

Using multiple methods to assess detection probabilities of riparian-zone anurans: implications for monitoring

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Abstract

Context. Both manual call surveys (MCS) and visual encounter surveys (VES) are popular methods used to monitor anuran populations. Recent statistical developments, specifically the development of occupancy models that permit the use of data from various survey methods to assess method-specific detection probabilities, provide a rigorous framework for evaluating the effectiveness of field methods.

Aim. To compare species-specific detection probabilities generated by MCS and VES and to evaluate the effectiveness of these methods throughout the activity season of several riparian-zone anuran species.

Methods. During 2010 and 2011, we sampled 21 sites along the Broad and Pacolet Rivers, in South Carolina, USA, using MCS and VES. Anuran species were surveyed across three seasons (fall, spring and summer) each year.

Key results. For six species, MCS resulted in a higher mean probability of detection, whereas VES resulted in a higher mean probability of detection for four species. In addition, survey date was an important influence on detection probability of most anurans when using MCS, but largely unimportant when employing VES.

Conclusions. Our findings indicated that VES are as effective as MCS for detecting some species of anurans, and for others, VES represent a more effective method. Furthermore, when using VES outside the breeding window, some anurans can be reliably detected, and in some cases, detected more easily than by using MCS.

Implications. We suggest that VES is a complimentary technique to MCS and a potentially important tool for population monitoring of anurans. VES can provide more flexibility for anuran researchers, as robust estimates of detection and occupancy can be obtained outside a narrow breeding window.

Additional keywords: active search, amphibian, manual call survey, South Carolina, survey method, visual encounter survey.

Received 4 March 2014, accepted 20 August 2014, published online 26 September 2014

Introduction

Manual call surveys (MCS) are a popular method used to detect anurans for ecological, behavioural and conservation-related investigations (e.g. Blair 1961; Woolbright 1985; Knutson *et al.* 2004; Price *et al.* 2005; Dorcas *et al.* 2010). In particular, using MCS to obtain anuran distribution data provides a relatively simple and cost-effective way to monitor populations across time and space (Droege and Eagle 2005; Weir *et al.* 2005; Dorcas *et al.* 2010). A major assumption of MCS is that peak anuran breeding windows are well understood and surveys are well timed to coincide with anuran reproductive activities. However, a central concern in any survey method, including MCS, is that of imperfect detection (MacKenzie *et al.* 2002, 2006). Species detection probability is defined as the probability of detecting at least one individual of a focal species during a sampling occasion, given that individuals of the species are present in the area (MacKenzie *et al.* 2002).

Although detection of a species confirms its presence, lack of detection does not necessarily confirm absence. Thus, estimates of site occupancy and abundance, and their relationships with measured covariates (e.g. habitat type) along with estimated probabilities of colonisation and local extinction will be biased unless methods are used that can account for imperfect detection (MacKenzie *et al.* 2009). During MCS, even within the peak breeding season for many species, calling does not occur each night and there are variations in calling behaviour because of abiotic and biotic conditions, which can lead to the incorrect inference of absence of a species (Gooch *et al.* 2006; Brandner *et al.* 2007; Cook *et al.* 2011). In addition, recent studies have shown that false positive errors (i.e. a species that is absent but erroneously detected) during anuran call surveys positively bias occupancy estimates, even when false positive detections occur only 1% of the time (Miller *et al.* 2011, 2012). For these reasons, it is becoming increasingly common for MCS monitoring

programs to standardise survey methodologies and account for factors that influence detection probability (Pellet and Schmidt 2005; Weir *et al.* 2005; Dorcas *et al.* 2010).

Another common amphibian survey method is visual-encounter surveys (or active searches; VES), where observers visually search for amphibians in a designated area for a prescribed amount of time (Crump and Scott 1994). VES may hold distinct advantages over MCS. For example, some species vocalise only in response to heavy rains (e.g. spadefoot toads, *Scaphiopus* spp.), call infrequently (e.g. gopher frogs, *Lithobates capito*), have relatively short breeding seasons (wood frogs, *Lithobates sylvaticus*), are uncommon (e.g. Pellet and Schmidt 2005), or may not be audible over the louder higher-pitch calls of their contemporaries (Doan 2003; Droege and Eagle 2005). As with MCS, VES are based on the assumption that all individuals are equally detectable; other major assumptions are that there are no observer-related biases and that individuals are recorded once during a survey (Vonesh *et al.* 2010). Studies have used VES to assess the habitat use by focal species (Burbrink *et al.* 1998; Adams *et al.* 2011) and to compare the effectiveness of techniques such as cover-objects versus quadrat methodologies (Doan 2003; Grover 2006) and diurnal versus nocturnal searches (Heard *et al.* 2006), but direct comparisons with MCS have not been conducted. Furthermore, knowledge of how time of year influences detection probabilities of anurans observed via VES is not as well understood as it is for MCS.

It has become increasingly common for amphibian researchers to use multiple methods to detect species (Brown *et al.* 2007; Mattfeldt and Grant 2007; Dahl *et al.* 2009; Farmer *et al.* 2009; Balas *et al.* 2012). Some studies have expanded MCS to include vocal imitation of advertisement calls, in an attempt to stimulate male frogs and improve detection along with other VES methods such as nocturnal spotlight surveys and diurnal visual searches (e.g. Heard *et al.* 2006). Other studies examining optimal survey design in the tropics have used a combination of pitfall and funnel traps, along with MCS and VES, and automated tape recording of anuran calls (e.g. Parris *et al.* 1999; Rödel and Ernst 2004). Survey method is one of the most important considerations when designing studies. For example, when little is known about the natural history of a species, incorporating several methods along with covariates of interest (e.g. day of year) can provide estimates of detection probability, which allows researchers to identify the most appropriate sampling method. If detection probability is influenced by the time of year or weather conditions, for example, survey protocols can be adjusted to minimise the chance of false absences. Traditionally, researchers using multiple survey methods either combined data from each method to generate detection probabilities (i.e. Price *et al.* 2011), or separately generated detection probabilities for each method to compare their utility (Bailey *et al.* 2004; Mattfeldt and Grant 2007). Using multiple, single-method analyses or combined methods analysis ignores information from all but the focal detection method (Nichols *et al.* 2008). Recent advances in modelling circumvent some of the drawbacks of either combining sampling data or conducting single-method comparisons. Specifically, multi-method models permit simultaneous use of data from all methods for inference about method-specific detection probabilities (Nichols *et al.* 2008).

In the present study, our objectives were to evaluate two common methods for surveying anurans, namely, MCS and VES, by using a statistical model that permits incorporation of both methods into a single model (Nichols *et al.* 2008). We examined the generated detection probabilities for anuran species by using both methods and then examined how day of year influenced the effectiveness of each method. Given the variation in life history of many anurans, for some species, we expected that VES would be comparable to MCS and sometimes preferable to MCS, and that during certain times of the year, one method would be preferable over the other.

Materials and methods

Study area

Study sites ($n=21$) were located along the Broad and Pacolet Rivers, in the Piedmont region of north-central South Carolina (Fig. 1). We used a geographic information system (ArcGIS 10.0; Environmental Systems Research Institute, Redlands, CA, USA), with layers from the National Wetland Inventory (<http://www.fws.gov/wetlands/>, verified 20 July 2013), and the 2006 National Land Cover Database (Fry *et al.* 2011) to identify ~200 riparian wetlands within our study area. We generated a circular buffer of 1-km radius around each site, a distance that encompasses a majority of the core terrestrial habitat used by most anuran species (Semlitsch and Bodie 2003), and chose final study sites on the basis of spatial independence (i.e. non-overlapping 1-km-radius circular buffers). After ground-truthing, we determined that 21 sites were sufficiently accessible for time-constrained active searches (Fig. 1; see Eskew *et al.* (2012) and Hunt *et al.* (2013) for more information on study site selection).

Data collection

During 2010 and 2011 we surveyed each site using MCS (Dorcas *et al.* 2010) and time-constrained VES (Crump and Scott 1994) to document anurans. During 2010, three anuran calling surveys were conducted in both spring and summer at every site and during 2011 three anuran calling surveys were conducted in winter, spring and summer at every site; these seasons corresponded to the peak breeding windows for species in our study (Table 1). In total, 15 MCS were conducted at each study site. Manual call surveys were conducted between 1845 hours and 0100 hours by two experienced anuran surveyors listening independently for 5 min and recording all species heard; any differences in species observed were reconciled before leaving the study site and questionable species identifications were eliminated (Eskew *et al.* 2012). In total, there were four experienced observers participating in the study; however, only two observers participated in each survey. During each MCS, the number of cars passing by was recorded, because this may interfere with the ability to detect frogs. The majority of sites were located in rural areas and had little to no road traffic and, in cases with moderate traffic, observers waited to begin the survey until all cars had passed. Some survey sites were located nearer to dams than others (see Eskew *et al.* 2012); however, the distance was not great enough to influence observer ability to detect calling frogs (i.e. the noise level was always relatively low), and we found that water releases were infrequent relative to the timing of our surveys.

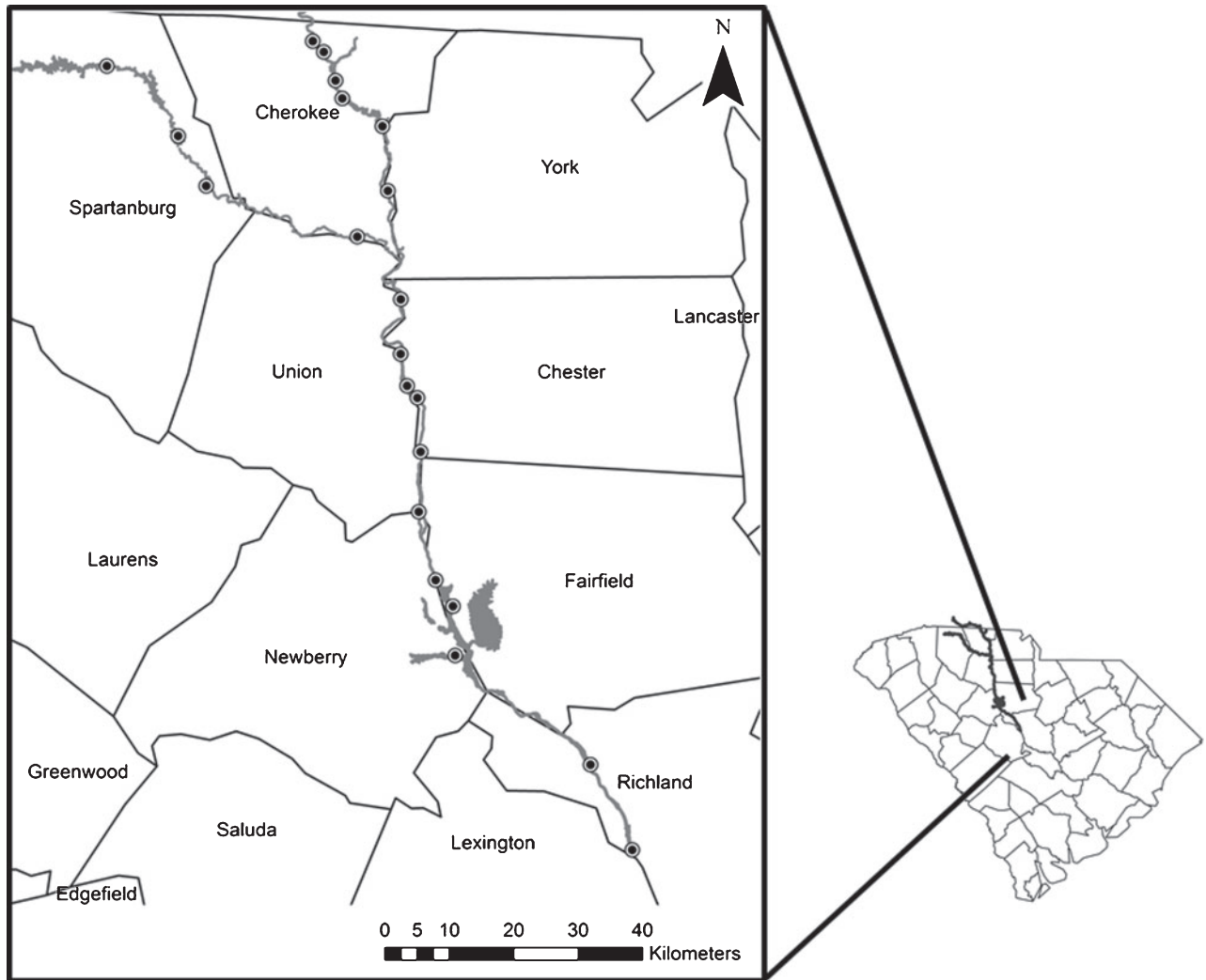


Fig. 1. Location map depicting South Carolina, USA. Inset shows locations of each anuran study site along both the Pacolet (upper left fork) and Broad River in South Carolina, USA; county boundaries are delineated on the South Carolina outline, and labelled on the study site inset.

Table 1. Proportion of sampling units where each species was observed (i.e. naïve estimate) and the number of times each species was detected, for each survey method (i.e. visual encounter surveys (VES) and manual calling surveys (MCS))
 In total, 12 repeat surveys were conducted for each survey method

Species	Common name	Naïve estimate (no. of detections)		Breeding window
		Active search	Call survey	
<i>A. americanus</i>	American toad	0.48 (16)	0.95 (40)	February to April
<i>A. fowleri</i>	Fowler's toad	0.90 (94)	1.00 (128)	April to July
<i>A. terrestris</i>	Southern toad	0.05 (1)	0.14 (4)	Late February to May
<i>A. crepitans</i>	Northern cricket frog	0.57 (86)	0.71 (66)	April to August
<i>H. cinerea</i>	Green treefrog	0.38 (20)	0.76 (65)	April to September
<i>H. chrysoscelis</i>	Cope's grey treefrog	0.90 (53)	0.95 (66)	April to August
<i>P. feriarum</i>	Upland chorus frog	0.43 (19)	0.90 (47)	November to early April
<i>P. crucifer</i>	Spring peeper	0.29 (11)	0.95 (102)	November to April
<i>G. carolinensis</i>	Eastern narrow-mouth toad	0.29 (18)	0.19 (4)	April to October
<i>L. catesbeianus</i>	Bullfrog	0.57 (33)	0.67 (52)	April to August
<i>L. clamitans</i>	Green frog	0.67 (39)	0.86 (45)	April to August
<i>L. palustris</i>	Pickerel frog	0.43 (13)	0.33 (12)	February to early April
<i>L. sphenoccephalus</i>	Southern leopard frog	0.81 (79)	0.62 (32)	December to early April
<i>S. holbrookii</i>	Eastern spadefoot	0.10 (3)	0.00 (0)	Year round

In addition, time-constrained VES were conducted at each site. During 2010, VES were conducted in summer ($n=3$) and fall ($n=2$) and, during 2011, VES were conducted in spring ($n=3$), summer ($n=3$) and fall ($n=2$) at each site; we assumed that we would detect focal species during these seasons, when activities such as breeding, ovipositing and foraging can be observed (Dorcas and Gibbons 2008). In total, 13 VES were conducted at each study site. Each survey consisted of two persons independently searching the site for 30 min to identify anuran species. A few searches were made by one person and these lasted 1 h. Each VES was conducted during daylight hours (i.e. 0900–1900 hours) and as much variation in microhabitat was sampled as possible, including surface cover objects (Vonesh *et al.* 2010). Search area was restricted to areas that we could hear calling amphibians from during MCS surveys. Anurans heard vocalising during VES were documented, along with any visual observations of species. All observed life-history stages were included during VES; however, the majority of observations encompassed adult and metamorphosing individuals (as compared with observations of tadpoles). For both survey methods, we recorded the number of days since rainfall and included this as a sampling covariate.

Data analyses

We used the model Nichols *et al.* (2008) developed for multiple detection methods that allows simultaneous use of data from all methods for inference about method-specific detection probabilities. This modelling approach applies to any situation in which multiple detection methods are used in the same locations and allows parameters to be modelled as functions of site or sample-specific covariates. The general model comprised one detection parameter, p^s_t , which is the probability of detection at occasion t by method s , given the sample unit is occupied and the species is present at the immediate sample station site, and two occupancy parameters, namely, ψ , which is the probability a unit is occupied, and θ_t , which is the probability a species is present at the immediate sample site at occasion t , given the sample unit is occupied. The two occupancy parameters, ψ and θ_t , permit the modelling of occupancy at two different spatial scales; however, for the present study, we focussed on the influence of survey method on detection probability and held the two occupancy parameters constant.

For each species, we used data from 12 VES conducted in summer, fall and spring (i.e. peak activity period) paired with data from 12 MCS conducted during summer, winter and spring (i.e. peak breeding period). Because we conducted more call surveys than active searches, we eliminated call survey dates that fell outside a particular species' window of peak calling activity (Table 1). Peak anuran activity varies from species to species and we were able to fit each species into a general category of spring–summer–fall or fall–winter–spring activity. For example, the northern cricket frog (*Acris crepitans*) was placed in the spring/summer/fall activity window because it breeds from April to August (Table 1) and is active into the fall months. This exercise identified which three MCS surveys could be eliminated before data analysis, for each species, such that each survey method would have the same amount of effort (i.e. 12 VES and 12 MCS).

To obtain estimates of the probability of detection for each species for each method, we used the Nichols *et al.* (2008) model within program PRESENCE 5.7 (Hines 2006), which estimates parameters using maximum likelihood estimation methods. We evaluated the following eight models examining different influences on detection probability of anurans: (1) constant (null model with no covariates on detection probability), (2) survey method, (3) day of year ('date'), (4) number of days since rain ('rain'), (5) date and rain, (6) survey method and date, (7) survey method and rain and (8) survey method plus date and rain.

To obtain the most accurate parameter estimation, all covariates were standardised by calculating z-scores (i.e. the mean was subtracted from each value and then divided by the s.d.) before analysis. Model selection was based on Akaike information criteria (AIC; Burnham and Anderson 2002). We used AIC values adjusted for small samples sizes (i.e. AICc), and assessed fit for each model set by using the MacKenzie–Bailey goodness-of-fit test (MacKenzie and Bailey 2004). We conducted the test for 1000 bootstrap iterations on the most parameterised models in each model set to generate estimates of the overdispersion factor, \hat{c} , and used the \hat{c} value to ensure a conservative estimation of goodness-of-fit (i.e. if $\hat{c} > 1$, we used QAICc values adjusted for overdispersion; Burnham and Anderson 2002). We examined Akaike weights to determine the strength of evidence for each model (Burnham and Anderson 2002). We assumed models with higher weights and lower AIC values were better able to explain variation in data and selected the models with substantial empirical support, which included models within $\Delta 2$ AICc (Burnham and Anderson 2002). In cases where there was no clear 'best' model, we computed model-averaged estimates (Buckland *et al.* 1997) for parameters of interest. We define 'best' to be a model within $\Delta 2$ AICc which has >50% of the weight and where the remaining 50% of the weight is spread relatively thinly among the remaining candidate models that are also within $\Delta 2$ AICc. Species-specific detection probabilities were derived using the inverse logit-transformation (i.e. $(\exp(\alpha))/(1 + \exp(\alpha))$) of parameter estimates. We estimated lower and upper 95% confidence intervals using the delta method (Ver Hoef 2012). Because it was impractical to summarise AIC results for eight candidate model sets for each species, we present the top models for each species.

Results

We detected the following 14 anuran species: American toad (*Anaxyrus americanus*), Fowler's toad (*Anaxyrus fowleri*), southern toad (*Anaxyrus terrestris*), northern cricket frog (*A. crepitans*), green treefrog (*Hyla cinerea*), Cope's grey treefrog (*Hyla chrysoscelis*), upland chorus frog (*Pseudacris feriarum*), spring peeper (*Pseudacris crucifer*), eastern narrow-mouthed toad (*Gastrophryne carolinensis*), American bullfrog (*Lithobates catesbeianus*), green frog (*Lithobates clamitans*), pickerel frog (*Lithobates palustris*), southern leopard frog (*Lithobates sphenoccephalus*) and eastern spadefoot (*Scaphiopus holbrookii*). The naïve occupancy and detection estimate varied among species for both MCS and VES (Table 1). Because *S. holbrookii* detections were so limited,

Table 2. Best-supported models for detection of anuran species, based on QAICc, selection criteria

The same eight candidate models were constructed for each species, from uncorrelated covariates. Best-supported models are in bold. AIC, Akaike information criteria; Δ QAICc, difference in QAICc relative to the top model; w, model weight; K, number of parameters in the model; Method, anuran survey method (VES or MCS); Day of year, day of year each survey was conducted; Days since rain, number of days since rain for a given survey

Species	Model	AICc	Δ QAICc	w	K	-2 log-likelihood	Parameter estimate (s.e.)				Day of year		Number of days since rain	
							Ψ -intercept	p-intercept	p-VES	p-MCS	p-VES	p-MCS	p-VES	p-MCS
<i>A. americanus</i>	$\Psi(\cdot)^\wedge, \theta(\cdot)^\wedge, p^B(\text{Date})$	323.64	0.00	0.57	4	313.14	4.94 (4.02)	-2.87 (0.23)	-	-	-0.13 (0.09)	-1.38 (0.22)	-	-
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	325.54	1.90	0.22	6	307.54	4.87 (4.00)	-2.97 (0.27)	-	-	-0.09 (0.09)	-1.47 (0.24)	-0.64 (0.31)	0.19 (0.17)
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	325.99	2.35	0.18	5	311.99	3.92 (2.54)	-	-2.70 (0.26)	-3.23 (0.42)	-0.07 (0.08)	-1.64 (0.34)	-	-
	Model averaged						4.59 (3.62)	-2.29 (0.19)	-0.49 (0.05)	-0.58 (0.08)	-0.11 (0.09)	-1.41 (0.24)	-0.14 (0.07)	0.04 (0.04)
<i>A. fowleri</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	648.63	0.00	0.73	6	630.63	2.12 (0.50)	-0.26 (0.15)	-	-	-0.51 (0.17)	1.24 (0.28)	0.06 (0.04)	0.84 (0.19)
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	650.58	1.95	0.27	7	627.96	2.06 (0.48)	-	-0.39 (0.17)	-0.02 (0.22)	-0.56 (0.17)	1.10 (0.30)	0.04 (0.15)	0.86 (0.20)
<i>A. terrestris</i>	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	57.47	0.00	0.44	2	52.80	-0.95 (0.73)	-1.87 (1.19)	-	-	-	-	-	-
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	57.98	0.51	0.34	3	50.57	-1.07 (0.72)	-	-2.71 (1.44)	-1.30 (1.28)	-	-	-	-
	Model averaged						-0.78 (0.57)	-0.82 (0.52)	-0.92 (0.49)	-0.44 (0.43)	-	-	-	-
<i>A. crepitans</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	530.38	0.00	0.55	5	516.38	1.21 (0.29)	-	0.39 (0.23)	-0.49 (0.24)	0.10 (0.08)	0.73 (0.27)	-	-
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	531.49	1.11	0.31	3	524.08	1.08 (0.28)	-	0.41 (0.24)	-0.15 (0.11)	-	-	-	-
	Model averaged						1.00 (0.25)	-	0.34 (0.20)	-0.32 (0.17)	0.06 (0.04)	0.40 (0.15)	-	-
<i>H. cinerea</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	354.84	0.00	0.54	5	340.84	0.70 (0.41)	-	-1.81 (0.33)	-0.98 (0.45)	-0.51 (0.32)	2.92 (1.13)	-	-
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	355.21	0.37	0.45	4	344.71	0.87 (0.39)	-1.57 (0.26)	-	-	-0.37 (0.27)	2.96 (0.70)	-	-
	Model averaged						0.77 (0.40)	-0.71 (0.12)	-0.98 (0.18)	-0.53 (0.24)	-0.44 (0.29)	2.90 (0.93)	-	-
<i>H. chrysoscelis</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	526.82	0.00	0.58	4	516.32	2.02 (1.06)	-1.25 (0.21)	-	-	-0.92 (0.27)	0.81 (0.25)	-	-
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	529.00	2.18	0.19	5	511.00	2.00 (1.08)	-	-1.41 (0.25)	-1.09 (0.25)	-1.04 (0.32)	0.69 (0.27)	-	-

(continued next page)

Table 2. (continued)

Species	Model	AICc	ΔQAICc	w	K	-2 log-likelihood	Ψ-intercept		p-intercept		Parameter estimate (s.e.)		Day of year		Number of days since rain	
							Ψ-intercept	p-intercept	p-VES	p-MCS	p-VES	p-MCS	p-VES	p-MCS		
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	529.02	2.20	0.19	6	515.02	2.05 (1.04)	-1.28 (0.20)	-	-0.93 (0.28)	0.82 (0.26)	-0.25 (0.17)	0.29 (0.16)			
	Model averaged						1.94 (1.02)	-0.97 (0.16)	-0.27 (0.05)	-0.21 (0.05)	0.76 (0.25)	-0.05 (0.04)	0.06 (0.03)			
<i>P. feriarum</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	306.14	0.00	0.97	5	292.14	1.02 (0.32)	-	-2.51 (0.24)	-2.01 (0.66)	0.35 (0.24)	-3.33 (0.50)	-			
<i>P. crucifer</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	412.65	0.00	0.85	5	398.65	0.87 (0.33)	-	-2.60 (0.34)	-1.20 (0.36)	0.46 (0.32)	-2.73 (1.00)	-			
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	416.41	3.76	0.13	4	405.91	0.71 (0.20)	-2.11 (0.24)	-	0.49 (0.28)	-4.95 (1.05)	-	-			
<i>G. carolinensis</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	151.68	0.00	0.93	3	137.68	-0.41 (0.30)	-	-0.56 (0.41)	-2.37 (0.61)	-	-	-			
<i>L. catesbeianus</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	439.26	0.00	0.44	4	428.76	1.53 (0.52)	-1.28 (0.19)	-	-0.19 (0.15)	0.74 (0.25)	-	-			
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	440.10	0.84	0.29	3	432.69	1.58 (0.52)	-	-1.43 (0.23)	-0.82 (0.21)	-	-	-			
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	441.18	1.92	0.17	5	427.18	1.53 (0.52)	-	-1.44 (0.23)	-1.07 (0.25)	-0.15 (0.21)	0.58 (0.27)	-			
	Model averaged						1.39 (0.47)	-0.56 (0.08)	-0.66 (0.11)	-0.42 (0.10)	-0.11 (0.10)	0.42 (0.16)	-			
<i>L. clamitans</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	441.53	0.00	0.58	4	431.03	1.78 (0.61)	-1.44 (0.19)	-	-0.29 (0.21)	0.72 (0.24)	-	-			
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	443.76	2.23	0.19	6	425.76	1.79 (0.60)	-1.47 (0.19)	-	-0.31 (0.21)	0.74 (0.24)	0.42 (0.18)	0.03 (0.18)			
<i>L. palustris</i>	$\Psi(\cdot), p(\cdot)$	200.71	0.00	0.65	2	196.04	1.01 (0.67)	-2.26 (0.41)	-	-	-	-	-			
	$\Psi(\cdot), p(\text{Method})$	203.41	2.70	0.17	3	196.00	1.01 (0.70)	-	-2.22 (0.46)	-2.31 (0.46)	-	-	-			
<i>L. sphenoccephalus</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	484.14	0.00	0.78	5	470.14	1.63 (0.56)	-	-0.25 (0.22)	-2.49 (0.41)	-0.08 (0.06)	-1.10 (0.36)	-			
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	488.04	3.90	0.11	3	480.63	1.66 (0.56)	-	-0.26 (0.22)	-1.54 (0.23)	-	-	-			

^AConstant probability of occupancy (i.e. $\Psi(\cdot), \theta(\cdot)$).
^BProbability of detection, which varies by model for each species, with or without inclusion of covariates that improve detection estimates.

method-specific detection probabilities for this species were not possible to estimate.

The best supported model for 10 anuran species indicated that detection varied by survey method (i.e. VES or MCS; Table 2, Appendix 1); for four of these species (*P. feriarum*, *P. crucifer*, *G. carolinensis* and *L. sphenoccephalus*), detection varied by survey method and, for six species, the best-supported model was determined from model averaging (*A. americanus*, *A. terrestris*, *A. crepitans*, *H. cinerea*, *H. chrysoscelis* and *L. catesbeianus*). For the remaining three species (*A. fowleri*, *L. palustris* and *L. clamitans*), survey method was unimportant and the best-supported model suggested either a constant probability of detection (*L. palustris*) or suggested that detection varied by date (*L. clamitans*) or date and days since rainfall (*A. fowleri*; Table 2).

For six species, MCS resulted in a higher mean (s.e.) probability of detection than did VES (*A. terrestris*: MCS 0.39 (0.38) vs VES 0.28 (0.15); *H. cinerea*: MCS 0.37 (0.17) vs VES 0.27 (0.05); *H. chrysoscelis*: MCS 0.45 (0.11) vs VES 0.43 (0.08); *P. feriarum*: MCS 0.12 (0.04) vs VES 0.08 (0.01); *P. crucifer*: MCS 0.23 (0.07) vs VES 0.07 (0.01); and *L. catesbeianus*: MCS 0.40 (0.09) vs VES 0.34 (0.06); Fig. 2). Conversely, for four species, VES resulted in a higher mean probability of detection than did MCS (*A. americanus*: VES 0.38 (0.04) vs MCS 0.36 (0.05); *A. crepitans*: VES 0.60 (0.36) vs MCS 0.38 (0.18); *G. carolinensis*: VES 0.36 (0.27) vs MCS 0.09 (0.02); and *L. sphenoccephalus*: VES 0.44 (0.39) vs MCS 0.08 (0.01); Fig. 2). For three species, however, both methods were equally effective and detection probabilities were identical (*A. fowleri*: 0.44 (0.25), *L. clamitans*: 0.46 (0.08) and *L. palustris*: 0.09 (0.02); Fig. 2).

In addition to survey method, date was an important factor influencing detection probability and was included in the best-supported model for 10 species (*A. americanus*, *A. fowleri*, *A. crepitans*, *H. cinerea*, *H. chrysoscelis*, *P. feriarum*, *P. crucifer*, *L. catesbeianus*, *L. clamitans* and *L. sphenoccephalus*; Table 2). For all summer-breeding frogs except *A. crepitans*, detection probability during the VES decreased with increasing day of year (i.e. decreased from spring to fall), which corresponded to between 12 April and 18 November each year (Figs 3, 4). Specifically, from mid-April to mid-November of each year, the estimated probability of detection during VES increased from 0.58 to 0.60 for *A. crepitans*, and decreased from 0.40 to 0.30 for *L. catesbeianus*, from 0.78 to 0.32 for *A. fowleri*, from 0.45 to 0.19 for *H. cinerea*, from 0.73 to 0.48 for *L. clamitans*, and from 0.80 to 0.17 for *H. chrysoscelis* (Figs 3, 4). For all summer-breeding frogs, detection probability during the MCS calling window increased with increasing day of year, which corresponds to between 9 April and 28 June each year (Figs 3, 4). Specifically, from early April to late June of each year, the estimated probability of detection during MCS increased from 0.25 to 0.60 for *A. crepitans*, from 0.22 to 0.60 for *L. catesbeianus*, from 0.21 to 0.95 for *A. fowleri*, from 0.002 to 0.99 for *H. cinerea*, from 0.22 to 0.80 for *L. clamitans*, and from 0.20 to 0.78 for *H. chrysoscelis* (Figs 3, 4).

For all winter-breeding frogs, detection probability during the active-search survey window varied slightly with increasing day of year (Fig. 5); the estimated probability of detection during VES decreased from 0.50 to 0.40 for *L. sphenoccephalus* and from 0.41 to 0.31 for *A. americanus*, and increased from 0.05 to 0.18 for *P. feriarum* and from 0.03 to

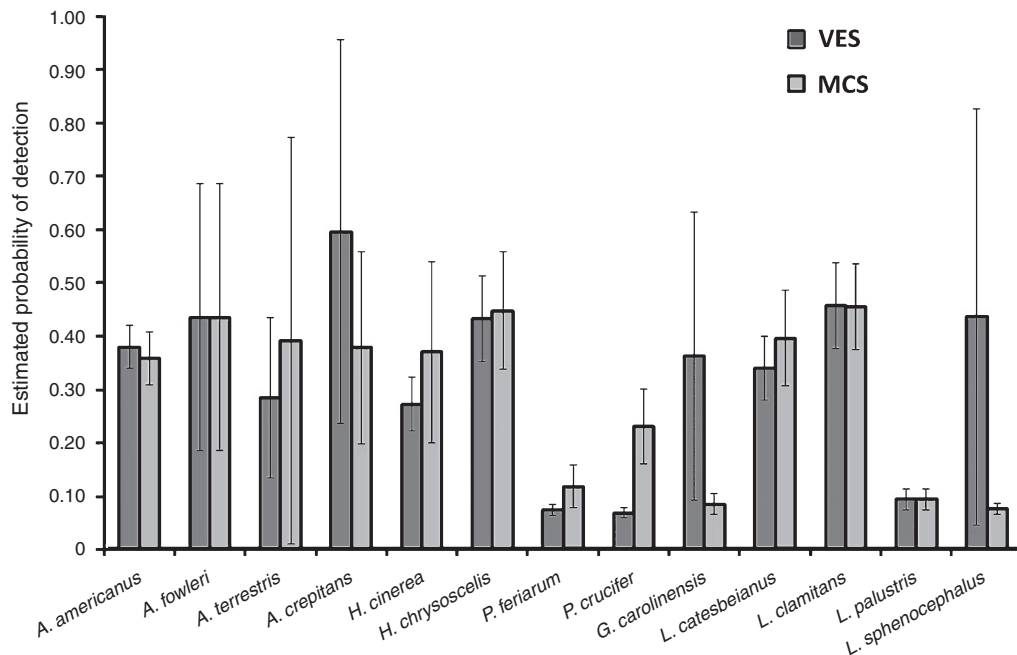


Fig. 2. Estimated conditional probability of detection (± 1 s.e.) for each anuran species along the Broad and Pacolet Rivers, South Carolina, USA. Estimates are based on repeat surveys using two different survey methods (MCS or VES).

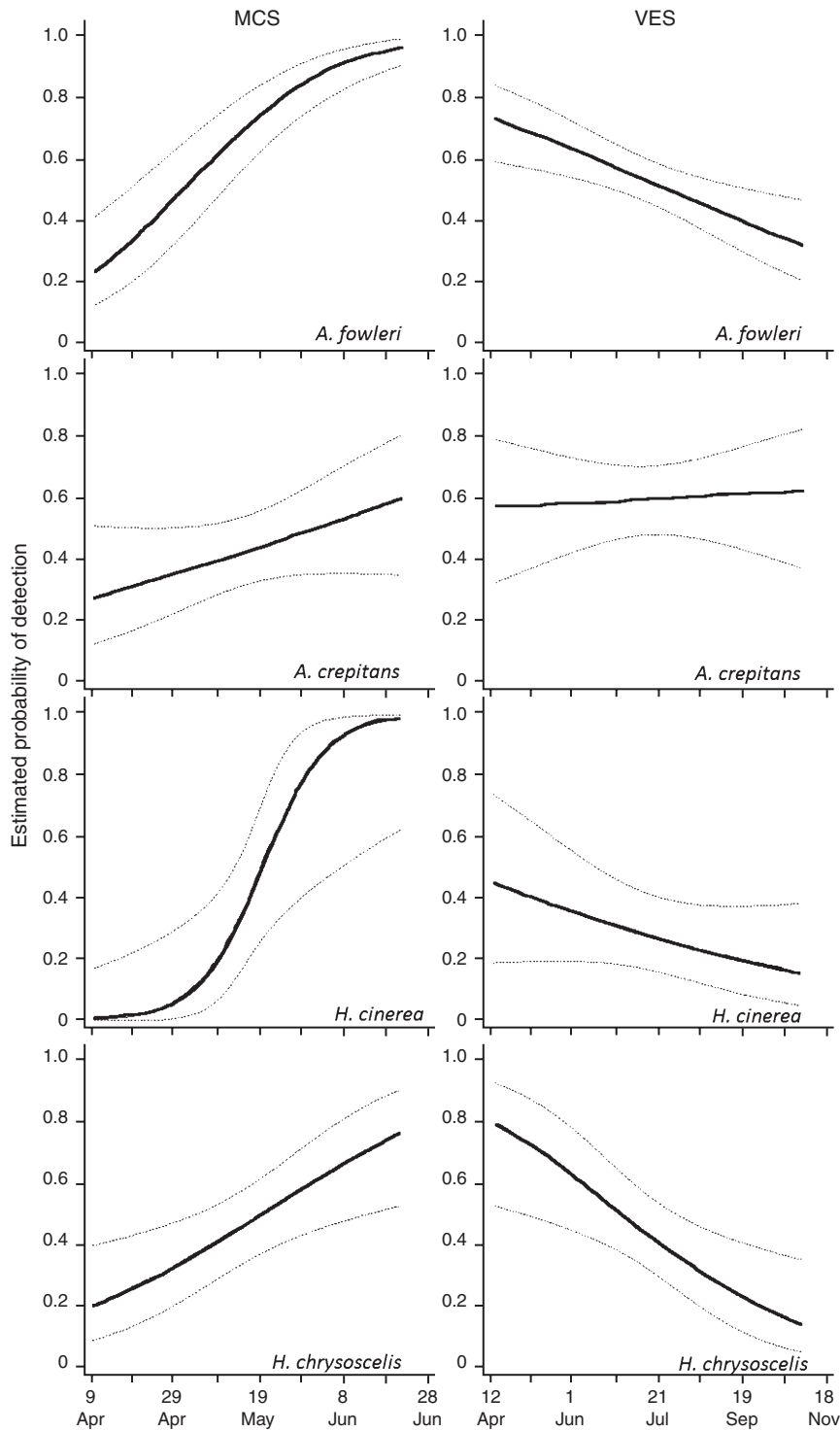


Fig. 3. Effect of date by survey method (MCS or VES) on conditional detection probability of summer-breeding anuran species along the Broad and Pacolet Rivers, South Carolina, USA. Solid lines represent the relationship between date and detection probability and dashed lines are the 95% CIs for estimates of the covariate effect.

0.18 for *P. crucifer* (Fig. 5). For all winter-breeding frogs, detection probability during the calling-survey time span decreased with increasing day of year (Fig. 5). Specifically,

from mid-February to mid-May of each year, the estimated probability of detection during MCS decreased from 0.38 to 0.02 for *L. sphenoccephalus*, from 0.98 to 0.01 for *P. feriarum*,

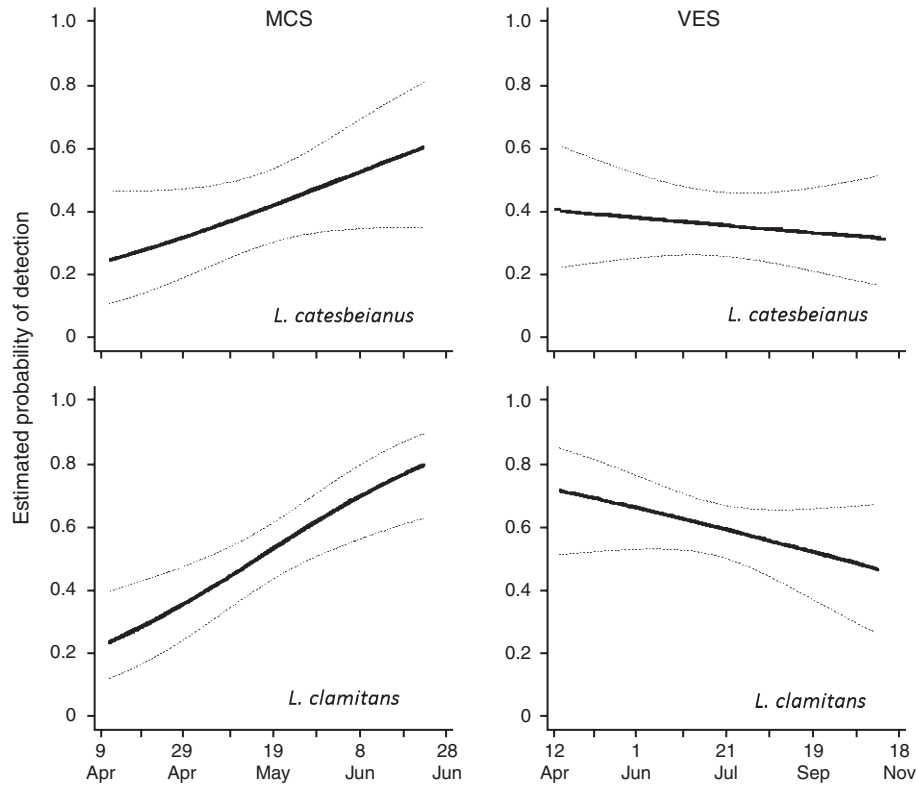


Fig. 4. Effect of date by survey method (MCS or VES) on conditional detection probability of summer-breeding anuran species along the Broad and Pacolet Rivers, South Carolina, USA. Solid lines represent the relationship between date and detection probability and dashed lines are the 95% CIs for estimates of the covariate effect.

from 0.89 to 0.05 for *A. americanus*, and from 0.98 to 0.01 for *P. crucifer* (Fig. 5).

Discussion

Our study has provided insight for monitoring anurans by implementing a modelling framework where data from both MCS and VES are evaluated simultaneously, resulting in method-specific detection probabilities. Our results provided strong evidence of variation in anuran detection probabilities among two different detection methods. Specifically, for 10 of 13 species, the best-supported model indicated that detection varied by survey method. Consistent with previous studies (e.g. Gooch *et al.* 2006; Steelman and Dorcas 2010), calling surveys were effective at detecting a wide range of anurans. Visual encounter surveys, however, were also effective at detecting a wide range of anuran species, and several species had a higher detection probability with VES than with MCS. Visual encounter surveys are likely to be under-used as a monitoring tool for anurans, perhaps because of a lack of information on their utility. Instead, VES are often used along with other methods in surveys for focal or rare species where the intent is geared toward complete coverage of all life stages to increase detection probability (e.g. Drost and Fellers 1996; Burbrink *et al.* 1998; Lips 1999; Lehtinen and Galatowitsch 2001).

Although both MCS and VES are effective methods, for certain species in our study, one method was most effective.

Specifically, VES represent a more effective method for detecting *A. crepitans*, *G. carolinensis* and *L. sphenoccephalus*, which is perhaps reflective of variation in species life history. For example, *G. carolinensis* and *L. sphenoccephalus*, like most anurans, can often be observed via vocalisations made during breeding; however, the breeding windows are wide (particularly for *L. sphenoccephalus*), calling by both species is sporadic, and for *G. carolinensis*, calling is usually initiated only by heavy rains (Brandt 1936; Dodd 2013). In addition, calls of both *G. carolinensis* and *L. sphenoccephalus* are easily masked by louder species (e.g. *H. cinerea* and *P. crucifer*; Conant and Collins 1998). Likely because both *G. carolinensis* and *L. sphenoccephalus* are active during the non-breeding period in a wide variety of aquatic and terrestrial habitats (Mitchell and Lannoo 2005; Dodd 2013), VES was a more reliable method of detection. *Acris crepitans*, another species with higher detection probabilities during VES, is active and conspicuous during the non-breeding season. Several other anuran species might also be more reliably detected using VES if their vocalisations are difficult to observe and their non-breeding habits permit detection (i.e. little grass frogs (*Pseudacris ocularis*) or species that exhibit explosive and/or short-lived breeding periods (e.g. *Scaphiopus* spp., *L. sylvaticus*, *L. capito*). In these cases, precisely timing MCS during this brief window is challenging (Dostine *et al.* 2013) and often not ideal because anuran call surveys are less effective during heavy rain (Weir *et al.* 2005).

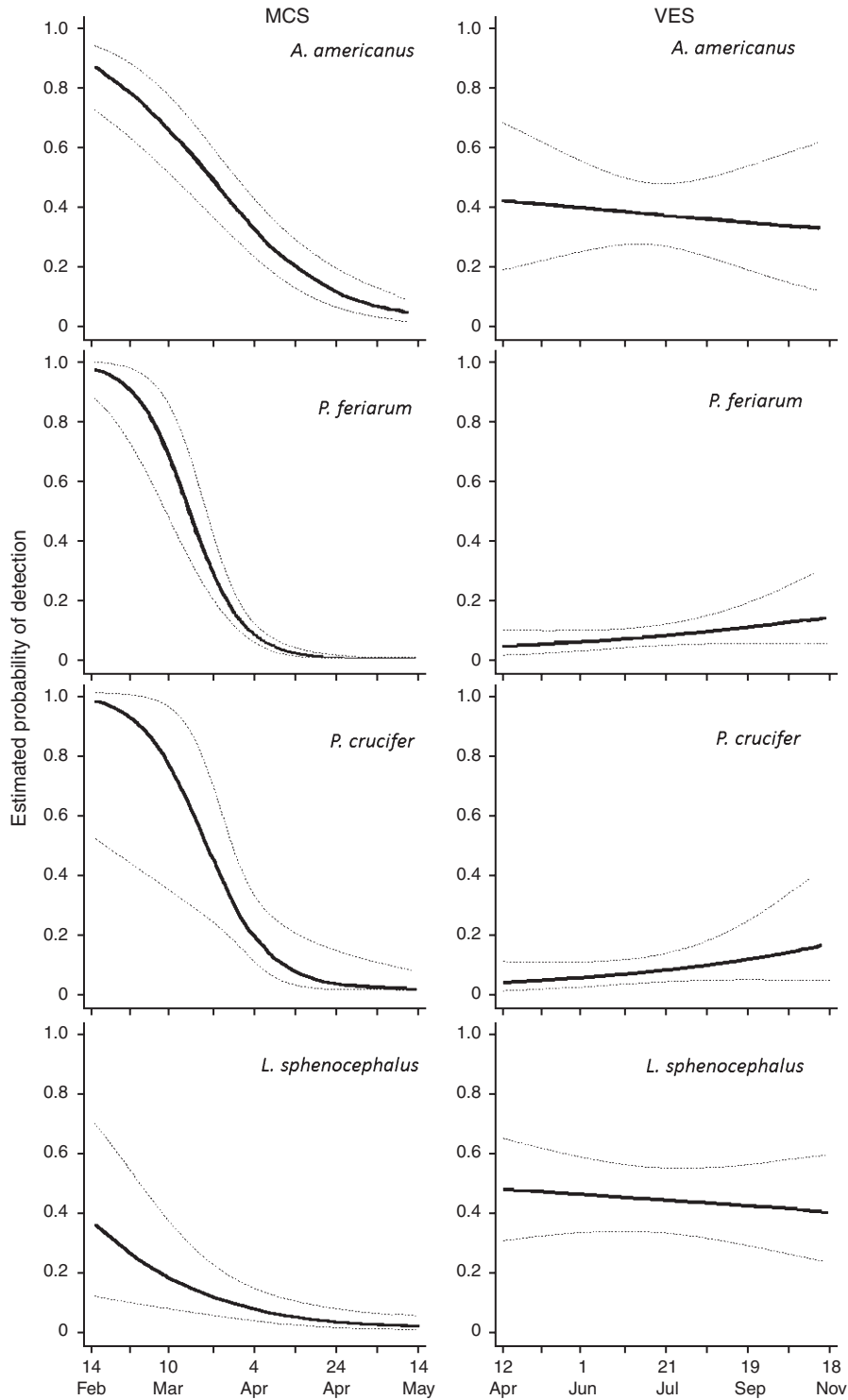


Fig. 5. Effect of date by survey method (MCS or VES) on conditional detection probability of winter-breeding anuran species along the Broad and Pacolet Rivers, South Carolina, USA. Solid lines represent the relationship between date and detection probability and dashed lines are the 95% CIs for estimates of the covariate effect.

We found that MCS represented a more effective detection method for *H. cinerea*, *P. feriarum*, *P. crucifer* and *L. catesbeianus*. These species are common, vocal, and calls can

be heard from a considerable distance (Dorcas et al. 2007). For a few species, however, both survey methods were equally effective (i.e. for *A. fowleri*, *L. clamitans* and *L. palustris*). In

addition, given the marginally larger detection probabilities of *A. americanus* using VES and of *H. chrysoscelis* using MCS, for these species, we also consider both survey methods to be similarly effective. For both *A. americanus* and *A. fowleri*, MCS and VES detection probabilities were very similar; MCS are effective because males of each species produce loud easily recognisable calls (Dorcas *et al.* 2007) but VES are also effective, perhaps because of their conspicuous tadpoles which school in large groups (Lefcort 1998) and the tendency for large numbers of metamorphs to forage for several weeks around the edge of the aquatic habitat from which they emerged (Beck and Congdon 1999; Dodd 2013). Likewise, VES had detection probabilities similar to those of MCS for *L. clamitans*, *L. palustris* and *H. chrysoscelis*; for *L. clamitans*, this may be because when startled, they emit conspicuous alarm calls as they leap into the water (Dorcas *et al.* 2007) and *L. palustris* may call in any month of the year in the southern United States (Conant and Collins 1998). Finally, for *H. chrysoscelis*, its tendency to call sporadically during the daytime likely accounts for the similarity in effectiveness of both survey methods.

Date was an important factor influencing detection probability of anurans, particularly regarding call surveys. For summer-breeding anurans, detection probability steadily increased toward the end of the summer survey windows, and likewise, for winter-breeding anurans, detection probability was highest toward the beginning of the winter survey windows. Previous studies have documented strong patterns in seasonal breeding activity and breeding windows are well established (Droege and Eagle 2005). However, for VES, the potential influence of date to increase or decrease the effectiveness of this survey method is not well known. Our results indicated that for VES, for most species, detection probability was relatively constant throughout the sampling window (i.e. April–November each year), although for a few species (*A. fowleri*, *H. chrysoscelis*, *H. cinerea* and *L. clamitans*), detection probability steadily decreased into the fall months. Furthermore, although we showed that VES are better for some species, we also highlighted that VES can provide adequate occupancy estimation, even when conducted outside the breeding window. For example, for *L. clamitans* and *A. fowleri*, VES conducted in early April resulted in a 60% probability of detection and, during MCS, it was not until late June, toward the end of the breeding season, that detection probabilities reached 60%. Similarly, for *H. chrysoscelis*, VES conducted in early April resulted in an 80% probability of detection and for *A. crepitans*, detection probabilities remained ~60% during the VES survey window; for both of these species, detection probabilities comparable to 80% and 60%, respectively, did not occur until late June. Therefore, we suggest that spring and fall VES can detect species that vocalise mostly during the summer months.

Management implications

The goals of a particular study should dictate the appropriate survey method; however, results of the present study highlighted the importance of estimating method-specific detection probabilities, which should prove especially useful in the design of multispecies surveys. We recommend the use MCS for anurans with broad calling windows and conspicuous

vocalisations, and VES for anurans that either vocalise sporadically or discreetly. Furthermore, we recommend the use of VES throughout the activity season, not just the breeding season, because we found that survey date was a largely unimportant predictor of detection using VES. Our results also suggested that VES can provide more flexibility for anuran researchers, because robust estimates of detection and occupancy can be obtained outside a narrow breeding window.

Acknowledgements

This research was supported with funding provided by the Broad River Mitigation Trust Fund administered through the South Carolina Department of Natural Resources. Additional funding was provided by the Duke Endowment through the Davidson Research Initiative and the Davidson College Department of Biology. We thank E. Eskew, S. Hunt, L. Witzzak, C. Williams, A. Domske, D. Millican, C. Oldham, R. Bauer, B. Abbuhl, and C. Ruder for assistance in the field and J. Micancin for his help in identifying cricket frog vocal recordings. For assistance with logistics related to the project we thank G. Vaughan, S. Bennett, B. Perry, and V. Vejđani. Finally, we thank D. Ramsey and two anonymous reviewers for statistical assistance and comments which greatly improved this manuscript.

References

- Adams, M. J., Pearl, C. A., Galvan, S., and McCreary, B. (2011). Non-native species impacts on pond occupancy by an anuran. *The Journal of Wildlife Management* **75**, 30–35. doi:10.1002/jwmg.29
- Bailey, L. L., Simons, T. R., and Pollock, K. H. (2004). Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications* **14**, 692–702. doi:10.1890/03-5012
- Balas, C. J., Euliss, N. H., and Mushet, D. M. (2012). Influence of conservation programs on amphibians using seasonal wetlands in the prairie pothole region. *Wetlands* **32**, 333–345. doi:10.1007/s13157-012-0269-9
- Beck, C. W., and Congdon, J. D. (1999). Effects of individual variation in age and size at metamorphosis on growth and survivorship of southern toad (*Bufo terrestris*) metamorphs. *Canadian Journal of Zoology* **77**, 944–951. doi:10.1139/cjz-77-6-944
- Blair, W. F. (1961). Calling and spawning seasons in a mixed population of anurans. *Ecology* **42**, 99–110. doi:10.2307/1933272
- Brander, S. M., Royle, J. A., and Eames, M. (2007). Evaluation of the status of anurans on a refuge in suburban Maryland. *Journal of Herpetology* **41**, 52–60. doi:10.1670/0022-1511(2007)41[52:EOTSOA]2.0.CO;2
- Brandt, B. B. (1936). The frogs and toads of eastern North Carolina. *Copeia* **1936**, 215–223. doi:10.2307/1436326
- Brown, G. W., Scroggie, M. P., Smith, M. J., and Steane, D. (2007). An evaluation of methods for assessing the population status of the threatened Alpine tree frog *Litoria verreauxii alpina* in southeastern Australia. *Copeia* **3**, 765–770. doi:10.1643/0045-8511(2007)2007[765:AEOMFA]2.0.CO;2
- Buckland, S. T., Burnham, K. P., and Augustin, N. H. (1997). Model selection: an integral part of inference. *Biometrics* **53**, 603–618. doi:10.2307/2533961
- Burbrink, F. T., Phillips, C. A., and Heske, E. J. (1998). A riparian zone in southern Illinois as a potential dispersal corridor for reptiles and amphibians. *Biological Conservation* **86**, 107–115. doi:10.1016/S0006-3207(98)00054-8
- Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: a Practical Information-theoretic Approach.' 2nd edn. (Springer-Verlag: New York.)
- Conant, R., and Collins, J. T. (1998). 'A Field Guide to Amphibians and Reptiles: Eastern and Central North America.' 3rd edn. (Houghton Mifflin Company: Boston, MA.)
- Cook, R. P., Tupper, T. A., Paton, P. W. C., and Timm, B. C. (2011). Effects of temperature and temporal factors on anuran detection probabilities at

- Cape Cod National Seashore, Massachusetts, USA: implications for long-term monitoring. *Herpetological Conservation and Biology* **6**, 25–39.
- Crump, M. L., and Scott, N. J., Jr (1994). Visual encounter surveys. In 'Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians'. (Eds W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster.) pp. 84–92. (Smithsonian Institution: Washington, DC.)
- Dahl, C., Novotny, V., Moravec, J., and Richards, S. J. (2009). Beta diversity of frogs in the forests of New Guinea, Amazonia and Europe: contrasting tropical and temperate communities. *Journal of Biogeography* **36**, 896–904. doi:10.1111/j.1365-2699.2008.02042.x
- Doan, T. M. (2003). Which methods are most effective for surveying rain forest herpetofauna? *Journal of Herpetology* **37**, 72–81. doi:10.1670/0022-1511(2003)037[0072:WMAMEF]2.0.CO;2
- Dodd, C. K. (2013). 'Frogs of the United States and Canada.' (Johns Hopkins University Press: Baltimore, MD.)
- Dorcas, M. E., and Gibbons, J. W. (2008). 'Frogs and Toads of the Southeast.' (The University of Georgia Press: Athens, GA.)
- Dorcas, M. E., Price, S. J., Beane, J. C., and Cross, S. S. (2007). 'The Frogs and Toads of North Carolina.' (North Carolina Wildlife Resources Commission: Raleigh, NC.)
- Dorcas, M. E., Price, S. J., Walls, S. C., and Barichivich, W. J. (2010). Auditory monitoring of anuran populations. In 'Conservation and Ecology of Amphibians'. (Ed. C. K. Dodd.) pp. 281–298. (Oxford University Press: Oxford, UK.)
- Dostine, P. L., Reynolds, S. J., Griffiths, A. D., and Gillespie, G. R. (2013). Factors influencing detection probabilities of frogs in the monsoonal tropics of northern Australia: implications for the design of monitoring studies. *Wildlife Research* **40**, 393–402.
- Droege, S., and Eagle, P. (2005). Evaluating calling surveys. In 'Amphibian Declines: the Conservation Status of United States Species'. (Ed. M. J. Lannoo.) pp. 314–319. (University of California Press: Berkeley, CA.)
- Drost, C. A., and Fellers, G. M. (1996). Collapse of regional frog fauna in the Yosemite area of the California Sierra Nevada. *Conservation Biology* **10**, 414–425. doi:10.1046/j.1523-1739.1996.10020414.x
- Eskew, E. A., Price, S. J., and Dorcas, M. E. (2012). Effects of river-flow regulation on anuran occupancy and abundance in riparian zones. *Conservation Biology* **26**, 504–512. doi:10.1111/j.1523-1739.2012.01842.x
- Farmer, A. L., Smith, L. L., Castleberry, S. B., and Gibbons, J. W. (2009). A comparison of techniques for sampling amphibians in isolated wetlands in Georgia, USA. *Applied Herpetology* **6**, 327–341. doi:10.1163/157075309X12470350858433
- Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., and Wickham, J. (2011). Completion of the 2006 National Land Cover Database for the Conterminous United States. *PE&RS* **77**, 858–864.
- Gooch, M. M., Heupel, A. M., Price, S. J., and Dorcas, M. E. (2006). The effects of survey protocol on detection probabilities and site occupancy estimates of summer breeding anurans. *Applied Herpetology* **3**, 129–142. doi:10.1163/157075406776984211
- Grover, M. C. (2006). Comparative effectiveness of nighttime visual encounter surveys and cover object searches in detecting salamanders. *Herpetological Conservation and Biology* **1**, 93–99.
- Heard, G. W., Robertson, P., and Scroggie, M. P. (2006). Assessing detection probabilities for the endangered growling grass frog (*Litoria raniformis*) in southern Victoria. *Wildlife Research* **33**, 557–564. doi:10.1071/WR04080
- Hines, J. E. (2006). 'PRESENCE (Version 5.7): Software to Estimate Patch Occupancy and Related Parameters. USGS-PWRC.' Available at <http://www.mbr-pwrc.usgs.gov/software/presence.html> [verified 1 August 2014].
- Hunt, S. D., Guzy, J. C., Price, S. J., Halstead, B. J., Eskew, E. A., and Dorcas, M. E. (2013). Responses of riparian reptile communities to damming and urbanization. *Biological Conservation* **157**, 277–284. doi:10.1016/j.biocon.2012.08.035
- Knutson, M. G., Richardson, W. B., Reineke, D. M., Gray, B. R., Parmelee, J. R., and Weick, S. E. (2004). Agricultural ponds support amphibian populations. *Ecological Applications* **14**, 669–684. doi:10.1890/02-5305
- Lefcort, H. (1998). Chemically mediated fright response in southern toad (*Bufo terrestris*) tadpoles. *Copeia* **1998**, 445–450. doi:10.2307/1447439
- Lehtinen, R. M., and Galatowitsch, S. M. (2001). Colonization of restored wetlands by amphibians in Minnesota. *American Midland Naturalist* **145**, 388–396. doi:10.1674/0003-0031(2001)145[0388:CORWBA]2.0.CO;2
- Lips, K. R. (1999). Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology* **13**, 117–125. doi:10.1046/j.1523-1739.1999.97185.x
- MacKenzie, D. I., and Bailey, L. L. (2004). Assessing fit of site occupancy models. *Journal of Agricultural, Biological and Ecological Statistics* **9**, 300–318.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2006). 'Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence.' (Academic Press: San Diego, CA.)
- MacKenzie, D. I., Nichols, J. D., Seamans, M. E., and Gutiérrez, R. J. (2009). Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* **90**, 823–835. doi:10.1890/08-0141.1
- Mattfeldt, S. D., and Grant, E. H. C. (2007). Are two methods better than one? Area constrained transects and leaf litterbags for sampling stream salamanders. *Herpetological Review* **38**, 43–45.
- Miller, D. A., Nichols, J. D., McClintock, B. T., Grant, E. H. C., Bailey, L. L., and Weir, L. A. (2011). Improving occupancy estimation when two types of observational errors occur: non-detection and species misidentification. *Ecology* **92**, 1422–1428. doi:10.1890/10-1396.1
- Miller, D. A., Weir, L. A., McClintock, B. T., Grant, E. H. C., Bailey, L. L., and Simons, T. R. (2012). Experimental investigation of false positive errors in auditory species occurrence surveys. *Ecological Applications* **22**, 1665–1674. doi:10.1890/11-2129.1
- Mitchell, J. C., and Lannoo, M. J. (2005). *Gastrophryne carolinensis* (Holbrook, 1836). Eastern narrow-mouthed toad. In 'Amphibian declines: conservation status of United States species'. (Ed. M. J. Lannoo.) pp. 501–503. (University of California Press: Berkeley, CA.)
- Nichols, J. D., Bailey, L. L., O'Connell, A. F. Jr, Talancy, N. W., Campbell, E. H., Grant, E. H. C., Gilbert, A. T., Annand, E. M., Husband, T. P., and Hines, J. E. (2008). Multiscale occupancy estimation and modeling using multiple detection methods. *Journal of Applied Ecology* **45**, 1321–1329. doi:10.1111/j.1365-2664.2008.01509.x
- Parris, K. M., Norton, T. W., and Cunningham, R. B. (1999). A comparison of techniques for sampling amphibians in the forests of south-east Queensland, Australia. *Herpetologica* **55**, 271–283.
- Pellet, J., and Schmidt, B. R. (2005). Monitoring distributions using call surveys: estimating site occupancy, detection probabilities, and inferring absence. *Biological Conservation* **123**, 27–35. doi:10.1016/j.biocon.2004.10.005
- Price, S. J., Marks, D. R., Howe, R. W., Hanowski, J., and Niemi, G. J. (2005). The importance of spatial scale for conservation and assessment of anuran populations in coastal wetlands of the western Great Lakes. *Landscape Ecology* **20**, 441–454. doi:10.1007/s10980-004-3167-6

- Price, S. J., Cecala, K. K., Browne, R. A., and Dorcas, M. E. (2011). Effects of urbanization on occupancy of stream salamanders. *Conservation Biology* **25**, 547–555. doi:[10.1111/j.1523-1739.2010.01627.x](https://doi.org/10.1111/j.1523-1739.2010.01627.x)
- Rödel, M. O., and Ernst, R. (2004). Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. *Ecotropica* **10**, 1–14.
- Semlitsch, R. D., and Bodie, J. R. (2003). Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* **17**, 1219–1228. doi:[10.1046/j.1523-1739.2003.02177.x](https://doi.org/10.1046/j.1523-1739.2003.02177.x)
- Steelman, C. K., and Dorcas, M. E. (2010). Anuran calling survey optimization: developing and testing predictive models of anuran calling activity. *Journal of Herpetology* **44**, 61–68. doi:[10.1670/08-329.1](https://doi.org/10.1670/08-329.1)
- Ver Hoef, J. M. (2012). Who invented the delta method? *The American Statistician* **66**, 124–127. doi:[10.1080/00031305.2012.687494](https://doi.org/10.1080/00031305.2012.687494)
- Vonesh, J. R., Mitchell, J. C., Howell, K., and Crawford, A. J. (2010). Rapid assessments of amphibian diversity. In 'Amphibian Ecology and Conservation: a Handbook of Techniques'. (Ed. C. K. Dodd Jr.). pp. 263–280. (Oxford University Press: Oxford, UK.)
- Weir, L. A., Royle, J. A., Nanjappa, P., and Jung, R. E. (2005). Modeling anuran detection and site occupancy on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. *Journal of Herpetology* **39**, 627–639.
- Woolbright, L. L. (1985). Patterns of nocturnal movement and calling by the tropical frog, *Eleutherodactylus coqui*. *Herpetologica* **41**, 1–9.

Appendix 1. Complete candidate model results for detection of anuran species along the Broad and Pacolet Rivers, South Carolina, USA

The same eight candidate models were constructed for each species, from uncorrelated covariates. Best supported models are in bold. AIC, Akaike information criteria; ΔQAICc, difference in QAICc relative to the top model; w, model weight; \hat{c} , overdispersion parameter estimated by dividing model deviance of the observed model by mean bootstrap model deviance; K, number of parameters in the model. Day of year, day of year each survey was conducted; Days since rain, number of days since rain for a given survey; Method, anuran survey method (VES or MCS)

Species	Model	AICc	ΔQAICc	w	K	-2 log-likelihood	\hat{c}
<i>A. americanus</i>	$\Psi(\cdot)^A, \theta(\cdot)^A, p(\text{Date})^B$	323.64	0.00	0.57	4	313.14	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	325.54	1.90	0.22	6	307.54	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	325.99	2.35	0.18	5	311.99	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	329.43	5.79	0.03	7	306.81	1.39
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	347.12	23.48	0.00	3	339.71	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain})$	349.05	25.41	0.00	5	335.05	
	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	356.29	32.65	0.00	2	351.62	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain})$	358.85	35.21	0.00	4	348.35	
<i>A. fowleri</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	648.63	0.00	0.73	6	630.63	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	650.58	1.95	0.27	7	627.96	0.63
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	667.23	18.60	0.00	4	656.73	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	667.80	19.17	0.00	5	653.80	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain})$	671.85	23.22	0.00	5	657.85	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain})$	677.55	28.92	0.00	4	667.05	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	689.56	40.93	0.00	3	682.15	
	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	696.20	47.57	0.00	2	691.53	
<i>A. terrestris</i>	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	57.47	0.00	0.44	2	52.80	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	57.98	0.51	0.34	3	50.57	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain})$	61.25	3.78	0.07	5	47.25	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	61.49	4.02	0.06	6	43.49	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain})$	62.50	5.03	0.04	4	52.00	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	62.93	5.46	0.03	4	52.43	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	64.13	6.66	0.02	5	50.13	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	65.60	8.13	0.01	7	42.98	1.10
<i>A. crepitans</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	530.38	0.00	0.55	5	516.38	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	531.49	1.11	0.31	3	524.08	
	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	534.35	3.97	0.08	2	529.68	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain})$	536.55	6.17	0.03	5	522.55	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	537.34	6.96	0.02	7	514.72	2.78
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	537.95	7.57	0.01	4	527.45	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain})$	538.50	8.12	0.01	4	528.00	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	543.65	13.27	0.00	6	525.65	
<i>H. cinerea</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	354.84	0.00	0.54	5	340.84	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	355.21	0.37	0.45	4	344.71	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	362.64	7.80	0.01	6	344.64	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	363.34	8.50	0.01	7	340.72	4.61
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	404.25	49.41	0.00	3	396.84	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain})$	410.30	55.46	0.00	5	396.30	
	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	435.67	80.83	0.00	2	431.00	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain})$	441.22	86.38	0.00	4	430.72	
<i>H. chrysoscelis</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	526.82	0.00	0.58	4	516.32	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	529.00	2.18	0.19	5	511.00	
	$\Psi(\cdot), \theta(\cdot), p(\text{Date}, \text{Rain})$	529.02	2.20	0.19	6	515.02	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date}, \text{Rain})$	532.27	5.45	0.04	7	509.65	6.30
	$\Psi(\cdot), \theta(\cdot), p(\cdot)$	550.47	23.65	0.00	2	545.80	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain})$	551.20	24.38	0.00	4	540.70	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	551.30	24.48	0.00	3	543.89	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain})$	552.77	25.95	0.00	5	538.77	
<i>P. feriarum</i>	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Date})$	306.14	0.00	0.97	5	292.14	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method}, \text{Rain}, \text{Date})$	313.07	6.93	0.03	7	290.45	6.21
	$\Psi(\cdot), \theta(\cdot), p(\text{Date})$	319.39	13.25	0.00	4	308.89	
	$\Psi(\cdot), \theta(\cdot), p(\text{Rain}, \text{Date})$	325.75	19.61	0.00	6	307.75	
	$\Psi(\cdot), \theta(\cdot), p(\text{Method})$	384.65	78.51	0.00	3	377.24	

(continued next page)

Appendix 1. (continued)

Species	Model	AICc	Δ QAICc	w	K	-2 log-likelihood	\hat{c}
<i>P. crucifer</i>	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	390.63	84.49	0.00	5	376.63	
	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	395.97	89.83	0.00	2	391.30	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	401.13	94.99	0.00	4	390.63	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date})$	412.65	0.00	0.85	5	398.65	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date})$	416.41	3.76	0.13	4	405.91	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date, Rain})$	420.88	8.23	0.01	7	398.26	4.46
	$\Psi(\cdot),\theta(\cdot),p(\text{Date, Rain})$	423.32	10.67	0.00	6	405.32	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method})$	431.35	18.70	0.00	3	423.94	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	437.70	25.05	0.00	5	423.70	
<i>G. carolinensis</i>	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	537.28	124.63	0.00	2	532.61	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	542.89	130.24	0.00	4	532.39	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method})$	151.68	0.00	0.93	5	137.68	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	158.10	6.42	0.06	7	135.48	
	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	160.65	8.97	0.01	3	153.24	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	166.02	14.34	0.00	5	152.02	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date})$	170.07	18.39	0.00	2	165.40	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain, Date})$	175.78	24.10	0.00	4	165.28	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date})$	175.80	24.12	0.00	4	165.30	
<i>I. catesbeianus</i>	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain, Date})$	183.19	31.51	0.00	6	165.19	2.06
	$\Psi(\cdot),\theta(\cdot),p(\text{Date})$	439.26	0.00	0.44	4	428.76	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method})$	440.10	0.84	0.29	3	432.69	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date})$	441.18	1.92	0.17	5	427.18	
	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	443.05	3.79	0.07	2	438.38	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	445.78	6.52	0.02	5	431.78	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date, Rain})$	445.80	6.54	0.02	6	427.80	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	448.07	8.81	0.01	4	437.57	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date, Rain})$	448.77	9.51	0.00	7	426.15	5.34
<i>L. clamitans</i>	$\Psi(\cdot),\theta(\cdot),p(\text{Date})$	441.53	0.00	0.58	4	431.03	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date, Rain})$	443.76	2.23	0.19	6	425.76	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date})$	444.74	3.21	0.12	5	430.74	
	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	446.71	5.18	0.04	2	442.04	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	447.78	6.25	0.03	4	437.28	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date, Rain})$	448.21	6.68	0.02	7	425.59	4.98
	$\Psi(\cdot),\theta(\cdot),p(\text{Method})$	448.89	7.36	0.01	3	441.48	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	450.54	9.01	0.01	5	436.54	
<i>L. palustris</i>	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	200.71	0.00	0.65	2	196.04	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method})$	203.41	2.70	0.17	3	196.00	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date})$	205.15	4.44	0.07	4	194.65	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	205.32	4.61	0.06	4	194.82	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date})$	206.76	6.05	0.03	5	192.76	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	208.80	8.09	0.01	5	194.80	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date, Rain})$	211.37	10.66	0.00	6	193.37	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date, Rain})$	214.34	13.63	0.00	7	191.72	3.22
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Date})$	484.14	0.00	0.78	5	470.14	
<i>L. sphenocephalus</i>	$\Psi(\cdot),\theta(\cdot),p(\text{Method})$	488.04	3.90	0.11	3	480.63	
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain, Date})$	488.62	4.48	0.08	7	466.00	6.61
	$\Psi(\cdot),\theta(\cdot),p(\text{Method, Rain})$	491.11	6.97	0.02	5	477.11	
	$\Psi(\cdot),\theta(\cdot),p(\cdot)$	514.39	30.25	0.00	2	509.72	
	$\Psi(\cdot),\theta(\cdot),p(\text{Date})$	516.53	32.39	0.00	4	506.03	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain})$	517.56	33.42	0.00	4	507.06	
	$\Psi(\cdot),\theta(\cdot),p(\text{Rain, Date})$	521.38	37.24	0.00	6	503.38	

^AConstant probability of occupancy (i.e. $\Psi(\cdot), \theta(\cdot)$).

^BProbability of detection, which varies by model for each species, with or without inclusion of covariates that improve detection estimates.