Journal of Herpetology, Vol. 45, No. 1, pp. 23–27, 2011

Assessing Long-Term Population Trends of Wood Frogs Using Egg-Mass Counts

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Abstract.—**In North America, most efforts to monitor pond-breeding anurans have focused on call surveys. Egg-mass counts offer an alternative monitoring strategy that has been used extensively in Europe because this technique can produce precise and accurate estimates of annual reproductive effort at many study sites. We surveyed egg masses of Wood Frogs (*Lithobates sylvaticus*) at 18 ponds for up to 16 years from 1993–2008 in the largest contiguous forest tract in southern New England. We detected an average of 441.5 ± 343.7 egg masses per pond. Based on annual egg-mass counts, coefficients of variation (CV) were slightly higher than previous estimates for this species. We detected no relationship between mean annual population size and CV or between length of time series and CV. Population fluctuations in these ponds exhibited evidence of annual synchrony, in part because annual fluctuations at individual ponds were large enough that it was difficult to assess differences in population trends among ponds. However, the overall trend suggests this population was probably increasing slightly, which was expected because ponds were located in contiguous forest that remained intact during the study. Egg-mass counts appear to represent a feasible technique to monitor Wood Frog populations, given that all local breeding ponds are monitored.**

Because many species of amphibians are declining, herpetologists need to implement effective monitoring programs to assess long-term changes in distribution and abundance (Blaustein et al., 1994; Storfer, 2003). However, designing effective monitoring programs may be difficult because amphibians can experience dramatic annual population fluctuations (Pechmann et al., 1989; Marsh, 2001). Thus, assessing long-term population trends can be challenging (Williams et al., 2002; Green, 2003).

Although a number of survey techniques are available (Heyer et al., 1994), North American herpetologists primarily use anuran call surveys to monitor populations during the breeding season (Weir et al., 2005). Anuran call surveys are efficient because large numbers of breeding sites can be surveyed rapidly along road-based routes. Yet, anuran call surveys typically provide an index to population size (Shirose et al., 1997; Weir et al., 2005) and, thus, are most useful for monitoring changes in site occupancy (MacKenzie et al., 2006; but see Driscoll, 1998).

Alternatively, egg-mass counts can accurately monitor trends in adult female annual breeding effort for selected species of amphibians (Grant et al., 2005; Paton and Harris, 2009). Although few North American biologists conduct egg-mass counts to assess long-term population trends (but see Sherman and Morton, 1993; Corn et al., 2000; Richter et al., 2003; Petranka and Holbrook, 2006), European herpetologists have been using egg-mass counts to monitor amphibian populations for several decades (Hazelwood, 1969; Cooke, 1985; Griffith and Raper, 1994; Loman and Andersson, 2007). Meyer et al. (1998) monitored population trends of Common Frogs (*Rana temporaria*) at three ponds near Bern, Switzerland, for up to 28 yr and only observed a negative trend when fish were introduced to one pond. Loman and Andersson (2007) used egg-mass surveys to monitor *Rana arvalis* and *R. temporaria* in Sweden over 17 yr at 120 ponds and documented significant annual population fluctuations, with negative population trends detected for populations breeding in habitats impacted by human land use.

An advantage of egg-mass counts is that they allow biologists to accurately track annual reproductive effort at many breeding ponds. Crouch and Paton (2000) documented a 1 : 1 ratio between the number of female Wood Frogs (*Lithobates sylvaticus*) entering ponds based on drift-fence captures and the number of egg masses counted in ponds. Therefore, North American biologists could use egg-mass counts to assess long-term population trends. However, determining how many sites should be monitored annually to estimate local or regional population trends with reasonable precision and accuracy is difficult. For example, Marsh (2001) suggested, based on a recent meta-analysis of 29 amphibian time series, it may be challenging to estimate statistical power of amphibian monitoring programs even if five years of data have been collected. He found a positive relationship between the number of years a population was monitored and the coefficient of variation (CV) in population size, that is, the magnitude of the population fluctuation increased as the monitoring period lengthened, and he found few studies where stabilization in CVs was documented.

Pond-breeding frogs may be particularly difficult to monitor because they exhibit more variation in population size than stream-breeding or terrestrial breeding species (Green, 2003). Species breeding in highly variable environments, such as seasonal ponds, may be particularly vulnerable if their populations fluctuate widely and undergo frequent localized extinctions because of loss of breeding or dispersal habitat. For example in Sweden, Common Frogs breeding in permanent ponds had more positive population trends than populations breeding in temporary ponds, whereas populations breeding in cropped fields generally showed negative trends (Loman and Andersson, 2007).

In this study, we quantified fluctuations in annual breeding effort by surveying Wood Frog egg-mass production from 1993 to 2008 in southern Rhode Island. Our objectives were to (1) quantify annual variation in egg-mass counts, (2) investigate whether ponds monitored for longer time series exhibited greater annual fluctuations, (3) assess whether smaller populations exhibited greater annual fluctuations, (4) assess whether ponds exhibited synchronous annual fluctuations or whether ponds tended to behave independently, and (5) assess overall long-term population trends for all ponds in this population. We assumed that, because this population was located in one of the largest contiguous forest tracts in southern New England, long-term trends for this population should be relatively stable or increasing. Habitat models suggest Wood Frogs are one of the few species in the region adapted to closed-canopy ponds (Skelly et al., 2005); thus, forest maturation should have a positive influence on breeding population sizes.

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TABLE 1. Annual variation in Wood Frog egg-mass counts at 18 ponds in southern Rhode Island from 1993–2008. CV = coefficient of variation.

Pond	$\bar{x}$	SD	Range	CV	Detrended CV	Years monitored
Midway Trail	1169.3	670.7	360–2,500	0.574	0.573	13
Carolina Management Area	1264.4	1193.3	215–3,,100	1.014	0.459	9
Brook Trail	858.0	247.5	437–1300	0.289	0.286	13
Mt. Tom Road	723.7	419.5	227–1,400	0.750	0.353	11
The Bog (TB)	704.5	439.4	0–1,581	0.689	0.491	15
E-Hun-tee	614.9	320.9	165–1,200	0.522	0.503	12
Barber Farm Fen	584.7	325.7	125–1,340	0.557	0.412	16
Frosty Hollow Pond	457.1	309.3	90–987	0.677	0.657	13
Rt. 165-Arcadia Trail	434.3	259.6	110–805	0.598	0.545	9
Shelter	406.3	159.0	160–600	0.391	0.384	12
Barber Farm North	256.8	85.5	172–375	0.333	0.211	4
Falls River	246.7	50.3	200–300	0.204	0.187	3
Twin Ponds Large	157.8	78.2	18–270	0.496	0.489	13
Twin Ponds Small	140.2	77.4	0–250	0.553	0.551	13
Frosty Hollow Road	98.4	39.8	31–155	0.404	0.339	8
Flat River Bridge	74.5	49.9	19–140	0.670	0.520	4
Leatherleaf Bog	28.9	58.1	0–200	2.010	1.779	13
Barber Farm Pond	0.0	0.0	0–0	0.0	0.0	16

MATERIALS AND METHODS

Fieldwork was primarily conducted in Arcadia Management Area in western Rhode Island from 1993 to 2008. Arcadia is one of the largest contiguous forest patches (5,665 ha) in southern New England. Mixed deciduous-coniferous forests in Arcadia are dominated by white pine (*Pinus strobus*), pitch pine (*Pinus rigida*), red maple (*Acer rubrum*), and a variety of oaks (*Quercus* spp.). Ponds were typically <0.05 ha at ordinary high water levels. Although pond hydroperiod was not systematically surveyed each year, we do know that most ponds dried completely in most years. In addition, FCG monitored a semipermanent pond (0.1 ha) in Carolina Management Area (954 ha) from 2001 to 2008. This pond was approximately 8 km south of Arcadia and occurred within a large forest tract (954 ha) dominated by trees of similar composition.

We felt that egg-mass counts could be an effective technique for monitoring annual fluctuations in Wood Frog populations because (1) their egg masses are conspicuous; (2) a single observer can accurately count Wood Frog egg masses, particularly because they usually are found in large communal aggregations (Crouch and Paton, 2000; but see Grant et al., 2005); (3) their eggs typically take at least three weeks to hatch; thus, observers have a relatively long survey window (Egan and Paton, 2004); and (4) this species is one of the most abundant pond-breeding amphibians in southern New England and, thus, is widespread (Egan and Paton, 2004).

To develop robust estimates of changes in population size, detection probabilities should be estimated (Grant et al., 2005; Mazerolle et al., 2007). However, we were unable to estimate egg-mass detection probabilities because we did not use double-observer methods (Grant et al., 2005), which were not available when this research was initiated. In addition, although we conducted multiple site visits to each pond every year, we could not estimate detection probabilities because we did not mark individual egg masses. Variation between site visits could have been the result of additional egg masses oviposited in ponds, because not all Wood Frog egg masses are deposited simultaneously (Crouch and Paton, 2002). We assumed a linear relationship between egg-mass counts and the actual population size. This was because a single experienced observer conducted all egg-mass counts over all years of the study. In addition, ponds were small, and we assumed that detection probabilities were relatively constant over space and time.

We conducted egg-mass surveys from mid-March to mid-April, with the survey period varying annually depending on local weather conditions. We typically surveyed ponds at least three times per year to obtain a maximum count. Although there is a tendency for egg masses of this species to be located toward the northern end of ponds (Seale, 1982), the observer would systemically search the entire pond in an effort to count all egg masses present. We only included ponds in subsequent analysis if they were monitored for at least eight years and had some egg masses detected. A total of 14 ponds met this condition.

We quantified the direction and magnitude of changes in annual population size using a method outlined by Houlahan et al. (2000) and Green (2003):

$$\Delta N = \log(N+1)_t - \log(N+1)_{t-1}, \tag{1}$$

where ΔN is a normalized estimate of the realized rate of increase (R) and can be calculated when populations recover from local extinction for one or more time intervals. Populations are increasing when ΔN is positive and decreasing when ΔN is negative. We calculated ΔN and its variance ($V_{\Delta N}$) for each time interval within each time series from all ponds to summarize population trends.

Marsh (2001) suggested the magnitude of population fluctuation could be related to local extinction risk and population size variation is relevant in amphibian conservation. To investigate the relationship between population size and the magnitude of population fluctuations, we calculated the CV in yearly population size, where CV = standard deviation/mean, and a detrended CV using a method outlined by the USGS (http://www.pwrc.usgs.gov/monmanual/cvs/ampcv/ampcvresults.cfm; accessed 10 May 2008 [hereafter USGS, 2008]). Then, we used linear models to investigate the relationship between counts and CV.

To assess overall population trends for all ponds, we used a mixed model in which we treated pond as a random effect to account for the lack of independence between repeated measures on each pond over the course of the study (Schabenberger and Pierce, 2001). Using Proc Mixed in SAS with the Maximum Likelihood (ML) method (Littell et al., 2006) to implement this repeated-measures model, we examined whether there was a linear trend in egg-mass counts over time. In addition, we hypothesized that if ponds were saturated, then populations would stabilize or decrease. Therefore, we also modeled population trends as a quadratic equation. We compared these linear and quadratic models using Akaike's Information Criterion (AIC) adjusted for small sample sizes (i.e., AIC_c; Burnham

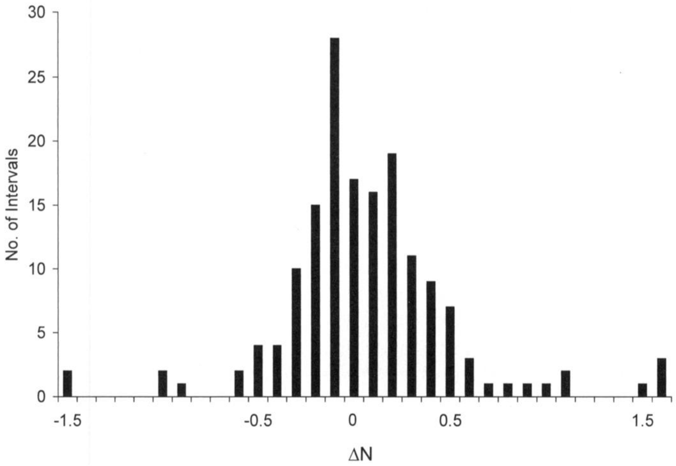

FIG. 1. Distribution of ΔN values for Wood Frog populations monitored in southern Rhode Island from 1993–2008.

and Anderson, 2002). We also developed another candidate model to examine whether there was an interaction between pond and time to determine whether populations among ponds fluctuated synchronously. Both repeated-measures models were developed using a log-transformed response (log [egg-mass count +1]) to meet model assumptions.

We conducted all statistical analysis using SAS (vers. 9.2). We present $\bar{x} \pm$ SD throughout.

RESULTS

We surveyed 18 ponds over an average of 10.9 ± 1.0 yr (range 3–16 yr; Table 1). All ponds except one, Barber Farm Pond, had breeding populations of Wood Frogs, with a mean of 441.5 ± 343.7 egg masses per pond per year (maximum = 3,100; Table 1). Of the 18 ponds we monitored, there were 160 census intervals. Declines (49.4%) were slightly more common than increases (46.7%), whereas 3.4% of census intervals exhibited no change. However, overall values of ΔN were positive ($\bar{x}$ = 0.021 ± 0.042; minimum = −2.66, maximum = 2.89, Fig. 1). Mean variance of ΔN was 0.259 ± 0.086. There were three crashes (population count = 0), yielding a crash rate of 0.019.

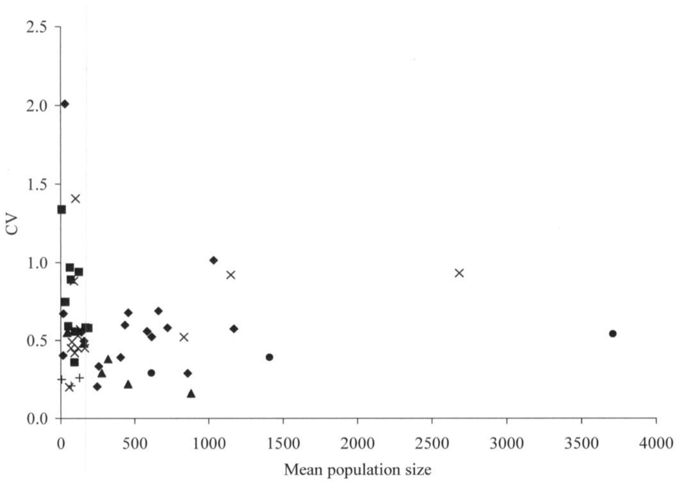

FIG. 2. Relationship between Coefficient of Variation (CV) and mean size of Wood Frog populations at breeding ponds. Data from this study in southern Rhode Island from 1993–2008 (◆), Petranka and Holbrook (2006) (■), J. W. Petranka and C. K. Smith (unpubl. data) (▲), Berven (1990) (×), and two studies of *Rana temporaria*: Elmberg (1990) (+) and Meyer et al. (1998) (●) are presented.

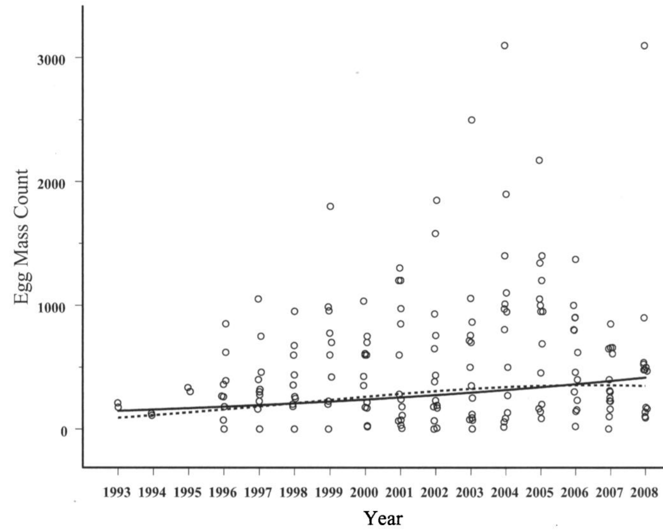

FIG. 3. Mixed linear (solid line) and quadratic (dotted line) trends in annual variation in a Wood Frog population in Rhode Island, based on egg-mass counts at 14 ponds from 1993–2008.

Coefficients of variation were relatively high for most ponds ($\bar{x}$ = 0.621 ± 0.404, range = 0.204–2.010), with detrended CV slightly lower ($\bar{x}$ = 0.514 ± 0.351, range = 0.187–1.780). We detected no relationship between mean annual population size and CV ($F_{1,12}$, $P = 0.58$; Fig. 2). In addition, we found no relationship between the number of years a pond was monitored and CV ($F_{1,12}$, $P = 0.93$).

Based on the repeated-measures models with pond treated as a random effect, we detected evidence of a positive linear trend in log-transformed counts of Wood Frog egg masses over all ponds over the 16-yr study period ($F_{1,155} = 15.9$, $P < 0.0001$; Fig. 3). Back-transforming model results to the raw data scale resulted in a slight exponential curve to the model fit, such that the effect of year increased slightly over time. The linear model suggested increases in Wood Frog egg masses in a given year of the study equaled 0.0699 × *exp* [4.9179 + 0.0699 (year)]. Over the 16 yr of the study, the estimated mean increase in Wood Frog egg masses was approximately 18.1 ± 5.6 egg masses per year. This linear model was similar in fit to another candidate model, suggesting a quadratic trend ($F_{1,154} = 2.9$, $P = 0.087$; Table 2). We found no evidence of an interaction among ponds and time (i.e., whether the trend over time differed significantly among ponds), because we could not obtain convergence with this model; $F_{13,142} = 1.2$, $P = 0.266$; Fig. 4), which suggests the pond × year interaction term is not appropriate for this model.

DISCUSSION

This study represents one of the largest long-term data sets for a North American pond-breeding anuran monitored using annual counts of egg masses. The magnitude of population fluctuations documented during this study was strikingly similar to Green's (2003) recent meta-analysis of pond-breeding frogs, which found ΔN values ranging from −2.634 to 2.340 compared to our estimates of −2.66 to 2.89. Thus, as Green (2003) documented, pond-breeding anurans exhibit large annual variation in population sizes.

The magnitude of population fluctuation we documented (detrended CV: $\bar{x}$ = 0.514 ± 0.351, range = 0.187–1.780) were much higher than other studies based on counts of Wood Frog egg masses (e.g., detrended CV: $\bar{x}$ = 0.346 ± 0.151, range = 0.157–0.546, $N = 6$; USGS, 2008) and for the European Common Frog (detrended CV: $\bar{x}$ = 0.323 ± 0.121, range = 0.214–0.538, $N = 6$; USGS, 2008; Fig. 1). Yet, the fluctuations from this study

TABLE 2. Model selection results from mixed linear and quadratic models used to examine annual variation in number of Wood Frog egg masses at ponds in Rhode Island from 1993–2008.

Model	No. of parameters	AIC_c[a]	ΔAIC_c[b]	w_i[c]
Quadratic trend	5	481.7	0	0.60
Linear trend	4	482.5	0.8	0.40

[a] Akaike's Information Criterion for small sample sizes (Burnham and Anderson, 2002)
[b] $\Delta AIC_c = AIC_{ci} - \min AIC_c$.
[c] $w_i = \exp[-(\Delta AIC_{ci}/2)]/\Sigma \exp[-(\Delta AIC_{ci}/2)]$.

were similar to overall estimates for Wood Frogs based on a variety of survey techniques (detrended CV: $\bar{x} = 0.543 \pm 0.296$, range = 0.157–1.409, $N = 20$; USGS, 2008). This variation leads to two issues that biologists need to consider when designing long-term monitoring programs. First, more sites will have to be monitored to obtain an estimate of long-term population trends for species that exhibit large annual fluctuations among years. Second, fluctuating populations are more vulnerable to local extinction events and, thus, are susceptible to extirpation unless recruits from adjacent ponds can help a local population to recover (Green, 2003).

This study took place in one of the largest contiguous forests in southern New England, which is presumably why most ponds had relatively large population sizes (67% of ponds averaged >250 breeding females annually and 39% averaged over 500 breeding females). This is typical for egg-mass counts in breeding ponds surrounded by contiguous forested tracts in Rhode Island (Egan and Paton, 2004). Thus, population fluctuations documented during this study represented apparent natural stochastic variation in annual population sizes, because there were no obvious anthropogenic habitat perturbations affecting fluctuations in this system. Given the magnitude of population fluctuations we documented was substantial, it is not surprising that the population trends for Wood Frogs in this forested section of Rhode Island remain uncertain. It is not clear whether this population is gradually increasing or may be exhibiting a slight decrease recently.

Marsh (2001) documented that CV increased with time series length in 27 of 29 time series he investigated. In contrast, we found no relationship between CV and series length. We also found no relationship between population size at breeding ponds and CV; thus, smaller populations as well as larger populations exhibited similar levels of fluctuations. In southern Rhode Island, ponds average 184 egg masses per pond, with <16% having <25 egg masses (Egan and Paton, 2004). Typically, we do not have to deal with ponds with few breeding individuals, but in other parts of their range, populations might be considerably smaller.

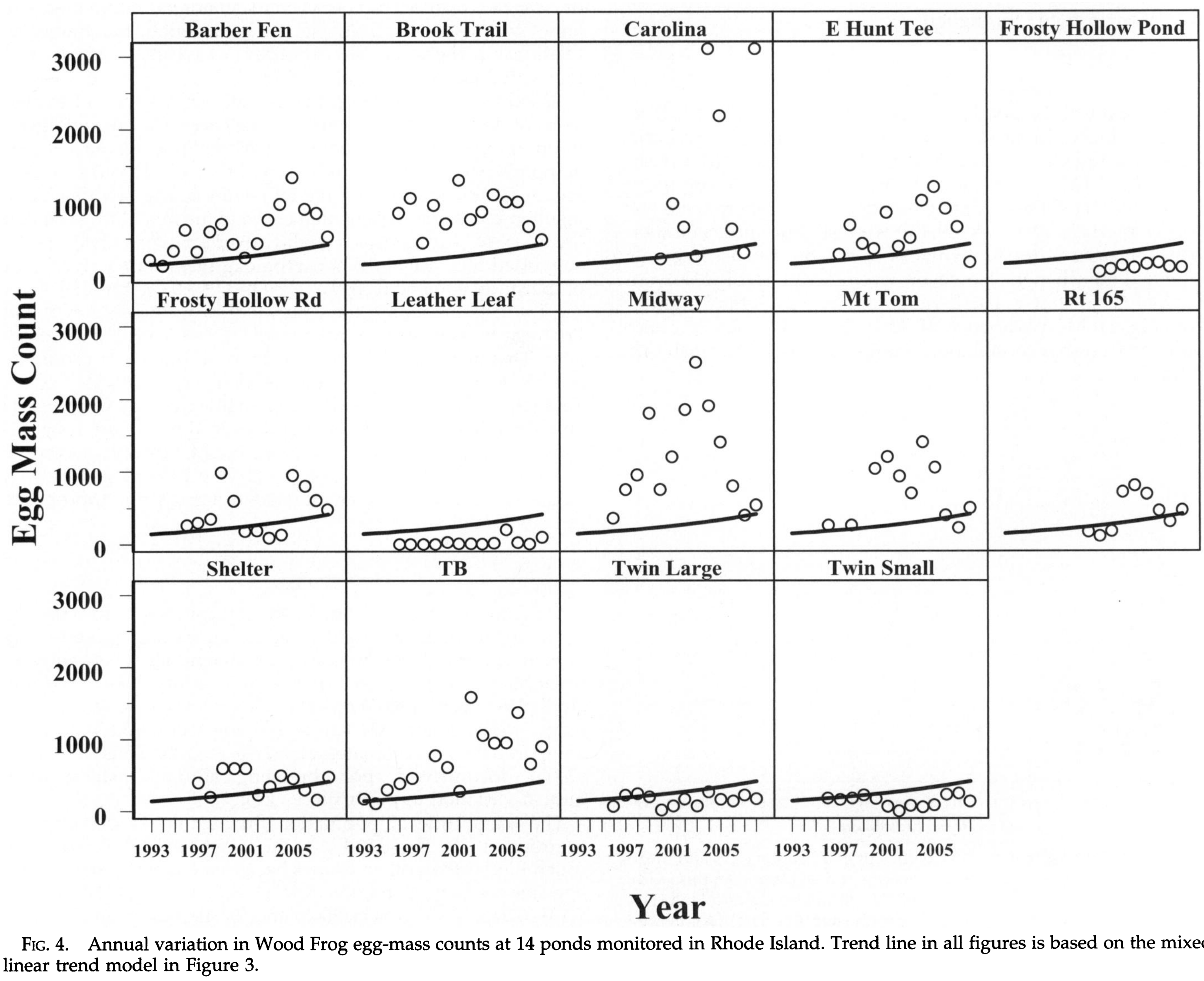

FIG. 4. Annual variation in Wood Frog egg-mass counts at 14 ponds monitored in Rhode Island. Trend line in all figures is based on the mixed linear trend model in Figure 3.

Finally, if the large CV we documented (detrended CV: $\bar{x}$ = 0.514 ± 0.351, range = 0.187–1.780) in southern Rhode Island holds true for other parts of the species' range, then relatively large numbers of ponds will have to be surveyed annually to develop reasonable estimates of population trends during short-term studies (<10 yr). Based on USGS (2008) calculations, about 44 ponds (CV = 0.5) to 71 ponds (CV = 0.8) would have to be surveyed annually for a 5-yr study with 90% power to detect a 3% annual decline at $\alpha = 0.2$. However, sample size requirements would decline substantially if the length of the study were increased to over 20 yr, with little difference in CV values.

Acknowledgments.—We thank the Rhode Island Department of Environmental Management for financial support for CJR's fieldwork. We thank two anonymous reviewers for making substantial improvements to earlier versions of this manuscript.

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Accepted: 25 May 2010.