Comparison of amphibian abundance in constructed vernal pools in two distinct habitats

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ABSTRACT

Construction and monitoring artificial wetlands for proactive conservation can help offset regional declines in amphibian abundance. We developed monitoring protocols and estimated abundance of three pool-breeding amphibians in constructed, high-altitude wetlands to determine site-specific differences in abundance and guide future research surrounding landscape and site-scale drivers of population dynamics. We found that pools in a forested site contained significantly greater numbers of amphibians than those in a meadow site. Within the meadow site, pools that drained prior to summer contained similar numbers of individuals as those that remained inundated, potentially contributing to source-sink dynamics. These results highlight the importance of site-specific factors in annual population fluctuations, and need to understand pool-scale drivers of abundance at fine temporal and spatial scales.

INTRODUCTION

Vernal pools are small, and usually ephemeral wetlands that form important habitat features in upland ecosystems (Calhoun and deMaynadier 2007). The pools recharge annually with water during spring in the Northeastern United States, and gradually lose water throughout the year, often draining completely by late summer or early autumn. This prevents fish and other aquatic predators from establishing and allows amphibians and their offspring to take advantage of a predator-free environment (Zedler 2003). As such, vernal pools are critical breeding sites for a number of amphibian species, many of which are declining globally more quickly than in the past (McCullum 2007), largely as a result of human impacts (McCullum 2007, Stuart et al. 2004, Windmiller et al. 2008). Habitat loss, alteration (including climate change), and fragmentation have been implicated as the primary drivers of amphibian declines during the past several decades (Cushman 2006, Semlitsch and Skelly 2007, Wake 1991). Additionally, a disproportionate number of species extinctions or extirpations have occurred at high-altitude (> 500 m elevation) pools during the past several decades (Gardner 2001).

One promising tool for conservation of pool-breeding amphibians and their habitats is the proactive construction of vernal pools (Kusler and Kentula 1989). However, some anthropogenic pools have been observed to function as ecological traps that can negatively affect amphibian

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populations (DiMauro and Hunter 2002). For example, pools that drain early in the year might attract breeding amphibians only to dewater before juveniles have metamorphosed (e.g., Calhoun et al. 2014, Seigel et al. 2006). As a result, evaluation of population responses following construction is critical to assessing utility of constructed pools for conservation. A number of factors including pool size, geographic location, hydrology, geology, and local ecology may also impact amphibian occupancy and population dynamics in seasonal pools (Calhoun et al. 2014, Semlitsch et al. 1996). Research also indicates that the presence of indicator species such as Spotted Salamander Ambystoma maculatum [Shaw 1802] is particularly sensitive to forest cover at local scales (Homan et al. 2004).

The timing and duration of post-construction surveys often limit the amount and type of information that is available regarding conservation value of constructed wetlands. Calhoun et al. (2014) recommended that vernal pools be monitored for a minimum 5-year period following construction in order to account for changes in colonization rates, hydrology, environmental variability, and other factors affecting the use of vernal pools. Importantly, it was recommended that monitoring studies focus on differential responses to local geology, hydrology, and land cover (Calhoun et al. 2014). Furthermore, amphibian populations may vary widely between years based on these and other factors (Semlitsch et al. 1996). As a result, consideration of stochastic variability in population fluctuations at both regional and local scales during climatically different years may be useful for understanding differences in population responses to habitat changes (Gardner 2001), and our ability to detect them.

In response to the need for information about stochastic changes in amphibian abundance in constructed, high-altitude wetlands, we undertook a study to investigate site-scale factors influencing the abundance of Jefferson Salamander Ambystoma jeffersonianum [Green 1827], Spotted Salamander, and Wood Frog Lithobates sylvatica [Le Conte 1825] in artificial pools created 5–10 years prior in the upper Susquehanna River watershed. The specific objectives of this study were to 1) develop a monitoring framework and estimate abundances of pool-breeding amphibians at two sets of anthropogenic vernal pools in distinct, isolated habitats 5–10 years after initial construction, and 2) determine whether or not abundance differed between these two sites despite annual fluctuations in an effort to guide further investigation into potential drivers of abundance. In order to accomplish these objectives, we used pit-fall traps (Gibbons and Semlitsch 1981) to collect amphibians during spring 2016 and 2017 breeding seasons at 15 high-altitude vernal pools across two sites. We estimated population abundance in each study pool using binomial mixture models that accounted for imperfect detection. Abundance was related to site-specific conditions and habitat characteristics of interest, including presence of permanent streams, hydroperiod, and site location. Because of their altitude, and the fact that the pools are located in the headwaters of a major Atlantic drainage, monitoring efforts have the potential to serve a large geographic area.
Field-Site Description

Twenty-one vernal pools were constructed as part of an amphibian conservation project by the Upper Susquehanna Coalition on the Rum Hill property of the State University of New York College at Oneonta Biological Field Station from 2007 through 2011 (Figure 1). The first pools (numbers 1–8) were constructed in an upland meadow during summer 2007 at an elevation of approximately 470 m above sea level. An additional 12 pools (9–21) were created in a nearby northern hardwood forest, about 570 m above sea level. Prior to spring 2016, none of the pools were studied to assess conservation value to pool-breeding amphibians over any appreciable time-frame.

A total of 15 artificially constructed vernal pools were monitored during the spring 2016 breeding season between the two sites (upper and lower; Figure 1). At the lower site (42°47′53.11″ N, 74°55′31.84″ W), all pools were surveyed (pools 1–8; Figure 1). One of these pools (pool 8) was not monitored during spring 2017 because it never filled with water during the 2016 season, and no amphibians were observed in the pool. We surveyed seven pools (9, 10, 11, 18, 19, 20, and 21; Figure 1) at the upper site (42°47′53.68″ N, 74°56′24.95″ W) to approximately balance the number of pools monitored at each site. We selected these seven pools to be representative of the geographic distribution of the pools over the upper site, and the same pools were surveyed during the 2016 and 2017 study seasons.

The soils at the lower site were predominantly composed of Manheim silt loam (80%) components that are poorly drained with 3–8% slopes, and moderately low water movement (NRCS 2016). These soils were adjacent to soils on all sides that were well drained and on steeper slopes (Figure 1). By comparison, soils at the upper site were characterized primarily by well-drained Mongaup (50%) and Hawksnest (30%) components with 1–8% slopes, moderately high water movement in the most restrictive layer (NRCS 2016). This site was surrounded by soils with relatively poorer drainage and water movement, and elevation gradients in surrounding soil units were generally much less steep than at the lower site (Figure 1). Canopy cover at pools in the upper site ranged from 0 to 100%, whereas there was no cover over at of the pools in the lower site and most were > 30 m to the nearest forest edge.

The two study years constituted somewhat disparate climatic conditions at the study sites. Whereas 2016 was drier than average, 2017 was a wetter than average spring in New York State. Likewise, a number of pools at the lower site drained completely by early June in 2015 and 2016, but none of the pools at either site drained prior to midsummer during 2017. As such, this study presents results from a varied climate regime that should be useful for drawing contrasts in breeding amphibian abundance during both wet and dry years.
METHODS

Amphibian surveys

We constructed pitfall traps around the perimeter of each study pool prior to the 2016 and 2017 breeding seasons using 0.5 m construction-grade silt fence. We erected fencing with wooden stakes placed every 3 meters around the perimeter of each pool, approximately 0.5 m from the shoreline. The bottom edge of fencing was closed with rocks and logs to create a more effective barrier to movement. At each pool we cut two openings in the fencing, with random orientations, and dug a small hole at each opening in which we placed a 1-gal bucket.

We conducted daily trap checks for amphibians from 19 March through 12 April 2016, and from 06 April through 30 April 2017. Amphibian activity was monitored each year prior to trap
construction to facilitate the earliest possible construction of traps. Terminal sampling dates were determined based on repeated zero counts at the majority of traps for a minimum of 1 week during each year. All amphibians collected in the traps were identified, recorded, and released immediately in accordance with SUNY Oneonta IACUC protocol number 2016-14.

Habitat characteristics

At the beginning of the survey period during the 2016 field season, we measured initial depth of each pool to characterize any gross differences, and we noted if the pool had a stream running through it (Table 1). We mapped each pool on 14 June 2016 using a global positioning system (GPS; Garmin eTrex 10, Garmin Ltd., Olathe, Kansas) and calculated area as a convex hull in QGIS (QGIS Development Team 2017). During June of each study year, we characterized summer water levels as being empty or inundated to determine whether or not abundance of each species differed between those pools that remained full throughout summer and those that dewatered prior to completion of metamorphosis by juveniles.

Abundance estimates

We used counts of amphibians in pitfall traps on each day to estimate abundance of each species in each pool during each year of the study period. It was evident that not all amphibians entering or exiting pools were caught in pitfall traps based on visual observations (probability of capture < 1.00). Therefore, we used a binomial mixture model (Royle 2004) that allowed for temporal separation of estimates (Dodd and Dorazio 2004) in order to estimate abundance during each week of sampling based on daily trap data, while accounting for imperfect detection of individuals within weeks.

We implemented the model using a Bayesian approach (see Kéry 2010). We assumed that amphibian count, at each \( i \)th pool during week \( j \) \( (N_{ij}) \) was represented by a Poisson distribution, described by parameter \( \lambda_{ij} \):

\[
N_{ij} \sim \text{Poisson}(\lambda_{ij})
\]

We used an uninformative prior distribution for abundance in each pool \( i \) during each week \( j \). For each pool during each week, the parameter \( \lambda_{ij} \) was assigned a prior on the log scale with a mean of zero and a variance of 10:

\[
\log(\lambda_{ij}) \sim \text{Normal}(0, 10)
\]
Table 1. Habitat characteristics of each vernal pool monitored on the Rum Hill property of the SUNY Oneonta Biological Field Station 16 March 2016 through 12 April 2016, including pool ID, site for each pool, presence of stream connecting a pool to others (yes or no), initial water depth, area, and summer water level (observed 14 June 2016).

<table>
<thead>
<tr>
<th>Pool</th>
<th>Site</th>
<th>Stream (Y/N)</th>
<th>Depth (cm)</th>
<th>Area (m²)</th>
<th>Summer water level</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Lower</td>
<td>Y</td>
<td>56</td>
<td>124</td>
<td>Inundated</td>
</tr>
<tr>
<td>2</td>
<td>Lower</td>
<td>Y</td>
<td>70</td>
<td>77</td>
<td>Empty</td>
</tr>
<tr>
<td>3</td>
<td>Lower</td>
<td>Y</td>
<td>74</td>
<td>112</td>
<td>Inundated</td>
</tr>
<tr>
<td>4</td>
<td>Lower</td>
<td>N</td>
<td>33</td>
<td>48</td>
<td>Empty</td>
</tr>
<tr>
<td>5</td>
<td>Lower</td>
<td>N</td>
<td>0</td>
<td>38</td>
<td>Empty</td>
</tr>
<tr>
<td>6</td>
<td>Lower</td>
<td>Y</td>
<td>34</td>
<td>69</td>
<td>Inundated</td>
</tr>
<tr>
<td>7</td>
<td>Lower</td>
<td>Y</td>
<td>27</td>
<td>32</td>
<td>Inundated</td>
</tr>
<tr>
<td>8</td>
<td>Lower</td>
<td>N</td>
<td>0</td>
<td>21</td>
<td>Empty</td>
</tr>
<tr>
<td>9</td>
<td>Upper</td>
<td>Y</td>
<td>34</td>
<td>41</td>
<td>Inundated</td>
</tr>
<tr>
<td>10</td>
<td>Upper</td>
<td>Y</td>
<td>53</td>
<td>37</td>
<td>Inundated</td>
</tr>
<tr>
<td>11</td>
<td>Upper</td>
<td>N</td>
<td>35</td>
<td>10</td>
<td>Inundated</td>
</tr>
<tr>
<td>18</td>
<td>Upper</td>
<td>N</td>
<td>49</td>
<td>35</td>
<td>Inundated</td>
</tr>
<tr>
<td>19</td>
<td>Upper</td>
<td>N</td>
<td>41</td>
<td>19</td>
<td>Inundated</td>
</tr>
<tr>
<td>20</td>
<td>Upper</td>
<td>N</td>
<td>34</td>
<td>13</td>
<td>Inundated</td>
</tr>
<tr>
<td>21</td>
<td>Upper</td>
<td>N</td>
<td>29</td>
<td>22</td>
<td>Inundated</td>
</tr>
</tbody>
</table>

In order to estimate detection probability for each species, we modeled counts in each pool during each week \(C_{ij}\) as the outcome of a binomial process (number of successes observed), with the distribution of \(C_{ij}\) described by parameters \(p_{ij}\) (probability of successful detection) and \(N_{ij}\) from the Poisson count model to link the likelihoods for detection probability and estimated population sizes:

\[
C_{ij} \sim \text{Binomial}(p_{ij}, N_{ij})
\]

We allowed detection probability to vary between pools, and specified uninformative priors on \(p\) for each week using a beta distribution with parameters \(a = 1\) and \(b = 1\).

We used Markov chain Monte Carlo (MCMC) methods to estimate model parameters in JAGS using the ‘R2jags’ package (Su and Yajima 2015) in R (R Core Team 2017). We used a burn-in of 50,000 runs, and simulated an additional 250,000 samples from each posterior distribution, saving every 50th sample to reduce autocorrelation between samples and increase the number of independent samples from the posterior distribution (Kruschke 2010). We ran
three Markov chains for each parameter, resulting in 12,000 samples from which to construct posterior distributions. We assessed convergence among the three chains for each parameter using the Gelman-Rubin convergence diagnostic (Gelman & Rubin, 1992), and visually inspected plots of Markov chains to ensure adequate mixing (Kruschke 2010).

Seasonal population abundance at each pool for each species was estimated using the week during which species abundance was greatest. We estimated the difference in mean seasonal abundance between pools at the upper site and lower site for each iteration of MCMC sampling. We used the same approach to estimate the mean difference in abundance of amphibians in pools with and without streams, and in pools that were inundated in mid-summer and those that were empty at the lower site. We assumed that where the 90% credible interval (CRI) did not contain zero those differences were statistically significant when $\alpha = 0.10$. Unless otherwise specified, all results are reported as mean (90% CRI).

RESULTS

Habitat measurements

The average area of vernal pools was 46.5 m$^2$. The largest pool was pool 1, which was approximately 124 m$^2$ (Table 1). Water depth was variable between pools and throughout the season at both sites. At the lower site, pools 4, 5, and 8 were empty during May 2015, prior to this monitoring effort. Pools 5 and 8 never filled with water during 2016, and there were zero amphibians collected in either of these pools. Pools 2 and 4 at the lower site contained water during the breeding period, when multiple species of amphibians were collected in the pool. However, this pool was empty by early June (Table 1). The pools at the upper site were filled with water throughout the study period, and higher numbers of all amphibian species were collected in pit fall traps than at the lower site.

Pools 1, 2, 3, 6, and 7 were all connected by a small stream that ran through the lower site (not shown on map). At the upper site, all pools retained water through early summer, and only pools 9 and 10 were ephemerally connected by a small drainage ditch that was likely dug by beavers (Table 1).

Wood Frog abundance

Wood Frog abundance was highly variable between years and pools. Wood Frog abundance in pools at the lower site was consistently low between years with the exception of pool 1, but few similarities were observed within pools at the upper site (Figure 2). Estimated seasonal abundance of Wood Frogs in pools at the lower site was 5 (CRI = 1–12) Wood Frogs in 2016 and was 28 (5–94) Wood Frogs per pool in 2017 (Figure 2). By comparison, estimated abundance of Wood Frogs in a given pool at the upper site was 99 (32–264) Wood Frogs in 2016, and was 146 (56–339) Wood Frogs in 2017 (Figure 2). Abundance within pools was highly variable between years at the upper site. The mean difference in seasonal abundance at the
upper and lower sites was about 95 (27–259) Wood Frogs per pool in 2016, and 118 (16–318) Wood Frogs per pool in 2017 (Figure 3). The CRI on these estimates did not overlap zero, indicating that the difference in abundance was statistically significant. When the estimates from 2016 and 2017 were averaged, we estimated a mean difference of 107 (25–293) Wood Frogs per pool between the upper and lower sites across years.

Figure 2. Estimated seasonal abundance of Wood Frogs (top panels), Jefferson Salamanders (middle panels), and Spotted Salamanders (bottom panels) by pool in lower and upper sites during spring 2016 (a–c) and spring 2017 (d–f). Note the use of different scales for y-axis to allow visualization of results across species.
Figure 3. Mean difference per pool between upper and lower sites in estimated seasonal abundance of Wood Frogs (top panels), Jefferson Salamanders (middle panels), and Spotted Salamanders (bottom panels) during spring 2016 (a–c) and spring 2017 (d–f).

At the lower site, the CRI for the difference in abundance between pools connected by streams and those not connected by streams at the lower site overlapped zero (mean difference = 0, CRI = -2–16), indicating little evidence that abundance differed between pools based on stream connectivity at the lower site during 2016. Similarly, we found insufficient evidence to support differences in abundance between pools that retained water through early summer and those that drained seasonally at the lower site during 2016 (mean difference = 5, CRI = -3–18). However, abundance was greater in pools connected by streams (mean difference = 33, CRI = 3–121) and in pools that retained water (mean difference = 44, CRI = 6–154) during the 2017 breeding season. When averaged across years, the mean difference in abundance for pools with and without streams was 36 (5–70), and the mean difference in abundance for pools that
remained full compared to those that drained was 45 (7–83). Thus, it seems that these differences are variable from one year to the next.

**Jefferson Salamander abundance**

Trends in the abundance of Jefferson Salamanders within pools were more consistent across years and sites than was the case for Wood Frogs, but were more variable than for Spotted Salamanders (Figure 2). For example, at the lower site abundance was consistently high at pools 2 and 4, and at the upper site abundance followed similar trends in abundance across pools between years (Figure 2). Estimated seasonal abundance of Jefferson Salamanders in pools at the lower site was 8 (2–18) individuals during 2016 and 6 (2–16) individuals during 2017, although abundance varied between pools and within pools between years (Figure 2). Estimated abundance of Jefferson Salamanders in a given pool was higher at the upper site in spring 2016 (mean = 28; CRI = 10–63) and 2017 (mean = 47; CRI = 18–106) than at the lower site (Figure 2). In 2016, pools at the upper site contained an average of 20 (1–60) more individuals than at the lower site, whereas a mean increase of 40 (10–101) Jefferson Salamanders per pool was estimated during the 2017 breeding season (Figure 3). When averaged across years, we estimated that pools at the upper site contained 30 (4–84) more Jefferson Salamanders on average than pools at the lower site.

We found little evidence for differences in abundance between pools connected by streams or differences in abundance between pools that retained water through early summer and those that drained seasonally based on overlap of 90% CRIs with zero in both years. Interestingly, the greatest abundance of Jefferson Salamanders at the lower site was documented in pool 4 during both years, which was drained by midsummer each year.

**Spotted Salamander abundance**

As with Jefferson Salamanders, abundance of Spotted Salamander abundance was somewhat coherent within pools between years at both the upper and lower sites. Abundance was highest in pools 3 and 6 at the lower site, and pools 9, 18, 19, and 21 at the upper site during both years (Figure 2). Seasonal abundance of Spotted Salamanders also was higher than that of Wood Frogs or Jefferson Salamanders across both years and sites (Figure 2).

At the lower site, we estimated a mean abundance of 16 (5–40) Spotted Salamanders per pool in 2016, and mean abundance of 35 (13–87) individuals in 2017. Estimated abundance of Spotted Salamanders in a given pool at the upper site during 2016 (mean = 108, CRI = 40–247) and 2017 (mean = 354, CRI = 243–479) was greater than at lower pools in either year (Figure 2). The mean difference in seasonal abundance at the upper and lower sites was about 92 (21–234) salamanders per pool in 2016, and 319 (197–450) individuals per pool during 2017 (Figure 3).

Across years, we estimated an increase in abundance of 205 (29–425) salamanders per pool at the upper site compared to the lower site. As with Jefferson Salamanders, we found no evidence to indicate differences in abundance based on stream connectivity or seasonal hydroperiod either within or across years.
DISCUSSION

This work represents the first attempt to quantify population dynamics of amphibians in recently constructed, high-altitude vernal pools on the Rum Hill property of the SUNY Oneonta Biological Field Station. We have successfully developed field protocols and statistical models that can be used as the basis for continued monitoring and for understanding regional population changes in the future; we were able to distinguish biologically meaningful differences between sites with respect to the abundance of multiple species that use the pools for breeding.

Monitoring and statistical considerations

The monitoring and statistical designs used in this study were adapted from previous work, and our results indicate that mixture models provide a useful tool for estimating trends in amphibian abundance across sites and through time based on daily counts from pit fall traps. However, we note that a priori consideration of observation error and temporal trends in abundance may be necessary due to the irregular migration of individuals, even during peak breeding times. Failure to account for changes in these processes through time has the potential to result in reduced accuracy and precision of estimates.

Overall, detection probabilities were low (generally less than 0.50; data not shown). It may be important to consider this for determining sampling intensity needed to estimate trends in abundance in this and other systems from binomial mixture models in future studies. The result of low detection probabilities in this study was a large amount of uncertainty in population estimates (Figure 2), and derived effect sizes of interest (Figure 3). While this likely increased Type II error rates, it did not appear to impede our ability to detect biological effects of interest in the present study given a priori establishment of Type I error rate ($\alpha = 0.10$) to account for expected uncertainty.

Uncertainty in estimated population sizes from this work also was likely inflated by lacunarity in migration behavior and resultant non-stationarity in trap counts from day to day. Trap numbers were low and contained a large number of zeros during much of the breeding season. These lulls were punctuated by large catches on days following what appeared to have been nights of mass migration into or out of vernal pools. As a result of this inconsistency, and the reliance of these models on repeat observations, estimated abundance from these data was highly uncertain. Future studies of breeding amphibians or species with similar migratory behaviors would benefit greatly from investigation of model formulations and (or) implementations that allow for estimation that accounts for large, temporal fluctuations in the state process (i.e. occupancy).

Despite uncertainty associated with population abundance, we were able to extract meaningful differences in abundance of all three species during this study. Therefore, this work should be useful for informing regional monitoring efforts, and may serve as a local baseline for quantifying changes in other populations. Furthermore, successful establishment of monitoring
and analysis protocols will promote the ability to track changes in these populations over time, and will serve to guide investigation at different spatial scales (e.g., pool scale) in the future.

**Implications for amphibian conservation**

By virtue of their location at the upstream extent of the Susquehanna River watershed, both sets of pools have been protected from extraneous effects of at least some factors known to affect amphibian populations globally, such as chemical pollution or contemporary land-cover modification (Gardner 2001). However, the mere creation of pools in a single region without other anthropogenic impacts does not mean that the two sites will be equally supportive of amphibian populations (Semlitsch 2002). Importantly, we have noted several trends in species distribution and abundance between these two distinct, although geographically proximal, sites in climatically divergent years that have the potential to inform proactive vernal pool construction in other regions. While annual fluctuations, and even local extinctions, are expected to occur stochastically due to philopatry (Waldman and Tocher 1998) and short lifespans (Marsh and Trenham 2000) regardless of habitat quality (Marsh 2001, Sjorgen 1991), the consistent difference between sites across years in the present study may indicate that habitat quality at the site (regional) scale is driving local species abundance in pools (Gardner 2001).

The vernal pools at the upper site tended to hold more individuals of all three study species during the breeding season than pools at the lower site in both years. Other studies have indicated that abundances of the species monitored are positively correlated with forest area in surrounding landscapes (e.g., Guerry and Hunter 2002, Laan and Verboom 1990, Pope et al. 2000). Calhoun et al. (2003) also indicated that a forested environment around a vernal pool improves water quality and serves as a terrestrial nursery for amphibian metamorphs, in addition to serving as important post-breeding and hibernation habitat for adults (Calhoun et al. 2014). Although pools 4, 7, and 8 were nearest the forest edge at the lower site, the pools at the lower site were generally concentrated in the center of a large meadow, whereas all pools at the upper site were located within the forest. As a result, this work appears to provide additional evidence for the importance of forest cover for successful colonization, reproduction, and survival of indicator species in vernal pools.

One of the primary differences between pools at the two sites investigated in this study was that a number of pools at the lower site drained during summer months, whereas pools at the upper site did not. At the site scale, this likely contributes to observed differences in abundances for the three study species (van Dyke et al. 2017). These differences may be attributable to differences in landscape-scale differences such as soil composition, drainage, and elevation gradients (Figure 1). However, at the lower site we noted no differences between those pools that have a tendency to drain during the summer and those that do not. This similarity could indicate that at least some of the pools at the lower site function as ecological traps. Pools that drained attracted breeding amphibians in similar abundance as those pools that held water throughout summer, but they dried too soon for larvae to metamorphose and leave in both 2015 (prior to this study) and 2016. The expected result is reduction of net productivity or local extinction during some years, with the most pronounced effects observed in those years following low-water years.
In this respect, it is possible that pools in the lower site mimic natural pools in the region and that some demographic rescue occurs during wet years due to the clustering of pools within this site (van Dyke et al. 2017). Ultimately, this question will require further investigation through the lens of metapopulation dynamics and pool-scale drivers, but it appears that the combined effects of reduced forest canopy and irregular hydrological cycles at the lower site contribute to lower amphibian abundance across species relative to the upper site at a landscape scale. Investigation into pool-scale differences in hydrology could further improve understanding of annual fluctuations at this site in the future.

One potentially interesting trend noted during this study was the difference between annual fluctuations in Wood Frog abundance between pools compared to fluctuations in salamander abundances, despite the limited number of years thus far. Changes in abundance of Wood Frogs in individual pools seemed to be somewhat sporadic from 2016 to 2017, and none of the pools appeared to attract breeding adults in consistently greater numbers than others across years. However, both Spotted and Jefferson Salamanders showed some consistency in their relative abundance between pools across sites and years (Figure 2). For example, Jefferson Salamanders were most abundant in the southeastern pools at the upper site in both years, and Spotted Salamanders were more abundant at the northeastern cluster of pools at the upper site in both years. These results may be due to the more limited dispersal ability of salamanders relative to Wood Frogs (Faccio 2003). This trend also may be due to high rates of site fidelity that has been reported for these species (Husting 1965, Savage and Zamudio 2005, Whitford and Vinegar 1966) despite interbreeding of breeding adults across similar scales (e.g., Zamudio and Wiezorek 2007), or it could be related to competitive interactions for space and resources (Semlitsch and Skelly 2007). Investigation of these questions in the future could further inform site choice and construction of anthropogenic vernal pools.

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