Biological Conservation 144 (2011) 1508–1515

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes

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A R T I C L E   I N F O

Article history:
Received 12 July 2010
Received in revised form 19 January 2011
Accepted 24 January 2011
Available online 21 February 2011

Keywords:
Aquatic snakes
Detectability estimates
Habitat use
Program PRESENCE
Site occupancy modeling
Wetland

A B S T R A C T

The species most in need of conservation or management are often also the most difficult to monitor, because of their rarity, secretive habits, or both. To combat these challenges, presence/absence (site occupancy) models can be used to track species occupancy at landscape scales. However, quantitative knowledge of detection probability (which is almost always <1) is required to reliably estimate site occupancy. Here, we present a case study that combines detection probabilities and site occupancy modeling to monitor a notoriously secretive guild of animals, North American aquatic snakes. Specifically, we use program PRESENCE to estimate detection probability (p) and probability of site occupancy (ψ) for seven snake species in relationship to site covariates, to understand the proximate and ultimate factors that influence habitat suitability. We were able to estimate p (3–46%) and ψ (12–96%) for each species and calculate the amount of unsuccessful effort necessary to declare absence of each species with statistical confidence (5–63 visits; 150–1890 trap-nights). We documented considerable interspecific variation in p and ψ; one species (*Nerodia fasciata*) was widespread and highly detectable, while another (*Agkistrodon piscivorus*) had low detectability despite its wide distribution. Five other species were secretive, or restricted to specific habitat types, or both, illustrating that complex and sometimes counterintuitive relationships exist between capture rate and occupancy. Incorporating p and ψ is essential to the success of large-scale monitoring programs for elusive species.

1. Introduction

Reptiles are suffering dramatic declines around the world due to overharvesting, habitat loss and degradation, environmental pollution, disease, climate change and persecution (Araújo et al., 2006; Garber and Burger, 1995; Gibbons et al., 2000; Todd et al., 2010). Reptile declines are especially troubling in light of the important trophic and ecological roles they play in ecosystems, where they often exist at high densities (Godley, 1980; Luiselli and Akani, 2002; Rodda et al., 2001). Despite their ecological importance, insufficient data are available to quantify the conservation status of most reptiles at either population or landscape scales (Gibbons et al., 2000). Worldwide, >82% of snake and >84% of lizard species have not been evaluated by the International Union for Conservation of Nature (IUCN) or are classified as having insufficient data to determine conservation status (IUCN, 2010). This discrepancy is largely caused by the inability of traditional field and data analysis techniques to circumvent unpredictability in reptile detection by researchers.

Snakes are generally considered the most difficult reptile group to study because of their cryptic behaviors, minimal or sporadic activity patterns, and frequent use of inaccessible (e.g., subterranean, arboreal, or aquatic) habitats (Parker and Plummer, 1987; Turner, 1977). Consequently, high-resolution data on geographic distribution are lacking for many species (Jenkins et al., 2009) and few situations exist where population densities have been accurately measured, or population trends tracked over time with confidence (Dorcas and Willson, 2009). When declines are suspected, it is extremely difficult or impossible to distinguish true rarity from poor or unlucky sampling, without knowledge of detection probability (Renken et al., 2004; Seigel et al., 1998; Shoemaker et al., 2009).

Site occupancy (presence/absence) modeling is recognized as an effective technique for monitoring populations of secretive species on a landscape scale (Harvey, 2005; Lõhmus, 2009; MacKenzie et al., 2003; Mazerolle et al., 2007), historically considered a daunting or even impossible task. Site occupancy modeling may be the only feasible metric for monitoring population status of some species,

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doi:10.1016/j.biocon.2011.01.020

such as those with recapture probabilities too low to use mark-recapture models effectively (Dorcas and Willson, 2009; Joseph et al., 2006; Pollock, 2006). For categorical, presence–absence data to be useful, however, estimates of species-specific detection probabilities must be incorporated into surveys (Kéry, 2002; Pellet and Schmidt, 2005).

Here, we provide the first estimates of detection probability and site occupancy for aquatic snake species, and use snakes as a case study for incorporating detection probability in site occupancy monitoring of rare and cryptic species. Specifically, we (1) surveyed twenty isolated wetlands for aquatic snakes, using multiple replicated sampling events, (2) calculated species-specific parameter estimates of detection probability (p) and site occupancy (ψ), using program PRESENCE (MacKenzie and Hines, 2002), and (3) compared single-season models (MacKenzie et al., 2002) to assess the ability of site-specific covariates to influence these two parameters. We estimated p and ψ for seven aquatic snake species – banded watersnake (*Nerodia fasciata*), Florida green watersnake (*Nerodia floridana*), glossy crayfish snake (*Regina rigida*), black swamp snake (*Seminatrix pygaea*), mud snake (*Farancia abacura*), rainbow snake (*Farancia erytrogramma*), and cottonmouth (*Agkistrodon piscivorus*) – which allowed us to understand how aspects of behavior and ecology influence patterns of detection probability and site occupancy.

2. Methods

2.1. Study sites

Between 30 May and 20 July 2006, we sampled aquatic snakes in 20 freshwater wetlands on the US Department of Energy's Savannah River Site, located in the upper Coastal Plain of South Carolina (Aiken and Barnwell Counties), USA. Wetlands were selected to represent a range of aquatic habitat types, but the majority of sites we surveyed were semi-permanent, open-water, herbaceous, depressional wetlands. For our analyses of aquatic snake detectability and site occupancy, we characterized wetlands in terms of their permanence (hydroperiod length), their distance from the Savannah River floodplain, and their abundance of prey. We used these variables to construct covariates for our analyses.

2.2. Field methods

Estimating detectability is accomplished by repeatedly visiting sites and comparing the outcome of equivalent sampling intervals (visits) made over a short time. At each wetland we set arrays of 30 cylindrical plastic minnow traps (model 700, N.A.S. Incorporated, Marblehead, Ohio) for five consecutive nights, using a single array-night as one sampling occasion (i.e., one visit). Passive traps are an effective method for sampling snakes because they reduce observer bias, integrate captures over time, and readily capture actively foraging aquatic snakes in a variety of microhabitats (Dorcas and Willson, 2009; Gunzburger, 2007; Rodda and Fritts, 1992; Willson et al., 2005, 2008; Winne, 2005). Depending on the size of the wetland, we set one, two or three trap arrays; thus, each night we made one to three visits to each wetland, for a total of 150, 300 or 550 trap-nights per wetland. We placed traps in shallow water with the funnels submerged and top of the trap 4–5 cm above water, to provide trapped animals with access to air. While traps were not initially baited, accumulation of prey items (fish and amphibians) through incidental capture resulted in natural baiting of traps (Keck, 1994; Winne, 2005). We examined traps every morning and removed captured snakes. We left captured fish and amphibians in the traps (to serve as bait), but we removed large crayfish, predacious diving beetles (Coleoptera: Dytiscidae) and giant water bugs (Hemiptera: Belostomatidae) because of their potential to injure or kill trap-mates, including snakes.

We transported newly-captured snakes to the laboratory where we marked each individually by branding ventral scales (Winne et al., 2006a). On the following day, we released snakes into the wetland within 10 m of their original capture location. Recaptured individuals were recorded and released immediately at their capture location. Although some individuals were not available for recapture during the 24 h following their initial capture, estimation of detection probability and site occupancy does not rely on recapturing individuals and requires only that sites be closed to changes in species occupancy, not individual occupancy (MacKenzie et al., 2006). We acknowledge that short-term removal of individuals may have added heterogeneity to our estimates of detection probability or, in the unlikely case that we captured all individuals in the sampling area on one day, violated the occupancy closure assumption, but these effects were almost certainly minor, given that individual capture probability of aquatic snakes is very low (<0.05; Willson et al., 2011).

2.3. Site covariates

We collected prey covariate data by counting the number of fishes, crayfish, large aquatic salamanders (*Siren* and *Amphiuma*) and larval or paedomorphic mole salamanders (*Ambystoma talpoideum*) captured on the first day of sampling at each wetland. The distance of each wetland from the river floodplain is related to the frequency of inundation during floods and the ease of dispersal to and from more permanent aquatic habitats. Straight-line distances between the wetland center and the Savannah River were measured using ArcView (Version 3.3, ESRI). Wetland permanence (hydroperiod) affects the ability of species with differing life-history attributes to persist through droughts (Willson et al., 2006; Winne et al., 2006b). Sixteen of the 20 wetlands studied had pre-existing data, which we used to assess permanence: we calculated wetland permanence as the proportion of each year a wetland held standing water, averaged over 5–12 years of available data. The permanence of the remaining four wetlands was estimated by comparing observations made between 2006 and 2009 to other heavily-studied wetlands (Davis and Janecek, 1997).

2.4. Data analyses

For each of seven aquatic snake species, we estimated detection probability and site occupancy across all wetlands using program PRESENCE (Version 2.4, Proteus Research and Consulting Ltd., Dunedin, New Zealand). PRESENCE estimates detection probability (p) and proportion of area occupied (site occupancy; ψ), assuming (1) sites are closed to changes in site occupancy at the species level during the study, (2) species are not detected if they are absent and may or may not be detected if they are present, and (3) detection at one site is independent of detection at all other sites (MacKenzie et al., 2002). Both p and ψ can be expressed as logit-functions of site-specific covariates such as habitat variables or the sympatry of other species.

We performed a Principal Components Analysis (PCA) on our six site covariates (wetland permanence, distance from floodplain, and abundance of each of the four prey types) and used the first two orthogonal factors (F1 and F2, Eigenvalues >1; cumulative variability 63.4%) in our models as covariates representing an underlying environmental gradient (Gannon, 2005). Doing so allowed us to avoid autocorrelation of site covariates and greatly simplified our modeling structure, while still permitting biological interpretation due to large differences in the contribution of each site covariate to each factor (Table 1).

Table 1
Results of a Principal Components Analysis (PCA) of six site covariates describing 20 wetlands in South Carolina, USA. Correlations between site covariates and the first two PCA factors (F1 and F2) and relative contribution of site covariates to these factors are indicated. The Eigenvalue for Factor 1 = 2.354; the Eigenvalue for Factor 2 = 1.449.

Site covariate	PCA F1		PCA F2	
	Contribution (%)	Correlation	Contribution (%)	Correlation
Wetland permanence (hydroperiod)	35.621	0.916	2.419	0.187
Distance from river floodplain	6.494	0.391	33.556	0.697
Fish abundance	13.331	0.560	15.973	−0.481
Crayfish abundance	22.580	−0.729	13.232	−0.438
Ambystoma talpoideum abundance	8.624	−0.451	22.588	0.572
Siren/*Amphiuma* abundance	13.351	0.561	12.232	−0.421

For each of the seven snake species, our model set in program PRESENCE contained eight models: the null (constant) model as a reference; three models where proportion of sites occupied was held constant, $\psi(.)$, and p was allowed to vary with each PCA factor individually and both factors together; three models where detection probability was held constant, $p(.)$, and ψ allowed to vary each PCA factor individually and both factors together; and a global model where both p and ψ included both factors (Gooch et al., 2006; Kirlin et al., 2006). Except for the global model, we did not include PCA factors in both terms simultaneously because of our low sample size ($n = 20$ wetlands); preliminary attempts to do so did not improve model fit or performance. Because of the short duration of sampling at each wetland (5 days) we did not model sampling covariates or allow p or ψ to vary over time. For two species, some models failed to converge and were excluded from analyses. We assessed model fit by estimating the mean dispersion parameter ($\hat{c}$) for the global model using 1000 parametric bootstraps as recommended by MacKenzie and Bailey (2004).

Models for each species were prioritized by Akaike weight (w_i) and small sample size-corrected Akaike Information Criterion values (ΔAIC_c; Akaike, 1973; Burnham and Anderson, 1998). Models for two species, *N. floridana* and *S. pygaea*, showed evidence of overdispersion ($\hat{c} = 6.57$ and $\hat{c} = 2.44$ respectively), and so we reranked these models using quasi-AIC$_c$ and multiplied standard errors for β values and parameters (p and ψ) by $\sqrt{\hat{c}}$. Where underdispersion was observed ($\hat{c} < 1$), we truncated $\hat{c}$ to 1 and used AIC$_c$ (Medeiros and Freed, 2009; White et al., 2001). In most instances, a single "best" model was not evident (i.e. several models were equivocally favored; $w_1/w_2 \leqslant 10$). We tested for differences between species in estimates of p and ψ from all equivocal models using a multi-way ANOVA with post-hoc multiple comparison procedures (Duncan's Multiple Range test).

Several methods have been proposed for calculating the amount of effort necessary to declare species absence at a site (Green and Young, 1993; Kéry, 2002; Solow, 1993). The method that best fits our data is a probability model presented by McArdle (1990), which uses detection probability to estimate the amount of effort (number of unsuccessful visits) necessary to declare absence of a species at a specified level of statistical confidence. We set a confidence level of 95%, and calculated the minimum number of visits necessary using p calculated from the most favored model for each species.

Despite its potential explanatory value, we were unable to use snake population density as a covariate in our models of detectability because of infrequent recaptures of most species. Alternatively, we correlated (Spearman correlation, due to non-normality of data) population density with estimated detection probability for the few cases where it was possible to estimate density using mark-recapture (*N. fasciata* at seven wetlands). For these cases, population size was estimated using the Lincoln–Peterson estimator (Heyer et al., 1994) and divided by the area sampled (30 m buffer of aquatic habitat around arrays) to estimate density.

3. Results

Thirty-five nights of aquatic trapping ($n = 7200$ trap-nights) at 20 wetlands yielded 319 captures of 230 individual snakes. Of the 11 species captured, we focus analyses on the seven most commonly captured species, all with at least three captures: four natricines, the banded watersnake (*N. fasciata*, $n = 201$ captures), black swamp snake (*S. pygaea*, $n = 49$), Florida green watersnake (*N. floridana*, $n = 24$), and glossy crayfish snake (*R. rigida*, $n = 5$), the xenodontine mud snake (*F. abacura*, $n = 28$) and rainbow snake (*F. erytrogramma*, $n = 3$), and the viperid cottonmouth (*A. piscivorus*, $n = 9$).

3.1. Detection probability and proportion of area occupied

Across all species and models, estimates of p were between 0.03 and 0.46, with standard errors from 0.02 to 0.31. Our models revealed interspecific variation in detection probability (Fig. 1; ANOVA $F_{6,43} = 53.8$, $p < 0.001$, $R^2 = 0.897$). Estimates of ψ varied from 0.12 to 0.96 across all species and models, with standard errors from 0.05 to 0.54, and also differed between species (Fig. 1; ANOVA $F_{6,43} = 78.68$, $p < 0.0001$, $R^2 = 0.927$). Post-hoc Duncan's Multiple Range Tests for p and ψ revealed five groups of species with significantly different means for each parameter, although group composition differed for p and ψ (Fig. 1).

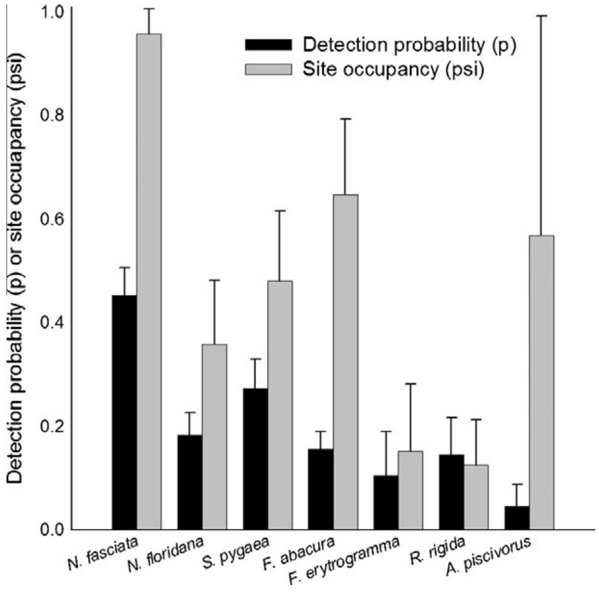

Fig. 1. Detection probability (p) and site occupancy (ψ) estimates for seven species of semi-aquatic snakes across 20 wetlands in South Carolina, USA, for most favored models, ($\Delta AIC_c = 0$). Statistically significant groupings for detection probability (p) are: *N. fasciata* > *S. pygaea* > *R. rigida*, *N. floridana* and *F. abacura* > *F. erytrogramma* and *A. piscivorus*; and for proportion of area occupied (ψ) are: *N. fasciata* > *F. abacura* and *A. piscivorus* > *S. pygaea* and *N. floridana* > *F. erytrogramma* > *R. rigida*. Bars represent ± 1 SE, adjusted for overdispersion where necessary.

3.2. Interspecific patterns of detectability and site occupancy

N. fasciata, the most commonly captured snake species, had the highest overall estimates for both detection (0.46) and site occupancy (0.96; Fig. 1). No species besides *N. fasciata* had a detection probability greater than 0.40. For the five other non-Viperid species, detectability and site occupancy varied considerably and were not necessarily intuitively related. Detectability was second-highest for *S. pygaea* ($p = 0.27$), whereas the other species were similarly difficult to detect ($p = 0.10–0.18$). *F. abacura* was the second-most widespread species ($\psi = 0.65$), followed by *S. pygaea* ($\psi = 0.48$) and *N. floridana* ($\psi = 0.36$). The most restricted species were *F. erytrogramma* and *R. rigida*, predicted to occur at only 15% and 13% of sites, respectively. *A. piscivorus* exhibited a particularly strong pattern of extremely low detectability using aquatic traps ($p = 0.05$) but relatively high site occupancy ($\psi = 0.57$).

The number of unsuccessful visits (where one visit = 30 traps set for one night) necessary to declare absence of a species with 95% confidence was inversely correlated with species detection probability (Fig. 2). We estimated that species with low detectability require substantial effort (high number of visits) to reject site occupancy given non-detection at a site, whereas those with high detectability require less effort. The minimum number of visits required to declare absence with 95% confidence ranged from five (i.e., 150 trap-nights) for *N. fasciata* to 63 (i.e., 1890 trap-nights) for *A. piscivorus* (Fig. 2).

3.3. Covariates

The PCA of wetland covariates yielded two factors with Eigenvalues >1, which explained 63.4% of the variation in the covariate data. The first factor (F1) was positively correlated with wetland permanence and abundance of prey types reliant on permanent wetlands (fish and large aquatic salamanders; Snodgrass et al., 1999; Table 1). The second factor (F2) was positively correlated with distance from the Savannah River floodplain (isolation from permanent water) and with abundance of the prey type most associated with nonpermanent wetlands, the paedomorphic salamander *A. talpoideum* (Snodgrass et al., 2000). Positive values for F1 indicate an association with more permanent wetlands that have large populations of fishes and large aquatic salamanders. Positive values for F2 imply an association with wetlands that are more isolated from the floodplain and have large populations of *A. talpoideum*.

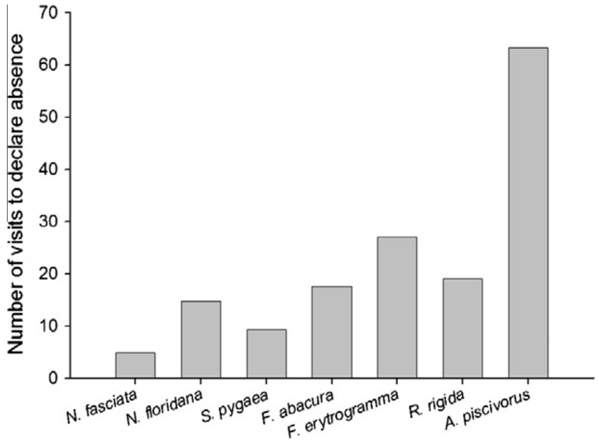

Fig. 2. Number of non-detecting visits (1 visit = 30 traps set for 24 h) necessary to declare species absence with 95% confidence for seven species of semi-aquatic snakes in South Carolina, USA, using the model with the highest overall Akaike weight for each species.

PRESENCE penalizes for the addition of parameters, promoting simplicity and parsimony (Mazerolle, 2004); in only one instance did the best model include more than one covariate (Table 2). Models which allowed site occupancy to vary with PCA factors were favored for only one species (*F. erytrogramma*), while models allowing detection probability to vary with one or both factors were favored for both *N. fasciata* and *S. pygaea*. For four of the seven species, the null model was the most favored (Table 2). However, as indicated by weight ratios ($w_1/w_2 \leqslant 10$), a single "best" model was rarely evident. The equivocal nature of all seven model sets complicates interpretation of covariate relationships.

Factor 1 was negatively correlated with detectability of *N. fasciata* and *S. pygaea* (Fig. 3) and positively correlated with both

Table 2
Models of site occupancy (ψ) and detection probability (p) for seven species of aquatic snakes in South Carolina, USA. Parameters (p and ψ) were fixed (.) or allowed to vary with PCA factors (F1 and F2) derived from six site covariates. For each species we include all models that converged out of the total set of eight, in descending order by rank, except those that carried < 1% of the model weight. Models are ranked according to their AIC$_c$ (second-order Akaike's Information Criterion corrected for small sample sizes) or QAIC$_c$ (quasi-AIC corrected for overdispersion) and w_i (model weight). Models in bold generated outputs shown in Fig. 3.

Model, by species	ΔAIC$_c$	w_i
Banded watersnake – *Nerodia fasciata*		
ψ(.), p(F1, F2)	**0.00**	**0.78**
ψ(.), p(F1)	2.97	0.18
ψ(F1, F2), p(F1, F2)	5.88	0.04
Green watersnake – *Nerodia floridana*	ΔQAIC$_c$	w_i
ψ(.), p(.)	0.00	0.41
ψ(.), p(F1)	**2.07**	**0.15**
ψ(.), p(F2)	2.29	0.13
ψ(F1), p(.)	2.44	0.12
ψ(F2), p(.)	2.51	0.12
ψ(.), p(F1, F2)	4.83	0.04
ψ(F1, F2), p(.)	5.28	0.03
Black swamp snake – *Seminatrix pygaea*	ΔQAIC$_c$	w_i
ψ(.), p(F1)	**0.00**	**0.48**
ψ(.), p(F2)	**1.40**	**0.24**
ψ(.), p(F1, F2)	2.44	0.14
ψ(.), p(.)	3.72	0.07
ψ(F1), p(.)	5.16	0.04
ψ(F2), p(.)	6.21	0.02
ψ(F1, F2), p(.)	8.01	0.01
ψ(F1, F2), p(F1, F2)	8.49	0.01
Mud snake – *Farancia abacura*	ΔAIC$_c$	w_i
ψ(.), p(.)	0.00	0.30
ψ(.), p(F1)	**0.87**	**0.20**
ψ(.), p(F2)	1.19	0.17
ψ(.), p(F1, F2)	1.92	0.12
ψ(F1), p(.)	2.16	0.10
ψ(F2), p(.)	2.48	0.09
ψ(F1, F2), p(.)	4.95	0.03
Rainbow snake – *Farancia erytrogramma*	ΔAIC$_c$	w_i
ψ(F2), p(.)	**0.00**	**0.54**
ψ(.), p(F2)	**0.97**	**0.33**
ψ(.), p(.)	2.97	0.12
Glossy crayfish snake – *Regina rigida*	ΔAIC$_c$	w_i
ψ(.), p(.)	0.00	0.39
ψ(F2), p(.)	**1.74**	**0.16**
ψ(.), p(F2)	2.14	0.13
ψ(F1), p(.)	2.22	0.13
ψ(.), p(F1)	2.24	0.13
ψ(F1, F2), p(.)	3.77	0.06
Cottonmouth – *Agkistrodon piscivorus*	ΔAIC$_c$	w_i
ψ(.), p(.)	0.00	0.38
ψ(F1), p(.)	2.07	0.13
ψ(.), p(F2)	2.33	0.12
ψ(F2), p(.)	2.40	0.12
ψ(.), p(F1)	2.50	0.11
ψ(F1, F2), p(.)	2.96	0.09
ψ(.), p(F1, F2)	5.16	0.03

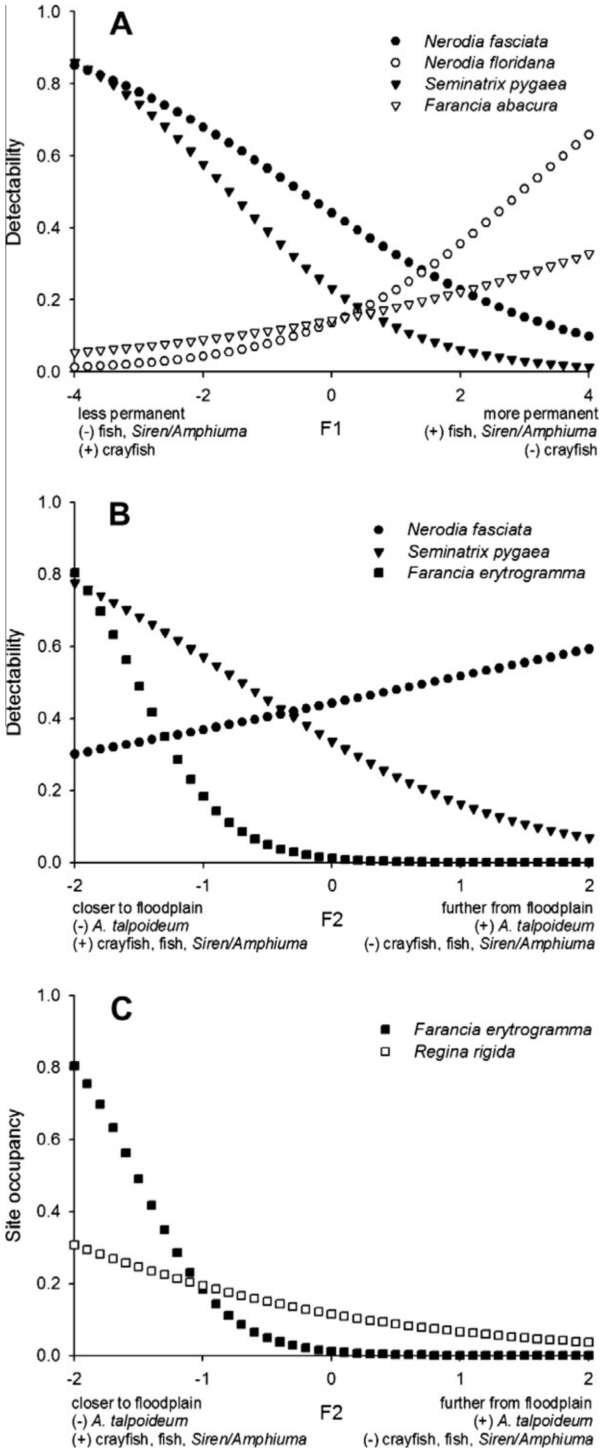

Fig. 3. Directional trends in detectability (p) and site occupancy (ψ) derived from coefficients for PCA covariates (β values) from most-favored and equivocal model outputs (indicated in Table 1). These include (a) effect of F1 on detectability of *Nerodia fasciata* ($\beta_p = -0.16 \pm 0.15$, $\beta_{F1} = 0.53 \pm 0.12$), *Nerodia floridana* ($\beta_p = -1.84 \pm 0.95$, $\beta_{F1} = 0.62 \pm 0.97$)*, *Seminatrix pygaea* ($\beta_p = -1.20 \pm 0.70$, $\beta_{F1} = -0.75 \pm 0.350$)* and *Farancia abacura* ($\beta_p = -1.78 \pm 0.26$, $\beta_{F1} = 0.27 \pm 0.21$), (b) effect of F2 on detectability of *Nerodia fasciata* ($\beta_p = -0.32 \pm 0.14$, β_{F2} 0.35 ± 0.12), *Seminatrix pygaea* ($\beta_p = -0.68 \pm 0.38$, β_{F2} -0.96 ± 0.45)* and *Farancia erytrogramma* ($\beta_p = -5.22 \pm 1.87$, β_{F2} -2.01 ± 1.14), and (c) effect of F2 on site occupancy by *Farancia erytrogramma* ($\beta_\psi = -4.40 \pm 3.05$, $\beta_{F2} = -2.91 \pm 2.41$) and *Regina rigida* ($\beta_\psi = -2.03 \pm 0.88$, β_{F2} -0.61 ± 0.74). Estimates of p and ψ were obtained by using the inverse logit function on β estimates obtained from model output files in PRESENCE. Standard errors are adjusted for overdispersion where necessary.*

detectability and site occupancy of *F. abacura*. Factor 2 was negatively correlated with detectability of *S. pygaea* and detectability and site occupancy of *F. erytrogramma* but was positively correlated with detectability of *N. fasciata* (Fig. 3). The slope of the relationship between PCA factors (representing the underlying environmental gradient) and estimated parameters (detectability or site occupancy; Fig. 3) suggests a gradient response for *S. pygaea* and *N. fasciata*, with both species being less detectable in permanent wetlands close to the floodplain. The detectability of *N. fasciata* in permanent wetlands is almost 10 times that of *S. pygaea* (F1 = 4.0, 9.9% and 1.4%, respectively), whereas the detectability of the two species is nearly identical in the most ephemeral ecosystems (F1 = −4.0, 86.1% for *S. pygaea* and 85.1% for *N. fasciata*; Fig. 3). In contrast, a threshold response exists between F2 and site occupancy for *F. erytrogramma*, with estimates of site occupancy falling from 0.80 to 0.18 as F2 increases from −2 to −1, and values of F2 > 0.1 resulting in site occupancy estimates of <0.01 (Fig. 3).

Although population density was estimable for only one species (*N. fasciata*) at seven wetlands we found a significant positive correlation between population density and detectability ($p = 0.04$) that explained a high proportion of the variance in detectability between sites for this species ($R^2 = 0.79$).

4. Discussion

Overall, detectability estimates for aquatic snakes were low compared to many other types of animals. Our estimates of detection probability ranged from 0.03 to 0.46 and comprised five statistically significant groups, indicating that considerable interspecific variability exits in snake detectability. These estimates are comparable to the few published for terrestrial snakes, including for *Sistrurus catenatus* in Canada (0.14–0.25; Harvey, 2005), for three species of European forest-edge snakes (0.23–0.70, 0.09–0.56 and 0.11–0.25; Kéry, 2002) and for pine-flatwoods snakes in the southeastern USA (0.00–0.17; Steen et al., in press). Published values for lizards are similar, including for *Oligodon otagense* in New Zealand (0.35–0.45; Roughton and Seddon, 2006) and for *Lacerta agilis* in the Netherlands (0.05–0.40; Kéry et al., 2009). Estimates for species which are detected aurally are generally greater, such as for five species of summer-breeding anurans in North Carolina (0.48–0.81; Gooch et al., 2006), and for four anuran species in Switzerland (0.743, 0.568, 0.438 and 0.288; Pellet and Schmidt, 2005), though all taxonomic groups show interspecific variation in detectability (Magurran and Henderson, 2003).

Relatively few studies of birds incorporate detection probabilities, in part because birds are very detectable – one study estimated that detectability of seventeen species of European birds ranged between 0.55 and 0.96 (Moore et al., 2004), depending on method, observer, species and time of day. The mean detectability of 150 Swiss bird species was 0.89 (SD 0.06, range 0.72–1.00), omitting one "extreme case of 0.50" (Kéry and Schmid, 2006). Estimated values for butterflies are similarly high (mean for 150 spp. = 0.61, SE = 0.01; Kéry and Plattner, 2007), due to the conspicuousness of these brightly-colored, flying, diurnal species. Other fully aquatic species may be quite difficult to detect (e.g., $p = 0.03$–0.33 for four species of minnow in Georgia, USA; Albanese et al., 2007), and estimates of p for nocturnal or fossorial species of birds and mammals show substantial range overlap with our estimates for aquatic snakes (e.g., 0.25–1.00 for seven species of small mammals in Indiana, USA; Gu and Swihart, 2004; 0.07–0.48 for 10 species of mesomammals detected using remote cameras in Massachusetts, USA; O'Connell et al., 2006; 0.09–0.63 for six species of nocturnal birds and mammals in southwestern Australia; Wintle et al., 2005).

Other cryptic species of herpetofauna are much easier to detect than snakes. For example, Bailey et al. (2004) found that detectability of Plethodontid salamanders in North Carolina varied between 0.51 and 0.87, depending on method and species, and was as low as 0.12 for a poor method when only a subset of sampling occasions was included. While it can be challenging to compare detectability across studies due to confounding factors such as differences in visit sizes, techniques and explanatory covariates, we can directly compare our estimates of snake detectability to the detectability of aquatic fishes and amphibians we captured in our minnow traps (1.00 for fishes and *A. talpoideum*, 0.96 ± 0.03 for crayfish, 0.32 ± 0.04 for *Siren* and 0.91 ± 0.05 for *Amphiuma*). Compared to estimates for other taxa, our estimates of 0.03–0.46 show that detecting snakes requires greater effort, although the low cost and high repeatability of our method makes it the most favored method for capturing aquatic snakes (Dorcas and Willson, 2009).

Species also varied substantially in site occupancy (0.12–0.96), and site occupancy was sometimes, but not always, intuitively related to capture frequency (Dorcas and Willson, 2009). *N. fasciata* represented 63% of total captures and had the highest estimates of both p and ψ (0.45 and 0.96, respectively), consistent with its unspecialized habitat requirements (Gibbons and Dorcas, 2004; Hebrard and Mushinsky, 1978) and the high efficacy with which it is sampled by minnow traps (only 5 visits necessary to declare absence with 95% confidence; Fig. 2). Both PCA factors contributed to the detectability of *N. fasciata*. Detectability exhibited a negative linear correlation with F1 (i.e., detection probability was lower in more permanent wetlands with denser populations of fish and large aquatic salamanders) and a positive linear correlation with F2 (i.e., detection probability was higher in wetlands that were far from the floodplain and had large populations of *A. talpoideum*). Site occupancy was high across the entire environmental gradient for both factors, demonstrating that detectability can vary substantially among occupied sites, even within a relatively common species. *N. fasciata* was the only species for which population density could be estimated at more than one site; a positive correlation between density and detectability indicated that abundance may be an proximate force driving detectability within species.

We predicted counterintuitive cases of relatively high site occupancy but low detectability for *N. floridana*, *S. pygaea*, and *F. abacura*, the last of which displayed a particularly strong case in which low detectability (0.16) was not indicative of rarity (low occupancy). It is likely that *F. abacura* either exists at lower population densities or is less prone to capture in aquatic traps than *N. fasciata*, but is present in most wetlands ($\psi = 0.65$). Detectability of *S. pygaea* was inversely correlated with F1, indicating lower detectability at wetlands with long hydroperiods. This trend is not surprising; although *S. pygaea* are known to occur in a variety of habitats (Gibbons and Dorcas, 2004), their diet on the Savannah River Site consists predominantly of amphibians, particularly aquatic salamanders such as *A. talpoideum*, which prefer isolated nonpermanent wetland habitats (Willson et al., 2010). Further, the ability of *S. pygaea* to aestivate within dried wetlands (Winne et al., 2006b) allows them to persist in nonpermanent wetlands more successfully than other aquatic snake species which exhibit dramatic population crashes in nonpermanent wetlands during severe droughts (Seigel et al., 1995; Willson et al., 2006). Though the null model was most favored for both *N. floridana* and *F. abacura*, covariate relationships from equivocal models predicted increased detectability with increases in F1 (i.e., more permanent wetlands with many fishes and large aquatic salamanders). These relationships are unsurprising given that *F. abacura* feed almost exclusively on aquatic salamanders and that *N. floridana* are vulnerable to local extirpation in nonpermanent wetlands during droughts (Willson et al., 2006).

For *F. erytrogramma* and *R. rigida* infrequent capture rates (low detectability) did appear to indicate rarity (low site occupancy). Highly-favored models including explanatory covariates of site occupancy were limited to *F. erytrogramma*, and were intuitively related to the specific needs of that species. A dietary specialist which primarily consumes a catadromous fish (American eel; *Anguilla rostrata*), *F. erytrogramma* requires wetlands with connectivity to permanent surface water (i.e. close to the river floodplain). The threshold relationship observed between site occupancy and F2 (Fig. 3) may correspond to the upstream dispersal limit of American eels. Despite also having a specialized diet of crayfish, *R. rigida* was our most difficult species to interpret due to a combination of few captures, low detectability, low site occupancy and a highly equivocal model set with weak covariate associations. Although we employed a methodologically rigorous method of estimating the parameters p and ψ, it apparently came at the expense of elucidating the particular effects of individual covariates. The equivocal nature of many of our model sets may be due in part to the "blurry" nature of our PCA factors (i.e., contribution of any one variable to a factor $\leqslant 35\%$), such that weight was distributed among several equivocal models rather than concentrated on the most-favored. Such issues should be considered when designing occupancy studies. Our understanding of covariate relationships could be improved by increasing sample size (# of wetlands), which would allow individual consideration of multiple covariates without using PCA, or by sampling sites that represent the entire environmental covariate gradient (e.g. sampling some highly ephemeral or extremely permanent wetlands).

Although the presence of *A. piscivorus* was confirmed at many of our 20 sites by opportunistic visual encounters, it was only detected using minnow traps at 6 of the 20 sites and made up only 2.82% of our total captures. Accordingly, our models predicted a case of high site occupancy ($\bar{x} = 0.60$) and extremely low detectability ($\bar{x} = 0.05$) for this species. Low captures of *A. piscivorus* in aquatic traps may reflect sedentary, ambush-oriented feeding behavior, in contrast to the more active foraging of the other six species of aquatic snake studied. Although an ontogenetic shift to more active foraging takes place in *A. piscivorus* (Eskew et al., 2009), most large adults have too large a head or body diameter to enter minnow traps and may be unable or unwilling to do so (Willson et al., 2008). We suggest that *A. piscivorus* is reluctant to enter aquatic traps and would be better surveyed using other techniques such as nocturnal visual encounter surveys.

Though others have suggested distance sampling (Buckland et al., 2001, 2004; Luiselli, 2006; but see Rodda and Campbell, 2002) or focal animal studies (Beaupre, 2002; Seigel et al., 1998) as potential methods for studying intractable snake populations, our results indicate that populations of secretive species, such as aquatic snakes, can be effectively monitored at a landscape scale through presence/absence monitoring. Despite the perceived rarity and secrecy of species like *F. erytrogramma*, with considerable effort it is possible to declare absence from a site with confidence; we estimated that up to 27 non-detecting visits (>810 trap-nights) are required to confidently reject absence of this species at a site. Although this represents an intense sampling effort, it is a substantial improvement over dismissing species such as *F. erytrogramma* as 'too secretive to study' (Steen, 2010). Of the seven species we studied, only three exhibited intuitive relationships between detectability and site occupancy (both high – *N. fasciata* – or both low – *F. erytrogramma* and *R. rigida*). The remaining species exhibited varying degrees of detectability but relatively high site occupancy, underscoring the fact that simple count-based indices may not be reliable indicators of abundance. We suggest that recognition of the disparity between site occupancy and detectability represents a major advance for the conservation of imperiled species inhabiting a critically imperiled habitat.

Many species are perceived as rare when they are merely secretive and not easily detected. Snakes are among the most secretive animals, leading to the perception that many species are impossible to monitor. This unfortunate generalization has led to a lack of information about the status of most snake populations, in spite of the fact that careful study design and a reasonable, quantifiable amount of effort can permit inferences and inform management decisions (Dorcas and Willson, 2009). Our study provides the first estimates of detectability and site occupancy for a North American snake guild and is a crucial first step in monitoring seldom seen aquatic snake species, many of which are suspected to be declining and occupy imperiled habitats (Todd et al., 2010). We incorporated data on environmental covariates to increase precision of parameter estimates, and found that even when doing so many snakes exhibit low detection probability. We demonstrated that monitoring secretive species on a landscape scale is possible using occupancy modeling, a promising new tool requiring only presence–absence data and sufficient effort to monitor species too secretive for traditional methods.

Acknowledgments

We would like to acknowledge the faculty and staff at the Savannah River Ecology Lab, especially J. Whitfield Gibbons, Judy Greene, Deno Karapatakis and Lindy Steadman. We also thank the following individuals for their assistance with field work: Kevin P. Durso, Sandy Durso, Evan A. Eskew, Chad A. Jennison, Tom M. Luhring, Rebecca L. Maska and Anna McKee; with data analysis: Greg Anderson, Robert J. Cooper, Mary C. Freeman, Scott J. Meiners and Todd Rasmussen; and for provisioning us with over a decade of hydrologic data: Evelyn Gaiser, Robert Lide and Ken McLeod. J.W. Gibbons, the Eastern Illinois University herpetology lab and one anonymous reviewer provided comments which improved the manuscript. This work was supported by the National Science Foundation through the Research Experiences for Undergraduates (REU) program to AMD and a Graduate Research Fellowship to JDW, and was supported by the Department of Energy under Award Number DE-FC09-96SR18546 to the University of Georgia Research Foundation. Animals were collected under South Carolina Department of Natural Resources scientific collection permits (G-06-04), and procedures used in the study were approved by the University of Georgia animal care and use committee (A2006-10069-0).

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