Behavioral and Survival Responses of Dragonflies to Drying Cues in Temporary Ponds: Implications for Effects of Climate Change

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Submitted in fulfillment of the senior thesis requirements of the Department of Environmental Science at Allegheny College and approved by the senior thesis committee.

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Aquatic organisms living in temporary habitats are especially vulnerable to climate change as increasing global temperatures lead to earlier spring melts and summer drying. Temporary-habitat specialists that rely on pond hydroperiods to complete their life cycles must adapt to these seasonal shifts to survive. The purpose of this study was to examine how drying and crowding affect aggression and cannibalism in the predatory dragonfly *Anax junius*. I conducted a microcosm experiment in which I manipulated water level and tank size to determine if the threat of drying and/or crowding, respectively, increased the frequency of cannibalism among *A. junius* larvae. I hypothesized that 1) combative interactions and cannibalism would increase with crowding as microcosm size decreases under both permanent and temporary conditions, 2) the most aggression and cannibalism would occur in the smallest microcosms due to higher encounter rates, and 3) the lowest levels of aggression and cannibalism would be observed in the largest microcosms as a result of lower encounter rates. I found that hydroperiod, pool size, and larval size all had a significant effect on dragonfly survivorship, but these factors had no significant impacts on behavior. Cannibalism on small larvae by large conspecifics increased with the acceleration of drying conditions across all microcosm sizes. These findings provide evidence that climate warming could cause changes in population interactions and size structures, potentially leading to gaps in age cohorts. As top predators, fluctuations in dragonfly populations could have cascading top-down and bottom-up effects on community structure.
Introduction

Climate change poses serious concerns for ecosystems worldwide (NOAA, 2016). The increasingly dry and warm climate expected to ensue with rises in annual global temperatures will likely interfere with a multitude of natural processes and ecosystem functions upon which we rely (IPCC, 2014). Rising global temperatures contribute to seasonal climate shifts (a phenomenon known as season creep), which prompt earlier winter melts, advanced springs and longer summers (Schwartz et al., 2006). Season creep is especially concerning for temperate climate areas across the Northern Hemisphere due to the fragile ecosystems located at this latitude (Robeson, 2004). Close analysis of average seasonal temperatures reveals warming in temperate areas to be significantly greater in winter and spring compared to summer and fall (Bonsol et al., 2001), and these higher temperatures could have dramatic effects on the structure of temporary habitat ecosystems and the life cycles of organisms found within them.

Temporary habitats, such as intermittent streams, shallow lakes, and vernal ponds, are experiencing dramatic changes in their hydroporiods and ecosystem functions as a result of climate shifts (Brooks, 2008). Such changes should directly impact the subset of species that are adapted to complete their life cycles in these habitats (Wellborn et al., 1996). Premature snowmelts due to increasing temperatures are causing temporary habitats to fill and dry earlier and at a faster rate (Schwartz et al., 2006). Although invertebrates living in semi-permanent or shallow permanent habitats can typically complete their lifecycles without special adaptations, those that rely on temporary habitats are faced with the challenge of adjusting their life cycles to seasonal changes in order to survive and reproduce effectively (Schwartz et al., 2006). Temporary-habitat specialists (organisms that respond to processes within temporary habitats) depend on the hydroporiods of aquatic habitats that dry during the early developmental stages of their life cycles (Pandit et al., 2009). Many of these organisms exhibit a diverse range of adaptations to early desiccation, revealing a promising sign that animals in temporary habitats should be particularly responsive to long-term changes in climate and hydroporiods (Strachan et al., 2014).

Responses to drying can be prompted by an array of cues, including temperature, photoperiod, events of wetting and drying, and water chemistry (Strachan et al., 2014). These cues influence behaviors, such as aestivation or hastening of life cycle events, which enable
habitats to survive and eventually complete development. Although some temporary-habitat specialists have shown flexibility in response to climate change, the degree of their flexibility remains relatively unknown (Lund et al., 2016). Studies examining the behavioral responses of organisms that depend on temporary habitats to changing habitat conditions are critical for determining which species will most likely have the ability to adapt to and survive climate change, and which will ultimately fall victim to its effects (Rosset and Oertli, 2011).

For aquatic invertebrates, cues such as increased temperature, decreased water depth, and changes in food accessibility induce behavioral and developmental flexibility (Harper and Peckarsky, 2006; Juliano and Stroffregen, 1994; Johansson et al., 2001). In most cases, there are costs associated with hastened development in response to the time constraints of a fast-drying habitat. For instance, increased developmental rates can cause adults to have smaller body sizes, which in turn can greatly reduce their potential fitness and defensive abilities (Loman and Claesson, 2003). Furthermore, organisms exposed to desiccation have decreased survival rates as well as weakened immune systems (Wickson et al., 2012; Gervasi and Foufopoulos, 2008). The costs of these trade-offs can have significant effects on ecosystem function and community structure (Meyer et al., 1999).

Species that live in temporary habitats develop rapidly during and after snowmelts in order to emerge in early summer before their habitats dry (Wissinger et al., 2003). Toward the end of their development, larvae become crowded and resources become increasingly scarce. These conditions can escalate the amount of aggressive interactions between larvae, including cannibalism (Wissinger et al., 1996). Crowding and declining water levels cue larvae to adjust their behavior and development. For instance, increased density of caddisfly larvae can proliferate aggressive behavior and durations of aggression, increase the number of mobbing and cannibalism incidents, and accelerate larval development (Lund et al., 2016). Furthermore, the presence of a protein supplement allays aggressive behaviors, indicating cannibalism to be a last-resort alternative when preferred protein sources are limited (Lund et al., 2016). These findings can be a useful model when making inferences about the behavioral and physiological responses of predatory temporary-habitat specialists to early drying.

Dragonflies (order Odonata) begin their lifecycle as aquatic insects that often rely on temporary freshwater habitats (McPeek, 1990). Temporary habitats at temperate latitudes are vulnerable to winterkill, and are thus fishless, allowing large-bodied invertebrates (such as
dragonflies) to retain the role as top predators (Wellborn et al., 1996). As the top invertebrate predators, dragonfly larvae play a significant role in the structure of freshwater food webs and in overall ecosystem function (McPeek, 1990). The breeding and emergence patterns of many dragonfly species often result in overlapping cohorts, causing a broad size distribution between the youngest and oldest individuals (Wissinger, 1988b). Although food availability is rarely limited due to the widely diverse diets of dragonfly larvae, cannibalism can be responsible for up to 95% of the total mortality of many species, making it a primary regulating mechanism of odonate population densities (Anholt, 1994). Dragonfly larvae rarely exhibit aggressive behaviors toward similarly sized dragonfly larvae under normal conditions, but smaller individuals are commonly subject to cannibalism by larger conspecifics (Wissinger, 1988a; Ferris and Rudolf, 2007). Cannibalism between like-sized dragonfly larvae is usually mediated by habitat structure, size and balancing the risk between eating and being eaten (Wissinger, 1988a).

As opportunistic predators, dragonfly larvae tend to eat anything they can detect and easily defeat (Pritchard, 1964). They are also highly territorial of their feeding sites, and are known to act aggressively against intruding conspecifics (Harvey and Corbet, 1985). Because of this, dragonfly larvae prefer to distribute themselves independently from each other as much as possible within their habitats. Vertical sticks and vegetation act as individual perches for dragonfly larvae to sit and wait for passing prey (Harvey and Corbet, 1986). For instance, *Anax junius* prefer to climb and perch on littoral vegetation (vegetation along the shore). This species relies heavily on their vision to detect prey, making their success rate of capturing prey directly dependent on the structure of their habitat and the intensity of prey activity (Folsom and Collins, 1984). Competitive interactions increase between larvae when resources are limited (Wissinger, 1988a); however, the underlying cues that trigger these behavioral responses have not fully been explored, and the effects of rapid habitat drying on the behavior of dragonfly larvae, to my knowledge, has yet to be investigated.

The purpose of this study was to examine the behavioral responses of *A. junius* in a controlled laboratory setting to drying cues encountered in their natural habitat. This species is often the top predator in long-during temporary habitats and shallow permanent habitats without fish (Wellborn et al., 1996). The combination of living in shallow fishless habitats that dry late in the season coupled with their long larval period (large body size) and lack of specialized
desiccation strategy (unlike short-lived temporary specialists) makes them a likely candidate for being vulnerable to seasonal creep; i.e. *A. junius* live in the types of habitats where early drying could result in crowding and eventually desiccation. In order to investigate this, I conducted a microcosm experiment in which I manipulated water level and tank size (simulating crowding in drying ponds as in Lund et al. 2016) to determine if the threat of drying and/or crowding increased the frequency of cannibalism among *A. junius* larvae. I hypothesized that combative interactions and cannibalism would increase with crowding as the habitats decrease in size under both permanent and temporary pond conditions, and the most aggression and cannibalism would occur in the smallest temporary pond simulations as a result of higher encounter rates. I also predicted the lowest levels of aggression and cannibalism would be observed in the largest permanent pond simulations due to lower encounter rates. Alternative hypotheses for this experiment were that (1) few aggressive behaviors would be observed due to the constant and sufficient food source availability throughout all simulations, or (2) the animals would instead be so aggressive that changes in crowding, water depth, and food availability have no influence on behavior; i.e., they are so aggressive that all of the these behaviors would be commonplace without the treatment of drying and/or crowding.

**Methods**

**Organism Collection/ Study Site:**

All *A. junius* and damselfly larvae were collected from semi-permanent ponds near Allegheny College in northwestern Pennsylvania. The primary source of *A. junius* larvae was collected from a pond located on State Game Lands 146 (41.733794, -79.974109). The damselflies that were supplied as a regular prey resource to *A. junius* during the experiment were collected at the same pond and/or at a semi-permanent beaver marsh on Allegheny’s Bousson Environmental Research Reserve (41.599392, -80.053044). Both species were collected by gently sweeping the edges of the ponds with D-frame nets. The organisms were transported in buckets to a laboratory setting. The study was conducted in microcosms housed in the aquatic research laboratory in Steffee Hall located on the Allegheny College campus. Damselfly larvae were replenished weekly following initial organism collection to maintain a fresh and constant food supply for the dragonfly larvae.
Microcosm Set-up/Maintenance:

I set up 30 aquarium habitats (15 permanent pond simulations, 15 temporary pond simulations), ten of each different aquarium size (large size: 37.85 liters; medium size: 18.93 liters; small size: 9.46 liters). The perches were made using cotton-tipped applicators (15.24 cm long). The cotton tips were removed from all wooden stems and fastened to the bottom of the aquaria, allowing the stick to stand vertically. The large aquaria each had three rows of 4 perches evenly spaced apart (12 perches total), the medium sized aquaria had two rows of 4 perches (8 perches total), and the small aquaria had two rows of 2 perches (4 perches total). At the bottom of each aquarium, a layer of sand sediment was spread evenly (roughly 1 cm deep). The water placed in the tanks was a 50/50 mixture of local pond water and dechlorinated tap water. All aquariums started out with the same water depths (roughly 14cm). While the depth of the 15 permanent habitat conditions remained constant throughout the experiment, the depths of the 15 temporary habitat conditions were decreased by 4cm every 4 days until their depths were only at 2cm. All aquaria were connected to an air pump with air stones for constant oxygen circulation.

Each aquarium initially contained 8 dragonflies: 1 large (mean body length ± 1SD = 36.5 mm ± 1.1 mm), 1 medium (mean body length ± 1SD = 25.5 mm ± 1.1 mm) and 6 small (mean body length ± 1SD = 21.0 mm ± 0.9 mm). These size ratios represented the size variation found in their natural habitat. For the dragonfly food source, 8 damselfly larvae were added to each aquarium. Each day, the numbers of dragonfly and damselfly larvae were counted, and damselflies were added to maintain an constant ratio across tanks and through time, assuring a sufficient food source for the dragonflies. To account for water evaporation, dechlorinated tap water was added to the aquariums as needed to maintain desired depths.

Data Collection:

The duration of the experiment was 16 days, beginning directly after a 24-hour acclimation period. Each day, a series of observations were taken of all 30 tanks, noting the distribution, location and size of all dragonflies. The survivors were also counted, and the sizes of the dead and alive were recorded. The water depths of the temporary pond conditions were decreased by 4cm every 4 days to imitate natural drying. The dragonflies in the temporary treatments were given two days to acclimate to the new depth. Focal observations were done three days after a water drawdown to assess behavior. For these observations, 12 tanks (two from
each of the six treatments) were chosen at random. One random individual from each of the twelve tanks was followed for a total of 15 minutes. The size and initial location of the dragonfly was recorded, along with its behaviors, specifically noting: (i) Total time active, (ii) Number of encounters with other individuals and the size of the other individuals, (iii) Number of aggressive encounters with other individuals and the size of the other individuals, (iv) Number of prolonged aggressive behaviors and the size of the other individuals involved, (v) Number of cannibalistic events and the size of the other individual, and (vi) Number of feeding encounters. When missing larvae or remnants of body parts were observed, cannibalism was assumed to have taken place.

**Data Analysis:**

Behavioral analysis was conducted using JMP Pro 12. I analyzed the effect of tank size and hydroperiod on behavior using a general linear mixed model in which tank ID was used as a random effect. The Cox Proportional Hazards Model in R was used to analyze the significance of tank size, hydroperiod and larval size on survivorship.

**Results**

**Survivorship**

Tank size, hydroperiod, and larval size all had a significant effect on survivorship (Table 1). Hydroperiod had the greatest effect on survivorship in the small tanks (Table 2). The most mortality occurred in the small tanks with the temporary hydroperiod treatment. All small and medium larval deaths were due to cannibalism by larger conspecifics. The cause of large larval deaths was uncertain.

<table>
<thead>
<tr>
<th>Table 1: Cox Proportional Hazards Model for the effects of tank size, hydroperiod, and larval size on survivorship.</th>
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<tbody>
<tr>
<td><strong>Factors</strong></td>
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<tr>
<td>Tank Size</td>
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<tr>
<td>Hydroperiod</td>
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<tr>
<td>Larval Size</td>
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</tbody>
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Survival rates in the large temporary hydroperiod treatment tanks closely resembled those in all the permanent hydroperiod treatment tanks (Figure 1). Mortality occurred on a regular step-wise basis rather than being pulsed following water drawdown days (days 4, 8, and 12) in the tanks with temporary hydroperiods (Figure 2A). Mortality proceeded at different rates across all treatments throughout the duration of the experiment. Tank size and hydroperiod were found to be the most influential factors on larval survivorship (Figure 2A). For example, the small sized tanks with temporary hydroperiods had the greatest amount of mortality, with deaths occurring at a steady rate throughout the experiment. The medium larvae were the most successful in terms of survival throughout the duration of the experiment (Figure 2B). The small larvae had the least success, dying relatively consistently at a faster rate than the larger conspecifics. The mortality of medium larvae occurred toward the end of the experiment, after many of the small larvae had already disappeared. The few deaths of the large larvae showed no distinct pattern.

**Table 2:** Total death summary indicating the amount of deaths per larval size in respect to permanent (P) and temporary (T) hydroperiods and tank size.

<table>
<thead>
<tr>
<th>Tank Size</th>
<th>Hydroperiod</th>
<th>Small Deaths</th>
<th>Medium Deaths</th>
<th>Large Deaths</th>
<th>Total Deaths</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>P</td>
<td>5</td>
<td>0</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Small</td>
<td>T</td>
<td>19</td>
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<td>1</td>
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</tr>
<tr>
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<td>P</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Medium</td>
<td>T</td>
<td>16</td>
<td>0</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Large</td>
<td>P</td>
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<td>0</td>
<td>0</td>
<td>2</td>
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<tr>
<td>Large</td>
<td>T</td>
<td>9</td>
<td>0</td>
<td>1</td>
<td>10</td>
</tr>
</tbody>
</table>

**Figure 1:** Proportion of larvae surviving throughout the 16-day duration of the experiment with respect to tank size and hydroperiod treatment.
Figure 2: Mean (±1 SE) total number of survivors per treatment at the conclusion of the experiment (A) and the proportion of small, medium and large Anax larvae surviving throughout the 16-day duration of the experiment (B).
**Behavior**

During the 15-minute behavioral observations, the total time that focal organisms were active was not affected by tank size ($p = 0.39$) or hydroperiod treatment ($p = 0.19$) (Figure 3), and there was no interaction between these main effects ($p = 0.76$).

![Figure 3: Mean (±1 SE) total time active in seconds of focal organism per 15-minute observation of each larva density treatment.](image)

Encounter rates did not differ across all treatments (Figure 4). For example, neither tank size ($p = 0.23$) nor hydroperiod ($p = 0.88$) affected total number of encounters that focal organisms had with other larvae during the 15-minute focal observations for each larval density treatment (Figure 4A). The effect of both treatments together on the amount of encounters was also not significant ($p = 0.74$). Likewise, encounters per capita were not affected by tank size ($p = 0.69$), hydroperiod ($p = 0.79$) or the interaction between tank size and hydroperiod ($p = 0.17$) (Figure 4B). The effects of tank size ($p = 0.70$), hydroperiod ($p = 0.79$), draw down intervals ($p = 0.59$), and the interaction between tank size and hydroperiod ($p = 0.18$), hydroperiod and draw down intervals ($p = 0.19$), and tank size and draw down intervals ($p = 0.62$) on encounters per capita were not significant (Figure 4C).
Figure 4: Mean (±1 SE) total number of encounters (A), encounters per capita (B), and encounters per capita in each draw down scenario (C) observed per 15-minute focal observation for each larval density treatment.
Discussion

In small lentic habitats (ponds, isolated marshes, woodland pools), habitat drying often results in smaller pool sizes, decreasing water depths, and increased crowding of organisms (Brooks, 2008; Wissinger et al., 1996). To study these effects on dragonflies, I conducted a microcosm experiment to closely observe the survivorship dynamics and behavioral responses of different sized conspecifics of the predatory habitat specialist, *A. junius*, to such drying cues observed in their natural habitat. I found that 1) hydroperiod, pool size, and larval dragonfly size all had a significant effect on survivorship, 2) cannibalism by the large larvae accounted for all mortality of small and medium larvae, and 3) both tank size and hydroperiod, as well as drawdown intervals, had no significant effect on the observed behavior of *A. junius* larvae. These results provide further evidence that the frequency of cannibalism between carnivore conspecifics increases with crowding (Johansson and Rowe, 1999; Rossi et al., 2011), and novel evidence that dragonfly activity remains relatively constant under both permanent and temporary habitat conditions.

Survivorship

Cannibalism of small individuals by larger conspecifics is a common occurrence that is well documented among predatory dragonfly larvae (Wissinger, 1988a; Ferris and Rudolf, 2007). My study provides further evidence of this phenomenon, as significantly more small larvae were cannibalized in proportion to medium and large larvae. Furthermore, I found that more cannibalism occurred in the temporary habitat simulations compared to permanent, with the most cannibalism transpiring in the small tanks under temporary conditions. The cannibalism of medium larvae by the large conspecific also occurred exclusively in small tanks under drying conditions where the population of small larvae had already been cannibalized completely. These findings can be analogous to Wissinger’s 1998a study that found cannibalism between like-sized dragonfly larvae to be typically mediated by habitat structure and size. As the environment deteriorated in the temporary habitat simulations and the number of small larvae available to cannibalize dwindled, the large larvae turned to cannibalizing larvae closer to their own size. As has been previously reported, dragonfly larvae rarely exhibit aggressive behaviors toward similarly sized dragonfly larvae under normal conditions (Wissinger, 1988b; Ferris and Rudolf,
2007), and the benefits (increased nutrition and the elimination of competitors) of trying to cannibalize a conspecific of a similar size must outweigh the potential costs (injury or death) (Elgar and Crespi, 1992). This could explain why I observed similar behavior as the large larvae began to cannibalize the medium larvae when smaller conspecifics were no longer present.

Conversely, in tanks where the largest conspecific was no longer present, no further cannibalism occurred. This could be attributable to the inability of the medium larvae to successfully capture and kill the small larvae without the likelihood of becoming a secondary victim (Wissinger et al, 1992). One interesting topic of further study would be to determine how the timing of *A. junius* egg laying potentially influences the size structure of their populations (hence increasing the availability of different sizes of potential conspecific prey). For instance, if females lay their eggs earlier in the season, their offspring would likely be the largest in the pond, and thus they would be able to eat the offspring from later clutches. In a temporary habitat, this would be highly beneficial, especially with increased rates of drying imposed by climate change.

**Behavior**

In previous studies examining the effects of drying on the behavior of aquatic insects, increased crowding due to decreasing water depths and smaller pool sizes were found to induce more encounters, aggression, and cannibalism among conspecifics (Lund et al, 2016; Johansson and Rowe, 1999; Rossi et al. 2011). I found that drying conditions do not significantly affect dragonfly larvae activity, at least during short-term focal animal trials. Throughout the duration of the experiment, the observed behavior of the larvae in both permanent and temporary habitat simulations across all tank sizes remained relatively consistent. Although this finding seems to contradict previous literature on the responses of aquatic invertebrates to drying conditions, I suspect the lifestyle of this particular species has much to do with this. Dragonfly larvae like *A. junius* are known sit-and-wait predators, and thus are not typically active under normal conditions (Harvey and Corbet, 1986). This is in contrast to actively foraging animals that spend most of their time collecting and gathering food (as in Lund et al., 2016). Instead, dragonfly larvae tend to rest on littoral vegetation, and because they rely on the traction of their perch to pull in their prey, they typically do not leave their perch unless forced away by the threat of larger conspecifics (Harvey and Corbet, 1985). This could explain why I observed very little
activity under both drying and nondrying conditions. The dragonfly larvae chose to stay on their perch despite stressed conditions, most likely because there was no added benefit to leaving their perches, especially since the traction of the perch aids in defense against competitors and catching passing prey.

It is well documented that competitive interactions increase between larvae when resources are limited (Wissinger, 1988b). In my study, the limiting resources were space, perches, and water depth (food availability was kept constant throughout the duration of the experiment). Although there was no significant increase in larval activity in either temporary or permanent hydroperiod conditions, cannibalism was much more prevalent under temporary habitat conditions. This provides evidence that dragonfly larvae can perceive drying cues and respond to them accordingly through eliminating competitors for food and cannibalizing smaller conspecifics to increase their protein intake under stressed habitat conditions. This could potentially have grave consequences on community structure as larger conspecifics eliminate the populations of younger cohorts, thus leaving a predator gap in aquatic ecosystems. This could also cause a decrease in adult dragonfly populations. Another future study might focus on how pond drying affects the spatial dynamics of larvae by measuring the distances between potential cannibals and victims. The simplest explanation for the effects of drying on dragonfly cannibalism is that it brings potential victims in increasingly close proximity to potential cannibals (Crowley et al., 1987).

Toward the end of my experiment, I observed “herding behavior” among the small larvae under temporary habitat conditions in the small tanks; i.e. groups of three or more small larvae gathered close together on the same perch, despite the availability of other perches. Although I did not specifically look out for these behaviors, they were observed regularly when habitat conditions were most stressed (the last 4 days of the experiment). I suspect this could be a defense mechanism against larger conspecifics. The potential benefits of this kind of behavior would make for an interesting topic of future study.

Conclusions

The results presented here along with findings of previous studies provide evidence that habitat drying can cause increased encounter rates among organisms, which can lead to higher
cannibalism rates (Lund et al, 2016; Johansson and Rowe, 1999; Rossi et al. 2011). In my study, drying conditions (decreased pool size and water depth) led to increased cannibalism of smaller larvae by larger conspecifics. In nature, this phenomenon could potentially lead to gaps in age cohorts, which could have cascading top-down and bottom-up effects on community structure as dragonfly larvae are among the top predators in fishless ponds. Gaps in cohort cycles in isolated temporary habitats are particularly concerning because they can lead to local extirpations. While permanent habitats are not likely to dry in the short term as a result of climate change, temporary and semi-permanent habitats are expected to experience dramatic hydroperiod changes even with slight variations in temperature, evaporation and precipitation. Research that focuses on the effects of habitat drying on organisms living in temporary habitats can help predict how climate change will influence the structure and functions of these freshwater ecosystems.
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Literature Cited


