ARTICLE

Evaluation of Listener-Based Anuran Surveys with Automated Audio Recording Devices

A. F. Shearin · A. J. K. Calhoun · C. S. Loftin

Abstract Volunteer-based audio surveys are used to document long-term trends in anuran community composition and abundance. Current sampling protocols, however, are not region- or species-specific and may not detect relatively rare or audibly cryptic species. We used automated audio recording devices to record calling anurans during 2006–2009 at wetlands in Maine, USA. We identified species calling, chorus intensity, time of day, and environmental variables when each species was calling and developed logistic and generalized mixed models to determine the time interval and environmental variables that optimize detection of each species during peak calling periods. We detected eight of nine anurans documented in Maine. Individual recordings selected from the sampling period (0.5 h past sunset to 0100 h) described in the North American Amphibian Monitoring Program (NAAMP) detected fewer species than were detected in recordings from 30 min past sunset until sunrise. Time of maximum detection of presence and full chorusing for three species (green frogs, mink frogs, pickerel frogs) occurred after the NAAMP sampling end time (0100 h). The NAAMP protocol's sampling period may result in omissions and misclassifications of chorus sizes for certain species. These potential errors should be considered when interpreting trends generated from standardized anuran audio surveys.

Keywords Anuran call surveys · Amphibian monitoring · Audio surveys · Automated audio recording devices · NAAMP

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Introduction

Accurate detection and abundance measures are essential for documenting trends in amphibian populations. Audio surveys are used extensively for long-term and rapid population monitoring of vocalizing anurans (Dorcas et al. 2009). Large-scale, volunteer-based audio survey programs, such as the North American Amphibian Monitoring Program (NAAMP; http://www.pwrc.usgs.gov/naamp/), are designed to monitor anurans over diverse spatial and temporal scales (Weir and Mossman 2005). NAAMP is a North American program instituted in 1997; in the US, it is a collaborative effort among state wildlife agencies, non-profit organizations, and the U.S. Geological Survey to document trends in anuran populations with volunteer-based call surveys (Weir et al. 2005). The unified sampling protocol adopted by participating states in 2001 (Weir and Mossman 2005) directs volunteers to identify calling anurans during a five-minute listening period at up to ten stops along a designated route. All surveys must begin 0.5 h after sunset or later and terminate by 0100 h. Each species identified during a listening period is assigned a Calling Index (CI) code from 1 to 3, with CI 1 representing non-overalapping individuals of that species calling and CI 3 representing a full chorus (Mossman et al. 1998; Weir and Mossman 2005). CI is correlated with the number of calling males for certain species, such as green frogs (*Lithobates clamitans* Latreille) (Nelson and Graves 2004), North American bullfrogs (*L. catesbeianus* Shaw) (Shirose et al. 1997), and Fowler's toads (*Anaxyrus fowleri* Hinckley) (Shirose et al. 1997), and it can be used to estimate relative abundance. Declining CI over multiple years often is used as an indicator of declining populations (Gibbs et al. 2005). Environmental variables, such as wind speed and cloud cover, also are noted at each NAAMP listening stop or at the start and end of the survey, as these conditions may affect calling initiation and detection (Weir et al. 2005). Standardized volunteer listener surveys are inexpensive, repeatable, applicable across multiple regions, and foster public involvement in amphibian research. Calling surveys alone, however, may be

insufficient for detecting species that call infrequently, vocalize outside the protocol's monitoring windows, or are rare and may require pairing with more intensive sampling methods such as pitfall traps or automated audio recording devices (Crouch and Paton 2002). Commission errors (false inclusions) also may obfuscate accurate assessment of population trends in long-term amphibian datasets (Lotz and Allen 2007; McClintock et al. 2010). Furthermore, species omissions and misclassification of CI can affect interpretations of long-term trends based on audio data (Lotz and Allen 2007), although models may correct for imperfect detections in some scenarios (e.g., Royle 2004; Nichols et al. 2007; Mackenzie et al. 2009; Miller et al. 2011).

The unified NAAMP protocol standardizes data collection across multiple regions and years; however, the generality of the protocol may lead to poor detection of species that require different survey parameters. The NAAMP sampling period is appropriate for detecting many species, such as Fowler's toads, which call most frequently within 2 h after sunset (Tupper et al. 2007). Species that call before or after this time period may not be detected. Southern leopard frog (*L. sphenocephalus* Harlan) for example, calls primarily from midnight until dawn in North Carolina and could be missed by surveys conducted during evening hours (Bridges and Dorcas 2000). In the northeastern United States, mink frogs (*L. septentrionalis* Baird) routinely call later than the 0100 h end time for NAAMP surveys. Peak mink frog detection usually occurs during 0300–0400 h following peak calling activity (Bevier et al. 2006). Surveys conducted before this time may fail to detect full choruses given that estimation of local population sizes would warrant such a distinction (Popescu and Gibbs 2009). While these studies indicate that audio surveys conducted before 0100 h may fail to detect certain species, there currently are no paired studies explicitly comparing species detections and CI classifications before and after the 0100 h NAAMP end time, although detection probabilities are known to vary throughout the NAAMP sampling window (Royle 2004; Weir et al. 2005).

Each state participating in NAAMP offers sampling guidance for dates with the best probabilities of detecting target species. In Maine, there are three sampling periods that target early spring (wood frog [*L. sylvaticus* Le Conte], spring peeper [*Pseudacris crucifer* Wied-Neuwied]), late spring (American toad [*Anaxyrus americanus* Holbrook], gray treefrog [*Hyla versicolor* Le Conte], pickerel frog [*L. palustris* Le Conte], northern leopard frog [*L. pipiens* Schreber]), and early summer (green frog, bullfrog, mink frog) breeders (Maine Amphibian Monitoring Program, www.maineaudubon.org). Guidance for when to sample within these periods is limited to temperature thresholds and the occurrence of light precipitation. Recommended sampling dates differ among the three Maine sampling regions (coastal, interior, northern Maine) and are based on anuran species present in each; however, the unified protocol requires that surveys be conducted during 0.5 h after sunset to 0100 h.

While general guidance simplifies the sampling protocol, environmental variables may significantly influence the probability of detecting certain species. Wood frogs and spring peepers may vary calling initiation by as much as 3 weeks based on environmental variables (Mossman et al. 1998). Other studies have documented the importance of environmental variables for predicting calling occurrence (e.g., Oseen and Wassersug 2002; Weir et al. 2005; Saenz et al. 2006; Steelman and Dorcas 2010). The number and effect of environmental variables on calling may differ among breeding strategies, with explosive breeders (e.g., wood frogs) influenced by fewer variables than their prolonged breeding counterparts (Wells 1977) that call over several weeks or months (e.g., green frogs) (Oseen and Wassersug 2002). Prolonged breeders must regulate calling effort over a longer period of time and thus are exposed to a greater range of environmental conditions (Wells 1977).

Automatic recording systems (ARS) may be useful for identifying sampling times and environmental variables that can improve detection of target anuran species. ARS are digital or cassette-tape based automated audio recording systems that can be programmed to record a specified interval over a given time period (Peterson and Dorcas 1992). They can be used to monitor sites over multiple nights, extended time periods, and under various environmental conditions. ARS also remove any potentially confounding effects of human disturbance during a survey. Recordings can be permanently archived and reviewed repeatedly by multiple listeners for accurate species identification and CI designation. Digital ARS data also can be manipulated with widely available software to improve recording quality, remove interference, and isolate audibly cryptic species that may be masked by louder species (Dorcas et al. 2009). ARS have been used extensively for detecting calling anurans (e.g., Steelman and Dorcas 2010), birds (e.g., Brandes 2008), and other vocalizing species.

We used ARS to monitor calling anurans at lakes and vernal pools in Maine to determine if the standardized NAAMP protocol detects and accurately describes calling choruses for all anuran species in our region. The specific objectives of our study were to (1) determine if surveys conducted during the NAAMP-specified time period (0.5 h past sunset to 0100 h) identified all species known to be present and captured the maximum CI for that night; (2) describe temporal calling patterns for anurans in central Maine; and, (3) describe environmental variables that predict calling occurrence.

Methods

Study Area

ARS were deployed during 2006–2009 at lakes and vernal pools in the Western and Interior Mountains and Foothills (12 lakes) and the Eastern Coastal Plain and Foothills (12 lakes and

four vernal pools) biophysical regions of Maine (Krohn et al. 1999) (Appendix 1). Lakes were characterized by permanent hydroperiods and surface areas from 1.4 to 10.1 ha. Vernal pools typically dried by the end of August, with surface areas ranging 0.02–0.7 ha at high water. Sites chosen were a subset of those surveyed for invertebrate, fish, and amphibian community composition (Schilling et al. 2008, 2009; Shearin 2012) and are located within Maine's 'central' NAAMP region (Zone 2) in Franklin, Hancock, Oxford, Piscataquis, and Washington Counties (Appendix 1). Nine anuran species (American toad, gray treefrog, North American bullfrog, green frog, pickerel frog, northern leopard frog, mink frog, wood frog, spring peeper) occur in this region (Hunter et al. 1999).

ARS Deployment

We used a combination of five, tape-based ARS (designed after Peterson and Dorcas [1992]) and five digital-based ARS developed at the University of Maine, Orono, to record calling anurans. Each digital ARS consisted of a USB recorder (iKEY® Plus, GCI Technologies Corporation, Edison, NJ), two-channel, eight event timer (DT-04, SuperFeeder®, Hermitage, TN), microcontroller-operated electronic trigger circuit, voltage regulator (12 to 5 volt DC), 4 GB capacity USB drive, stereo microphone (iKEY® Plus, GCI Technologies Corporation, Edison, NJ), aluminum, 1 m tripod (DT-120D, Fox®), waterproof case (Pelican™ Products, Inc., Torrance, CA, $24 \times 18 \times 11$ cm), and two 6-volt DC batteries. Microphones were housed in a 20 cm-long section of 5 cm diameter polyvinylchloride (PVC) piping to prevent wind and rain interference (see Peterson and Dorcas 1992). Digital and tape-based ARS were deployed haphazardly among 24 lakes and vernal pools during the duration of our study. ARS were often removed from a site once a species was detected, and the number of deployment days and sampling occasions varied by site and year. We placed a single ARS within 0.5 m of shoreline under vegetation to provide protection from sunlight and to reduce interference from wind and precipitation. ARS were programmed to record an approximate 2 min audio clip every hour from 0.5 h past sunset until sunrise. This time interval constituted a single recording night and maximized the number of nights and recordings per night captured by each ARS deployment.

Recording Analyses

Only nights containing recordings from all hours between 0.5 h past sunset and sunrise were used for analysis. Time (minutes) past sunset was noted for each recording. Recordings were assigned a Julian date (DAY) based on the start date of each recording night. Audio recordings were reviewed by one of five listeners. A single listener also reviewed random recordings from each night to ensure that all listeners correctly and consistently assigned CI values. CI code (1–3) for each species per recording was assigned following NAAMP detection protocols: CI 1 for individuals with no overlap between calls, CI 2 for overlapping individuals, and CI 3 for a constant, overlapping chorus (Weir and Mossman 2005). We also created an additional category (CI 0) for no calls.

We used environmental data collected nightly from the nearest weather station within 30 km (National Oceanic Atmospheric Administration weather stations, http://lwf.ncdc.noaa.gov/oa/climate/stationlocator.html). We determined maximum (MAXT) and minimum (LOWT) temperature, relative humidity (HUMID) at 2,400 h, precipitation during the recording night (PRECIP), and presence (1) or absence (0) of precipitation within 24 h prior to the recording. The fraction of the moon illuminated for each night (MOON) (Weir et al. 2005) was obtained from the U.S. Naval Observatory (http://www.usno.navy.mil/USNO/astronomical-applications/data-services/frac-moon-ill). Cloud cover (CLD) and wind speed (WIND) at midnight during each recording session were obtained from Weather Underground (www.wunderground.com). Cloud cover was converted to a sky condition code based on NAAMP categories from 0 (clear or few clouds) to 8 (showers). Wind speeds were categorized as Beaufort wind speed codes from 0 (wind speed <1.6 km per hour) to 5 (wind speeds 30.6 to 38.6 km per hour), which is consistent with NAAMP protocols.

Individual audio recordings were classified as falling within the NAAMP sampling time period (0.5 h past sunset to 0100 h; NAAMP) or within a COMPLETE recording session (0.5 h past sunset to sunrise; COMPLETE). Recordings occurring from 0.5 h past sunset until 0100 h occurred during both the NAAMP and full night sampling intervals, and therefore were classified as both NAAMP and COMPLETE. Recordings occurring from 0100 h to sunrise were outside the NAAMP sampling interval, and therefore were classified only as COMPLETE. A single recording (INDIVIDUAL) was chosen randomly from each recording night within the NAAMP sampling time to represent a typical NAAMP survey that identifies species at a site and assigns a CI during a single five-minute listening period. We determined the number of species identified for the randomly chosen INDIVIDUAL sessions as well as the median number of species for all the NAAMP (0.5 h past sunset until 0100 h) and COMPLETE (any time between 0.5 h past sunset and sunrise) sessions for each recording night. Paired median numbers of species from INDIVIDUAL, NAAMP, and COMPLETE sessions were compared across nights with Wilcoxon Signed Rank Tests, because data were not normally distributed (Sprent and Smeeton 2001). We determined the number of times each species was detected during the INDIVIDUAL, NAAMP, and COMPLETE sessions and calculated the percentage of nights the INDIVIDUAL and NAAMP sessions omitted species compared with the COMPLETE session. We also determined the median CI for

each species for the NAAMP and COMPLETE recording sessions and compared these with the INDIVIDUAL CI for each recording night with Wilcoxon Signed Rank Tests. We calculated the percentage of sessions that the INDIVIDUAL session CI (as a proxy for a typical NAAMP sampling night) over- or underestimated the median CI.

We also wanted to determine if NAAMP volunteers in Maine were surveying during the entire NAAMP sampling time period. We accessed data for 2006–2009 from the Maine NAAMP website (http://www.pwrc.usgs.gov/naamp; accessed 15 March 2011) and identified survey end times for each route per sampling time period and year. We identified the time of night for which 80 % of surveys were completed (NAAMP volunteer end time). We randomly selected individual recordings from within the NAAMP protocol time period truncated by the NAAMP volunteer end time and determined species detected and their respective CI. We calculated the median CI for each species and calculated the percentage of nights these matched the median CI from the COMPLETE session. We also determined the total number of detections by species pooled over route, sampling period, and year during 2006–2009.

Time as a Predictor of Species Detection and Maximum Calling Index

We used logistic regression to model the relationship between time (minutes after sunset) of INDIVIDUAL sessions and the probability of detecting a calling species. We did not include environmental or date variables in this analysis, because the NAAMP sampling time period remains static throughout the sampling season. Thus, we wanted to determine if species could be detected during the NAAMP sampling time period for all nights and conditions when a species is present, as would be the realistic case for volunteers conducting NAAMP surveys. Only recordings from COMPLETE sessions where a species was detected at least once were used for this analysis. Each recording was classified as a 1 (CI 1, 2, 3), or 0 (CI 0). Time was included in the model as both a first and second order term to produce a quadratic relationship between time and calling probability. Similar models were created to describe the relationship between time and the probability of detecting a CI 3, including only audio recordings with CI values 1, 2, or 3 and classified as 1 (CI 3) or 0 (CI 1, 2). We did not detect CI 3 for pickerel frogs; therefore, we used CI 2 as the maximum chorus value for this species (Crouch and Paton 2002). We included only COMPLETE nights during which a species was present, which limited number of recording sessions for a given site or year and required pooling our analysis over these variables. Model fit for each species was evaluated with likelihood ratio tests comparing models with and without time (null model) as a predictor (Agresti 2007). We added the time with the greatest detection probability to the earliest and latest observed sunset time during which a species was detected to determine if predicted peak times of detection and CI 3 were within the NAAMP specified sampling period.

Environmental Variables as Predictors of Species Detection

We used an information theoretic approach to determine the best generalized mixed model describing the probability of detecting each species during the full survey season (April to August) based on environmental variables (Burnham and Anderson 2002). Mixed models are useful for analyzing unbalanced data, separating between-group and between-individual effects, and for datasets with nested fixed effects (Veysey et al. 2009; Zuur et al. 2009). We pooled hourly environmental variables and species detections over the COMPLETE session to generate a single summary value for each COMPLETE night, because hourly environmental data recorded at weather stations may not represent hourly changes in environmental conditions at the recording sites. The response term was detection or nondetection of a given species on each night. Among explanatory variables we considered, the fixed effects in our models including nine environmental variables typically collected as part of the NAAMP sampling protocol (DAY, the quadratic day term DAYSQ, MOON, WIND, CLD, LOWT, the quadratic temperature term LOWTSQ, PRECIP, PRECIP24) and one interaction term (MOON*CLD) (Weir et al. 2005). HIGHT ($|r| > 0.20$, $P < 0.01$ for all variables except MOON) and HUMID ($|r| > 0.30$, $P < 0.001$ for all variables except WIND and CLD) were correlated with other variables and dropped from the analysis. LOWT, LOWTSQ, DAY, and DAYSQ were centered to reduce autocorrelation between the main and quadratic term. Random variables included YEAR and SITE and were initially fit as SITE nested within YEAR with the notation (1|YEAR/SITE). The initial model was fit with maximum likelihood estimation. We dropped individual terms based on smallest coefficient values and refit the model to achieve the smallest AIC value. Model parameter fit for the best model was estimated with restricted maximum likelihood estimation with the REML function in R (Zuur et al. 2009). We examined the effect of random variables with variance estimates. SITE and YEAR were first unnested and fit as individual random variables with the command (1|SITE) + (1|YEAR) for small (<0.001) or large (>20) variance estimates. If variance for either random effect remained too large or small, we dropped the term as a random effect, and the model was refit with the variable as a fixed effect. If this failed to correct the variance estimate of the remaining random term, we refit the model as a logistic model pooled over site and year.

We created additional models for four species targeted during early (wood frogs, spring peepers) and late (gray treefrogs, northern leopard frogs) spring NAAMP sampling

periods in Maine. NAAMP monitoring for these species is limited to a 3 to 4 week window in April and a minimum temperature threshold (5.6 and 10 °C for the early and late spring breeders, respectively [Maine Amphibian Monitoring Protocol, www.maineaudubon.org]). Of these species, wood frogs and northern leopard frogs are considered explosive breeders and may be less affected by temporal changes in environmental variables than spring peepers and gray tree frogs, which have longer breeding periods (Oseen and Wassersug 2002). Limiting this analysis to April allowed us to examine small changes in environmental variables that could affect calling behavior and thus detection probabilities. We used logistic regression to determine which environmental variables examined in the full season (April to August) model were most important for predicting species calling during April. We pooled over site and year as there were too few replications in the April dataset for each variable to create random effects in generalized mixed models. The quadratic terms DAYSQ and LOWTSQ were excluded from the models, because our target species call beyond April and thus were not expected to follow a quadratic pattern for April alone. An information theoretic approach was used to determine the best model. All statistical analyses were performed in R Statistical Software version 2.11.1 (R Development Core R Team 2010).

Results

Comparison of Recording Sessions

We collected recordings for 137 COMPLETE (0.5 h past sunset to sunrise) sessions, 75 % of all nights that ARS were deployed. Each session contained 7 to 12, two- to three- minute recordings made hourly after sunset. Eight species were recorded during the study: gray treefrog, bullfrog, green frog, pickerel frog, leopard frog, mink frog, wood frog, and spring peeper. One additional species (American toad) found in Maine was not recorded with ARS; however, it was detected at our survey sites with visual encounter surveys (Shearin 2012). The number of nights and dates each species was recorded varied by year and species (Table 1).

The number of species detected and their CI differed by recording session. Fewer species were detected during INDIVIDUAL sessions (median no. species±1 SE: 1±0.09) than during the NAAMP (2±0.10 species; Wilcoxon Z statistic=−6.86, $P<0.001$) and COMPLETE (2±0.10; Wilcoxon Z statistic=−7.31, $P<0.001$) recording sessions. The number of times a species was omitted during the INDIVIDUAL and NAAMP sessions compared with COMPLETE sessions differed by species (Table 2). Species were omitted more frequently during INDIVIDUAL sessions than during NAAMP. Approximately 80 % of Maine NAAMP

surveys during 2006–2009 were completed by 2,300 h (Appendix 2). Number of species detections by NAAMP volunteers varied by species (Table 1). The median CI differed significantly by recording session for some species (Table 2). INDIVIDUAL session CIs were congruent with COMPLETE session median CIs for greater than 50 % of recording nights for all species (Table 2). INDIVIDUAL calling codes from the NAAMP volunteer end time truncated session were congruent with COMPLETE median calling codes for >50 % of recording sessions for all species except mink frogs (Table 2).

Time as a Predictor of Species Presence and Maximum Calling Index

CI varied temporally and among species (Appendix 3). Mean CI for six species did not exceed CI 2 for the COMPLETE session, whereas, the mean CI for gray tree-frogs and spring peepers exceeded CI 2 within 2 and 4 h of sunset, respectively, and declined thereafter. The predicted time of maximum detection probability varied among species (Fig. 1). Maximum predicted detection probability also varied by species and exceeded 80 % for all species except pickerel frogs. The time of maximum probability for detecting a CI 3 (or CI 2 for pickerel frogs) also varied among species (Fig. 2). We were least likely to detect a CI 3 for bullfrogs and leopard frogs; the probability of detecting this value was <50 % throughout the sampling night. For each species, the maximum detection probability and detection of CI 3 occurred at different times, except for gray treefrogs (Table 3). For this species, both maximum detection probability and detection of CI 3 was greatest 32 min after sunset and declined throughout the night.

Environmental Variables as Predictors of Species Presence

Multiple environmental variables were predictive of presence during the full sampling period for seven of eight species (Appendix 4). Bullfrog presence was explained only by date (DAY and DAYSQ). Multiple environmental variables also were needed to predict calling during April by early spring breeders, and these models differed from models for the full sampling time period (Appendix 4). Leopard frogs were detected only in April, and there were no differences among variables included in final models among sampling seasons.

Discussion

Species Omissions and Calling Index Underestimates

We compared anuran species and their respective CI detected during the NAAMP-specified time period with those detected during the COMPLETE recording session. INDIVIDUAL

Table 1 Species detections by year, species omissions by recording session, and species detections reported by NAAMP volunteers during 2006–2009. INDIVIDUAL session is abbreviated as 'INDIV'

Species	Dates detected	Total no. nights detected	No. detections by year (No. nights, No. sites)				No. omissions by session type		No. detections by NAAMP volunteers (% of all NAAMP detections)
			2006 (29, 24)	2007 (40, 11)	2008 (65, 12)	2009 (13, 3)	INDIV	NAAMP	
Gray treefrog	16 Apr-18 Jul	66	9	10	43	4	14	0	624 (14)
Bullfrog	1 Jun-21 Jul	35	13	17	2	3	10	3	200 (4)
Green frog	3 May-11 Aug	62	21	25	8	8	18	4	605 (13)
Pickerel frog	18 Apr-7 Jun	6	0	2	4	6	5	2	81 (2)
No. leopard frog	17–21 Apr	7	0	0	7	0	2	1	18 (<1)
Mink frog	23 Jun-4 Aug	12	9	3	0	0	8	3	30 (<1)
Wood frog	16 Apr-5 Jun	20	0	3	15	2	5	1	680 (<1)
Spring peeper	16 Apr-3 Jul	60	3	9	42	6	9	0	1886 (42)

sessions consistently detected one fewer species than COMPLETE sessions. Species omitted during an INDIVIDUAL sampling session may be detected during subsequent surveys. For example, gray treefrogs were omitted during 21 % of INDIVIDUAL sessions compared with detections for COMPLETE sessions; however, no omissions occurred for the entire NAAMP session. This indicates that multiple surveys conducted during random sampling times within the NAAMP time period should eventually detect this species. For other species, however, omissions spanned the duration of the NAAMP sampling session. INDIVIDUAL

session omission rates for pickerel frogs and mink frogs were 83 and 67 %, respectively, and omission rates for the NAAMP session were 33 and 25 %, respectively. The predicted time of maximum detection of both species occurred after 0100 h. Surveys conducted during the NAAMP time period (i.e., ending by 0100 h) are likely to omit these species.

CI underestimates may be particularly problematic if used as an indicator of population size. For example, bullfrogs are considered invasive outside their native range (Ficetola et al. 2007), and CI is sometimes used as a surrogate for its population size (Shirose et al. 1997). While bullfrogs called

Table 2 Percentage of INDIVIDUAL session Calling Index (CI) randomly selected from NAAMP (0.5 h after sunset to 0100 h) and truncated NAAMP (0.5 h after sunset to 2300 h) sessions that match, overestimate, or underestimate the median CI for the COMPLETE session, and paired Wilcoxon Signed Rank tests for median CI by species and recording session. Significant differences at $\alpha=0.05$ are noted in bold type

Species	INDIVIDUAL CI comparisons with COMPLETE session						Wilcoxon signed rank results for CI comparisons					
	NAAMP session			Truncated NAAMP session			INDIVIDUAL-COMPLETE		INDIVIDUAL-NAAMP		COMPLETE- NAAMP	
	% of total nights detected[a]			% of total nights detected[a]			Z	P	Z	P	Z	P
	Match	Under	Over	Match	Under	Over						
Gray treefrog	62	6	32	58	9	33	−4.18	**<0.01**	−1.43	0.15	4.56	**<0.01**
Bullfrog	77	17	6	71	26	3	1.03	0.30	0.42	0.68	−1.10	0.27
Green frog	62	28	13	55	40	8	1.65	0.10	−0.53	0.60	−2.60	**0.01**
Pickerel frog	67	33	0	50	33	17	1.00	0.32	−1.00	0.32	−1.41	0.16
No. leopard frog	86	0	14	71	0	29	−1.00	0.32	−1.00	0.32	N/A[b]	N/A[b]
Mink frog	58	33	8	33	42	25	1.41	0.16	1.13	0.26	−0.45	0.65
Wood frog	60	10	30	60	20	20	−0.58	0.56	1.10	0.27	2.26	**0.02**
Spring peeper	62	10	28	60	12	28	−2.67	**0.01**	0.32	0.75	3.20	**0.00**

[a] Percentages for each species may not add up to exactly 100 % due to rounding. See Table 1 for total number of nights detected by species

[b] The comparison between the COMPLETE and NAAMP sessions for northern leopard frogs was not performed, because values were identical for these two session types

Fig. 1 Logistic regression models relating time (minutes past sunset) to the probability of detecting eight Maine amphibian species: **a** gray treefrog, **b** bullfrog, **c** green frog, **d** pickerel frog, **e** northern leopard frog, **f** mink frogs, **g** wood frog, and, **h** spring peeper
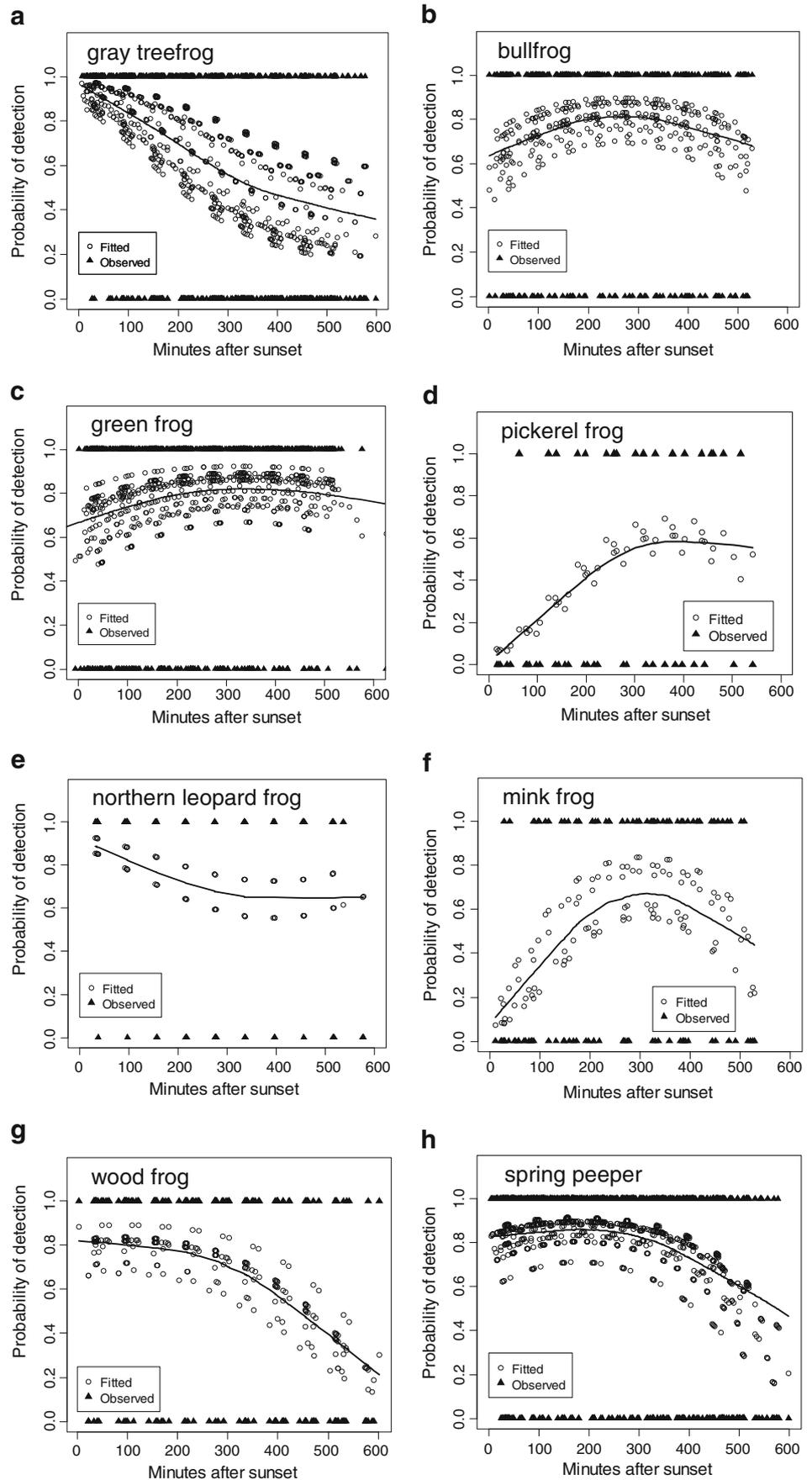
Fig. 2 Logistic regression models relating time (minutes past sunset) to the probability of detecting a maximum Calling Index (CI) for eight Maine amphibian species: **a** gray treefrog, **b** bullfrog, **c** green frog, **d** pickerel frog, **e** northern leopard frog, **f** mink frog, **g** wood frog, and, **h** spring peeper. CI 3 was used as the maximum CI value for species all but pickerel frogs; CI 2 was used as the maximum CI for this species, because CI 3 was not detected
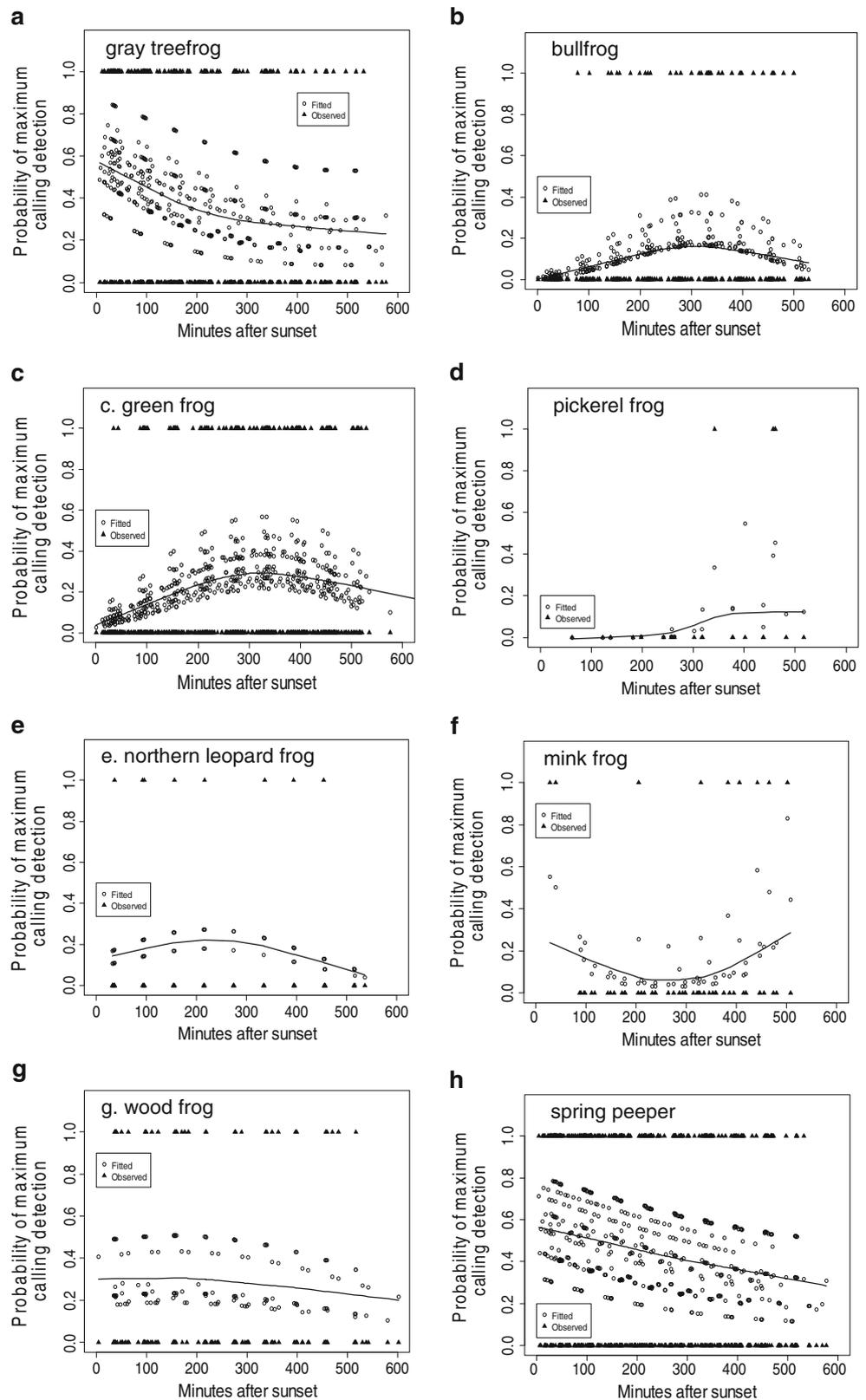
throughout the sampling period in our study area, the time of predicted peak detection occurred just before or after 0100 h, which is 2 h after most NAAMP volunteer surveys in the area

ceased. Bridges and Dorcas (2000) also reported peak calling times after 0100 h for this species. While naïve occupancy estimates can be corrected using detection probabilities (e.g.,

Table 3 Predicted times maximizing detection probability and maximum Calling Index (CI) detection by species. Time of night intervals were created by adding the predicted minutes after sunset to the earliest and latest sunset times observed during sampling periods for each species. Species are arranged in chronological order of detection times

[a] CI 3 not detected; [b] CI 2 used as maximum value

Species	Predicted min. after sunset maximizing detection (Time of night)	Predicted min. after sunset maximizing CI 3 detection probability (Time of night)
Gray treefrog	32 (1953–2102 h)	32 (1953–2102 h)
No. leopard frog	32 (1955–1958 h)	216 (2259–2302 h)[a]
Wood frog	100 (2100–2123 h)	154 (2154–2217 h)
Spring peeper	159 (2200–2308 h)	32 (1953–2101 h)
Bullfrog	275 (2403–0100 h)	319 (2447–0144 h)
Mink frog	298 (0101–0128 h)	502 (0425–0452 h)
Green frog	335 (0103–0205 h)	325 (2453–0155 h)
Pickerel frog	422 (0225–0319 h)	402[b] (0205–0259 h)

Weir et al. 2005), surveys that consistently omit or underestimate abundance due to improper sampling times may fail to adequately describe population trends.

In our study area, two additional species, northern leopard frogs and mink frogs, are of particular conservation concern. Northern leopard frogs are declining throughout their range (Hinshaw 1999) and are listed as a Species of Special Concern in Maine (www.maine.gov.ifw/wildlife/species/endangered_species/specialconcern). We detected this species on only seven COMPLETE nights (~5 %) during our study, an observation consistent with reports by NAAMP volunteers during the same period (14 detections, <1 %). Infrequent detections suggest that this species either is rare or is missed by audio surveys. Maine represents the southern range for mink frogs (Stockwell 1999), and their distribution may be particularly sensitive to climate change (Popescu and Gibbs 2009). We predicted that the best full chorus detection time for this species is around 0400 h, which is consistent with observations by Bevier et al. (2006). The mink frog CI for INDIVIDUAL sessions selected from both the full NAAMP and volunteer-truncated NAAMP sessions underestimated the median CI for 33 and 42 % of COMPLETE sessions, respectively. It is likely that surveys conducted during the NAAMP time period consistently underestimate CI and thus may fail to detect small changes in CI (such as from CI 3 to 2) that may reflect changes in population sizes.

Species detection and detection of a full chorus may not be represented equally by volunteer-based listener surveys. Time of survey with the greatest probability of detection for four species did not overlap with the time with the greatest probability of detecting their full chorus. For example, the best time to detect a full northern leopard frog chorus occurred 3 h after the best time to detect presence, although both times occurred within the NAAMP protocol sampling time. This may have implications for chorus size estimates within individual routes, where there is a greater probability of detecting full choruses at stops sampled later in the run. This discrepancy may not affect occupancy models, however, relative abundance estimates may be underestimated with this truncated sampling time without correcting for the latent CI (the maximum CI achievable at a site) (Royle 2004; Royle and Link 2005; MacKenzie et al. 2009). For example, mink frog CI underestimates in our study increased from 33 % to 42 % of nights for NAAMP sessions truncated at 2300 h.

Environmental Variables as Predictors of Peak Calling

Time is often a predictor of anuran calling, however, other variables may influence temporal calling patterns. In our study, time was modeled separately and then removed from analyses to examine environmental variables alone. This method allowed us to predict which date or environmental variable most affected calling so that we could determine which conditions within these breeding times optimized species or full chorus detection. Environmental variables affecting calling differed among species. For example, precipitation generally is thought to positively affect anuran calling, and volunteers may be instructed to conduct surveys on nights with light rain above a certain temperature threshold. Our results are consistent with other studies (Oseen and Wassersug 2002; Saenz et al. 2006; Steelman and Dorcas 2010) that found no effect of precipitation on calling occurrence by bullfrogs, pickerel frogs, and northern leopard frogs. Rain also was not associated with calling detection for bullfrogs and pickerel frogs in Maryland (Weir et al. 2005). As reported by Bevier et al. (2004), increased precipitation negatively affected calling detection for mink frogs; the occurrence of precipitation in the 24 h preceding the recording, however, positively affected calling detection for this species. In contrast to Saenz et al. (2006), we found a negative relationship between precipitation and calling by spring peepers. Precipitation was included in the final model for April-only spring peeper detection, although this variable appeared to have little effect. The contrast between our study and Saenz et al. (2006) highlights the need to consider survey location when determining effects of environmental variables on calling patterns. Saenz et al. (2006) surveyed amphibians in eastern Texas, where prolonged periods with no precipitation are common. In contrast, Maine is

characterized by cool springs and summers with frequent precipitation. Precipitation likely is not a limiting factor in our region, and thus heavy rains may affect calling through other mechanisms.

Wind speed negatively affected calling detection in green frogs, northern leopard frogs, and mink frogs in our study. Wind has also been reported to have a negative effect on detection of green frogs, and other ranids, in Maryland (Weir et al. 2005). However, Oseen and Wassersug (2002) found no effect of wind on green frogs, wood frogs, or spring peepers in New Brunswick, Canada, although they did see an effect on bullfrogs. As recommended in the NAAMP protocol, in our study we did not examine recordings from nights with wind codes greater than three, thus, it is unlikely that the negative effect of wind speed on calling detection in our study was the result of direct interference from wind.

We found that different combinations of variables predicted calling probability among species. This finding was similar for anurans in Maryland (Weir et al. 2005), thus suggesting the need for volunteers to record multiple environmental variables during surveys. Ideally, environmental data should be collected concurrently with call data (Dorcas et al. 2009). Additional environmental variables not routinely collected by volunteers also may be important. For example, water temperature was a strong predictor of calling by bullfrogs and green frogs, although this variable became less important later in the breeding season (Oseen and Wassersug 2002).

We also found differences in predictive environmental variables between April-only and full-season surveys for early spring breeders. For example, northern leopard frogs were detected only in April, and wood frogs were the only explosive breeder that called beyond April. In contrast to Oseen and Wassersug (2002), we found that additional variables were needed to predict calling during April compared with the full season. Date was the strongest predictor for the full season and had a negative effect on the probability of detecting wood frogs. This species called primarily during April and early May, therefore, it is likely that other environmental variables had less effect as breeding declined. Fewer variables were needed to predict calling by gray treefrogs and spring peepers during the full season compared with April alone. Since calling grows more energetically expensive with warmer temperatures as a function of increased calling rates toward the end of the breeding season (Taigen et al. 1985; Wells et al. 1996), it is possible that individuals calling later in the season are responding to cues that minimize energy expenditure. Spring peepers, for example, were not strongly affected by cloud cover and low temperatures in April. Over the full sampling season, however, calling was positively affected by temperature and negatively affected by precipitation and the cloud cover-moon interaction. Individuals reduced calling on nights where precipitation may have interfered with call transmission and on moonlit cloudless nights, when individuals potentially were more visible to predators (Weir et al. 2005).

One weakness in our dataset was the inclusion of multiple sites with single surveys (COMPLETE nights). Models described in MacKenzie et al. (2006) can model detection probabilities for datasets with missing observations, although these models assume that detection probabilities for a given species are equal among sites. Since we did not make this assumption with our dataset, our study may therefore underestimate site occupancy given imperfect detection. Thus, our study should not be used as a proxy to other NAAMP-related modeling studies (e.g., Royle 2004; Royle and Link 2005; Weir et al. 2005; Weir et al. 2009; Miller et al. 2011). Instead, our study describes entire night calling patterns throughout the night, beyond typical monitoring periods, that typically are not included in analysis of audio data and can be used to inform preexisting NAAMP detection and occupancy modeling. Furthermore, our study illustrates that additional survey effort may not be required to precisely model calling patterns for certain species in Maine (those that call primarily during the NAAMP time period). Using our naïve detection probabilities, gray treefrogs for example were always detected during the NAAMP interval and not detected during only 21 % of INDIVIDUAL sessions.

Our study also contributes to modeling the maximum attainable CI ('latent CI') (Royle 2004; Royle and Link 2005), which is derived from the observed CI, with greater observed CI values indicating a greater potential latent CI for a given site and species (Royle 2004; Royle and Link 2005). These models are built on values derived from a limited (e.g., NAAMP volunteer-truncated) sampling time, which may underestimate the true latent CI for species that routinely call in greater abundance or activity (depending on the definition of CI as an indicator of population size or activity level) during the post-NAAMP period. For example, at one site with multiple COMPLETE night surveys, we recorded mink frog CI values of (0, 1, 1) and (1, 2, 2) during NAAMP and COMPLETE sessions, respectively, resulting in a predicted lower latent CI for the former due to sampling bias rather than actual differences in abundance. Full night audio surveys, such as those presented here, can thus be used to evaluate whether modeled latent CIs are accurate or a reflection of the truncated NAAMP sampling interval. Current detection and occupancy modeling corrects for imperfect detection during the NAAMP sampling period; however, pairing NAAMP surveys with a subset of ARS-based full night surveys will allow researchers to determine the precision and effectiveness of these corrections across multiple species.

The longer NAAMP listening period at each stop accounts for resumption of normal calling activity following potential surveyor-induced disturbances (e.g., arrival at the

site or passing cars) at the beginning of the survey period, although few studies (e.g., Granda et al. 2008) have examined surveyor impacts on calling patterns. Because ARS are remote and automated, human disturbance during the recording period is not an issue. While the 2 min time intervals used in our study allowed us to collect recordings hourly over several nights, this abbreviated time interval may have affected detection of certain species. There is no consensus on an ideal time interval for anuran call surveys. However, this abbreviated time interval may affect detection of certain species. Shirose et al. (1997) found no difference in detecting North American bullfrogs between 3 and 5 min surveys, and Gibbs et al. (2005) proposed that 1 min surveys detected most species in New York State (USA). In contrast, other studies (Crouch and Paton 2002; Pierce and Gutzwiller 2004) found that 10–15 min surveys are needed for detecting at least 90 % of species. It is possible that our abbreviated recordings failed to detect all calling species. Additional studies are needed to determine the optimum recording interval to detect all calling anurans using ARS while accounting for nocturnal calling patterns.

Standardized volunteer-based audio surveys track long-term and regional changes in anuran populations. A unified sampling time period (0.5 h past sunset to 0100 h) allows for standardized data comparisons across sites and years. Most species are captured during this time period; however, our study suggests that it may not be sufficient for detecting certain species, such as pickerel frogs and mink frogs, and their full choruses in Maine. Further, certain species, such as northern leopard frog, were rarely detected in our study and were likewise rarely detected in NAAMP data for the same period. Whereas other studies have considered only a single site (e.g., Steelman and Dorcas 2010) or season (e.g., Oseen and Wassersug 2002), we suggest expanding survey efforts across multiple sites and seasons for pickerel frogs and mink frogs to better describe temporal calling patterns and relationships with environmental variables. Although detectability estimates can correct for false absences, consistently missing a species due to improper sampling times may underestimate occupancy even when detectability corrections are applied. Studies with longer survey times and additional sampling periods targeting rarely detected species may improve accuracy of the current NAAMP sampling protocol.
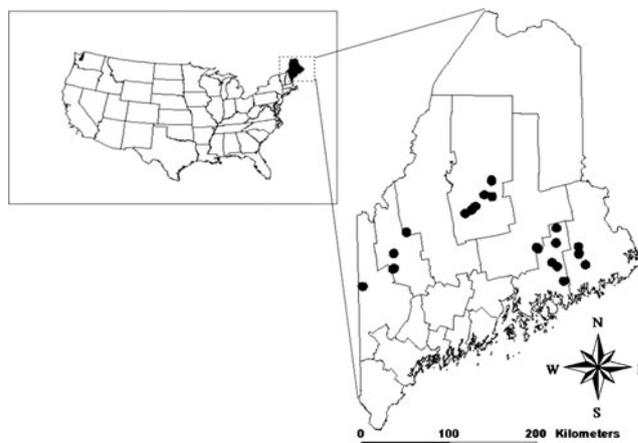
Appendix 1

Fig. 3 Locations of lakes and vernal pools where we deployed ARS during 2006–2009. Lakes ($n=24$) and vernal pools ($n=4$) are denoted by *circles*. Sites in close proximity to one another may not appear as independent circles due to overlapping
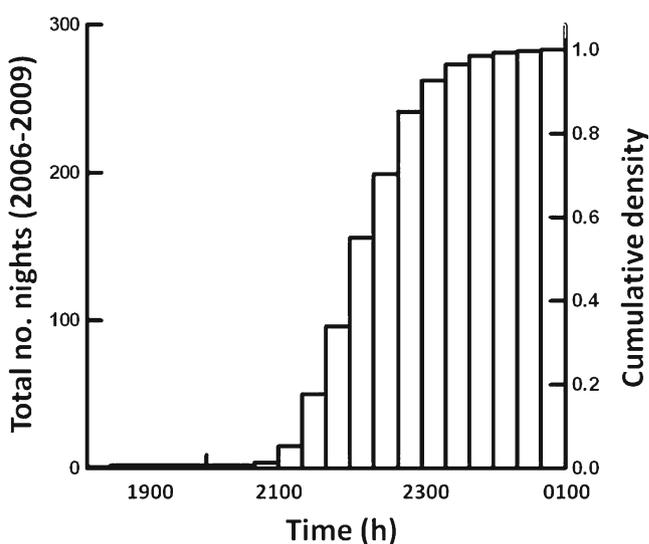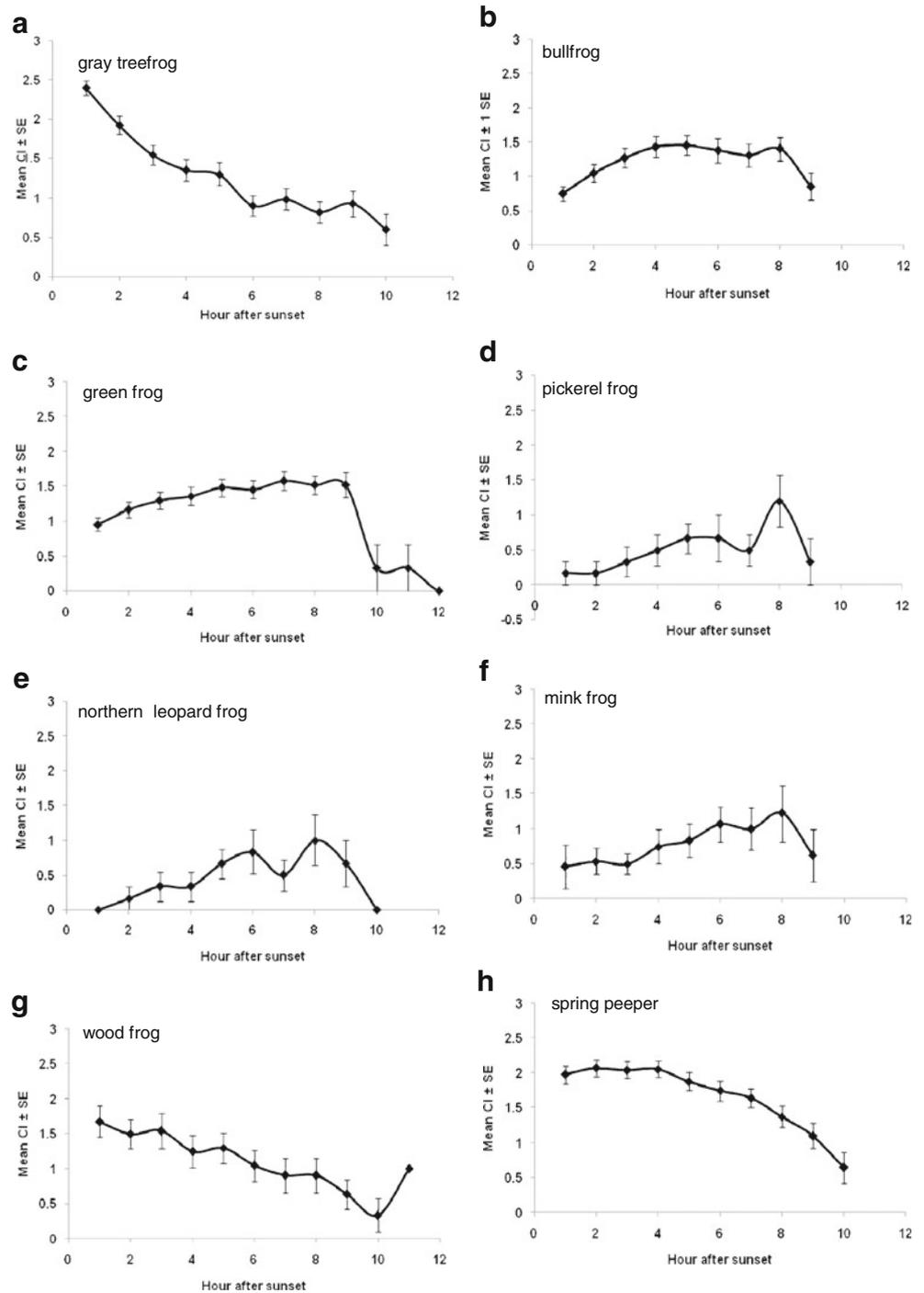
Appendix 2

Fig. 4 Cumulative density of survey end times for NAAMP volunteers during 2006–2009

Appendix 3

Fig. 5 Mean Calling Index
(CI) ± 1 standard error by hour
after sunset for eight species: **a**
gray treefrog, **b** bullfrog, **c**
green frog, **d** pickerel frog, **e**
northern leopard frog, **f** mink
frog, **g** wood frog, and, **h** spring
peeper. Individual recordings
originally measured in minutes
after sunset were grouped into
hours after sunset to produce
mean CI

Appendix 4

Table 4 Parameter estimates for variables retained in best models fit by generalized mixed models and stepwise logistic regression for predicting detection of calling amphibians by environmental variables for all species during the full sampling season (April – August) and spring breeders (April only). Significant parameters at $\alpha=0.05$ are in bold text

Species	Full year models				April only models		
	Variables	Coefficient ± SE	P	Random effects	Variables	Coefficient ± SE	P
Gray treefrog	DAY	−0.01±0.01	0.30	1|YEAR/SITE	MOON	3.36±2.36	0.15
	DAYSQ	−0.002±0.0005	**<0.001**		CLD	−5.54±3.26	0.09
	MOON	1.78±1.31	0.17		MOON*CLD	5.06±3.61	0.16
	CLD	0.46±0.32	0.15				
	PRECIP	−0.96±0.45	**0.03**				
	MOON*CLD	−1.11±0.55	**0.04**				
Bullfrog	DAY	0.07±0.02	**<0.001**	1|SITE+1|YEAR	n/a	n/a	n/a
	DAYSQ	−0.001±0.0003	**0.001**				
Green frog	DAY	0.09±0.02	**<0.001**	1|SITE+1|YEAR	n/a	n/a	n/a
	DAYSQ	−0.002±0.0004	**<0.001**				
	WIND	−1.08±0.45	**0.02**				
	LOWT	−0.10±0.05	**0.04**				
	LOWTSQ	0.02±0.008	0.06				
	PRECIP	0.33±0.21	0.11				
Pickerel frog	LOWT	−0.51±0.33	0.12	Logistic model	n/a	n/a	n/a
	LOWTSQ	−0.08±0.05	0.10				
Northern leopard frog	DAY	−1832.11±2485.84	0.46	Logistic model	DAY	−1.66±1.42	0.24
	DAYSQ	−19.55±26.52	0.46		MOON	54.65±37.70	0.15
	WIND	73.02±105.83	0.46		WIND	7.08±5.04	0.16
	LOWT	−179.55±261.68	0.49		LOWTCTR	1.34±1.29	0.30
	LOWTSQ	−19.05±27.80	0.49				
Mink frog	DAY	0.46±0.20	**0.02**	Logistic model	n/a	n/a	n/a
	DAYSQ	−0.005±0.002	**0.03**				
	MOON	0.71±1.32	0.59				
	WIND	−0.56±0.68	0.41				
	CLD	−0.06±0.28	0.84				
	LOWT	0.06±0.51	0.91				
	LOWTSQ	0.02±0.04	0.64				
	PRECIP	−0.82±0.64	0.20				
	PRECIP24Y	0.21±0.003	0.99				
Wood frog	DAY	−0.75±0.52	0.15	1|SITE	DAY	−0.44±0.17	**0.01**
	DAYSQ	−0.008±0.007	0.23		MOON	−11.07±4.81	**0.02**
	LOWT	0.23±0.15	0.13		WIND	−1.73±0.83	**0.04**
	PRECIP	−3.23±3.26	0.32		CLD	−7.63±3.21	**0.02**
					LOWT	0.41±0.20	**0.04**
					MOON*CLD	10.02±4.29	**0.02**
Spring peeper	DAY	−0.13±0.03	**<0.001**	1|SITE	DAY	0.15±0.20	0.44
	DAYSQ	−0.003±0.0006	**<0.001**		MOON	0.02±0.35	0.95
	MOON	1.34±1.26	0.28		WINDCODE	−1.19±1.18	0.31
	CLD	0.90±0.40	**0.02**		CLDCODE	0.005±0.006	0.14
	LOWT	0.21±0.10	**0.04**		LOWT	0.26±1.50	0.86
	PRECIP	−0.56±0.26	**0.03**		PRECIP	0.02±0.0003	0.99
	MOON*CLD	−1.29±0.61	**0.04**				

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