Estimating Relative Population Density of Many Species from Trap Data^{1,2}

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Insects are easily caught by a large number of trapping techniques, including sex attractants, light traps, pan traps, and pheromone traps. These kinds of data are relatively easy to come by, but their interpretation is not so straightforward when one wishes to compare several species. In this note, I describe a method that uses trap data to estimate indirectly the relative population size of many populations. Basically the technique is to estimate *relative* trapping efficiencies for several species and to use this information to calculate relative population estimates from trap data.

If one considers the trap as a predator that "eats" more than one insect species, then the measurement of preference in selective predation can apply. Preference reflects any deviation from random sampling of prey (CHESSON, 1978) and so its measure should be independent of prey density. A variety of measures are available, but the most meaningful was originally proposed by MANLY et al. (1972), and theoretically derived by CHESSON (1978). CHESSON derived the probability of a predator eating a prey (or a trap capturing an insect) of type i given that there are n_j of prey type j and m prey types, as P_i where

$$P_i = \alpha_i n_i \left(\sum_{j=1}^m \alpha_j n_j \right)^{-1}.$$

The α_i are measures of preference and equal the probability of capturing a prey type i given the predator encounters the prey, times the probability of encounter. Since only relative measures of α_i are of interest for measuring preference, these are normalized so that they sum to 1. These normalized α_i measure the ease of capture of prey type i relative to all the other prey, and so will be called *relative capture efficiencies*.

The estimation of α from capture data is straightforward. When prey population density is not affected by trapping (n_i constant), α_i is estimated by the maximum likelihood estimator (MLE)

$$\hat{\alpha}_i = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j} \quad \text{CHESSON (1978)} \quad (1)$$

where r_i is the number of captures from a population of n_i of prey type i , and there are m total number of prey types. When prey populations are depleted by trapping, the approximate moment estimator of α_i is

$$\hat{\alpha}_i = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^m \ln((n_{j0} - r_j)/n_{j0})} \quad \text{MANLY et al. (1972)} \quad (2)$$

where n_{i0} is the number of prey type i before predation. The actual MLE can be found but equation (2) is adequate in most cases (CHESSON, 1978). Formulae for the bias, variance, covariance and statistical tests for both estimates are given by MANLY (1974).

Using equation (1), numerical examples are given to illustrate that α is independent of prey density and to show how one interprets α . Suppose there are 1,000 individuals of each of two insect species, called A and B, and that the trap catches 50 of each. Absolute capture efficiencies are 0.05 in both species and $\hat{\alpha}_A = \hat{\alpha}_B = 0.5$. If instead there are 1,000 A's and 2,000 B's, but the trap works with the same absolute efficiency catching 50 A's and 100 B's, again $\hat{\alpha}_A = \hat{\alpha}_B = 0.5$. However, if absolute efficiencies change, so that A's are caught more efficiently (50/1,000) than B's (30/1,000), then $\hat{\alpha}_A = 0.625$ and $\hat{\alpha}_B = 0.375$. Thus the measure of α does not depend on the population size of the prey but only on the relative efficiency of capture. Larger α 's indicate relatively more efficient capture, and equal α 's indicate equal absolute capture efficiency. For more than 2 species, α can be estimated simultaneously for all species or pair-wise for each species pair. If one is interested in only a subset of the species, α can be estimated for

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only that subset. In other words, we can select subsets of the trap sample so that the α 's are best estimated, or vice versa, that the relative population sizes are best estimated. To estimate the α 's experimentally, one simply releases known numbers of insects at equal distances and counts the number caught in the traps. Based on MANLY's (1972) tables on bias and standard error in the estimation of α , ideal conditions for these experiments are large n_1 and n_2 , low absolute capture efficiency, and an n_1/n_2 ratio between 0.25 and 4. These conditions minimize both the bias and standard error of α .

Relative capture efficiencies (α_i) may not depend on population density even when absolute capture (r_i) does. For example, if the r_i follow a Holling Type II functional response, then α does not depend on density and is estimated by equations (1) and (2) (CHESSON, 1983).

The estimation equations (1) and (2) can be used to calculate relative population size when the α 's do not explicitly depend on density. Both are equation in $2m+1$ unknowns. For $m=2$, there are 5 unknowns, and if we know α , r_1 , and r_2 , then clearly the relative population sizes of n_1 and n_2 can be calculated. From equation (1), we calculate

$$\frac{n_1}{n_2} = \frac{(1-\alpha_1)r_1}{\alpha_1 r_2}$$

and implicitly from equation (2)

$$\frac{\alpha_1}{1-\alpha_1} = \frac{\ln((n_{10}-r_1)/n_{10})}{\ln((n_{20}-r_2)/n_{20})}.$$

For m insect types, we can calculate the relative population size using trap catch data and previously determined α values for all types simultaneously or for all pairwise combinations. In addition, given this set of relative population densities, the absolute population density for each species in the entire species assemblage can be determined by estimating the absolute capture efficiency for only one species. That is, one can eliminate the messy problem of estimating absolute capture efficiencies for all species of interest and one can concentrate attention on only one species. Indeed, one can choose a species that is particularly easy to handle and work with.

The major limitation of this method is that rela-

tive capture efficiencies (α_i) are likely to vary with the environment. For example, critical temperature and critical wind speeds for flight vary from species to species. To the extent that these can be predicted, they should be avoided when using the method proposed here. However, variation in relative capture efficiency will be worth investigating in its own right. In general, variation in trap catch size depends on variation in both the environment and insect biology. In estimating relative capture efficiencies, environmental variation is minimal, so differences in relative capture efficiency will reflect interesting biological differences.

This method might be most useful when the study insect is difficult to sample by other methods, such as moths in sex attractant traps. Pheromone traps are a special case, and can be used if the pheromones can be mixed to attract more than one species, e.g. the pheromones of *Carposina niponensis* WALS. and *Grapholita molesta* BUSCK (SATO et al., 1981), or when adjacent traps can be used, e.g. *Homona magnanima* DIAK. and *Adoxophyes* sp. (TAMAKI et al., 1983).

To summarize, first one estimates the α 's in preliminary experiments and determines the constancy of the α 's. One then calculates relative population densities from trap data and the previously estimated α 's, and when desired, calibrates them all with one absolute population estimate.

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