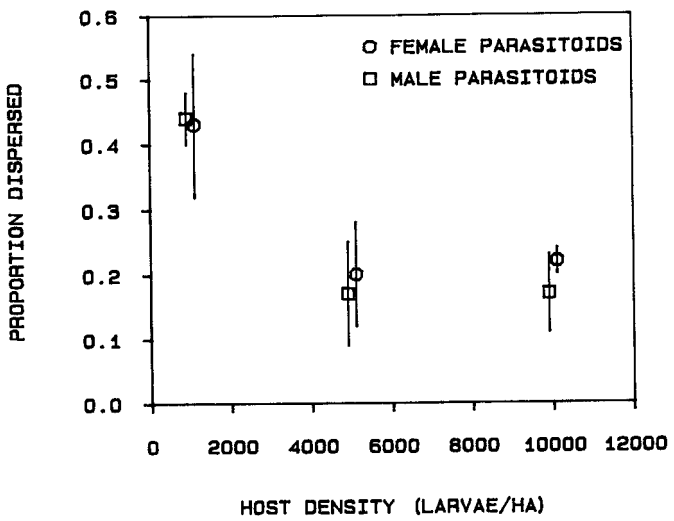

FIG. 1. Proportion of recaptured *M. croceipes* that had dispersed out of plot in which they were released. Proportion that dispersed decreased significantly with host density in release plot ($F = 7.48$, $p = 0.01$, $r^2 = 0.62$). Points are means; vertical bars are standard errors.

The two types of records collected most often in estimating dispersal are (1) the number of marked insects released and the location and time of release, and (2) the location, time, and label of captured insects. Release of laboratory reared and marked insects makes determination of the number, location, and time of release straightforward. Unfortunately, labeling insects by treating host plants in the field can make the numbers released and the time of release uncertain. Furthermore, some methods of recapture, e.g. light or pheromone traps serviced at long intervals, can make the time of recapture uncertain. Several steps can be taken to avoid these problems: emergence traps or quadrat samples can be used to estimate the number of marked insects emerging from labeled plots; host plants can be destroyed to narrow the release period; and recapture traps can be serviced more frequently. However, variation in the estimate of number released and time of release or recapture would have to be taken into account in calculations of mean and variance in dispersal rate, perhaps by the delta method (Seber 1982).

Using data on location and time of release and recapture, one can calculate several measures of dispersal. A basic variable is the net dispersal distance of each insect from time of release or eclosion to the time of recapture. Note that this is not the distance the insect has traversed; net dispersal distance will always be less than or equal to the distance traversed (Fig. 2). Depending on how insects disperse, net dispersal distance at recapture can under or over estimate net dispersal distance for the lifetime of an insect. However, if insect age and the time between release and recapture are known, the age distribution of net dispersal rates, and thus net lifetime dispersal distances, can be calculated. From net dispersal distances or rates, corrected for dilution of recaptures with distance from release site (see below), one can determine the frequency distribution of dispersal distances or rates.

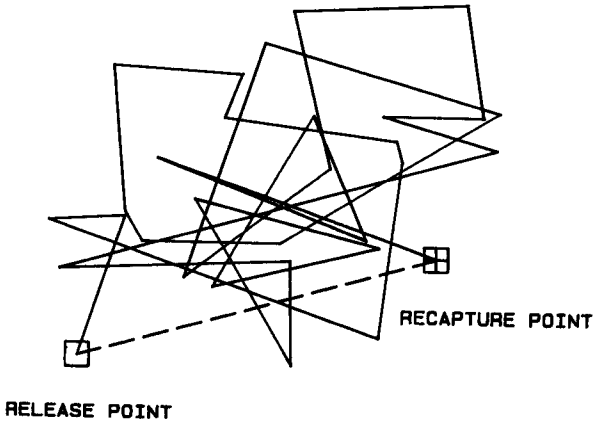

FIG. 2. Path traversed vs net dispersal distance in mark-recapture studies. Solid line is hypothetical path insect might follow; dotted line is net dispersal distance from release to recapture, given this path.

These variables can be used to estimate parameters of various models of dispersal. Skellam (1951) proposed a diffusion model for movement of living organisms, analagous to molecular diffusion:

$$P(r, t) = (2r / a^2t)\, e^{-r^2 / a^2t}$$

where $P(r,t)$ is the probability of dispersing to distance r by time t, and a^2 is the mean-squared displacement (=velocity x mean free path x flight time, where mean free path is the mean distance between turns). One can estimate mean squared displacement by fitting this model to the frequency distribution of net dispersal distances corrected for dilution with distance. The correction is crucial because, as Peart (1985) has pointed out, the probability of dispersing a distance $[P(r)]$ is not the same as the density of dispersants at that distance $[D(r)]$ (Fig. 3) simply because area increases with distance from the release site. Peart (1985) showed that the two curves are related:

$$P(r) = 2 \pi r D(r)$$

Thus, absolute measures of dispersal distance must be corrected for dilution with distance from the release site.

An argument against the use of mark-recapture estimates of dispersal distance is that often only a small proportion of the insects are recaptured and this small proportion may not be a random sample of the population of marked insects. There are two possible forms of nonrandom recaptures. One is that the method of recapture collects a biased sample within the study area; the other is that a portion of the population disperses rapidly out of the study area and goes undetected. The only apparent solutions are to use as unbiased a recapture technique as possible, to collect over as large an area as possible, and to recognize the limits of the conclusions one can draw.

Because adults are usually the most mobile stage of insects, most studies of dispersal have concentrated on adults. But trace element labels could work well for tracing larval or nymphal dispersal. Such dispersal may be important for the spread of plant and insect diseases. Another potential use for trace element labels lies in measuring immigration as opposed to emigration. For example, host plants can be treated so that the eggs of the insects feeding on them are labeled (Hayes and Hopper 1987, Jackson et al. 1988). Thus, one could label a field, collect eggs, and determine the proportion of eggs that were oviposited by insects that emerged from that field versus by insects that immigrated from elsewhere.

POPULATION SIZE

For mark-recapture estimates of population size, one must know the number of marked insects released into the population. Usually, one must also know the time of release to account for subsequent losses from the marked population because of mortality and dispersal. Thus, if one marks insects by treating host plants in the field, similar problems arise in estimating populations size as were discussed above for estimating dispersal rate, and the same solutions apply. However, releasing insects that have been reared in the laboratory or in field cages allows much more precise estimates of number released and time of release.

Another constraint on using trace element labels for estimating population size is that one must kill the insects to detect the mark. Thus, trace element labels cannot be used in multiple marking studies, e.g. the Schnabel census (Schnabel 1938) or the Jolly-Seber method (Jolly 1965 and Seber 1965), where recaptured insects are marked with a new mark and released again into the population.

Assuming that one has succeeded in marking a known number of insects in the population of interest, how does one use this information to estimate population size? In answering this question and also in discussing estimation of mortality, I have drawn heavily on the excellent book by Seber (1982) on estimating animal abundance.

The simplest mark-recapture model is the Lincoln-Petersen index. Here one samples a population with a known number of marked insects and uses the ratio of marked (m) to

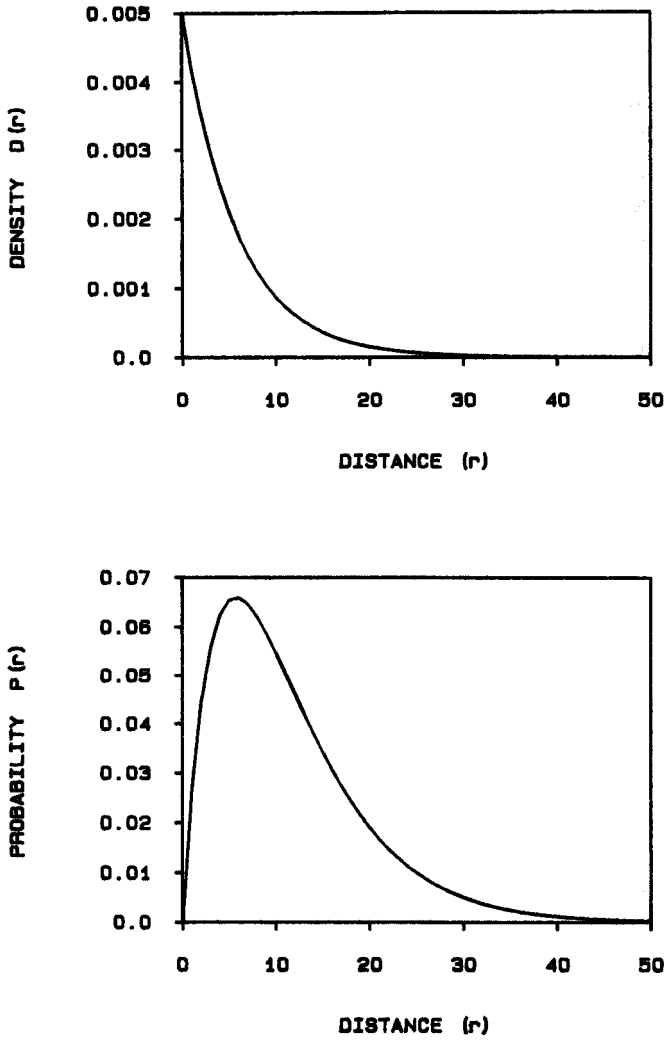

FIG. 3. The number of insects per area per insect released that reach distance r [$D(r)$] compared to probability of dispersal of an insect to distance r [$P(r)$] (after Peart 1985).

total (n) insects in the sample to estimate the ratio marked (M) to total (N') in the population. In other words,

$$m / n = M / N'$$

and

$$N' = M\ n\ / m.$$

One has to assume (1) no recruitment, mortality, immigration, or emigration has occurred between releasing the marked insects and sampling the ratio of marked to total insects, (2) marking does not affect catchability, (3) insects do not lose marks between release and recapture, and (4) the sample is a simple random sample of the population. This estimate is biased for small samples, and Chapman (1951) has given a less biased estimate:

$$N^* = (M+1)(n+1) / (m+1) - 1,$$

which is unbiased if $M+n > N$. If $M+n < N$, the expected value of N^*, given M and N, is given by

$$E\ [N^* \mid M,n] = N - bN$$

where the bias b is $\exp[-(M+1)(n+1)/N)]$. For b to be small, nM/N should be greater than 4, if $m > 6$ one can be 95% confident that this is true and thus that N^* is unbiased. Since N^* is asymptotically normally distributed, one can use the variance in N^*,

$$V[N^*] = (M+1)(n+1)(M-m)(n-m) / (m+1)^2(m+2),$$

to generate an approximate 95% confidence interval for N^*:

$$N^* \pm 1.96 \sqrt{V[N^*]}.$$

Robson and Regier (1964) give charts for determining the sample sizes needed for the Lincoln-Petersen index to give various levels of precision in estimating various sized populations. For example, if one wants the index to deviate from the true mean by less than 10% with 95% confidence, one must mark and release 10,000 insects and collect 1,000 to estimate a population of 40,000. With the same number marked and released, one must collect 10,000 to estimate a population of 300,000. Thus, large efforts are needed to get precise estimates.

Even if some of the assumptions underlying the Lincoln-Petersen estimate are violated, one can sometimes still estimate population density. Probably the most frequently violated assumption for insect populations is that they are closed, i.e. there is no recruitment (from births or maturation), no mortality, no immigration, and no emigration. If there is mortality or emigration and the marked and unmarked insects die or emigrate at the same rate, such losses will not affect the Lincoln-Petersen estimate because

$$E\ [m / n \mid M] \cong pM / pN' = M / N',$$

where p is the probability of surviving from release to recapture. On the other hand, if there is recruitment or immigration and recruits and immigrants can be distinguished, they can be subtracted from n, the total in the sample, and cause no problems with the analysis. If recruits and immigrants cannot be distinguished, N' is still a valid estimate, but now for the population at the time of the sample, not at the time of the release. If there are simultaneous losses (from mortality or emigration) and additions (from recruitment or immigration) to the population, Lincoln-Petersen type estimates must be replaced by open population estimates, one of which is described next.

Assume marked insects are released into an open population with variable recruitment and mortality and repeated samples are then taken from the population. The expected value

of the ratio of marked insects to total insects in the ith sample (m_i/n_i), given the number of marked and unmarked insects in the population at the time of the i^{th} sample (M_i, N_i), is just the ratio of marked to unmarked insects in the population, i.e.

$$E\,[m_i / n_i \mid M_i, N_i] = M_i / N_i.$$

Parker (1955) suggested plotting m_i/n_i against t_i (the time at which the i^{th} sample is taken) and extrapolating to get M_O/N_O. Thus, if one regresses, m_i/n_i against t_i, the y-intercept (y_O) is equal to M_O/N_O, so that $N_O = M_O/y_O$, and one can estimate a confidence interval for y_O, and thus for N_O. The arcsin square-root transformation is often necessary to homogenize variances and normalize residuals of the ratio m_i/n_i. In several mark-recapture experiments, I used this method to estimate density of *M. croceipes*; results from one experiment are shown in Fig. 4.

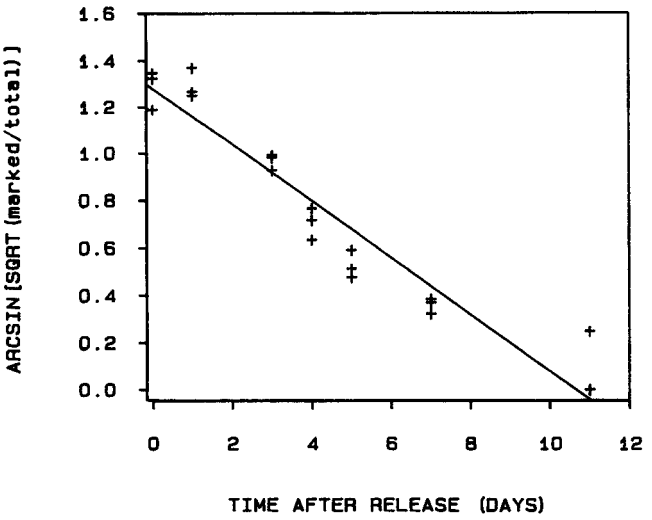

FIG. 4. Proportion of marked *M. croceipes* adults in samples (m_i/n_i) versus time after release (t_i) of marked parasitoids into a population. Arcsin[sqrt(m_i/n_i)] = 1.397-0.120 t, and $N_O = M_O / [\sin(1.397)]^2 = 3222$. Variables are defined in text.

MORTALITY

In populations with no emigration, mortality can be estimated from the rate of decline in recaptures of marked insects after releases are stopped. For this method, per capita probability of recapture must not vary much with age or time. If a cohort of insects of the same known age have been released over a short period, one can estimate age-specific survival, l_X, age-specific deaths, $d_X = l_X - l_{X+1}$, and age-specific mortality rate, $q_X = d_X/l_X$. If a significant proportion of marked insects in the population are removed through recaptures, this loss must be accounted for in calculating mortality.

In populations with emigration, mortality can still be estimated from the rate of decline in recaptures of marked insects, but the rate of decline has to be corrected for emigration. One must have an estimate of dispersal rate and a model of how insects disperse, e.g. the model of Skellam (1951) given above. One can then use the model to estimate the

proportion of marked insects which have dispersed beyond R, the radius of the study area, by time t since release:

$$P(r > R,t) = \int_R^{\infty} (2r/a^2t)\, e^{-r^2/a^2t}\, dr$$

where r is distance from the release point and a^2 is the mean-square displacement per unit time. An application of this model to *M. croceipes* is shown in Fig. 5.

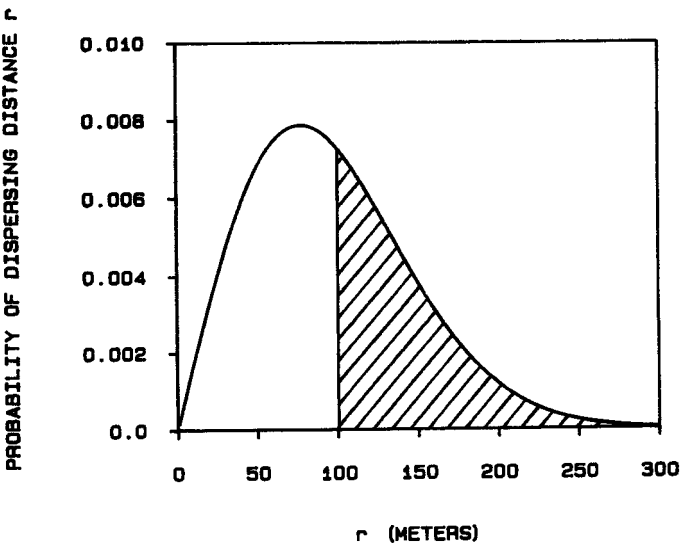

FIG. 5. Probability of dispersal to various distances from release site [P(r)] for *M. croceipes*. Shaded area is proportion of population predicted to have dispersed beyond study area [P(r>R|t)], given time since release (t=3 days) and mean-square displacement (a^2) measured within study area. Variables are defined in text.

Using this proportion, one can estimate the deaths (d_t) in each time interval t:

$$d_t = m_t - m_{t+1} / [1 - P(r > R,t)]$$

where m_t is the number of marked insects recaptured in the study area at time t. If a cohort of insects of the same known age have been released over a short period, d_t is equal to d_x. An application of this method for estimating survivorship of *M. croceipes* is given in Fig. 6.

If one treats mortality as a stochastic process, an estimate of mean and variance can be derived (Chiang 1960). If Q_x is the probability of dying in the age interval x to x+1, it can be estimated by $Q'_x = d_x/l_x$, and its variance can be estimated by

$$V'[Q'_x] = \frac{(1 - d_x/l_x)\, d_x/l_x}{l_x} [1 + (1/l_x) - (1/l_o)].$$

Assuming that Q'_x was asymptotically normally distributed and using the survivorship curve corrected for dispersal shown in Fig. 6, I calculated 95% confidence intervals for age-specific mortality rate of *M. croceipes* (Fig. 7).

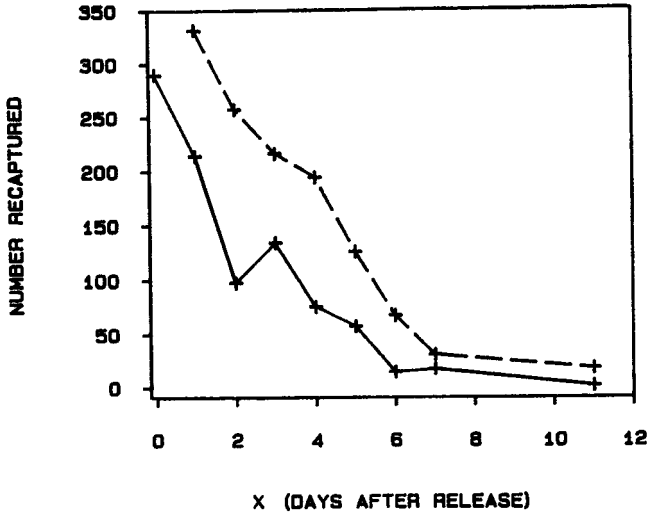

FIG. 6. Number of recaptures of *M. croceipes* (m_t) versus time after release of marked parasitoids (t). Solid line is actual recaptures; dotted line is recaptures corrected for dispersal from study area. Variables are as defined in text.

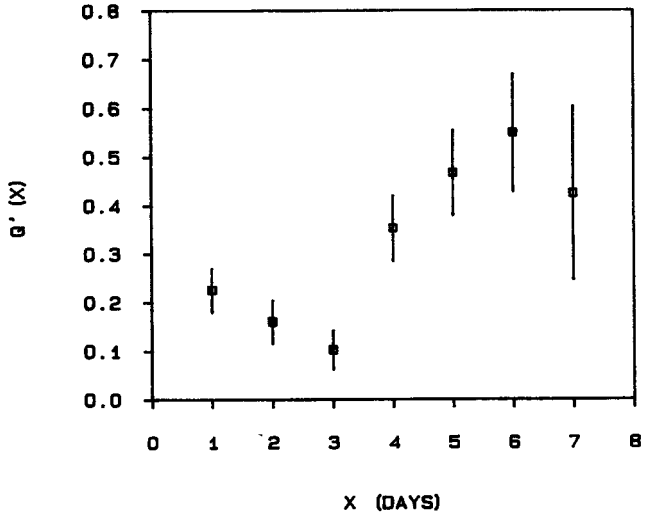

FIG. 7. Probability of dying [$Q'(x)$] versus age (x) for *M. croceipes* in the field. Points are expected values; vertical bars are 95% confidence intervals.

TROPHIC RELATIONSHIPS

Predators and parasitoids, as well as herbivores, can be labeled in the field (Graham et al. 1978a, Payne and Wood 1984). This opens the possibility of using trace elements to study trophic interactions at three or more trophic levels. Unfortunately, it may prove difficult to get quantitative data, e.g. number of prey eaten per time or amount of host plant biomass consumed. Two processes are likely to contribute to high variation in elemental concentrations among herbivores, predators, and parasitoids (here I will use 'predator' and 'prey' to refer to consumer and consumed in general). First, variation in elemental concentration among prey tissues and differential consumption of prey tissues could lead to high variance in elemental concentrations at the next trophic level. Second, decline in trace element concentration after cessation of feeding on labeled food could lead to high variance in concentration among prey and thus high variance in concentration among predators. For these reasons, trace elements are probably better suited for delineating trophic webs. However, even for this purpose caution is needed in interpreting negative data, i.e. evidence that a particular prey species is not attacked. If a predator population is exposed to labeled prey and then sampled and found not to be labeled, this could be because (1) the predator does not attack this prey, (2) the sample missed the individuals that ate labeled prey, or (3) the sample contained predators that ate labeled prey but did not pick up the element or eliminated the element before being caught. These problems could be addressed with a combination of laboratory experiments and sampling theory, but trace element tracers are probably best used for positive identification of trophic links.

CONCLUSIONS

Although many reports on the method of trace element labeling have been published in the 20 years since it was first proposed, few applications have been published. Perhaps this is because of the great amount of labor needed for recapturing and analyzing labeled insects in sufficient numbers to make valid statistical inferences. Fortunately, automated machines for rapidly detecting very small quantities of trace elements have become available in recent years, and these machines have reduced the labor of analyzing for trace elements. However, the labor of collecting large numbers of insects in the field remains. Nevertheless, many techniques are available for analyzing data from mark-recapture studies, and trace elements are promising labels for measuring some rather intractable ecological variables.

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