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Evaluating the non-consumptive, positive effects of a predator in the persistence of an endangered species

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ABSTRACT

Failure to consider both the consumptive and non-consumptive effects of predators on prey can lead to erroneous conclusions about the net effect of the relationship. The predatory devil crayfish, *Cambarus diogenes* Girard functions as an ecosystem engineer constructing extensive burrow systems through aquatic habitats. Despite crayfish posing a serious predation threat, preliminary data indicate that the federally endangered Hines Emerald dragonfly larvae, *Somatochlora hineana* Williamson regularly inhabit crayfish burrows. During late summer, *S. hineana* larval habitat dries up; leaving crayfish burrows as some of the only wetted habitats. Thus, *C. diogenes* can affect *S. hineana* through both direct, negative and indirect positive effects. We examined the positive role of crayfish burrows as drought refuges, and the threat of predation by *C. diogenes* on *S. hineana* larvae. Monthly field sampling indicated that *S. hineana* use open channel areas in spring and early summer moving into burrow systems in mid summer when channel areas normally dry. Laboratory experiments and field observations confirmed that crayfish prey on *S. hineana* larvae. Adult crayfish were a larger predation threat than juvenile crayfish. Despite their negative predatory impact, removal of crayfish from burrows in the field did not enhance densities of *S. hineana* larvae. Although *S. hineana* may face the threat of predation in burrows, they face a greater risk of desiccation if they remain in the open channel. These results lead to the counterintuitive conclusion that the maintenance of a predator is important for conserving an endangered prey species.

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1. Introduction

Interactions between the biotic community and the physical environment play an important role in regulating populations (Connell, 1961; Paine, 1966; Dayton, 1971; McPeek, 1990; Corti et al., 1997). Abiotic factors can be a key factor controlling species abundance and distribution, allowing only species with the appropriate life history, morphology and behaviors to survive and reproduce (Wiggins et al., 1980; Wilbur, 1987). However, biotic factors, such as predators, can also have direct effects on prey populations regulating the patterns of abundance and distribution of prey (Sih et al., 1985). The relative importance of abiotic and biotic factors in regulating population persistence can change along a physical gradient (i.e. habitat permanence) (Bertness and Callaway, 1994; Wellborn et al., 1996; Bertness and Leonard, 1997); therefore, it is important to consider the influence of both factors when studying the mechanisms regulating populations and community structure. In this study, we evaluated the role of predation by crayfish and desiccation on the population persistence of

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the federally, endangered Hine's Emerald dragonfly, *Somatochlora hineana* (Williamson, 1931).

Although predators have negative effects on the prey species they consume, it has frequently been observed that predators may have a net positive effect on prey populations through indirect, non-consumptive effects (Sih et al., 1998). One type of indirect effect that has rarely been considered in the context of endangered prey involves predators as ecosystem engineers. Ecosystem engineers are defined as organisms that directly or indirectly control the availability of resources to another organism by causing physical state changes in biotic or abiotic materials (Jones et al., 1997). Animals, such as beavers, elephants and alligators, have been referred to as ecosystem engineers because their behaviors and activities modify the physical habitat in some way, which in turn allows for the colonization or persistence of many other organisms (Jones et al., 1994; Finlayson and Moser, 1991). Such modifications may help ameliorate physical and abiotic stressors that would otherwise have strong negative impacts on other species associated with such habitats.

One type of abiotic stressor that can strongly regulate populations and communities, particularly within intermittent aquatic habitats is desiccation (Wiggins et al., 1980; Schneider and Frost, 1996). Aquatic organisms that inhabit temporary waters must possess adaptations to either complete development before stream drying, tolerate drought conditions, or respond behaviorally to avoid desiccation (i.e., migration) (Wiggins et al., 1980; Williams, 1996). Additionally, the availability of refugia is also important for the persistence and recovery of aquatic organisms in drying systems. The presence of an ecosystem engineer can ameliorate the threat of desiccation by creating such refugia. For example, during droughts alligator wallows (dug out depressions; "gator holes") often provide crucial refuge for other aquatic organisms that are not resistant to desiccation (Finlayson and Moser, 1991). Although the benefits of such refuges are clear, they also concentrate prey into a small area often making them more vulnerable to predators. Therefore, it is often difficult to predict the relative impact of desiccation and predation on prey populations because of the indirect positive effects of a predator as an ecosystem engineer.

Populations of *S. hineana* have been steadily declining primarily due to habitat destruction (Soluk et al., 1998, 2000). Larvae of *S. hineana* inhabit small, flowing stream and wetland habitats that are temporary and experience frequent drying that can extend for several months (Soluk et al., 1998, 2000). Odonate larvae are not generally viewed as drought tolerant, and most species are thought to survive periods of drying as adults or eggs (Wiggins et al., 1980; Corbet, 1999). However, *S. hineana* have a four year larval life cycle (Soluk et al., 1998), therefore, the likelihood of the larvae experiencing multiple drought periods is high. Manipulation and alteration of *S. hineana* habitat may exacerbate the threat of desiccation causing further negative impacts on the species. Therefore, it is important to understand the relative impact of desiccation on the densities of *S. hineana* larvae.

Another threat to *S. hineana* larvae is predation by the red devil crayfish, *Cambarus diogenes* (Girard 1852). *C. diogenes* is a naturally occurring predator and is ubiquitous throughout *S. hineana* larval habitat where they are predominant predators in terms of numbers and biomass. Crayfish are omnivores and can have effects across multiple trophic levels, including strong effects on aquatic invertebrates (Lodge et al., 1994; Charlebois and Lamberti, 1996; Nystrom et al., 2001). Crayfish are not only predators, but some species can function as ecosystem engineers (Creed and Reed, 2004; Usio and Townsend, 2004; Zhang et al., 2004). Specifically, burrowing crayfish dig their burrows deep enough so that they can reach groundwater during drought periods and can avoid freezing in the winter (Grow and Merchant, 1980). Burrows have been identified as microhabitats for invertebrates, such as amphipods and isopods (Creaser, 1931). Therefore, these burrows may play a vital role in the ecology of *S. hineana* by serving as refuges for the larvae when the habitat undergoes seasonal drying in mid-summer to early fall.

Preliminary studies have indicated that *S. hineana* larvae inhabit occupied crayfish burrows (Soluk et al., 2000). Therefore, we wanted to quantitatively examine the patterns of burrow use and interactions between *S. hineana* larvae and the devil crayfish, *C. diogenes*. Specifically, this study aims to understand the threat of desiccation and benefits of burrows as a refuge during drought for *S. hineana* larvae. Additionally, we evaluated the negative predatory effect *C. diogenes* has on *S. hineana* larvae while inhabiting burrows. Ideally, we would evaluate the trade-off between the threat of desiccation and predation simultaneously; however, this design was not possible due to the constraints of working with an endangered species. Therefore, we had to use a combination of field and laboratory studies with *S. hineana* and with a surrogate dragonfly species to understand the interaction between a native predator and its endangered prey.

Conservation biologists often used surrogate species as representatives when addressing specific threats facing threatened or endangered species (Savino and Miller, 1991; Beyers, 1995; Caro and O'Doherty, 1999). However, when choosing a surrogate, it is important to choose a species that resembles the focal species both taxonomically and ecologically. *Somatochlora williamsoni* Walker was chosen as a surrogate for *S. hineana*. Morphologically, the two species of *Somatochlora* are very similar; obvious differences include the absence of dorsal spines and a lower density of cuticular hair on *S. williamsoni*. Behaviorally, both are nocturnally active and show similar patterns of nighttime movement (Pintor and Soluk, personal observation). Furthermore, *S. williamsoni* co-occurs with *C. diogenes* and occasionally co-occurs in low numbers with *S. hineana*. Therefore, we were confident that *S. williamsoni* was the best surrogate to further elucidate the interaction between *S. hineana* and *C. diogenes*.

2. Methods

2.1. Monthly field sampling

We used monthly field sampling to evaluate the use crayfish burrows by *S. hineana* larvae in comparison to the open channel. We predicted that densities of *S. hineana* would be lower in the burrow than in the open channel while the channel

contained flowing water, but would be higher in the burrows when the channel was dry. These predictions are based on the preliminary observations that there is a significantly higher abundance of prey for the dragonflies to exploit in the stream channel than in crayfish burrows while the stream contains flowing water (Pintor, unpublished data).

Furthermore, we compared the change in *S. hineana* density from the month prior to and following the onset of drought conditions to evaluate the threat of desiccation. In 2002, drought conditions set in during the month of July, therefore we compared the change in density from June to August. Ideally, desiccation could be directly evaluated in the field by manipulating the presence or absence of burrows and observing mortality of marked individuals following stream drying. However, the endangered status of *S. hineana* makes this type of experimentation and manipulation unethical.

Crayfish burrows and adjacent channel areas were sampled monthly from May through September in 1999 and 2002. Sampling took place at the Mud Lake North Wildlife Refuge in Door County, Wisconsin. We estimated larval densities in burrows along a 20-m section of stream channel by sampling using a manual bilge pump (Jabsco- "Amazon Universal" ©) to extract the contents of the burrow. Burrow remained intact throughout the course of the sampling, thereby allowing us to sample the same set of burrows each month. Three 7.57 L (8-quart) samples were taken in sequence from each burrow system. Each sample was strained through a 500 mm-mesh net and all *S. hineana* larvae were removed live from the samples. Following measurement, larvae were returned to the burrows from which they were taken. When the channel was dry, filtered water (500 mm-mesh) from the adjacent stream was added to the burrow to facilitate pumping.

Adjacent channel sampling was conducted on each date in conjunction with the burrow sampling. Specifically, eight samples were obtained by disturbing a 30.48 cm^2 area upstream of a 30.48-cm^2 d-frame net (500 mm-mesh). Samples were taken along a 40-m reach of the stream at 5-m intervals. Samples were processed in the field to remove all *S. hineana* larvae. Following measurement, larvae were returned to the location from which they were taken.

Density estimates for the channel sampling were reported in area (number of larvae/m^2), whereas density estimates from the crayfish burrows were reported as mean number of larvae per burrow. We used ANOVAs to compare the change in density of larvae in the month before and after drought conditions in the two microhabitats.

Finally, we compared the water temperature within both microhabitats to further understand whether crayfish burrows provided a more stable abiotic environment for *S. hineana* larvae. Temperature was measured with temperature logging devices that recorded the temperature every hour. Temperature was monitored in four crayfish burrows using a StowAway Tidbit® (Onset corporation) attached to a cord tied to a stake outside the burrow entrance. Temperature loggers were heavy enough to remain at least six inches below the burrow entrance. StowAway® (Onset corporation) temperature loggers were placed in the stream channel outside of one of the monitored burrows.

2.2. Laboratory predation experiment

The US Fish and Wildlife Service permitted the use of 10 *S. hineana* larvae in direct predation experiments with crayfish in order to confirm a direct predator–prey link between *S. hineana* and *C. diogenes*. Additionally, it has been suggested that juvenile and adult crayfish exhibit different diet preferences, such that adults prefer aquatic plants and detrital material, whereas juveniles prefer invertebrates (Abrahamsson, 1966; Momot et al., 1978). Therefore, we conducted a simple lab experiment using both juvenile and adult *C. diogenes* and a range of sizes of *S. hineana* larvae to determine whether *C. diogenes* directly consumed *S. hineana*. We also used a surrogate species, *S. williamsoni*, to further understand the size relationship between *S. hineana* larvae and *C. diogenes*.

Dragonfly larvae and crayfish were split into two categories based on size (head width and carapace length, respectively); equivalent in size to *S. hineana* larvae in the 1st/2nd year and 3rd/4th year classes, and crayfish by stage (juvenile, ⩽20 mm and adult, >20 mm). We used a 2 × 2 factorial design to compare the interactions of each category of dragonfly larvae with each category of crayfish in order to determine which sizes of dragonfly larvae were most vulnerable to juvenile crayfish. Within each group, predation trials were conducted by exposing one dragonfly larva to a single crayfish within a simple arena for a 24-h period. Experiments were performed in a greenhouse facility at the Illinois Natural History Survey maintained at 21 °C under a 12 L:12 D photoperiod. The experiment was conducted in white tubs (38.7 cm diameter, 20.32 cm depth) lined with white sand as a substrate and filled with ambient temperature, de-chlorinated tap water. One 30.5 cm piece of PVC pipe was placed in the tub as a daytime refuge for the crayfish. *Cambarus diogenes* is a nocturnally active species and remain in burrows until nighttime (Pintor and Soluk, unpublished data).

Crayfish and dragonflies were starved for 12 h prior to the start of the experiment. Both the crayfish and the dragonfly larvae were measured (carapace and chelae length and head width, respectively) and were randomly assigned to an experimental arena. Both were allowed to acclimate for 2 h in the tub, separated by a partition. After 2 h, the partition was removed and the experiment was run for 24 h. Following the 24 h period, the tubs were checked and the outcome recorded. A Kruskal–Wallis one-way analysis of variance was used to test for significant differences between treatment groups (SYSTAT Version 10). With the ranks and test statistic obtained from the Kruskall–Wallis ANOVA, non-parametric multiple comparisons were used to see which of the four categorical treatment groups differed from each other (Conover, 1999).

2.3. Field predation experiment

To determine the threat of predation within natural crayfish burrows, we manipulated the presence of crayfish in burrows and observed the response of *S. hineana* larval densities. The experiment was conducted at Mud Lake North Wildlife Refuge in Door County, WI. Initial density estimates of *C. diogenes* and *S. hineana* larvae were made through a combination of trapping and burrow pumping. Crayfish were trapped from

a burrow for two consecutive days. Following the second day of trapping, the burrows were pumped out with a manual bilge pump (see field sampling methods above) to remove any remaining crayfish and any S. hineana larvae. All S. hineana larvae and crayfish collected were measured (head width and total length for dragonflies, carapace and chelae length for crayfish). In all treatments, dragonfly larvae were returned to burrows. In predator treatments, crayfish were returned to the burrows.

Following the initial estimates, the treatments were applied and subsequent densities were recorded at weeks 2 and 4. Three treatments were assigned randomly to 18 burrows (6 replicates/treatment). Cages were used in the treatments to prevent crayfish from re-entering a burrow. Treatments were: (1) cage-closed, crayfish removed and then excluded, (2) cage-open, crayfish removed but not excluded, and (3) cageless reference. Caged-closed treatments restricted large juvenile and adult crayfish from entering the burrow while allowing S. hineana larvae to move freely in and out of the burrow.

Burrows were monitored during the 4-week experiment. Treatments without crayfish were examined for signs that indicated the presence of crayfish in the enclosure, i.e., a plugged burrow entrance or fresh chimney pellets. Burrows were also monitored to prevent tampering, clogging, or dislodgement of the mesh cage. We used a repeated-measure ANOVA to examine if the presence of crayfish had a negative effect on the density of S. hineana larvae within crayfish burrows. All statistical analyses were conducted using Systat 10.0® (SPSS, 2001).

3. Results

3.1. Monthly field sampling

Data from 1999 were not included in the analysis because of the absence of water during part of the sampling period might have altered sampling efficiency. Therefore, analysis of the monthly field sampling was conducted on only the 2002 data. During the summer of 2002 the channel dried as normal, but localized rainstorms rewetted the channel for short periods that coincided with sampling events. As predicted, sampling indicated that densities of S. hineana larvae within crayfish burrows were lower than within the channel while there was flowing water (Fig. 1). However, following the onset of drought conditions densities within burrows increased, as densities within the drying channel decreased. Furthermore, the change in density between the channel and burrows were significantly different, with densities in the burrows showing a positive change while a negative change was observed within the stream channel (ANOVA, $F_{1,14}$, $p = 0.037$; Fig. 2).

Comparisons of the abiotic environment showed that the approximate annual mean temperature inside the burrow (8.4 ± SE 0.1 °C) was lower than that in the channel, (9.6 ± SE 0.1 °C). Although the mean annual temperature was higher in the open channel, the lowest temperature reached inside the burrow was 1.31 °C, whereas the lowest temperature in the stream channel was −0.2 °C. Alternatively, during the summer the burrow temperatures were lower than within the channel (May–mid-July). The temperature range inside
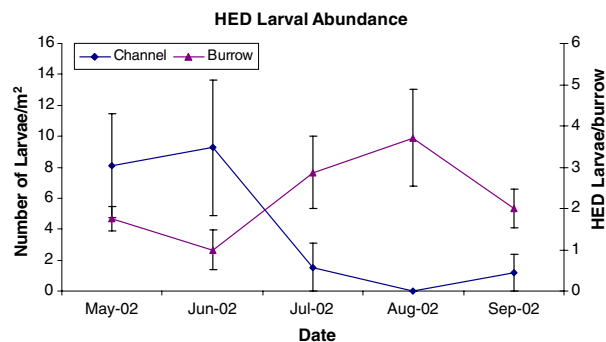

Fig. 1 – Mean S. hineana densities (±SE) in burrows and in the open channel of a small streamlet in the Mud Lake North Wildlife Area (Door County, WI, USA) from May through September 2002. Burrow density was calculated using mean number of larvae per burrow and mean number of burrows per m² stream channel. Densities of S. hineana larvae were lower within crayfish burrows while the stream contained flowing water. However, once stream drying occurred in July, burrow densities increased, while densities decreased within the stream channel.
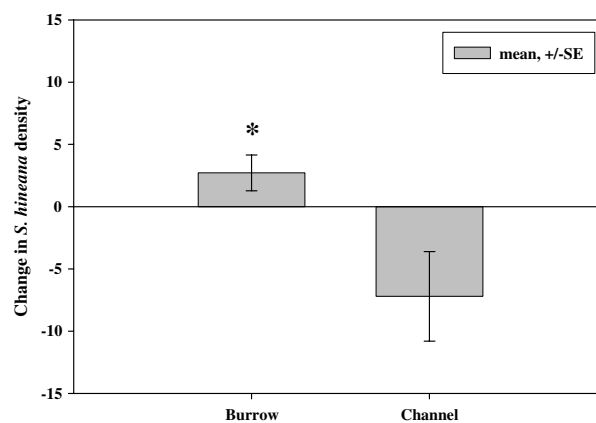

Fig. 2 – Change in S. hineana density following drought, open channel verses crayfish burrows. Results of an ANOVA showed a significant difference in the change in S. hineana density between habitats. Densities within the burrow increased following stream drying, while those in the open channel decreased (ANOVA, $F_{1,14}$, $p = 0.037$).

the burrow was also smaller in comparison to the stream channel (burrow range 30.5–1.3 °C; channel range 38.1 to −0.2 °C).

3.2. Laboratory predation experiment

Results showed that Cambarus diogenes will readily consume S. hineana larvae. Three of the seven S. hineana larvae used in the trials were killed and consumed by C. diogenes. Although we were given the intentional take of 10 S. hineana larvae, we were convinced that they were in fact, not distasteful to C. diogenes after the third larvae was consumed. Therefore, we continued the trials using S. williamsoni to further understand the size relationship between Somatochlora larvae and C. diogenes.
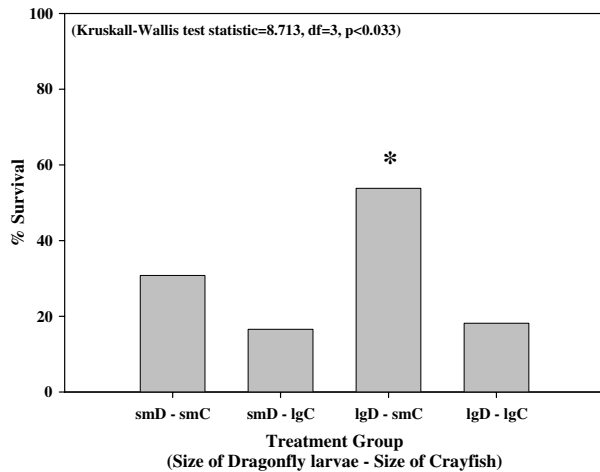
Fig. 3 – Outcome of laboratory predation trials with *S. hineana* and *S. williamsoni*. Significantly more larvae survived in trials between 3rd and 4th year dragonfly larvae and juvenile crayfish in comparison to all other treatment groups. Results suggest that larvae above a 3.5 mm headwidth may have a size refuge from juvenile crayfish under 20 mm carapace length.

In total, 55 trials were conducted using *S. williamsoni* of all size classes, and 7 trials with *S. hineana* ($n = 62$). Of the 62 trials, *Somatochlora* larvae were killed in 42 trials; 67.7% of larvae tested were killed. Kruskal–Wallis one-way ANOVA indicated a significant difference between treatment groups (test statistic = 8.713, df = 3, $p < 0.033$) (Fig. 3, Table 1). Multiple comparisons indicated significant differences between the juvenile crayfish vs. 3rd and 4th year larvae and all three other treatment groups (Fig. 3, Table 1). In general, small, juvenile crayfish seem unable to kill large *S. hineana* and *S. williamsoni* larvae. *Somatochlora* larvae survived best in interactions in which the larva had at least a 3.5 mm headwidth and the crayfish was below a 16 mm carapace length. This indicates that *Somatochlora* larvae are vulnerable to all but the smallest size class of crayfish, typically those hatched in the spring of any given year.

3.3. Field predation experiment

Repeated-measures ANOVA indicated that there was no treatment effect of crayfish on *S. hineana* larval densities in burrows ($F_{2, 15} = 0.055$; $p = 0.947$; power = 0.87 and 0.47 for an
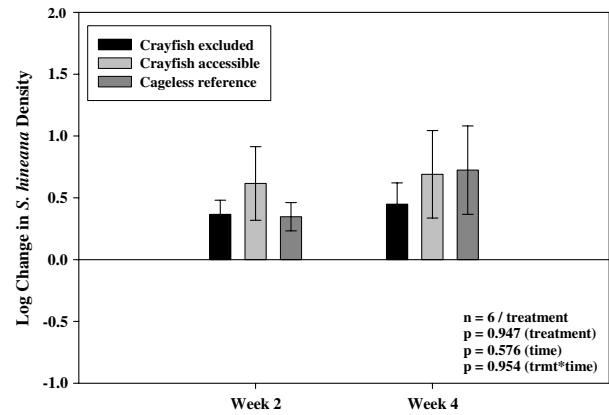

Fig. 4 – Changes in mean number (±SE) of *S. hineana* larvae in burrows with varying degrees of access by crayfish over a 4-week period. Changes are expressed as deviation from the initial density at two different time intervals. Repeated-measures ANOVA showed no significant overall treatment effect, ($F_{2, 15} = 0.055$; $p = 0.947$, power = 0.87 and 0.47 for an 80% and 50% change in density at $\alpha = 0.05$, respectively). Additionally, there was no significant effect of time ($F_{1, 15} = 0.326$, $p = 0.576$) or time * treatment interaction ($F_{2, 15} = 0.048$, $p = 0.954$).

80% and 50% change in density at $\alpha = 0.05$, respectively; Fig. 4). Additionally, there was no significant effect of time ($F_{1, 15} = 0.326$, $p = 0.576$) or time * treatment interaction ($F_{2, 15} = 0.048$, $p = 0.954$).

Periodic videotaping of the burrow entrances indicated that the closed-cage structures were effective in keeping out crayfish, while allowing *S. hineana* larvae to move freely in and out of the burrows. Furthermore, daily observations of burrow entrances did not reveal any signs of crayfish present in closed-caged treatments, i.e., no plugged entrances or chimneys.

4. Discussion

Although, *Somatochlora hineana* larvae are capable of surviving without water longer than many other odonates, drying still poses a significant threat (Soluk et al., 1998, 2000). Therefore, without refuges containing free water, population densities of *S. hineana* larvae are likely to significantly decline during drought conditions. In our study crayfish burrows were the only part of the habitat that consistently contained free water

Table 1 – Kruskal–Wallis one-way ANOVA			
Multiple comparisons			
	CP0–HW0	CP0–HW4	CP20–HW0
CP0–HW0	–		
CP0–HW4	10.04 > 6.42[*]	–	
CP20–HW0	4.03 < 9.34	11.99 > 8.20[*]	–
CP20–HW4	1.50 < 9.56	11.53 > 8.45[*]	0.46 < 9.74
Test statistic = 8.713. $p = 0.033$ with df = 3.			

throughout the summer and it is clear that they are used extensively as a drought refuge by *S. hineana* larvae. Crayfish burrows appear to represent more than just a temporary refuge from drought conditions for *S. hineana*. The thermal environment within the crayfish burrows was more stable and water inside the burrows never froze during the winter. Crayfish burrows thus appear to represent both a refuge from drought and a refuge from extreme winter conditions for *S. hineana* larvae.

Although crayfish burrows have advantages in terms of stability of hydrological and thermal environments, there are a number of reasons for not occupying burrows year-round. When the open channel is not frozen or dry, burrows presumably would not be the favored habitat due to the lower abundance of prey in comparison to the open channel (Pintor and Soluk, unpublished data). Our results matched this predication indicating that larval abundance in burrows was lower than in the open channel when the stream contained flowing water. However, once stream drying occurred densities in the channel dropped and subsequently increased in the burrows. This concentration of larvae in crayfish burrows in the dry period is similar to that observed for fish in alligator wallows during periods of drought.

Another potential negative consequence of *S. hineana* larvae moving into burrows may be that it increases the risk from cannibalism. Because this species has a four-year larval life cycle, the overlapping generations can include a broad range of sizes that typically is associated with high rates of cannibalism in odonates (Morin, 1984; Robinson and Wellbourn, 1987; Van Buskirk, 1989). Although densities in burrows increased, analysis of the size distribution of larvae in the crayfish burrows indicate that multiple size classes coexisted within any individual burrow in every month (Pintor, unpublished data). Further evaluation is needed to understand the contribution of cannibalism to survivorship of *S. hineana*.

Although prediction by conspecifics may not strongly regulate densities of *S. hineana*, larvae must still contend with crayfish predators. Results of the laboratory experiment confirm that crayfish do prey on *S. hineana* larvae. Although results did indicate that there is some size refuge of larger *Somatochlora* larvae from juvenile crayfish, in total, more than 65% of the larvae of all sizes were killed by most sizes of crayfish. Therefore, is the risk of being eaten by a crayfish larger than the risk of desiccation if the stream dries? A study looking at the drought resistance of a congener, *Somatochlora semicircularis*, found that larvae could survive in a desiccation chamber for on average 311 h (Willey and Eiler, 1972). Therefore, one would not expect larvae in a dry channel bed to withstand drought conditions for longer than approximately 13 days. Drought conditions typically last at least one to two months within *S. hineana* larval habitat and are then followed by winter, during which the streambed is frozen. Therefore, if the stream dries out there is little to no chance of survival.

Although crayfish can and will eat *Somatochlora* larvae if they enter into a burrow, results of the field predation experiment suggest that there is a better chance of survival than if they remain in a dry channel for more than 13 days. Crayfish removal from burrows did not have a significant positive effect on *S. hineana* densities suggesting that there is not a strong risk of predation within burrows. The presence of some *S. hineana* in the burrows while the stream contained flowing water in the spring may also suggest that predation by crayfish may not be as great a threat for larvae in burrows as might be assumed. If burrows were extremely dangerous places, then we would have expected all *S. hinenana* larvae to leave the burrows whenever the channel contained flowing water. Instead, we unexpectedly found that larvae used the burrows at least to some extent, throughout the entire sampling period. There is a problem, however, with using this observation to suggest that burrows are not risky places, in that *C. diogenes* is also abundant in the channel where they actively forage away from their burrows. Therefore, the threat of predation by crayfish might be as high in the channel as in the burrows.

Although it is typical to view predator–prey relationships as winner-loser situations in this case it is clear that the non-trophic interaction with crayfish plays an important part in the ecology of *S. hineana* larvae. Crayfish are predators of *S. hineana* larvae, however, they also function as ecosystem engineers by modifying the habitat and physically creating refuge space that can be used by other organisms. Although *S. hineana* may face the threat of predation when entering into a crayfish burrow, the alternative is death from desiccation in a dry streambed or freezing during the winter. The 4–5-year larval life cycle of *S. hineana* essentially requires that the larvae have a stable microhabitat to take refuge in through the annual seasonal drought.

Their ability to exploit crayfish burrows may also explain why *S. hineana* larvae are typically the predominant odonate species present in most habitats where they are found. For example, surveys for exuvia within the larval habitat in Wisconsin found that more than 95% of the exuviae collected were *S. hineana* (Foster and Soluk, 2004). In contrast, surveys in an adjacent permanent stream found that only 1.2% (10 out of 863) of the exuvia collected in 1999 and 2.9% (15 out of 521) collected in 2000 were *S. hineana* (Foster, 2001) while the others were a wide array of taxa (Foster, 2001). Given that these habitats were less than 50 m apart it is clear that while eggs of many other dragonfly species may be laid in *S. hineana* habitat these species are unable to complete their life cycles in these areas.

This research strongly highlights the importance of basic behavioral and ecological knowledge in the conservation of critically threatened and endangered species. Without this research we would not have known of the positive, indirect effects of crayfish. Therefore, it might have seemed appropriate to reduce crayfish abundance to enhance *S. hineana* abundance. Obviously such a recommendation would have detrimental effects on this endangered species because we would have inadvertently reduced critical refuge space. In conclusion, efforts to enhance or conserve populations of an endangered species must evaluate both the trophic and non-trophic interactions between predator and prey. Understanding the subtleties of both direct and indirect interactions may be fundamental both for understanding the basic ecological processes governing community structure, and for making sound decisions about the conservation of individual species within threatened, natural ecosystems.

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