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SNAKES IN THE GRASS: SECRETIVE NATURAL HISTORIES DEFY BOTH CONVENTIONAL AND PROGRESSIVE STATISTICS

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***Abstract*.—Standardized efforts to passively sample for upland snakes often result in low detection probabilities, yet this methodology is often used to determine differences in relative abundance. Estimating abundance of upland snakes using a model that incorporated detection probabilities did not generate useful results because detection rates were too low. These results indicate researchers interested in quantifying relative abundances of upland snakes should focus on increasing sampling efforts in an attempt to raise detection probabilities, regardless of the preferred analysis.**

Key Words.— Detection probability; occupancy modeling; relative abundance; reptile

OVERVIEW

Recent work has described developments in model selection and occupancy modeling while demonstrating the importance of incorporating detection probabilities into analysis (Mackenzie et al. 2006). The general sentiment among herpetologists is the field has not fully embraced these methodological advances despite their ability to refine our understanding of amphibians and reptiles (Mazerolle et al. 2007). When detection probabilities are not incorporated into analyses, researchers are in danger of misinterpreting patterns of distribution. A comprehensive review of detection probabilities and occupancy estimation is beyond the scope of this essay, although the topic has been covered extensively elsewhere, including in relation to amphibians and reptiles (Mazerolle et al. 2007).

Snakes are generally secretive and cryptic animals difficult to survey or recapture with current methods. This is not a particularly groundbreaking observation: the difficulties associated with estimating snake population parameters are well known (Parker and Plummer 1987). The effort associated with simply establishing snake absence from a particular area may be substantial (Kéry 2002). The cryptic natural histories of this group of animals would seem to make it particularly essential to incorporate detection probabilities into analyses when comparing parameters associated with snake populations or assemblages.

The purpose of this essay is to discuss some of the problems encountered when attempting to integrate detection probabilities into analyses comparing groups of upland snakes captured via passive trapping and to stress that a renewed focus on improving our ability to detect these animals is necessary to substantially further our knowledge of how populations vary over time or space.

WHAT IS THE LEVEL OF SAMPLING EFFORT REQUIRED TO STUDY RELATIVE ABUNDANCE?

When it is difficult to simply establish whether a species is present or absent (Kéry 2002), we should be even more cautious when making inferences about the relative number of individuals captured. Yet, snake studies have generally not included detection probabilities. To investigate population or community-level responses to habitat modification or habitat selection, investigators often use passive traps with boxes, pitfall traps, or funnel traps. The relative number of snakes captured among plots or treatments is then analyzed to make inferences (e.g., Russell et al. 2002; Renken et al. 2004; Cagle 2008; Todd and Andrews 2008; Bateman et al. 2009; Perry et al. 2009).

It is well established that raw counts are an unreliable means of estimating population sizes for cryptic species (e.g., Williams et al. 2002; Bailey et al. 2004; Lind et al. 2005) and the typical method of overcoming this hurdle is to conduct a mark-recapture study. However, many snake species are difficult to capture once, let alone multiple times making mark-recapture analysis less feasible. An additional difficulty relates to defining population boundaries. As individuals may wander widely, large home ranges make it difficult to know with certainty that a particular study site encompasses a single individual's movement patterns, let alone that of the population. An abundance estimate is of little value unless there is also an associated unit of area, and the area being sampled is difficult to define for terrestrial forms that range across the landscape.

Species associated with a discrete habitat type, (e.g., wetlands or communal hibernacula) are sometimes captured with enough regularity to permit mark-recapture analyses (Lind et al. 2005; Koons et al. 2009; Rose et al. 2010). For most upland snake species though, recaptures are a relatively rare event making mark-recapture techniques difficult (Turner 1977; Parker and Plummer 1987). An alternative is to estimate abundance with models requiring only presence/absence data (e.g., Royle and Nichols 2003) and they have been suggested as a potentially viable strategy for snake analyses when individuals are infrequently recaptured (Dorcas and Willson 2009).

When conducting preliminary analyses associated with my dissertation proposal, I set upon several datasets of snakes captured in Longleaf Pine (*Pinus palustris*) forests, eager to devise an analysis that incorporated the detection probabilities recent papers had convinced me were so important. The datasets I examined were based on upland snakes captured in box traps (Burgdorf et al. 2005) and spanned from two to four years. In delving into the data, I came upon a Catch-22. Although incorporating detection probabilities may refine analysis of snake populations, most species in my study were captured so infrequently that meaningful results were not obtainable.

For example, over four years at Ichauway (the Joseph W. Jones Ecological Research Center in southwestern Georgia), 52 Copperheads (*Agkistrodon contortrix*) and 45 Pinesnakes (*Pituophis melanoleucus*) were captured within 16 box trap arrays. Both species were captured relatively frequently, as compared to other detected species, and in numbers comparable to each other. When I attempted to calculate detection probabilities using a model (Royle and Nichols 2003) with Program Presence (Hines 2006), I obtained detection probabilities of 0.01 for Copperheads and 0.00 for Pine Snakes (estimates are rounded; Steen et al. in press). Despite relatively large samples sizes (for snakes), given the length of study and number of traps, their record of presences and absences was so sparse as to make them virtually undetectable as far as the model was concerned.

Neither Copperheads nor Pinesnakes are considered rare on the site, but two Southern Hog-nosed Snakes (*Heterodon simus*), which are of conservation concern (Tuberville et al. 2000), were also captured. Despite catching many fewer Southern Hog-nosed Snakes than the aforementioned species, calculated detection probabilities for all three species were indistinguishable (0.00, Steen et al., in press). Thus, it is likely models are unable to differentiate between rare species or species that are relatively common but rarely detected. When detection probabilities are low, confidence intervals and standard errors are so large the reliability of these estimates is minimized.

Small sample sizes are a thorn in the side of these recent statistical advances (as they have been for more traditional analyses). To calculate detection probability, a species detected at least once at a site is assumed to be present for the study's duration. Frequently, a single individual snake may be the only representative for a species within a particular trap in a given study. If a species was only detected once at one or two sites (again, not a farfetched scenario) but assumed to be present and available for capture the entire time at these sites, current models will determine the species' detection probability to be extremely low. If the probability of detecting a species when it is present is very low, we will not have high confidence the species is really absent where it was not detected.

Consequently, model outputs will indicate the species is present at all or nearly all sites, but undetected; standard errors and confidence intervals around detection probabilities will be exceedingly large. Abundance estimates derived from the distribution of these detection probabilities (i.e., as specified within Royle and Nichols 2003, for example) will range from the seemingly reasonable to the grossly ridiculous (e.g., thousands of snakes present, Steen et al. in press). The model I used (Royle and Nichols 2003) assumes a positive relationship between abundance and detectability, but if detectability is low, then the model is of limited utility in generating abundance estimates.

Is it valid to assume a species detected once is likely present during every sampling occasion over the course of the study? Often, I would say yes. Exceptions would occur when a species is detected in the course of dispersing to hibernacula (Brown and Parker 1976), undertaking other seasonal movements to disparate habitats, such as when pursuing prey (Shine and Madsen 1997), or responding to periodic environmental conditions (e.g., drought, Willson et al. 2006). In most cases, I would argue, if a passive trap is set in suitable habitat for a particular species, and barring the aforementioned scenarios, the snake is likely present the entire time even when detected only once. Unfortunately, however, acknowledging the assumption of continual occupancy of rarely detected species, while necessary from a statistical standpoint, only confirms we have a limited ability to sample for snakes.

Knowledge of natural history and common sense is key in all field studies, and passive trapping is no exception. It is not appropriate, for example, to assume a highly aquatic snake captured in an upland trap during what was obviously an isolated terrestrial foray is present over the course of a study. Similarly, little to no weight should be given to non-detections when the species is known to be dormant due to environmental conditions and sampling occasions during these times should not be included when calculating detection probabilities.

Do I agree with the sentiments outlined within Mazerolle et al. (2007), in that herpetologists must account for detection probabilities in future analyses? Absolutely. My point here is although sophisticated model selection techniques and models that incorporate detection probabilities are available, they are not yet applicable for hard-to-sample species such as upland snakes. When these sophisticated analyses are used for infrequently captured species, they are likely to generate nonsense values.

The point is not that recent advances in modeling and detection probability are flawed, but that we lack the ability to collect samples robust enough to differentiate between snakes that are truly rare and those that are infrequently detected, between a group of one species with a few individuals and a group of the same species with many individuals. Corresponding abundance estimates will be similar for snakes captured relatively frequently and for those captured only a handful of times, with little confidence in any estimates. Passive trapping may represent our best chance to capture or survey for large, upland snake species, but this should not be taken to mean it is an effective methodology when the goal relates to population or community-level questions.

That it is nearly impossible to acquire sensible results in analyses that incorporate detection probabilities suggests 1) observed values are unlikely to give reliable indication of how many individuals are actually present and 2) researchers should focus on methods that increase detection probabilities. Until we do so, we cannot integrate the recent statistical advances that others have convinced us are important (Mazerolle et al. 2007). The point of this essay is two-fold. First, to bring attention (temporarily) away from the allure and promise of sophisticated analyses to note they cannot overcome the secretive biology of many snakes. Second, to note a prevailing methodology (i.e., passive traps) used to sample for upland snakes is typically unsuitable in generating samples sizes robust enough to appropriately answer population level questions.

This is not to say passive trapping for snakes has not and will not continue to generate important information. For example, our knowledge of life history for many species is due in large part to this methodology (e.g., see the cumulative work of H.S. Fitch) and may be effective at determining snake species richness, although a level of effort is necessary that exceeds typical studies of the subject. In addition, pitfall traps and other sampling methods have been successful at capturing hundreds of small, litter dwelling or fossorial snakes in a relatively short period of time (e.g., Todd and Andrews 2008; Patrick and Gibbs 2009); many more individuals than would be expected of larger, upland species. These species may be suitable for integrating detection probabilities into abundance estimates and I echo Mazerolle et al's (2007) call to do so.

WHERE DO WE GO FROM HERE?

If we desire to compare groups of upland snakes, we must strive to increase our ability to detect them. Longer term sampling efforts have been proposed as necessary to monitor trends in reptile populations (Tinkle 1979), due to natural fluctuations in population sizes, variation in detection probability, or both. I agree these long-term studies are necessary given the potentially long life spans of snakes, among other factors. However, the ability to accurately determine population trends is not enhanced in any given year when studies are conducted for a longer period of time. When sampling yields low capture success, there is little reason to suggest a 100 year survey will give a better indication of population trends than a study of 10 years. There is just a ten-fold increase in the amount of values with wide confidence intervals.

Increasing length of study does not substantially increase detection probabilities or their precision within any reasonable amount of time for many upland snake species (Steen et al. in press). One could conceivably increase detection probabilities by increasing the amount of time considered a sampling occasion, assuming you are more likely to detect a species at least once over a relatively long time frame, but at least for most snakes, these time frames may need to consist of the pooled captures over perhaps 5, 10, or more years of study. The logistic efforts associated with this type of study, however, preclude this strategy in most scenarios. In addition, the longer the study the greater likelihood of violating the assumption that a species detected once is present over the entire duration.

INCREASING SAMPLING EFFORT

Instead of repeating the same methodology for a longer period of time, a more productive strategy would be to increase sampling effort within a given period of time. Steen et al. (in press) noted potentially promising trends among a population of one species, North American Black Racers (*Coluber constrictor*), when the number of traps included in analysis increased; but cautioned this was observed only for the one species captured most frequently. Once we are relatively confident in our ability to simply detect a species (although we can aspire to reach 100% detection probability, this is not required), we can take the next step and attempt to quantify abundances from this information. For other taxa, thresholds of detections have been identified below which it is likely not feasible to estimate abundances (e.g., Joseph et al. 2006). It may be beneficial to determine these values for snakes. Increasing sampling also enables the researcher to gather enough data to determine, via back-calculation, the effort required to confidently conclude a species is absent (e.g., McArdle 1990; Kéry 2002).

Vast increases in sampling effort are required to advance our understanding of populations for many upland snake species. This essay should be not be used to excuse future researchers from considering detection probabilities with the reasoning that it would not have generated meaningful results. Our inability to calculate detection probabilities with confidence should be considered an indication of limitations associated with sampling methodology. This will not be remedied by either inaction or repetition.

ADDITIONAL METHODOLOGY

Passive trapping is, and will likely continue to be, one of our most effective tools for sampling snakes. Yet, there is room for improvement. Perhaps our ability to detect upland snakes will increase when passive trapping is used in conjunction with other innovative or novel methods. Avenues for further exploration include baited traps (Rodda et al. 1999), which have met with some success in capturing Brown Tree Snakes, (*Boiga irregularis*). Researchers have successfully used detector dogs to locate chelonians (Cablk and Heaton 2006) and there may be promise in using these animals to find snakes (Engeman et al. 2002). There are a myriad of methods and techniques for catching and studying snakes (Fitch 2001; Dorcas and Willson 2009) and the cumulative or comparative efforts of different techniques employed intensively are likely to be useful in raising detection rates.

Detection rates may be raised through focused sampling efforts that take into account basic natural history information. Although we lack this information for many species, it is essential in guiding more advanced study (Greene 2005). Radio telemetry holds great promise in elucidating snake habitat use and movement patterns (e.g., Blouin-Demers and Weatherhead 2001) and trap placement may be informed by studies that incorporate this technique.

What if we are unable to increase upland snake detection probabilities to what may be considered a reasonable level? To avoid abandoning field studies that elucidated trends in snake populations, we must interpret findings of such studies with caution and consideration. Setting out a number of traps, counting the number of animals captured, and then interpreting these data as indicators of the relative preference for a given treatment should not be considered valid practice. Given the low and varied detection probabilities that have been documented for upland snakes, researchers are reasonably assured at documenting varying numbers of animals in different areas. There is little compelling evidence to suggest, however, that these numbers are representative of the number of present animals, and it is not statistically defensible to infer habitat preference, among other parameters, from raw counts. Given the potential rarity of the study organisms and their low detectability, presence-absence surveys may be a more accurate way of examining snake populations (e.g., Pollock 2006). If studies that quantify relative abundance continue without efforts to increase detection rates, it is essential to formulate *a priori* hypotheses regarding the species of interest. If results are found according to expectation, at least some degree of confidence can be attributed to interpretations.

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