MONITORING OF POND BREEDING AMPHIBIANS AT CAPE COD NATIONAL SEASHORE, 2004

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EXECUTIVE SUMMARY

Given the abundance and significance of freshwater wetlands at Cape Cod National Seashore (CACO), the important role amphibians play in them, and concerns that global, regional, and local factors (pollution, disease, road kill, development) may alter the abundance, distribution, and structure of amphibian communities, long term monitoring of pond breeding amphibians was initiated in 2003. It is part of the park's long term ecological monitoring program, and consists of two components. Vernal pond egg mass counts monitor the abundance and distribution of spotted salamanders (*Ambystoma maculatum*) and wood frogs (*Rana sylvatica*). Anuran call counts monitor abundance, distribution, and habitat association of the park's anurans (frogs and toads). In addition, data on each pond's physical and chemical attributes and vegetation are collected.

In spring 2004, three counts of egg masses were conducted in 40 vernal ponds. Based on each pond's maximum count, a total of 5322 spotted salamander masses and 86 wood frog masses were present. Spotted salamanders occurred in 29 ponds, from Eastham to the limit of glacial deposits at High Head, Truro. Wood frog egg masses were recorded in 11 ponds in Eastham. There were no significant differences in spotted salamander egg mass counts from 2003 to 2004, no significant trend over the past three or four years, nor any relationship between egg mass counts and rainfall during the breeding migration season. There were no significant trends in wood frog egg mass counts. Given the lack of long term data, the lack of significant trends is not surprising.

Analysis of landscape and within-pond factors found spotted salamander abundance to be correlated negatively with water color and positively with submerged aquatic vegetation (SAV). Darkly colored water has been linked to low embryonic survival and lower populations elsewhere. The amount of SAV reflects pond hydroperiod (time water is present) and suggests that the largest populations of spotted salamanders occur at vernal ponds that hold water longest. This is consistent with research conducted elsewhere. Abundance of wood frogs was also negatively correlated with color. Compared to other areas of the Eastern United States, the CACO landscape, particularly Eastham, supports a widespread and very abundant population of spotted salamanders, but a limited and small population of wood frogs. Lack of forested wetlands, a critical habitat for wood frogs but not spotted salamanders, appears to be responsible for this difference.

Anuran call counts were conducted weekly at 30 freshwater sites for 15 consecutive weeks, from mid-April to late July. Counts consisted of visiting ponds after dark, listening for five minutes, and recording the abundance of species heard as an index value ranging from 0 to 3. Seven species of frogs and toads, all the species known to occur at CACO except for eastern spadefoot toads (*Scaphiopus holbrookii*), were recorded at least once. In descending order, the most widespread species were spring peepers (*Pseudacris crucifer*), green frogs (*Rana clamitans*), Fowler's toads (*Bufo fowleri*), bullfrogs (*Rana catesbiana*), pickerel frogs (*Rana palustris*), wood frogs (*Rana sylvatica*) and grey treefrogs (*Hyla versicolor*). Analysis of species occurrence and site features, and seasonal patterns indicate that habitat use and breeding season chronology of species here are similar to other anuran communities in the Northeastern U.S

INTRODUCTION

Cape Cod National Seashore (CACO) supports a great abundance and diversity of freshwater wetlands. Few landscapes in the region contain such a wealth of wetlands, which in turn support many regionally uncommon species of wetland-dependent flora and fauna. Among these, amphibians play a significant role in the energy flow, biomass, and community structure of freshwater wetlands, and contribute significantly to terrestrial ecosystems as well. Consequently, monitoring of pond breeding amphibians was initiated in 2003 as a component of freshwater wetland monitoring in the Cape Cod National Seashore prototype monitoring program (Roman and Barrett 1999). Specific rationale for the program includes concerns for individual habitats and species, as well as questions related to changes in abundance, distribution, and structure of the park's amphibian communities in the face of potential impacts from acid deposition, road mortality, groundwater borne and air borne contaminants, habitat changes, and groundwater withdrawal (Paton et al. 2003).

Pond breeding amphibian monitoring at CACO consists of two components; monitoring occurrence and abundance of the vernal pond breeding species spotted salamander (*Ambystoma maculatum*) and wood frog (*Rana sylvatica*) through egg mass counts, and monitoring occurrence and relative abundance of the breeding anuran community park wide, in a range of wetland types, through the use of anuran call counts. Since these components entail distinct methods, target organisms, and sample sites, each will be reported on separately.

VERNAL POND EGG MASS COUNTS

Introduction

Monitoring of egg masses in vernal ponds in 2004 was a combination of activities called for in the CACO Amphibian Monitoring Protocol (Paton et al. 2003), plus a collaboration with the United States Geological Survey (USGS) Amphibian Research and Monitoring Initiative (ARMI). The USGS ARMI work in 2004 employed a proportion of area occupied (PAO) approach to determine the proportion of available vernal ponds occupied by spotted salamanders and wood frogs and the role of within-pond and adjacent landscape variables in determining occupancy. USGS randomly selected 40 known vernal ponds at CACO, and randomly assigned them a priority for inclusion in the sampling effort (Grant et al. 2004). A total of 40 ponds were sampled. These included the 20 called for in CACO's Pond Breeding Amphibian Monitoring Protocol (Paton et al. 2003) and 30 of the 40 called for by the USGS ARMI protocol. Ten ponds sampled belonged to both groups (Appendix 1).

Methods

Counts of spotted salamander and wood frog egg masses were conducted at 40 vernal ponds in 2004. Ponds ranged geographically from Eastham to Provincetown and include most of the Eastham vernal pool complex (figs. 1-3). Three counts were conducted between 29 March 2004 and 5 May 2004. At each count, the entire pond was searched carefully and methodically, and all egg masses found were enumerated. For each species at a given pond, the highest of the three counts or maximum count was used as the measure of abundance (Cook and Boland 2005). At each count, maximum water depth (at a marked point determined to be the deepest point in the pond), air and water temperature were recorded (Paton et al. 2003). Maximum pond length and width (Jung 2002) were also measured at each count, and the maximum values used to calculate pond size. Analysis of a suite of water quality parameters was conducted, based on water samples collected in April. Analysis was conducted at the North Atlantic Coastal Lab, North Truro, using methods described in Boland and Cook (2004).

Analysis of between year (2003 *vs* 2004) differences in maximum egg mass counts was conducted by a paired t-test. Trends in egg mass counts were analyzed using linear regression, as recommended by Paton et al. (2003). Spotted salamander trend analysis was conducted for the period 2001 through 2004 based on seven ponds, using data for spotted salamanders from 2001 from Paton et al. (2003) to augment our own, and from 2002 through 2004, based on 14 ponds. Trends in wood frog egg mass counts from 2002 to 2004 were based on nine ponds.

In addition, since there is a significant positive correlation between annual breeding effort in *Ambystoma* salamanders and rainfall during the breeding migration season (Semlitsch 1987), the effects of rainfall-related variation in total egg mass counts were removed using partial correlation (Pechmann et al. 1991). Since wood frogs and spotted salamanders in Massachusetts migrate to breeding ponds in March and April, the total rainfall for these two months, as recorded at a Cape Cod National Seashore rain gauge in Eastham, was used to estimate migration season rainfall.

Data from 2004 were analyzed to explore relationships between egg mass counts and physical, chemical, and ecological attributes of ponds and their adjacent areas. Many water quality parameters (Appendix 2) were highly significantly correlated (e.g. pH and alkalinity ($r=0.8208$, $p<0.0001$), conductivity and chloride ($r=0.9437$, $p<0.0001$). As was done in 2003, to remove these redundant variables and simplify analysis, only pH, conductivity, and color (Absorbance Coefficient at 440 nanometers (AbsCo440)) were retained for use in analysis. Methods for measuring the ecological attributes of ponds and adjacent areas are based on the ARMI protocol (Jung 2002). The adjacent landscape parameters measured were distance to nearest paved road, number of vernal ponds within 250 meters, and percent of woodland, paved road, field, wetland, and residential development within 50 meters. Within-pond parameters were area, maximum depth, pH, conductivity, absorbance, and percent of pond occupied by leaf litter, woody debris, submerged aquatic vegetation (SAV), moss, emergent, shrubs, and trees.

Figure 1. Vernal pond egg mass count sites in Eastham.

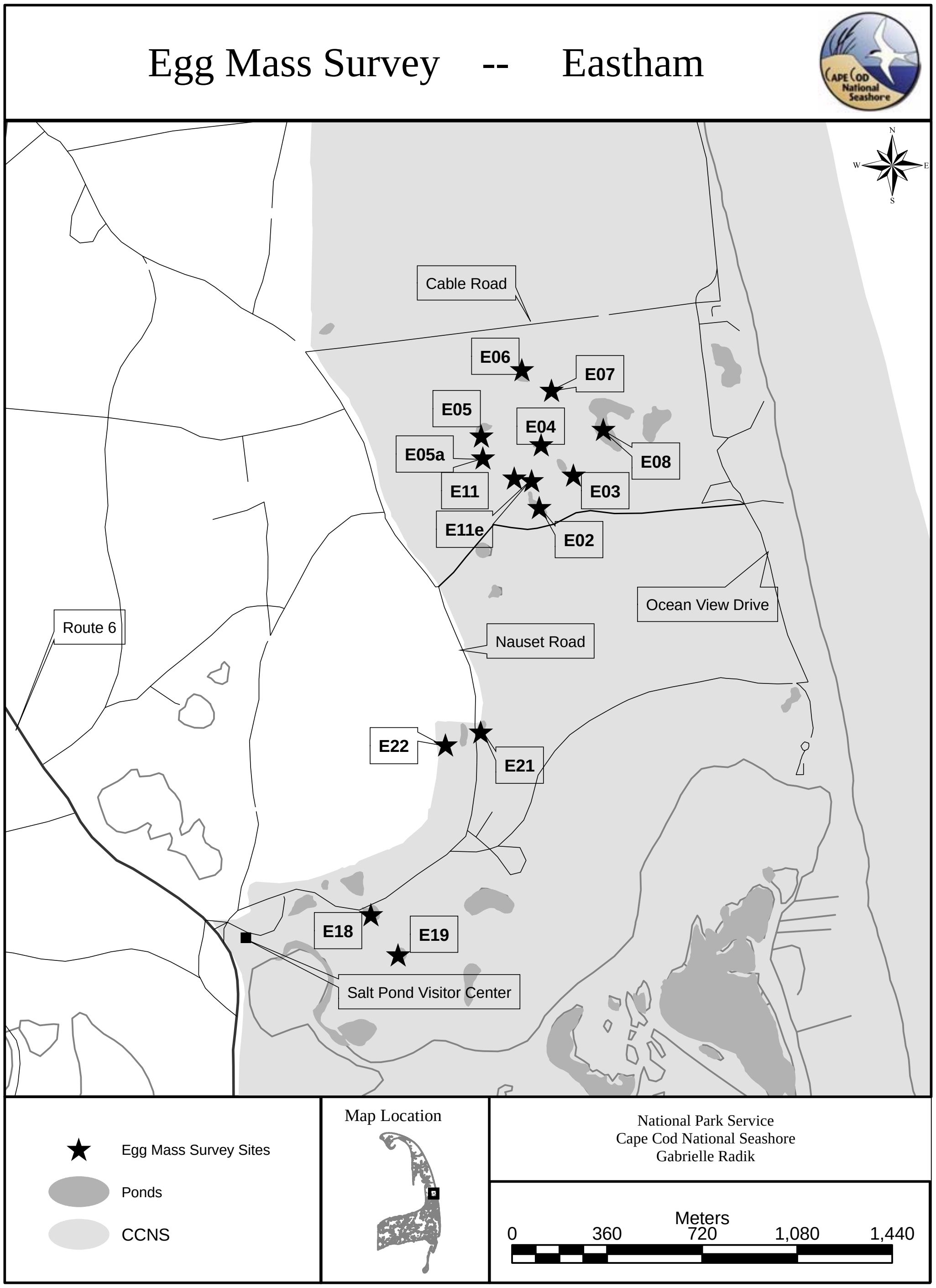


Figure 2. Vernal pond egg mass count sites in Truro and Wellfleet.

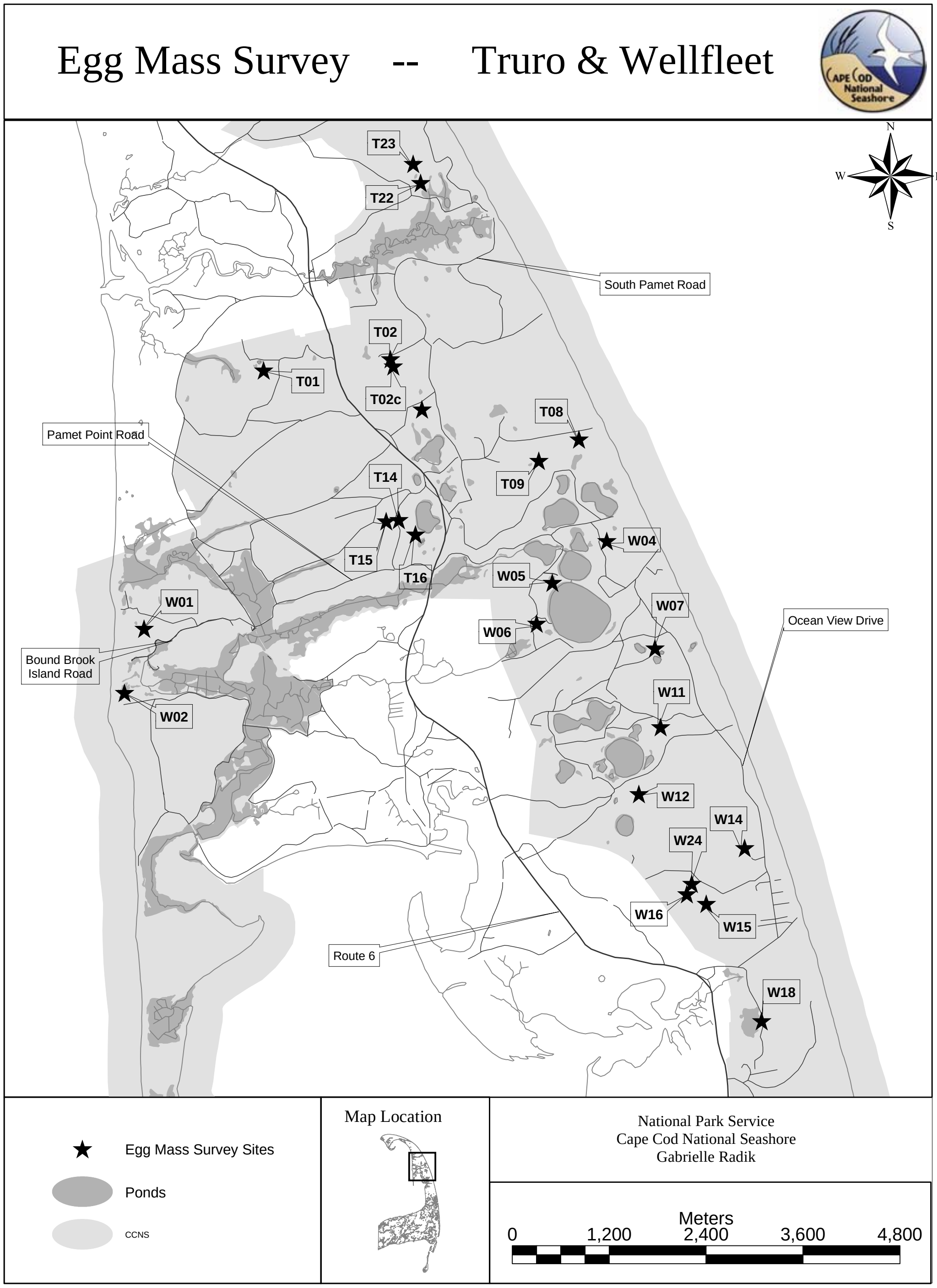
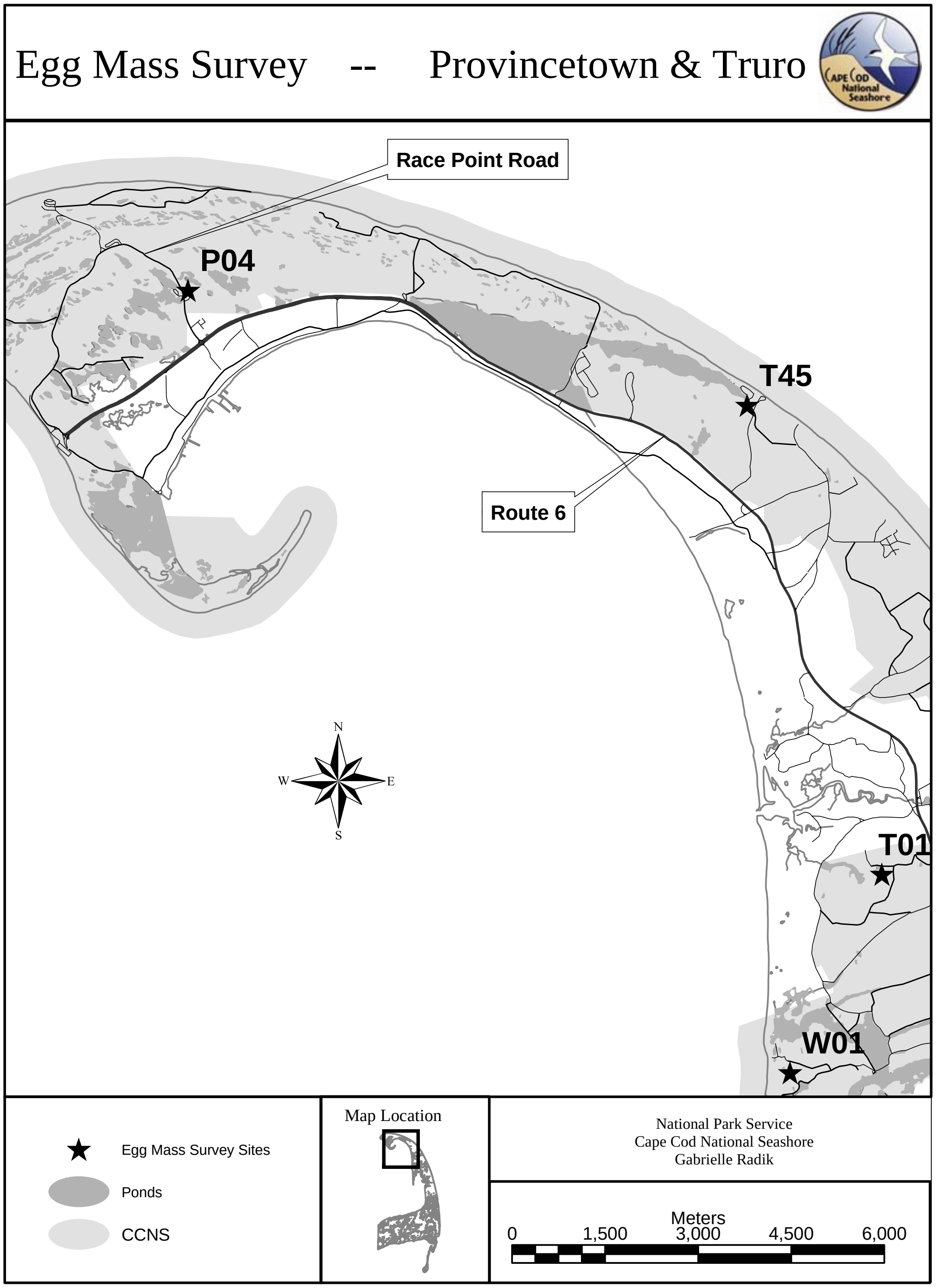


Figure 3. Vernal pond egg mass count sites in North Truro and Provincetown.



The relationship between egg mass counts and habitat parameters was analyzed using forward stepwise multiple regression, with variables entered and removed at critical values of p = 0.05 and p = 0.10, respectively (Egan 2001). Percentage data were arcsine transformed prior to analysis. Remaining habitat variables (Appendix 3) were tested for normality using the Shapiro-Wilks test of program STATISTICA (Statsoft 2000). Those not meeting assumptions of normality were transformed to best meet assumptions of normality using either the square root or log transformation procedures detailed in Zar (1996). Analysis was performed separately on within-pond and adjacent landscape variables. Since the known range of spotted salamanders at CACO only extends to High Head, pond P04 was excluded from the spotted salamander analysis. Similarly, since wood frogs are only known to occur in Eastham and into South Wellfleet as far as W18, only ponds within this known range were included in the wood frog analysis.

Results

Spotted Salamander Egg Mass Counts

Of the 40 ponds sampled, a total of 5322 spotted salamander egg masses were detected in 29 (73%). Within its known range at CACO (i.e. omitting P04) the naïve occupancy rate (percentage of sampled ponds at which it was recorded) is 74% (29/39). Mean (± SE) number of egg masses per pond were 133 ± 33 for all 40 ponds, 136 ± 34 for all 39 ponds within the known range of spotted salamanders at CACO, and 183 ± 42 for the 29 ponds where egg masses were detected (range 4 to 778). Maximum counts occurred primarily in replicate three and two (table 1), as they did in 2003 (Cook and Boland 2004).

Maximum egg mass counts were generally lower in 2004 than 2003. For 20 ponds with two year's data, the total number of egg masses declined from 5450 to 4986. Counts increased at five ponds and decreased at 14 (table 2). Mean increase per pond was 113 egg masses, whereas mean decline was 47. Differences in egg mass counts between 2003 and 2004 were not significant (t=0.948, df=19, p=0.355). For the seven ponds with data from 2001 to 2004, the trend in combined egg mass counts was positive (slope=0.32) but not significantly different from zero (p=0.68). Four of the seven ponds had positive slopes and three negative. None deviated significantly from zero (table 3). For the 14 ponds with data from 2002 to 2004, the trend in combined egg masses was negative (slope =-0.97), but not significantly different from zero (p=0.16) (table 4). Three of the 14 ponds had positive slopes and 11 were negative. Only E11 deviated significantly from zero (slope= -1.0, p=0.04) (table 4). Yet, for the period from 2001 to 2004, there was no deviation from zero at E11 (slope=-0.04, p=0.96) (table 3).

After correcting for rainfall, the trend in combined egg mass count from 2001 through 2004 was not significant (r= -0.9071, p=0.277), nor was the correlation between egg mass count and migration season rainfall (r = -.0719, p=0.281).

Table 1. Spotted salamander egg mass counts by replicate for 2004 at Cape Cod National Seashore. Bold indicates maximum count.

Pond	Rep 1	Rep 2	Rep 3	Maximum
	3/29-4/19	4/12-5/04	4/26-5/05	
E02	0	2	**12**	12
E03	0	20	**21**	21
E04	0	463	**532**	532
E05	16	**687**	573	687
E05a	0	248	**297**	297
E06	3	**396**	263	396
E07	0	167	**193**	193
E08	0	64	**93**	93
E11	0	114	**124**	124
E11east	0	0	**4**	4
E18	0	2	**5**	5
E19	0	**52**	28	52
E21	0	106	**179**	179
E22	0	**778**	617	778
P04	0	0	0	0
T01	186	**541**	511	541
T02	36	**95**	91	95
T02C	2	**8**	6	8
T04*	n/a	0	0	0
T08	0	0	0	0
T09	0	0	0	0
T14	0	**16**	13	16
T15	0	18	**27**	27
T16	0	0	0	0
T22	0	0	0	0
T23	0	**63**	54	63
T45	0	0	0	0
W01	34	333	**362**	362
W02	19	14	**28**	28
W04	0	0	0	0
W05	0	2	**9**	9
W06	0	0	**25**	25
W07	96	**499**	415	499
W11**	n/a	0	0	0
W12	0	0	0	0
W14	0	6	**12**	12
W15	0	45	**114**	114
W16	0	14	**48**	48
W18	0	27	**102**	102
W24	0	0	0	0
Total	392	4780	4758	5322

*Rep 1: 4/19; Rep 2: 5/04

**Rep1: 4/15; Rep2: 4/27

Table 2. Maximum count (MC) of spotted salamander egg masses in ponds with data from 2003 and 2004.

Pond	2003 MC	2004 MC	Change	%Change
E02	50	12	-38	-76%
E03	38	21	-17	-45%
E04	633	532	-101	-16%
E05	767	687	-80	-10%
E05a	315	297	-18	-6%
E06	575	396	-179	-31%
E07	269	193	-76	-28%
E08	250	93	-157	-63%
E11	254	124	-130	-51%
E11east	24	4	-20	-83%
E21	261	179	-82	-31%
E22	486	778	292	60%
P04	0	0	0	0%
T01	544	541	-3	-1%
T15	22	27	5	23%
W01	489	362	-127	-26%
W06	27	25	-2	-7%
W07	338	499	161	48%
W15	64	114	50	78%
W18	44	102	58	132%
Sum	5450	4986	-464	-9%

Table 3. Trend analysis of spotted salamander egg mass counts at seven CACO vernal ponds from 2001 through 2004.

Pond	2001 MC	2002 MC	2003 MC	2004 MC	Slope	R^2	*p*
E03	48	25	38	21	-0.71	0.50	0.29
E04	503	1227	633	532	-0.19	0.04	0.81
E05	174	596	767	687	0.84	0.70	0.16
E06	168	599	575	396	0.43	0.18	0.57
E07	92	226	269	193	0.59	0.35	0.41
E11	101	359	254	124	-0.04	0.00	0.96
E11e	0	29	24	4	0.06	0.00	0.94
All	1086	3061	2560	1957	0.32	0.10	0.68

Table 4. Trend analysis of spotted salamander egg mass counts at 14 CACO vernal ponds from 2002 through 2004.

Pond	2002 MC	2003 MC	2004 MC	Slope	R^2	*p*
E02	30	50	12	-0.47	0.22	0.69
E03	25	38	21	-0.23	0.05	0.86
E04	1227	633	532	-0.93	0.86	0.25
E05	596	767	687	0.53	0.28	0.64
E05a	677	315	297	-0.89	0.78	0.31
E06	599	575	396	-0.92	0.84	0.26
E07	226	269	193	-0.43	-0.62	0.71
E08	243	250	93	-0.85	0.71	0.36
E11	359	254	124	-1.00	1.00	0.04
E11east	29	24	4	-0.94	0.89	0.21
E21	434	261	179	-0.98	0.96	0.13
E22 (Turtle Pond)	910	486	778	-0.30	-0.81	0.80
W06	8	27	25	0.81	0.66	0.39
W15	81	64	114	0.65	0.42	0.55
All	5444	4013	3455	-0.97	0.94	0.16

Wood Frog Egg Mass Counts

A total of 86 egg masses were recorded from 11 of 40 ponds sampled (28%). Within its known range at CACO the naïve occupancy rate was 73% (11/15). Mean (± SE) number of egg masses per pond were 2.15± 0.8 for all 40 ponds, 5.73± 1.76 for all 15 ponds within the known range of wood frogs at CACO, and 7.82 ± 2.08 for the 11 ponds where egg masses were detected in 2004 (range 1 to 22). Maximum counts occurred primarily in replicate two (table 5).

Of 12 ponds in Eastham with data from 2003 and 2004, nine contained a total of 61 egg masses in 2003 and 75 egg masses in 2004 (table 6). Differences in egg mass counts between years were not significant (t=-0.4693, df=11, p=0.65). For nine ponds with data from 2002 to 2004, the trend in combined egg masses was positive, but did not differ significantly from zero (slope=0.99, *p*=0.08). Six ponds had a positive slope and three were negative. None deviated significantly from zero (table 7).

After correcting for rainfall, the trend in combined egg mass count from 2002 through 2004 was not significant (r=0.0504, *p*=0.795) nor was the correlation between egg mass count and migration season rainfall (r = -.8775, *p*=0.318).

Table 5. Summary of wood frog egg mass counts for 2004 season at Cape Cod National Seashore. Bold indicates maximum count.

Pond	Rep 1 Total 3/29-4/19	Rep 2 Total 4/12-5/04	Rep 3 Total 4/26-5/05	Maximum
E02	0	0	0	0
E03	0	**1**	0	1
E04	2	**4**	1	4
E05	0	**16**	2	16
E05a	0	**6**	2	6
E06	0	**2**	0	2
E07	0	**8**	7	8
E08	0	0	0	0
E11	0	**2**	1	2
E11east	0	0	0	0
E18	0	0	**2**	2
E19	0	**9**	0	9
E21	12	**22**	10	22
E22	0	**14**	1	14
P04	0	0	0	0
T01	0	0	0	0
T02	0	0	0	0
T02C	0	0	0	0
T04*	no data	0	0	0
T08	0	0	0	0
T09	0	0	0	0
T14	0	0	0	0
T15	0	0	0	0
T16	0	0	0	0
T22	0	0	0	0
T23	0	0	0	0
T45	0	0	0	0
W01	0	0	0	0
W02	0	0	0	0
W04	0	0	0	0
W05	0	0	0	0
W06	0	0	0	0
W07	0	0	0	0
W11**	no data	0	0	0
W12	0	0	0	0
W14	0	0	0	0
W15	0	0	0	0
W16	0	0	0	0
W18	0	0	0	0
W24	0	0	0	0
Total	14	84	26	86

*Rep 1: 4/19; Rep 2: 5/04

**Rep 1: 4/15; Rep 2: 4/27

Table 6. Maximum count of wood frog egg masses in ponds with data from 2003 and 2004.

Pond	2003 MC	2004 MC	Change	%Change
E02	0	0	0	0%
E03	1	1	0	0%
E04	1	4	3	300%
E05	16	16	0	0%
E05a	15	6	-9	-60%
E06	16	2	-14	-88%
E07	7	8	1	14%
E08	0	0	0	0%
E11	1	2	1	100%
E11east	0	0	0	0%
E21	2	22	20	1000%
E22	2	14	12	600%
Sum	61	75	14	23%

Table 7. Trend analysis of wood frog egg mass counts at nine CACO vernal ponds from 2002 through 2004.

Pond	2002 MC	2003 MC	2004 MC	Slope	R^2	*p*
E03	0	1	1	0.87	0.750	0.33
E04	2	1	4	0.66	0.423	0.55
E05	0	16	16	0.87	0.750	0.33
E05a	9	15	6	-0.33	0.107	0.79
E06	8	16	2	-0.43	0.182	0.72
E07	3	7	8	0.95	0.893	0.21
E11	0	1	2	1.00	1.000	**
E21	11	2	22	0.55	0.301	0.63
E22	19	2	14	-0.29	0.081	0.82
All	52	61	75	0.99	0.984	0.08

<u>Environmental Conditions</u>

Pond water temperatures in 2004 averaged 6.32, 10.23, and 13.47 °C for replicates one, two, and three respectively (table 8). For 19 ponds with complete water temperature data for 2003 and 2004, the mean water temperature was 9.02 °C in 2003 and 9.48 °C in 2004. Differences in water temperature were not significant between ponds ($F_{18, 76}$=0.7169, p=0.78) nor between years ($F_{1,76}$=0.34, p=0.56).

Maximum water depth in 2004 (table 9) ranged from 4 to 83 centimeters (cm), with a mean of 39.75 cm and a standard deviation of 20.43. For 20 ponds measured in 2003 and 2004, the mean maximum depth in 2003 (76.2 cm) was significantly greater than in 2004 (41.8 cm) (t=14.042, df=19, p=0.0000001). Total rainfall during the breeding migration season was 32.8 cm in 2001, 26.5 cm in 2002, 26.7 cm in 2003, and 24.9 cm in 2004.

Table 8. Water temperature (°C) of the forty ponds where egg mass counts were conducted in 2004, for each of three sampling replicates

Pond	Rep 1	Rep 2	Rep 3
E02	5.0	9.0	7.5
E03	6.0	10.0	12.0
E04	2.0	11.0	12.3
E05	11.0	10.0	12.0
E05a	9.0	8.5	9.8
E06	4.0	9.5	15.9
E07	5.0	10.0	13.5
E08	8.0	9.0	11.8
E11	3.0	8.0	7.4
E11east	dry	8.0	17.5
E18	6.0	11.0	9.9
E19	6.0	11.5	10.8
E21	5.5	9.0	14.0
E22	7.0	8.5	11.0
P04	5.0	6.0	17.5
T01	8.5	12.0	16.0
T02	6.5	19.0	19.5
T02C	8.0	15.0	16.0
T04*	no data	12.0	dry
T08	6.5	dry	dry
T09	dry	dry	17.0
T14	6.5	11.0	16.0
T15	6.5	10.0	13.5
T16	7.0	10.0	11.0
T22	8.0	11.0	17.0
T23	6.0	8.0	12.0
T45	6.5	22.0	19.0
W01	5.0	10.0	15.0
W02	7.0	10.0	16.7
W04	6.0	10.0	15.8
W05	7.0	9.5	16.0
W06	6.0	10.0	15.0
W07	6.5	7.0	21.7
W11*	no data	7.0	9.5
W12	3.5	9.4	9.0
W14	8.0	11.0	9.5
W15	7.0	6.0	12.5
W16	5.5	5.4	11.0
W18	7.5	10.5	10.4
W24	dry	5.5	9.0
Mean**	6.3	10.2	13.5

*Sites were added to survey during Rep2 period
**mean based only on ponds with water temperature data from all three replicates

Table 9. Maximum depth (cm) recorded during egg mass counts in 2003 and 2004. Mean represents the mean of the maximum depth recorded during three replicates in 2003 and three replicates in 2004.

Pond	Max Depth 2003	Max Depth 2004	Mean Depth 2003	Mean Depth 2004
E02	59.0	30.0	51.75	26.67
E03	60.5	21.0	52.63	17.33
E04	71.0	32.0	63.00	27.00
E05	80.0	43.0	69.00	37.00
E05a	78.0	35.0	66.50	28.33
E06	87.0	51.0	79.00	44.00
E07	50.0	20.0	46.25	28.67
E08	65.0	43.0	61.50	37.67
E11	67.0	37.0	57.00	34.67
E11east	58.0	18.0	49.50	10.67
E18	***	60.0	***	50.00
E19	***	82.0	***	70.00
E21	106.0	53.0	100.50	52.00
E22	102.0	60.0	96.25	58.33
P04	77.0	40.0	75.00	37.67
T01	82.0	52.0	74.00	49.00
T02	***	26.0	***	20.67
T02C	***	27.0	***	22.67
T04	***	4.0	***	2.00
T08	***	5.0	***	1.67
T09	***	17.0	***	5.67
T14	***	79.0	***	74.67
T15	90.0	75.0	82.00	69.67
T16	***	20.0	***	18.67
T22	***	83.0	***	79.67
T23	***	49.0	***	45.33
T45	***	40.0	***	35.67
W01	74.0	56.0	62.50	51.67
W02	***	50.0	***	46.00
W04	***	41.0	***	31.00
W05	***	50.0	***	44.67
W06	56.0	36.0	53.00	31.33
W07	102.0	70.0	94.00	64.67
W11	***	16.0	***	15.00
W12	***	30.0	***	21.33
W14	***	24.0	***	18.50
W15	86.0	27.0	70.75	21.00
W16	***	40.0	***	37.67
W18	74.0	37.0	66.00	26.67
W24	***	11.0	***	6.33

***denotes sites that were not sampled in specified year

Pond area ranged from 0.5 to 33825 $meter^2$, with a mean of 2211 and a standard deviation of 5761. All ponds were acidic: pH ranged from 4.01 to 5.86, with a mean of 4.692 and a standard deviation of 0.515. Conductivity ranged from 31.5 to 221 µS/cm, with a mean of 73.37 and standard deviation of 40.51. Color, measured as the absorption coefficient at 440 nanometers (AbsCo440), ranged from 0.921 to 92.581, with a mean of 29.99 and standard deviation of 20.85. Physical parameters of individual ponds where egg mass counts were conducted are in Appendix 3.

<u>Habitat Parameters and Spotted Salamander Egg Mass Counts</u>

Woodland habitat comprised from 10 to 100% of pond adjacent habitat. Only a few ponds had any roads, field, wetland, or residential use within 50 m, and in these instances, those habitat and land use categories almost always accounted for only 5 to 10% of the adjacent zone (Appendix 3). Of the adjacent landscape parameters, none were significant enough to be entered into the regression model. Within-pond vegetation tended to be a mix of both shrubby and emergent plants. Emergent vegetation comprised from 0 to 85% of a pond (mean 30%) and shrubby vegetation from 0 to 80% (mean 19%). Ponds heavily dominated by shrubs tended to lack emergent vegetation, and vice versa (Appendix 3). Of the within-pond parameters, only color (AbsCo440) and %SAV were entered into the regression model (model adjusted $R^2 = 0.491$, $F_{2,36} = 18.387$, p <0.000). Color was a significant variable, with a standardized regression coefficient (*Beta*) of -0.449 (p=0.001), as was %SAV (*Beta*=0.416, p=0.003).

<u>Habitat Parameters and Wood Frog Egg Mass Counts</u>

Of the landscape variables, only road distance was entered into the model (model adjusted $R^2 = 0.370$, $F_{1,14} = 9.217$, p =0.01). Distance to paved road was a significant variable, with a standardized regression coefficient (*Beta*) of -0.644 (p=0.01). Of the within-pond variables, only color was entered into the regression model (model adjusted $R^2 = 0.459$, $F_{1,14} = 12.858$, p <0.003). Color was a significant variable, with a standardized regression coefficient (*Beta*) of -0.705 (p<0.003).

Discussion

<u>Temporal Trends in Spotted Salamander Egg Mass Counts</u>

Annual variation in reproductive effort of *Ambystoma* salamanders is well documented. Numbers of egg masses deposited in a pond in a given year reflect both the size of the adult population and the proportion of that population that bred. Breeding populations vary more than adult populations, and long term data show orders of magnitude variation in breeding populations (reproductive effort) that is highly correlated with rainfall during the breeding migration season (Semlitsch 1987, Pechmann et al. 1991). Yet, data on spotted salamander collected by Shoop (1974) over a five year period in eastern Massachusetts do not show this correlation.

The data collected to date at CACO are short term and generally show variation in reproductive effort within the same order of magnitude (table 3, 4). A similar degree of annual variation over the short term has been found in spotted salamander populations elsewhere in Massachusetts (Shoop 1974, 5 years), Alabama (Blackwell et al. 2004, 6 years), Ohio (Brodman 2002, 12 years), and the Appalachia region (Petranka et al. 2004, 10 years). Given the limited data, several more years of monitoring will be necessary for meaningful trend analysis.

Spatial Variation in Spotted Salamander Egg Mass Counts

The influence of within-pond and adjacent landscape attributes on numbers of spotted salamander egg masses has been moderately well studied. In Pennsylvania, the number of eggs present in ponds was positively correlated with pH and pond size, and negatively correlated with total cations and silica (Rowe and Dunson 1993). In Ontario, number of eggs in ponds was positively correlated with alkalinity (Clark 1986, cited in Petranka 1998). In Rhode Island, spotted salamander occurrence was associated with presence of woodland habitat (Egan 2001) and number of eggs in ponds was negatively correlated with road density. Beyond those landscape features, large numbers of egg masses were more likely to be deposited in larger ponds with greater canopy closure, extensive shrub cover and persistent non-woody vegetation, and relatively longer hydroperiod (Egan and Paton 2004). Similarly, in eastern Massachusetts, viable populations of spotted salamanders were associated with relatively large (>1000 m^2), deep (>1 m), fishless, permanent or semi-permanent ponds with relatively open canopies in a well drained, topographically varied, unfragmented forested landscape (Windmiller 1996). In New Hampshire, numbers of spotted salamander egg masses were positively correlated with hydroperiod, amount of forest and agriculture, and distance to road (Mattfeldt 2004).

The ponds monitored at CACO are fewer than the numbers sampled in the some of the above works and were chosen for monitoring based, in part, on their known use by spotted salamanders. In addition, they are inside the park, in a relatively uniform forested landscape. Thus, the ponds monitored here at CACO probably represent a much narrower range of conditions than would be found in a random sample of vernal ponds from a larger geographic area. Consequently, the parameters that differentiate between ponds in a broad scale analysis may not be informative at the park scale. For example, whereas Windmiller (1996), Egan (2001), and Mattfeldt (2004) found that landscapes with low road density and high woodland habitat were positively correlated with occurrence and larger populations of spotted salamanders, all of the ponds monitored at CACO meet this description. The lack of any significant relationship between egg mass counts and adjacent habitat features is due to the fact that all ponds are essentially in woodlands with very low road density. With only one exception (W14), from 90 to 100% of their adjacent area is occupied by woodland and only 6 of 40 ponds have any paved roads within 50 meters (Appendix 3).

The analysis of the relationship of egg mass counts to within-pond features found a significant negative relationship with color (AbsCo440) and a positive relationship to percent SAV. This model explained 49.1% of all variability in numbers of egg masses in a pond. In general, there was a tendency for ponds with darker water (higher color value) to have fewer egg masses and ponds with more SAV to have more. The degree of color in woodland vernal ponds reflects the presence of humic compounds (tannins) formed by plant decomposition (Cuthbert and del Giorgio 1992). At CACO, most vernal ponds are highly colored and acidic, with acidity mostly due to organic acids (Portnoy 1990). Portnoy (1990) also found a significant negative relationship between color and hatching success, as did Jackson (1990), and suggested that a negative relationship between spotted salamander breeding abundance and color was due to the long term effects of lower survival and recruitment at high color sites. At CACO in 2004, color was negatively correlated with depth (Spearman's R= -0.39, p=0.015), area (R= -.41, p=0.01) pH (R= -57, p= 0.0001) and alkalinity (R = -0.63, p=0.00001) and positively correlated with conductivity (R=0.46, p=0.003). In essence, ponds that are smaller, shallower, more acidic, with lesser buffering capacity and greater concentration of dis-associated ions tend to have higher color values and fewer egg masses. Rowe and Dunson (1993) had similar findings in Pennsylvania, with numbers of egg masses positively correlated with pH and volume, and negatively with conductance.

Since the presence of SAV in vernal ponds is indicative of ponds with longer hydroperiods (Egan and Paton 2004), percent SAV was considered a surrogate measure of hydroperiod. As such, the strong positive relationship between egg mass counts and SAV (hydroperiod) is consistent with findings from Rhode Island (Egan and Paton 2004), eastern Massachusetts (Windmiller 1996), New Hampshire (Mattfeldt 2004), and coastal Maine (Baldwin and Vasconcelos 2003). Also, given the positive relationship between hydroperiod and reproductive success in other *Ambystoma* species at a single pond over time (Semlitsch 1987, Pechmann et al. 1991), and the well established philopatry of spotted salamanders, it seems logical that among a group of vernal ponds, those with longer hydroperiods would tend to support larger populations. Thus, ponds with longer hydroperiods and less colored waters tend to support larger populations of spotted salamanders.

Landscape analysis throughout the Northeast U.S. has shown that the ideal landscape for spotted salamanders is a non-urbanized, non-fragmented, roadless, forested landscape with well drained soils and moderately hilly topography, containing long hydroperiod vernal ponds (Windmiller 1996, Gibbs 1998, Egan 2001, Guerry and Hunter 2002, Egan and Paton 2004, Mattfeldt 2004, Rubbo and Kiesecker 2005). This describes much of the CACO landscape, particularly the Eastham vernal pools area. This complex of ponds in close proximity, with varied hydroperiods and with many supporting large numbers of spotted salamanders appears exceptional. For example, whereas Windmiller (1996) found only 12 of 94 (13%) ponds occupied by spotted salamanders in the largely urbanized landscape in eastern Massachusetts had more than 104 egg masses (indicative of a viable population of 500 adults) eight of 14 (57%) ponds sampled in Eastham in 2004 did.

Further evidence that CACO provides an optimal landscape for spotted salamanders is seen in comparisons of naive occupancy rates and mean numbers of egg masses per pond between CACO and other geographic areas. At CACO, the 39 vernal ponds within the known range of spotted salamanders had a naive occupancy rate of 74% (29 of 39) and a mean number of egg masses per pond of 136 (range 0 to 778, SE=33.8, includes ponds not occupied). Naive occupancy rate and mean number of egg masses/pond reported from elsewhere include: 67% (33/49) and 25.9 (range 0-217, SE=7) from New Hampshire (Mattfeldt 2004); 78% (28/36) and 45.4 (range 0-747, SE=21.1) in Rhode Island (Egan 2001); 49% (94/193) and 21.0 (range 0-374) in Concord, Massachusetts (Windmiller 1996); 70% (7/10) and 31.5 (range 0-230, SE=22.4) in Maryland (Albers and Prouty 1987); and 90% and 124 (SE=24.4) in western Virginia (Petranka et al. 2003a). In Pennsylvania, Rowe and Dunson (1993) report median numbers of spotted salamander egg masses/pond in four different regions of the state as 65 (range 0-456), 12 (range 0-195), 48 (range 0-361), and 146 (3-1298). In northeast Maine, occupancy rate was 52% (Guerry and Hunter 2002) and in three regions of the state, it varied from 66.3% to 93.3 % (71% overall) (Calhoun et al. 2003). These comparisons indicate that there are few areas where spotted salamanders are as widespread and abundant as CACO.

While CACO is noteworthy in that it appears to be a high quality landscape for supporting robust populations of spotted salamanders, urbanization, road construction, increased traffic volume, groundwater withdrawal, and habitat fragmentation all have the potential to reduce spotted salamander abundance. These stressors will likely have their greatest impacts outside of CACO, suggesting that CACO will become increasingly more important regionally for maintaining viable populations. However, considering that the negative effects of forest habitat alteration and road impacts can extend up to 300 meters (Windmiller 1996), there is also potential for these impacts to extend into the park.

Temporal Trends in Wood Frog Egg Mass Counts

Annual variation in reproductive effort in wood frogs is also well documented. Berven (1990) noted that breeding population size in Maryland varied by a factor of 10 over a seven year period and that breeding effort (number of egg masses) sometimes varied by a factor of 20 between consecutive years. Crouch and Paton (2000) found that numbers of egg masses in a pond varied by a factor of two to three from one year to the next, and in a group of Virginia ponds, numbers of breeding females sometimes varied annually by a factor of 10 to 20 (Berven and Grudzien 1990). Such variation primarily reflects a time-lagged response to variation in juvenile recruitment (Berven 1990, Petranka et al. 2003a) which in turn is a function of larval density and hydroperiod. A Maryland population was regulated by density-dependant factors affecting larval survival (i.e. survival was negatively correlated with number of eggs deposited) and hydroperiod. Larval survival at short hydroperiod ponds could vary dramatically between years due to pond drying whereas at the opposite extreme, more permanent ponds had lower larval survival, presumably due to presence of more predators (Berven 1990). Variation in numbers of breeding females (each wood frog egg mass represents one female, Crouch and Paton 2000) at CACO (tables 6 and 7) falls within this range of variation. The lack of significant trends is not surprising, given the short term nature of the data.

Spatial Variation in Wood Frog Egg Mass Counts

Similar to spotted salamanders, wood frog occurrence and abundance is generally associated with an unfragmented, roadless, forested landscape (Gibbs 1997, Egan 2001, Guerry and Hunter 2002, Egan and Paton 2004, Mattfeldt 2004, Porej et al. 2004, Rubbo and Kiesecker 2005). However, some subtle landscape level differences between these two species appear to exist, such as adjacent forested wetlands being a critical habitat component for wood frogs (Egan 2001). Though both wood frogs and spotted salamanders typically breed in fishless vernal ponds, there is a growing body of literature demonstrating that wood frog abundance is greatest in vernal ponds with short and intermediate hydroperiods and spotted salamander abundance is greatest in long hydroperiod vernal and semi-permanent ponds (Berven 1990, Rowe and Dunson 1993, Paton et al. 2000, Babbitt et al. 2003, Calhoun et al. 2003, Mattfeldt 2004, Egan and Paton 2004). While pond hydroperiod seems to be the most important within-pond factor, egg mass abundance of both species was also positively linked to ponds with extensive woody and non-woody emergent vegetation in Rhode Island (Egan and Paton 2004) and to pond volume and dissolved organic carbon in Pennsylvania (Rowe and Dunson 1993).

The significant negative relationship between wood frog abundance and color parallels the results discussed above for spotted salamanders, and reflects the fact that these two species are ecologically similar. In contrast, the significant negative relationship between wood frog abundance and distance to paved roads is inconsistent with studies demonstrating negative impacts of roads on amphibian breeding abundance (Egan and Paton 2004, Mattfeldt 2004). However, we suspect that this relationship is an artifact of our study's relatively small sample size (only 15 ponds), the small numbers of wood frog egg masses present (mean=5.73 egg masses/pond), and the fact that two of CACO's top three sites for wood frogs, E21 and E22, are close to a paved road.

Wood frogs at CACO present a number of paradoxes. Their known distribution is limited to Eastham and South Wellfleet. Within this distribution they appear widespread, yet uncommon. The naive occupancy rate at CACO, within its known range, is high (73%), and compares favorably with other regions: e.g.17% in southwest Ontario (Hecnar and M'Closkey 1996); from 78% to 100% in Virginia (Petranka et al 2003a,b); 86%, 11%, and 8% in rural, urban, and suburban Pennsylvania (Rubbo and Kiesecker 2005); 43% in Ohio (Porej et al. 2004); 88% (Mattfeldt 2004) and 48% (Babbit et al. 2003) in New Hampshire; 75% (Egan 2001) and 69% (Egan and Paton 2004) in Rhode Island; 82% in northeast Maine (Guerry and Hunter 2002), and in three regions of Maine, 39%, 51%, and 23% (Calhoun et al. 2003). In contrast, wood frog abundance at CACO is comparatively very low. Within its known range at CACO, the mean number of egg masses per pond (including ponds not occupied) is only 5.73. Similar studies, sampling multiple sites across a landscape, report a much greater abundance (mean number of egg masses/pond): e.g. 47.7 in New Hampshire (Mattfeldt 2004); 169 (Egan 2001) and 131 (Crouch and Paton 2000) in Rhode Island; 86.5 (Berven and Grudzien 1990) and 124 (Petranka et al. 2003b) in Virginia. Comparison with these and other studies (e.g. Rowe and Dunson 1993, Calhoun et al. 2003) indicates that wood frogs are not abundant at CACO.

The contrasting widespread distribution and abundance of spotted salamanders versus the localized rarity of wood frogs at CACO presents a puzzling situation for which several explanations were considered. Lazell (1976) describes a model of post-glacial colonization of Cape Cod by amphibians and reptiles in which more "northern" or cold adapted species are the first to arrive. Since wood frogs are the most northerly amphibian in North America they would be expected to precede, not follow spotted salamanders, which do not range as far north (Conant and Collins 1998). While the wood frog appears to be expanding its range onto the outer Cape and has recently been recorded as far out as South Wellfleet, spotted salamanders extend out much farther, to High Head in Truro.

Since most landscape level analyses find occurrence and abundance of these two species to be linked to the same factors, the forested and relatively unfragmented, roadless landscape full of vernal ponds at CACO, which appears ideal for spotted salamanders, should seemingly be so for wood frogs as well. While these two species appear to be highly correlated at a coarse landscape level, there is some evidence suggesting subtle differences at a finer scale. For example, Porej et al. (2004) found that while both spotted salamander and wood frog presence at breeding ponds were positively associated with a forested "core", wood frog presence also was correlated with the larger landscape being forested. Similarly, Egan (2001) found that the amount of forested upland within 1000 m of breeding ponds had a greater effect on wood frog abundance than on spotted salamanders.These findings suggest that wood frogs, which emigrate greater distances from their breeding ponds than spotted salamanders (Berven and Grudzien 1990, Madison 1997), extend their use of the landscape much further away from breeding ponds than do spotted salamanders, and hence require a more extensively forested landscape. Given that forest habitat at CACO is still in the process of recovering from colonial era deforestation (Eberhardt et al. 2003), if wood frogs were more sensitive to the extent of forest than spotted salamanders, they would be expected to be less common. While they are in fact less common, since wood frogs at CACO occur primarily in Eastham, where deforestation was more extensive than in Wellfleet or Truro (Eberhardt et al. 2003), it seems unlikely that the extent of woodland habitat is limiting the range and abundance of wood frogs at CACO.

Another subtle difference between wood frogs and spotted salamanders is the length of their larval period and consequent pond hydroperiod requirements. In Rhode Island, wood frogs required a minimum hydroperiod of 16.4 weeks, whereas for spotted salamanders it was 20 weeks (Paton et al. 2000). As noted above, wood frogs are most abundant and dominant in intermediate-duration vernal ponds whereas spotted salamanders are most abundant and dominant in long-duration vernal and semi-permanent ponds. In two of three regions studied in Maine, numbers of wood frog egg masses were negatively correlated with numbers of spotted salamander egg masses, and spotted salamander abundance was greatest in semi-permanent ponds (Calhoun et al. 2003). Similarly, in Pennsylvania, wood frogs dominated in areas where ponds tended to be low volume and spotted salamanders dominated in an area where pond volume was greater (Rowe and Dunson 1993). These studies suggest that landscape level abundance of wood frogs relative to spotted salamanders may be a function of which hydroperiod types dominate the landscape. While detailed hydroperiod data are not yet available to include in analysis of CACO's egg mass data, pond maximum depth data (Appendix 3) were normally distributed, suggesting that a broad range of hydroperiods with many intermediate depth ponds are present within our study area. The low numbers of wood frog egg masses, even at intermediate depth ponds, suggests that their rarity at CACO is not related to pond hydroperiod.

Another factor potentially determining the number of wood frog egg masses in a pond is the negative correlation between egg mass abundance and number of adjacent vernal ponds (Mattfeldt 2004). Isolated ponds contain greater numbers of egg masses (Calhoun et al. 2003), suggesting that when many ponds are in close proximity, reproductive effort is spread among them (Mattfeldt 2004). This seems plausible and likely very adaptive, and the ponds used by wood frogs at CACO are in fact in close proximity to other vernal ponds. Yet, even the total number of wood frog egg masses (86 found in 11 ponds) is less than most of the pond means detailed above. Clearly, wood frogs are uncommon at CACO, and neither extent of forested upland, hydroperiod, nor proximity to other vernal ponds seems to be a factor.

One other subtle difference between spotted salamanders and wood frogs is that wood frogs appear to require a more complex landscape to support seasonal shifts in habitat use. Whereas non-breeding spotted salamanders are primarily fossorial, spending most of their time underground in mammal burrows (Faccio 2003, Regosin et al. 2003a), wood frogs appear to move from breeding ponds in the spring to moist lowland forests in the summer and back to forested uplands adjacent to breeding ponds for hibernation (Regosin et al. 2003b). Wood frog occurrence and abundance at ponds in Rhode Island was positively linked to amount of nearby forested wetlands (Egan 2001). Given the positive relationship between survival of adult wood frogs and rainfall (Berven 1990), it would appear that wood frogs are more sensitive to dessication pressures and forested wetlands provide an important summer micro-habitat. CACO has few forested wetlands, with the largest, “Red Maple Swamp”in Eastham. Eastham is also the primary range of wood frogs here, suggesting that the rarity of wood frogs at CACO is due to a lack of forested woodlands.

ANURAN CALL COUNTS

Methods

Anuran call counts were conducted at a total of 30 sites (figs. 4-6), selected in a stratified random design to sample across the range of freshwater wetlands present at CACO, as well as along the length of the park’s long axis from Eastham to Provincetown (Paton et al. 2003). Each site was sampled weekly, for 15 consecutive weeks, beginning on April 13 and extending until July 22. The thirty sites were divided into three groups of 10 (survey routes one, two, and three). Within a given week, one survey route was sampled each night, such that a complete sampling of all 30 ponds occurred over the course of three nights, nearly always Tuesday, Wednesday, and Thursday.

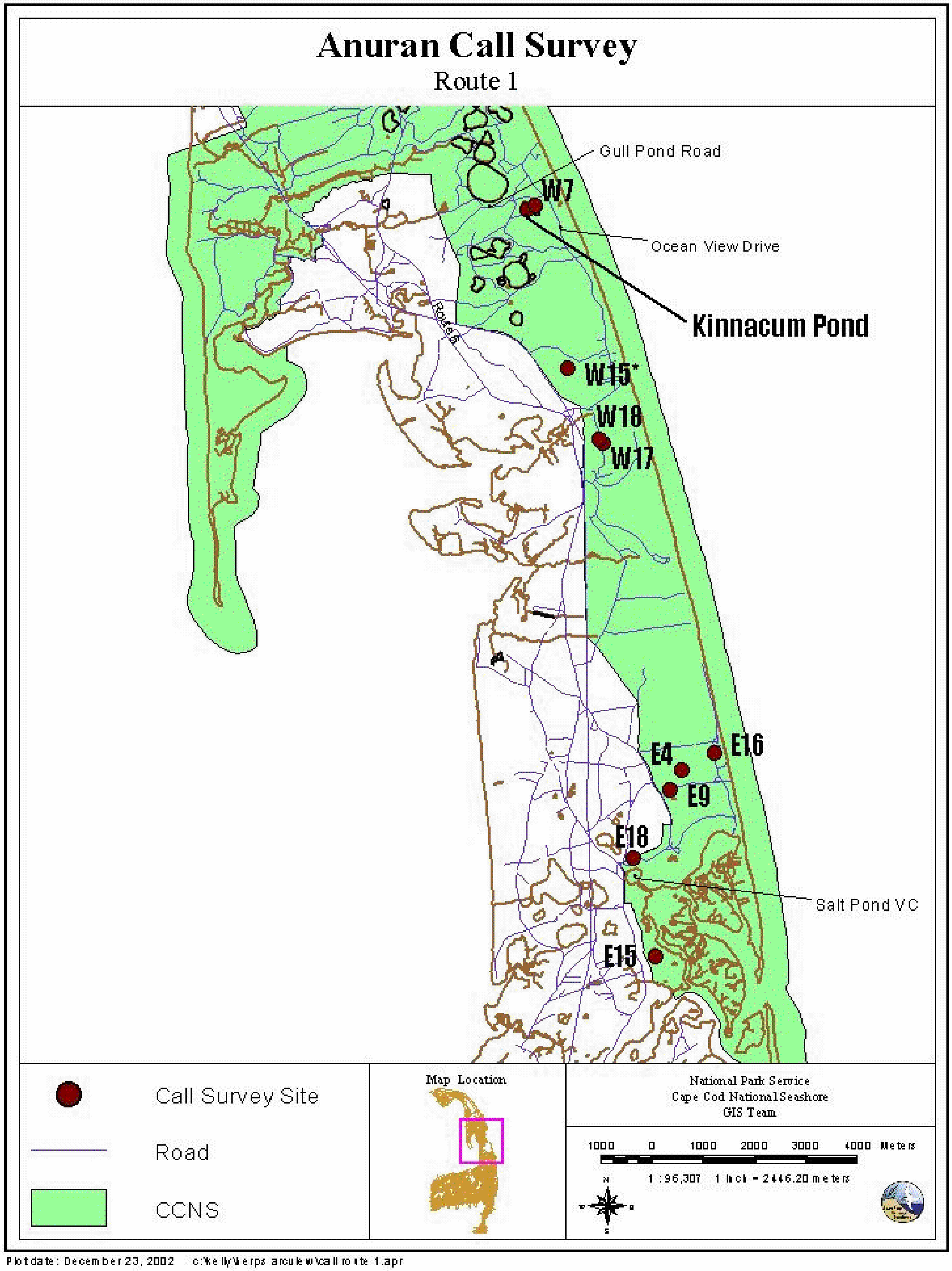


Figure 4. Anuran call survey Route 1.

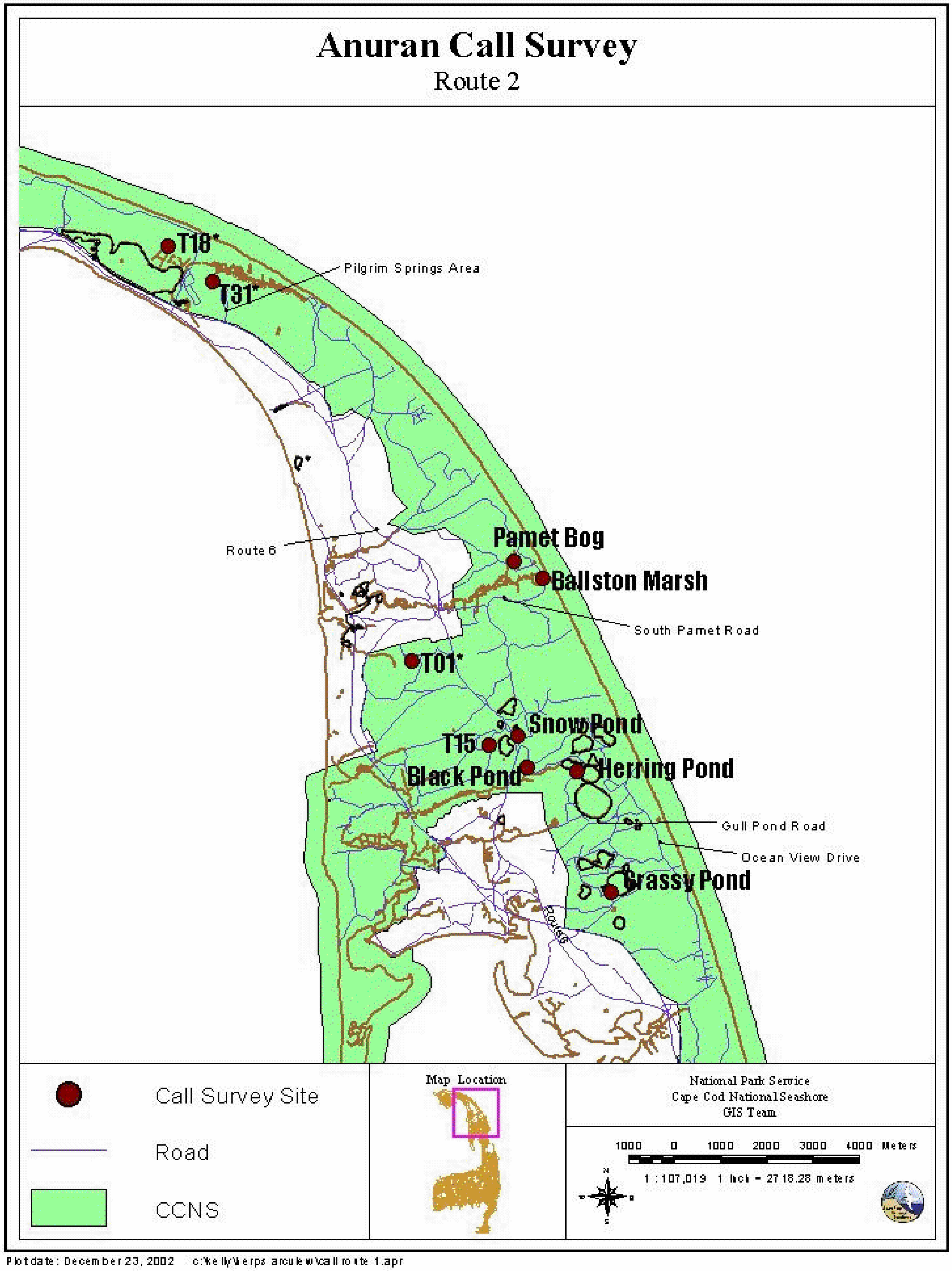


Figure 5. Anuran call survey Route 2.

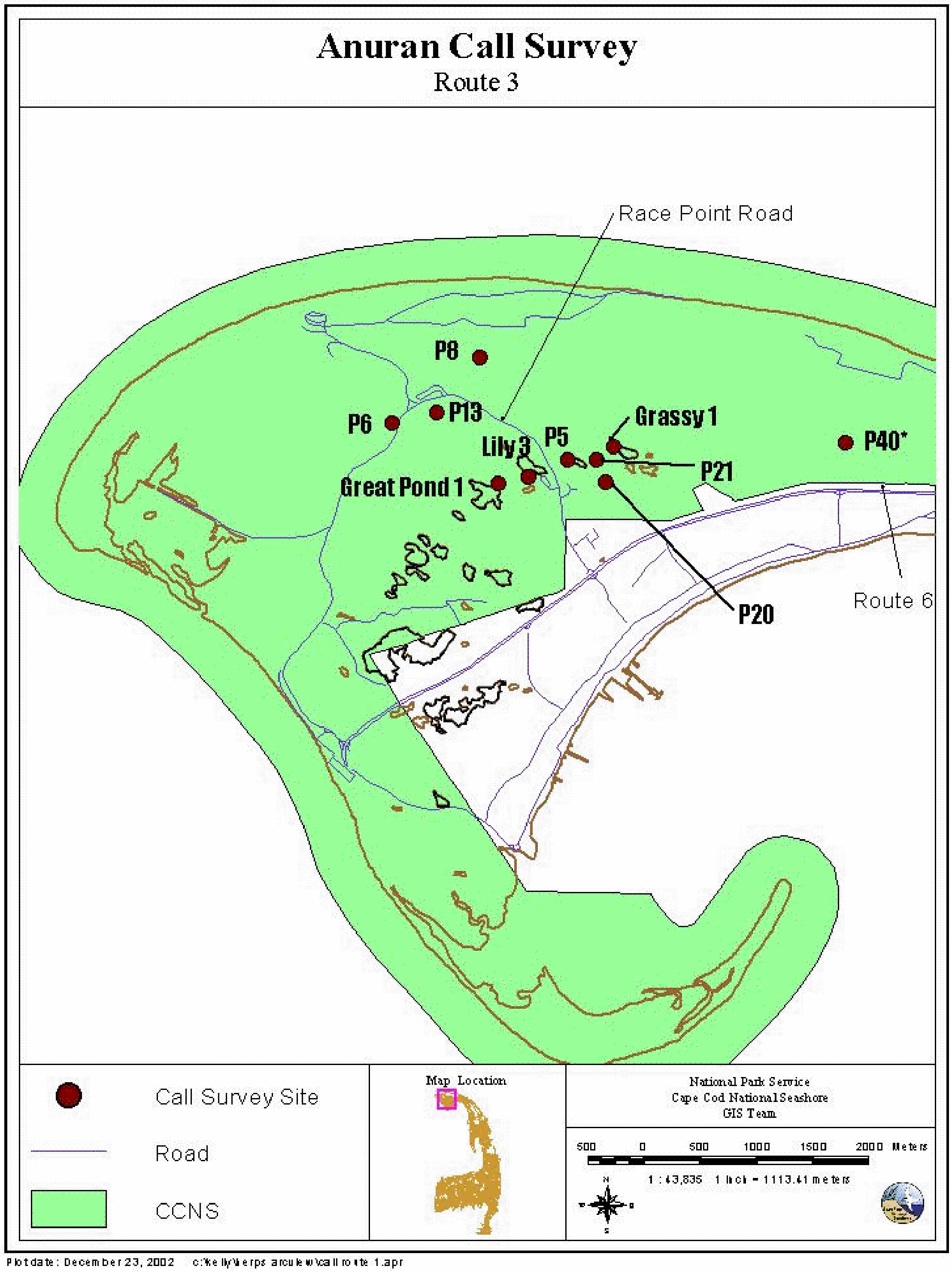


Figure 6. Anuran Call Survey Route 3.

Nightly sampling occurred from 30 minutes after sunset until ca. midnight – 0100 hours, and consisted of listening for and identifying anuran vocalizations. Vocalizations were scored according to an index value that ranged from zero to three (Mossman et al. 1998). In addition, data on air and water temperature, sky, wind, and precipitation conditions were recorded. See Paton et al. (2003) for further details of sampling procedure. Water samples from the 30 call count ponds were collected and analyzed in conjunction with those collected from ponds where egg mass counts were conducted.

Call count data were used as a measure of distribution based on sites recorded, and a measure of abundance based on the calling index. For each species, abundance at a particular site was based on the maximum index value recorded (Stevens et al. 2002). As a measure of a species' overall abundance at sites where it was present, the mean of these maxima was calculated (based only on sites where the species was present).

For each species recorded over the course of the season, program PRESENCE (MacKenzie et al. 2002) was used to estimate detection probability (probability of detecting a species at a site on a given sampling occasion, given it is actually present at the site) and determine the role of sampling covariates (air and water temperature) in detectability. The data set was reduced by only including data from the first to last week (inclusive) when a given species was recorded. PRESENCE was also used to estimate site occupancy rates (proportion of sites that species is estimated to occur at) for each species detected, and the relationship of each species occurrence to site covariates. One group of site covariates was based on hydroperiod (temporary, semi-permanent, or permanent) and a second group related to water chemistry (pH, conductivity, and color (AbsCo440)) (table 10). Temporary ponds were defined as ponds that dry out every or nearly every year. Conversely, semi-permanent ponds were defined as ponds that retain water in most years but dry out infrequently. Permanent ponds retain standing water even during droughts.

The process of constructing and selecting models to explain detectability and occurrence with PRESENCE involved first determining the best model for detectability. Pre-defined models for constant ($p(.)$) and time dependent ($p(t)$) probability of detection were run, and compared to custom models of detectability based on air and water temperatures recorded during sampling events. PRESENCE calculated the Akaike Information Criterion (AIC) for each model and, based on differences in AIC and a model weighting procedure detailed in Cooch and White (2001), the best model for explaining detectability was selected. Additional models testing the role of hydroperiod and water chemistry in explaining occurrence (ψ) were built upon the best detectability model. AIC weighting was used to determine the most informative hydroperiod and water chemistry covariates and a final model, containing both of these two covariates (and the detectability covariate) was constructed. These four models, plus a null model (constant occurrence, constant detectability) were compared based on AIC weighting, and the best overall model determined.

Between-year differences in each species' abundance were analyzed based on maximum index values using the Sign Test. Between year differences in occupancy rates and mean abundance for the entire community were analyzed with the Wilcoxon paired sample test.

Results

A total of seven species were recorded. Spring peepers (*Pseudacris crucifer*, PSCR) were the most widespread. They were detected at 27 sites and, at those sites, had a mean maximum index value of 2.81. Grey treefrogs (*Hyla versicolor*, HYVE) were least widespread, detected at just one site, and least abundant with a mean maximum index value of 1.0 (table 10). Site occupancy rates estimated by PRESENCE ranged from 0.033 for gray treefrogs to 0.900 for spring peepers, and generally were very similar if not identical to a species' naive rate. Spring peepers were the most detectable (probability of detection=0.7259) and Fowler's toads the least detectable (p=0.2265) (table 11). There was a moderate but non-significant correlation between occupancy rate and abundance (Spearman's R=0.61, *p*=0.15).

In terms of seasonal chronology, spring peepers and wood frogs began calling earliest, at week one (4/12/04), and Fowler's toads (*Bufo fowleri*, BUFO) and Pickerel frogs (*Rana palustris*, RAPA) in week two (4/19/04). Green frogs (*Rana clamitans*, RACL) were first recorded in week four (5/3/04) and Grey treefrogs and bullfrogs (*Rana catesbiana*, RACA) in week nine (6/7/04). Breeding season duration (number of weeks from first to last records, inclusive) was shortest for wood frogs (one week) and longest for Fowler's toads and green frogs (12 weeks) (fig. 7).

The best models for explaining detection and occurrence varied by species. For wood frogs, Fowler's toads, and gray treefrogs, detectability was positively associated with air temperature. For the remaining four species detectability varied by sampling occasion but was not related to either temperature parameter (table 11, 12).

Table 10. Anuran call count maximum index values and site covariates. Mean maximum represents the mean of maximum values for a species based only on sites where the species was recorded. Hydro=hydroperiod and Cond=conductivity.

Route	SiteID	RASY	RACL	RACA	PSCR	RAPA	BUFO	HYVE	# Species	Wetland Type	Hydro	pH	Cond	AbsCo 440
1	E04	0	2	0	3	0	0	0	2	Vernal Pool	Temp	4.80	39.6	10.1332
1	E09	1	2	0	3	0	0	1	4	Vernal Pool	Temp	5.12	40.5	14.2786
1	E15	0	1	0	3	0	0	0	2	Swamp-red maple	Temp	4.10	159.0	62.1810
1	E16	2	1	0	3	0	0	0	3	Vernal Pool	Temp	4.60	198.9	60.5689
1	E18	2	1	0	3	0	0	0	3	Vernal Pool	Temp	5.85	115.0	16.3513
1	Kinnacum	0	1	2	3	0	3	0	4	Kettle Pond	Perm	4.97	74.7	0.2303
1	W07	0	1	1	3	1	0	0	4	Vernal Pool	Temp	5.57	94.5	11.0544
1	W15	0	0	0	3	0	0	0	1	Vernal Pool	Temp	4.50	45.9	41.6843
1	W17	0	0	0	3	0	0	0	1	Swamp-white cedar	Temp	4.01	169.2	31.7814
1	W18	0	0	0	3	0	0	0	1	Vernal Pool	Temp	4.05	162.0	36.8480
2	Ballston Marsh	0	1	1	3	0	3	0	4	Riparian Marsh	Perm	7.11	4545.0	4.6060
2	Black Pond	0	1	0	0	0	0	0	1	Riparian Marsh	Perm	6.13	123.3	1.8424
2	Grassy Pond	0	2	1	3	0	0	0	3	Kettle-shallow	Semi	4.77	62.1	13.5877
2	Herring Pond	0	1	1	1	2	1	0	5	Kettle Pond	Perm	6.67	135.9	1.1515
2	Pamet Bog	0	1	3	3	1	1	0	5	Bog	Perm	4.65	218.7	35.6965
2	Snow Pond	0	1	1	3	2	0	0	4	Kettle Pond	Perm	6.02	81.9	1.8424
2	T01	0	1	0	3	0	0	0	2	Vernal Pool	Semi	4.72	36.0	30.8602
2	T15	0	0	0	0	0	0	0	0	Vernal Pool	Temp	4.64	49.5	24.8724
2	T18	0	0	0	3	0	1	0	2	Dune Slack	Temp	6.13	81.9	20.4967
2	T31	0	3	0	3	0	0	0	2	Vernal Pool	Temp	4.60	72.9	20.7270
3	Grassy1	0	2	0	3	0	1	0	3	Interdune pond	Perm	5.17	96.3	17.5028
3	Great Pond 1	0	3	1	3	0	1	0	4	Interdune pond	Perm	6.18	78.3	7.5999
3	Lily3	0	2	0	3	0	1	0	3	Interdune pond	Semi	5.52	72.9	13.3574
3	P05	0	1	0	3	0	2	0	3	Dune Slack	Semi	4.41	118.8	32.2420
3	P06	0	0	0	3	0	3	0	2	Dune Slack	Temp	6.08	111.6	3.6848
3	P08	0	0	0	2	0	0	0	1	Dune Slack	Temp	4.94	100.8	5.7575
3	P13	0	1	0	3	0	3	0	3	Dune Slack	Temp	4.83	104.4	29.9390
3	P20	0	2	0	3	0	0	0	2	Interdune pond	Perm	4.79	87.3	15.6604
3	P21	0	0	0	0	0	0	0	0	Vernal Pool	Temp	4.37	83.7	38.9207
3	P40	0	0	0	1	0	1	0	2	Dune Slack	Temp	5.92	99.9	8.5211
Mean Max Index		1.67	1.48	1.38	2.81	1.50	1.75	1.00						
Total # Ponds		3	21	8	27	4	12	1						

Table 11. Analysis of anuran call count data by program PRESENCE. Best model is the best model explaining occurrence (ψ) and detectability (p). Naïve is the naive occupancy rate (frequency of occurrence). The estimated site occupancy rate is ψ, and (p) is the average probability of detection for each species, obtained using the constant probability of detection model (p(.)).

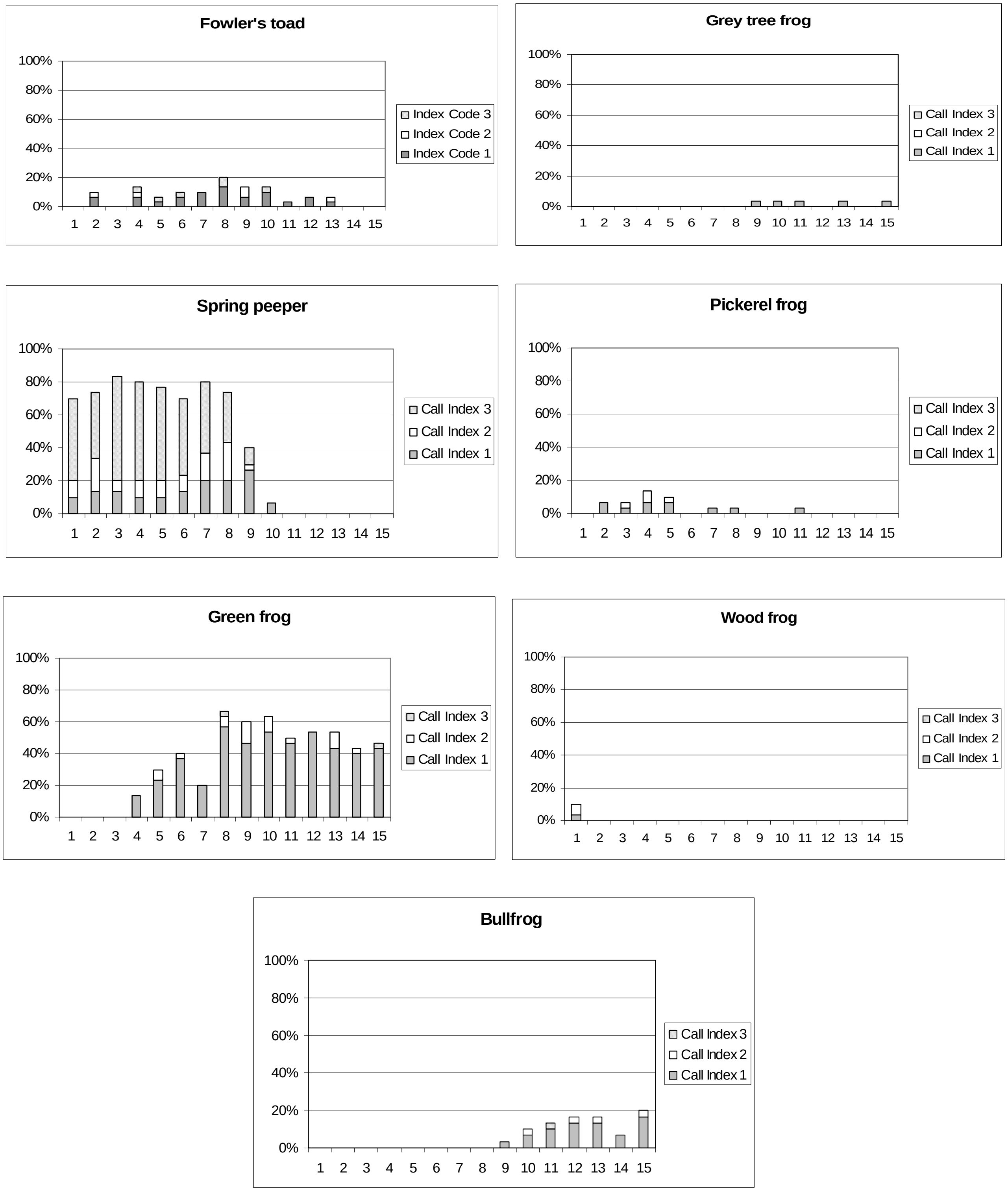
Species	Best Model	naïve	Ψ	*p*
BUFO	Ψ(.) p(air)	0.4000	0.4172	0.2265
HYVE	Ψ(cond) p(air)	0.0333	0.0333	0.7142
PSCR	Ψ(.) p(t)	0.9000	0.9000	0.7259
RACA	Ψ(perm) p(t)	0.2667	0.2677	0.4770
RACL	Ψ(perm,semi) p(t)	0.7333	0.7333	0.6174
RAPA	Ψ(perm) p(t)	0.1333	0.1333	0.3449
RASY	Ψ(perm) p(air)	0.1000	0.1750	0.3162

Table 12. Coefficients for parameters included in best model for each species by Program PRESENCE.

Species	Parameter	Coefficients
BUFO	air temp	0.0888
HYVE	conductivity	-0.1481
	air temp	19.1396
PSCR	time	
RACA	permanent	2.9517
	time	
RACL	permanent	26.2209
	semi-permanent	26.8724
	time	
RAPA	permanent	2.3026
	time	
RASY	permanent	-673.5742
	air temp	114.8825

The most important parameter influencing species occurrence was hydroperiod, which affected four of seven species (table 11, 12). Wood frogs had a strong negative coefficient for permanent water, indicating association with non-permanent ponds. Conversely, pickerel frogs and bullfrogs had positive coefficients for permanent water, and green frogs had positive coefficients for both permanent and semi-permanent water, indicating an association with relatively permanent water bodies. Gray treefrogs had a weak negative association with conductivity, based on the fact that the one pond they occurred at was among the lowest sites for this parameter. Spring peeper and Fowler's toad occurrence was not explained by any of the parameters analyzed.

Figure7. Seasonal variation in calling index values over course of sampling for each species encountered.



Species site occupancy rates and mean maximum index values in 2004 were generally similar to those of 2003 and there were no significant between-year differences in abundance for any species (table 13).Community-level patterns of occupancy and abundance did not differ significantly between years (Wilcoxon matched pairs test p=0.87 for mean maximum abundance, p=0.12 for naïve occupancy rate, and p=0.31 for estimated occupancy rate).

Table 13. Comparison of naive and estimated site occupancy rates and mean maximum calling index for anuran species detected in 2003 and 2004. Z and *p* obtained from the sign test of each species' between–year abundance.

Species	2003 naïve	2004 naive	2003Ψ	2004Ψ	2003 Mean	2004 Mean	Z	*p*
SCHO	0.100	0.000	0.100	0.000	3.00	0.00	1.15	0.25
BUFO	0.500	0.400	0.502	0.417	1.87	1.75	1.44	0.15
HYVE	0.100	0.033	0.333	0.033	1.00	1.00	0.71	0.48
PSCR	0.900	0.900	0.900	0.900	2.56	2.81	0.67	0.51
RACA	0.267	0.267	0.272	0.268	1.33	1.38	0.50	0.62
RACL	0.700	0.733	0.700	0.733	1.43	1.48	0.60	0.55
RAPA	0.170	0.133	0.170	0.133	1.80	1.50	0.50	0.62
RASY	0.067	0.100	0.067	0.175	1.00	1.67	0.50	0.62

Discussion

While too soon to detect trends, the first two year's data suggest that the park's anuran community may be fairly stable in terms of distribution and abundance. Occupancy rates and species abundance varied little between years (table 13) and there was no difference in community level patterns. The few differences involved species difficult to detect or with limited distributions, such as spadefoot toads, gray treefrogs, and wood frogs. Spadefoot toads and wood frogs are explosive breeders with short breeding seasons, and are not well suited for monitoring by nighttime calling surveys (Crouch and Paton 2002, Paton et al. 2003). These species are detected on few occasions, such that small year to year differences may appear large For example, spadefoots were detected in full chorus at three sites in 2003 and none in 2004. Gray treefrogs were detected at three sites in 2003 and only one in 2004.

Of the eight anurans known to occur at CACO, seven were recorded in 2004. Only spadefoot toads, already noted as difficult to monitor using this protocol, were missed. However, spadefoot eggs were observed at other CACO sites, indicating this species bred in 2004. For the seven species recorded, patterns of habitat use were similar to those observed in 2003 and pretty much conform to known habitat affinities for these species (Lazell 1976, Klemens 1993). Distributions of some species, however, continue to be puzzling. Gray treefrogs were only recorded in Eastham in 2004, though they had been recorded in Provincetown in 2003. This species, first recorded at CACO in Eastham in 2001, has never been recorded in Wellfleet or Truro, despite what appears to be suitable breeding habitat. While wood frogs were only recorded during surveys in Eastham, one was heard calling at W18 in South Wellfleet, on April 13, prior to a calling survey. As discussed above, the distribution and abundance of wood frogs seems to be limited by a lack of summer habitat (forested wetlands) rather than a lack of vernal pond breeding sites. Pickerel frogs were only recorded at a small number of sites from northern Wellfleet and Truro and seemingly correspond to the distribution of their suitable habitat, permanent clearwater ponds. Similarly, the remaining species are fairly widespread and have a distribution that essentially reflects the distribution of their preferred habitats.

Site occupancy rates of CACO anurans show both similarities and differences compared to other areas sampled with anuran call counts. Spring peepers were most widespread at CACO (occurring at 90% of sites) as well as in Southern Rhode Island (68% of sites) (Crouch and Paton 2002) and Prince Edward Island, Canada (90%)(Stevens et al. 2002). However, while both Crouch and Paton (2002) and Stevens et al. (2002) found wood frogs to be the second most widespread species (occurring at 65% and 83% of sites, respectively), wood frogs are the most geographically restricted CACO anuran, occurring only in Eastham and South Wellfleet. Their naïve occupancy rate in 2004 was 10%. This difference is likely due to two factors. While woodland vernal pond habitat is widespread at CACO, wood frogs have only been recorded during surveys from vernal ponds in Eastham. As discussed previously, this limited range and abundance seems to be the result of limited forested wetland at CACO. In addition, since wood frogs typically breed in small vernal ponds, some of this disparity is due to sampling bias. Ponds sampled by Crouch and Paton (2002) and Stevens et al. (2002) tended to be smaller than those sampled at CACO, and thus more likely to be used by wood frogs.

Green frogs, the second most widespread species at CACO and a species of permanent water bodies, had a 73% naive occupancy rate here, but only 32% in Rhode Island. This difference is also likely due to differences in the size and permanence of sample sites. For the remaining species, occupancy rates were similar to those reported by Crouch and Paton (2002). In addition, patterns of seasonal chronology and breeding season duration were also similar to those reported from southern Rhode Island (Crouch and Paton 2002), though the breeding season on Cape Cod is generally a few weeks later in the year.

RECOMMENDATIONS

While we have attempted some trends analysis with these limited data, a more in-depth analysis should be conducted after five consecutive years. In addition to trends, this analysis should look at annual variability, power, and sampling frequency to determine if protocol modifications are called for. Until this more in-depth analysis is completed, we plan to continue annual monitoring.

For both egg mass counts and anuran call counts, further research and consideration should be given to identifying, defining, measuring, and analyzing pond and landscape parameters and their relationship to the distribution and abundance of target species. In particular, the relationship of wood frog presence and abundance to extent of forested upland and wetlands should be examined. Additional monitoring of pond water depth and hydroperiod is also needed to better characterize ponds, and collecting groundwater data should also be considered.

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Appendix 1. Ponds sampled for egg masses in 2004 at Cape Cod National Seashore.

Name	Town	Easting	Northing	Protocol
E02	E	420291	4633806	Both
E03	E	420420	4633929	Both
E04	E	420298	4634044	CACO
E05	E	420071	4634077	Both
E05A	E	420077	4633994	Both
E06	E	420225	4634328	Both
E07	E	420337	4634250	CACO
E08	E	420533	4634102	Both
E11	E	420196	4633918	CACO
E11east	E	420262	4633908	CACO
E18	E	419653	4632264	PAO
E19	E	419756	4632112	PAO
E21	E	420069	4632956	CACO
E22	E	419936	4632907	CACO
P04	P	401405	4657852	Both
T01	T	412586	4648436	CACO
T02	T	414157	4648575	PAO
T02C	T	414190	4648487	PAO
T04	T	414546	4647955	PAO
T08	T	416490	4647582	PAO
T09	T	415993	4647319	PAO
T14	T	414260	4646585	PAO
T15	T	414104	4646568	CACO
T16	T	414467	4646406	PAO
T22	T	414530	4650759	PAO
T23	T	414436	4650994	PAO
T45	T	410416	4655998	PAO
W01	W	411106	4645239	PAO
W02	W	410864	4644444	PAO
W04	W	416834	4646324	PAO
W05	W	416160	4645808	PAO
W06	W	415966	4645301	Both
W07	W	417431	4644996	CACO
W11	W	417499	4644021	PAO
W12	W	417231	4643191	PAO
W14	W	418540	4642523	PAO
W15	W	418064	4641832	Both
W16	W	417823	4641952	PAO
W18	W	418750	4640381	CACO
W24	W	417886	4642081	PAO

Both=ARMI PAO and CACO protocol pond
PAO=ARMI PAO protocol only pond
CACO=CACO protocol pond, not on PAO list

Appendix 2. Water quality data collected from all amphibian monitoring sites in 2004.

Pond	Date	pH	Alkalinity	Conductivity	Cl^- mg/L	Cl^- (mM)	SO_4^{-2} mg/L	SO_4^{-2} (mM)	$Cl:SO_4$ (molar)	AbsCo440
Ballston Marsh	04/30/04	7.11	29.0	4545.0	1600.0	45.130	480.9	5.004	9.019	4.606
Black Pond	04/29/04	6.13	4.0	123.3	27.4	0.773	5.5	0.057	13.504	1.842
E02	04/29/04	4.57	-1.9	39.6	6.4	0.181	0.6	0.006	28.913	12.206
E03	04/29/04	4.68	-1.8	45.8	5.9	0.166	0.5	0.005	31.985	14.509
E04	04/29/04	4.80	0.1	39.6	17.8	0.502	2.5	0.026	19.300	10.133
E05	04/29/04	4.80	0.0	48.6	31.5	0.889	1.1	0.011	77.623	4.376
E05a	04/29/04	5.49	2.3	45.0	28.4	0.801	5.4	0.056	14.256	0.921
E06	04/29/04	4.77	-0.1	46.8	13.2	0.372	1.2	0.012	29.817	13.357
E07	04/29/04	4.74	0.0	36.9	23.5	0.663	2.2	0.023	28.954	9.212
E08	04/29/04	4.47	-3.0	36.0	8.3	0.234	0.7	0.007	32.140	13.588
E09	04/29/04	5.12	0.2	40.5	8.4	0.237	0.7	0.007	32.528	14.279
E11	05/03/04	4.65	-1.5	45.9	7.7	0.217	0.5	0.005	41.744	17.503
E11east	05/03/04	4.82	-1.0	57.6	8.3	0.234	0.8	0.008	28.123	40.303
E15	04/29/04	4.10	-5.4	159.0	34.1	0.962	1.5	0.016	61.622	62.181
E16	04/29/04	4.60	-0.4	198.9	33.4	0.942	1.4	0.015	64.668	60.569
E18	04/29/04	5.85	1.2	115.0	9.1	0.257	0.9	0.009	27.407	16.351
E19	04/22/04	5.71	3.2	59.5	11.2	0.316	1.0	0.010	30.359	11.976
E21	04/29/04	5.71	1.5	31.5	5.3	0.149	0.8	0.008	17.958	6.679
E22	04/29/04	4.01	-5.3	64.0	5.4	0.152	0.9	0.009	16.264	8.521
Grassy_W	04/29/04	4.77	-0.9	62.1	12.4	0.350	1.2	0.012	28.010	13.588
Grassy1_P	05/03/04	5.17	0.0	96.3	22.9	0.646	2.7	0.028	22.990	17.503
Great1_P	04/29/04	6.18	2.5	78.3	18.3	0.516	2.3	0.024	21.567	7.600
Herring	04/29/04	6.67	4.4	135.9	31.6	0.891	4.7	0.049	18.225	1.152
Kinnacum	04/29/04	4.97	-0.4	74.7	17.1	0.482	2.4	0.025	19.313	0.230
Lily Pond 3	04/29/04	5.52	0.5	72.9	18.3	0.516	1.4	0.015	35.432	13.357
P04	05/03/04	4.40	-3.3	78.3	10.8	0.305	0.9	0.009	32.528	49.975
P05	05/03/04	4.41	-3.1	118.8	24.6	0.694	1.5	0.016	44.454	32.242
P06	04/29/04	6.08	5.2	111.6	26.1	0.736	2.2	0.023	32.158	3.685
P08	04/29/04	4.94	-0.3	100.8	22.9	0.646	3.4	0.035	18.257	5.758
P13	04/29/04	4.83	-0.7	104.4	25.0	0.705	1.4	0.015	48.404	29.939
P20	05/03/04	4.79	-0.7	87.3	18.9	0.533	1.6	0.017	32.019	15.660
P21	05/03/04	4.37	-3.4	83.7	12.1	0.341	1.3	0.014	25.230	38.921

Pond	Date	pH	Alkalinity	Conductivity	Cl^- mg/L	Cl^- (mM)	SO_4^{-2} mg/L	SO_4^{-2} (mM)	$Cl:SO_4$ (molar)	AbsCo440
P40	05/03/04	5.92	3.4	99.9	21.5	0.606	0.9	0.009	64.754	8.521
Pamet Bog	04/30/04	4.65	-1.4	218.7	46.2	1.303	2.2	0.023	56.923	35.697
Snow Pond	04/29/04	6.02	0.6	81.9	18.7	0.527	2.7	0.028	18.774	1.842
T01	04/30/04	4.72	-0.2	36.0	32.1	0.905	3.2	0.033	27.191	30.860
T02	04/23/04	5.18	1.1	46.0	6.9	0.195	0.6	0.006	31.172	23.491
T02C	04/23/04	4.35	-4.7	90.6	10.1	0.285	0.8	0.008	34.222	92.581
T04	05/04/04	4.06	-6.9	80.0	7.0	0.197	0.5	0.005	37.949	56.193
T09	05/04/04	4.05	-6.5	101.6	11.8	0.333	1.1	0.011	29.078	76.229
T14	04/23/04	4.35	-3.1	74.2	10.5	0.296	1.0	0.010	28.462	26.485
T15	04/30/04	4.64	-0.3	49.5	11.9	0.336	1.9	0.020	16.977	24.872
T16	04/23/04	4.61	-1.8	55.6	5.3	0.149	1.6	0.017	8.979	53.430
T18	04/30/04	6.13	18.0	81.9	17.3	0.488	5.5	0.057	8.526	20.497
T22	04/23/04	4.46	-2.7	74.9	12.9	0.364	0.6	0.006	58.279	50.666
T23	04/23/04	4.69	-1.3	89.9	18.1	0.511	1.1	0.011	44.602	27.866
T31	05/03/04	4.60	-1.5	72.9	558.4	15.750	57.3	0.596	26.416	20.727
T45	04/23/04	4.49	-2.5	162.5	36.5	1.030	1.4	0.015	70.670	22.339
W01	04/30/04	5.08	0.5	64.8	13.3	0.375	0.9	0.009	40.057	20.266
W02	04/22/04	5.86	4.6	221.0	49.5	1.396	1.9	0.020	70.619	30.169
W04	04/22/04	4.26	-2.8	132.8	26.2	0.739	2.5	0.026	28.407	27.636
W05	04/23/04	4.05	-6.5	97.8	11.3	0.319	1.4	0.015	21.879	60.799
W06	04/30/04	4.24	-4.7	90.0	13.9	0.392	0.9	0.009	41.864	61.951
W07	04/29/04	5.57	0.7	94.5	23.2	0.654	2.3	0.024	27.342	11.054
W11	04/22/04	4.31	-3.5	63.9	6.0	0.169	0.9	0.009	18.071	33.854
W12	04/22/04	4.45	-2.8	68.5	4.1	0.116	0.3	0.003	37.045	26.945
W14	04/22/04	4.76	-1.1	79.5	16.3	0.460	0.6	0.006	73.639	36.387
W15	04/30/04	4.50	-2.3	45.9	14.0	0.395	1.7	0.018	22.323	41.684
W16	04/22/04	4.50	-2.2	53.9	7.6	0.214	1.0	0.010	20.601	20.497
W17	04/30/04	4.01	-6.1	169.2	32.8	0.925	3.3	0.034	26.942	31.781
W18	04/30/04	4.05	-5.2	162.0	32.7	0.922	2.3	0.024	38.538	36.848
W24	05/05/04	4.27	-3.5	35.8	0.9	0.025	0.9	0.009	2.711	46.751

Appendix 3. Maximum counts of spotted salamander (AMMA) and wood frog (RASY) egg masses, within-pond variables (columns 3-12) and adjacent habitat variables (columns 13-19). Columns 8-19 are % cover.

Site	AMMA	RASY	depth	area	pH	conduct	AbsCo	SAV	lily	emerg	shrub	tree	woods	roadall	paved	field	resid	adjpool	rd dist
E02	12	0	30	1635	4.57	39.6	12.21	1	0	10	80	0	97	3	0	0	0	6	530
E03	21	1	21	780	4.68	45.8	14.51	1	0	85	5	0	97	3	0	0	0	6	565
E04	532	4	32	1728	4.8	39.6	10.13	3	2	88	3	0	100	0	0	0	0	10	454
E05	687	16	43	2108	4.8	48.6	4.38	20	0	65	0	0	100	0	0	0	0	6	355
E05a	297	6	35	520	5.49	45	0.92	2	0	50	0	0	100	0	0	0	0	4	414
E06	396	2	51	1334	4.77	46.8	13.36	6	4	61	0	0	100	0	0	0	0	3	185
E07	193	8	34	720	4.74	36.9	9.21	2	0	80	3	0	100	0	0	0	0	5	258
E08	93	0	43	4756	4.47	36	13.59	2	1	29	20	0	100	0	0	0	0	5	397
E11	124	2	37	800	4.65	45.9	17.50	40	0	70	5	0	100	0	0	0	0	6	506
E11east	4	0	18	65	4.82	57.6	40.30	0	0	2	0	0	100	0	0	0	0	6	569
E18	5	2	60	575	5.85	115	16.35	0	0	15	80	0	90	5	5	5	0	3	31
E19	52	9	82	1560	5.71	59.5	11.98	4	3	7	40	0	100	0	0	0	0	3	206
E21	179	22	53	319.2	5.71	31.5	6.68	21	20	70	0	0	85	5	5	10	0	1	19
E22	778	14	60	33825	4.01	64	8.52	0	0	40	40	1	94	1	1	0	5	1	35
P04	0	0	40	237.12	4.4	78.3	49.98	0	0	1	6	10	98	0	0	0	0	6	88
T01	541	0	52	2442	4.72	36	30.86	50	45	45	3	0	97	3	0	0	0	1	277
T02	95	0	26	51.6	5.18	46	23.49	5	0	5	0	0	100	0	0	0	0	5	492
T02C	8	0	27	270.4	4.35	90.6	92.58	0	0	55	0	0	100	0	0	0	0	5	453
T04	0	0	4	1	4.06	80	56.19	nd	nd	nd	nd	nd	100	0	0	0	0	4	157
T08	0	0	5	0.5	nd	nd	nd	nd	nd	nd	nd	nd	98	0	0	0	0	1	1483
T09	0	0	17	6	4.05	101.6	76.23	0	0	0	0	0	100	0	0	0	0	1	945
T14	16	0	79	880	4.35	74.2	26.48	0	0	6	15	10	100	3	0	0	0	2	558
T15	27	0	75	494	4.64	49.5	24.87	0	0	0	20	2	95	5	0	0	0	1	557
T16	0	0	20	214.2	4.61	55.6	53.43	0	0	0	5	5	97	3	0	0	0	3	359
T22	0	0	83	1568	4.46	74.9	50.67	5	3	7	75	1	100	0	0	0	0	1	120
T23	63	0	49	1599	4.69	89.9	27.87	0	0	10	60	5	100	0	0	0	0	1	402
T45	0	0	40	488.4	4.49	162.5	22.34	0	0	45	10	5	97	3	3	0	0	1	35
W01	362	0	56	1200	5.08	64.8	20.27	2	0	0	70	5	100	0	0	0	0	1	1262
W02	28	0	50	13884	5.86	221	30.17	1	0	80	10	0	10	3	3	57	0	0	42
W04	0	0	41	780	4.26	132.8	27.64	0	0	0	5	0	96	2	0	0	2	2	572
W05	9	0	50	9760	4.05	97.8	60.80	0	0	10	20	5	89	5	0	0	4	0	1004

Site	AMMA	RASY	depth	area	pH	conduct	AbsCo	SAV	lily	emerg	shrub	tree	woods	roadall	paved	field	resid	adjpool	rd dist
W06	25	0	36	1344	4.24	90	61.95	0	0	0	10	5	97	3	3	0	0	0	48
W07	499	0	70	1369	5.57	94.5	11.05	21	20	45	5	1	100	0	0	0	0	0	247
W11	0	0	16	364	4.31	63.9	33.85	0	0	3	90	0	100	0	0	0	0	0	84
W12	0	0	30	405	4.45	68.5	26.95	0	0	35	5	0	100	0	0	0	0	2	65
W14	12	0	24	70	4.76	79.5	36.39	0	0	60	0	0	10	0	0	0	0	0	246
W15	114	0	27	81.25	4.5	45.9	41.68	1	0	5	0	0	100	0	0	0	0	3	827
W16	48	0	40	50.7	4.5	53.9	20.50	1	0	0	10	0	100	0	0	0	0	4	925
W18	102	0	37	144.5	4.05	162	36.85	0	0	10	15	1	95	5	0	0	0	1	729
W24	0	0	11	1.25	4.27	35.82	46.75	0	0	0	2	0	100	0	0	0	0	2	954

Appendix 4. Program PRESENCE model comparison, by species. AIC is the Akaike Information Criterion, w_i is the model weight, ψ is the site occupancy rate, "naïve" is the naive detection rate, and *p* detection is the average probability of detection.

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
BUFO	ψ(.) p(air)	3	191.817	0.000	0.474	0.417	0.400	
BUFO	ψ(pH) p(air)	4	192.820	1.003	0.287	0.415	0.400	
BUFO	ψ(perm,pH) p(air)	4	193.814	1.997	0.175	0.418	0.400	
BUFO	ψ(perm) p(air)	4	196.048	4.231	0.057	0.417	0.400	
BUFO	ψ(.) p(.)	2	200.181	8.364	0.007	0.420	0.400	0.227

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
HYVE	ψ(cond) p(air)	4	12.886	0.000	0.504	0.033	0.033	
HYVE	ψ(.) p(air)	3	14.769	1.882	0.197	0.033	0.033	
HYVE	ψ(perm, cond) p(air)	5	14.878	1.992	0.186	0.033	0.033	
HYVE	ψ(perm) p(air)	4	16.041	3.154	0.104	0.033	0.033	
HYVE	ψ(.) p(.)	2	21.144	8.258	0.008	0.033	0.033	0.714

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
PSCR	ψ(.) p(t)	11	276.403	0.000	0.456	0.900	0.900	
PSCR	ψ(semi) p(t)	12	277.494	1.092	0.264	0.900	0.900	
PSCR	ψ(pH) p(t)	12	278.316	1.913	0.175	0.900	0.900	
PSCR	ψ(semi, pH) p(t)	13	279.337	2.935	0.105	0.900	0.900	
PSCR	ψ(.) p(.)	2	340.630	64.228	0.000	0.900	0.900	0.726

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
RACA	ψ(perm) p(t)	9	106.506	0.000	0.684	0.268	0.267	
RACA	ψ(perm, semi) p(t)	10	107.403	0.896	0.279	0.268	0.267	
RACA	ψ(AbsCo440) p(t)	9	110.075	3.569	0.019	0.268	0.267	
RACA	ψ(.) p(t)	8	114.635	8.129	0.012	0.268	0.267	
RACA	ψ(.) p(.)	2	116.190	9.684	0.005	0.270	0.267	0.477

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
RACL	ψ(perm, semi) p(t)	15	347.522	0.000	0.871	0.733	0.733	
RACL	ψ(perm, semi, pH) p(t)	16	349.435	1.914	0.128	0.733	0.733	
RACL	ψ(.) p(t)	13	354.808	7.287	0.001	0.733	0.733	
RACL	ψ(pH) p(t)	14	356.273	8.751	0.000	0.733	0.733	
RACL	ψ(.) p(.)	2	390.079	42.557	0.000	0.733	0.733	0.617

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
RAPA	ψ(perm) p(t)	12	72.583	0.000	0.688	0.133	0.133	
RAPA	ψ(perm, pH) p(t)	13	74.268	1.685	0.128	0.133	0.133	
RAPA	ψ(pH) p(t)	12	74.552	1.969	0.096	0.133	0.133	
RAPA	ψ(.) p(t)	11	74.646	2.063	0.087	0.133	0.133	
RAPA	ψ(.) p(.)	2	79.244	6.661	0.001	0.135	0.133	0.345

Species	Model	# param	AIC	Δ AIC	w_i	ψ	naive	p detection
RASY	ψ(perm) p(air)	4	21.496	0.000	0.551	0.175	0.100	
RASY	ψ(.) p(air)	3	22.220	0.724	0.267	0.167	0.100	
RASY	ψ(.) p(.)	2	23.505	2.009	0.074	0.316	0.100	0.316
RASY	ψ(AbsCo440) p(air)	4	23.658	2.162	0.063	0.157	0.100	
RASY	ψ(perm, pH) p(air)	5	24.013	2.517	0.044	0.158	0.100	