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Ecology, Volume 77, Issue 3 (Apr., 1996), 880-884.

Ecology, 77(3), 1996, pp. 880–884

MARK–RESIGHT POPULATION ESTIMATION WITH IMPERFECT OBSERVATIONS[1]

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Abstract. Minta and Mangel (1989) developed a Monte Carlo method for estimating population size from mark–resight data in which there is considerable variability in the resighting frequencies among individuals and irregular census surveys. Their method assumed that sightings were perfect, so that all animals present (marked or unmarked) were resighted. We describe an updated version that allows a proportion $1 - p$ of the individuals present to be overlooked during censusing. We compare confidence interval coverage for the original method and the updated method using simulated data sets, describe a method to estimate p, and evaluate how error in estimating p affects confidence interval coverage. The updated method for estimating a confidence interval performs considerably better than the original estimate. We find that p can be overestimated by 30% or underestimated by 10% and the confidence interval generated still includes the true population size 90% of the time. This technique may improve confidence interval estimates for small and threatened populations.

Key words: mark–resight; Monte Carlo; observation error; population estimate; resighting error; sightability; simulations.

INTRODUCTION

Minta and Mangel (1989) proposed a method for estimating population size from mark–resight data for small, heterogeneous populations. Their method, based on Monte Carlo simulation, both allows the experimental freedom of either continuous or heterogeneous surveys and includes individual variation in sightability characteristic of different populations. White (1993) noted that if observations are imperfect (i.e., not all available animals are seen), the Minta–Mangel (MM) estimate, because it is conditioned on the sighting information, may not generate a sufficiently wide confidence interval; White proposed a corrected method based on the hypergeometric distribution.

Imperfect sighting of animals can arise in a number of ways. For example, in cetacean populations, resighting surveys may be heterogeneous in time and space for these seldom-seen animals (Scott et al. 1990). Often greater than half of a population's members can be identified by natural markings on the dorsal fin. Furthermore, observation error probably occurs because an individual may swim under the water's surface and not be recorded although it is present during an aerial sweep.

The original MM method was developed for estimating population size of northern mammals by radiocollaring individuals and resighting tracks in the snow. Snow melt or falling branches may obscure some of the tracks, contributing to observation error. Birds and primates that remain camouflaged easily may be overlooked so that estimates of their populations also require correction for imperfect observations.

In this brief article, we (i) confirm White's observation, (ii) propose a correction of the MM method, and (iii) validate that the revised method works. To do this, we first simulate mark–resight data from a known population size with imperfect sightability, compute a confidence interval under the false assumption of perfect sightability, and tabulate how frequently this confidence interval includes the known population size. Then, we revise the MM population estimate to correct for observation error in resighting animals and affirm that the known population lies within the new confidence interval. Since this method requires that census-takers estimate the proportion of animals present that they observe, we describe a method for computing the observation probability from resight data collected simultaneously by two census-takers. Finally, we evaluate how error in the estimate of observation probability affects confidence interval coverage.

METHODS

The accuracy of the Minta–Mangel population estimate with imperfect observation

The original MM algorithm estimates the total number of unmarked individuals in a population through a Monte Carlo method based upon the frequencies of resighting marked individuals and the total sightings of unmarked individuals (Minta and Mangel 1989). The observed frequencies of resighting marked animals are scaled by the total number of marked animals to estimate the probability distribution of sighting frequencies, which we denote by $S_o(k) = \Pr\{\text{animal will be resighted } k \text{ times}\}$.

[1] Manuscript received 7 March 1994; revised 6 January 1995; accepted 7 July 1995; final version received 11 September 1995.

Next, one randomly draws individuals from the distribution $S_o(k)$ and sums the sighting frequency associated with each individual until the total number of randomly chosen sightings equals the empirically observed number of resightings of unmarked animals. As advocated by White (1993), to reduce bias we only accept samples in which cumulative sightings exactly equal the number of observations of unmarked individuals and reject samples in which sightings exceed this number. One could modify the stopping rule to continue drawing individuals beyond the exact number of unmarked observations if these individuals were drawn from the group with 0 resightings, only stopping when an individual with >0 resightings was drawn. This is a modest modification of the program that might improve confidence interval coverage, particularly if there are a large number of marked animals with 0 resightings. However, our method will only underestimate the true population size N by an average of $\Sigma_{i=0}^{\infty} i(S_o(0))^i(1 - S_o(0)) = S_o(0)/(1 - S_o(0))$, where $S_o(0)$ is the probability an individual is never resighted. The upper bound on the confidence interval could be enlarged by this amount if there were a large number of marked animals that were never resighted. At least 50% of the marked individuals must have 0 resightings for this average bias to be as much as a single individual.

Repeating this procedure 10 000 times leads to an empirical frequency distribution of estimates for the number of unmarked animals. The point estimate of population size is the mode of this frequency distribution of unmarked animals. An empirical 95% confidence interval around the peak of the frequency distribution contains 9500 of the total 10 000 population estimates.

To evaluate the accuracy of this method when animals that are present may not be sighted, we started with a population of known size N (we used $N = 40$) and simulated mark–resight data similar to those that would be collected empirically. First, each individual was randomly "marked" with Bernoulli probability 15/40. Independently of each individual's marked or unmarked status, we randomly assigned each animal a chance of being available for resight from a uniform distribution ranging from 0.3 to 0.6. Finally, we specified the probability p that an animal that was present would be resighted. For each simulated day of censusing, an animal was designated as present or absent during a survey according to its probability of being available for sighting, and then was seen by the census-taker with probability p. After $n_{\max} = 10$ d of censusing, we tabulated (1) the distribution of resighting frequencies for the marked individuals and (2) the total number of resightings of unmarked individuals.

We calculated a 95% confidence interval for the population size with the MM algorithm and checked how often this confidence interval included the actual population size N. For a given observation probability p, we averaged the results from 100 sets of simulated data and MM estimates. Repeating this procedure for each of 10 observation probabilities ($p = 0.1, 0.2, \ldots, 1$) determined the largest observation error $(1 - p)$ allowable to estimate a 95% confidence interval.

Updating the MM population estimate to account for imperfect sighting

When we know that an individual may be present but not sighted, two modifications to the MM algorithm correct for imperfect observations in both the marked and the unmarked sightings. First, the observed sighting distribution of marked animals $S_o(k)$ must be used to construct an estimate for the "true" distribution of the frequencies of individuals that are available for sighting, $S_t(n)$. Individual sighting frequencies are then drawn from this updated distribution. Second, only a randomly chosen fraction of these sightings are summed, using the binomial probability p to determine if a potential sighting is included in the sum. This procedure expands the confidence interval from the case of perfect observations.

To begin, we need to find $S_t(n)$. Since we no longer assume that the sighting distribution of marked animals is based on perfect observations, an animal observed k times could have been present $k, k + 1, k + 2, \ldots, n_{\max}$ times. Suppose that $G_k(n)$ is the probability that an individual is present n times given that it is seen k times. Then by Bayes' theorem

$$G_k(n) = \frac{\Pr(\text{observed } k \mid \text{present } n)\Pr(\text{present } n)}{\Pr(\text{observed } k)} \tag{1}$$

In Eq. 1, Pr(observed k | present n) is a binomial distribution.

There are two obvious choices as a prior distribution Pr(present n) for the probability that an animal is present n times during resighting efforts. One is the uniform prior Pr(present n) $= 1/n_{\max}$. A second possibility is the noninformative prior in which the data change the location, but not the shape, of the posterior distribution (Box and Tiao 1973). Mangel and Beder (1985) showed that when estimating the parameter n in the binomial distribution, using the uniform prior results in essentially the same posterior distribution as that obtained using the noninformative prior. Since the noninformative prior is so much harder to compute than the uniform prior, we stay with the latter. Thus, we assume a uniform prior, so that

$$G_k(n) = \frac{\binom{n}{k} p^k (1 - p)^{(n-k)} \frac{1}{n_{\max}}}{\sum_{m=k}^{n_{\max}} \left[\binom{m}{k} p^k (1 - p)^{(m-k)} \frac{1}{n_{\max}}\right]}, \quad \text{for } n = k, k + 1, k + 2, \ldots, \tag{2}$$

which simplifies to

$$G_k(n) = \frac{\binom{n}{k}(1-p)^n}{\sum_{m=k}^{n_{\max}} \binom{m}{k}(1-p)^m}. \quad (3)$$

From a Bayesian viewpoint, $G_k(n)$ is an estimate of the prior for the sighting distribution $S_t(n)$ informed by the estimated magnitude of observation error. The observed sighting distribution $S_o(k)$ is the likelihood, so that

$$S_t(n) = \sum_{k=0}^{n} G_k(n) S_o(k). \quad (4)$$

In the modified MM algorithm, the numbers of times that individuals are available for resighting are generated using the Bayesian estimate of the distribution $S_t(n)$. This accounts for imperfect observation ($p < 1$) of marked individuals.

To correct for imperfect observation of unmarked individuals, some of the times that each individual is available for resighting are selected as actual resights according to a binomial random variable with probability p. These resightings are summed until the empirically observed number of unmarked sightings is reached. The confidence interval (CI) is computed as before. We averaged the results from 100 simulated sets of data for each value of p to determine the percent of time the updated CI estimate included the true population size.

Determining the probability of sighting

We now describe a simple method that can be used to determine the probability of successfully sighting an individual. To do so, we assume that the resighting process is modified so that two searchers work essentially simultaneously (e.g., Estes and Jameson 1988). Ignoring whether resighted individuals are marked or not, we then have a number of resighted individuals (C) that both searchers detect and a number of resighted individuals (K) that one of the searchers detects. Assuming that each searcher has the same probability of resighting an animal, the probability that both searchers sight a particular individual is p^2, the probability that one of them encounters a particular individual is $2p(1 - p)$ and the probability that neither of them encounters a particular individual is $(1 - p)^2$. If there are N individuals present during resighting, the observed data will follow a multinomial distribution

$$\Pr\{C=c, K=k\} = \frac{N!}{c!k!(N-c-k)!}[p^2]^c[2p(1-p)]^k[(1-p)^2]^{N-c-k}. \quad (5)$$

We view Eq. 5 as the likelihood function for p and N, given the data c and k, with the restrictions that $0 < p < 1$ and that $N \geq (c + k)$. The maximum likelihood estimate for p is

$$p_{\text{MLE}} = \frac{2c + k}{2N}. \quad (6)$$

However, N is unknown in Eq. 6. To determine the maximum likelihood estimate for N, we consider the likelihood ratio

$$\frac{L(p, N+1 \mid c, k)}{L(p, N \mid c, k)} = \frac{(N+1)(1-p)^2}{N+1-c-k}. \quad (7)$$

Setting this ratio equal to 1, which is the analog—for a discrete variable—of setting the derivative equal to 0 (see Mangel and Beder 1985), and solving for N gives the maximum likelihood estimate

$$N_{\text{MLE}} = \text{Int}\left(\frac{c + k - 1 + (1-p)^2}{1 - (1-p)^2}\right). \quad (8)$$

Since we are only interested in p, we ignore the constraint that N_{MLE} must be an integer, substitute Eq. 8 into Eq. 6 and simplify to obtain

$$2p_{\text{MLE}}{}^2 + p_{\text{MLE}}(2c + k - 4) - 2c = 0. \quad (9)$$

This equation has one positive root <1 for the cases of interest here.

An alternative to (9) is to use the method of moments to estimate p (e.g., Estes and Jameson 1988). This can be found by noting that the expected value of K is $2p(1 - p)N$ and that the expected value of C is p^2N. Thus, given values $K = k$ and $C = c$, we can eliminate N and find that

$$p_{\text{moment}} = \frac{2c}{k + 2c}. \quad (10)$$

We prefer the Maximum Likelihood Estimate of p, but the two methods give similar values for the estimate of the probability of sighting.

Effect of error in estimate of p *on* CI *coverage*

We evaluate how uncertainty in estimating p affects confidence interval coverage. For example, suppose the actual probability of observing individuals is 0.5, but because of error in estimating this actual value of p, a value of 0.7 is used to compute the confidence interval for the population size. To assess this effect, we simulate mark–resight data with one value of p but compute a confidence interval with a different, therefore incorrect, estimate of p. The greatest difference between the estimate and the true value of p for which 95% of simulated data fall within the CI indicates the acceptable error in estimating p. In these computations we used $p = 0.5$ as the actual observation probability.

RESULTS

With the original MM estimate, any level of imperfect observation decreased confidence interval cover-

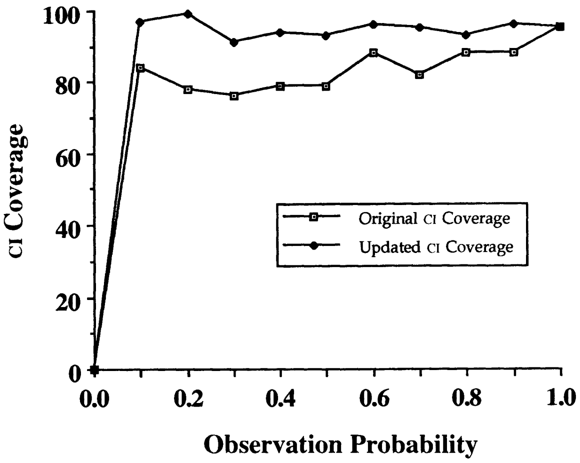

FIG. 1. The fraction of simulated data sets in which the true population size was contained in the 95% confidence interval (CI) determined from the frequency distribution of estimates of population size for the original Minta–Mangel method and the updated method in which imperfect observation is accounted for.

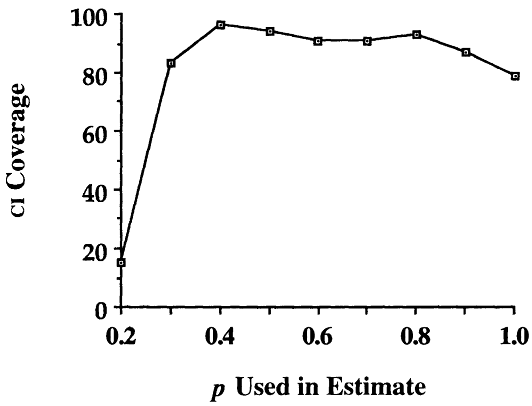

FIG. 2. The fraction of simulated data sets in which the true population size was contained in the 95% confidence interval (CI) determined from the frequency distribution of estimates of population size for the case in which the probability p that individuals present are also observed = 0.5 but for which values of p in the range 0.2 to 1.0 are assumed.

age below 95% (Fig. 1). The updated method improved CI coverage for all values of p tested, and for most values of p it increased coverage to at least 95%. However, particularly for low values of p, this correction did not always boost CI coverage above 95%, although it always brought the coverage above 91%. Averaging the results from more sets of data could resolve this. Thus, the updated method improved the confidence interval when observations were imperfect.

CI's calculated with an incorrect value of p resulted in >90% coverage if the mistaken value of p was ≤30% higher than the actual value (Fig. 2). However, low estimates of p could be only 10% beneath the actual p for 90% coverage. The flatness of the curve in Fig. 2 for values of p from 0.4 to 0.8 shows that CI coverage does not differ drastically for a range of p values. The drop-off for underestimates of p indicates that it is better to overestimate p than to underestimate p. The reason for this is the reciprocal nature of the relationship between p and the estimate of the number of unmarked individuals, so that the curve relating the two is steeper for lower values of p. Hence, underestimating p changes the estimate of the number of unmarked individuals more sharply than overestimating p.

DISCUSSION

This method of estimating a confidence interval is useful in censusing small or threatened populations where individuals can be recognized, show individual variation in behaviors that affect sightability, and may be seen rarely, thus requiring prolonged and irregular census surveys. In such small and heterogeneous populations, estimates based on the assumption of a Gaussian distribution, centered around the mean number of resightings per individual, are hard to justify.

A key assumption common to this and all other mark–resight population estimates is that an individual's probability of being resighted is independent of its marked or unmarked status. Therefore, a study must be designed so that the method of capturing individuals to mark is different from or occurs in different local points than does resighting. For example, traps for marking animals may be placed in several locales such as watering holes frequented by a large number of individuals, while resighting surveys are made along a number of transects that are systematically arranged to cover the habitat. Thus, if there are "sight happy" individuals made apparent by outstanding coloration or vocalization, the original capture and marking would be independent of subsequent differences in resight probability. If the probabilities of marking and of resighting individuals are not independent, then the population's true size may be larger than that obtained from the estimated confidence interval. Even with this caveat, mark and resight methods remain some of the most valuable and most used methods for estimating population abundance. Consequently, we must strive to develop the best possible methods.

One may implement the technique we have outlined for estimating population sizes on a personal computer. The only data necessary in addition to that collected during the original formulation of the MM algorithm are the results of a simultaneous survey to estimate p. This method promises to be especially useful to census threatened populations for which accurate knowledge of confidence intervals is essential.

ACKNOWLEDGMENTS

The work of S. N. Gardner was partially supported by a NSF Predoctoral Fellowship and that of M. Mangel by NSF Grant BSR 91-17603. This paper is funded in part by a grant from the National Sea Grant College program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA36RG0537 (93–94), project number 31-F-N, through the California Sea Grant College, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. The U.S. Government is authorized to reproduce and distribute this material for governmental purposes. This work was partially completed while M. Mangel was Varon Visiting Professor at the Weizmann Institute of Science. He thanks Lee Segel and Zvi Artstein for their wonderful hospitality. The method of Eqs. 5–8 (but not 9) arose in collaboration with Ron Nickel and Warren Rodgers many years ago on search by A-7s. Copies of the method described here are available from the author upon request.

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