

Teresa Chen  
Hellenthal

Importance of behavior and visual stimuli on species preference in  
interodonate predation

**Abstract**

Intraguild predation and cannibalistic activity often regulate odonate population. These behaviors are often affected by both mechanical and visual stimuli. Most often, activity of both predator and prey are important in determining species preference. Larval species of *Cordulia shurttleffi*, *Libellula* sp, and *Leucorrhinia* sp were used. Both *C.Shurttleffi* and *Libellula* are sit and wait foragers while *Leucorrhinia* is an active forager. Large larvae were paired with small of both the same species and of a different species to examine any species preference. Results showed that predation seemed to be higher on *Leucorrhinia* paired with *Cordulia*. Other pairwise responses showed no significant differences. This can be explained by a greater reliance on mechanical and behavioral cues of *C.Shurttleffi*. Active foraging prey increases encounter rates with predators, while sit and wait foragers often hide among the debris. Species preference seemed to be less dependent on visual cues and thus it was concluded that species recognition did not take precedence among larvae in order to avoid predation of the same species.

**Introduction**

Odonate predation on other odonates is a common feature in natural habitats. Intraguild predation and cannibalism can often affect communities of aquatic dragonfly larvae (Odonata: Anisoptera). These activities have been shown to regulate population densities and bring numbers below the carrying capacity of the environment by suppressing them before overexploitation and mass starvation occur (Johannson, 1992).

Dragonfly larvae are commonly the most dominant and most abundant invertebrate predators in the littoral zone of lentic habitats, reaching densities of more than 1000 individuals per meter squared (Johannson, 1992). Differences in oviposition time, asynchronous hatching, and development rates produces a wide range of instars within the immature life cycle, and thus larval populations are commonly age and size-structured (Johannson, 1992; Wissinger, 1988).

Cannibalism involves the process of eating individuals of the same species, whereas intraguild predation addresses odonate predation on other odonates. Because the intensity of cannibalism often increases as alternative food decreases, this type of activity has been suggested as a powerful strategy for predators to overcome periods of low prey density, which may lead to stable or cyclic populations (Johannson, 1992). Larvae similar in size are potential competitors, whereas larvae disparate in size can interact as predators and prey (Wissinger, 1988). It has been shown that cannibalism is uncommon if larvae are of the same instar, frequent if larvae differ by one instar, and certain if a 2-instar size difference is present (Hopper and Crowley, 1996).

Studies have shown that odonate larvae vulnerability to intraguild predation varies between species (Johannson, 1992). These differences can be attributed to habitat use, morphology, alternative prey, and body size, but may also be the result of variances in behavior (Johannson, 1992). Therefore, different foraging activities may significantly influence predation. In contrast, escape abilities may also directly affect preference for prey and vulnerability to capture.

It has been proposed that in response to vertebrate predators, odonate larvae have evolved two main lifestyles (Johannson, 1992). In the presence of predatory vertebrates, low activity and low energetic rates should be most beneficial, thus suggesting a “slow” pattern of behavior. However, a “fast” lifestyle with high activity and rapid energetic rates may be favored in the absence of vertebrate predators. Therefore, differences in habitats establish behavioral traits that may affect rates of predation.

Foragers have been classified in two main groups: active foragers and “sit and wait” foragers (Resetarits, 1998; Johannson 1993). Larvae of different species rely on different stimuli, such as vision and movement (Johannson, 1993), to detect prey. These behaviors are linked to both the environment and preferences for hunting during the daytime and during nighttime hours. Furthermore, different species often exemplify variances in strike speed and

reactive distance as well (Johannson, 1993; Johannson, 1992). In conjunction with these predatory behaviors, odonate larvae as prey also show differences in escape abilities, which are most often habitat related (Johannson, 1993). All factors considered, these behaviors exhibit variances in both encounter rates and capture efficiency among different species of anisopteran larvae.

However, it may also be possible that odonate larvae are able to differentiate those of the same species. This could especially be true of the dragonfly naiads that rely heavily on visual cues for prey capture. This study used dragonfly larvae of 3 different species: *Cordulia shurttleffi*, *Leucorrhinia*, and *Libellula*. *C. Shurttleffi* larvae are distinctly dissimilar in appearance compared to both *Leucorrhinia* and *Libellula*, however, *Leucorrhinia* and *Libellula* are fairly similar in appearance. Additionally, both *Leucorrhinia* and *Libellula* are from the same family classification (Libellulidae). Therefore, this study examines the importance of appearance in species recognition to avoid predation. However, it is possible that differences in behavioral traits and environmental adaptations may outweigh visual cues in determining cannibalistic behaviors.

### **Natural habitat description**

Larvae of the dragonfly *Leucorrhinia* were most common in Tuesday Lake. A small proportion of Aeshnids and zygopterans were noted, however *Leucorrhinia* dominated the odonate population in this region. Tuesday Lake is a deep lake surrounded by mixed forest and a large sphagnum mat. Although the lake originally supported a dense population of minnows, bass from Peter Lake were moved to Tuesday and minnows from Tuesday were transferred to Peter Lake in 1985. The dominant zooplankton includes *Bosmina*, *Eucyclops*, and *Keratella*.

Ed's Bog supports mainly populations of *Cordulia* and *Libellula*. The bog is relatively small in comparison to other bogs found on the University of Notre Dame Environmental Research Center property (UNDERC). A dense growth of trees surrounds the water's edge. Although tadpoles inhabit Ed's Bog, the bog is fishless and does not support any other aquatic vertebrate species. The dominant zooplankton includes *Alona*, *Ceriodaphnia*, *Daphnia*, *Diaptomus*, *Keratella*, *Chaoborus*, and *Cyclops*.

Dragonfly larvae of *Cordulia* and *Libellula* inhabit Forest Service Bog. The surface is overgrown with sphagnum and is surrounded by a dense forest; however, it does extend as close to the water's edge in comparison to Ed's Bog. Additionally, Forest Service Bog does not support any fish life. The dominant zooplankton includes *Daphnia* and *Keratella*.

### **Materials and Methods**

Using dip nets, dragonfly larvae of genus *Libellula*, *Leucorrhinia*, and *Cordulia* were collected from Tuesday Lake, Forest Service Bog, and Ed's Bog. Larvae were most commonly located under bog mats. Experiments and aquariums were carried out and maintained in the lab at the University of Notre Dame Environmental Research Center in Land O'Lakes, WI. Larvae were maintained in the lab in glass aquaria (51cm x 25cm x 32cm) filled approximately  $\frac{3}{4}$  full with tap water. Mesh netting was placed in aquariums to provide a substrate, thus reducing encounters and any cohort cannibalism as a result of thigmotaxis. Larvae were separated into tanks based on genus and relative size. Aquariums were maintained at approximately 28° C. Larvae were fed zooplankton collected from Hummingbird Lake. All aquariums were equipped with aerators to provide proper oxygen.

The purpose of this study was to determine if species recognition affected cannibalistic behaviors and intraguild predation among Odonata Anisoptera larvae. Larvae were paired using

3 different combinations. Both head widths and body lengths were measured prior to conducting experiments. Head width is the most reliable and integrative measure of overall size in dragonfly larvae (Schutte, 1999). No records of instar size were found and thus instars were based on a mean growth ratio of 1.27mm per molt for hemimetabolous insects (Schutte, 1997). It has been shown that cannibalism is certain (100%) if a two-instar size difference is present (Hopper et al., 1996). Therefore, large larvae used were at least twice the size of the smaller.

Large larvae of *Cordulia* were paired with both *Libellula* and *Leucorrhinia*. In order to test sibling recognition, 1 large larva was placed with 3 smaller of the same genus and 3 smaller of a different genus. To ensure cannibalistic behaviors, large larvae received no food at least 48h before being assigned to treatments.

Based on external characteristics, it can be seen that *Libellula* and *Leucorrhinia* (Family Libellulidae) are very similar in appearance. Therefore, large *Libellula* were placed with 3 small *Libellula* and 3 small *Leucorrhinia* to test if the results would vary because of their similarity in appearance. Experiments were set up in small plastic aquaria (28cm x 16cm x 10 cm) containing rocks as a substrate. Compartments were filled halfway with tap water. All compartments were equipped with aerators to provide proper oxygen and longer survival times. Large windows in the lab provided natural light conditions.

Larvae were checked once daily. All instances of cannibalism and intraguild predation have been shown to occur within the first 4d of observation (Hopper et al., 1996). Pairs were classified into two categories: those that experienced cannibalism and intraguild predation within 4d and those in which larvae survived the 4d period. Pairs were excluded in which the large larvae perished with no signs of predation on larvae. Pairs in which no sign of predatory behavior was exhibited on larvae within the first 4d were also excluded. Experiments were carried out until all larvae were eaten.

## Results

Size and growth ratios within replicates are represented by head width and body length and are shown in Table 1. All measurements were recorded in cm and measurements were taken for both large and small larvae. Similarities in size and instar number among small larvae show that predation between small larvae was reduced. The differences between measurements for large and small larvae guarantee increased cannibalistic activity. Analysis of fecal composition revealed larval remnants, thus confirming intraguild predation.

### 100% consumption time per species

Total time required for all 3 larvae of each species to be consumed was examined. The effects of species preference and recognition within replicates showed no significant difference when studied according to time needed for all 3 of each species to be consumed.

Large *CorduliaShurtleffi* exposed to small *C. shurtleffi* and *Libellula sp* showed a similarity in eating preference and therefore no change was apparent (ANOVA, N=7, P=0.16). On average, when placed with small *Leucorrhinia sp.*, large *C. shurtleffi* consumed all 3 within  $7.29 \pm 1.34$  days and consumed all *C. shurtleffi* in  $10.14 \pm 1.81$  days, showing no significant difference in total consumption time (ANOVA, N=7, P=0.228). A correlation in time was also seen in trials containing large *Libellula sp* and small *Leucorrhinia sp* and *Libellula sp* (ANOVA, N=8, P=0.196).

### Median consumption time per species

It is possible that the first larva of a possibly preferred species may have been consumed by chance. Though the third may have been preferred, it is possible that it became more difficult to locate (decreased abundance) as a result of decreased encounter rate, and thus not consumed

as quickly. Therefore, comparisons among time required to consume 2 of 3 larvae per species were made.

Large *Libellula sp* paired with small *Libellula sp* and *Leucorrhinia sp* showed no preference for either species (ANOVA, N=8, P=0.59). Although not significant, a slight difference was seen in eating preference among large *C. shurttleffi* placed with small *C. shurttleffi* and *Libellula sp* (ANOVA, N=9, P=0.063). Thus it is possible that some large *C. shurttleffi* larvae were indeed exhibiting preferential behavior by consuming the *Libellula sp* more quickly.

A comparison among median consumptions for *C. shurttleffi* and *Leucorrhinia sp* placed with large *C. shurttleffi* showed a significant difference among values (ANOVA, N=7, P=0.017). As a result, predation of *Leucorrhinia sp* was higher within trials (Figure 1).

#### **Average consumption time within replicates**

An examination of average time required to consume each larva was also conducted to interpret cannibalistic behaviors. No significant differences were seen for either trials using large *C. shurttleffi* with small *C. shurttleffi* and *Libellula sp* (ANOVA, N=9, P=0.13) or trials using large *Libellula sp* with small *Leucorrhinia sp* and *Libellula sp* (ANOVA, N=8, P=0.18). However, a preference for *Leucorrhinia sp.* over *C. Shurttleffi* was noted when large *C. shurttleffi* were offered a choice (ANOVA, N=7, P=0.032) (Figure 2).

#### **Conclusion**

Regarding cannibalism and intraguild predation, differences in preference for one odonate species over another may depend on either the significance of predator and prey behavior or as the significance of visual cues for the predator. Visual and mechanical cues have

been shown to be important for prey detection in odonate larvae (Johannson, 1992). Visual information is received by facet eyes and mechanoreceptors on antennae and legs receive mechanical stimuli (Johannson, 1992).

If in fact, larvae rely heavily on visual cues during foraging activity, identification and recognition of similar species may motivate larvae to select prey of a different species to avoid predation. Thus, it may come of greater ease for *Cordulia* to recognize same species cohorts when paired with *Libellula* or *Leucorrhinia*, as a result of greater differences in appearance. *Leucorrhinia* and *Libellula*, however, exhibit more similarities in external characteristics and thus it may be more difficult for the large larvae to distinguish between the two. Because *Cordulia* have been studied to move most at night, vision seems of subordinate importance (Johannson, 1992). Richard (1960) found that prey capture was only slightly affected when eyes were made inactive, compared to inactivation of mechanoreceptors (Johannson, 1992). Thus, visual cues come secondary in predatory behavior of *Cordulia* and a heavier reliance is most likely placed on stimuli from the prey itself, such as movement and exposure.

*Cordulia* have a sit and wait behavior in capturing prey and do not often leave their well-hidden positions among benthic debris (Johannson, 1992). In the laboratory trials, *Cordulia* were most commonly observed as being located near the rocky habitat provided and were rarely seen dwelling in more open areas of the plastic aquaria. Encounter rates to predators should increase with increasing prey activity (Johannson, 1993). Thus, large *Cordulia* larvae may have seen an increased exposure to the active forager, *Leucorrhinia*, in comparison to the sit and wait foraging behavior of *Libellula*. Johannson (1993) found that *Aeshna juncea* had lowest predation on larvae with sit and wait foraging mode and highest predation on *Leucorrhinia dubia* (an active forager).



Trials in which large *Libellula* were paired with *Leucorrhinia* should also exhibit similar results to those of trials pairing *Cordulia* and *Leucorrhinia* because *Libellula* are also sit and wait foragers. However, no significant difference was seen upon analysis. This may be due to increased prey activity as a result of conspecific interference (Johannson, 1992). Therefore, perhaps the behavior and activity of one group of larvae influenced the other. Furthermore, in the presence of predators, a reduction in foraging activity could reduce predation risk for prey (Johannson 1992). It is possible that the actively foraging *Leucorrhinia* may have reduced activity in the presence of large *Libellula* odonates, thus balancing activity to the level of the small *Libellula* larvae. Additionally, although capture rate on sedentary prey is often low because of decreased encounters with predators, capture success is often higher with slow-moving prey in comparison to fast-moving prey (Johannson, 1992). Particular larvae have also been shown to have poor escape capabilities. Larvae may be detected and captured by predators even though they do not move, indicating an absence of active predator avoidance (Johannson, 1993). Increased movement from sit and wait larvae could be explained by the need to find suitable shelter (Johannson, 1992). If this were to occur, behavior of the two different larvae would be comparable. Small plastic aquaria and a simple substrate of small rocks may have provided rather unnatural laboratory conditions, which could have increased exposure to normally hidden sit and wait foragers.

In contrast, *Libellula* and *Cordulia* are both sit and wait foragers, and therefore would have similar exposure rates to large *Cordulia*. In this case, differences in preference would rely more strongly on predator activity or random movement of prey. Many sit and wait predators often require the stimulus of moving prey while actively hunting predators may utilize other modes for prey location and identification (Resatarits, 1998).

Analysis of 100% consumption time showed no significant differences in results, although both median and average consumption times both showed significant differences with paired treatments of *Cordulia* and *Leucorrhinia*. This may be due to satiation of the predator. After a given period of time, large larvae become satisfied and less motivated to attack prey (Johansson, 1992). Differences in sizes of large larvae between trials may also affect results because larger larvae require increased amounts of sustenance and will remain more active in predatory behavior until fulfilled. Additionally, as prey density increases, handling time takes up an increased proportion of total time and as a result, the predator may spend all of its time handling prey (Johansson, 1992). Therefore, as prey density increases, adverse effects would result in decreased time spent handling prey.

In order to run trials with the least amount of error, small larvae were not offered any food during treatments because of decreased predatory behavior in the presence of alternative prey (Hopper & Crowley, 1996; Wissinger, 1988). Decreased food availability has been shown to increase instar duration (Wissinger, 1988), however hunger of small larvae could affect activity, especially in active foragers. Improper nourishment for small larvae could also lead to decreased activity. On the other hand, if starvation posed as a threat to the small larvae, predator-prey interactions could arise between small larvae, especially if size differences between larvae existed.

During collection, *Libellula* and *Cordulia* were found to coexist in several habitats, however, neither was found with *Leucorrhinia*. Placing *Cordulia* and *Libellula* with *Leucorrhinia* under laboratory conditions may affect behavior because the two do not coexist under natural conditions. Active foragers are often not found in habitats with fish because of increased encounter rates and therefore fast growing larvae are associated with habitats without fish (Johansson, 1993). Different species of odonates differ considerably in sensitivity towards

fish predators due to morphological and behavioral characteristics (Arnqvist and Johannson, 1998). Of the collection sites, only Tuesday Lake contained small minnows, all other collections were made from bogs and fishless lakes. *Leucorrhinia* larvae were relatively abundant in Tuesday Lake and although this does not coincide with Johannson (1993), minnows were artificially relocated to Tuesday, which may explain the continued prevalence of *Leucorrhinia* in the lake. Additionally, presence of minnows may have affected odonate population; however, it could have also altered behavior, making the larvae less active foragers. Furthermore, *Leucorrhinia* may have altered the timing of activity, switching consumption of prey to the nighttime as a mechanism to withstand living with fish (Swisher, et. al, 1998), thus synchronizing their behavior to that of the large predatory *Cordulia*.

Additionally, it is possible that *Libellula* and *Cordulia* larvae may develop at an increased rate as a result of presence in fishless lakes, which may have altered size differences among larvae during the course of the experiment. Timing of development also varies among species, which could also vary sizes among small larvae. Not only could this cause a change to predator-prey relations among small larvae, but studies also show that aquatic insects generally select large sized prey until handling differences and increased probability of prey escape outweigh the returns gained from eating large prey (Johannson, 1993). These alterations could easily have made certain prey more or less preferred to the larger larvae.

In the presence of waterborne environmental cues of fish predators, *Leucorrhinia* have been found to exhibit defensive spine morphology (Arnqvist and Johannson, 1998). Benefits of exaggerated spine shape involve costs such as reduced growth, reduced fecundity, or delayed reproduction (Johannson and Samuelsson, 1994). Because of piercing and chewing mouthparts, defensive spines offer little defense against invertebrate predators. A critical body length of about 10-12mm must be obtained before spines become of benefit to odonate larvae (Johannson

and Arnqvist, 1998). In this size range, odonate larvae are less sensitive to invertebrate predation and move into the range where they are more exposed to fish predation (Johansson and Arnqvist, 1998). Many of the small larvae used in trials fall into this size range and although it may not present sufficient defense against the larger larvae, perhaps morphological changes may have affected behavior in the *Leucorrhinia* larvae. Additionally, while exaggerated spine shape may not have posed difficulty in consumption to the larger larvae, spines may have affected reaction norms of the large larvae to the *Leucorrhinia*.

Although trials were not run using large active foraging predators, future studies should be done to analyze inter-odonate behavior and recognition. As an active forager, *Leucorrhinia* may have relatively equivalent encounter rates to both species of larvae and consumption may then have greater reliance on escape capabilities and predator avoidance of the prey, rather than capture success and encounter rates of the predator. *Leucorrhinia* have been found to be more active during the day and night (Johansson, 1992). More prey was eaten at night, but higher capture efficiency under light conditions suggests more reliance on vision in *Leucorrhinia* (Johansson, 1992). Eyes are found to be more important in prey detection in the genus *Leucorrhinia* than in larvae of other bottom-living genera (Johansson, 1992). If *Leucorrhinia* are truly more dependent on visual cues as opposed to the movement and mechanical cues of larvae, then perhaps this genus of odonate larvae may be able to distinguish its own species.

Based on the results and analysis, it can be seen that preference of a particular species of anisopteran larvae was most dependent on behavioral components as opposed to visual. Decreased reliance on visual cues in prey detection results in decreased prey identification. Thus, in this case, it cannot be concluded that odonate larvae are capable of successful species recognition to avoid predation.

## Predator - Cordulia

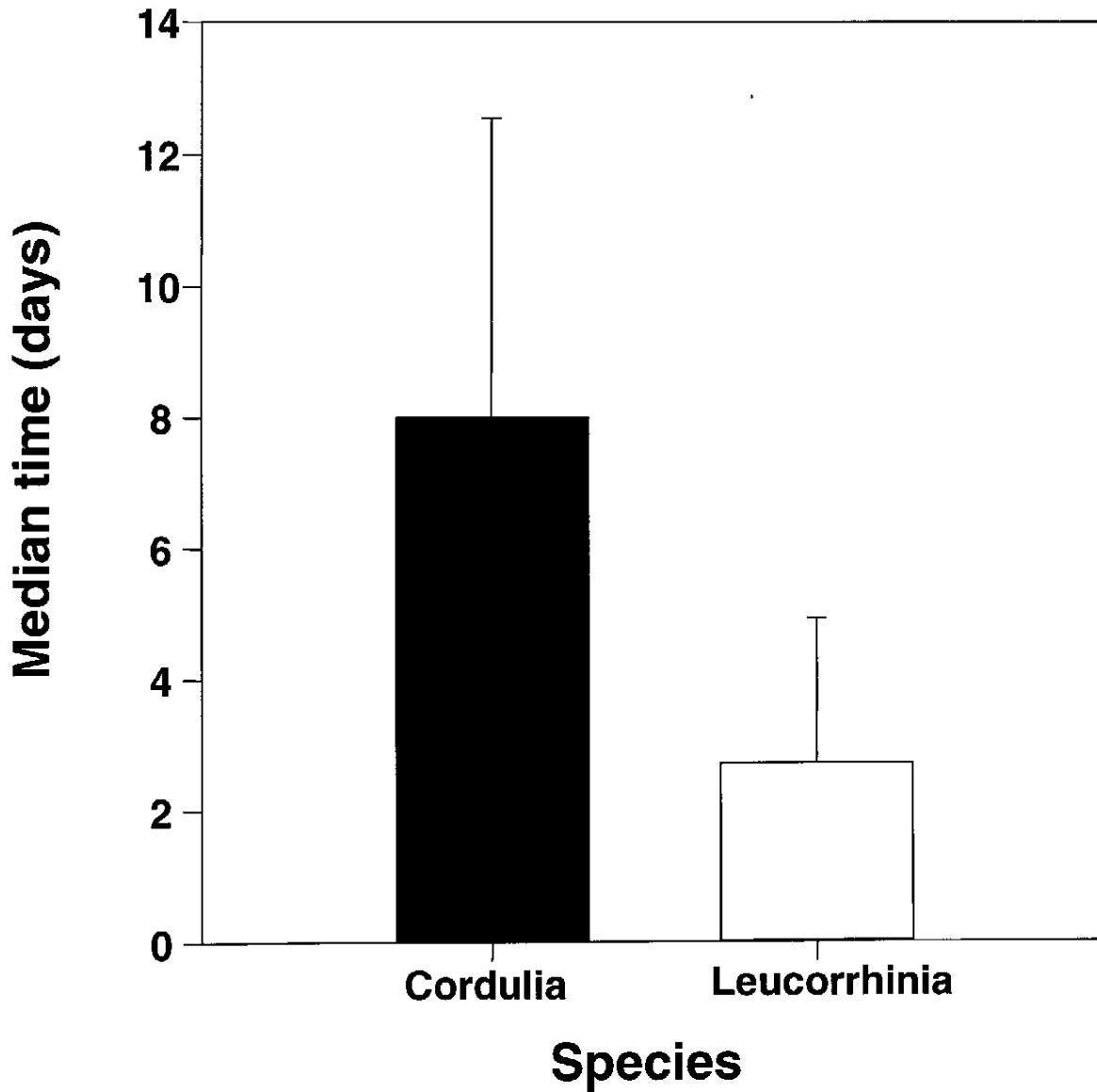


Figure 1- One-way analysis of variance, ANOVA. Analysis of median consumption time for large *C.shurtleffi* paired with small *C.shurtleffi* ( $8.000 \pm 4.546$ ) and *Leucorrhinia* sp. ( $2.714 \pm 0.837$ ). Median time represents the average number of days required for 2 of 3 larvae within each species to be consumed.

## Predator - Cordulia

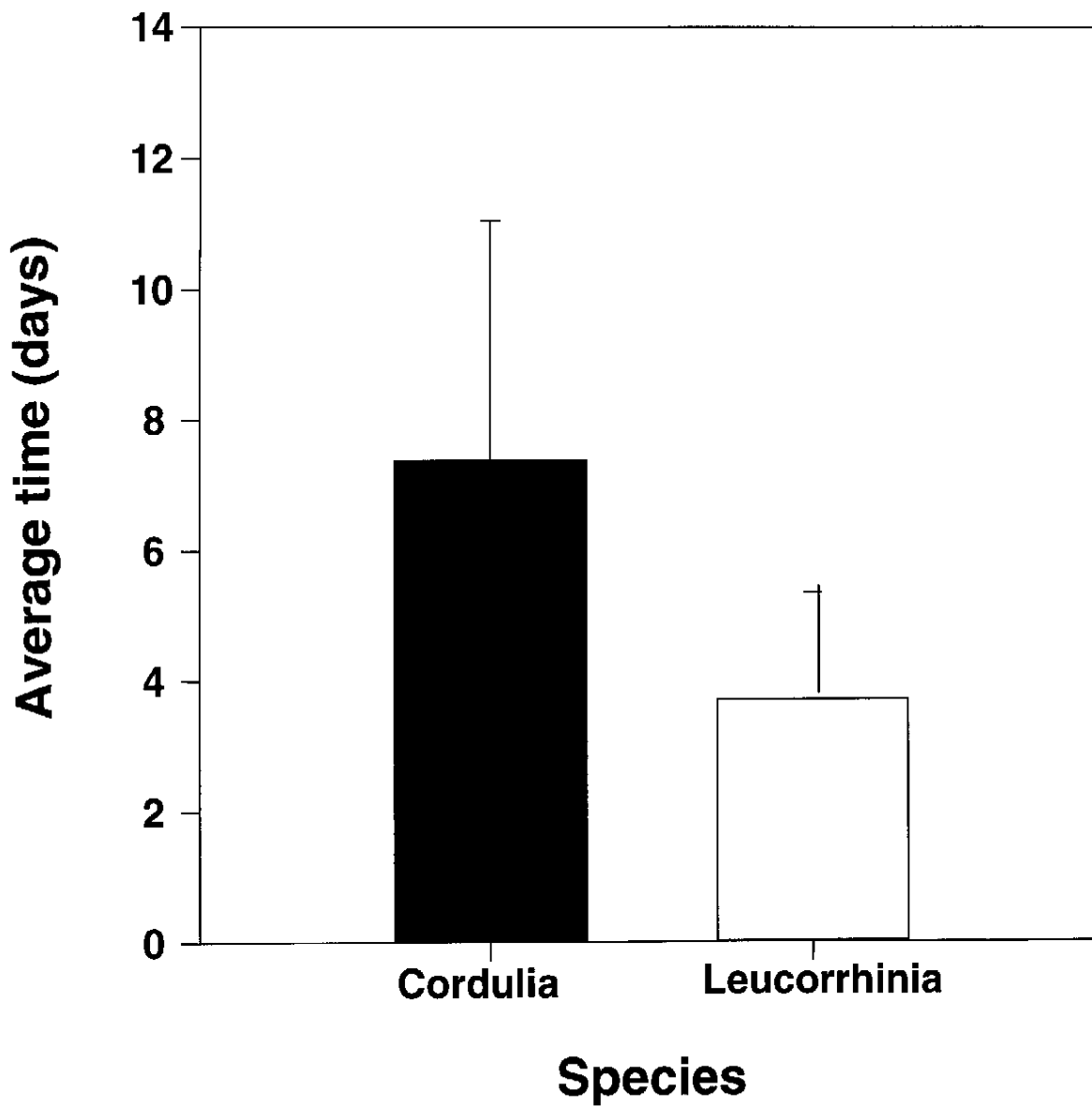


Figure 2- ANOVA, one-way analysis of variance. Analysis of average consumption time for large *C.shurtleffi* paired with small *C.shurtleffi* ( $7.381 \pm 3.656$ ) and *Leucorrhinia sp* ( $3.713 \pm 1.627$ ). Average time for each larvae (per species) within replicates to be consumed.

I	Body length	Head width	Growth ratio
Cordulia	2.1	0.6	
Cordulia	0.9	0.3	2
Leucorrhinia	0.9	0.3	2
2			
Cordulia	2.1	0.65	
Cordulia	0.8	0.2	3.25
Leucorrhinia	1	0.3	2.2
3			
Cordulia	1.6	0.5	
Cordulia	1	0.3	1.67
Leucorrhinia	0.8	0.3	1.67
4			
Cordulia	1.5	0.5	
Cordulia	1	0.3	1.67
Leucorrhinia	0.8	0.3	1.67
5			
Cordulia	1.6	0.5	
Cordulia	1	0.3	1.67
Leucorrhinia	0.8	0.3	1.67
6			
Cordulia	1.6	0.5	
Cordulia	1	0.3	1.67
Leucorrhinia	0.9	0.3	1.67
7			
Cordulia	1.4	0.5	
Cordulia	1	0.3	1.67
Leucorrhinia	0.9	0.3	1.67

Table 1 - Body lengths and head widths of large *C.shurttleffi* paired with small *Leucorrhinia* sp and *C.shurttleffi*. Growth ratios (head width comparison) are based on a mean growth of 1.27mm per instar for hemimetabolous insects.

1	Body length	Head width	Growth ratio
Cordulia	2.2	0.7	
Cordulia	0.9	0.4	1.75
Libellula	0.8	0.3	2.3
2			
Cordulia	2.2	0.6	
Cordulia	1	0.3	2
Libellula	1.1	0.3	2
3			
Cordulia	2.1	0.6	
Cordulia	1	0.3	2
Libellula	1.2	0.35	1.7
4			
Cordulia	1.8	0.6	
Cordulia	1	0.3	2
Libellula	1.1	0.3	2
5			
Cordulia	2	0.6	
Cordulia	0.9	0.3	2
Libellula	1	0.4	1.5
6			
Cordulia	2.2	0.7	
Cordulia	1.2	0.4	1.75
Libellula	1.2	0.4	1.75
7			
Cordulia	2.3	0.65	
Cordulia	1.2	0.3	2.2
Libellula	1.1	0.35	1.86
8			
Cordulia	2	0.6	
Cordulia	1	0.3	2
Libellula	1	0.3	2
9			
Cordulia	2	0.6	
Cordulia	0.9	0.3	2
Libellula	1.2	0.4	1.5

Table 2- Body lengths and head widths of large *C.shurttleffi* paired with small *Libellula* sp and *C.shurttleffi*. Growth ratios (based on head width comparison) are based on a mean growth of 1.27mm per instar for hemimetabolous insects.

	1	Body length	Head width	Growth ratio
Libellula	2	0.6		
Libellula	1	0.3		2
Leucorrhinia	1	0.3		2
2				
Libellula	1.5	0.5		
Libellula	0.8	0.3		1.67
Leucorrhinia	0.8	0.3		1.67
3				
Libellula	1.4	0.5		
Libellula	0.8	0.3		1.67
Leucorrhinia	0.8	0.3		1.67
4				
Libellula	1.5	0.5		
Libellula	1.1	0.3		1.67
Leucorrhinia	0.9	0.3		1.67
5				
Libellula	1.4	0.4		
Libellula	1.1	0.3		1.33
Leucorrhinia	0.9	0.3		1.33
6				
Libellula	1.7	0.5		
Libellula	1.1	0.3		1.67
Leucorrhinia	0.8	0.3		1.67
7				
Libellula	1.7	0.6		
Libellula	1.1	0.3		2
Leucorrhinia	1.2	0.4		1.5
8				
Libellula	1.5	0.5		
Libellula	1	0.3		1.67
Leucorrhinia	1.7	0.2		2.5
9				
Libellula	1.4	0.5		
Libellula	1.1	0.3		1.67
Leucorrhinia	0.9	0.3		1.67

Table 3- Body lengths and head widths of large Libellula sp paired with small Libellula sp and Leucorrhinia sp. Growth ratios (head width comparison) are based on a mean growth of 1.27mm per instar for hemimetabolous insects.



## Literature Cited

1. Johannson, F. 1992. Predator life style and prey mobility: a comparison of two predatory odonate larvae. *Arch. Hydrobiol.* **126**(2): 163-173.
2. Johannson, F. 1993. Diel feeding behavior in larvae of four odonate species. *Journal of Insect Behavior* **6**(2): 253-264.
3. Schutte, C. 1997. Life history of *Neurothemis tullia* (Drury) in a tropical rainfed ricefield (ANISOPTERA: Libellulidae). *Odonatologica* **28**(1): 1-11.
4. Schutte, C. 1999. Egg development and early instars in *Cordulegaster boltonii immaculifrons* selys- a field study (ANISOPTERA: Cordulegastridae). *Odonatologica* **26**(1): 83-87
5. Wissinger, S.A. 1988. Effects of food availability on larval development and inter-instar predation among larvae of *Libellula lydia* and *Libellula luctuosa* (Odonata: Anisoptera). *Canadian Journal of Zoology* **66**: 543-549.
6. Hopper, K.R., Crowley, P.H. 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. *Ecology* **77**(1): 191-200.
7. Swisher, B.J., Soluk, D.A., Wahl, D.H. 1998. Non-additive predation in littoral habitats: influences of habitat complexity. *OIKOS* **81**(1): 30-37.
8. Johannson, F. 1992. Effects of zooplankton availability and foraging mode on cannibalism in three dragonfly larvae. *Oecologia* **91**: 179-183.
9. Johannson, F. 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behavior and zooplankton availability. *OIKOS* **60**: 80-87.
10. Resetarits, W.J. 1998. Differential vulnerability of *Hyla chrysoscelis* eggs and hatchlings to larval insect predators. *Journal of Herpetology* **32**(3): 440-443.
11. Johannson, F., Samuelsson, L. 1994. Fish-induced variation in abdominal spine length of *Leucorrhinia dubia* (Odonata) larvae? *Oecologia* **100**: 74-79.
12. Arnqvist, G., Johannson, F. 1998. Ontogenetic reaction norms of predator-induced defensive morphology in dragonfly larvae. *Ecology* **79**(6): 1847-1858.

### 100% Consumption Time per Species

Group	N	Mean	Std Dev	SEM	P
Cordulia	9	6.667	2.693	0.898	0.159
Libellula	9	4.667	3.014	1.014	
Libellula	8	11.75	4.062	1.436	0.196
Leucorrhinia	8	8.75	4.743	1.667	
Cordulia	7	10.143	4.776	1.805	0.228
Libellula	7	7.286	3.546	1.34	

### Median Consumption Time per Species

Group	N	Mean	Std Dev	SEM	P
Cordulia	9	3.778	2.587	0.862	0.063
Libellula	9	1.889	1.167	0.389	
Libellula	8	7.375	5.975	2.112	0.591
Leucorrhinia	8	6	3.78	1.336	
Cordulia	7	8	4.546	1.718	<b>0.017</b>
Leucorrhinia	7	2.714	2.215	0.837	

### Average Consumption Time within Replicates

Group	N	Mean	Std Dev	SEM	P
Cordulia	9	3.999	2.008	0.669	0.129
Libellula	9	2.703	1.37	0.457	
Libellula	8	7.625	3.556	1.257	0.179
Leucorrhinia	8	5.334	2.894	1.023	
Cordulia	7	7.381	3.656	1.382	<b>0.032</b>
Leucorrhinia	7	3.713	1.627	0.615	