CHAPTER 15

Overcoming Low Detectability in Snake Conservation Research: Case Studies from the Southeast USA

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Abstract—Goals of conservation research include detecting and monitoring changes in abundance, understanding species interactions, detecting extinction events of imperiled species, and detecting colonization events and spread of non-native species. Achieving these goals is difficult or impossible when the target species is rarely encountered or when the number of individuals detected is unrelated to the true population size, as is often the case with snakes. Here, we review the challenges that low species-level and individual-level detection probability cause for snake conservation research, present four case studies demonstrating approaches we have used to overcome low detection probability, and highlight priority areas for future research and method development.

Keywords—Capture-mark-recapture; experimental design; methods; occupancy; sampling; statistics

Introduction

Despite historical underappreciation and public misconception, snakes are gaining popularity as study organisms (Shine and Bonnet 2000). In fact, snakes have emerged as model organisms for a variety of questions in organismal biology and physiology. However, population and community-level research on snakes is still rare, presenting a serious impediment to snake conservation and management (Mullin and Seigel 2009). Indeed, many snake species are thought to be rare or threatened, but in most cases population sizes are unknown and it is difficult to know whether species are truly absent from areas where they have not been detected. The lack of knowledge about snake population ecology is fundamentally driven by the low probability of encountering a species or individual of most snake species (i.e., low detection probability). Resulting from a combination of secretive behavior, cryptic coloration, low and sporadic activity, and low abundance, the issue of low detection probability can make it difficult to document which snake species occur at a location, let alone to obtain sample sizes adequate for many research questions. Further, low and variable detection probability can result in misleading perceptions of abundance and biased estimates with unrealistically high precision (Banks-Leite et al. 2014, Guillera-Arroita et al. 2014b). For example, research on invasive *Boiga irregularis* (Brown Treesnakes) on Guam found no relationship between the number of snakes observed during surveys and true snake abundance (Rodda et al. 2007). Low detection probability presents a particular challenge for formal estimation of demographic parameters such as abundance, survival, and recruitment, because the mathematical approaches used in these types of studies usually require recapturing individuals over time (Dorcas and Willson 2009). Fortunately, advances in our understanding of snake behavior, sampling technologies, and analytical approaches are improving our ability to study secretive snakes. Our goals in this chapter are to review data on snake detection probability and to present case studies from our own research that have allowed us to overcome low detection probability and ask meaningful questions about snake population ecology and management.

Detection probability in snake research

Most snakes are cryptic in both morphology and behavior, and many occupy habitats that are difficult (if not impossible) to non-destructively sample. These factors make snakes among the most difficult group of vertebrates for biologists to detect−on par with caecilians, some fossorial or aquatic salamanders and lizards, secretive marsh birds, owls, and some nocturnal mammals (Bobay et al. 2018, Colli et al. 2016, Specht et al. 2017). The difficulties studying snakes are exacerbated by the infrequent activity of many species, which has been detailed by three decades of radiotelemetry studies (e.g., Macartney et al. 1988, Jorgensen et al. 2008, Ward et al. 2013).

Understanding detectability has many applications in wildlife research; we focus primarily on two of the most widespread applications: estimating probability of species occurrence via occupancy modeling of detection/non-detection data and estimating abundance via capture-mark recapture (CMR). These and related (e.g., distance sampling, binomial mixture modeling, etc.) approaches can be implemented within a frequentist (i.e., probability of the data, given the hypothesis) or Bayesian (i.e., probability of the hypothesis, given the data) statistical framework. However, there are some circumstances (e.g., low sample sizes or complicated data structures) where a Bayesian approach may be favored. Consequently, Bayesian approaches are increasingly common in ecology, particularly hierarchical models that consist of a nested sequence of proba-

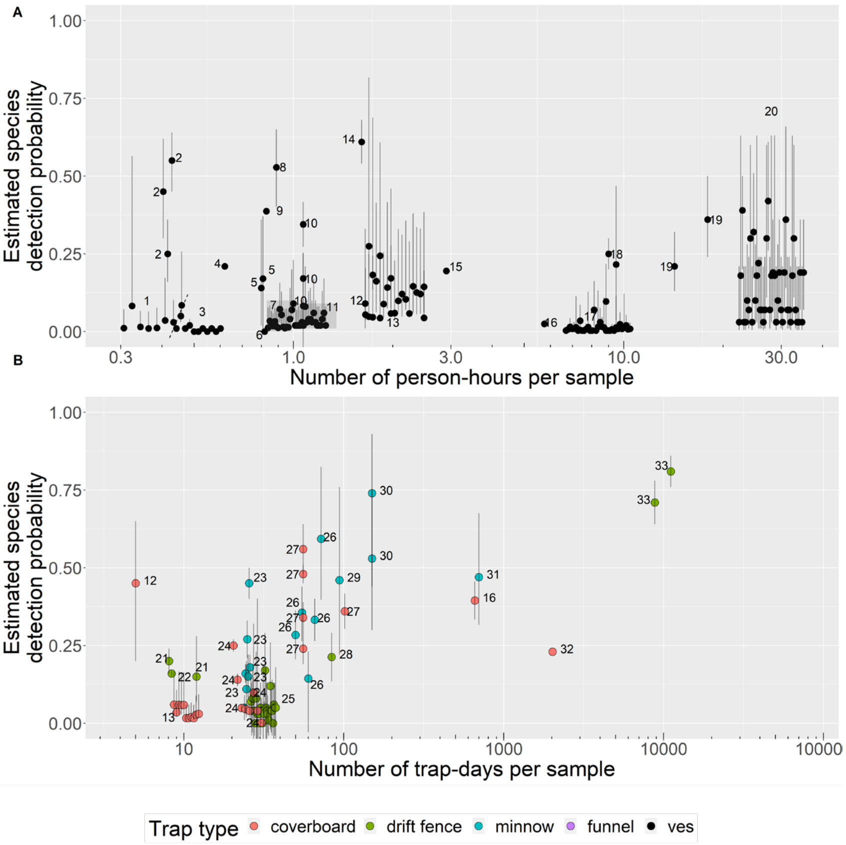

Fig. 1. Estimated species detection probability ($p_{species}$ ± 1 SE or 95% CI) of snakes compared to effort (number of person-hours for visual encounter surveys; A; number of trap-days for trapping; B). Drift fences may be equipped with funnel, box, or pitfall traps, coverboards, or a combination. For studies with many species, points are slightly horizontally offset for visibility. Studies referenced are **1** Homyack et al. 2016; **2** Kéry 2002; **3** Guzy et al. 2019b; **4** Hartel et al. 2009; **5** Oldham 2016; **6** Nafus et al. 2020; **7** Royal et al. 2022 ; **8** J.A. Crawford et al. 2020; **9** Graitson et al. 2020; **10** Snyder 2019; **11** Hunt et al. 2013; **12** Michael et al. 2012; **13** Royal et al. 2022; **14** Conelli et al. 2009 and Mebert et al. 2011; **15** Abrahão 2007; **16** Ward et al. 2017; **17** Zipkin et al. 2020; **18** Durso 2011; **19** Bauder et al. 2017; **20** Fraga et al. 2014; **21** Mitrovich et al. 2018; **22** Kim et al. 2018; **23** Durso et al. 2011; **24** Maritz et al. (unpubl.); **25** Steen et al. 2012a, b; **26** Vogrinc et al. 2018; **27** King and Vanek 2020; **28** Button et al. 2019; **29** Halstead et al. 2015a,b; **30** Rose et al. 2019; **31** Hansen et al. 2017; **32** Bonnet et al. 2016; **33** Sutton et al. 2013. See also Rodda et al. 1999 for catch-per-unit-effort of snakes in traps, which includes many studies without formal detection estimates not plotted here. The data and metadata for this plot are available online at 10.6084/m9.figshare.13286672.

bility models for observed (i.e., the data we collect) and unobserved random variables (i.e., latent variables) such as the probability of occupancy or estimated abundance. Refer to Kéry and Royle (2015) for more information on these approaches.

When discussing detectability, it is critical to differentiate between CMR and occupancy: these two analytical approaches have different goals, and detection probability has different meanings in each context. Further, the term detection probability can be confusing because despite different meanings, detection probability is typically denoted using a lowercase '*p*' in the models and literature of both approaches. *Individual* detection probability in CMR studies refers to the probability of capturing a particular individual snake, whereas *species* detection probability in occupancy studies refers to the probability of directly or indirectly (e.g., sign, tracks, DNA) encountering any individual of that species (at least one; occupancy studies reduce captures to detection (1) or non-detection (0) for each survey). To avoid confusion, we will hereafter refer to individual and species detection probability as $p_{individual}$ and $p_{species}$, respectively. Detection probability in either approach is not fixed for any species, site, or situation, but rather is a function of the behavior of the target species, efficacy of the capture method and/or observer, amount of effort expended per sample, and attributes of the survey (e.g., environmental conditions, season). For occupancy studies, $p_{species}$ is also a function of the density of the target species. Some studies define "capture probability" as a joint probability of species presence and its detection, which cannot be compared to $p_{species}$ from occupancy models (Rota et al. 2017, Timm et al. 2020, Mizsei et al. 2020). When designing either type of study, controlling for covariates of detection probability through sampling design (i.e., a study design that constrains spatial and temporal variation in sampling) is desirable but practically challenging, especially when many determinants of snake activity and catchability are still unknown (Eskew and Todd 2017, Siers et al. 2018).

Species (Fig. 1) and individual (Fig. 2) detection probabilities of snakes are often substantially lower than those for many other taxa (Durso et al. 2011), rarely exceeding 0.50, and vary dramatically among species, systems and studies. We collected 102 studies that provided estimates of either species (*n* = 59) or individual (*n* = 49) detection probabilities for one or more snake species, of which 61 also quantified the associated effort in person-hours or trap-nights. All 102 studies represented 185 species from 5 families (species-level: 89, individual-level 137) and were conducted in 18 countries on five continents. Species detection probabilities from published studies of snakes (Fig. 1) ranged from essentially 0 for many species to 0.81 for *Agkistrodon contortrix* captured in drift fences in Alabama, USA (Sutton et al. 2013). Large sample definitions (see below) such as lumping annual captures (Sutton et al. 2013, Graitson et al. 2019) or using many trap-nights (*n* = 60; Vogrinc et al. 2018), were needed to achieve $p_{species}$ > 0.50 for select species (Fig. 1). However, even with high effort per sample, $p_{species}$ was still very low in most cases. In studies where species detection

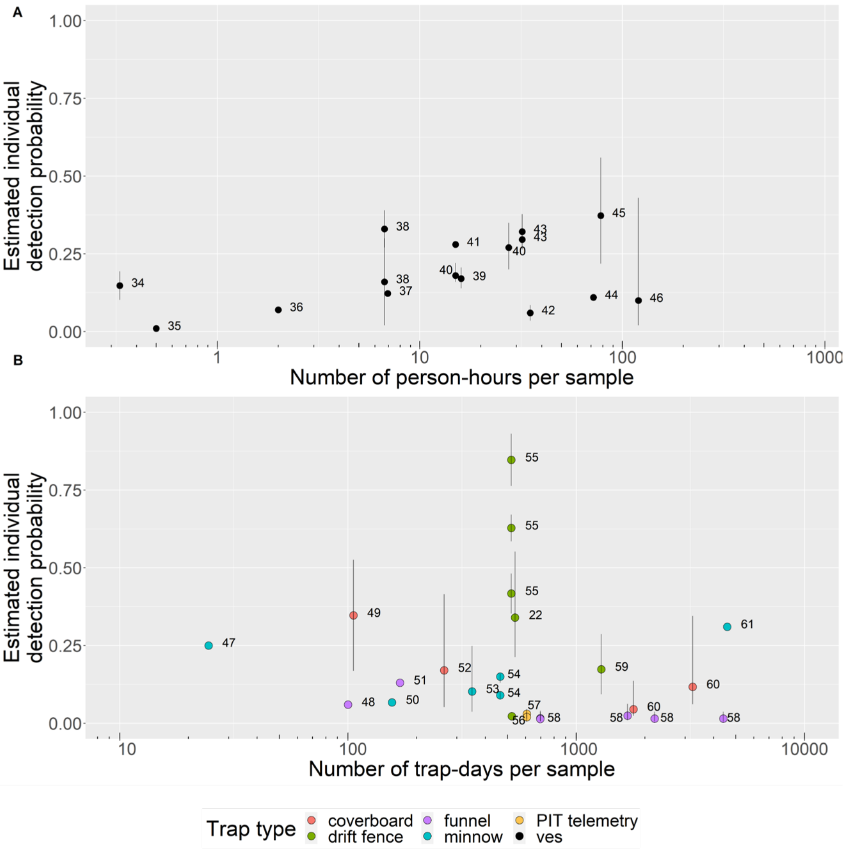

Fig. 2. Estimated individual detection probability ($p_{\text{individual}}$ ± 1 SE/CI95) of snakes compared to effort (number of person-hours for visual encounter surveys; A; number of trap-days for trapping; B). Drift fences may be equipped with funnel, box, or pitfall traps, coverboards, or a combination; "funnel" denotes stand-alone terrestrial traps. Studies referenced are **22** Kim et al. 2018; **34** Harvey 2005; **35** Dorcas and Willson 2013; **36** Christy et al. 2010; **37** Koons et al. 2009; **38** Shelton et al. 2017; **39** Lind et al. 2005; **40** Henderson et al. 2021;**41** Lyet et al. 2009; **42** Maritz and Alexander 2012; **43** Webb et al. 2002, 2003; **44** Jaramillo-Alba et al. 2020; **45** Flatt et al. 1997; **46** Guimarães et al. 2014; **47** Cecala et al. 2010; **48** Boyarski et al. 2008; **49** Hileman et al. 2015; **50** Rose et al. 2013; **51** Tyrrell et al. 2009; **52** Sewell et al. 2015; **53** Wylie et al. 2010; **54** Willson et al. 2011; **55** Diller and Wallace 2002; **56** Reeder et al. 2015; **57** Leuenberger et al. 2019; **58** Wood et al. 2020; **59** Halstead et al. 2011a; **60** Ovaska et al. 2021; **61** Hansen et al. 2015. The data and metadata for this plot are available online at 10.6084/m9.figshare.13286672.

probabilities exceeded 0.50 on shorter timescales, surveys were exclusively conducted during optimal seasons and conditions when basking activity is most common, which is possible only through a detailed understanding of the annual activity cycle of extensively-studied temperate European snake species (e.g., Kéry 2002, Conelli et al. 2009, Mebert et al. 2011, Graitson et al. 2019, 2020). Species detection probabilities also sometimes exceeded 0.50 when implanted passive integrated transponder (PIT) tags were used to enhance detection (Oldham et al. 2016), although detection probabilities varied widely among surveys and sites using this method. At the opposite extreme, visual encounter surveys of snakes in the Amazon rainforest never exceeded 0.50, despite samples that consisted of 15 times as many person-hours as the European surveys (Fraga et al. 2014). Individual detection probabilities > 0.50 (Fig. 2) were only achieved in a population where neonate snakes were marked following birth in captivity and released at a site near a routinely used hibernaculum and rookery over a period of 7 years (Diller and Wallace 2002). Along railways and at relatively small grassland and open rocky sites in Belgium, recapture rates of *Coronella austriaca* during favorable weather were ~0.50 (Graitson et al. 2020).

Overcoming low species detection probability (Occupancy Studies)—Occupancy studies typically aim to evaluate factors influencing species occurrence, and they use sampling designs that consist of repeated surveys of multiple sites, termed "detection/non-detection" surveys which are often colloquially called 'presence/absence,' however non-detection does not necessarily indicate true absence. Overcoming low p_{species} in occupancy studies is less daunting than in population monitoring (CMR) studies, but still is not trivial (Steen 2010, Durso and Seigel 2015). For many decades, the detection/non-detection data used for occupancy modeling were considered more-or-less useless (MacKenzie 2005, Vojta 2005), but studies that estimate both occupancy (ψ) and detection probability (p_{species}) from these data have become a new standard for hard-to-detect species.

The first step in designing an occupancy study is selecting the best capture/survey method. Because occupancy does not require recapture of individuals, it is usually best to use whichever method yields the highest encounter rate; for snakes, this is often a method that allows experienced observers to cover a lot of ground and focus on searching the best microhabitats within a sampling area. Trapping can be a superior method for aquatic species (see Case Study 1) or those that are attracted to bait. Non-traditional methods like using eDNA (Hunter et al. 2015) or wildlife detector dogs (Engeman et al. 1998a,b, Stevenson et al. 2010) can also enhance species detection. However, using eDNA techniques may still result in low detection probability, particularly for semi-aquatic snakes (e.g., Giant Gartersnake [*Thamnophis gigas*]; Halstead et al. 2017), and the utility of eDNA in terrestrial systems is limited (Kucherenko et al. 2018). Further, because non-traditional methods like eDNA rely on indirect signals of species presence (i.e., they sometimes fail to confirm an individual's presence during a survey), care must be taken to avoid false positives as one assumption of occupancy models are that species are not misidentified (MacKenzie et al. 2017). Other occupancy model assumptions are that site-occupancy status does not change during the survey period, the probability of occupancy and detection are constant across all sites (or if heterogeneous, are modeled using site or survey-level covariates), and detection of species at each site are independent (reviewed in MacKenzie et al. 2017). Finally, combining data from multiple different methods may have advantages (namely, increasing p_{species}), but doing so without explicitly estimating how detection differs by method sacrifices inter-study comparability based on effort (Fig. 2b).

The next step is defining a sample (i.e., number of person-hours, traps, or other units of effort over which detection or non-detection will be assessed; sometimes also called a 'survey' or 'visit') and deciding on the number of samples per site. Researchers must also carefully consider how sites are delineated, because inference about occupancy for a location will be affected by issues of scale and species' home range size and movement patterns. For example, survey methodologies such as road or trail transects may violate occupancy assumptions if sites are not independent of one another. Most occupancy models perform best when all sites are visited the same number of times (balanced sampling), although missing surveys can be accommodated when there are study design or sampling limitations (MacKenzie et al. 2017). When species are uncommon, greater effort per sample will result in higher p_{species}, but will reduce the number of samples that can be conducted. Figure 1 shows how p_{species} varies among species, study systems, and with effort per sample. Almost half of the studies we reviewed did not quantitatively report one or more crucial elements of sample definition that allow for inter-study comparison, such as site area, number of person-hours, or number of traps. Given the utility of this literature for guiding study design, we strongly encourage authors to clearly define the sample in publications, giving ranges and medians if effort varied among visits, and to report transformed, model-averaged parameter estimates in addition to those from top ranked models.

A trade-off also exists between the number of sites and the number of samples per site, given a fixed cost/effort. For example, a budget for a landscape-scale study incorporating a large number of sites may not allow for many repeat surveys, and depending on expected detection probability for certain species, fewer sites with more repeat surveys may instead be necessary. This trade-off has led some to suggest that estimating p_{species} is only worthwhile when occupancy is high ($\psi > 0.50$) and p is low (< 0.50), especially when the number of sites (sample size) is relatively small (Durso and Seigel 2015). MacKenzie and Royle (2005) provide information on the optimal distribution of sites and surveys given different expected combinations of p_{species} and ψ, and they explain when unbalanced designs may be more efficient. One such approach, called 'removal sampling,' is to stop sampling a site after the first detection of the target species and move to the next unsampled site. This is especially efficient when prior information about detectability exists (Halstead et al. 2011b, 2014; Fig. 1); continuing to sample a site where detection has already occurred only informs the detection process, whereas sampling additional sites provides more information about occupancy—the parameter of interest. Other survey designs and analytical techniques that minimize per-site survey effort, such as single-visit 'time-to-detection' occupancy modeling (Lele et al. 2012, Halstead et al. 2018) and using presence-only data (Royle et al. 2012), have not yet been applied to snakes, and their utility for snake research is likely limited because those methods require high detection probability (Guillera-Arroita et al. 2014a, García-Díaz et al. 2019). Analytical methods that can incorporate data from opportunistic or incidental encounters of individual snakes outside of pre-defined sites/sampling periods would be welcome, such as models implemented within a Bayesian framework that incorporate prior information for sites known to be occupied by a species (Tourani et al. 2020, Huberman et al. 2020). Likewise, recent approaches incorporating citizen science data of non-target species as inferred absences (when target species data are limited) are valuable, especially when using these minimal inputs to estimate persistence to inform status assessments and conservation decisions (e.g., B.A. Crawford et al. 2020)

Often, sampling under an occupancy framework (i.e., repeated low-intensity surveys across many spatially independent sites) yields few captures of many snake species. This is particularly true for studies aimed at sampling the overall herpetofaunal community or those not targeting specific snake taxa. Occupancy models for species with few detections often fail or lack the power to detect significant covariate relationships (Welsh et al. 2013, Fraga et al. 2014, Dénes et al. 2015). In such situations, authors must restrict their analyses and/or conclusions to one or a few focal snake taxa with sufficiently high captures, or exclude snakes from analyses all together. However, biostatisticians have recently introduced hierarchical community occupancy models (Dorazio et al. 2006, Zipkin et al. 2009, Pacifici et al. 2014) that simultaneously model occupancy of multiple species, often using Bayesian inference. These models maintain separate estimates for species-specific occurrence and detection probabilities, while relating these data to a broader analysis of species richness, thus combining species- and community-level attributes into one framework (Dorazio et al. 2006, Zipkin et al. 2009, Hunt et al. 2013). This approach can improve precision of individual parameter estimates, particularly for rare species, by considering them in the context of the larger community (Dorazio and Royle 2005, Dorazio et al. 2006), and can often identify guild- or community-level relationships, even when data for most species are too sparse to be meaningful on their own (see Case 2, below). Few published studies have applied community occupancy models to snake research (Homyack et al. 2016, Guzy et al. 2019b, Zipkin et al. 2020), but results from other herpetofauna have been promising (e.g., Hunt et al. 2013, Bush et al. 2017, Guzy et al. 2018, 2019a). Other promising modeling approaches that may benefit sparse snake datasets include multi-state occupancy models in which sites can be assigned to discrete states (e.g., Nichols et al. 2007, Miller et al. 2012). For example, these states could include (1) sites that are unoccupied, (2) occupied by few individuals, or (3) occupied by many individuals; flexibility can be included to allow sites to transition from one state to another. A benefit of this approach is that the proportion of sites in each state provides some index of abundance, which can be further informed by covariates expected to influence the probability of a site being in a specified state.

Finally, citizen science databases (e.g., web-based platforms containing georeferenced species occurrence records from opportunistic surveys at large spatial scales and verified by experts), can aggregate large numbers of observations into datasets that allow researchers to gain new insight into ecological and conservation questions (e.g., Hines 2011, Todd et al. 2016, Maritz et al. 2018). However, to date most citizen science databases focusing on amphibians and reptiles lack the ability for users to report search effort information, limiting the utility of their data for occupancy modeling (O'Donnell and Durso 2014). Citizen science projects that have successfully generated standardized or effort-corrected data for occupancy and other ecological modeling of other taxa include the U.S. Geological Survey (USGS) North American Amphibian Monitoring Program (NAAMP; Weir et al. 2005, 2009), and eBird (Johnston et al. 2019), whereas those that generate opportunistically collected, non-effort-corrected data include HerpMapper (www.herpmapper.org) and iNaturalist (www.inaturalist.org). Promisingly, participants in some citizen science programs appear more likely to report observations of snakes than those of other species (Price and Dorcas 2011).

Overcoming low individual detection probability (CMR Studies)—The goal of CMR sampling is typically to estimate demographic parameters such as abundance, survival, and recruitment. Meaningful CMR analyses usually rely on relatively high *individual* detection probability ($p_{\text{individual}}$), and parameter estimates become more precise by reducing variation in detection probability. Because $p_{\text{individual}}$ reflects the likelihood of capturing (or recapturing) a particular individual snake, it is not directly affected by abundance of the target species. Thus, $p_{\text{individual}}$ is often low when superficially surveying a large area. Likewise, achieving high $p_{\text{individual}}$ in CMR studies is not necessarily related to a high catch per unit effort (CPUE). When a species is rare but detectable, meaningful data for abundance estimation may result from studies with low CPUE but frequent recaptures of a few individuals (though ability to estimate survival may be limited; Halstead et al. 2015a). Alternatively, studies of species that are abundant but have low $p_{\text{individual}}$ may fail to yield meaningful CMR data (i.e., few recaptures) despite a high overall number of captures. For example, Fitch's (1975, 1999) pioneering long-term CMR study of *Diadophis punctatus* (Ringneck Snake) in Kansas included >22,800 captures, but recapture rates were <20%. Even more strikingly, a five-year CMR study of *Storeria dekayi* (DeKay's Brownsnake) in Illinois yielded only 44 recaptures of >3,000 marked individuals (I. Gross, Auburn University and S.J. Mullin, Arkansas State, pers. comm.). The aim of CMR sampling should generally be to maximize recaptures of a reasonable sample size of individuals, while minimizing variation in $p_{\text{individual}}$ by sampling in as standardized a way as possible. Figure 2 shows how $p_{\text{individual}}$ is related to effort in a variety of snake species.

Careful selection of a species/system that offers high individual detection probability is critical to the success of CMR studies. Study systems that are particularly amenable to CMR are those with a geographically well-defined population with minimal movement in/out (i.e., habitat 'islands'), those that are small in area, and those with habitat that is uniform and easy to sample. Detailed discussions of species and field methods are beyond the scope of this chapter (see McDiarmid et al. 2012, Graeter et al. 2013, Dodd 2016), but ideal species for CMR are those that are inherently catchable due to high activity, conspicuous behavior, or ease of sampling with particular methods (e.g., traps). Species that occur at high densities are also desirable, yielding a large sample size of recaptured individuals for analysis. In some cases, $p_{\text{individual}}$ can be increased by using technologies that help observers locate individual snakes, such as detection dogs (Stevenson et al. 2010), burrow cameras (Buskirk and Fiedler 1986), or PIT tag scanners (Oldham 2016, Oldham et al. 2016). To maximize recapture, high-intensity sampling of a relatively small area is usually preferable for CMR; however, small study areas may suffer from detection heterogeneity due to animals leaving the study area (i.e., temporary or permanent emigration). Temporal distribution of sampling events will usually reflect the goals of the study and are described in detail elsewhere (Dorcas and Willson 2009, Rodda 2012).

Modern CMR analytical methods allow researchers to account for sources of variation in $p_{\text{individual}}$, thereby improving precision of parameter estimates. Models can be divided into two broad categories: (1) 'closed' models that assume no birth, death, immigration, or emigration within the study period and are usually used to estimate abundance; and (2) 'open' models that are conducted over longer timeframes and typically usually used to estimate survival. 'Closed' models provide the most flexibility in accounting for heterogeneity in $p_{\text{individual}}$ and can account for variation due to time (e.g., season or sampling event), sampling covariates, capture history (i.e., trap-happy or trap-shy responses), individual covariates (e.g., body size, age, sex, reproductive status, body condition; Bonnet and Naulleau 1996, Pike et al. 2008, Bauwens and Claus 2018). With 'closed' models, individual heterogeneity in $p_{\text{individual}}$ can also be accounted for by including an individual-level random effect on p (e.g., Dorazio and Royle 2003). Finally, the most powerful group of CMR models are those that combine both 'open' and 'closed' models via the 'robust design' sampling approach (Pollock 1982, Kendall and Nichols 1995). 'Robust design' allows an 'open' analysis of survival across widely spaced primary intervals and 'closed' analyses of capture probability and abundance across closely spaced secondary intervals with minimal violation of model assumptions. 'Robust design' analyses are also the only family of models that allow for estimation of temporary emigration, a form of heterogeneity in which a portion of the population is essentially uncatchable ($p_{\text{individual}} = 0$) during a sampling event (Kendall et al. 1997). The importance of temporary emigration in herpetological research was first demonstrated by Bailey et al. (2004), who found that on average, 87% of individuals in a population of woodland salamanders were unavailable for capture (below ground) during sampling events, and would not be accounted for in typical 'closed' population analysis of their dataset (see also O'Donnell and Semlitsch 2015, Lardner et al. 2015, Rodda et al. 2015; Henderson et al. 2021). Although the 'robust design' framework has seldom been applied to snakes (but see Rose et al. 2018 and Case 3, below), its capacity for incorporating temporary emigration may allow researchers to account for periods of inactivity and cryptic behavior characteristic of many snake species. However, 'robust design' models are generally 'data-hungry' and may fail if detection probabilities or sample size (number of individuals) is low. Recently, spatial capture-recapture (SCR) models have emerged that explicitly incorporate the spatial distribution of captures into the abundance estimation process (Royle et al. 2013). These SCR models may prove particularly useful for situations where sampling is not uniform across the area of interest (introducing heterogeneity in capture probability due to location) or in cases where the boundaries of the population are not well defined. However, these models have only recently been applied to herpetofauna (Hileman et al. 2015, Muñoz et al. 2016, Schmidt et al. 2017), and model assumptions should be carefully considered in order to apply them appropriately to the unique biology of snakes.

Individual detection probability of some snakes may be so low that CMR is unlikely to yield useful results under even the best circumstances. For such species, alternative methods must be employed or developed. If survival is the primary parameter of interest, researchers may use methods such as radiotelemetry that allow direct tracking of individuals over time, essentially making $p_{\text{individual}} = 1$ (e.g., Halstead et al. 2012). Methods for abundance estimation that do not require recapture of individuals have been developed, but they have seldom been applied to snakes and in many cases seem unlikely to work. For example, distance sampling is a method that calculates abundance based on the assumptions that (1) detection probability (p) decreases with distance (d) from a survey point or transect and (2) all individuals along the transect are detected (i.e., $p = 1$ when d = 0). However, these assumptions seem unlikely to be valid for any snake population. The only attempt to validate distance sampling for snake populations resulted in severely biased estimates of population density compared to those generated using CMR (Rodda and Campbell 2002). Finally, Bradke et al. (2018) found that the ratio between estimates of genetic effective population size (N_e) measured using the linkage disequilibrium method and census population size (N_c) of reproductively mature adult *Sistrurus catenatus* (Eastern Massasauga Rattlesnake) measured using mark-recapture were similar between two sites (between 0.27 and 0.30). However, validation of CMR using genetic techniques is time-consuming, expensive, and still requires capturing (but not recapturing) numerous individuals. Also, the stability of this ratio has not been determined for any other snakes and is affected by life history, environmental characteristics, and demography. Given these limitations, we encourage snake researchers to think outside of the box and develop novel approaches for abundance estimation that do not require recapture of individuals, and to ideally capitalize on aspects of snake biology that predispose them to capture. For example, below (Case 4) we describe a novel abundance estimation method that does not rely on recapturing individuals and takes advantage of the fact that many secretive snakes are most frequently encountered while crossing roads (Willson et al. 2018).

Case Studies:

Conservation research frequently involves assessing relationships between species occurrence (occupancy) or abundance and anthropogenic stressors or management actions. Below, we summarize four published case studies where we have overcome low detectability of snakes to determine occupancy or abundance. The first two cases involved estimating occupancy. In the first case, we evaluated habitat covariates that best predicted occupancy of several poorly understood semi-aquatic snake species, as well as changes in occupancy (declines in occurrence across the landscape) of those species during extreme drought. In the second case study, we evaluated occupancy responses of snakes to riparian buffer width within managed forests and demonstrated the value of community occupancy models for similar datasets with sparse detections of snakes. The final two case studies involved estimating snake abundances. In Case 3, we use intensive CMR sampling within a 'robust design' framework to estimate abundance of aquatic snakes within isolated wetlands, with the ultimate goal of assessing the roles of snakes as secondary consumers within wetland food webs. Our final case study used a novel method for estimating snake abundance from road survey data to generate the first estimates of density for a secretive and declining upland snake species, the Southern Hognose Snake (*Heterodon simus*). Our focus here is on the approaches used to overcome low detectability, and thus we encourage readers to consult references cited therein for greater detail on methods and context of the research as it applies to snake conservation.

Case 1: Occupancy of Semi-aquatic Snakes in South Carolina—In conjunction with long-term studies of aquatic snake population and community dynamics in wetlands of the southeastern U.S. Coastal Plain, we were interested in understanding landscape scale patterns of occurrence (occupancy) and abundance of semi-aquatic species (Durso et al. 2011, Vogrinc et al. 2018). We were particularly interested in determining: (1) whether rarely encountered species were truly rare (i.e., had low occupancy); (2) wetland and landscape characteristics that best predicted occupancy of aquatic snake species; and (3) whether species occupancy declined during extreme droughts. We used repeated sampling of 20 freshwater wetland sites using aquatic minnow traps and occupancy modeling to estimate species detection (p) and occupancy (ψ) probabilities for 7 semi-aquatic snake species. We also determined the influence of wetland characteristics (e.g., wetland isolation, water permanence, and prey abundance) on occupancy probability. We defined our sample as an array of 30 minnow traps set for 1 night, and we conducted 5–15 samples per wetland within a 1-week period.

Our approach was sufficient to estimate p and ψ for all seven species, but a limited number of sites and low species detection probability resulted in wide confidence intervals for some species and limited our ability to detect effects of site covariates on occupancy. Species detection probability ranged from 0.46 ± 0.05 (mean ± SE per 30 trap-nights) for *Nerodia fasciata* (Banded Watersnake) to 0.05 ± 0.04 for *Agkistrodon piscivorus* (Cottonmouth), indicating that for *A. piscivorus*, 63

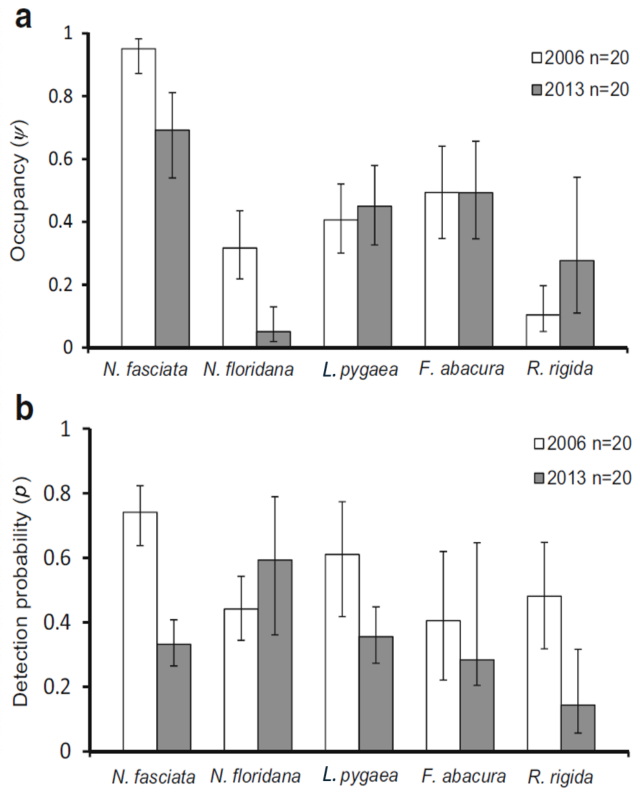

Fig. 3. Pre-drought (open bars) and post drought (grey bars) (a) occupancy and (b) species detection probability estimates for five species of semi-aquatic snakes across 20 wetlands in South Carolina. Error bars represent 95% confidence intervals. Reprinted from Vogrinc et al. (2018).

unsuccessful sampling events (i.e., 1,890 trap-nights) would be needed to determine species absence with 95% confidence. Site occupancy estimates ranged from 0.96 ± 0.05 for *N. fasciata* to 0.13 ± 0.09 for *Liodytes rigida* (Glossy Crayfish Snake) and 0.17 ± 0.13 for *Farancia erytrogramma* (Rainbow Snake). In addition to providing the first estimates of occupancy and species detection probability for some of these poorly understood species, our results revealed that perceptions of rarity may be spurious. For example, *Farancia abacura* (Mud Snake) and *A. piscivorus* both exhibited low detection probability ($p < 0.2$), but relatively high occupancy ($\psi > 0.6$), suggesting that higher effort or alternative capture methods might be needed to study these species. Conversely, our results confirmed that *F. erytrogramma* and *L. rigida* are both rare ($\psi < 0.2$) and secretive ($p < 0.2$). Although our ability to detect covariate (habitat) relationships with species occupancy was limited by small sample size ($n = 20$ wetlands), we found support for higher occupancy probability of *F. erytrogramma* and *R. rigida* at wetlands that were closer to river floodplain habitat and had more crayfish prey, whereas *N. fasciata* and *L. pygaea* (Black Swampsnake, formerly *Seminatrix pygaea*) were more detectable (and therefore presumably more abundant) in wetlands with shorter hydroperiods that lacked fish.

We expanded upon this research by repeating occupancy sampling at the same wetland sites seven years later, following an extreme drought in the region (Vogrinc et al. 2018). By estimating p and ψ before and after drought (Fig. 3), we were able to determine that watersnakes (*Nerodia floridana* [Eastern Green Watersnake] and *N. fasciata*) experienced substantial reductions in occupancy over this period, with *N. floridana* being nearly extirpated from the study region. *Nerodia fasciata* also declined substantially in detection probability ($p = 0.69$ pre-drought; $p = 0.33$ post-drought), presumably indicating a reduction in abundance that decreased p_{species}. Conversely, occupancy of *L. pygaea*, *F. abacura*, and *R. rigida* did not change significantly during drought. Taken together, these studies informed conservation of secretive aquatic snakes by better understanding their levels of site occupancy, habitat requirements, and responses to drought. We found that some species were truly rare, whereas others seemed rare due to low detectability but were actually relatively widespread. Similarly, species differed strongly in habitat preferences and responses to drought, with *Nerodia* suffering major declines during extreme drought periods. Thus, climate change and habitat alteration may have profound but species-specific effects on aquatic snake populations.

Lessons Learned—Despite the substantial effort required to conduct repeated sampling events across 20 wetlands, this study was still limited by a relatively small sample size. Combining samples (i.e., using a 60 trap-night sampling unit) for the second study (Vogrinc et al. 2018) allowed us to achieve relatively high species detection probabilities (>0.3) for most species, but our ability to detect covariate relationships or use dynamic occupancy models (which provide estimates of extinction and colonization) was still limited by the number of sites and sampling events (only two sampling sessions that were widely separated in time). In general, careful consideration of statistical power, given expected effect sizes and detection probabilities of the target species is critical for optimizing allocation of effort across sites (for example and guidelines see Halstead et al. 2015a; MacKenzie and Royle 2005). Finally, it is likely that community occupancy models (see below) would have improved our analyses for rare species.

Case 2: Using Hierarchical Community Occupancy Models to Examine Occupancy Responses of Snake Assemblages—As part of best management practices within managed timber forests, forested buffers are frequently retained alongside streams. The width of these buffers is often variable and determined by factors such as stream permanence, topography, and soil type. We conducted a large-scale occupancy study to evaluate the conservation value of riparian buffers for preserving herpetofaunal biodiversity within managed forests of west-central Arkansas, USA (Guzy et al. 2019a,b). Specifically, we surveyed 102 headwater stream sites 4 times each (sample = 30-min visual and cover object survey), recording species observed, along with several variables that could explain variation in herpetofaunal detection probability (e.g., temperature, soil moisture, humidity). Although our sampling methodology was designed to target salamanders, surveys yielded some snake detections, with the typical pattern of few captures across many species (Table 1). Here, we extend those analyses to demonstrate the power of community occupancy models to yield meaningful

Table 1. Summary of captures, model-estimated occupancy and species detection probabilities, and species-specific mean parameter estimates for the effect of riparian buffer width, for 9 snake species across 102 headwater stream sites within managed forests in the Ouachita Mountains, Arkansas, USA (Guzy et al. 2019b). Three groups of models were used: (1) single species occupancy models; (2) a community occupancy model that included all snake species; and (3) a community model for all reptile species (including box turtles and several lizard species with higher capture numbers). Values within parentheses represent 95% credible intervals. Bold values indicate strong relationships (i.e., credible intervals do not contain zero).

Species	Number of captures	Mean Occupancy*	Mean Detection*	Parameter Estimates from Riparian Buffer Width Models		
				Single Species	Snake Assemblage	Reptile Assemblage
Agkistrodon contortrix	2	0.52 (0.04–0.97)	0.01 (0.00–0.04)	8.87 (–6.15– 23.61)	1.27 (–0.22–2.74)	**1.63 (0.27–2.83)**
Agkistrodon piscivorus	20	0.79 (0.23–0.99)	0.06 (0.03–0.13)	0.14 (–4.53– 6.64)	0.94 (–0.19–2.12)	1.23 (–0.08–2.54)
Coluber constrictor	2	0.60 (0.06–0.98)	0.01 (0.00–0.04)	2.03 (–15.05–21.02)	1.17 (–0.52–2.67)	**1.55 (0.01–2.81)**
Diadophis punctatus	9	0.66 (0.12–0.97)	0.03 (0.01–0.09)	4.4 (–8.11–16.67)	1.07 (–0.28–2.40)	**1.42 (0.04–2.66)**
Lampropeltis triangulum	1	0.50 (0.02–0.97)	0.01 (0.00–0.04)	–0.36 (–18.54–18.32)	1.07 (–0.74–2.60)	1.47 (–0.26–2.77)
Nerodia erythrogaster	3	0.46 (0.02–0.96)	0.02 (0.00–0.07)	5.49 (–1.14–14.96)	1.21 (–0.11–2.63)	**1.55 (0.20–2.79)**
Opheodrys aestivus	1	0.57 (0.03–0.98)	0.01 (0.00–0.03)	–3.64 (–21.85–15.07)	1.00 (–1.03–2.55)	1.42 (–0.41–2.75)
Pantherophis obsoletus	3	0.43 (0.02–0.95)	0.02 (0.00–0.07)	9.21 (–2.90–22.07)	**1.34 (0.01–2.75)**	**1.67 (0.38–2.83)**
Storeria occipitomaculata	2	0.49 (0.03–0.97)	0.01 (0.00–0.05)	7.3 (–5.03–22.39)	1.27 (–0.02–2.65)	**1.59 (0.27–2.81)**
Riparian Buffer Mean Assemblage Response	–	–	–	–	**1.15 (0.04–2.23)**	**1.54 (0.64–2.49)**

*Estimates are from Reptile Assemblage model

information from these types of datasets. We analyze data for nine snake species in three stages: (1) single-species occupancy models for each snake species; (2) a community occupancy model that included all snake species; and (3) with a community occupancy model for all reptile species (i.e., including box turtles and several lizard species with higher capture numbers).

Single-species occupancy models are a popular method for population and community monitoring because they incorporate repeated low-intensity surveys at each location to account for two important sources of variation, space and imperfect detection (Bailey et al. 2004). Thus, many sites can be surveyed (i.e., large-scale inference) to provide estimates of the proportion of area occupied by a species. More recently, statistical approaches (i.e., hierarchical community occupancy models) have been developed that extend single-species occupancy models to incorporate data for several species in the same model, providing both species-specific and community-level estimates of detection and occupancy probability, and estimates of species richness (e.g., Dorazio and Royle 2005, Zipkin et al. 2009, Homyack et al. 2016). Under this framework, individual species-level estimates are generated using a combination of the data for that species and the average estimate of those parameters for the entire community (Pacifici et al. 2014). Therefore, one advantage of using community occupancy models is that estimates for data-poor species with few detections are improved by borrowing information from data-rich species with many detections. Importantly, borrowing information is only appropriate if the species that are sharing information have some degree of relatedness (Pacifici et al. 2014), such as taxonomic similarity or shared life-histories. Therefore, group-level parameters can be included in these models that specify which groups to borrow information from (e.g., taxonomic groups, functional guilds).

In our analysis, single-species occupancy models failed to detect an influence of riparian buffer width on any of the nine snake species, as evidenced by nonsensical mean parameter estimates with wide credible intervals that contained zero (Table 1). Conversely, the snake assemblage model revealed a positive influence of riparian buffer width on occupancy of the snake assemblage overall, and a positive response for *Pantherophis obsoletus* (Black Rat Snake) with a credible interval that did not overlap zero. Finally, when other reptiles (primarily lizards) were included in the reptile assemblage community model, the positive assemblage response to riparian buffer width was strengthened, and this model extended meaningful estimates to six individual snake species, while also narrowing the error around the most frequently detected species (*A. piscivorus*). Results of the reptile assemblage model indicate that mean species detection probability varied from 0.01 for several species to 0.06 for *A. piscivorus* (Table 1). Average occupancy estimates varied from 0.43 for *P. obsoletus* to 0.79 for *A. piscivorus*.

Lessons Learned—This case study demonstrates that community occupancy models can be a useful method for incorporating sparse data from multiple species. These models can identify covariate relationships across a species assemblage, even when data for most or all species are too sparse to be meaningful in isolation (Pacifici et al. 2014). Likewise, 'borrowing' data from common species can inform analyses for rare species, particularly when species in the assemblage have similar behavior or ecology. Similarly, when many species are considered together, inference on data-rich species may become more precise. For example, in our study, the snake with the most detections, *A. piscivorus,* had high overall occupancy (0.79) but unlike other reptile species, was not strongly influenced by riparian buffer width in any of our model formulations. However, as we included more species, and thus more data, the measure of error around the buffer width parameter estimate for *A. piscivorus* became more precise (Table 1). In our case, we were able to include data from infrequently encountered snakes and ultimately determine that there is variation among herpetofaunal species regarding how wide riparian buffers should be to maximize occupancy (Guzy et al. 2019b). Thus, forestry management actions may differentially affect taxonomic groups and species. Importantly, analyses in this case study would be further improved with a sampling methodology targeted to increase snake detections (e.g., more effort per survey or different sampling techniques).

Case 3: Using Intensive CMR to Estimate Abundance of Semi-aquatic Snakes—As part of the same research project described in Case 1, we wanted to accurately estimate density of aquatic snakes and assess their role as secondary consumers within wetland ecosystems. We were able to achieve these goals by selecting an ideal study site/system and carefully designing our field sampling and analytical approach. For details of this research see Willson et al. (2011) and Willson and Winne (2016).

Our study site for this research was Ellenton Bay, a 5–10 ha (depending on water levels) Carolina Bay freshwater wetland located on the U.S. Department of Energy's Savannah River Site in South Carolina, USA. Several characteristics of this site made it ideal for aquatic snake population studies and CMR abundance estimation. First, the snakes inhabiting Ellenton Bay comprised discrete populations that were isolated from other aquatic systems by >1 km of upland habitat, thereby limiting movement of animals into and out of each population. Second, the wetland was large enough to support a large population (i.e., sample size) of snakes, but small enough that we could sample the entire periphery of the wetland with high intensity, thereby maximizing individual capture probability and minimizing heterogeneity in capture probability that could result from under-sampling portions of the study site. Finally, the habitat within the wetland consisted of open-canopy shallow water (<1 m) with relatively uniform thick emergent vegetation. The uniformity of the habitat facilitated standardized sampling effort across the site and was ideal for our sampling method (aquatic trapping).

The snake community at Ellenton Bay was dominated (~95% of captures) by two species, *N. fasciata* and *L. pygaea*. In addition to being abundant (yielding a large sample size of captures), these focal species had several other characteristics that made them amenable for CMR population estimation. First, both were readily sampled using aquatic minnow traps, which allowed for efficient, high-intensity sampling that was less sensitive to observer biases and short-term variation in detection probability than other methods (e.g., visual surveys, Dorcas and Willson 2009). Second, these snakes were consistently active (except in winter) and did not exhibit the strong ontogenetic shifts in diet or behavior which can result in undersampling of some age classes. For example, juvenile Brown Treesnakes (*Boiga irregularis*) prefer lizard prey, which greatly reduces their capture probability in rodent-baited traps that are highly effective at capturing adults (Rodda et al. 2007). Similarly, the vast majority of young *Vipera berus* (European Adder) evaded capture for their first 2–4 years of life, likely because of their preference for dense vegetation and small size (Bauwens and Claus 2018).

Snake sampling consisted of 6–10-day bouts of high intensity trapping of the entire population (465 traps set in a continuous transect around the wetland perimeter). Surveys were conducted monthly from March to October and traps were checked daily. All snakes were individually marked by ventral branding (Winne et al. 2006) and returned to their capture location within 12 h. The temporal structure of the resulting capture data (short 'secondary' sampling periods [days], within widely-spaced 'primary' sampling periods [months]) allowed for 'robust' CMR analysis (see above), which combines open and closed modeling approaches and allows for evaluation of many factors that can affect detection, including temporary emigration.

One year of sampling yielded a total of 2,857 captures of 1,023 individual *N. fasciata* and *L. pygaea*, with an overall recapture rate of 64%. CMR analyses revealed several factors that strongly influenced $p_{\text{individual}}$, including species, season (highest capture probability in the mid-summer), and importantly, a strong trap-happy response (i.e., recapture probability higher than initial capture probability). *Nerodia fasciata*, for example, had recapture probabilities that were five times higher (>25% daily) than initial capture probability in the summer months, likely due to snakes learning to associate traps with food (accumulated amphibian prey). Failing to account for this major source of heterogeneity in capture probability would have led to a dramatic (3-fold) underestimation of population size. Finally, we found evidence for sex-specific random temporary emigration in *L. pygaea*, with 19% of males and 36% of females unavailable for capture during a given primary sampling period. Accounting for these sources of variation in $p_{\text{individual}}$ allowed us to generate reasonably precise (SE < 10% of mean) estimates of abundance for these two species (Fig. 4). We were then able to couple abundance estimates with measurements of individual growth, mass conversion efficiency, and diet to demonstrate that aquatic snakes consume >37 kg per ha of amphibian biomass annually in this system (Willson and Winne 2016). This research demonstrates the role of snakes as secondary consumers within ecosystems, providing important justification for snake conservation on the grounds of their important roles within food webs.

Lessons Learned—This case study demonstrated that it is possible to generate meaningful abundance estimates for some snake species with sufficient effort and conditions that are conducive to population research. However, in hindsight, there are always ways to improve a study. For example, heterogeneity in $p_{\text{individual}}$ may have resulted from spatial variation in sampling (i.e., center of the wetland was under-sampled). Thus, a sampling scheme based on a grid of equally spaced traps might have improved precision of analytical results. Furthermore, using a

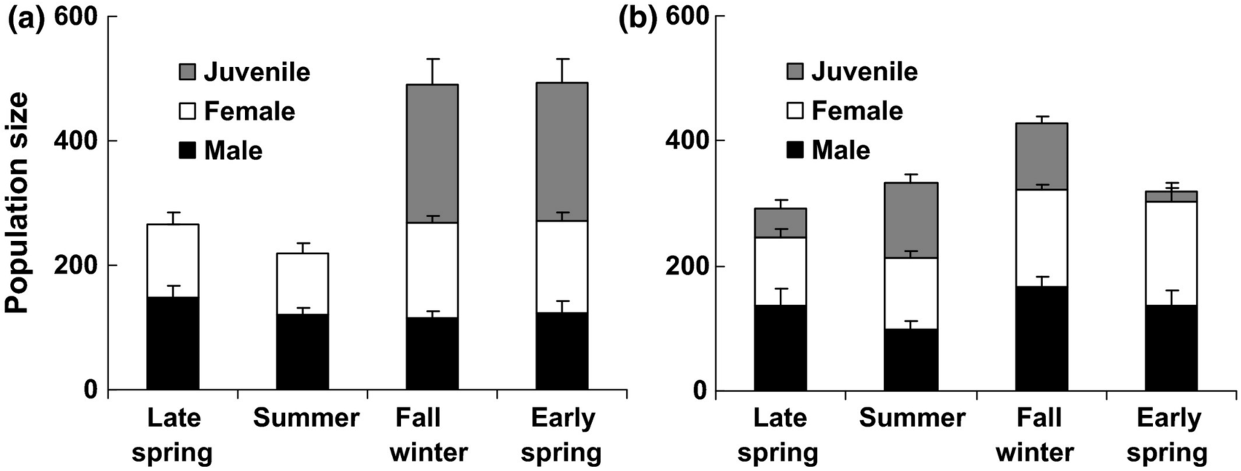

Fig. 4. Population size estimates (± 1 SE) of (a) *Nerodia fasciata* and (b) *Liodytes pygaea* at Ellenton Bay, South Carolina, USA estimated over a one-year period using robust-design analysis in program MARK. Models included time-varying and independent (i.e., allowing for a behavioral response to traps) capture and recapture probabilities for both species and sex-specific constant random temporary emigration for *L. pygaea*. Reprinted from Willson and Winne (2016).

spatial-capture-recapture (SCR) approach would likely alleviate the need to sample the entire population (i.e., the whole wetland) and allow for sampling more intensively within a smaller sampling area, thereby increasing $p_{\text{individual}}$.

Case 4: Road-based Density Estimation for Southern Hognose Snakes—Some snake species are so secretive (i.e., low $p_{\text{individual}}$) that CMR is unlikely to ever yield precise and unbiased abundance information. Not surprisingly, these species are often those that are perceived to be rare or declining, and thus are of high conservation concern. Understanding abundance of these species requires development of innovative field and analytical techniques that overcome low recapture probability. We recently developed a novel abundance estimation method that takes advantage of the fact that many rare and secretive snakes are most frequently encountered crossing roads (Willson et al. 2018). We demonstrated this method using existing data for imperiled Southern Hognose Snakes (*Heterodon simus*) in the sandhills of North Carolina, USA (Fig. 5). Despite documented declines in geographic range (Tuberville et al. 2000) and proposal for federal listing, no estimates of abundance existed for *H. simus* anywhere in its range, presenting a fundamental hurdle for future conservation or management of the species.

Fig. 5. Imperiled Southern Hognose snakes (*Heterodon simus*) are most often found crossing roads through xeric habitats in the southeastern USA. Measuring crawling speeds of naturally crossing individuals allowed us to calculate the probability of detecting snakes that crossed during systematic road surveys. Photo by J.D. Willson.

Our technique used an understanding of snake spatial movement patterns (based on radio-telemetry) and road crossing behavior to estimate snake density from frequency of snake observations during systematic road surveys. In short, our method assumed that a snake would be detected during a road survey if its road crossing location and time coincided with the survey vehicle. Thus, to translate encounter frequencies into densities, we needed to know (1) the probability that a snake will cross the road during a survey and (2) our probability of detecting a snake that does cross during the survey time. To estimate the probability that a snake would cross the road during a survey, we created individual-based spatial movement simulation models (for more detail see Willson et al. 2018). We then parameterized those models with spatial movement metrics (movement distance, frequency, orientation towards home range center and road) derived from species-specific radiotelemetry data. Next, we used data on snake road crossing speed and average vehicle speed to calculate the probability that a snake would be detected if it crossed the survey route during a survey. Taken together, these pieces of information allowed us to generate a relationship between encounter frequency of snakes on roads and density, which was compared to empirical road data for the species to generate a density estimate and explore sensitivity of that estimate to assumptions and variation in model parameters.

We demonstrated our method using an existing database of radiotelemetry and road survey data for *H. simus* collected by Jeff Beane of the North Carolina State Museum of Natural Sciences (for more detail see Beane et al. 2014). We supplemented

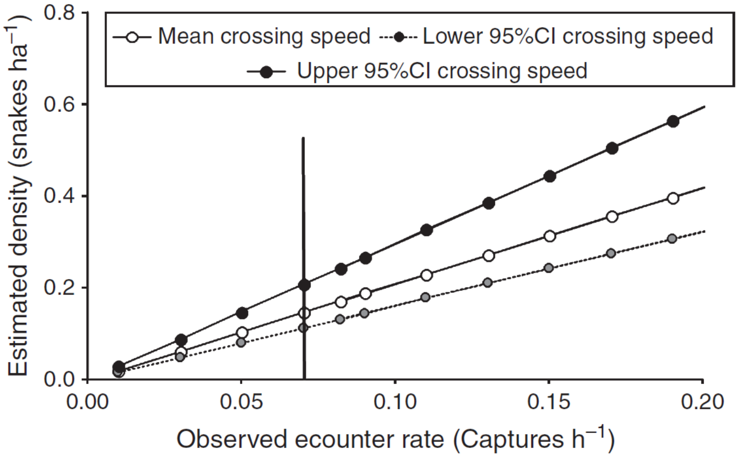

Fig. 6. Relationship between observed encounter rate (live captures per hour of road survey) and estimated density of *Heterodon simus*, bounded by the 95% confidence interval of road crossing speeds observed in behavioral observations. Vertical bold line indicates mean observed encounter frequency (0.082 live snakes per h) across 656 hours of survey time over nine years in the North Carolina Sandhills. Reprinted from Willson et al. (2018).

these data with our own measurements of crossing speed from wild *H. simus* encountered naturally crossing roads, as well as additional radiotelemetry data collected by Tracey Tuberville of the University of Georgia's Savannah River Ecology Laboratory. Movement models were used to generate a relationship between road encounter frequency and predicted density (Fig. 6), which, when compared to the long-term average encounter rate of 0.08 live *H. simus* per hour of road survey, yielded a density of 17.14 *H. simus* per square kilometer (0.17 per ha). This was the first density estimate for *H. simus* and was lower than those for congeners (Platt 1969), suggesting that *H. simus* exist at low density and/or may be declining, even in strongholds such as the North Carolina Sandhills (Tuberville et al. 2000, Willson et al. 2018).

Lessons Learned—Our road-based density estimation method may be the only available method to estimate abundance of secretive snakes that are most frequently captured on roads, such as *H. simus*. However, this technique is new, and ideally should be validated using an experimental system or a species that is amenable to both this method and CMR. Moreover, the model currently has several assumptions and limitations that deserve consideration, including the following (see Willson et al. 2018 for expanded discussion):

1. The model currently assumes that roadside habitats have snake densities similar to those of the broader landscape/study area.
2. Abundance estimates are sensitive to the behavior of the snake relative to the road (i.e., avoidance or attraction). Road responses can be incorporated into the model, but such data are lacking for most snake species (Andrews and Gibbons 2005).
3. Our movement model assumes linear movement between telemetry relocations and models movements as a biased random walk within a homogeneous landscape. Thus, current models are best suited for species that move infrequently and inhabit relatively homogeneous landscapes and may be inadequate for modeling movement of highly mobile species or those that are heterogeneously distributed.

Conclusions

Despite perceptions of rarity for many species, snake conservation research has lagged behind amphibians, lizards, and turtles, principally resulting from the difficulties associated with low detectability of most snake species. Our four case studies demonstrate approaches, both novel and traditional, for overcoming low detectability to answer meaningful questions related to snake conservation. In Cases 1, we used traditional occupancy methods to evaluate occupancy rates, habitat associations, and responses to extreme drought in poorly known semi-aquatic snake species. In Case 2, we explored community occupancy models to improve analytical tractability for infrequently encountered snakes and ultimately, we were able to assess species and community-level occupancy response to riparian buffer widths within managed forests. Cases 3 and 4 involved estimation of snake abundance. In Case 3 we used robust-design CMR sampling to rigorously estimate abundance of aquatic snakes within an isolated wetland, ultimately demonstrating that they are important secondary consumers and thus important components of wetland food webs. Finally, in Case 4 we developed a novel abundance estimation method based on road survey data, which shows promise as perhaps the only currently feasible method for estimating density of some rare snakes that are not amenable to CMR methods, such as the declining Southern Hognose Snake (*Heterodon simus*). We hope that these case studies will provide a model for similar conservation research on poorly understood snake species that are targets for management and conservation, as well as inspiring continued efforts develop new field and analytical approaches, as well as adapt existing methods to the unique ecologies of snakes.

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