SAMPLING ELUSIVE SPECIES IN KARST ENVIRONMENTS: DESIGN AND DEMOGRAPHIC MODELING CONSIDERATIONS

BRET A. COLLIER[1], DANTÉ B FENOLIO[2]
[1]Institute of Renewable Natural Resources, Texas A&M University, College Station, Texas 77843
[2]Atlanta Botanical Garden, Center for Conservation Research, 1345 Piedmont Ave, Atlanta, GA 30309

One of the primary difficulties associated with populations endemic to cave ecosystems is estimating basic biological parameters such as abundance, survival, and recruitment. As many karst systems can be perturbed, determining estimates of demographic variables are central to evaluating whether anthropogenic or environmental influences cause variation in population distribution and trajectories. Currently, sampling design and inference methods for demographic parameters are readily available and widely applied to a range of terrestrial fauna. Our objective is to provide an overview of potential sampling designs and demographic estimation methodologies which would be amenable for use on a variety of subterranean species. We will discuss concepts associated with spatial and temporal constraints contingent on the biology of the species under study, provide examples of potential sampling designs applicable to subterranean systems, and outline estimation techniques addressing issues associated with estimation of observability, presence/absence, abundance, survival and recruitment estimation, and transience associated with temporary and permanent emigration. While general and applicable, few sampling designs or modeling applications have been applied to karst species, likely due to perceived difficulties associated with low species abundance, limited spatial and temporal distribution, and unobservable states. However, we suggest that further investigation be directed towards design and application of common estimation approaches to further our understanding of the fauna existing in subterranean ecosystems.

1. Introduction

Scientific research is frequently driven by hypotheses-based experimental studies on mechanisms impacting populations across their range. Experimental studies where system perturbations are planned and implemented necessitate a much different design than studies focused on inventory or monitoring. However, perhaps the most difficult but most important part of developing a study is explicitly defining what the survey's focus will be and how those data will be used to evaluate population trajectory and demography. Logistical limitations, such as those found in most cave environments, will limit researchers to mensurative designs in lieu of replicated experimentation. However, mensurative research can provide a wealth of information on population dynamics and the causal relationships between environment and demography. Thus, as ecologists, our objective is to collect and use information to make inferences regarding population growth, trajectory, or demography (Thompson et al. 1998). However, as complete enumeration of populations is infeasible in most cases, we rely on a combination of sampling survey design and model-based inferences to maximizing information collected on populations of interest while minimizing costs of the sampling effort (Thompson 2002).

The primary difficulties in studying cave environments are associated with sampling designs and resulting demographic inferences (Benedetti-Cechi et al. 1996, Culver et al. 2004). Sampling designs for cave systems have similar limitations as those found in terrestrial or marine systems; thus cave sampling designs must address general issues associated with spatial configuration across landscapes and within unique cave systems, temporal variation associated with seasonality of resources within cave systems, and enumeration variation, or the inability of ecologists to accurately census populations. However, specific issues affecting sampling in cave systems differ from those found when sampling terrestrial or marine systems. For example, cave systems may be more buffered from climactic changes or seasonal extremes (Dowling, 1956; Poulson and Culver, 1969; Barr and Holsinger, 1985; Fenolio et al. 2005), but, issues of sample survey coverage and detectability are paramount to demographic studies of cave organisms (Schneider and Culver, 2004). Our focus within this paper is to discuss some general topics relating to sample survey design and resulting inference and to discuss several approaches which might be amenable for cave systems. Obviously our review will not be all encompassing of all literature on both sampling and caves, but we will note alternative literature for the interested reader.

2. Study Focus

When designing a study to evaluate population dynamics, the study species is perhaps the most important factor on which to base design decisions. After positing a question and reviewing literature, one must determine study feasibility based on a host of factors. Research questions and survey designs for species of interest which are widely distributed in low abundance differ from species which are restricted in range and locally abundant. Accessibility to the target population's habitats are requisite, although structural or spatial limitations will influence observability of the target population. In addition, given we can access habitat where the species is expected to be located, the next questions are addressed. First, is the species present or absent? If present, can we allocate enough effort to adequately sample the species, e.g., are we able to catch/locate the species on a regular basis? Each of these questions must be addressed and answered, via either literature review or a pilot study (Thompson et al. 1998) before intensive efforts studying population dynamics are attempted.

Because our ability to experimentally perturb cave systems is somewhat limited, we often focus on different forms of population assessment as a way to evaluate population state(s). Monitoring is critical to our understanding of factors causing variation in populations as monitoring allows for population assessments over time and space (Thompson et al. 1998, Yoccoz et al. 2001) and provides the ability to readily identify conservation issues and potential solutions (Thomas 1996). Inventories typically measure population status during the survey period, but are not concerned with persistence, size, or mechanism affecting population change after the survey period. Inventories often focus on species richness or diversity (Nichols et al. 1998, Cam et al. 2002, Schneider and Culver 2004). Inventories can also focus on species abundance within a cave during a single time frame (Benedetti-Cecchi et al. 1996). Within the context of monitoring, when future impacts are temporally and spatially defined, impact assessments can be used to determine what effects perturbations have on populations. Impact assessment require explicit knowledge of the upcoming disturbance, otherwise sub-optimal designs are warranted (Morrison et al. 2008). However, using long-term monitoring, we suggest that impact assessments can be used to correlate changes in populations to biological (Fenolio et al. 2005; Fenolio et al. 2006) or anthropogenic (e.g., Schwartz, 1976; Crunkilton, 1984; Weaver, 1987) phenomenon.

3. Sample Survey Design for Observational Research

Because we cannot assume a census when studying natural populations, the primary purpose of sampling is to collect data from a randomly selected subset of the population of interest and use those data to estimate population parameters (abundance, survival, recruitment) while accounting for nuisance parameters (observability, detectability) and evaluating the impacts of process-based (temporal and spatial) and sampling-based (enumeration) variation (Thompson et al. 1998, Williams et al. 2002, Morrison et al. 2008). Inductive inference and measurements of uncertainty are tied to probabilistic sampling designs (Cochran 1977), and non-probabilistic sampling based on judgment/convenience do not allow for valid inference to be made regarding the study population. Because the range of sampling and inference topics which could be associated with sampling troglobitic/stygobitic populations are extensive, we will focus on applications that illustrate methodologies we suggest would be applicable. We acknowledge that this list is not all-encompassing, and that alternative designs should be evaluated.

4. Designs for Parameter Estimation

Currently, there are countless approaches for estimating population demographic parameters (e.g.,occupancy abundance, survival, recruitment, fidelity) as well as nuisance parameters (detection or capture probabilities) when a complete census is infeasible or impossible. When designing a study to track the dynamics of a natural population over time and space, it is highly unlikely to expect that you will detect all of the organisms of interest within your sampling frame. The issue of detection probability has permeated the field of population dynamics research recently with both manuscripts and books highlighting the importance of estimating detection (Anderson 2001, 2003, Thompson 2002, Williams et al. 2002, Thompson 2004, Morrison et al. 2008). Estimation of nuisance parameters has become pervasive in ecological literature, often superseding discussion of population parameter of interest as demographic parameters can rely on multiple nuisance parameters for accurate prediction. As a simple example outlining the necessity of estimating nuisance parameters, consider the general estimator provided by Pollock et al. (2004) which addresses issues associated with observability of the sampled population, via both detectability and availability to be detected. The estimator from Pollock et al. (2004)

$$\hat{N} = \frac{C}{P_{area}\hat{p}_a\hat{p}_{d|a}}$$

where $\hat{N}$ is the population size, C is the uncorrected count or population index, P_{area} is the proportion of the total area surveyed, $\hat{p}_a$ and $\hat{p}_{d|a}$ represent the probability of being available for sampling, and for being detected given that the species was available to be sampled, respectively. The historical approach would be to equate $\hat{N} = C$ under the aforementioned assumptions. However, $\hat{p}_{d|a}$, $\hat{p}_a$, and P_{area} each have different ramification for estimates of $\hat{N}$. Not accounting for the amount of an area available for sampling (P_{area}) would only allow inferences to be made to the available component of a population (Pollock et al. 2004) while ignoring the effects of $\hat{p}_{d|a}$ and $\hat{p}_a$ would likely bias estimates of $\hat{N}$ low (e.g., as $\hat{p}_i \rightarrow 1$ then $C \rightarrow \hat{N}$). The primary reason we chose this example is that this general estimator highlights the need to account for sample availability (observability and detection), which we see as being issues paramount to study of subterranean species in environments which we will discuss in the next section.

Because complete enumeration of natural populations is difficult, biometricians have developed a suite of methods appropriate for estimating population demographic parameters based on capture-recapture of marked individuals. In capture-recapture studies, populations are sampled >2 times with individuals are marked upon capture and the frequency of recapture of marked and unmarked individuals is recorded during each occasion. Marks can be based on unique characteristics of individuals, PIT (passive integrated transponder) tags, radio-tags, genetic tags, unique vocalization, repeated observation, and a host of other marking techniques (Morrison et al. 2008, pp. 175). Typically, recaptures occur through harvest, trapping, resighting (Williams et al. 2002). There are typically 4 population parameters of primary interest to ecologists; abundance, survival, and recruitment, and immigration/emigration rates. Methods available for estimating these parameters are not mutually exclusive, but can be broken into general categories of closed and open population models (Amstrup et al. 2005) with different approaches falling under each type (e.g., closed captures, multiple observers, Cormack-Jolly-Seber) and several approaches that combine different methods to estimate a set of parameters from the same data (e.g., robust designs, multi-state models) (see Amstrup et al. (2005; pp. 4) for a methods flowchart). While we focus our discussion of parameter estimates on models for abundance, survival, and recruitment using on capture-recapture style approaches, we also note that a variety of techniques for estimating abundance that do not rely on capture-recapture approaches are available (Williams et al. 2002).

The Peterson-Lincoln model is one of the original population abundance estimator models and is the forerunner of all current modeling applications. Under the Peterson-Lincoln model, a sample (n_1) is captured, marked, and released during the first sampling occasion (t_1). A second sample (n_2) is taken at a later time (t_2), and the number of previously marked individuals recaptured (m_2) are recorded. Using these data, population size is estimated as $\hat{N} = n_1 n_2 / m_2$. Based on this original design, closed capture population models (Otis et al. 1978) are used when the researcher is confident that the population in question is unchanged due to births, deaths, or movements into and out of the population during the survey period(s). Closed capture models have expanded from addressing issues associated with variation due to behavioral or temporal factors to a class of models which now allow for evaluations of heterogeneity associated with groups, classes, states, or values unique to individuals (Williams et al. 2002) and have been expanded for either discrete or continuous time modeling (Chao and Huggins 2005). Closed capture models are highly flexible and can be applied not only to situations where individuals are captured and released, but to systems based on multiple-observer surveys as well (double observers, Nichols et al. 2000).

Determining viability of populations often requires information on survival and recruitment, which, when combined with estimates of abundance would allow researchers to model populations dynamics over time. Estimation of survival and recruitment requires models that relax the assumption of population closure (no movements in or out of a population during the sampling period). Thus, population models which allow modeling of gains based on reproduction/emigration and losses due to mortality and emigration are described as open models. Open population models have been developed under variety of different modeling methods and assumptions over the past 50 years. Open population models using the Cormack-Jolly-Seber (CJS) parameterization are conditioned on the capture and release of marked individuals within the population (Williams et al. 2002), while Jolly-Seber parameterizations include an additional component for modeling unmarked individuals in the population (Nichols 2005). Another option for recruitment estimation is based on reverse-time models (Nichols et al. 2000) or an application of common CJS models wherein by reversing the capture histories and conditioning on the individuals captured during the last time period, inferences can be made on recruitment rates into the population and the various importance of recruitment or survival to population growth rates.

Modeling approach we suggest, which use marked individuals and are very applicable to sampling and demographic parameter estimation in karst environments, are those using robust designs. Robust design modeling (Pollock 1982, Kendall et al. 1995) is an approach in which open and closed models are combined; wherein, periods having short times between sampling events are modeled as closed populations and time between these periods are modeled as open populations. Hence, estimation of abundance and capture probabilities can be garnered from the closed periods, while estimates of survival and recruitment can be determined using data collected from individuals captured between the closed periods (i.e., the open periods). Use of robust design models is well suited for cave systems in that questions regarding population size can be addressed using the 'closed' sampling periods. As a brief example, imagine sampling in a system where salamanders are seasonally clustered in a known portion of the subsurface habitat (Fenolio et al. 2006; Fenolio et al, in prep). Optimally we suggest structuring the secondary sampling period to occur when salamanders are clustered, due to available resources. The primary sampling periods could occur annually or seasonally or given some time frame that is biologically relevant for estimating survival and movements. Estimation of gains and losses to the populations will be determined over the primary periods while abundance is estimated over the secondary periods.

Robust designs also provide a framework for evaluation of temporary emigration, or the probability that an individual is unavailable for capture during the sampling occasion (Kendall et al. 1997). Unavailability for sampling is an important consideration in cave systems, as cracks, fissures, and other small human inaccessible places all limit the ability of sampling technique to adequately expose all individuals to sampling efforts. The availability to be captured must be incorporated into our estimates of capture probabilities and hence other population parameters. For this, robust design methods are recommended. We also see future applications for parameter estimation combining robust design models under a multi-state framework (Schwarz 2005). Under a multi-state framework, interest is in estimating the transition probability between various states (e.g., breeding/non-breeding, movements between locations) while robust designs could be used to estimate abundance and demographic parameters associated with the temporal frame during which the above states occur.

One final topic relates to use of presence-absence surveys (Mackenzie et al. 2006). We suggest that estimation of occupancy (probability that a species is present in a location) has some relevance to surveys for subterranean species distributed in cave systems across a landscape. Estimates of species richness are often tied to the number of caves surveyed (Schneider and Cluver 2004, Culver et al. 2004) and methods that use presence/absence of species at different locations could be used to determine the likelihood that the species is present at locations where it was not detected (Nichols et al. 1998). An example application of presence/absence surveys at the macro-level could evaluate the distribution of a species by surveying caves across a region (Culver et al. 2004), or, at the micro-level one could survey specific habitats (pools, runs, etc.) within a cave system and evaluate covariates (distance from mouth, temperature) which could influence species presence. The primary benefit from application of presence/absence approaches is that under a viable sampling design, they allow estimation of the likelihood a species is present, even if undetected, and allow for incorporation of potential covariates to determine what information best predicts presence to aid in future sampling plans.

We have provided some general thoughts on potential designs which could be applied in cave studies that could use capture-mark-recapture/resight information to estimate population parameters. Obviously, there is a host of literature on population parameter estimation methods available and we have only scratched the surface of potential approaches which could be applicable to subterranean systems. We suggest interested readers see works by Otis et al (1978), Kendall et al. (1995), Thompson et al. (1998), Williams et al. (2002), Thompson (2004) and Amstrup et al. (2005).

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