

## Combining Data Sources to Understand Drivers of Spotted Salamander (*Ambystoma maculatum*) Population Abundance

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**ABSTRACT.**—Robust methods for estimating abundance of wetland-breeding amphibian species, such as mark–recapture, are often resource intensive. This limits our ability to study the processes that influence species abundance. Alternatively, more efficient sampling methods, such as indices based on visual encounter surveys (VES) (e.g., egg masses), may be biased by variability in detection probabilities and species biology (e.g., no. of egg masses per female). We combine data sources (i.e., VES and capture–mark–recapture) to provide an efficient technique for monitoring wetland-breeding amphibians. Our study focuses on understanding factors that determine local abundance of Spotted Salamanders, *Ambystoma maculatum*, in Pennsylvania. We first estimated abundance for a subset of wetlands using single-season, capture–mark–recapture data and then verified egg-mass counts collected from a wider network of wetlands as an unbiased index of abundance. We found a strong correlation between estimated adult abundance and estimated egg-mass abundance with an estimated ratio of one egg mass per adult per breeding effort. We next determined the factors that best explained variation in estimated *A. maculatum* egg-mass abundance and consequently, adult abundance among sites. Our “best-fit” model included effects for wetland hydroperiod and quadratic effects of mean water temperature. We also report positive, but weak, association with two co-occurring amphibian species, Jefferson Salamanders, *A. jeffersonianum* and Wood Frogs, *Lithobates sylvaticus*. We demonstrate how combining sampling approaches can provide efficient abundance estimates in wetland ecosystems. In particular, positive co-occurrence among species indicates shared habitat preferences that may enable us to predict the presence of difficult-to-detect species using only VES.

Ephemeral wetland systems support complex plant (Keeley and Zedler, 1998; Deil, 2005), invertebrate (Batzer and Wissinger, 1996; Wellborn et al., 1996; Brooks, 2000; Babbitt et al., 2003), and amphibian communities (Duellman and Trueb, 1986; Pechmann et al., 1989; Semlitsch et al., 2015). By definition, ephemeral wetlands are temporary water features that form in low spots across the landscape during heavy spring precipitation or snowmelt, and dry partially or entirely during summer months (Zedler, 2003). This definition encompasses temporary water features such as vernal pools (Colburn, 2004), seasonal forest pools (Brooks, 2005), and seasonally flooded marshlands (Batzer and Wissinger, 1996). A key difference between ephemeral systems and permanent freshwater habitats is the dynamic hydroperiod, which describes seasonal and annual fluctuations in wetland inundation (Brooks and Hayashi, 2002; Brooks, 2005). In the case of ephemeral systems, these fluctuations create an environment with few aquatic predators (Moler and Franz, 1987; Brooks, 2009). This particular attribute of ephemeral wetlands results in unique community assemblages that are well adapted to the harsh conditions that accompany wetland drying (Pechmann et al., 1989; Snodgrass et al., 2000; Babbitt et al., 2003; Baber et al., 2004).

Community turnover of wetland-breeding amphibians is strongly associated with wetland hydroperiod (Semlitsch et al., 1996; Skelly et al., 1999; Snodgrass et al., 2000; Babbitt et al., 2003). Amphibian species adapted to ephemeral wetlands generally develop rapidly, which increases the probability of metamorphosis before wetland desiccation (Wellborn et al., 1996). In contrast, species inhabiting permanent wetlands are more likely to experience increased predation and competition pressures and as such, are slow developing and cryptic (Snodgrass et al., 2000). The presence or high abundance of aquatic predators in permanent, freshwater bodies excludes

amphibian species that do not exhibit efficient antipredator defenses (Babbitt et al. 2003). Therefore, ephemeral wetlands are critical for maintaining and promoting regional biodiversity (Semlitsch and Bodie, 1998; Snodgrass et al., 2000; Brooks, 2009; Greenberg et al., 2015). Consequently, we must monitor, assess, and mitigate effects on ephemeral wetlands because of changes in water availability that can occur from environmental change (e.g., climate change; Greenberg et al., 2015).

Monitoring of wetland-breeding amphibians typically is conducted using survey methods that quantify species occupancy or local abundance (Homan et al., 2004; Buskirk, 2005). Most commonly, researchers estimate these metrics through capture–mark–recapture studies (CMR; Whitford and Vinegar, 1966; Gamble et al., 2006; Grayson et al., 2011) or visual encounter surveys (VES; Crouch and Paton, 2000; Calhoun et al., 2003; Grant et al., 2005). CMR methods are useful tools to examine how local environmental factors affect demographic parameters, such as survival, recruitment, and dispersal, that contribute to spatiotemporal variation in abundance (e.g., Unglaub et al., 2015). Nonetheless, CMR methods are resource intensive, making their use difficult when a large number of wetlands have to be surveyed or when species are not easily captured. Estimated indices of abundance with the use of VES data are an efficient alternative but may be biased by imperfect detection (Grant et al., 2005; Mazerolle et al., 2007) and can be similarly biased by the biology or ecology of a species. Linking data across these two survey methods could mitigate the limitations associated with each and provide an efficient technique for monitoring wetland-breeding amphibians.

The Spotted Salamander, *Ambystoma maculatum* (Shaw, 1802), is a relatively common wetland-breeding amphibian, yet is rarely observed outside of the spring breeding season when it migrates in large numbers to seasonally inundated wetlands (Sexton et al., 1990; Egan and Paton, 2004). Annual population sizes can be easily assessed in a large number of wetlands during this short (approx. 1–3 wk; pers. obs.) breeding season

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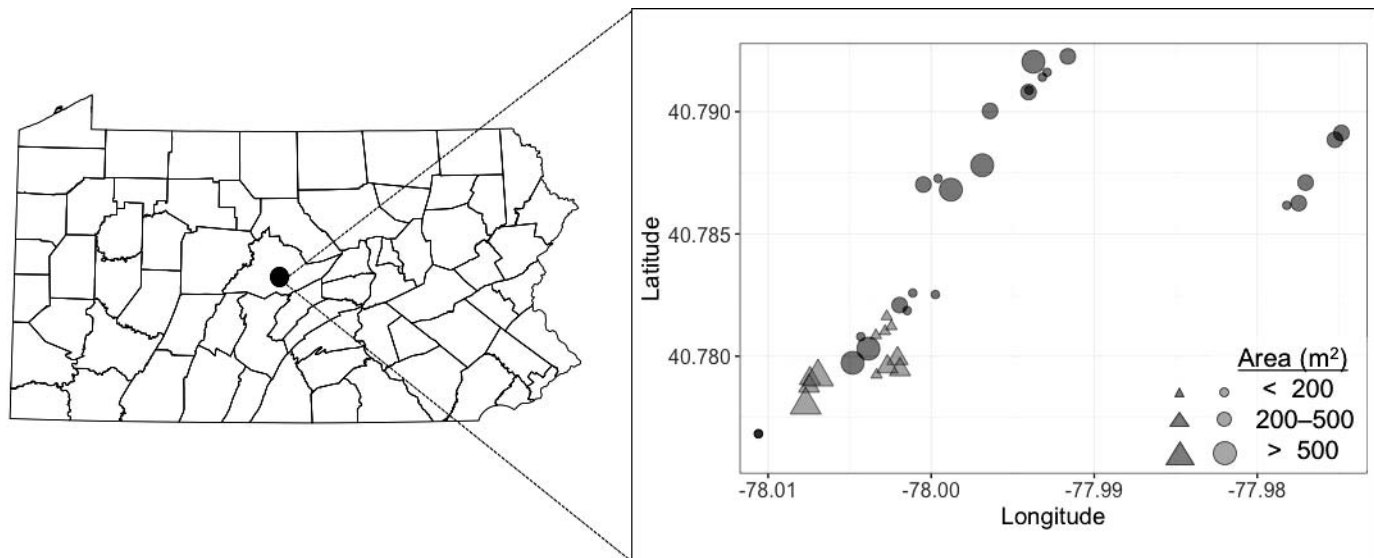


FIG. 1. Study area location within Pennsylvania and individual wetland sites within the study area. Red triangles indicate wetlands surveyed with CMR and VES, whereas gray circles indicate wetlands surveyed using only the VES method.

(Egan and Paton, 2004). In combination with individual spot patterns (Chase et al., 2015), these attributes make this a convenient target species for CMR studies. In addition, *A. maculatum* lay easily detectable egg masses (Crouch and Paton, 2000; Egan and Paton, 2004; Grant et al., 2005) that are often used to approximate adult abundance (e.g., Faccio, 2011), though such indices have rarely been validated (see Crouch and Paton, 2000 and Fellers et al., 2017, for examples in other species). Our goals for this study were twofold. First, we validate the use of VES to index adult population abundance for *A. maculatum*. To achieve this, we compared adult CMR abundance estimates and egg-mass count data collected using double-observer VES. Second, we determine the abiotic and biotic characteristics that best explain the observed variation in our egg-mass counts after accounting for imperfect detection (Grant et al., 2005; Mazerolle et al., 2007).

In addition to wetland hydroperiod, water temperature (Smith-Gill and Berven, 1979; Berven and Gill, 1983), wetland area (Werner et al., 2007), vegetation composition, and canopy cover (Skelly et al., 2002; Halverson et al., 2003; Werner et al., 2007) have been related to wetland-breeding amphibian abundance, individual fitness, and species richness. Specifically, we test the effects of wetland hydroperiod, area, and water temperature on the density (estimated abundance per square meter) of *A. maculatum* egg masses across a network of ephemeral wetlands in central Pennsylvania. We predicted that wetlands of longer hydroperiod would have higher densities of *A. maculatum* egg masses, assuming these sites were not occupied by fish or other large, aquatic predators that might influence the magnitude or direction of this effect. Previous research also has shown that high con- and heterospecific densities have been associated with reduced growth and survival of larval amphibians (Semlitsch, 1987). We tested the effects of two co-occurring wetland-breeding amphibian species, Jefferson Salamanders, *A. jeffersonianum* and Wood Frogs, *Lithobates sylvaticus*, on *A. maculatum*. We predicted that *A. jeffersonianum* and *L. sylvaticus* would negatively influence our target species through direct predation of larvae or eggs (or both), or competition between developing larvae for shared resources. By achieving our goals, we demonstrate how

combining sampling approaches can provide efficient, unbiased abundance estimates in wetland ecosystems while understanding the environmental factors that determine local population abundance of *A. maculatum* in central Pennsylvania.

#### MATERIALS AND METHODS

**Study System.**—We surveyed 37 ephemeral wetlands of State Game Lands No. 176 in central Pennsylvania in 2015 (Fig. 1). Sites ranged in area from 24 m<sup>2</sup> to 1,945 m<sup>2</sup> ( $x = 360$  m<sup>2</sup>) and vary in observed, mean hydroperiod (i.e., length of inundation). The most abundant wetland-breeding amphibians in our study area were Spotted Salamanders, *A. maculatum*, Jefferson Salamanders, *A. jeffersonianum* (Green, 1827) and Wood Frogs, *Lithobates sylvaticus* (LeConte, 1825). Our study focuses on understanding the environmental factors determining local abundance of Spotted Salamanders, *A. maculatum*, which inhabit lowland deciduous forests throughout the eastern United States and southern Canada (Petranka, 1998). Adults of this species migrate from the surrounding terrestrial landscape, where they overwinter, to wetlands with the onset of spring precipitation to breed (Shoop, 1965; Sexton et al., 1990). Often, annual sex ratios are male biased throughout the breeding season, as females frequently skip years between breeding efforts, arrive at wetlands later in the breeding season, and generally are less abundant (Husting, 1965; Whitford and Vinegar, 1966; Sexton et al., 1990; Patrick et al., 2008). In our study system, *A. maculatum* larvae hatch ~1 mo after oviposition and metamorphose into subadults by early summer (Rowe and Dunson, 1995). As with other wetland-breeding amphibian species, oviposition, larval development, and subadult dispersal vary by region and are heavily influenced by local weather patterns (Brodman, 1995; Rowe and Dunson, 1995; Petranka, 1998).

**Capture-Mark-Recapture.**—We first conducted an intensive CMR study (Otis et al., 1978) to estimate sex-specific adult abundance during the 2015 breeding season at a subset of 12 of our 37 monitored wetlands. CMR sites ranged in area from 102 m<sup>2</sup> to 1,175 m<sup>2</sup> ( $x \pm SD = 348 \pm 297$  m<sup>2</sup>). We deployed minnow traps (Grayson et al., 2011; Piovia-Scott et al., 2011) from the onset of spring thaw until overall capture rates declined to <5% of

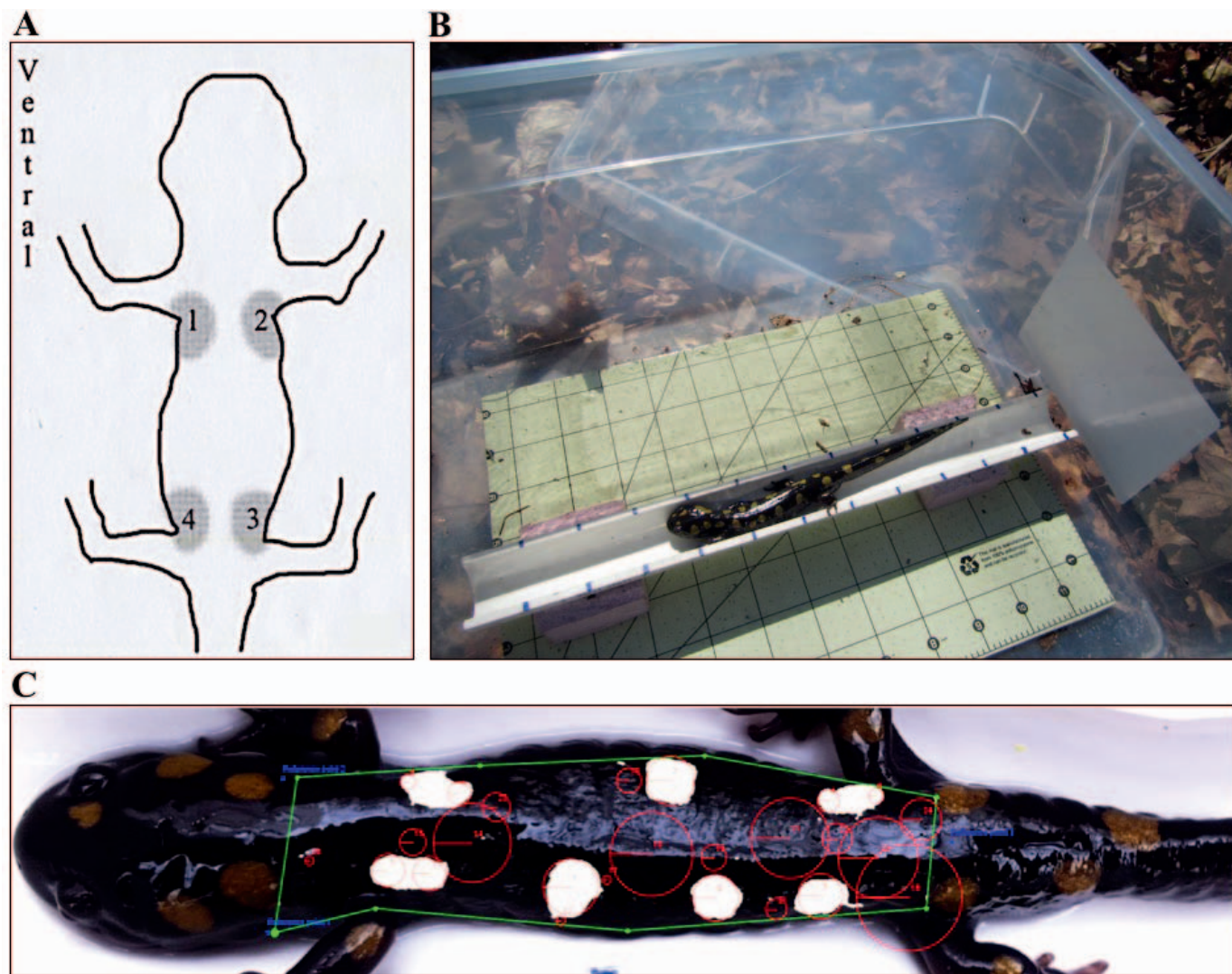


FIG. 2. Diagram depicting the (A) placement of VIE marks, (B) standardized processing station for photographing all captured *Ambystoma maculatum* individuals, and a (C) straightened and cropped image as displayed in I3S, the identification software used to identify individuals via unique dorsal spot patterns, as highlighted here, which can then be used to construct individual encounter histories.

daily captures achieved at peak migration ( $t = 13$  d). To ensure that trapping effort was comparable across sites, the number of traps deployed at each site varied in proportion to wetland size. Traps were consistently placed in shallow water at 10-m intervals along the wetland perimeter and baited with 15.25-cm green glow sticks, which have increased amphibian capture rates (Grayson and Roe, 2007; Bennett et al., 2012; Antonishak et al., 2017). Traps were checked daily and all animals were released at the location of their capture.

We used visual implant elastomer (VIE) (Northwest Marine Technology, Shaw Island, Washington USA) to mark salamanders with a site-specific “batch code” (Davis and Ovaska, 2001; Phillips and Fries, 2009; Sapsford et al., 2015). This allowed us to verify which animals were recaptures, minimizing the probability that animals were falsely identified as a new individual (Stevick et al., 2001). Elastomer marks were placed in four standardized positions on the ventral surface adjacent to limbs (Fig. 2A; Davis and Ovaska, 2001; Phillips and Fries, 2009; Muñoz et al., 2016) using a pattern unique to the wetland of first capture. All *A. maculatum* were photographed each time they were captured regardless of whether they were identified via batch mark as a recaptured individual. We standardized

photographs in the field with the use of a consistent processing station (Fig. 2B). We then determined individual identification using photograph identification software (Interactive Individual Identification Software I3S; Hartog and Reijns, 2014). Photographs were straightened and cropped to increase uniformity before image analysis. We used the unique dorsal patterns of *A. maculatum* to “fingerprint” each image (Chase et al., 2015) and compare with potential matches in our photographic database (Fig. 2C). Matches were manually verified and recorded if found in the first 20 options presented by I3S. This enabled us to observe matching proficiency by the program. Individuals listed in field records as “recaptured” and not positively matched in the first 20 options by I3S were manually searched for in the database using the batch mark.

We then estimated sex-specific adult abundance for each of the 12 CMR sites, using Huggins’ closed population model (Huggins, 1989) in Program MARK (White and Burnham, 1999). We created a balanced candidate model set that included sex-, site- and capture-day effects on (re)capture probabilities (see Appendix 1 for full candidate set). Models were ranked on the basis of the Akaike information criterion adjusted for small sample size (AICc; Akaike, 1973); estimates reported and used

in all subsequent analyses are from the “best-fit” model with the lowest AICc.

*Visual Encounter Surveys.*—After adult emigration from breeding wetlands, we conducted double-observer VES (Grant et al., 2005) to count the number of *A. maculatum* egg masses present in all 37 wetlands. Although the focus of these VES was *A. maculatum*, we also performed concurrent egg-mass counts for *A. jeffersonianum* and *L. sylvaticus* to understand the influence of heterospecific egg-mass densities on our target species. We also collected data on various wetland characteristics, such as water temperature and wetland size at the time of these VES. Each site was instrumented with an iButton Temp Logger (#DS1921G-F5; Embedded Data Systems, LLC, Lawrenceburg, Kentucky USA), allowing us to determine the duration of water inundation in the basin (Earl and Semlitsch, 2015).

In the context of our VES, egg masses may have been obstructed by vegetation or were difficult to detect in tannin-stained water (Grant et al., 2005). Moreover, *A. maculatum* egg masses can be opaque, clear, or green in color depending on the presence of particular proteins or symbiotic algae (Hardy and Lucas, 1991; Ruth et al., 1993; Grant et al., 2005), which may also influence detectability in dark water or larger wetlands. Therefore, our ability to conduct a complete census was severely constrained (Mazerolle et al., 2007). Instead, we estimated the probability of detecting *A. maculatum* egg masses,  $p_{VES}$ , using the Royle (2004) *N*-mixture model in the R package “unmarked” (Fiske and Chandler, 2011). The Royle model requires repeated count data from >2 encounter occasions (e.g., counts from two independent observers) to estimate abundance while accounting for imperfect detection (Royle, 2004; Kéry et al., 2005). We estimated a constant detection probability and used  $\text{offset}(\ln[\text{area}])$  to model the density of *A. maculatum* egg masses (estimated abundance per square meter) from our double-observer VES data.

Our analysis of among-wetland differences in estimated egg-mass density focused on site characteristics previously hypothesized to influence *A. maculatum* population processes (Egan and Paton, 2004; Semlitsch and Skelly, 2007; Gould et al., 2012) and for which we collected standardized data across all 37 wetlands. We included an effect for proportionately scaled area measurements (i.e.,  $\ln[\text{area}]$ ), but also included an effect for wetland size (i.e., area) in the candidate model set, though these two measures were never included in the same model. We categorized wetlands on the basis of the time of drying in 2015 to account for heterogeneity between sites. Wetlands that dried before larval *A. maculatum* metamorphosis were categorized as shorter duration ( $n = 27$ ; mean time to drying = 47 d), whereas wetlands that retained water throughout larval development were designated as longer duration ( $n = 10$ ; mean time to drying = 148 d). This classification, although coarse, allowed us to capture general differences among basins in wetland hydroperiod, which is known to influence the occurrence patterns (Egan and Paton, 2004; Davis et al., 2017a) and community structure (Rowe and Dunson, 1995; Buskirk, 2005; Davis et al., 2017b) of wetland-breeding amphibians. We restricted the model set to ensure that hydroperiod and wetland size were never included in the same model. We also included linear as well as quadratic effects of mean water temperature, and the density of egg masses (mean count per square meter) of *A. jeffersonianum* and *L. sylvaticus* as covariates in our candidate model set. Models were ranked on the basis of the AIC; estimates reported and used in all subsequent analyses are from the best-fit model with the lowest AIC.

TABLE 1. Total number of captures and number of unique *Ambystoma maculatum* captured in 2015 ( $n = 12$  wetlands).

Site	Total number of captures		Number of unique individuals	
	Male	Female	Male	Female
CMR 01	426	100	308	91
CMR 02	382	91	250	83
CMR 03	94	6	55	5
CMR 04	65	2	30	2
CMR 05	208	19	91	18
CMR 06	47	3	25	3
CMR 07	73	8	45	8
CMR 08 <sup>a</sup>	55	11	44	11
CMR 09 <sup>a</sup>	143	18	107	15
CMR 10	223	13	94	12
CMR 11 <sup>a</sup>	68	5	48	5
CMR 12 <sup>a</sup>	121	16	79	13

<sup>a</sup> Trapping occurred over 12 rather than 13 d.

*Validating Egg-Mass VES.*—We used a linear model to understand the relationship between estimates of sex-specific adult and egg-mass abundance at each CMR site.

## RESULTS

*Capture–Mark–Recapture.*—Image analysis using I3S alone yielded positive matches of 88.0% of individuals recorded as recaptured. Our use of photograph identification and batch marking increased our identification success by 9.2%, matching 97.3% of individuals recorded in the field as recaptures. We processed 2,197 capture events and used I3S to identify 1,176 unique males and 266 unique females across our 12 CMR wetlands (see Table 1 for site-specific captures).

Our best-fit model allowed capture ( $p$ ) and recapture probabilities ( $c$ ) to vary equally (i.e.,  $p = c$ ) as a function of capture day and sex (see Appendix 1 for model selection results), indicating that an individual’s behavioral response to capture had little effect on its probability of recapture. Estimated sex-specific abundance and sex ratios for each CMR site can be found in Table 2. Estimates of male abundance ranged from  $X$  (95% confidence interval) = 27.42 (24.19, 30.65) to 364.65 (335.82, 393.48), whereas female abundance ranged from 6.73 (0.00, 14.82) to 472.56 (284.95, 660.17) across our 12 CMR sites. Male-to-female sex ratios derived from these abundance estimates ranged from 0.77 : 1 to 4.89 : 1 ( $X = 1.1 : 1.0$ ). The maximum probability of capture during the sampling period was 0.72 (0.68, 0.76) across all sites, with two additional peak capture probabilities (0.44 [0.40, 0.48] and 0.31 [0.29, 0.33]) corresponding to two rain events. The mean number of capture events per individual across all sites ranged from 1.25 (1.11, 1.39) to 2.37 (2.10, 2.64); ( $X = 1.38$  [1.16, 1.60]) for males and 1.00 to 1.23 (0.90, 1.56) ( $X = 1.08$  [1.02, 1.14]) for females (see Appendix 2 for mean capture rates).

*Visual Encounter Surveys.*—Egg-mass counts for *A. maculatum* ranged from 0 to 550 in wetlands of area 40 m<sup>2</sup> and 1,590 m<sup>2</sup>, respectively. Mean egg-mass counts for *A. jeffersonianum* ranged from 0 to 187 in wetlands of area 40 m<sup>2</sup> and 390 m<sup>2</sup>, respectively, whereas mean counts for *L. sylvaticus* ranged from 0 to 113 in wetlands of area 40 m<sup>2</sup> and 1,180 m<sup>2</sup>. Our estimated detection probability indicated that, on average, observers were only able to detect 69% of *A. maculatum* egg masses present in a wetland ( $\hat{p}_{VES} = 0.69$  [0.67, 0.71]). Double-observer counts for *A. maculatum*, *A. jeffersonianum*, and *L. sylvaticus* egg-mass surveys,



TABLE 2. Estimated sex-specific adult abundance with 95% confidence intervals (CI) and estimated sex ratio for *Ambystoma maculatum* ( $n = 12$  wetlands).

Site	$\hat{N}_{\text{male}}$	95% CI		$\hat{N}_{\text{female}}$	95% CI		Estimated sex ratio (M : F)
CMR 01	337.86	325.28	350.44	306.09	195.76	416.42	1.10
CMR 02	364.65	335.82	393.48	472.56	284.95	660.17	0.77
CMR 03	60.33	55.49	65.17	16.82	3.35	30.29	3.59
CMR 04	32.91	29.36	36.46	6.73	0.00	14.82	4.89
CMR 05	99.82	93.49	106.15	60.54	30.26	90.82	1.65
CMR 06	27.42	24.19	30.65	10.09	0.00	20.18	2.71
CMR 07	49.36	44.99	53.73	26.91	9.11	44.71	1.83
CMR 08	64.18	53.28	75.08	62.63	22.67	102.59	1.02
CMR 09	156.07	138.47	173.67	85.40	36.20	134.50	1.82
CMR 10	103.11	96.68	109.54	40.36	19.02	61.70	2.55
CMR 11	70.01	58.60	81.42	28.47	3.78	53.17	2.46
CMR 12	115.23	100.33	130.13	74.01	29.42	118.60	1.56

as well as estimated *A. maculatum* egg-mass abundance, can be found in Figure 3. Our best-fit model relating estimated egg-mass density to abiotic and biotic site characteristics included effects for wetland hydroperiod ( $\hat{\beta} = 0.534$  [0.418, 0.650]) and density of *A. jeffersonianum* ( $\hat{\beta} = 0.046$  [0.038, 0.054]) and *L. sylvaticus* ( $\hat{\beta} = 0.051$  [0.043, 0.059]) egg masses, as well as quadratic effects of mean water temperature (Table 3; Appendix 3). Wetlands of longer hydroperiod were predicted to have more egg masses, and predicted egg-mass density was maximized at  $\sim 15^{\circ}\text{C}$ . We present all predicted relationships and 95% prediction intervals from our best-fit model in Figure 4.

**Validating Egg Mass VES.**—We found a strong relationship between estimated female abundance and estimated egg-mass abundance ( $\hat{\beta} = 1.06$  [0.92, 1.20];  $P < 0.001$ ;  $R^2_{\text{adj}} = 0.95$ ; Fig. 5A). This result translates to an average of one egg mass per female per breeding effort. The estimated relationship between male abundance and estimated egg-mass abundance ( $\hat{\beta} = 1.25$  [0.91, 1.59];  $P < 0.001$ ;  $R^2_{\text{adj}} = 0.82$ ) indicates an egg mass-to-adult male ratio of  $\sim 1.25 : 1$  (Fig. 5B).

## DISCUSSION

Combining field VIE batch marking with photograph recognition software greatly improved our CMR efficiency and increased our identification success, thereby allowing for more accurate

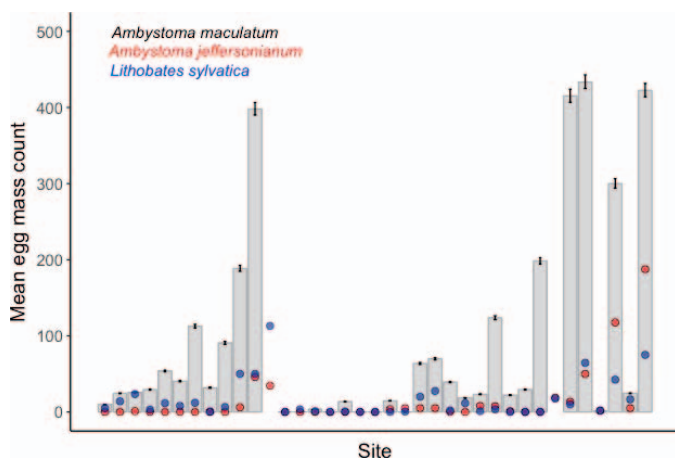


FIG. 3. Estimated *Ambystoma maculatum* egg-mass abundance (gray; counts adjusted for 0.69 detection probability) and 95% confidence intervals as well as mean double-observer egg-mass counts for *A. jeffersonianum* (red) and *Lithobates sylvaticus* (blue) for all 37 wetlands monitored via VES in 2015.

individual encounter histories. Our CMR analysis revealed male-biased sex ratios that align with previous studies that report male-to-female sex ratios ranging from 1 : 1 (Blanchard 1930) to 1.39 : 1 (Husting, 1965) and 1.86 : 1 (Sexton et al., 1990). Additionally, our results highlight that (re)capture probabilities vary widely throughout the breeding season, and are likely linked with high rainfall events (Sexton et al., 1990). We also detected variation in (re)capture probabilities among the sexes, likely the result of differences in behavior (e.g., length of stay in the wetland; Strickland et al., 2015) and physiology (e.g., reduced metabolic rate and locomotor performance in gravid females; Finkler et al., 2003). Our low number of female recaptures resulted in relatively imprecise estimates of adult female abundance, and likely led to an overestimation of true female abundance in wetlands where we never recaptured marked females. Future research should therefore focus on assessing these differences in (re)capture probabilities by using multiseason CMR data to better inform estimates, particularly with regard to female abundance.

Double-observer egg-mass VES are an efficient method to survey breeding effort (Egan and Paton, 2004; Grant et al., 2005; Skidds et al., 2007). Egg masses of *A. maculatum* are relatively easy to detect from the time of oviposition to hatching (Crouch and Paton, 2000; Grant et al., 2005) and in some instances, can be easily observed in wetlands up to 2 mo posthatching (Skidds et al., 2007). Although previous studies have reported high detection probabilities (e.g., Grant et al., 2005; Faccio, 2011), we found that detection of *A. maculatum* egg masses was much less than 1, indicating that abundance estimates based solely on VES count data would be biased low. Furthermore, if we instead relied on mean egg-mass counts and did not correct for imperfect detection in our VES, our estimated egg mass-to-adult ratio would be  $< 1 : 1$  (see Appendix 4). Our survey method, however, was not able to account for individual heterogeneity in detection (i.e., not all egg

TABLE 3. Estimated Poisson regression coefficients ( $\hat{\beta}$ ) and 95% confidence intervals (CI) for our “best-fit” model predicting *Ambystoma maculatum* egg-mass density in 2015 ( $n = 37$  wetlands).

Predictor	$\hat{\beta}$	95% CI	
<b>Abiotic</b>			
Mean water temperature	5.226	4.077	6.375
Mean water temperature <sup>2</sup>	-0.179	-0.140	-0.218
Wetland hydroperiod	0.534	0.419	0.650
<b>Biotic</b>			
<i>Ambystoma jeffersonianum</i> (AJEF)	0.046	0.038	0.054
<i>Lithobates sylvaticus</i> (LSYL)	0.051	0.043	0.059

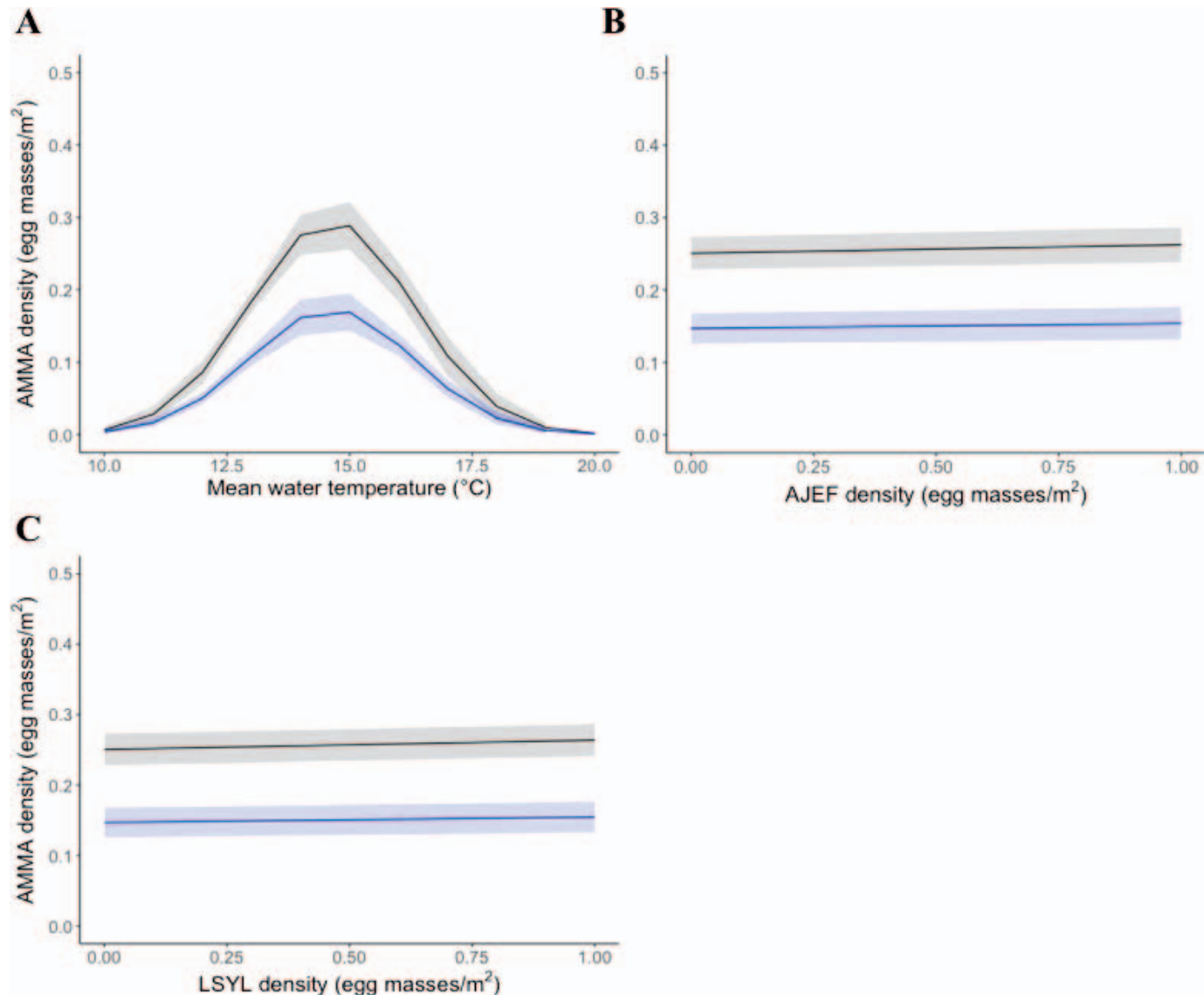


FIG. 4. Relationship between predicted density of *Ambystoma maculatum* (AMMA) egg masses and (A) mean water temperature (°C), (B) *A. jeffersonianum* (AJEF) egg-mass density (mean count/m<sup>2</sup>), and (C) *Lithobates sylvaticus* (LSYL) egg-mass density (mean count/m<sup>2</sup>) for wetlands of shorter (blue) and longer (black) hydroperiod. Regression lines show predicted slopes with 95% prediction intervals.

masses in a wetland had the same probability of being detected). A more robust approach, such as individually marking egg masses (e.g., Hels and Buchwald, 2001; Fellers et al., 2017), would further increase precision and reduce potential bias (Grant et al., 2005). Nevertheless, we demonstrate a strong correlation between estimated adult abundance and estimated egg-mass abundance, suggesting that VES data adjusted for imperfect detection can be a valid means of estimating *A. maculatum* population abundance in ephemeral wetlands with minimal survey effort. VES indices are common but in each case, they need to be validated because 1) detection can vary from site to site and year to year, and 2) the biology of a species (e.g., the number of egg masses deposited per female or the proportion of a population on the surface) can lead to biased indices (e.g., by underestimating population size) that would have low correlation to true abundance.

Our work suggests a quadratic relationship between mean water temperature and *A. maculatum* egg-mass density. Average water temperature has been shown to influence the duration of breeding and egg-mass incubation, thereby affecting breeding

success of *A. maculatum* (Brodman, 1995). In addition, the trade-off between hatching time and larval size is likely to regulate survival and population abundance (Light and Bogart, 1989). For instance, low water temperatures are associated with high levels of dissolved oxygen (Kern et al., 2013), but may result in longer embryonic and larval development, which may reduce breeding success in ephemeral wetlands. By contrast, hot temperatures may accelerate the rate of embryonic and larval development but increase larval mortality because of anoxia. In addition, accelerated rates of development may result in a smaller body size at metamorphosis, which has been linked to lower survival after juvenile emigration (e.g., Altwegg and Reyer, 2003; Chelgren et al., 2006; Schmidt et al., 2012) and lifetime reproductive output in amphibians (e.g., Berven, 1990). Water temperature is also correlated to canopy openness and, as a result, wetland productivity (Skelly et al., 2002), which has also influenced species richness (Skelly et al., 2014) and individual growth (Skelly et al., 2002).

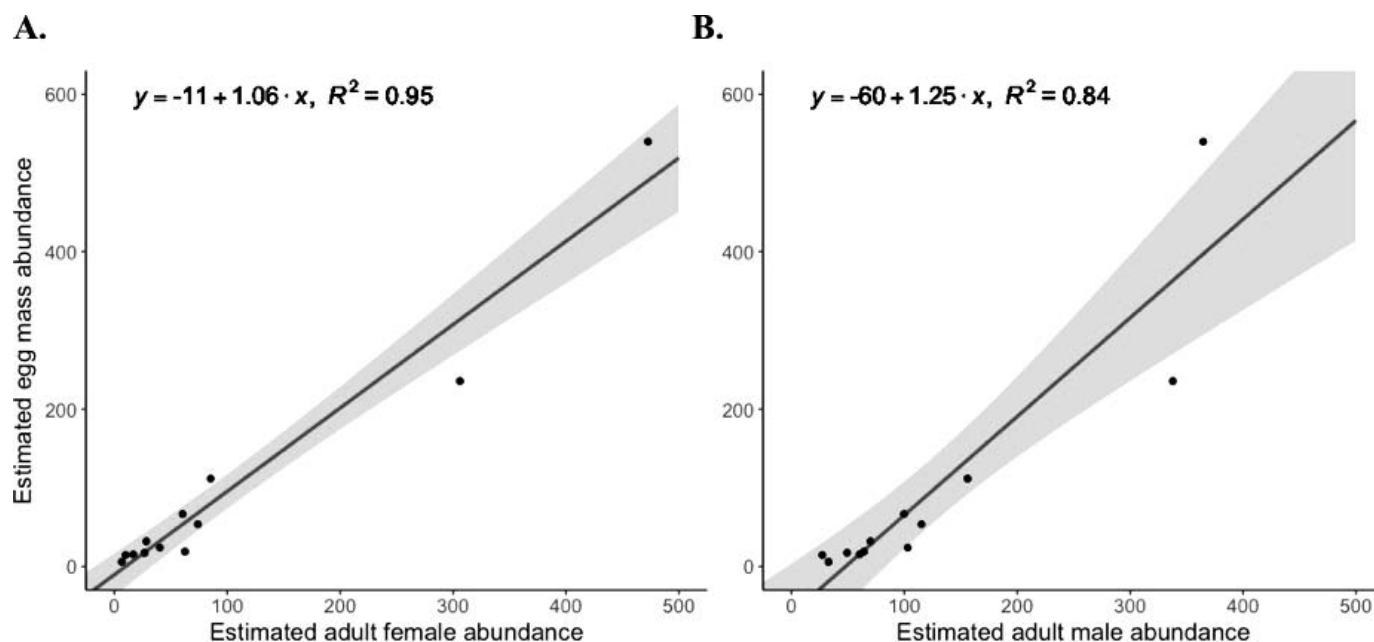


FIG. 5. Estimated *Ambystoma maculatum* egg-mass abundance as a function of estimated adult (A) female and (B) male abundance for our 12 CMR wetlands in 2015. Egg-mass abundances were estimated using an *N*-mixture model in the R package “unmarked,” whereas sex-specific adult abundances were estimated using Huggins’ closed population model in Program MARK. Regression lines show predicted slopes with 95% prediction intervals.

As expected in a network where all wetlands dry, we also observed a positive relationship between estimated *A. maculatum* egg-mass abundance and wetland hydroperiod. When considering strictly ephemeral wetlands, sites of longer hydroperiod had on average more egg masses than wetlands of shorter hydroperiod. Numerous studies have also shown a similar relationship between this covariate and wetland-breeding amphibian occurrence (Egan and Paton, 2004; Skiddds et al., 2007). More important, however, our coarse, binary classification does not adequately capture the fine-scale dynamics of hydroperiod that structure population-level processes. In addition, none of our monitored wetlands was known to contain fish, the aquatic predator that primarily influences wetland breeding amphibian occurrence (Babbitt et al., 2003; Binckley and Resetarits Jr., 2003; Hamer and Parris, 2013; Davis et al., 2017a,b), which may limit the extrapolation of our results beyond ephemeral and semipermanent wetlands.

We also found that density of *A. jeffersonianum* and *L. sylvaticus* egg masses were positively related to the density of *A. maculatum* egg masses, though the magnitude of these effects was much smaller than those reported for abiotic variables (see Table 3). These positive relationships are likely an artifact of a shared set of habitat preferences among the three species, but may also indicate heterospecific attraction (Buxton and Sperry, 2017). Previous studies focused on quantifying interactions between larval *A. maculatum* and *A. jeffersonianum* have shown these species to select different microhabitats and exhibit behavioral differences in temporal and spatial activity patterns (Brodman, 1996, 1999; Walls and Williams, 2001). At low densities of either species, therefore, we might not expect to see a negative correlation between *A. maculatum* and *A. jeffersonianum* at the wetland-level scale (Brodman, 1996). Furthermore, Walls and Williams (2001) demonstrated that the presence of *L. sylvaticus* in experimental pond units can alleviate negative interspecific interactions between *A. maculatum* and *A. jeffersonianum*. This may also explain the positive correlation

between *A. maculatum* and *L. sylvaticus* egg-mass counts, despite the fact that *L. sylvaticus* has preyed upon egg masses and developing embryos of *A. maculatum* (Petranka et al., 1998; Walls and Williams, 2001).

Approaches that integrate multiple data types are becoming more common for modeling population demographics (e.g., Besbeas et al., 2002, 2005; Smith et al., 2012; Tingley et al., 2016). For example, the combination of amphibian occupancy and CMR data has already increased our understanding of movement behavior (e.g., Tournier et al., 2017) and the influence of habitat suitability on amphibian demography (e.g., Unglaub et al., 2015). In a formal integrated population model, the data types are integrated into a single joint estimator allowing for uncertainty to be shared among the data types (Besbeas et al., 2003; Abadi et al., 2010; Chandler and Clark, 2014). Our work is an important first step in developing a formal integrated estimator of abundance that combines egg mass and CMR abundance estimates. Future work will focus on developing such a model for multiyear data, allowing us to determine demographic processes that affect changes in local population sizes. The more limited approach we take here, however, provides an efficient and effective way of monitoring ephemeral wetland-breeding species that are seldom observed outside of the breeding season. Although our results are specific to *A. maculatum* in small vernal pools, they provide a framework for combining data to validate indices in other systems. In addition, our results provide further insights regarding site characteristics that maximize local *A. maculatum* and that are likely to affect other amphibians and nonamphibians using ephemeral wetlands (Egan and Paton, 2004).

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APPENDIX 1. Full candidate set of models used to estimate adult abundance using Program MARK ( $n = 12$  wetlands).

Detection structure	Effect	AICc	$\Delta$ AICc
$p = c$	occasion + site + sex	6,225.48	0.00
$p \neq c$	occasion + sex	6,322.01	96.52
$p = c^a$	<b>occasion + sex</b>	<b>6,327.55</b>	<b>102.07</b>
$p = c$	occasion + site	6,395.41	169.93
$p \neq c$	occasion + site	6,446.61	221.13
$p \neq c$	occasion + site + sex	6,457.15	231.67
$p = c$	occasion	6,583.59	358.11
$p \neq c$	occasion	6,584.98	359.49
$p \neq c$	site + sex	12,068.21	5,842.73
$p \neq c$	site	12,170.20	5,944.72
$p \neq c$	sex	12,210.37	5,984.89
$p = c$	site + sex	12,214.19	5,988.71
$p = c$	site	12,333.44	6,107.96
$p = c$	sex	12,350.32	6,124.84
$p \neq c$	—	12,351.31	6,125.83
$p = c$	—	12,498.89	6,273.40

<sup>a</sup> Bold indicates that all estimates and standard errors are reported from this model; parameter values in the “best-fit” model(s) according to AICc were unreliable because of insufficient recapture data on female individuals.

APPENDIX 2. Mean number of encounters for male and female individuals by site, across the sampling period.

Site	Male	95% CI <sup>a</sup>	Female	95% CI
CMR 01	1.38	1.30 1.46	1.10	1.04 1.16
CMR 02	1.53	1.45 1.61	1.10	1.02 1.18
CMR 03	1.71	1.49 1.93	1.20	0.81 1.59
CMR 04	2.17	1.78 2.56	1.00	1.00 1.00
CMR 05	2.29	2.05 2.53	1.06	0.94 1.18
CMR 06	1.88	1.63 2.13	1.00	1.00 1.00
CMR 07	1.62	1.38 1.86	1.00	1.00 1.00
CMR 08	1.25	1.11 1.39	1.00	1.00 1.00
CMR 09	1.34	1.22 1.46	1.20	0.98 1.42
CMR 10	2.37	2.10 2.64	1.08	0.92 1.24
CMR 11	1.42	1.26 1.58	1.00	1.00 1.00
CMR 12	1.53	1.37 1.69	1.23	0.90 1.56

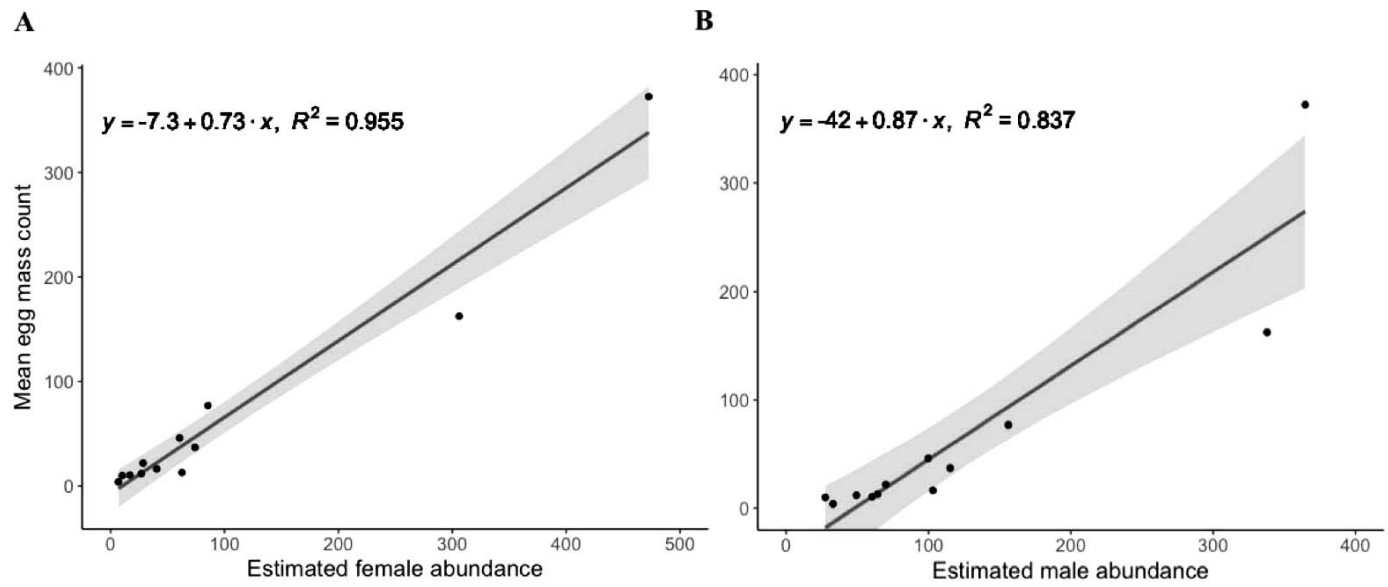
<sup>a</sup> CI = confidence interval.

APPENDIX 3. Model selection results for  $N$ -mixture model estimating egg-mass density from double-observer egg-mass counts corrected for imperfect detection ( $n = 37$  wetlands). Detection was constant in all models.

Effect	AIC	$\Delta$ AICc
<b>Temp + temp<sup>2</sup> + AJEF + LSYL + hydroperiod<sup>a,b</sup></b>	<b>1,519.27</b>	<b>0.00</b>
Temp + AJEF + LSYL + hydroperiod	1,579.02	59.75
Temp + temp <sup>2</sup> + ln(area) + AJEF + LSYL	1,618.75	99.48
Temp + temp <sup>2</sup> + AJEF + LSYL	1,647.35	128.08
Temp + LSYL + hydroperiod	1,648.49	129.22
AJEF + LSYL + hydroperiod	1,649.89	130.62
Temp + temp <sup>2</sup> + AJEF + hydroperiod	1,663.92	144.65
Temp + temp <sup>2</sup> + LSYL + hydroperiod	1,675.85	156.58
LSYL + hydroperiod	1,688.34	169.07
Temp + ln(area) + AJEF + hydroperiod	1,782.61	263.34
Temp + temp <sup>2</sup> + ln(area) + AJEF	1,802.97	283.71
Temp + ln(area) + AJEF + LSYL	1,806.03	286.76
AJEF + hydroperiod	1,843.31	324.04
Temp + temp <sup>2</sup> + ln(area) + LSYL	1,847.77	328.50
Temp + temp <sup>2</sup> + AJEF	1,850.88	331.61
Temp + temp <sup>2</sup> + LSYL	1,856.52	337.25
ln(area) + AJEF + LSYL	1,861.16	341.89
Temp + AJEF + LSYL	1,876.05	356.78
AJEF + LSYL	1,905.64	386.37
Temp + ln(area) + LSYL	1,947.06	427.79
ln(area) + LSYL	1,963.03	443.76
Temp + LSYL	1,974.95	455.68
LSYL	1,983.92	464.65
Temp + hydroperiod	2,009.99	490.73
Hydroperiod	2,021.56	502.29
Temp + temp <sup>2</sup> + hydroperiod	2,047.71	528.44
Temp + temp <sup>2</sup> + area + AJEF	2,063.06	543.79
Temp + ln(area) + AJEF	2,080.13	560.86
Area + AJEF + LSYL	2,102.30	583.03
ln(area) + AJEF	2,115.18	595.91
Temp + temp <sup>2</sup> + area + LSYL	2,164.07	644.80
Area + LSYL	2,203.76	684.49
Temp + AJEF	2,227.79	708.52
AJEF	2,234.30	715.03
Temp + temp <sup>2</sup> + ln(area)	2,336.50	817.23
Temp + temp <sup>2</sup>	2,353.03	833.76
Temp + temp <sup>2</sup> + area + AJEF + LSYL	2,383.13	863.87
Temp + area + AJEF	2,505.67	986.40
Area + AJEF	2,521.68	1,002.41
ln(area)	2,547.78	1,028.51
Temp + ln(area)	2,549.50	1,030.23
Temp + temp <sup>2</sup> + area	2,554.05	1,034.78
Temp	2,637.03	1,117.76
Temp + area + AJEF + LSYL	2,641.75	1,122.48
—	2,641.99	1,122.72
Temp + area	2,725.09	1,205.82
Area	2,755.23	1,235.96
Temp + area + LSYL	2,814.42	1,295.16

<sup>a</sup> Bold indicates the “best-fit” model according to AICc and the model from which all estimates and 95% confidence intervals are reported.

<sup>b</sup> AJEF = *Ambystoma jeffersonianum*; LSYL = *Lithobates sylvaticus*.



APPENDIX 4. Mean egg-mass counts (not corrected for imperfect detection) for *Ambystoma maculatum* as a function of estimated (A) female and (B) male abundance for our 12 CMR wetlands in 2015. Regression lines show predicted slopes with 95% prediction intervals.