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## Modeling Anuran Detection and Site Occupancy on North American Amphibian Monitoring Program (NAAMP) Routes in Maryland

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**ABSTRACT.**—One of the most fundamental problems in monitoring animal populations is that of imperfect detection. Although imperfect detection can be modeled, studies examining patterns in occurrence often ignore detection and thus fail to properly partition variation in detection from that of occurrence. In this study, we used anuran calling survey data collected on North American Amphibian Monitoring Program routes in eastern Maryland to investigate factors that influence detection probability and site occupancy for 10 anuran species. In 2002, 17 calling survey routes in eastern Maryland were surveyed to collect environmental and species data nine or more times. To analyze these data, we developed models incorporating detection probability and site occupancy. The results suggest that, for more than half of the 10 species, detection probabilities vary most with season (i.e., day-of-year), air temperature, time, and moon illumination, whereas site occupancy may vary by the amount of palustrine forested wetland habitat. Our results suggest anuran calling surveys should document air temperature, time of night, moon illumination, observer skill, and habitat change over time, as these factors can be important to model-adjusted estimates of site occupancy. Our study represents the first formal modeling effort aimed at developing an analytic assessment framework for NAAMP calling survey data.

Most male anuran species in North America vocalize to attract females for breeding. The North American Amphibian Monitoring Program (NAAMP), initiated in 1997 and patterned after the North American Breeding Bird Survey (Robbins et al., 1986; Peterjohn, 1994), is a roadside calling survey designed to monitor anuran populations by their vocalizations (Weir and Mossman, 2005). NAAMP is a collaborative effort among state natural resource agencies, non-profit organizations, and the U.S. Geological Survey (USGS). While USGS provides central coordination and database management, state partners recruit and train volunteers to identify local anurans by their unique vocalizations and to conduct the calling surveys following the NAAMP protocol. Since 2001, a unified protocol has been adopted by 17 states, primarily in the eastern United States (Weir and Mossman, 2005). One of the primary objectives of NAAMP is to determine whether anuran populations are changing over time at state, regional, and larger geographic scales.

Following the unified protocol, at each survey site observers record species presence based on vocalizations detected and assign a calling index value from 1, indicating individuals calling without overlap, to 3, a full chorus (for further discussion, see Mossman et al., 1998; Weir and Mossman, 2005). One important difficulty with this method is the lack of a precise and well-

defined relationship between the calling index and the abundance of anurans at a sample site (but see Nelson and Graves, 2004; Stevens and Paszkowski, 2004). Consequently, no explicit linkage exists with between-year variation in calling index data and population change.

To address this dilemma, it is possible to employ alternative population metrics that can be estimated from calling survey data and, therefore, are more appealing for use in a monitoring context. One possibility is to shift focus from calling index data or numbers of individuals in a population to numbers of sample units occupied by anuran species. Indeed, site occupancy has been identified by the USGS Amphibian Research and Monitoring Initiative (ARMI; Hall and Langtimm, 2001) as the primary focus of current monitoring efforts as indicated by the following statement from the ARMI webpage (<http://armi.usgs.gov/monitoring.asp>): "The most promising national variable to date is one based on species presence. Documenting shifts in species presence through time will provide important data for assessing changes in amphibian status. The 'proportion of area occupied' (PAO) by an amphibian species has been identified by ARMI as the only metric which so far meets the Program criteria for being nationally interpretable and regionally adaptable." Anuran occupancy can be estimated based on detection/nondetection data obtained from replicated visits to multiple sample sites (Geissler and Fuller, 1986; Bayley and Peterson, 2001; MacKenzie et al., 2002; Tyre et al., 2003). In

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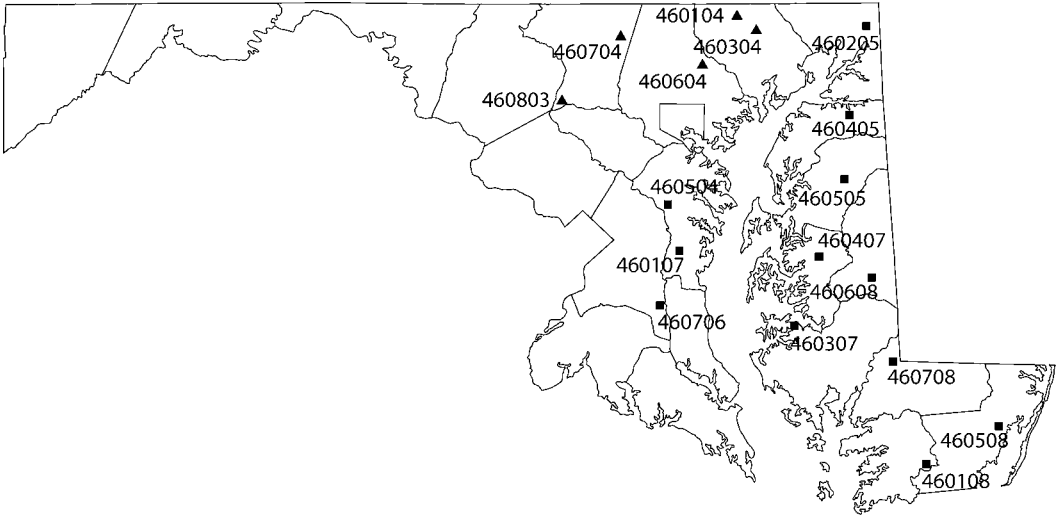


FIG. 1. North American Amphibian Monitoring Program (NAAMP) routes in the (■) Upper Coastal Plain and (▲) Northern Piedmont physiographic regions of Maryland.

addition to being efficient for large-scale monitoring efforts, site (or "patch"), occupancy is often viewed as a state variable in metapopulation studies (Hanski, 1992, 1994; Hanski and Gilpin, 1997). Its utility in a monitoring context is based on the heuristic notion that site occupancy is related to population size, which can be established in certain situations (Royle and Nichols, 2003).

One important benefit of using site occupancy as a measure of population state is that, under common sampling designs, these models enable a formal treatment of detectability. This is important because a species might not always be detected where it is present, yielding a null or false zero (see Moilanen, 2002), which can be the result of environmental conditions or other extraneous influences. Many studies that seek to explain patterns in population change ignore variation in detection altogether, instead focusing on modeling detection/nondetection data using various procedures (e.g., logistic regression; Hames et al., 2002; Reunanen et al., 2002; Bradford et al., 2003; Fewster, 2003; Knapp et al., 2003; Sanders et al., 2003) which fail to properly partition variation in detection from that in occurrence. Ignoring detectability can lead to biased estimates of site occupancy (MacKenzie et al., 2002; Tyre et al., 2003; Gu and Swihart, 2004). It is important to note that this bias is not constant but can depend on a myriad of factors that vary from one sampling occasion to the next, across years, and geographically (Grant et al., 2005). In anuran surveys, factors that may influence detectability include environmental conditions (e.g., temperature), observer skill, and noise disturbance. Consequently, it is critical that the

detection process be modeled so that detection bias-adjusted estimates of demographic state variables, such as site occupancy, can yield accurate comparisons across space and time.

Herein we use data collected on NAAMP routes in eastern Maryland to investigate factors that influence anuran detection probability and site occupancy. Our primary goal is estimation of baseline "detection bias-adjusted" site occupancy as a metric for anuran population changes. Our secondary objective is to develop an analysis protocol for NAAMP data.

#### MATERIALS AND METHODS

NAAMP routes used in this study were previously generated during the initiation of NAAMP efforts using a stratified random design with 10 listening stop locations placed at least 0.8 km apart (see Weir and Mossman, 2005). In Maryland, stop locations were positioned near potential breeding habitat (e.g., pond, stream, roadside ditch) but without regard to the initial presence or absence of calling anurans.

There are 19 anuran species found in Maryland (Harris, 1975; White and White, 2002). Because of phenological differences in calling between eastern and western Maryland, we surveyed 17 routes within eastern Maryland. Sampling windows for eastern Maryland in 2002 were 1–31 March, 15 April to 17 May, and 1–30 June. Of these 17 routes, five were located in the Northern Piedmont and 12 were in the Upper Coastal Plain physiographic regions (Fig. 1) as defined by Bystrak (1981).

*Field Methods.*—In a variation on the NAAMP protocol, where one survey is conducted in each

of three sampling windows (Weir and Mossman, 2005), employees at the USGS Patuxent Wildlife Research Center, trained by LAW and REJ, conducted three surveys within each of the three sampling windows. Each employee thereby surveyed their own assigned routes a total of nine times. Additionally, NAAMP volunteers trained by the Maryland coordinator were independently conducting single surveys per sampling window at all routes except one (460504; Fig. 1), which did not have an assigned NAAMP volunteer. Three routes (460107, 460508, and 460704; Fig. 1) had more than one volunteer assigned. Following the NAAMP unified protocol (Weir and Mossman, 2005) USGS employees and NAAMP volunteers began each survey at least one-half hour past sunset and finished prior to 0100 h, listening for 5 min at each stop.

We were interested in investigating factors thought to influence detection probability, and we considered all parameters currently required by the NAAMP protocol as those that may influence detection. To test whether optional parameters in the NAAMP protocol affected detection probability, USGS employees recorded start time of the listening period and the number of cars that passed at each stop. Any optional parameters collected by volunteers were also included in analyses. Two additional covariates (moonlight, rainfall) that are not part of the NAAMP protocol were considered as possible influences on detection probability. Moonlight data, characterized as the percent of moon illuminated on each survey night, were obtained from the U.S. Naval Observatory (available via <http://aa.usno.navy.mil/data/docs/MoonFraction.html>) where 0.00 is a new moon, 0.50 is a first and last quarter moon, and 1.00 is a full moon. Rainfall data, classified as a binomial (yes/no) with respect to any measurable rain within 48 h prior to surveys, were obtained from weather stations nearest to each route using data synthesized from the National Weather Service, the National Oceanic and Atmospheric Administration, and the National Climatic Data Center (available via <http://www.anythingweather.com>). Finally, we examined one potential interaction, a cloud cover by moon illumination effect. Ferguson (1960) noted an absence of adult *Bufo fowleri* (Fowler's Toad) on nights with a full moon and clear skies. Because nocturnal visual predators may have an advantage on a moonlit, clear night, anuran calling activity may decrease on such a night compared to a moonlit but cloudy night.

**Landscape Analysis.**—We also considered landscape covariates (Table 1) that may contribute to variation in site occupancy. Prior to conducting the calling surveys, we confirmed the location of each stop and recorded latitude and longitude

TABLE 1. Descriptions of Geographic Information System coverages used to model anuran site occupancy, the land cover and wetland layers were combined and evaluated for relative percent composition within a 1 km radius surrounding each site. Table 3 and Appendix 1 use the abbreviated codes provided here.

Coverages	Type	Description	Code
National Land Cover Data (NLCD) 30 m raster digital data	cultivated	≥ 75% agricultural (hay pastures, row-crops, orchards, etc.) and recreational areas (parks, golf courses, etc.)	AGR
	developed	≥ 30% constructed materials	DEV
	natural	≥ 25% tree and/or shrub canopy cover as well as sparsely vegetated areas due to clear-cuts, fires, floods, etc.	
Maryland DNR wetlands 1:12,000 m polygon data	all	tidal deepwater and wetlands with variable salinity	EST
	palustrine emergent	nontidal wetlands ≤ 8 ha characterized by primarily rooted, herbaceous hydrophytes	PEM
	palustrine forested	nontidal wetlands ≤ 8 ha characterized by primarily woody vegetation	PFO
	open water	nontidal standing water characterized by little or no vegetative cover, or channels periodically or continuously flowing (palustrine, lacustrine, and riverine)	POP

and estimated position error using a Garmin® GPS III Plus Personal Navigator™ receiver. Based on these stop coordinates, we calculated the areas and relative percent composition of land cover and wetland types within a 1-km buffer around each survey stop using a geographic information system (GIS; ArcGIS™ V8.2, Environmental Systems Research Institute, Redlands, CA). We chose a 1-km buffer to represent a reasonable area of landscape influence on amphibian metapopulations (Vos and Stumpel, 1995; Knutson et al., 1999). Although the home range of most anurans is less than 1 km<sup>2</sup>, the dispersal distances recorded for some species exceed 1 km, such as *Rana catesbeiana* (American Bullfrog; Ingram and Raney, 1943). To spatially analyze site occupancy using landscape variables, we combined general land cover data with detailed wetland data. We obtained 30 m digital raster land cover data from the USGS National Land Cover Dataset (NLCD), based on LandSat imagery circa 1992

(currently available from <http://seamless.usgs.gov>), and wetland data from the Maryland Department of Natural Resources (MD DNR) at 1:12,000 scale (downloaded from <http://dnrweb.dnr.state.md.us/gis/data/data.asp>). The MD DNR wetlands layer generally includes all photo-interpretable wetlands  $\geq 0.5$  acres (2023 m<sup>2</sup>), but some wetlands  $\leq 3$  acres (12,141 m<sup>2</sup>) obscured by evergreen forest cover may have been missed. We generalized both NLCD land cover classes and MD DNR wetland classes as described in Table 1.

**Model Development.**—We modeled detection probability and site occupancy according to the methods described by MacKenzie et al. (2002). A number of factors are thought to influence both detection probability and site occupancy (see above). To evaluate these factors, we considered logit models of the form (for detection probability):

$$\text{Eq (1)} \quad \text{logit}(p_{it}) = \beta_0 + \sum_{k=1}^{k_p} \beta_k \cdot u_{kit}$$

where  $u_{kit}$  is the value of (detection) covariate  $k = 1, 2, \dots, k_p$  for the observation collected at route/stop  $i$  and sampling occasion  $t$ . An analogous model for occupancy was considered:

$$\text{Eq (2)} \quad \text{logit}(\psi_i) = \alpha_0 + \sum_{k=1}^{k_\psi} \alpha_k \cdot v_{ki}$$

where  $v_{ki}$  is the value of (occupancy) covariate  $k = 1, 2, \dots, k_\psi$  for route/stop  $i$ . We assumed that occupancy status did not change over the course of the study, that is, that the sites were “closed” with respect to occupancy (for further discussion of the closure assumption, see MacKenzie et al. 2002). The likelihood of the observed data is a function of the  $[p_{it}]$ ,  $[\psi_i]$  parameters (see MacKenzie et al., 2002). This likelihood was maximized to obtain estimates of these model parameters (Tables 2 and 3).

To allow for the possibility of within-season variation in detection probability, we incorporated a sinusoidal function of “day-of-year” specifically, omitting other covariates for clarity:

$$\text{Eq (3)} \quad \text{logit}(p_{it}) = \beta_0 + \beta_1 \cdot \cos\left(\frac{2\pi t}{365} + \beta_2\right)$$

where  $\beta_1$  and  $\beta_2$  characterize the amplitude and phase shift of a sinusoid within a period of 365 days (an annual cycle). This model is essentially the logistic analog of “harmonic regression” (Bloomfield, 1976) and admits the possibility that calling activity of anurans is strongly seasonal and that detection should vary in relation to calling activity. Additional covariates can be added to this model according to Eq. (1). It is conceivable

that no seasonal variation in detection is discernable over the course of the study period given environmental effects such as temperature and time after sunset. This possibility must be considered and so the seasonal parameters  $\beta_1$  and  $\beta_2$  were included as a pair in the model selection described below, thus allowing for their possible omission from the best-fit model.

Direct interpretation of  $\beta_0$ ,  $\beta_1$ , and  $\beta_2$  under this model is awkward. The intercept  $\beta_0$  is the base detection probability (on the logit-scale) at one-quarter cycle (approximately 91 days) from the time of the maximum, and  $\beta_1$  and  $\beta_2$  are the amplitude and phase as stated previously. Although the interpretation is mathematically precise, it is more straightforward to interpret the intercept and sinusoidal terms together as implying a baseline detection probability that varies depending on day-of-year. This can be depicted graphically given estimates of the three parameters (Fig. 2). Also, it is convenient to represent these parameters in terms of two quantities that are more easily interpreted: the timing of the peak,  $t_{\max}$ , and detection probability at the maximum (the amplitude,  $p_{\max}$ ). These quantities are below:

$$\text{Eq (4)} \quad t_{\max} = \frac{|\beta_2| \cdot 365}{2\pi} \quad \text{and}$$

$$\text{Eq (5)} \quad p_{\max} = \frac{e^{\beta_0 + \beta_1}}{1 + e^{\beta_0 + \beta_1}}$$

In addition to those described above, several other covariates were considered as possible additive effects on detection probability including observer skill, cloud cover, wind conditions, and the interaction of cloud cover with moon.

Variation among observers is known to be important in many wildlife studies, such as the Breeding Bird Survey (Link and Sauer, 1998) and Christmas Bird Count (Sauer et al., 1994; Link and Sauer, 1999). Because of the diverse observer pool in this study, we suspected observer abilities would be an important source of variation in detection probability. To simplify the modeling of observer effects, we did not consider random effects models used in similar studies (e.g., Link and Sauer, 1998). Instead, we devised a scoring system to evaluate observer experience loosely based on Shirose et al. (1997), in which we classified observers using three criteria: self rating, rating by trainer, and other biological experience. For self and trainer rating we used a 1–3 scale for beginner, intermediate, and advanced, respectively. Other biological experience was assessed by asking observers seven questions, such as the number of years as a NAAMP observer and whether the person had participated in other fieldwork either as a volunteer or professional. Each question was worth one-half point for

TABLE 2. Parameter estimates contained in the best model, selected using Akaike's Information Criterion (AIC), for factors influencing detection probability. Factor weights are shown in parentheses. Variables are defined as follows: Cars (number of cars that pass), Moon (moon illumination), MnSky (moon and sky interaction), Obs (observer skill), Rain (rainfall within 48 h), Season (day of year), Sky (cloud cover), Temp (air temperature, linear), Temp<sup>2</sup> (air temperature, quadratic), Time (time after sunset, linear), Time<sup>2</sup> (time after sunset, quadratic), and Wind (wind speed using Beaufort scale).

Species	Cars	Moon	MnSky	Obs	Rain	Sky	Temp	Temp <sup>2</sup>	Time	Time <sup>2</sup>	Wind
<i>Bufo americanus</i>	-0.106 (0.94)	0.655 (0.67)	—	(0.05) 0.321 (0.78)	—	(0.08) -0.157 (0.89)	0.052 (0.76)	-0.0074 (0.57)	-0.214 (0.99)	—	(0.07) — (0.18)
<i>Bufo fowleri</i>	—	(0.06)	—	(0.00) 1.010 (1.00)	—	(0.06)	0.256 (1.00)	-0.0076 (0.94)	—	(0.06)	-0.268 (1.00)
<i>Hyla chrysoscelis</i>	-0.135 (0.83)	-1.292 (1.00)	-0.645 (0.95)	—	(0.06)	0.533 (1.00)	0.146 (1.00)	—	2.837 (1.00)	-0.740 (1.00)	— (0.13)
<i>Hyla versicolor</i>	0.204 (1.00)	0.284 (0.99)	0.838 (0.96)	0.685 (0.99)	-0.375 (0.62)	-0.95 (1.00)	0.151 (1.00)	-0.016 (1.00)	1.309 (1.00)	-0.277 (1.00)	— (0.07)
<i>Pseudacris crucifer</i>	—	(0.33)	0.614 (1.00)	—	(0.14)	(0.47)	0.028 (1.00)	-0.008 (1.00)	0.503 (1.00)	0.047 (0.76)	— (0.05)
<i>Pseudacris feriarum</i>	-0.246 (1.00)	—	(0.09)	—	(0.07)	—	(0.06)	—	-0.286 (1.00)	—	0.326 (1.00)
<i>Rana catesbeiana</i>	—	(0.06)	-0.729 (1.00)	—	(0.10)	(0.10)	0.056 (1.00)	—	-0.138 (0.96)	0.079 (0.91)	-0.376 (1.00)
<i>Rana clamitans</i>	—	(0.34)	—	(0.00) 1.245 (1.00)	—	(0.07)	(0.021) 0.040 (0.98)	—	0.221 (1.00)	—	-0.422 (1.00)
<i>Rana palustris</i>	0.243 (1.00)	-1.445 (1.00)	—	—	(0.05)	(0.15)	—	—	—	(0.06)	-0.235 (0.59)
<i>Rana sphenoccephala</i>	—	(0.10)	—	(0.00)	0.505 (1.00)	—	0.053 (0.99)	-0.013 (0.99)	—	(0.01)	— (0.08)

a maximum score of 3.5. These three categorical scores were averaged to obtain a final numerical score, which could range from 0.67–3.17. Actual scores ranged from 0.83–3.0.

In addition to seasonal and observer effects, we considered the following other factors thought to influence detection: number of cars passing as an indicator of noise disturbance, moon illumination, sky conditions (cloudiness), interaction of moon and sky conditions, rainfall in preceding 48 h, air temperature, time, and wind speed. Several of our collected parameters were adjusted. We converted start time to minutes after sunset. Both wind speed and cloudiness were recorded as ordered categorical variables. Although wind codes are sequential representing increasing wind, cloud cover codes representing increasing levels of cloudiness are sequential only from 0–2; no data were recorded above this range. For purposes of model fitting, these were treated as ordinary regression variables to yield a more parsimonious description while preserving the essential quantitative nature of both variables. For air temperature and time, both linear and quadratic effects were considered, allowing for the possibility of “optimal” calling conditions and hence “optimal” detection.

We also considered additive effects on occupancy by including landscape covariates. These covariates are compositional (they sum to 1), inducing an identifiability constraint into the model, in which the intercept must either be omitted from the model or one of the covariates must be removed to ensure that model parameters are identifiable. We chose to omit the “natural” category (Table 1). Although this decision does not influence the essential character of the model, care must be taken when interpreting parameter estimates. Because a particular parameter estimate is not contained in the model does not imply that its effect is zero. Omission of elements of the composition amounts to a reduced model in which two or more effects are equal but not necessarily zero.

**Model Selection.**—Introducing these six landscape effects on occupancy in addition to the 12 detection effects yields a model set of  $2^{18}$  possible models. Although this has been considerably reduced by a priori exclusion of some interactions (i.e., all interactions not previously mentioned), this still represents a substantial number of models to consider. Because fitting all possible models was prohibitive, we adopted a stepwise model selection procedure under which factors are added sequentially according to AIC (Burnham and Anderson, 1998). Using the stepwise procedure, about 140 models were fit for most species. Because it would be impractical to summarize AIC results for all selected models even for a single species, we present the top five models

TABLE 3. Parameter estimates contained in the best model, selected using Akaike’s Information Criterion (AIC), for factors influencing occupancy including observed ( $\psi_{\text{obs}}$ ) and modeled ( $\psi_{\text{model}}$ ) occupancy rates. Factor weights are shown in parentheses. Occupancy variable descriptions provided in Table 1.

Species	Intercept	AGR	DEV	EST	PEM	PFO	POP	$\psi_{\text{obs}}$	$\psi_{\text{model}}$
<i>Bufo</i>									
<i>americanus</i>	12.58	−13.32 (1.00)	−37.11 (1.00)	−164.84 (1.00)	— (0.07)	−41.96 (1.00)	— (0.08)	0.379	0.603
<i>Bufo fowleri</i>	−2.21	— (0.11)	— (0.27)	— (0.6)	— (0.13)	44.82 (1.00)	47.59 (0.99)	0.462	0.524
<i>Hyla</i>									
<i>chrysoscelis</i>	−1.09	— (0.07)	— (0.08)	— (0.07)	— (0.44)	19.76 (1.00)	— (0.33)	0.349	0.486
<i>Hyla</i>									
<i>versicolor</i>	−0.06	— (0.33)	— (0.28)	— (0.07)	— (0.10)	— (0.07)	— (0.07)	0.373	0.479
<i>Pseudacris</i>									
<i>crucifer</i>	2.49	— (0.10)	— (0.05)	−13.82 (1.00)	— (0.22)	33.18 (1.00)	— (0.04)	0.959	0.960
<i>Pseudacris</i>									
<i>feriarum</i>	−1.70	— (0.06)	−9.26 (0.93)	— (0.18)	30.91 (0.51)	19.67 (1.00)	−31.43 (0.79)	0.308	0.350
<i>Rana</i>									
<i>catesbeiana</i>	−0.66	— (0.40)	— (0.07)	— (0.06)	— (0.07)	6.49 (1.00)	55.92 (1.00)	0.497	0.533
<i>Rana</i>									
<i>clamitans</i>	−0.46	1.28 (0.73)	— (0.06)	−15.38 (1.00)	— (0.05)	7.99 (1.00)	— (0.08)	0.598	0.625
<i>Rana</i>									
<i>palustris</i>	−0.65	— (0.13)	— (0.41)	— (0.09)	— (0.25)	−4.89 (0.87)	— (0.08)	0.254	0.280
<i>Rana</i>									
<i>sphenocephala</i>	−3.45	— (0.06)	24.93 (1.00)	— (0.06)	— (0.07)	35.52 (1.00)	65.29 (1.00)	0.260	0.505

and factor weights to gauge the overall importance of each factor for each species. The factor weight for a particular factor is calculated by summing up the AIC weight of each model in which the factor appears (Burnham and Anderson, 1998:140). Factor weights are a means of gauging the relative importance of many factors. We used the free software package R, by the R Foundation for Statistical Computing, for all calculations (downloaded from <http://www.R-project.org>).

RESULTS

We present the results for the 10 species that were observed at > 25% of our survey points ( $\psi_{\text{obs}}$ , Table 3): *Bufo americanus* (American Toad), *Bufo fowleri* (Fowler’s Toad), *Hyla chrysoscelis* (Cope’s Gray Treefrog), *Hyla versicolor* (Gray Treefrog), *Pseudacris crucifer* (Spring Peeper), *Pseudacris feriarum* (Southeastern Chorus Frog), *Rana catesbeiana* (American Bullfrog), *Rana clamitans* (Green Frog), *Rana palustris* (Pickerel Frog), and *Rana sphenocephala* (Southern Leopard Frog).

Generally, the top 10–20 models showed that detection probability and occupancy only varied by the inclusion or omission of one or two factors when compared with the model selected as “best” based on AIC values. Because the model set was so large the top five models varied little with respect to AIC values. We present only the top five models (Appendix 1) and their factor weights (Tables 2 and 3) for each species.

*Detection Factors.*—In the top five models for all species, season explained variation in detection probability ( $N = 10$ ). The season term was generally the first added in the stepwise procedure with a factor weight of 1.0 (Table 2). Because the season term is a sinusoidal function,

we present the results graphically (Fig. 2). The parameter estimates that describe these detection probability sinusoids are given in Table 4. For more direct interpretation, this table also includes the derived parameters  $t_{\text{max}}$  and  $p_{\text{max}}$ , which are functions of  $\beta_0$ ,  $\beta_1$  and  $\beta_2$ .

Air temperature explained the variation in detection probability for eight of the 10 species. Of these species, the best models contained a quadratic temperature ( $\text{temp}^2$  in Table 2) effect for five species such that there was a positive linear coefficient and negative quadratic coefficient, implying an “optimal” calling temperature. The expression for optimum temperature was  $\text{temp}_{(\text{opt})} = -a/2b$  where  $a$  is the linear coefficient and  $b$  is the quadratic coefficient. The models were fit using temperature deviations from the mean observed temperature during the study (17.2°C), and the units of the estimated optimum are degrees from the mean. Thus, for the five species where the best model contained a quadratic in temperature (Fig. 3), these optimal temperature values were *B. americanus* (21°C), *B. fowleri* (34°C), *H. versicolor* (22°C), *P. crucifer* (19°C), and *R. sphenocephala* (19°C). For the remaining three species, detection increased as temperature increased (Table 2).

Time explained the variation in detection probability for seven of the 10 species (Table 2). For three of these species, detection had a linear relationship with time after sunset. The remaining four species had a nonlinear (quadratic) relationship with time, and detection probabilities for two of these species exhibited a peak during the time of sampling.

Other factors also contributed to the variation in detection probability for more than half of the

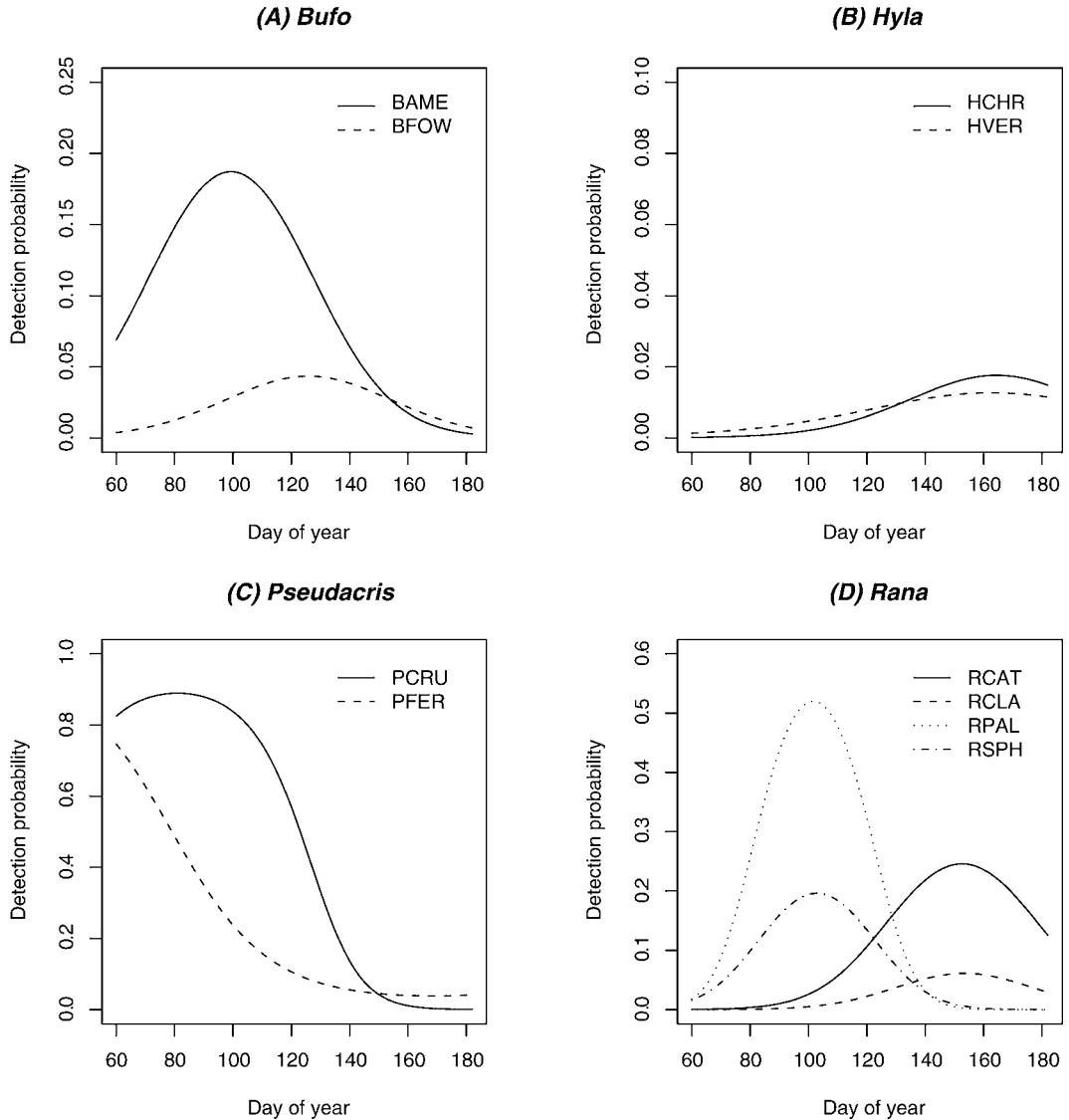


FIG. 2. Estimated seasonal detection probabilities during the NAAMP sampling period for Maryland (1 March through 30 June 2002) for 10 anuran species: *Bufo americanus* (BAME), *Bufo fowleri* (BFOW), *Hyla chrysoscelis* (HCHR), *Hyla versicolor* (HVER), *Pseudacris crucifer* (PCRU), *Pseudacris feriarum* (PFER), *Rana catesbeiana* (RCAT), *Rana clamitans* (RCLA), *Rana palustris* (RPAL), and *Rana sphenoccephala* (RSPH).

species (Table 2). For example, moon illumination explained variation in detection probability for six of 10 species. The interaction between moon and cloud cover further explained variation in detection for only two of these species. Observer ability explained the variation in detection probability for five of the 10 species, where detection probability increased with increasing observer ability. Although the number of cars that passed during the listening period explained variation in detection probability for five of 10 species, detection of only three of these decreased

with increased traffic. Wind also explained the variation in detection for five of 10 species; for four of these species, detection probability decreased as wind increased.

**Occupancy Factors.**—Observed occupancy ranged from 0.253 for *R. palustris* to 0.959 for *P. crucifer* (Table 3). Accounting for imperfect detectability adjusts the observed occupancy to account for differences in detection probability. For *P. crucifer*, the observed and modeled occupancy were not appreciably different (0.959 vs. 0.960). The difference between modeled and



TABLE 4. Parameter estimates for seasonal influence on detection probability, including intercept ( $\beta_0$ ), amplitude ( $\beta_1$ ), and phase of the sinusoid ( $\beta_2$ ). Also provide are the timing of the peak ( $t_{\max}$ ) and detection probability at the maximum ( $p_{\max}$ ). For all species season had a factor weight of 1.0.

Species	$\beta_0$	$\beta_1$	$\beta_2$	$t_{\max}$	$p_{\max}$
<i>Bufo americanus</i>	-6.61	5.15	-1.71	99	0.19
<i>Bufo fowleri</i>	-7.38	4.28	-2.17	126	0.04
<i>Hyla chrysoscelis</i>	-7.87	3.85	-2.83	164	0.02
<i>Hyla versicolor</i>	-6.24	1.89	-2.80	163	0.01
<i>Pseudacris crucifer</i>	-6.22	8.31	-1.39	81	0.89
<i>Pseudacris feriarum</i>	0.10	3.33	0.24	-14	0.97
<i>Rana catesbeiana</i>	-7.68	6.55	-2.63	153	0.25
<i>Rana clamitans</i>	-9.25	6.52	-2.64	153	0.06
<i>Rana palustris</i>	-16.52	16.60	-1.75	102	0.52
<i>Rana sphenoccephala</i>	-11.86	10.45	-1.77	103	0.20

observed occupancy was greatest for *B. americanus* and *R. sphenoccephala* (Table 3).

#### DISCUSSION

The models we developed accounted for variation in detection probability caused by environmental conditions as well as other extraneous sampling influences (e.g., variation among observers) and variation in occupancy caused by the surrounding landscape. The results of model selection suggest that, for more than half of the 10 species, detection probabilities vary most with season (i.e., day-of-year), air temperature, time, and moon illumination.

**Detection Factors.**—As expected, we found substantial seasonal variation in detectability even within the anuran breeding season. NAAMP sampling windows focus sampling during the breeding activity of these species. The modeling framework that we employed allows more precise targeting of particular species or at least adjustment of data collected at suboptimal times so that the sample period need not be truncated to ensure closure.

Although none of the best models included all required NAAMP parameters, based on model selection, detection of individual species varied with respect to some combination of all required covariates. Thus, we believe that the suite of required covariates should remain unchanged, but additional covariates may be important to consider when analyzing NAAMP data. The modeling framework presented in this paper can be used to improve NAAMP and other anuran calling surveys. For example, factors that influence detection should be considered in survey design and in the comparison of population state metrics across space and time.

Air temperature generally explained variation in detection for seven species; we found

quadratic temperature effects on detection probability for five of these species (Table 2) indicating a peak temperature for detection. Similarly, Johnson and Batie (2001) found that the greatest proportion of species-specific detections occurred during optimal temperature ranges. This information on the effect of ambient temperature on detection probability can be used to guide or restrict sampling to yield higher detection probabilities. Time after sunset explained the variation in detection probability for seven species (Table 2), although the effect was not consistent across all species. Our results for time effects for these species (except *B. americanus*) are generally in agreement with previous studies showing that detection increases as time after sunset increases (Bishop et al., 1997; Bridges and Dorcas, 2000). Note that these studies only considered linear time effects, whereas in our modeling, we considered the possibility of quadratic time effects.

Based on model selection, variation in detection for some species may be related to other factors such as moonlight, observer experience, extraneous noise (e.g., passing cars), and wind. Few studies have examined effects of moonlight on anuran activity (movement: Fitzgerald and Bider, 1974; calling: Johnson and Batie, 2001). Model selection suggests that moonlight may influence detection probability, although the response may be species-specific and further study is warranted. Stepwise selection is known to build overly complex models (Chatfield, 1995) resulting in risk that some selected factors may be spurious. Results such as increased detection with increasing wind for *P. feriarum* and increased detection of *H. versicolor* and *R. palustris* with increased traffic may represent spurious effects.

The importance of observer variation in these types of studies has been previously established (Sauer et al., 1994; Shirose et al., 1997; Link and Sauer, 1998, 1999). We accounted for this possible source of variation in our models by employing an observer experience-based scoring system. We did not test interobserver agreement, because observers were not simultaneously surveying the same routes. For half of the species, results from model selection indicate that observer experience may influence detection probability (Table 3). In previous studies, establishing species presence (i.e., detection) was not related to observer experience (Shirose et al., 1997; Genet and Sargent, 2003). Our modeling framework may be improved by replacing the current observer scoring system with one that rates observers based on a test of their ability to correctly identify calls. To address this need, NAAMP has developed an online testing tool in which observers will be evaluated on their ability to identify anuran calls

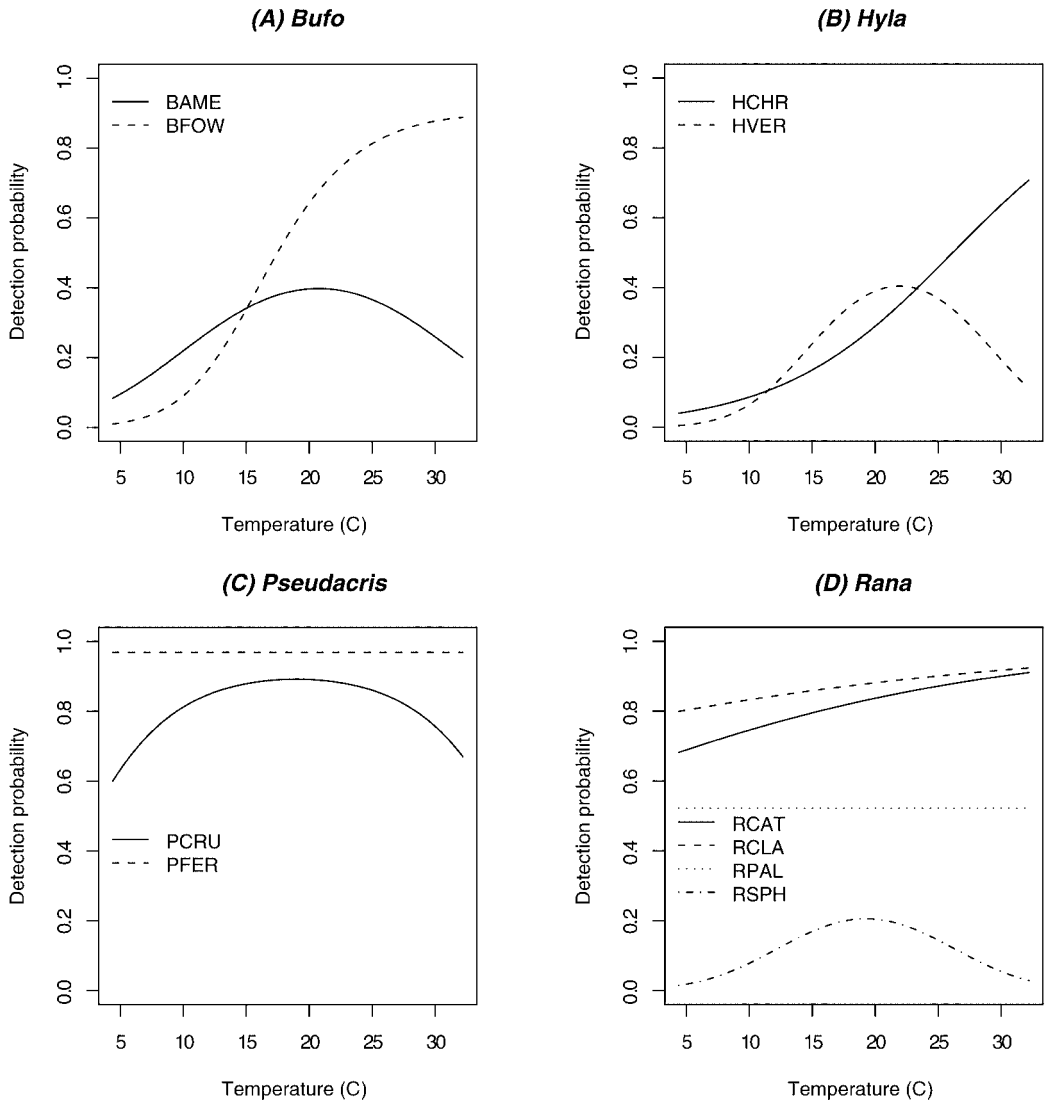


FIG. 3. On NAAMP routes in Maryland, the estimated detection probabilities with respect to air temperature for 10 anuran species: *Bufo americanus* (BAME), *Bufo fowleri* (BFLOW), *Hyla chrysoscelis* (HCHR), *Hyla versicolor* (HVER), *Pseudacris crucifer* (PCRU), *Pseudacris feriarum* (PFER), *Rana catesbeiana* (RCAT), *Rana clamitans* (RCLA), *Rana palustris* (RPAL), and *Rana sphenoccephala* (RSPH).

from randomly selected audio files (available at <http://www.pwrc.usgs.gov/frogquiz/>).

At 24°C, we found *H. versicolor* detection began to decrease, whereas *H. chrysoscelis* detection continued to increase (Fig. 3B). For both species during vocalization, the number of pulses per second increases as air temperature increases; at any given temperature *H. chrysoscelis* has more pulses per second than *H. versicolor* (Gerhardt, 1978). Gerhardt (1978) found the pulses per second of *H. versicolor* reach the range of *H. chrysoscelis* at 24°C. Thus, it is possible that observers confused the warm-temperature vo-

calization of *H. versicolor* for the calls of *H. chrysoscelis*, potentially confounding our results for these two species. This suggests the possibility of false positives and, thus, potentially violating a fundamental assumption of the models considered here (i.e., MacKenzie et al., 2002). To avoid the risk of false positives, these species could be treated as a complex or data restricted to low temperature observations. Alternatively, one could employ models that allow for false positives, which are currently under development (e.g., J. A. Royle and W. A. Link, unpubl.).

Although our results did not consistently show decreased detection with increased numbers of passing cars, this type of extraneous noise should be considered in estimates of detection because it can lead to biases that vary temporally. Without such correction, the appearance of negative population trends could result from lower detection rates caused by increased noise disturbance during sampling rather than actual population change.

Previous studies suggest that calling activity of some anurans may be related to wind conditions (Johnson and Batie, 2001; Oseen and Wassersug, 2002). Similarly, we found that detection of four of five species decreased with increased wind, although our surveys were confined to the low wind requirements of the NAAMP unified protocol (Weir and Mossman, 2005).

*Occupancy Factors.*—We present detection bias-adjusted site occupancy as a metric of population demographics. Not all species are detected equally; using detection bias-adjusted site occupancy can account for these differences (Table 3). In our study, routes were surveyed nine to 15 times allowing naïve estimates of site occupancy to approach the model-adjusted estimates. NAAMP routes are surveyed three to four times per year; we would expect that fewer visits would increase the difference between naïve and model-adjusted occupancy. By accounting for detection bias through modeling, differences in sampling conditions (e.g., temperature, time, etc.) during surveys from year-to-year will not obscure emerging population trends.

The proportion of palustrine forested wetland habitat surrounding a survey point explained variation in site occupancy for nine of 10 species. For seven of these species, occupancy increased with the prevalence of this habitat. This implies that these species exhibit a preference (or, for the remaining two species, a lack of preference) for palustrine forested habitat, but these species use several other habitat types for breeding (Hulse et al., 2001; White and White, 2002). NAAMP routes are located randomly, stratified by habitat with stop locations placed at potential breeding habitat (see Weir and Mossman, 2005). Future improvements in the resolution of digital land cover data will allow increased precision of habitat characterization permitting better interpretation of habitat associations in relation to population trends (Falardeau and DesGranges, 1991; Bishop et al., 1997).

*Conclusions.*—NAAMP is a relatively new monitoring program with the potential to generate substantial amounts of data on amphibian distributions and the status of populations. Consequently, the development of an analysis framework for NAAMP data is critically important. We believe that the site-occupancy model-

ing framework we employed is useful in this regard because it yields a summary of anuran metapopulation status (site occupancy) that may be useful for assessment of temporal and geographic variation in anuran populations. In addition, this framework facilitates the evaluation of factors that influence the detectability of anurans, and such information can be useful in development or modification of anuran sampling protocols. For example, our results suggest that data collected during NAAMP and other anuran calling surveys should include commonly collected parameters such as air temperature and time of night (e.g., Bishop et al., 1997; Johnson and Batie, 2001; Oseen and Wassersug, 2002) but also moon illumination and observer skill that are not presently components of the NAAMP protocol. Also, we demonstrated that seasonal variation can be accommodated in the model specification for detection probability; therefore delineating "sampling windows" may not be necessary for analyzing NAAMP data. Finally, our results indicate a strong relationship between site occupancy and land use for several species; however, our dataset only includes one year of data. Because land use patterns across the United States are undergoing rapid change, documenting habitat characteristics of sample locations over time may improve model-adjusted estimates of site occupancy. Although some possibility exists for extending the types of models considered here to make direct use of the calling index data (Royle, 2004; Royle and Link, 2005), our framework yields a metric of population state that we believe is useful in monitoring and conservation assessment, when the goal is to evaluate change in population state over time and in relation to change in landscape and other environmental features.

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APPENDIX 1. For 10 anuran species, the top five models using Akaike's Information Criterion (AIC). See variable descriptions in Table 1 and Table 3.

Species models	Detection factors												Occupancy factors							AIC	Weight
	Cars	Moon	MnSky	Obs	Rain	Season	Sky	Temp	Temp <sup>2</sup>	Time	Time <sup>2</sup>	Wind	AGR	DEV	EST	PEM	PFO	POP			
<i>Bufo americanus</i>																					
1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	1	0	1	0	692.4	0.234	
2	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	0	1	0	693.6	0.074	
3	1	1	0	1	0	1	1	1	1	0	1	0	0	1	1	1	0	1	0	693.9	0.052
4	1	0	0	0	0	1	1	0	0	1	0	0	1	1	1	0	1	0	694.2	0.039	
5	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	0	1	0	694.2	0.037	
<i>Bufo fowleri</i>																					
1	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1	1	948.6	0.181	
2	0	0	0	1	0	1	1	1	1	0	0	1	0	0	0	0	1	1	949.0	0.121	
3	0	0	0	1	0	1	0	1	1	0	0	1	0	1	0	0	1	1	949.4	0.082	
4	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0	1	1	949.8	0.058	
5	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	1	1	1	949.8	0.054	
<i>Hyla chrysoscelis</i>																					
1	1	1	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1	0	607.2	0.135	
2	1	1	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	607.5	0.100	
3	1	1	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	607.5	0.094	
4	1	1	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	607.6	0.086	
5	1	1	1	1	0	1	1	1	1	0	1	1	1	0	0	0	1	0	608.3	0.044	
<i>Hyla versicolor</i>																					
1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	723.1	0.161	
2	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	723.2	0.140	
3	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	723.8	0.081	
4	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	724.1	0.059	
5	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	724.1	0.058	
<i>Pseudacris crucifer</i>																					
1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	1	0	1579.3	0.090	
2	0	1	0	0	1	1	0	1	1	1	1	0	0	0	1	0	1	0	1579.7	0.061	
3	1	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	1	0	1579.7	0.056	
4	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	1579.8	0.056	
5	1	1	0	0	1	1	0	1	1	1	1	0	0	0	1	0	1	0	1579.8	0.056	

## APPENDIX 1. Continued.

Species models	Detection factors												Occupancy factors						AIC	Weight
	Cars	Moon	MnSky	Obs	Rain	Season	Sky	Temp	Temp <sup>2</sup>	Time	Time <sup>2</sup>	Wind	AGR	DEV	EST	PEM	PFO	POP		
<i>Pseudacris feriarum</i>																				
1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	625.0	0.140
2	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	625.1	0.136
3	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1	626.0	0.051
4	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	626.2	0.045
5	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	626.2	0.045
<i>Rana catesbeiana</i>																				
1	0	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	1	1	1031.9	0.211
2	0	1	0	1	0	1	0	1	0	1	1	1	1	0	0	0	1	1	1032.4	0.123
3	0	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	1	1	1032.7	0.093
4	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1033.2	0.057
5	0	1	0	1	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1033.2	0.056
<i>Rana clamitans</i>																				
1	0	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0	1	0	1196.7	0.089
2	0	0	0	1	0	1	0	1	1	1	0	1	1	0	1	0	1	0	1196.7	0.086
3	1	0	0	1	0	1	0	1	1	1	0	1	1	0	1	0	1	0	1197.0	0.065
4	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	1	0	1197.0	0.064
5	1	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0	1	0	1197.1	0.061
<i>Rana palustris</i>																				
1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	537.1	0.061
2	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	537.1	0.061
3	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	537.1	0.060
4	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	537.2	0.058
5	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	537.5	0.042
<i>Rana sphenoccephala</i>																				
1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	490.4	0.193
2	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	1	1	490.8	0.132
3	0	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	491.4	0.072
4	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	1	1	491.7	0.054
5	0	1	0	1	1	1	0	1	1	0	0	0	0	1	0	0	1	1	491.8	0.051