



Research Article

Ecological and Methodological Factors Affecting Detectability and Population Estimation in Elusive Species

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ABSTRACT Although mark-recapture methods are among the most powerful tools for monitoring wildlife populations, the secretive nature of some species requires a comprehensive understanding of the factors that affect capture probability to maximize accuracy and precision of population parameter estimates (e.g., population size and survivorship). Here, we used aquatic snakes as a case study in applying rigorous mark-recapture methods to estimate population parameters for secretive species. Specifically, we used intensive field sampling and robust design mark-recapture analyses in Program MARK to test specific hypotheses about ecological and methodological factors influencing detectability of two species of secretive aquatic snakes, the banded watersnake (*Nerodia fasciata*), and the black swamp snake (*Seminatrix pygaea*). We constructed a candidate set of a priori mark-recapture models incorporating various combinations of time- and sex-varying capture and recapture probabilities, behavioral responses to traps (i.e., trap-happiness or trap-shyness), and temporary emigration, and we ranked models for each species using Akaike's Information Criterion. For both banded watersnakes and black swamp snakes we found strong support for time-varying capture and recapture probabilities and strong trap-happy responses, factors that can bias population estimation if not accommodated in the models. We also found evidence of sex-dependent temporary emigration in black swamp snakes. Our study is among the first comprehensive assessments of factors affecting detectability in snakes and provides a framework for studies aimed at monitoring populations of other secretive species. © 2011 The Wildlife Society.

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With anthropogenic impacts on global ecosystems expanding at an alarming rate, recognition of the critical need to monitor animal populations is growing rapidly. For some species or situations, population monitoring can be as simple as taking direct census counts. However, in most cases, census counts provide an incomplete assessment of population status because detection probabilities are <1 and may vary among individuals or over time (Pollock et al. 2002, Mazerolle et al. 2007). Mark-recapture models allow for incorporation of detectability into estimates of population size and vital rates (e.g., survivorship) and they have a long tradition as powerful tools in wildlife management (reviewed in Pollock et al. 1990). However, when capture, and especially recapture, rates are low, mark-recapture analyses quickly lose power, generating imprecise parameter estimates with large associated standard errors (Kendall et al. 1995), a factor that can hamper effective management of wildlife populations.

The application of mark-recapture techniques to particularly secretive species confronts the researcher with a unique set of challenges. For example, capture and recapture probability are often considered nuisance parameters when

studying easily observed species (Murray and Patterson 2006). When detectability is low, however, understanding variation in capture probability is critical. Identifying and accounting for biological or methodological factors that contribute to low or variable detection probabilities can significantly improve the accuracy and precision of parameter estimates in secretive species (Bailey et al. 2004b,c). For example, application of advanced mark-recapture methods recently revealed that subterranean behavior was a major factor influencing capture probability of woodland salamanders (Bailey et al. 2004b). The appropriate modification of mark-recapture models increased capture and recapture probabilities and dramatically improved precision of population estimates (Bailey et al. 2004b,c). Such advances in mark-recapture analytical methods have provided a variety of tools to researchers interested in monitoring populations of secretive species (e.g., Pollock 1982, Norris and Pollock 1996, Kendall et al. 1997, Pledger 2000, Bailey et al. 2004a, Yang and Chao 2005). However, few studies provide a comprehensive approach for implementing these techniques to optimize monitoring of species with low capture probability. We used aquatic snakes as a study system for applying mark-recapture techniques to improve accuracy and precision of population parameter estimates for species that are poorly understood and notoriously difficult to sample.

Snakes are among the most secretive of all terrestrial vertebrates. Although snakes often occur at high densities (e.g., Fitch 1975, Godley 1980, Sun et al. 2001), there are numerous reports in which rates of capture per unit sampling effort are abysmally low or in which many snakes are marked,

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but few, if any, are ever recaptured (Dorcas and Willson 2009). Low recapture rates have led some authors to label snakes as generally more difficult to study than other species, or to question the feasibility of using mark-recapture methods to estimate snake population parameters altogether (Fitch 1987, Parker and Plummer 1987, Shine 1987). Indeed, standard errors associated with snake population size and vital rate estimates are often large (reviewed in Parker and Plummer 1987; but see exceptions in Brown 2008) and in many cases, assumptions of mark-recapture models are grossly violated. However, secretive behavior is just one of several potential and not mutually exclusive phenomena that can contribute to low capture probability in snakes and other elusive wildlife. Specifically, several factors may deflate capture and recapture probability or may result in biased or imprecise abundance and vital rate estimates. We discuss 2 of these factors, unequal catchability, and temporary emigration.

Historically, the 2 most popular abundance estimators were the demographically closed Lincoln–Peterson index (Lincoln 1930; discussed in detail in Pollock et al. 1990) and the demographically open Jolly–Seber model (Seber 1982). Classically, both of these models assume constant and equal capture probability across all individuals and sampling occasions (Pollock et al. 1990). Numerous authors have suggested that this assumption is seldom met, as capture probability is likely to vary among demographic groups (e.g., sexes, sizes, or reproductive classes), over time (e.g., across seasons, years, or with environmental conditions) or based on an animal's prior capture experience (e.g., animals may become trap-happy or trap-shy). The mistake of assuming constant capture probability in models when variation actually exists can substantially bias estimates of abundance or recruitment (Pollock et al. 1990, Bailey et al. 2004*b*). Evidence suggests that the behavior of many species can lead to violation of the equal catchability assumption. For example, although few studies have estimated capture probability in snakes, reproductive female Aspik vipers (*Vipera aspis*) are much more catchable by visual encounter surveys than are non-reproductive females (Bonnet and Naulleau 1996). Also, Gragg et al. (2007) demonstrated that prey abundance has a strong influence on capture probability of brown treesnakes (*Boiga irregularis*) in baited traps; application of rodenticide in surrounding habitats reduced prey abundance and increased snake capture probability by 22–65%.

Temporary emigration occurs when a portion of the population of interest is alive and affiliated with the population (i.e., has not permanently emigrated), but is unavailable for capture during a sampling interval (Kendall et al. 1997). Temporary emigration can result from a variety of factors, including behavior (e.g., inactivity) or aspects of the sampling method or design. For example, if sampling is not homogenous across the population, temporary emigration can result from animals moving between well- and under-sampled areas. If random temporary emigration exists, but is not accounted for, capture probability will be underestimated and the precision of parameter estimates will be

reduced (Kendall et al. 1997, Bailey et al. 2004*b*). Further, the presence of non-random (e.g., Markovian) temporary emigration can substantially bias estimates of capture probability and survival (Kendall and Nichols 1995).

Recent decades have seen rapid advances in the statistical analysis of mark-recapture data. Software packages (e.g., Program MARK; White and Burnham 1999) are currently available that allow stratified analyses, wherein individuals are divided into demographic groups that may differ in capture probability (Mazerolle et al. 2007), and allow the inclusion of individual covariates that may affect capture probability (Pollock 2002). Moreover, mark-recapture analyses have been developed that allow for incorporation of unequal catchability and temporary emigration (Pollock et al. 1990, Kendall et al. 1997). Particularly powerful is the so-called robust design analysis, which uses a combination of demographically open and closed population models to estimate both abundance and survivorship with minimal violation of model assumptions (Pollock et al. 1990, Kendall et al. 1995, Bailey et al. 2004*b*). First introduced by Pollock (1982) and formalized by Kendall et al. (1995), the closed robust design model consists of a series of widely spaced primary sampling intervals, across which survivorship is estimated using an open model approach. Each primary sampling interval consists of several short secondary samples (often successive days), across which abundance and capture probability parameters are estimated, assuming demographic closure. Because closed models are used within secondary sampling intervals, these models can incorporate time-varying capture probabilities and trap responses. Perhaps most importantly, robust design models are currently the only models that can estimate rates of temporary emigration to increase precision of other parameter estimates in the model (Kendall et al. 1997). Despite the obvious advantage of robust design analyses, their implementation requires careful study design. Consequently, these methods have only recently been applied to herpetofauna and have not been used to estimate temporary emigration in snakes (Savarie et al. 2001, Mazerolle et al. 2007, Dorcas and Willson 2009).

We used aquatic snakes as a case study in monitoring secretive species with the goal of understanding how behavioral and methodological factors, including time- and sex-varying capture and recapture probabilities, behavioral responses to traps (i.e., trap-happiness or -shyness), and random temporary emigration, influence estimation of population parameters. Using high-intensity robust-design sampling, we monitored populations of two secretive aquatic snakes, the black swamp snake (*Seminatrix pygaea*) and banded watersnake (*Nerodia fasciata*), inhabiting an isolated wetland in South Carolina, USA. The black swamp snake is considered the smallest semi-aquatic snake in North America and is endemic to the Coastal Plain of the Southeastern United States (Gibbons and Dorcas 2004). Because the black swamp snake is highly aquatic, seldom leaving aquatic habitats or basking above water (Gibbons and Dorcas 2004, Winne et al. 2006*b*), its abundance and status across much of its range are largely unknown and it is considered a species of concern in South Carolina,

Georgia, and Alabama. The banded watersnake is larger and is ubiquitous in the Southeastern United States, occurring in virtually all types of aquatic habitats (Gibbons and Dorcas 2004). We expected that both behavioral and methodological factors would affect detectability in the two snake species and that by accounting for these factors we could improve accuracy and precision of population parameter estimates for these notoriously secretive species.

STUDY AREA

Ellenton Bay was an isolated Carolina bay freshwater wetland located on the Department of Energy's Savannah River Site in the Upper Coastal Plain of South Carolina, USA. Ellenton Bay was characterized by shallow water (generally <1 m deep) and abundant emergent vegetation. Although water levels were variable across years (Willson et al. 2006, Winne et al. 2006b), the bay typically held water year-round and could achieve a surface area of approximately 10 ha in wet years. However, during our sampling period (from May 2005 to May 2006), water levels remained constant with the wetland surface area covering approximately 5.4 ha. Severe droughts rendered Ellenton Bay dry on ≥ 3 occasions in the past 3 decades, most recently during 1987–1990 and 2000–2003. Thus, since at least 1990, Ellenton Bay was devoid of fish, crayfish, and large, permanently aquatic salamanders (*Siren sp.* and *Amphiuma means*), and both black swamp snakes and banded watersnakes fed primarily on amphibians within the wetland (Willson et al. 2010). Importantly, Ellenton Bay was a discrete wetland isolated from other wetlands by an extensive matrix of forested uplands; the closest large wetland was 3.2 km away. Despite extensive sampling, only 2 of >1,000 marked banded watersnakes were documented moving between Ellenton Bay and other wetlands. The closest known population of black swamp snakes was 5.7 km from Ellenton Bay and black swamp snakes were never documented moving between Ellenton Bay and other wetlands.

METHODS

Capture Methods

We captured snakes at Ellenton Bay from May 2005 to May 2006. Within this period, we designed a temporal sampling regime to fit Pollock's (1982) robust design. Robust design requires a demographically open study period punctuated by primary sampling intervals that each consist of a series of secondary samples within which demographic closure is assumed. To meet this framework, we sampled snakes monthly (primary samples) from May to September 2005 for 10 consecutive days (secondary samples) and for 6 consecutive days in the additional primary periods of October 2005, March 2006, and April–May 2006.

We captured snakes using plastic minnow traps (Model 700; N.A.S Incorporated, Marblehead, Ohio), the most effective method for capturing these species in heavily vegetated aquatic habitats (Willson et al. 2005, 2008). During each primary sampling period, we set 465 traps spaced

approximately 2 m apart in a continuous transect around the aquatic periphery of the wetland. We placed traps in shallow water with the uppermost portion of the trap above water to prevent drowning of captured snakes. Although we did not intentionally bait traps, incidental capture of amphibians resulted in natural baiting of traps (Seigel et al. 1995, Winne 2005). We checked traps daily in the early morning and recorded each snake's capture location to within 10 m.

Following capture, we recorded sex (by inspection of tail morphology or cloacal probing), snout-vent length (SVL), and body mass for each snake captured. We then marked each snake with a unique code by branding ventral scales (Winne et al. 2006a) before releasing it at its capture location on the day of capture. Importantly, robust design studies assume that all individuals are available for capture on all sampling occasions within a primary period. Because we always released snakes on their day of capture, all individuals were available for capture within the wetland on each day of sampling.

For simplicity, we restricted analyses to animals born before the study started. We identified banded watersnakes born during the study (2005 young-of-year) by their body size and excluded them from analyses. Black swamp snakes are small enough at birth that they can escape through the mesh of minnow traps and are therefore uncatchable until they reach approximately 200 mm SVL (Willson et al. 2008), at an age of >9 months (J. D. Willson and C. T. Winne, Savannah River Ecology Laboratory, unpublished data). Thus, we included all captured black swamp snakes in mark-recapture analyses. Our capture histories for both species included sex as a grouping factor to allow for testing of sex-specific effects on the parameters of interest in our model selection procedure. Virtually all mature females of both species are reproductive during years when the wetland holds water (Winne et al. 2006b; J. D. Willson and C. T. Winne, unpublished data). Thus, we did not separate adult females into reproductive and non-reproductive groups. All snakes were collected under South Carolina Department of Natural Resources Scientific Collection permits (G-05-03 and G-06-04), and our procedures were approved by the University of Georgia Animal Care and Use Committee (A2003-10024-C2 and A2006-10069-0).

Mark-Recapture Modeling

The primary goal of our mark-recapture analysis was to examine factors affecting detectability of 2 secretive aquatic snake species. We used an overall model selection procedure that included the following steps: 1) we identified 8 a priori candidate models that offered contrasting biological representations of the role of capture probability, recapture probability, and temporary emigration in our study species, 2) we used our most highly parameterized candidate model to evaluate the role of sex in these factors, and 3) where sex effects on parameters were supported, we modified our 8 candidate models to include sex effects for those parameters and then compared the fit of the 8 candidate models using Akaike's Information Criterion (AIC; Akaike 1973).

We used Program MARK (White and Burnham 1999) to construct and evaluate mark-recapture models. We used the Huggins closed captures form of the robust design model, deriving population estimates separate from the model likelihood, a method that generally performs better with sparse data resulting from small samples sizes or infrequent recaptures (Huggins 1989, 1991; L. L. Bailey, Patuxent Wildlife Research Center, personal communication). We assumed capture and recapture probabilities within primary periods to be constant (i.e., no day-to-day variation among consecutive secondary samples). More general models are possible (Kendall et al. 1997), but they are heavily parameterized, often failing to computationally converge when recapture rates are low or the number of primary periods is great. Thus, our most heavily parameterized model included capture (p) and recapture (c) probabilities that varied among primary periods and also allowed for a behavioral response to traps (i.e., $p \neq c$) and constant random temporary emigration (γ).

In their evaluation of detection parameters of woodland salamanders using robust design, Bailey et al. (2004b) fixed survivorship at plausible values because the short duration of their primary sampling intervals led to parameter estimates that were often nonsensical and unstable. Similarly, we initially allowed survival to vary with other parameters in our model selection procedure but found that these models resulted in annual survivorship estimates of <30%. We felt that this was unrealistically low because both of these species are long-lived (capable of living ≥ 10 –15 yr), because in 2006 we recaptured >30% of banded watersnakes marked in 2005 (suggesting yearly survivorship >30%) and because this population was rapidly growing during our study (J. D. Willson and C. T. Winne, unpublished data). Consequently, in our a priori selection of candidate models, we fixed survival rates based on annual survival estimates from unpublished Cormack Jolly–Seber models of banded watersnakes and black swamp snakes at Ellenton Bay that used biannual samples from 2005 to 2008. These models yielded much more plausible 2005–2006 survival estimates of 0.92 and 0.88 for banded watersnakes and black swamp

snakes, respectively, and found no support for sex differences in survival during 2005–2006. Models with survivorship fixed based on longer-term data with sampling intervals of appropriate length for survival estimation produced results that were qualitatively equal to those in which survivorship was fixed; specifically, capture and recapture rates were similar between fixed-survivorship and variable-survivorship models in all seasons and the order of model rankings was identical, such that models with time-varying capture and recapture probabilities, behavioral responses, and sex-dependent temporary emigration for black swamp snakes were always favored (see below). The only substantive difference in parameter estimates was that estimated rates of temporary emigration dropped from 19% to 4% and from 36% to 29% for male and female black swamp snakes, respectively.

As a final assurance that our fixed survival rates did not substantially alter our conclusions, we repeated our model selection procedure (see below) using conservative yearly survival estimates of 0.50 and 0.70 for both species. This wide range of survivorship values did not alter model rankings, demonstrating that our results are robust to survivorship assumptions. We used month as a common denominator between our primary periods and adjusted interval lengths in Program MARK accordingly. Therefore, we converted yearly survival rates into monthly rates of 0.993 for banded watersnakes and 0.989 for black swamp snakes.

We first established 8 candidate models (Table 1) to evaluate support for the presence of temporary emigration (γ) as well as behavioral responses to traps and temporal variation in capture and recapture probabilities among primary periods. We constructed these models to test all possible parameter combinations and we organized them as follows: 1) Models 1 and 2 were heavily parameterized, allowing for behavioral responses to traps ($p \neq c$) and capture and recapture probabilities that varied across primary sampling periods; 2) Models 3 and 4 allowed for behavioral responses ($p \neq c$) but did not allow p and c to vary over

Table 1. A priori candidate models designed to evaluate support for temporary emigration, behavioral responses to traps, and time-varying capture probability in aquatic snakes at Ellenton Bay, South Carolina, USA, from May 2005 to May 2006.

Model ^a	Parameters					
	Temporary emigration		Capture probability			
	None $\gamma(.) = 0$	Constant, random $\gamma(.)$	Constant time, no trap response $p(.) = c(.)$	Time-specific, no trap response $p(t) = c(t)$	Constant time, trap response $p(.), c(.)$	Time-specific, trap response $p(t), c(t)$
1		X ^b				X
2	X					X
3		X ^b			X	
4	X				X	
5		X ^b		X		
6	X			X		
7		X ^b	X			
8	X		X			

^a Models: γ = temporary emigration, p = initial capture probability, c = recapture probability, (.) = parameter constant, (t) = parameter varies over primary (monthly) periods.

^b Models 1, 3, 5, and 7 allow γ to vary between the sexes in black swamp snakes (see Methods Section).

Table 2. Variations of the most parameterized candidate model (Model 1) evaluating support for sex effects in capture probability, recapture probability, or temporary emigration in aquatic snakes at Ellenton Bay, South Carolina, USA, from May 2005 to May 2006.

Model ^a	Parameters			
	Temporary emigration		Capture probability	
	Constant, random	Sex-specific	Time-specific, trap response	Time-specific, sex-specific, trap response
	$\gamma(\cdot)$	$\gamma(sex)$	$p(t), c(t)$	$p(\bar{t}sex), c(\bar{t}sex)$
1a	X		X	
1b		X	X	
1c	X			X
1d		X		X

^a Models: γ = temporary emigration, p = initial capture probability, c = recapture probability, (sex) = parameter different between males and females, (\cdot) = parameter constant, (t) = parameter varies over primary (monthly) periods.

primary periods; 3) Models 5 and 6 allowed p and c to vary over primary periods but did not include a behavioral response to traps ($p = c$); and 4) Models 7 and 8 were the simplest models we tested, including no behavioral response to traps and constant p and c among primary periods. Models 1, 3, 5, and 7 included constant random temporary emigration, whereas we fixed temporary emigration at zero in Models 2, 4, 6, and 8.

Accounting for possible sex differences greatly increased the number of alternative models required to test all parameter permutations. Rather than including all sex-varying model permutations in our primary model selection procedure, we first evaluated sex differences in detectability and availability parameters (p , c , and γ) by modifying the most parameterized candidate model (Model 1 above; see Table 2). Our permutations of this model included: 1a) no sex differences in parameters, 1b) sex differences in γ , 1c) sex differences in p and c , and 1d) sex differences in all 3 parameters. If there was support for sex differences in any of these parameters, we allowed the affected parameter to vary between the sexes when subsequently testing the 8 candidate models to evaluate detectability (Table 1).

RESULTS

During 69 sampling days at Ellenton Bay we obtained 1,392 captures of 414 individual banded watersnakes and 1,286 captures of 495 black swamp snakes. Captures were highest in summer for both species (Fig. 1). However, banded watersnakes displayed a more uniform seasonal pattern of captures than did black swamp snakes, with high capture rates from May to September and reduced capture rates in October and March. Black swamp snakes displayed a more strongly unimodal pattern of captures, with peak numbers of snakes captured in August and September and low capture rates in October and March. Through time, captures of new, previously uncaptured individuals declined rapidly in both species relative to total captures. However, despite intense sampling, we captured new individuals in all months and the percentage of snakes that we recaptured plateaued at approximately 80% and 70% of total captures after the first 3 months of sampling for banded watersnakes and black swamp snakes, respectively (Fig. 1).

For banded watersnakes, variations of Model 1 that we used to evaluate sex effects were ranked comparably and carried nearly equal weight, with a ΔAIC_c of only 1.2 separating the 4 models. Consequently, because there was no unequivocal support for sex differences in p , c , or γ for banded watersnakes, we did not allow parameters to vary between the sexes for this species in our primary model selection procedure. In contrast, for black swamp snakes, Model 1b (sex effects in γ) carried the greatest support of the 4 variants of Model 1, differing from the next best model by a ΔAIC_c of 4.9. Thus, in subsequent analyses, we included a sex effect in γ for black swamp snakes.

We found strong support for time-varying capture and recapture probabilities across months for both species (Tables 3 and 4). For banded watersnakes, the 3 highest ranked models included time-varying p and c and all models

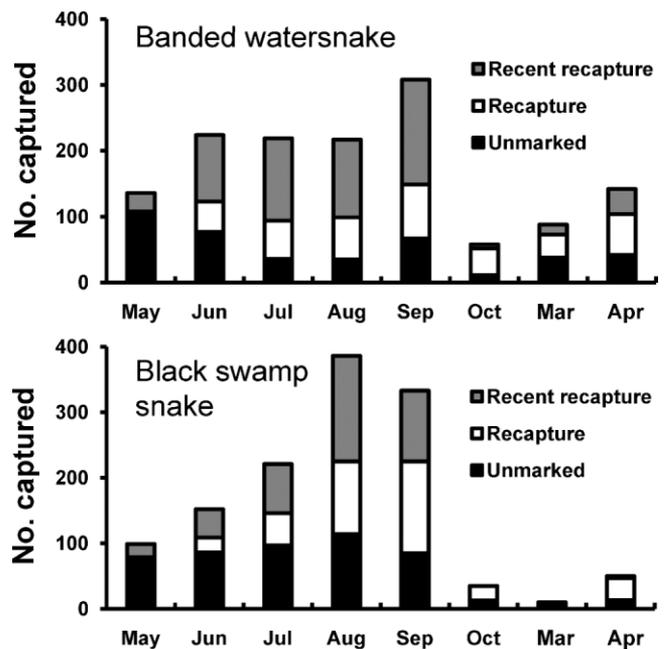


Figure 1. Capture summary for banded watersnakes and black swamp snakes at Ellenton Bay from May 2005 to May 2006. Bars represent total numbers of snakes captured in minnow traps, broken down into naive, unmarked individuals (black bars), snakes recaptured from previous primary sampling intervals (open bars), and recent recaptures within primary sampling intervals (gray bars).

Table 3. Model rankings for banded watersnakes sampled at Ellenton Bay, South Carolina, USA, from May 2005 to May 2006. Models are listed in decreasing order of support using Akaike's Information Criterion (corrected for small sample size; AIC_c).

Model ^a	Description			No. parameters	ΔAIC _c	AIC _c wt
	γ	p	c			
2	0	(t)	(t)	16	0	0.69
1	(.)	(t)	(t)	17	1.57	0.31
5	(.)	(t)	(t) = p	9	106.32	0
4	0	(.)	(.)	2	115.44	0
3	(.)	(.)	(.)	3	117.45	0
7	(.)	(.)	(.) = p	2	265.02	0
6	0	(t)	(t) = p	8	576.37	0
8	0	(.)	(.) = p	1	782.96	0

^a Models: γ = temporary emigration, p = initial capture probability, c = recapture probability, (.) = parameter constant, (t) = parameter varies over primary (monthly) periods.

Table 4. Model rankings for black swamp snakes sampled over a 1-yr period at Ellenton Bay, South Carolina, USA, from May 2005 to May 2006. Models are listed in decreasing order of support using Akaike's Information Criterion (corrected for small sample size; AIC_c).

Model ^a	Description			No. parameters	ΔAIC _c	AIC _c wt
	γ	p	c			
1	(sex)	(t)	(t)	18	0	0.99
2	0	(t)	(t)	16	8.93	0.01
5	(sex)	(t)	(t) = p	10	17.79	0
6	0	(t)	(t) = p	8	126.88	0
3	(sex)	(.)	(.)	4	310.74	0
4	0	(.)	(.)	2	312.67	0
7	(sex)	(.)	(.) = p	3	369.21	0
8	0	(.)	(.) = p	1	640.60	0

^a Models: γ = temporary emigration, p = initial capture probability, c = recapture probability, (sex) = parameter different between males and females, (.) = parameter constant, (t) = parameter varies over primary (monthly) periods.

with constant p and c had ΔAIC_c of ≥100 compared with the top-ranked model. For black swamp snakes, all models with constant p and c were ranked last, with ΔAIC_c values ≥300 units greater than the top-ranked model. Likewise, we found strong support for behavioral responses to traps (p ≠ c) in both species, with the top 2 models for each species containing a behavioral response (Tables 3 and 4). Initial capture probabilities (p) for banded watersnakes were low (range: 0.02–0.05) and consistent over time (Fig. 2). Banded watersnakes showed a strongly positive behavioral response to traps (i.e., trap happiness) with recapture probabilities (c) several times greater than p in all seasons (range: 0.06–0.26). Moreover, recapture probabilities showed strong temporal variation, with high recapture probabilities (>0.25) in July and August. Conversely, black swamp snakes exhibited strong temporal variation in both capture and recapture probabilities, with high values of both parameters in summer and near-zero values in spring (Fig. 2). Maximum initial capture probability estimates for black swamp snakes were substantially greater than those for banded watersnakes, approaching 0.10 in July and August. Black swamp snakes exhibited a trap-happy behavioral response similar to banded watersnakes, with recapture probability always greater than initial capture probability. However, the strength of the behavioral response varied over time in black swamp snakes, with a strong trap-happy response (c ≫ p) in June and July and nearly equal capture and recapture probabilities in August and September.

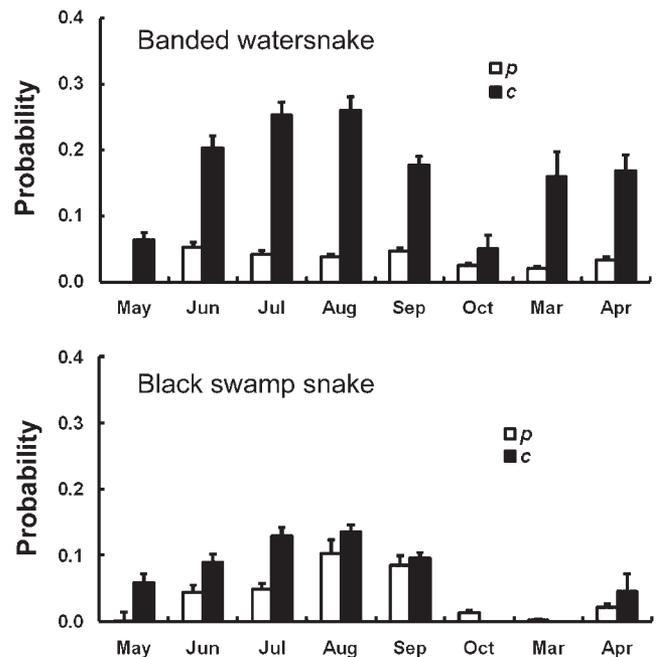


Figure 2. Seasonal variation in capture (p) and recapture (c) probabilities (±1 SE) for banded watersnakes and black swamp snakes at Ellenton Bay in 2005 and 2006. We generated parameter estimates for each species from the most parsimonious model for each species, each of which included independent, time-varying, but not sex-varying capture and recapture probabilities.

The most strongly supported model for banded watersnakes (Model 2) included time-varying capture probability with a behavioral response and no temporary emigration (i.e., γ fixed at zero; Table 3). Thus, we conclude that there was little support for random temporary emigration in this banded watersnake population. Conversely, we found support for random temporary emigration in black swamp snakes. The most strongly supported model for black swamp snakes (Model 1) included time-varying capture probability with a behavioral response and γ that differed between the sexes (Table 4). This model was separated by a ΔAIC_c of ≥ 8.9 compared with less-supported models. Estimates of temporary emigration parameters (γ) from this model were 0.19 ± 0.09 and 0.36 ± 0.08 for male and female black swamp snakes, respectively.

DISCUSSION

In both aquatic snake species we found evidence that capture and recapture probabilities were not equal, suggesting that the use of standard open population models would violate some modeling assumptions and yield biased estimates of population sizes and vital rates. Interpreting variation in detection probability parameters requires careful consideration of factors that influence capture rates using a given sampling method. Several capture methods are commonly used in snake population monitoring, including baited and unbaited traps, visual searches or road censuses, and turning of natural or artificial cover objects (i.e., coverboards; Dorcas and Willson 2009). Because each of these methods targets snakes undertaking different activities, capture rates obtained using different methods may reflect different biological or behavioral attributes of snakes (Dorcas and Willson 2009). For example, road censuses only detect snakes that are actively moving through habitat, presumably engaged in activities such as foraging, mate-searching, or dispersal, whereas cover objects generally capture snakes that are inactive or thermoregulating. Thus, seasons or environmental conditions favorable for activity might produce high capture rates in road censuses but few snakes captured under coverboards. Although we did not intentionally bait our traps, they readily accumulated aquatic prey, which were frequently consumed by snakes within traps (Seigel et al. 1995, Winne 2005). Thus, our capture rates were primarily indicators of foraging activity. This idea is supported by an experimental study conducted at Ellenton Bay that demonstrated increased capture rates associated with presence of prey in traps (Winne 2005).

We found clear support for temporal variation in capture and recapture probabilities in both banded watersnakes and black swamp snakes, which was not unexpected; activity patterns of many ectotherms are strongly dependent on environmental conditions, resulting in highly seasonal patterns of activity in temperate regions (Gibbons and Semlitsch 1987). Both banded watersnakes and black swamp snakes displayed generally unimodal temporal patterns of capture and recapture probability with rates that peaked in summer. High capture rates likely reflect foraging activity, with the highest foraging rates occurring during months when warm

air and water temperatures facilitate rapid digestion and allow for both diurnal and nocturnal activity. Many snakes exhibit reduced foraging during seasons that correspond with mating or gestation (Bonnet et al. 1998, Gregory et al. 1999). However, we found no strong support for variation between sexes in capture or recapture probabilities and did not see a noticeable reduction in detectability parameters during seasons when female snakes were pregnant. Although unexpected, this may be partly because females of both species feed during pregnancy (Winne et al. 2006*b*, J. D. Willson and C. T. Winne, unpublished data) and because the homogeneity of the aquatic habitat does not result in spatial conflicts between foraging and thermoregulation (Winne et al. 2006*b*). Failure to account for the time-varying capture probabilities we observed would result in decreased precision of parameter estimates and apparent variation in abundance among seasons.

Behavioral response to capture, manifested as a difference in capture probability between unmarked (initial capture probability) and previously marked (recapture probability) animals, has long been appreciated as a factor that can bias abundance and vital rate estimation (Nichols et al. 1984). Trap responses have been documented in a variety of animal taxa, particularly birds and small mammals (Nichols et al. 1984) but have seldom been tested for in snakes or other herpetofauna (Dorcas and Willson 2009). We found compelling evidence of behavioral responses to traps; in both species recapture probability was always greater than initial capture probability, indicating a strong trap-happy response. This positive trap response is likely due to bait accumulation in traps; greater recapture rates presumably reflect an association of traps with feeding opportunities. Trap happy responses are frequently associated with baited traps in other taxa (Pollock et al. 1990) and it is likely that our results apply to most situations where snakes are sampled with baited traps. The only other study to explicitly examine trap responses in snakes noted a positive, but ephemeral, behavioral response in brown treesnakes sampled using baited arboreal funnel traps (Tyrrell et al. 2009). It is important to consider, however, that snakes sampled using other methods may exhibit different responses. For example, it is plausible that snakes sampled using coverboards might exhibit trap-shy responses associated with the lack of reward (food), stress of being captured, or perhaps degradation of the microclimate under coverboards after frequent turning. Indeed, negative trap responses have been noted in terrestrial salamanders sampled using cover objects (Bailey et al. 2004*b*). In our study, banded watersnakes exhibited stronger trap responses than black swamp snakes, with recapture probability up to 5 times greater than initial capture probability for banded watersnakes in some seasons. This disparity might simply be due to the larger size and mobility of banded watersnakes compared to black swamp snakes, which could facilitate banded watersnakes foraging more widely to locate traps. Finally, capture and recapture probabilities did not always vary synchronously in our system. For example, banded watersnakes displayed a weak behavioral response in cooler months (e.g., Oct, when initial capture and

recapture probabilities were comparable) but showed strong trap-happiness in the summer (e.g., Jul and Aug, when recapture probability was >5 times greater than initial capture probability). This temporal variation in trap response strongly suggests seasonal differences in foraging rates. Because digestion is slower at lower temperatures, in cooler months snakes may exhibit longer refractory periods between feedings, reducing their likelihood of being captured multiple times within a sampling period.

Behavioral responses violate the equal catchability assumption of simplistic closed population models such as the Lincoln–Peterson estimator (Lincoln 1930), resulting in considerable bias in estimates of abundance or vital rates (Nichols et al. 1984, Pollock et al. 1990, Hines and Nichols 2002). Specifically, failure to account for a trap-happy response leads to underestimation of abundance whereas a trap-shy response results in abundance overestimation (Nichols et al. 1984, Pollock et al. 1990). For example, the most strongly supported model (Model 2, which included a behavioral response to traps) yielded an estimated total banded watersnake abundance of 306 individuals in August. The comparable model that did not incorporate a trap-happy response (Model 5) yielded an estimated abundance 3 times lower (111 individuals). Standard open population models, such as the Jolly–Seber model (Seber 1982), do not distinguish between capture and recapture probabilities and cannot incorporate behavioral responses. Most studies that have used mark-recapture to estimate population size in snakes either used these open models or have focused on abundance estimation using closed models and not reported support for, or strength of, behavioral responses (e.g., Whiting et al. 1996, Lourdais et al. 2002). Our results demonstrate that pronounced trap responses can exist in snakes and that these responses, if unaccounted for, can strongly bias abundance estimates. We advise researchers to evaluate trap responses in any study attempting to estimate abundance of snakes or other elusive wildlife species, especially for studies that use baited traps as a primary capture method.

Temporary emigration can result from a combination of an animal's physical location, its behavior, and efficacy of the capture method across habitats and behaviors. Among animal groups, reptiles and amphibians might be particularly likely to exhibit inherent temporary emigration due to their low energetic requirements, which allow them to undergo prolonged periods of inactivity. Moreover, many reptile and amphibian species use habitats that are difficult to sample (e.g., subterranean or arboreal habitats), which can lead to a large portion of the population being unavailable for capture much of the time. For example, Bailey et al. (2004*b*) documented high rates of temporary emigration in terrestrial salamanders, with an average of 87% being below ground and unavailable for capture during each primary sampling period. Temporary emigration models have also been used to evaluate populations of amphibians that are only sampled effectively at breeding sites (e.g., Bailey et al. 2004*a*, Fretey et al. 2004). These models allow for estimation of the non-breeding segment of the population that is unavailable for capture during surveys each year (Bailey et al. 2004*a*).

Snakes, which have low energetic demands and frequently use difficult-to-sample habitats, may also exhibit inactivity due to digestion, pregnancy, or ecdysis. However, despite the theoretical likelihood of temporary emigration occurring in snake populations, studies have heretofore lacked the appropriate sampling designs (i.e., robust design) to examine this possibility.

We found evidence for moderate levels of temporary emigration in black swamp snakes, with 19% of males and 36% of females being unavailable for capture during a given primary sampling period. In contrast, support for temporary emigration in banded watersnakes was equivocal. This difference between the species leads us to believe that temporary emigration in black swamp snakes likely reflects spatial distribution of the species within the wetland and reduced movement (i.e., smaller home range) of black swamp snakes in comparison to banded watersnakes. It is likely that limited movement of black swamp snakes due to small body size or more limited foraging activity precluded a segment of the population from encountering our trapping array during a primary sampling interval. Conversely, banded watersnakes may forage more widely, allowing all individuals to encounter traps. The difference in temporary emigration rates between the sexes in black swamp snakes could be due to more extensive movement of males from mate-searching behavior or to reduced movement of females during pregnancy, as is typical of many snakes (Gibbons and Semlitsch 1987, Gregory et al. 1987). Regardless of its cause, more extensive movement by males would result in a larger proportion of the male population encountering traps within sampling each period, compared to females. Finally, it is unlikely that behavioral inactivity contributed strongly to temporary emigration in these species. Both banded watersnakes and black swamp snakes are consistently active within the wetland during the months we sampled and regularly enter traps and feed during ecdysis and pregnancy (Winne et al. 2006*b*; J. D. Willson and C. T. Winne, unpublished data). Moreover, our use of long (10-day) primary sampling periods minimized the chance that snakes would remain inactive during the entire interval due to digestion, at least in warmer months.

Failure to account for random temporary emigration, where it exists, does not bias estimates of overall abundance in open population models (i.e., superpopulation size sensu Kendall et al. 1997, Bailey et al. 2004*b*), but does reduce precision of vital rate estimates (Kendall et al. 1997, Bailey et al. 2004*b*). However, because closed population models assume a static population, these models will underestimate abundance when a portion of the population has temporarily emigrated and thus is unavailable for capture within the sampling period. Consequently, our analysis using robust design is necessary to generate precise and unbiased abundance estimates in situations where random temporary emigration exists (e.g., black swamp snakes).

MANAGEMENT IMPLICATIONS

Precise and accurate estimation of population parameters requires an understanding of factors that influence capture

probability, but few studies have specifically addressed capture probability in snakes (but see Gragg et al. 2007, Tyrrell et al. 2009). We found strong evidence of several aspects of sampling methodology and snake behavior that, if not accounted for, can result in biased or imprecise population size or vital rate estimates. Thus, we recommend caution when analyzing snake mark-recapture data and strongly suggest evaluating factors that influence detectability and which may violate assumptions of some mark-recapture models. Robust design is the most appropriate sampling method allowing for estimation of abundance and vital rates over demographically open time scales without violating assumptions about population closure or equal capture probability. Thus, robust design sampling shows great promise for improving the efficacy of mark-recapture studies of secretive species, including snakes. Although some snakes may be inherently elusive, in many cases careful study design and consideration of factors that can artificially deflate capture and recapture probabilities can make precise monitoring of snake populations feasible.

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