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Application of Population Estimation to Pond Breeding Salamanders

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ABSTRACT

Accurate estimation of population size is essential for understanding the dynamics and structure of natural populations as well as for assessing conservation status. For pond-breeding salamanders, the application of mark/recapture models to partial drift fence studies or studies where trespass rates cannot be accurately determined are straightforward. Between 17 February 1998 and 1 June 1998 we marked 1150 salamanders and had 300 recaptures. Using four closed mark/recapture models (Schnabel, Schumacher-Eschmeyer, Tanaka, and Marten), we found deviations in model assumptions rendering the Schnabel, Schumacher-Eschmeyer, and Tanaka estimates invalid. With the Marten model, we estimated a population size of 1,061 (95% C.I. 777< N < 1,436). Considering the problems we encountered with the marking regime and drift fence, we present some recommendations on the use of mark/recapture estimators for drift fence studies.

INTRODUCTION

Collecting information concerning a population's size and related parameters (e.g., mortality and recruitment) is the first step in understanding the dynamics and structure of natural populations (Seber, 1973). With the growing concern over loss of biodiversity and mysterious declines in specific taxa such as amphibians (Wake, 1991), precise estimates of population size become increasingly important. It is impossible to determine if a species is declining if we have no precise current or historical records of population size. In the case of pond-breeding salamanders, one can effectively census the entire breeding population by intercepting migrating individuals with a terrestrial drift fence and pitfall trap array (Gibbons and Semlitsch, 1981). When the drift fence completely encircles the pond, the number of individuals marked, or raw census size, is usually given as an estimate of population size. However, because most pond-breeding salamanders are fossorial, some individuals may enter or leave the pond undetected, even when using a complete drift fence (Semlitsch, 1983a,b). The number of "trespassers" is easily determined by marking all individuals as they are encountered in the exterior pitfall traps.

Any unmarked individuals encountered in interior pitfall traps are trespassers. Population size is estimated simply by adding the number of trespassers to the raw census size. Trespass rates range from 9 to 50% depending upon the situation (Trenham et al., 2000; Beneski et. al, 1986). In addition, within a single population trespass rates can vary yearly and by sex (Trenham et al., 2000). Thus, ignoring trespass can lead to erroneous population estimates.

Trespass rates cannot always be accurately estimated. For example, many breeding ponds cannot be completely encircled by a drift fence because of size or shoreline complexity. In addition, flooding or damage to a drift fence reduces the accuracy of the trespass rate estimate. We believe that census data collected from a partial or compromised drift fence can be combined with mark/recapture models to develop robust population size estimates. We illustrate this point using closed mark/recapture models on drift fence data of unisexual salamanders of the *Ambystoma jeffersonianum* complex. We also provide background information on mark/recapture models of population estimation and present general recommendations for applying population size estimators, especially when using the drift fence-pitfall trap method for monitoring pond-breeding amphibians.

METHODS

Background

The literature contains many population estimation models based on mark/recapture (see summaries in Seber, 1973; White et al., 1982; Nichols, 1992), all of which include two basic assumptions: equal catchability among individuals (includes the effects of behavioral changes due to marking or experimental design) and no mark loss (tag loss, regrowth of clipped toes, or errors in recording and reading marks). All models fall into two classes, open or closed. Closed models are simpler because they do not require individual marks, but they do include the additional assumption of population closure (i.e., the effects of immigration, emigration, natality, and mortality are minimal). The familiar Lincoln/Petersen index is the simplest closed model and requires a single marking and single recapture period. Robust closed models require multiple sampling periods. Open models do not assume population closure and allow the estimation of survivability and recruitment, but require the construction of individual capture histories.

Study Site

Our study focused on an ephemeral pond basin bordered by mesic forest in Kickapoo State Park (KSP), Vermilion County, Illinois, USA. The basin holds water for periods varying from a few days to more than one year, but usually only after fall and winter precipitation (Phillips unpubl. data). During years of average precipitation, the pond is circular and approximately 30m in diameter, but because the basin is very shallow, heavy rains can cause the pond diameter to increase to more than 100m making it difficult to completely encircle the pond with a drift fence. This pond and two smaller, adjacent basins are the only known breeding locations for members of the *A. jeffersonianum* species complex in Illinois. Members of this complex are listed as endangered in Illinois and an accurate estimate of population size is needed to establish a long-term management plan for the salamanders and the surrounding forest. Three other species of ambystomatid salamanders breed in the pond; marbled salamander, *Ambystoma opacum*; spotted salamander, *A. maculatum*; and smallmouth salamander, *A. texanum*.

Procedures

We surrounded the pond with a drift fence constructed of aluminum window screening 40 cm high buried a few cm in the ground. We placed drop-cans at 4.4 m intervals along the inside and outside the 127m circumference fence. We checked drop-cans after all precipitation events between 10 February to 16 April 1998. We anesthetized the unisexual polyploids in MS-222 and clipped the outside front left toe with a sterile razor blade. After recovery in de-chlorinated water, we released all salamanders on the opposite side of the fence.

Data analysis

Permit restrictions prevented us from clipping more than one toe per individual and therefore from giving salamanders unique marks. This meant we could only consider closed models. We chose the Schnabel (1938) and three regression methods (Schumacher and Eschmeyer; 1943; Tanaka, 1951; 1952; Marten, 1970) to estimate the number of migrating adults during a single breeding season. We addressed the validation of equal catchability and population closure using linear regression as outlined by Krebs (1989). This was accomplished by examining the relationship between the recapture rate at time i (y_i) and the cumulative number of individuals available for recapture in the t^{th} sample (M_t). If the regression is significant and the y-intercept equals zero, the assumptions of equal catchability and population closure are met. Because salamander toes do not regenerate within the time frame of our study, mark loss was not a factor. For the Tanaka model, we calculated Tanaka's γ parameter, which determines how well the model fits the data. Good fit is achieved if the 95% confidence interval bounds 1 (Seber, 1973). We calculated all population estimates in Excel 2000® and analyzed all statistics in SPSS® ver. 6.1.4.

RESULTS

Heavy rains during our study flooded our drift fence twice allowing salamanders to enter and leave the pond unnoticed and making it impossible to estimate trespass rate. We marked 1150 unisexual polyploids and had 300 recaptures. The majority of individuals arrived in modes (Table 1). The range among the four population estimates is large suggesting we captured from half to all of the breeding polyploids (Table 2). The relationship between y_i and M_t was not significantly linear, but the y-intercept did not significantly differ from zero ($y_i = 0.000304M_t + 0.173814$, $r^2 = 0.129$, with $p = 0.0659$ for slope = 1, and $p = 0.226$ for y-intercept = 0, $n = 27$). Tanaka's model did not fit the data ($\gamma = 3.32$, 95% C.I. $2.99<\gamma < 3.65$) either. Marten's model yielded a population estimate below the actual number of individuals marked, although the number actually marked was bracketed by the confidence interval.

DISCUSSION

Model Comparisons and Fit

Several factors can be used to assess the performance of our four population estimates. First is our test of population closure and equal catchability. Because we failed to validate these assumptions, the more restrictive Schnabel and Schumacher-Eschmeyer methods will yield erroneous results. Both estimates are three times greater than the number of individuals we marked and would require that 75% of the individuals circumvented our drift fence. Even though our entire fence was flooded twice after the initial migration, we consider 75% trespass rate during the initial migration to be unrealistic. Second, Tanaka's γ indicates this model does not fit the data well. In contrast, the Marten model has an estimate less than the census size, but the confidence interval bounds our census size. Because Marten's model is even more relaxed to the assumption of closure (Marten, 1970; Seber, 1973), interpreting our results using this model is reasonable. Under Marten's model, the Kickapoo population of unisexual *Ambystoma* contained between 1150 (our census size) and 1436 individuals. Although this seems like a large interval, it provides a baseline estimate required for management decisions and future studies of the unisexual salamanders at KSP. Further, it is better than a simple census size because it accounts for some rate of error and the statistical comparisons with future studies.

Previous Studies at Kickapoo State Park

The first record of unisexual *Ambystoma* at KSP is from 1978, when only a few individuals were captured (Morris, 1981). In 1980, Morris (1981) captured 333 individuals using the same drift-fence pitfall trap methods as the present study. Drift fence estimates of 106, 95, and 210 were made from 1990 to 1992, respectively (Phillips et al., 1997). Our census size is an order of magnitude greater than most of the previous estimates. This may represent a significant increase in the number of the polyploid *Ambystoma* at KSP over the past 20 years. However, because none used trespass rate or mark/recapture methods, only our raw census size can be compared.

Comparisons with Other Studies

Even with the recent summary of mark/recapture population estimation methods given by Donnelly and Guyer (1994), little research has been directed toward estimating pond-breeding salamander population size. Although many researchers collect the data necessary to estimate breeding population size, they usually only report the raw census size. Others have applied mark/recapture models, but do not explicitly address the appropriate assumptions. A literature survey yielded only four drift fence studies that used either trespass rate or mark/recapture methods to estimate population size of ambystomatid salamanders. Beneski et. al (1986) estimated population size of *A. macrodactylum* and by using capture efficiency of the drift fence (the inverse of trespass rate) as a correction factor. Trenhman et al. (2000) adjusted their drift fence captures by their trespass number to achieve a robust population size estimate of *Ambystoma californiense*. Two studies used closed mark/recapture models to estimate population size of *A. talpoideum* and *A. macrodactylum*, but did not explicitly address the underlying assumptions (Raymond and Hardy 1990; Fukumoto and Herrero 1998; respectively).

Recommendations for Use of Mark/Recapture Models

First, consideration of model options should take place before the study begins (Donnelly and Guyer, 1994) so that certain model classes are not omitted. Open models are preferable to closed models, but require that individual salamanders be given unique marks. Although it may be difficult and expensive to individually mark amphibians, both survivability and recruitment data can be obtained from open models. These parameters can play an important role in management strategies. Further, both open and closed models can be combined to obtain results for long-term studies. Pollock (1982) outlined a methodology whereby closed model estimates are used for secondary periods (i.e., within years) and open models used for primary periods (i.e., between years).

Second, the appropriate assumptions must be explicitly addressed regardless of which model is chosen. If assumptions are violated, one must investigate how various models perform under deviations from each assumption. For example, Marten's model is more relaxed to deviations from equal catchability than other models (Marten, 1970; Otis et al., 1978). Other options for deviations from equal catchability include segmenting the population into classes such as sex or age, and then performing a population estimate of each class (Marten, 1970). If salamanders were not given unique marks and population closure is not supported, then none of the standard population methods reported in the literature, including the Lincoln/Petersen index, are appropriate. Depending on the severity of the deviations, statistical estimation based on mark/recapture may be impractical.

Third, after data have been collected and several models applied, explicit justification for choosing among competing estimates should be given. Some models allow for direct testing of fit (e.g. Tanaka and Jolly-Seber models) and specialized programs have been developed to test competing models (Otis et al., 1978). Even in the best-planned studies, the evaluation process may converge on more than one estimate. For those situations, researchers may follow Seber's (1973) recommendation of using different methods in tandem, such as removal sampling and quadrat sampling along with mark/recapture. When the estimate is finally obtained, it can serve as a basis for comparison with future studies and even allow for direct statistical testing among populations or across time in the same population. Only with accurate estimates can trends in population size be documented.

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Table 1. Mark/recapture data for the 1998 field season for a population of unisexual clonal salamanders of the genus *Ambystoma* at Kickapoo State Park, Vermilion County, Illinois. M_t is the cumulative number of individuals marked and y_i is the proportion of recaptures in the i^{th} sample.

Date	Marked	M_t	Recaptured	Total	y_i
2/17/98	5	5	0	5	0.000
2/18/98	91	96	2	93	0.022
2/19/98	0	96	5	5	1.000
2/20/98	9	105	1	10	0.100
2/26/98	2	107	0	2	0.000
2/27/98	247	354	6	253	0.024
3/3/98	5	359	0	5	0.000
3/6/98	1	360	3	4	0.750
3/9/98	246	606	50	296	0.169
3/16/98	3	609	1	4	0.250
3/17/98	2	611	4	6	0.667
3/18/98	422	1033	108	530	0.204
3/19/98	5	1038	4	9	0.444
3/20/98	26	1064	25	51	0.490
3/23/98	2	1066	0	2	0.000
3/27/98	1	1067	13	14	0.929
3/28/98	39	1106	17	56	0.304
3/29/98	5	1111	2	7	0.286
3/31/98	8	1119	4	12	0.333
4/1/98	9	1128	20	29	0.690
4/4/98	12	1140	6	18	0.333
4/7/98	2	1142	1	3	0.333
4/8/98	7	1149	23	30	0.767
4/12/98	0	1149	2	2	1.000
4/14/98	0	1149	1	1	1.000
4/16/98	0	1149	2	2	1.000
5/1/98	1	1150	0	1	0.000
Total	1150		300	1450	

Table 2. Model estimates, estimated proportion of the population captured, and confidence intervals for the Schnabel (1938), Schumacher-Eschmeyer (1943), Tanaka (1951,1952) and Marten (1970) estimators for a population of unisexual clonal salamanders of the genus *Ambystoma* studied in 1998 at Kickapoo State Park, Vermilion County, Illinois.

Estimator	Estimate	95% C. I.
Schnabel	3,661	3,247 < N < 4,152
Schumacher-Eschmeyer	3,554	2,817 < N < 4,812
Tanaka	970	806 < N < 1,168
Marten	1,061	777 < N < 1,436