
EFFECTS OF TEMPERATURE AND TEMPORAL FACTORS ON ANURAN DETECTION PROBABILITIES AT CAPE COD NATIONAL SEASHORE, MASSACHUSETTS, USA: IMPLICATIONS FOR LONG-TERM MONITORING

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Abstract.—To evaluate the efficacy of calling surveys, we studied effects of temperature and temporal factors (diel, seasonal, annual) on detection probabilities for anurans of southeastern Massachusetts, USA. We used automated recording systems (ARS) to quantify diel chronology during one field season, and conducted calling surveys to investigate seasonal and annual variation in calling at 103 wetlands over six years at Cape Cod National Seashore. Five species detected with ARS called primarily between sunset and midnight, with mean calling time of *Anaxyrus fowleri* and *Lithobates sylvaticus* nearer to sunset than *Pseudacris crucifer*, *Lithobates catesbeianus*, or *Lithobates clamitans*. Of eight species recorded during calling surveys (the preceding five plus *Scaphiopus holbrookii*, *Hyla versicolor*, and *Lithobates palustris*), detection probabilities of all but *Scaphiopus holbrookii* and *Lithobates sylvaticus* varied seasonally. Peak detection periods ranged from 11 to 33 days and peak period detection probabilities ranged from 0.06 for *Scaphiopus holbrookii* to 0.84 for *Pseudacris crucifer*. There was strong to moderate support for models with annual variation for all species except *Hyla versicolor*. Detectability was affected more by surface water temperature than by air temperature, but models with both received greater support in five species. For six species, models with temperature and seasonal effect received the greatest support, indicating that detectability is a function of both temperature and day of year. Durations of peak calling periods were long enough and detection probabilities high enough to effectively monitor six of the eight species with calling surveys.

Key Words.—ambient temperature; annual variation; anuran monitoring; calling anuran surveys; diel calling; seasonal variation

INTRODUCTION

Anuran calling surveys are widely used to study landscape ecology (Gagne and Fahrig 2007; Eigenbrod et al. 2008), evaluate restoration efforts (Stevens et al. 2002), and monitor population trends (Weir et al. 2009). One reason for the extensive use of calling surveys is their cost effectiveness (Weir and Mossman 2005), but many temporal and environmental factors can influence calling behavior of anurans (Oseen and Wassersug 2002; Saenz et al. 2006), and reduce detection probabilities (MacKenzie et al. 2006). Ignoring detection probabilities can lead to biased estimates of occupancy (Mazzerole et al. 2007): calling surveys should be conducted when detection probabilities are highest to maximize precision and efficiency (Shirose et al. 1997; Dorcas et al. 2009).

Weir et al. (2005) found that detection probabilities for

calling anurans varied most with temporal (date, time of night) and environmental factors (air temperature, moonlight, wind). Other studies (Todd et al. 2003; Gooch et al. 2006; Kirlin et al. 2006; Saenz et al. 2006) reached similar conclusions, but also found water temperature and rainfall patterns to be important. Collectively, these studies indicate that factors influencing detectability of anurans during calling surveys vary among species, as well as geographically within a species. Because anuran detection probability can be so variable, any study or monitoring program using calling surveys must consider local chronology (e.g., diel, seasonal, and annual variation in calling) and environmental factors (weather conditions, air and water temperature) when determining when to sample and the number of surveys needed.

One of the most widespread uses of calling surveys is the North American Amphibian Monitoring Program

(NAAMP), which is a long-term monitoring program to assess population trends of calling amphibians at regional or national scales (Weir and Mossman 2005). NAAMP observers survey along random roadside routes during regionally-determined sampling periods when detection probabilities are thought to be highest, but confirmation or refinement of these sampling periods is needed for many regions (Weir and Mossman 2005). Crouch and Paton (2002) quantified calling phenology of seven anuran species in southern Rhode Island, USA, and made monitoring recommendations based on sampling 31 wetlands for a single season. However, a multi-year study of *Anaxyrus fowleri* in eastern Massachusetts showed that peak calling periods varied among years and survey windows based on a single season underestimated the breadth of a species' long-term calling period (Tupper et al. 2007). Thus, multi-year data are needed to better define calling survey periods.

Our objectives were to assess variation in anuran detection probabilities at Cape Cod National Seashore, Massachusetts, USA due to air or water temperature and at three temporal scales (diel, seasonal, and annual). We also wanted to estimate interspecific variation in detection probabilities during peak calling periods and use these estimates to determine the number of survey events and sample sites needed to obtain given levels of probability and precision (MacKenzie et al. 2006). Our results, which are among the first to assess annual variation in detection probabilities of North American anurans, allow us to refine recommendations for monitoring anurans with calling surveys in southern New England and assess the feasibility of calling surveys for localized monitoring.

MATERIALS AND METHODS

Study site and site selection.—We conducted fieldwork within and adjacent to Cape Cod National Seashore (17,646 ha) in Barnstable County, Massachusetts (Tupper et al. 2007). Using a stratified random design and the Cowardin et al. (1979) wetland classification scheme, we selected 103 wetlands for the development and implementation of a long-term anuran monitoring program (Paton et al. 2003; Tupper and Cook 2008). We surveyed five types of wetlands: lacustrine wetlands; seasonally-flooded ponds in a woodland landscape; seasonally-flooded ponds in a dune grass (*Ammophila breviligulata*) landscape; riverine marshes; and forested swamps (Paton et al. 2003).

Diel variation.—To quantify diel variation in calling activity, we used automated recording systems (ARS; Dorcas et al. 2009) at four wetlands in 2001. Each ARS operated 24 h per day and sampled calling anurans every 30 min by recording for 30 s. For each 30 s “sample” we recorded time, species calling, and a calling index

value (0–3) following NAAMP guidelines (Weir and Mossman 2005). Dates of ARS operation were based on anuran calling data from Rhode Island (Crouch and Paton 2002) and extended from 26 March to 31 July. We monitored two seasonally-flooded ponds in Eastham, Massachusetts where *Lithobates sylvaticus* and *Pseudacris crucifer* were known to breed, from 26 March to 31 July and 26 March to 23 April, respectively. We monitored a cranberry bog in Wellfleet with *A. fowleri* from 28 April to 26 June and a riverine wetland with *Lithobates clamitans* and *L. catesbeianus* on the Upper Pamet River in Truro, from 27 June to 31 July.

Because time of day data are on a circular scale, we used circular statistics software (Oriana 3.0, Kovach Computing Services, Wales, UK) to compare mean time of calling within and among species. For each species recorded at two or more ponds (i.e., *P. crucifer*, *L. clamitans*, *L. sylvaticus*), we first used the Watson-Williams F-test (Zar 1998) to test for interpond differences in mean calling time. Results from these tests were non-significant (i.e., $P > 0.05$), thus we pooled data among ponds for subsequent analyses involving these three species. We then tested for inter-specific differences in calling chronology, again using the Watson-Williams F-test. The Rayleigh uniformity test (Batschelet 1981) was used to determine if calling was uniformly distributed over a 24-hr period.

Seasonal, annual, and temperature variation.—In 2001, we conducted calling surveys from 23 March to 5 September, whereas in 2003–2007, we surveyed from 10 April to 24 July. We surveyed 103 wetlands on 346 evenings total ($\bar{x} \pm SD = 57.7 \pm 7.3$ evenings annually) over six field seasons (i.e., years), with 3,767 5-min surveys completed in total (627.8 ± 118.4 5-min surveys annually). We surveyed from 30 to 67 sites annually (53.8 ± 17.9) with the number of temporal replicates at a site in any given year ranging from 4 to 24 (11.66 ± 4.35). Over the course of the 6-yr study, the total number of surveys at a site ranged from 4 to 100 (36.57 ± 34.06). We surveyed 21 sites in all six years, nine in five years, five in four years, 32 in three years, and 36 in only a single year.

With the exception of surveys to detect *L. sylvaticus* in 2001 (93 of 3,777 sampling events; ~ 2%), we began surveys from 0–30 min after sunset and typically ended around midnight. We rotated the sampling order of wetlands weekly to reduce potential temporal sampling bias. We used a total of four trained and experienced observers over the six-season sampling period. One observer conducted surveys in all six years and the remaining three observers for one, two, and three years, respectively.

We recorded up to four potential calling index values (0–3) at each site during a 5-min survey following NAAMP guidelines (Weir and Mossman 2005). We also recorded date, time, wind speed (Beaufort scale), sky

conditions, and ambient temperature (to the nearest 0.5° C) during each sampling event (Weir and Mossman 2005). We used a thermometer placed 1.5 m high for 5 min to measure air temperature at the survey station. We measured surface water temperature by placing a thermometer 1–3 cm below the water’s surface nearest the listening station, which was located at a central point on the wetland’s shoreline.

We used a maximum likelihood-based approach to estimate detection probabilities for each species, which is the conditional probability that a species was detected at site *i* during survey *t* (p_{it}), assuming it was present, using program PRESENCE 2.3 (MacKenzie et al. 2006). With PRESENCE, equal sampling effort is not required at all sites (MacKenzie et al. 2006). For this study, we were only interested in factors that might affect detection probabilities (*p*). For all models, we held site occupancy (ψ), colonization (γ), and extinction (ϵ) probabilities constant, while allowing detection probabilities (*p*) to vary. The effects of season (i.e., date) were modeled as a linear date function (Julian date) or a quadratic date function (Julian date + Julian date²; Weir et al. 2005) and annual variation was modeled using the “seasonal effects” model in PRESENCE.

We assessed effects of ambient temperature on calling anuran detection probabilities by incorporating these parameters as sampling covariates. Detection probability may be most affected by air or surface water temperature, depending on species (Gooch et al. 2006; Steelman and Dorcas 2010). Fouquette (1980) concluded that using both air and water temperatures were good predictors of the body temperatures of calling anurans. We therefore compared models with both air and surface water temperature by adding temperature covariates, individually and in tandem, to the best temporal models for each species.

We ranked competing models based on Akaike Information Criterion (AIC) by calculating the differences between each candidate model and the model with the lowest AIC (Δ_i AIC). We then used the Akaike weight (w_i) for each model (the estimated probability that a particular model is the best model) to guide final model selection (Burnham and Anderson 2002). However, because effective sample size (number of sites) relative to number of parameters was not very large (i.e., < 40), we based model comparison on AICc, a small sample bias adjustment to AIC (MacKenzie et al. 2006). In addition, we removed models identified by PRESENCE as having errors of convergence in the variance-covariance matrix.

We used output from the quadratic date function (Julian date + Julian date²) models to calculate detection probability for a species over the course of the field season. We then defined “peak calling period” as the range of dates, centered on the date of maximum detection probability (Max *p*), during which the daily

detection probability (*p*) exceeded 0.9 * Max *p*. We calculated the “detection probability during peak calling period” as the mean value of *p* for the dates within the “peak calling period.”

To aid planning and development of more localized monitoring programs in our region, such as at a park or wildlife refuge, we applied the “peak period” detection probabilities and site occupancy rates from our long term data to estimate “optimal” sampling effort (temporal and spatial) needed. MacKenzie and Royle (2005) define an “optimal” sampling strategy as one that provides an 85% to 95% probability of confirming that a target species occupies a site. Thus, for each species, we estimated the number of sampling occasions per site needed to achieve 90% and 95% probability of detecting the target species at least once during its peak calling period in a given year, at sites where present, using the formula $p^* = 1 - (1 - p)^k$, where *p* = detection probability and *k* = number of sampling occasions/site (MacKenzie and Royle 2005). In addition, for each species, we calculated the number of wetlands necessary to sample to estimate ψ with a standard error of 0.05 and 0.1, using equation 6.3 in MacKenzie et al. (2006).

RESULTS

Diel variation.—The five species detected with ARS each had specific time of day when frequency of calling was highest (Fig. 1) and the mean calling time, relative to sunset, varied significantly among species ($F = 11.65$, $df = 4,3934$, $P < 0.001$). Pairwise comparisons identified two groups of species whose mean calling times differed significantly (Table 1). Most calling by *L. sylvaticus* and *A. fowleri* occurred prior to or immediately after sunset whereas *P. crucifer*, *L. clamitans*, and *L. catesbeianus* had peak calling later in the evening (Table 1, Fig. 1).

TABLE 1. Mean calling time, in minutes relative to sunset, for species recorded by automated recording systems and results of Raleigh test of uniformity for each species. Vector length (*r*) is a measure of calling time concentration ranging from zero to one, with larger values indicating a more concentrated calling distribution and “n” is number of detections. Homogenous groups (a) or (b) were determined by Watson-Williams F Test pairwise comparisons.

Species	n	Mean Time	<i>r</i>	99% Confidence Interval		Rayleigh Z	<i>P</i>
				Lower Limit	Upper Limit		
<i>A. fowleri</i> (b)	87	101	0.92	75	187	73.4	<0.0001
<i>P. crucifer</i> (a)	1397	199	0.56	181	217	436.3	<0.0001
<i>L. catesbeianus</i> (a)	232	222	0.72	191	254	120.4	<0.0001
<i>L. clamitans</i> (a)	2089	206	0.29	174	237	169.2	<0.0001
<i>L. sylvaticus</i> (b)	134	55	0.44	-23	134	25.5	<0.0001

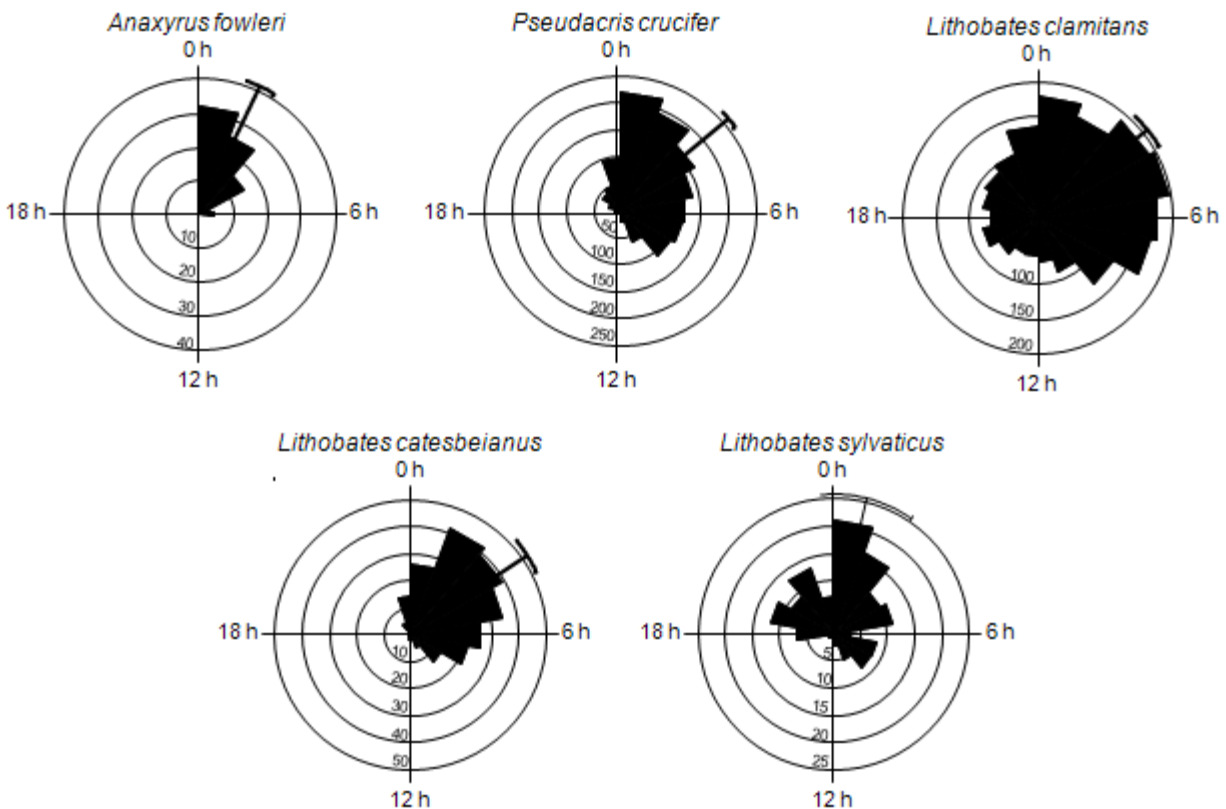


FIGURE 1. Frequency distribution of anuran calling detected with automated recording systems in relationship to sunset (0 h) at Cape Cod National Seashore. Length of bar represents number of 30 second “samples” in which calls were detected, within each time period. Mean and 99% confidence interval are shown.

Relatively high vector length values (r) for *A. fowleri* (0.919) and *L. catesbeianus* (0.721) indicate that calling in these species was concentrated around the mean calling time, whereas calling of *P. crucifer* (0.559), *L. clamitans* (0.285), and *L. sylvaticus* (0.436) was less concentrated (Table 1).

Seasonal, annual and temperature variation.—Each of the eight species recorded had a distinctive calling season, which for data pooled over the six years extended over 19 days for *L. sylvaticus* (28 March–15 April), 39 days for *S. holbrookii* (1 May–8 June), 49 days for *Hyla versicolor* (6 June–23 July), 74 days for *L. palustris* (11 April–23 June), 89 days for *A. fowleri* (20 April–17 July), 88 days for *L. catesbeianus* (6 May–2 Aug), 114 days for *P. crucifer* (19 March–9 July), and 141 days for *L. clamitans* (11 April–29 August).

For all species except *S. holbrookii* and *L. sylvaticus*, there was strong support for models that included a seasonal variation component (Julian date + Julian date²) in detection probabilities (Appendix 1). *Pseudacris crucifer* had the earliest “peak detection period”, followed by *L. palustris*, *A. fowleri*, and *S. holbrookii*,

whereas peak detection periods for *H. versicolor*, *L. clamitans*, and *L. catesbeianus* were later in the season (Table 2, Fig. 2). We were unable to model this effect for *L. sylvaticus*, likely because of insufficient sampling in late March and early April.

There was strong support for models with an annual variation component for *S. holbrookii*, *A. fowleri*, *P. crucifer*, and *L. catesbeianus*, and moderate support for *L. clamitans*, *L. palustris*, and *L. sylvaticus* (Appendix 1). Quadratic date models showed annual variation in peak timing and/or probability of detection for these species (Appendix 2). The length of the calling season varied annually and the first and last dates of calling based on pooled data produced a wider “calling window” than recorded in any given year (Table 3).

Detection probability of all species except *S. holbrookii* was also affected by ambient temperature (Appendix 3). Although both air and surface water temperature were highly correlated (Spearman’s $r = 0.841$, $P < 0.0001$), surface water temperature had a greater influence on detection probabilities. For the seven species affected by temperature, models with only water temperature were more heavily weighted than comparable

TABLE 2. Inter-specific variation in detection probability, showing maximum detection probability (Max p), date of Max p , peak calling period, duration of peak calling period in days, and mean detection probability during the peak calling period (Peak Period p).

Species	Max p	Date of Max p	Peak Period	Duration	Peak Period p
<i>S. holbrookii</i>	0.057	24-May	19 May to 29 May	11	0.056
<i>A. fowleri</i>	0.387	6-Jun	25 May to 19 June	26	0.373
<i>H. versicolor</i>	0.336	30-Jun	23 June to 7 July	15	0.325
<i>P. crucifer</i>	0.868	10-May	24 April to 26 May	33	0.842
<i>L. catesbeianus</i>	0.693	13-Jul	30 June to 26 July	27	0.669
<i>L. clamitans</i>	0.785	3-Jul	13 June to 24 July	42	0.760
<i>L. palustris</i>	0.574	12-May	2 May to 21 May	20	0.554

ones with air temperature. However, for *A. fowleri*, *P. crucifer*, *L. catesbeianus*, *L. clamitans*, and *L. palustris*, models with both water and air temperature were more heavily weighted than models with water alone. Moreover, for all species except *S. holbrookii* and *L. sylvaticus*, models that included both temporal components (seasonal and/or annual variation) and temperature components (water or water and air) were the most heavily supported. Temperature covariates had positive coefficients, indicating that anurans were more likely to vocalize on warmer nights. Also, as the calling season progressed for a given species, mean surface water temperatures associated with both calling and non-calling events increased, suggesting that temperature thresholds for calling increased as the breeding season

progressed (Appendix 4).

The “optimal” number of sampling occasions per site during the peak calling season for each species ranged from 2 to 101, with ≤ 6 for six of the eight species (Table 4). Increasing the probability of at least one detection from 90% to 95% required a slight increase in number of sampling events. The number of wetlands needed to survey ranged from 8–33 to obtain a SE for ψ of 0.1, and from 32–132 to obtain a SE for ψ of 0.05.

DISCUSSION

Diel phenology.—Anuran species in a locale may differ in the timing of their daily peak calling (Mohr and Dorcas 1999) plus, at the intra-specific level, diel calling

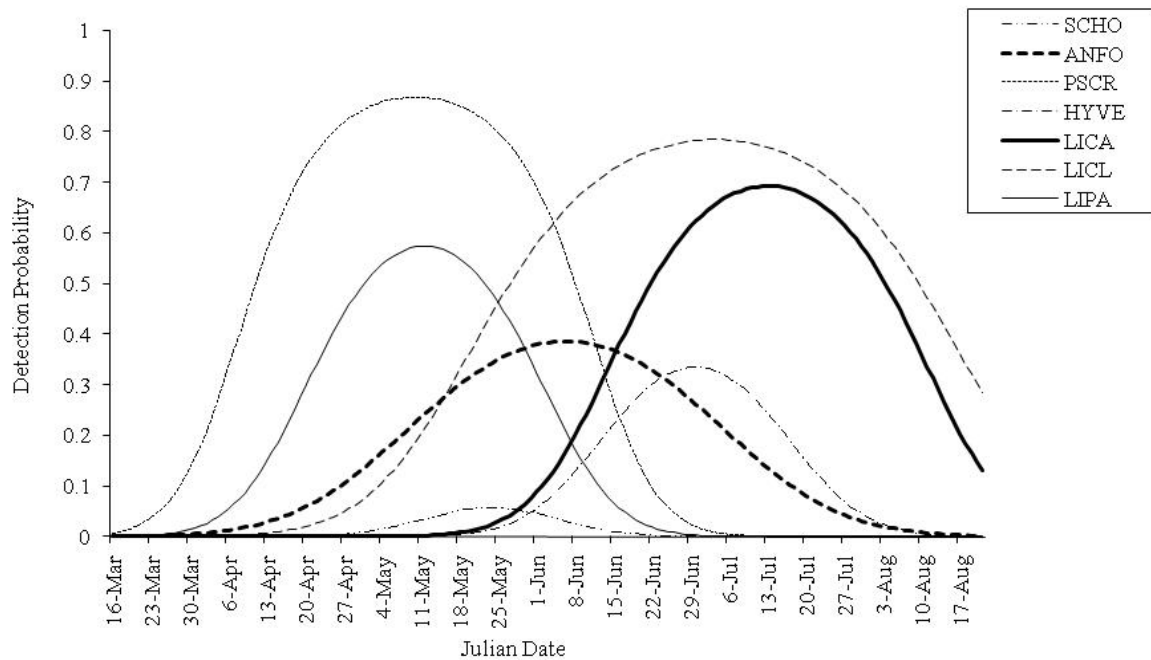


FIGURE 2. Seasonal variation in detection probabilities of calling anurans during 5-minute calling surveys at Cape Cod National Seashore, based on model $\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{julian} + \text{julian}^2)$ in Appendix 1. SCHO = *Scaphiopus holbrookii*, ANFO = *Anaxyrus fowleri*, HYVE = *Hyla versicolor*, PSCR = *Pseudacris crucifer*, LICA = *Lithobates catesbeianus*, LICL = *L. clamitans*, LIPA = *L. palustris*.

TABLE 3. Annual variation in length of observed calling season for eight species of anurans at Cape Cod National Seashore.

Species	Number of Days in Calling Season						All Years Pooled
	2001	2003	2004	2005	2006	2007	
<i>S. holbrookii</i>	0	34	0	5	36	1	39
<i>A. fowleri</i>	69	78	80	85	85	65	89
<i>H. versicolor</i>	0	29	43	43	43	34	49
<i>P. crucifer</i>	101	75	72	87	79	93	114
<i>L. catesbeianus</i>	56	45	44	50	59	80	88
<i>L. clamitans</i>	120	79	80	79	108	94	141
<i>L. palustris</i>	53	64	64	65	51	44	74
<i>L. sylvaticus</i>	9	1	1	0	1	8	20

patterns may vary geographically. For example, on Cape Cod, *L. catesbeianus* and *L. clamitans* call at peak levels near midnight, whereas both species often do not call at peak levels until 0400 h in South Carolina (Mohr and Dorcas 1999). Similarly, *L. sylvaticus* in New Brunswick, Canada called almost exclusively from sunset to sunrise (Oseen and Wassersug 2002) while in Rhode Island this species generally calls diurnally (Crouch and Paton 2000). During the present study on Cape Cod, most *L. sylvaticus* calling occurred diurnally or within two hours after sunset.

Given this potential for variation and the significant role time of day plays in the detectability of most species (Weir et al. 2005), we concur with Bridges and Dorcas (2000) that diel variation should be quantified locally to ensure that monitoring occurs during times of day when detection probabilities are high. However, in contrast to Mohr and Dorcas (1999) and Bridges and Dorcas (2000), our results agree with others (e.g., Johnson and Batic 2001; Todd et al. 2003; Weir et al. 2005) in finding that current NAAMP guidelines to survey from 30 min after sunset to 0100 h (Weir and Mossman 2005) are generally appropriate. Calling surveys designed to monitor *L. sylvaticus* in coastal New England should be earlier in the day than current NAAMP guidelines (i.e., between \pm two hours from sunset).

Seasonal variation.—Inter-specific variation in the seasonality and detectability of calling anurans is well-known (Bishop et al. 1997; Corn et al. 2000; Crouch and Paton 2002). The seasonal chronology we documented conformed to regional patterns previously described for New England (Babcock and Hoopes 1940). Similarly, the inter-specific variation in duration of “peak calling period” that we found largely agrees with previous research in northeastern North America (Crouch and Paton 2002; Oseen and Wassersug 2002; Weir et al. 2005; de Solla et al. 2006), although populations of these same

TABLE 4. Number of sampling occasions needed during a species’ peak detection period to achieve 90% and 95% probability of at least one detection at an occupied site, and estimated number of wetlands needed to sample to obtain standard errors of 0.05 and 0.1 for estimates of Ψ (based on 90% probability of at least one detection).

Species	mean ψ	peak period p	Number of sampling occasions needed to achieve:		Number of wetlands needed to obtain:	
			90% probability of at least one detection	95% probability of at least one detection	ψ SE of 0.05	ψ SE of 0.1
<i>S. holbrookii</i>	0.116	0.056	41	53	48	12
<i>A. fowleri</i>	0.643	0.373	5	7	132	33
<i>H. versicolor</i>	0.109	0.325	6	8	45	11
<i>P. crucifer</i>	0.952	0.842	2	2	32	8
<i>L. catesbeianus</i>	0.386	0.669	3	3	102	26
<i>L. clamitans</i>	0.790	0.760	2	3	98	24
<i>L. palustris</i>	0.200	0.554	3	4	76	19
<i>L. sylvaticus</i>	0.344	0.024	95	124	111	28

species in more southerly portions of their range have longer calling seasons and peak periods (Saenz et al. 2006).

Because the chronology of peak detection periods for a species tends to vary by latitude and elevation (Berven 1982; de Solla et al. 2006), it is important to identify these periods locally. For example, the peak calling date for *P. crucifer* on Cape Cod was 10 May, as opposed to 5 May in Rhode Island (Crouch and Paton 2002). Similar comparisons of other species are as follows: *H. versicolor*, 30 June vs. 11 June; *L. catesbeianus*, 13 July vs. 24 July; *L. clamitans*, 3 July vs. 15 July; *L. palustris*, 12 May vs. 5 May in Rhode Island (Crouch and Paton 2002). Thus, even for areas less than 130 km apart and at similar elevations, peak calling dates were up to 19 days apart. Weir and Mossman (2005) noted the need to refine NAAMP seasonal sampling periods in many regions and our data suggest the following four sampling periods for maximum detection in the Cape Cod region: early spring (18 March–7 April) for *L. sylvaticus*; mid-spring (1 May–21 May) for *P. crucifer* and *L. palustris*; late spring (27 May–16 June) for *A. fowleri*; and early summer (26 June–16 July) for *L. clamitans*, *H. versicolor*, and *L. catesbeianus*.

In addition to variation in the timing of peak detection periods, there is both inter and intra-specific variation in peak detection probabilities. The former may be due to differences in calling strategies, length of breeding periods, and strength of vocalization (de Solla et al. 2005) and the latter may reflect differences in abundance (MacKenzie et al. 2006). Given the relationship between detection probability and sampling effort needed to detect a species (MacKenzie et al. 2006), local

estimates of peak period detection probability are important in developing local monitoring programs. The species with the greatest detection probability on Cape Cod, *P. crucifer* ($p = 0.84$), was also the most detectable species in Rhode Island ($p = 0.96$; Crouch and Paton 2002), Maryland ($p = 0.89$; Weir et al. 2005) and Ontario (de Solla et al. 2005), but was less detectable in east Texas ($p = 0.38$; Saenz et al. 2006). In contrast, peak period detection probabilities of Cape Cod *A. fowleri*, *H. versicolor*, *L. catesbeianus*, and *L. palustris* were in the middle of the range of published values for these species (Crouch and Paton 2002; de Solla et al. 2005; Gooch et al. 2006; Saenz et al. 2006).

Annual variation.—Annual variation in calling intensity and chronology occurs in many species (Corn et al. 2000; Saenz et al. 2006) and because of highly variable temperatures in early spring, may be greater for explosive, early season breeders such as *L. sylvaticus* than for species that breed later (Crouch and Paton 2000; Oseen and Wassersug 2002). However, our results indicate that annual variation in timing and/or probability of detection occurs in most anuran species on Cape Cod, regardless of the time of the year they call. Thus, we concur with Tupper et al. (2007) that survey windows be expanded to incorporate annual variation in peak calling periods. Moreover, considering intra-specific variation in calling between nearby sites (Todd et al. 2003; Gooch et al. 2006) and the low detection probabilities of some species (de Solla et al. 2005; Weir et al. 2005), we agree that multiple samples within a species' "peak calling period" would result in more detections (de Solla et al. 2005) and allow for better estimation of detection probabilities (Gooch et al. 2006) than one sample per survey period.

Ambient temperature.—The influence of temperature on anuran calling behavior is well established, and many studies have shown it can affect detectability (e.g., Pellet and Schmidt 2005; Gooch et al. 2006). Surface water temperature, rather than air, is generally the best predictor of body temperature for calling anurans (Brattstrom 1963; Fouquette 1980). Five of the eight species we detected were always immersed in water while calling (*S. holbrookii*, *L. catesbeianus*, *L. clamitans*, *L. palustris*, and *L. sylvaticus*) whereas *A. fowleri*, *H. versicolor*, and *P. crucifer* called either while immersed in water or from shoreline areas. In Ontario, where water temperature was the most common predictor of anuran calling, *L. catesbeianus*, *L. clamitans*, and *L. sylvaticus* also called from water (Oseen and Wassersug 2002). In our study, water temperature had a greater effect on detection than air temperature. However, for five of the eight species, the most heavily weighted model included both surface water and air temperature.

Our study suggests that anuran calling surveys in

coastal New England should be conducted on nights when surface water temperatures exceed threshold values (e.g., $\geq 10^\circ\text{C}$). However, from a practical perspective, air temperature may be the more useful of these two variables, because it is easier to forecast and monitor. We found that anurans on Cape Cod rarely called when air temperatures were $< 7^\circ\text{C}$, which suggests the current NAAMP air temperature threshold (5.6°C) may be too low.

Time and temperature interactions.—For six of eight species (all but the two species of "explosive breeders," *S. holbrookii* and *L. sylvaticus*) the top models included air and/or water temperature and the quadratic date function, indicating that detection probabilities were affected by ambient temperatures and day of year. In Maryland, air temperature exerted a quadratic effect on detectability of *A. fowleri*, *H. versicolor*, and *P. crucifer*, and detection probabilities declined at temperatures above "optimal" (Weir et al. 2005). Similarly, calling in Ontario anurans declined at surface water temperatures above a species-specific "peak" (Oseen and Wassersug 2002) and in east Texas, air temperature above 24°C had a negative effect on calling in *L. catesbeianus* and *H. versicolor* (Saenz et al. 2006).

During this study, the threshold water temperature for calling appeared to increase as the calling season progressed for *A. fowleri*, *H. versicolor*, *L. catesbeianus*, and *L. clamitans* (Appendix 4). However, for species that breed early in the year, such as *P. crucifer* and *L. palustris*, this effect reversed itself in late season, and calling occurred, on average, on cooler occasions. These results suggest that calling activity and detectability are products of a more complex array of factors than date and temperature, and that these exogenous factors are proxies for underlying endogenous ones. Calling in anurans is androgen dependant and androgens fluctuate seasonally in concert with reproductive behavior (Wilczynski et al. 2005). Considering that water temperature is highly correlated with time of year (Oseen and Wassersug 2002), it suggests that the decline in anuran calling associated with high temperatures at the end of a species' calling season is due to declining hormone levels.

Application to a local monitoring program.—The NAAMP protocol is designed to assess anuran population trends over a large regional scale, but may also be adapted for more localized monitoring, such as in a specific park or preserve (e.g., Paton et al. 2003). The ability to do so with finite resources requires that the number of sample sites and sampling occasions be balanced to achieve desired levels of precision (MacKenzie et al. 2006). For most species on Cape Cod, the "peak calling period" is long enough and the number of sampling occasions and sample sites needed are small enough to be logistically feasible. Based on this study,

we recommend that each wetland be surveyed three times in mid-spring (1 May–21 May) for *P. crucifer* and *L. palustris*; five times in late spring (27 May–16 June) for *A. fowleri*; and six times in early summer (26 June–16 July) for *L. clamitans*, *H. versicolor*, and *L. catesbeianus*.

Although the number of sampling occasions needed to achieve 95% probability of one detection is equal to or only slightly more than needed for 90% probability, the number of sample sites needed to obtain a standard error of ψ of 0.05 is substantially more than for 0.10 (Table 4). This suggests that this level of precision is impractical. Moreover, calling surveys may not be appropriate for all anurans that breed in coastal New England. For example, *L. sylvaticus* is an explosive, early season breeder with a short calling season and low detectability in calling surveys (Oseen and Wassersug 2002; de Solla et al. 2005) that may be more effectively monitored with egg mass counts (Crouch and Paton 2000). *Scaphiopus holbrookii* is also an explosive breeder that generally lacks a well-defined breeding season and is thought to only breed in association with heavy rains (Saenz et al. 2006). On Cape Cod they typically breed for a few consecutive nights and may not breed every year. Consequently, this species is difficult to monitor with routine calling surveys and our “peak calling period” for this species should be interpreted with caution. Breeding of *S. holbrookii* on Cape Cod has been recorded from early April through late August: emergence and breeding are tied more to high ground water tables concurrent with temperatures exceeding 10° C (Gosner and Black 1955) than heavy rainfall or any specific month. Monitoring *S. holbrookii* would require locating known or likely breeding ponds, monitoring ground or surface water levels to determine when emergence is likely, and then conducting calling surveys during or after rainfall events or egg mass surveys soon thereafter.

Calling surveys are a relatively inexpensive method for surveying many anuran species at a large number of sites. Using calling surveys to monitor occupancy rates of wetlands by anurans may provide useful information on long-term population trends (Weir et al. 2009). However, because calling anurans are not always detectable and resources to conduct surveys are limited, biologists need to carefully consider, as locally as possible, factors affecting anuran calling to ensure that surveys are conducted during periods of peak detectability. Moreover, target species must be sufficiently detectable to generate estimates of occupancy with levels of precision that will allow for detection of trends. Our research on Cape Cod anurans shows that for six of eight species we recorded, duration of peak calling periods are long enough and detection probabilities high enough to effectively monitor them with calling surveys.

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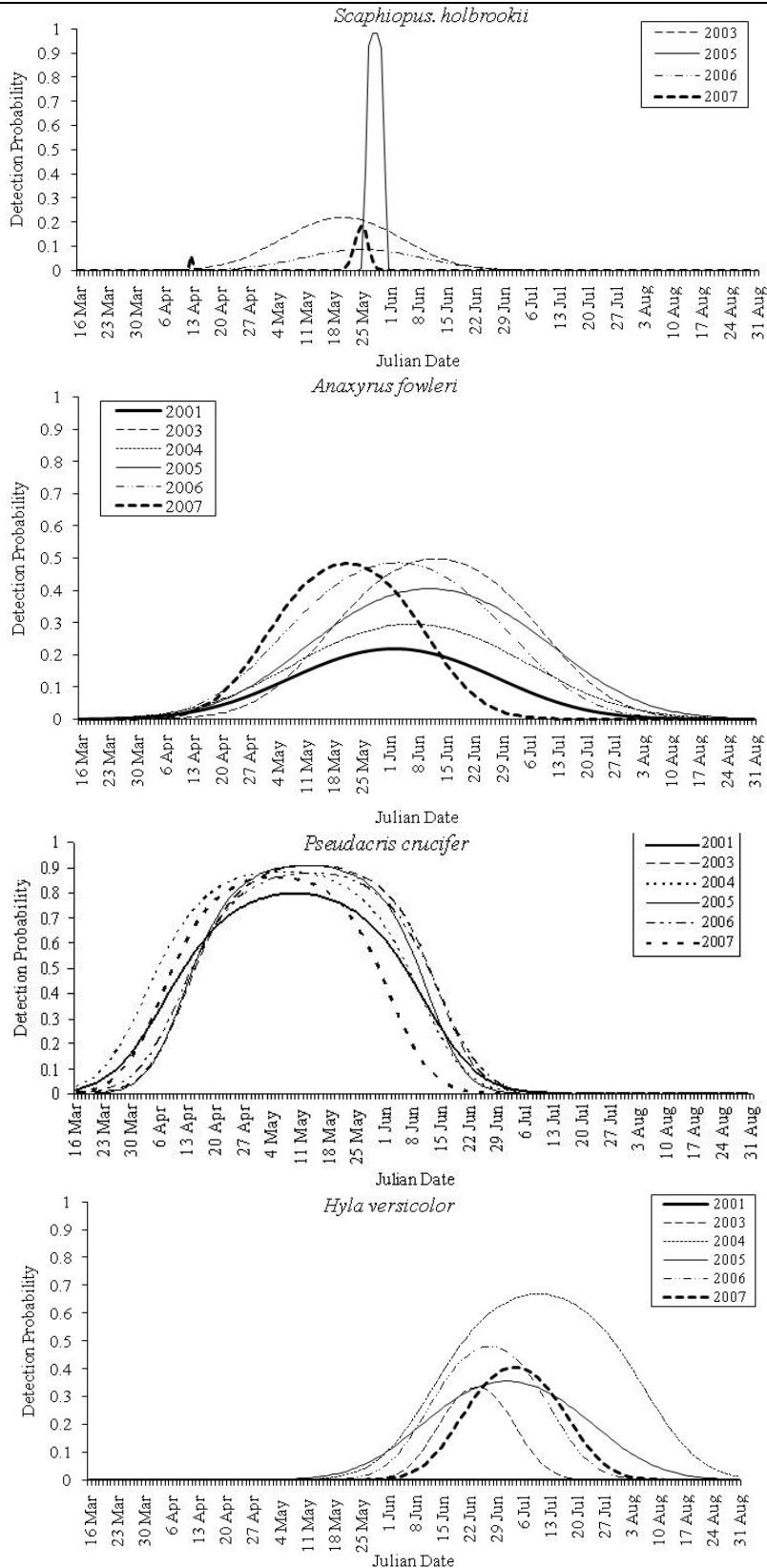
PETER PATON is a Professor and Chair of the Department of Natural Resources Science at the University of Rhode Island. He and his students conduct research on the impacts of anthropogenic factors affecting amphibian and avian populations throughout southern New England. (Photographed by anonymous)

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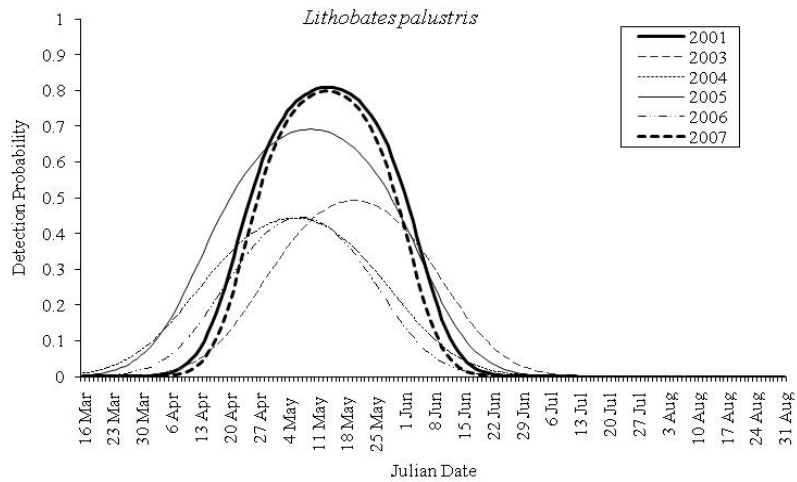
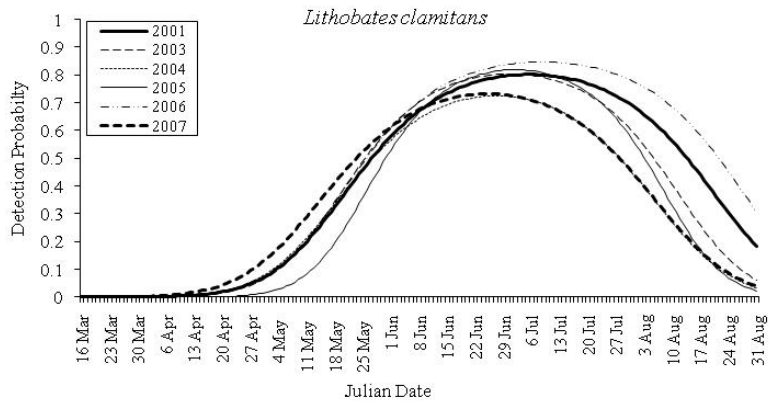
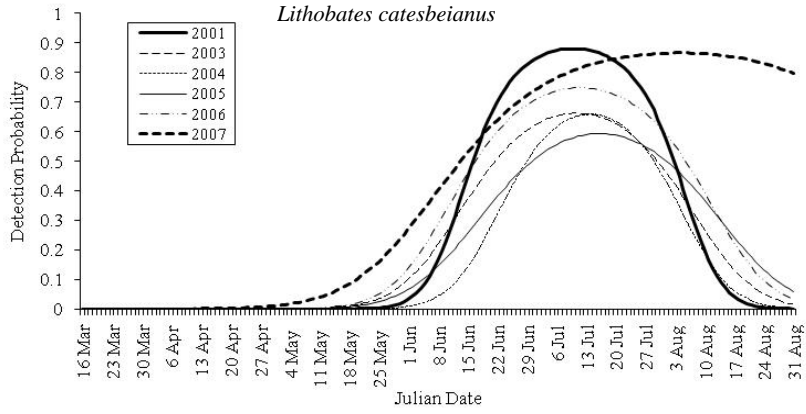
APPENDIX 1. Model selection assessing seasonal and annual variation in detection probabilities of calling anurans at Cape Cod National Seashore using adjusted Akaike's Information Criterion (AIC_c). Lower case j = julian date, ann = annual, w_i = model weight, K = number of parameters

Model	AIC _c	ΔAIC _c	w _i	K
<i>Scaphiopus holbrookii</i>				
ψ(·), γ(·), ε(·), p (ann)	276.74	0	0.993	9
ψ(·), γ(·), ε(·), p (·)	286.73	11.52	0.007	4
<i>Anaxyrus fowleri</i>				
ψ(·), γ(·), ε(·), p (j+j ² +ann)	2124.36	0	1.000	12
ψ(·), γ(·), ε(·), p (j+j ²)	2156.69	32.33	0.000	6
ψ(·), γ(·), ε(·), p (ann)	2252.37	128.01	0.000	9
ψ(·), γ(·), ε(·), p (j)	2297.81	173.45	0.000	5
ψ(·), γ(·), ε(·), p (·)	2298.59	174.23	0.000	4
<i>Hyla versicolor</i>				
ψ(·), γ(·), ε(·), p (j+j ²)	315.93	0	1.000	6
ψ(·), γ(·), ε(·), p (j)	338.42	22.49	0.000	5
ψ(·), γ(·), ε(·), p (·)	370.89	54.96	0.000	4
ψ(·), γ(·), ε(·), p (ann)	380.36	64.43	0.000	9
<i>Pseudacris crucifer</i>				
ψ(·), γ(·), ε(·), p (j+j ² +ann)	2788.32	0	1.000	12
ψ(·), γ(·), ε(·), p (j+j ²)	2805.20	16.88	0.000	6
ψ(·), γ(·), ε(·), p (j)	3652.53	864.21	0.000	5
ψ(·), γ(·), ε(·), p (ann)	4843.48	2055.16	0.000	9
ψ(·), γ(·), ε(·), p (·)	4850.33	2062.01	0.000	4
<i>Lithobates catesbeianus</i>				
ψ(·), γ(·), ε(·), p (j+j ² +ann)	1007.00	0	1.000	12
ψ(·), γ(·), ε(·), p (j+j ²)	1025.84	18.84	0.000	6
ψ(·), γ(·), ε(·), p (j)	1129.30	122.3	0.000	5
ψ(·), γ(·), ε(·), p (ann)	1425.52	418.52	0.000	9
ψ(·), γ(·), ε(·), p (·)	1435.54	428.54	0.000	4
<i>Lithobates clamitans</i>				
ψ(·), γ(·), ε(·), p (j+j ²)	3154.3	0	0.877	6
ψ(·), γ(·), ε(·), p (j+j ² +ann)	3158.22	3.92	0.124	12
ψ(·), γ(·), ε(·), p (julian)	3433.8	279.5	0.000	5
ψ(·), γ(·), ε(·), p (ann)	4180.87	1026.57	0.000	9
ψ(·), γ(·), ε(·), p (·)	4192.78	1038.48	0.000	
<i>Lithobates palustris</i>				
ψ(·), γ(·), ε(·), p (j+j ²)	652.99	0	0.547	6
ψ(·), γ(·), ε(·), p (j+j ² +ann)	653.37	0.38	0.453	12
ψ(·), γ(·), ε(·), p (j)	762.65	109.66	0.000	5
ψ(·), γ(·), ε(·), p (·)	848.18	195.19	0.000	4
ψ(·), γ(·), ε(·), p (ann)	851.23	198.24	0.000	9
<i>Lithobates sylvaticus</i>				
ψ(·), γ(·), ε(·), p (·)	190.13	0	0.848	4
ψ(·), γ(·), ε(·), p (ann)	193.56	3.43	0.152	9
ψ(·), γ(·), ε(·), p (j)	650.62	460.49	0.000	5
ψ(·), γ(·), ε(·), p (j+j ²)	652.88	462.75	0.000	6
ψ(·), γ(·), ε(·), p (j+j ² +ann)	667.47	477.34	0.000	12

APPENDIX 2. Annual variation in detection probabilities of seven species of anurans based on calling surveys at Cape Cod National Seashore based on model $\psi(\cdot, \gamma(\cdot), \varepsilon(\cdot), p(\text{julian} + \text{julian}^2))$ for each year.



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Cook et al.—Effects of temporal and temperature factors on anuran detection probabilities.

APPENDIX 3. Model selection combining air and water temperature with best temporal model of anuran detection probabilities at Cape Cod National Seashore. Water and air columns provide coefficient values and standard error (SE) for water and air temperature covariates of the most heavily weighted model for a species. Lower case j = julian date, ann = annual, w_i = model weight, K = number of parameters, wt = water temperature, at = air temperature.

Model	AIC _c	ΔAIC _c	w _i	K	Water (SE)	Air (SE)
<i>Scaphiopus holbrookii</i>						
ψ(.), γ(.), ε(.), p (ann)	276.74	0	1.000	9		
<i>Anaxyrus fowleri</i>						
ψ(.), γ(.), ε(.), p (j+j ² +ann+wt+at)	1548.89	0	0.971	14	0.56 (0.01)	0.52 (0.01)
ψ(.), γ(.), ε(.), p (j+j ² +ann+wt)	1555.9	7.01	0.029	13		
ψ(.), γ(.), ε(.), p (j+j ² +ann+at)	1906.77	357.88	0.000	12		
ψ(.), γ(.), ε(.), p (j+j ² +ann)	2124.36	575.47	0.000	12		
<i>Hyla versicolor</i>						
Ψ(.), γ(.), ε(.), p (j+j ² +wt)	257.81	0	0.650	7	0.64 (0.2)	
Ψ(.), γ(.), ε(.), p (j+j ² +wt+at)	259.05	1.24	0.350	8		
ψ(.), γ(.), ε(.), p (j+j ² +at)	283.41	25.6	0.000	7		
ψ(.), γ(.), ε(.), p (j+j ²)	315.93	58.12	0.000	6		
<i>Pseudacris crucifer</i>						
ψ(.), γ(.), ε(.), p (j+j ² +ann+wt+at)	2071.21	0	0.950	14	0.62 (0.03)	0.41 (0.03)
ψ(.), γ(.), ε(.), p (j+j ² +ann+wt)	2077.71	5.9	0.050	13		
ψ(.), γ(.), ε(.), p (j+j ² +wt+at)	2578.02	510.9	0.000	13		
ψ(.), γ(.), ε(.), p (j+j ² +ann)	2788.32	717.11	0.000	12		
<i>Lithobates catesbeianus</i>						
ψ(.), γ(.), ε(.), p (j+j ² +ann+wt+at)	870.62	0	0.557	14	0.57 (0.01)	0.48 (0.01)
ψ(.), γ(.), ε(.), p (j+j ² +ann+wt)	871.08	0.46	0.443	13		
ψ(.), γ(.), ε(.), p (j+j ² +ann+at)	946.23	75.61	0.000	13		
ψ(.), γ(.), ε(.), p (j+j ² +ann)	1007	136.35	0.000	12		
<i>Lithobates clamitans</i>						
ψ(.), γ(.), ε(.), p (j+j ² +wt+at)	2343.03	0	0.898	8	0.55 (0.01)	0.49 (0.01)
ψ(.), γ(.), ε(.), p (j+j ² +wt)	2347.38	4.35	0.102	7		
ψ(.), γ(.), ε(.), p (j+j ² +at)	2960.79	617.76	0.000	7		
ψ(.), γ(.), ε(.), p (j+j ²)	3154.3	811.27	0.000	6		
<i>Lithobates palustris</i>						
ψ(.), γ(.), ε(.), p (j+j ² +wt+at)	586.57	0	0.684	8	0.55 (0.01)	0.47 (0.01)
ψ(.), γ(.), ε(.), p (j+j ² +wt)	588.11	1.54	0.317	7		
ψ(.), γ(.), ε(.), p (j+j ² +at)	627.76	41.19	0.000	7		
ψ(.), γ(.), ε(.), p (j+j ²)	652.99	66.42	0.000	6		
<i>Lithobates sylvaticus</i>						
ψ(.), γ(.), ε(.), p (wt)	110.58	0	0.745	5	0.12 (0.05)	
ψ(.), γ(.), ε(.), p (wt+at)	112.72	2.14	0.255	6		
ψ(.), γ(.), ε(.), p (at)	156.12	45.54	0.000	5		
ψ(.), γ(.), ε(.), p (.)	190.13	79.55	0.000	4		

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APPENDIX 4. Mean (\pm SE) surface water temperatures ($^{\circ}$ C) when anurans were detected (solid square-solid line) or not detected (open diamond-dashed line) during calling surveys at Cape Cod National Seashore. Data are only from sites where a given species was recorded at least once during the study period.

