

Effects of Light and Fish on Behavior of Three Odonate Genera

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Abstract

This experiment studied the predatory interactions between benthivorous fish (Lepomis macrchirus) and odonates of the genera Enallagma, Leucorrhinia, and Ladona. Their behavior was monitored in response to three experimental conditions: tap water, fish odor and predatory fish that were prevented from reaching the larvae. Twelve hourly observations were made under both light (8 observations) and dark (4 observations) conditions for each trial.

While there were no observed effects of the treatments on the frequency and distance of movement of the larvae, behavioral differences were observed between the genera. The genera also increased the frequency of their movements in dark conditions. Furthermore, members of the genus Enallagma were observed to remain in nonconspicuous positions more often under light conditions than when under dark conditions. These factors suggest behavioral adaptation to visual predators.

Behavior in Odonata

Introduction

It is well known that the benthic and pelagic communities of a lake are linked by biological and chemical pathways (Wetzel 1979; Golterman 1990). The trophic interactions connecting these two communities have not been as well defined in the literature, but predation by fish on invertebrates may represent a substantial benthic-pelagic link (Morin 1984, Hodgson and Kitchell 1987, Henrikson 1988, McPeck 1990, Johnson 1991, Macchiusi and Baker 1991 and 1992, Wiseman et al. 1993). In particular, Odonates often provide a substantial portion of the diet of these predatory fish (Hodgson and Kitchell 1987, Martin et al. 1991).

Predation by fish may have a large impact on the odonate assemblage of a basin (Morin 1984, Pierce 1988). For example, Martin et al. (1991) concluded that benthivorous fish in Bays Mountain Lake, TN induced semivoltine development in the Epitheca larvae found in that basin. This occurred through the removal of larvae growing at a rate consistent with univoltinism, making the population appear semivoltine.

McPeck (1990) found that species of Enallagma, which dominated fishless lakes, were highly susceptible to predation and incapable of co-existing with benthivorous fish. Nilsson (1981) concluded that the behavior of Leucorrhinia larvae played a role in their inability to co-exist with benthivorous fish (their increased vulnerability to predation). He found that Leucorrhinia hid less and moved further than other odonates studied, regardless of the presence or absence of fish. Henrikson (1988) found Leucorrhinia dubia only in lakes without fish. Experimentally, Leucorrhinia dubia was more susceptible to predation by benthivorous fish than species which were taken from lakes containing fish because they lacked antipredator behavior, which she defined as: 1) the feigning of death and then escape following an attack and 2) decreased activity during light conditions.

The extent to which odonates are susceptible to predation by benthivorous fish is dependent upon larval size and behavior (McPeck 1990). Smaller species tend to dominate in basins that contain fish, while larger species dominate in those basins that are fishless (Morin 1984, Dixon and Baker 1988). Johnson (1991) separated odonate larval behavior into two categories, "fast" and "slow" lifestyles. Odonates with a "fast" lifestyle actively search for food and move often during light conditions. Odonates with a "slow" lifestyle exhibit ambush foraging behavior and remain hidden in light conditions, making them less susceptible to predation. There are two mechanisms through which benthivorous fish can effect changes in the behavior (slow vs. fast lifestyle) of the odonate assemblage of a basin, one is the adaptation of individual behavior to the presence of fish, and the second is the removal of more active species by these predacious fish. (Johnson 1991, Macchiusi and Baker 1991 and 1992, Wiseman et al. 1993). The removal of the more active species, those with a fast lifestyle, from the odonate assemblage of a basin occurs because

Behavior in Odonata

fish are visual predators, attracted to odonates which are easily visible because of their movements (Henrikson 1988).

In this experiment I examined the behavioral changes of three odonate genera (Ladona, Leucorrhinia and Enallagma) The behavioral characters which I examined were frequency of movement, distance of movement and orientation to substrate, in response to the presence and odor of benthivorous fish. This was done in order to determine: 1) which genera would respond to the presence of predators, and 2) which environmental cues cause this response. I hypothesized that Ladona would show little response because this genera spends much of its time buried in the substrate, and that Leucorrhinia would also show little response because it has been previously shown to have difficulty coexisting with fish (Henrikson 1988). However, members of the genus Enallagma spend much of their time climbing, and in otherwise exposed areas. Therefore, I expected these larvae to respond to the experimental conditions to a greater degree than either Ladona or Leucorrhinia.

Materials and Methods

This experiment examined the effects of the presence of a fish predator on the behavior of members of the odonate genera Ladona, Leucorrhinia and Enallagma. The frequency and distance of movement of larvae along with their position in relation the substrate was examined. These variables were monitored in response to the following conditions: 1) tap water that had never contained fish, 2) water which had previously contained fish and which, therefore, presumably contained their odor and 3) the presence of predacious fish (Bluegill) which were prevented from reaching the larvae.

Experiments were conducted in ten gallon aquaria. A layer of sediment 0.5-1.5 cm deep was placed in the bottom of each aquarium. The sediment was collected from Central Long Lake at a depth of approximately 1 meter and had been previously picked and microwaved in order to remove or kill any organisms present. A grid constructed of metal brackets and fishing line was placed in each tank at a height of three inches from the bottom. The grid served two purposes: preventing the fish from reaching the larvae, and providing a coordinate system (each square measured 2.5 cm on a side) on which to chart the movement of the larvae. Five dowels, each 1.15 cm in diameter and 3.45 cm in length were placed in an approximately circular arrangement in the bottom of each tank to provide structure on which the larvae could climb. Lighting was maintained on a near natural 14:10 Light:Dark photoperiod. Hourly observations were made beginning at 1 PM and ending at 12 AM, with the last four observations made in the dark using a red light.

The larvae in this experiment were collected using dip nets (at depths ranging from approximately 0.5-2.5 meters) in Central Long Lake and from a marsh habitat, both on the property of the

Behavior in Odonata

University of Notre Dame's Environmental Research Center in Wisconsin. Neither habitat supported large populations of benthivorous fish at the time of the experiment, but Central Long Lake did prior to 1991. The fish used in this experiment were bluegills (Lepomis macrochirus) and were collected by angling from Bay Lake. They were held for at least one week prior to being used in an experiment in order to acclimate them to captivity. The fish were not fed for 48 hours before an experiment.

Each day at 12 PM the larvae were marked with a small dot of Whiteout on their wingpads before being placed in the tanks, in order to make them easier to see during observations. The number of individuals of each species to be used, treatments performed for each species and tank they were assigned to was determined randomly in order to prevent any bias that may have occurred due to position of the tanks, lighting or day of the year. Each larvae was used only once. The only exceptions were the tap water treatments, which were performed in the same tanks each day. Each hour, the position of each larvae within the grid was recorded, and a record was kept of the position of the larvae relative to the substrate, recorded as either buried, on top of the substrate, on the side of a dowel, on the top of a dowel or on the grid.

Due to time constraints and failed trials I was unable to complete an equal number of replicates for each species and treatment (Table 1). Statistical analysis was performed using the SYSTAT statistics program.

Results

Data obtained for the frequency and distance of movement of the larvae was analyzed by three-way ANOVA (Table 2). Differences in the frequencies of movement were observed between the Odonate genera, with increased activity evident under dark conditions (Figure 1). Data obtained for the distance of movement of the larvae indicated similar trends (Figure 2).

During trials, the vertical position of the larvae was recorded as either on the grid, on top of a dowel, on the side of a dowel, on top of the substrate, partially buried or buried. For analysis of the data these positions were grouped as either conspicuous (on the grid, on top of a dowel and on the side of a dowel) or inconspicuous (on top of the substrate, partially buried and buried) (Figure 3). These two groups were chosen because the first three positions indicate climbing behavior which would expose the larvae to the view of a predator, while the second three positions did not expose the larvae to the view of fish.

Behavior in Odonata

	<i>Enallagma</i>	<i>Ladona</i>	<i>Leucorrhinia</i>
Tap Water	7	6	7
Fish Odor	9	9	7
Fish	4	7	7

Table 1. The number of replicates completed for each species and experimental condition.

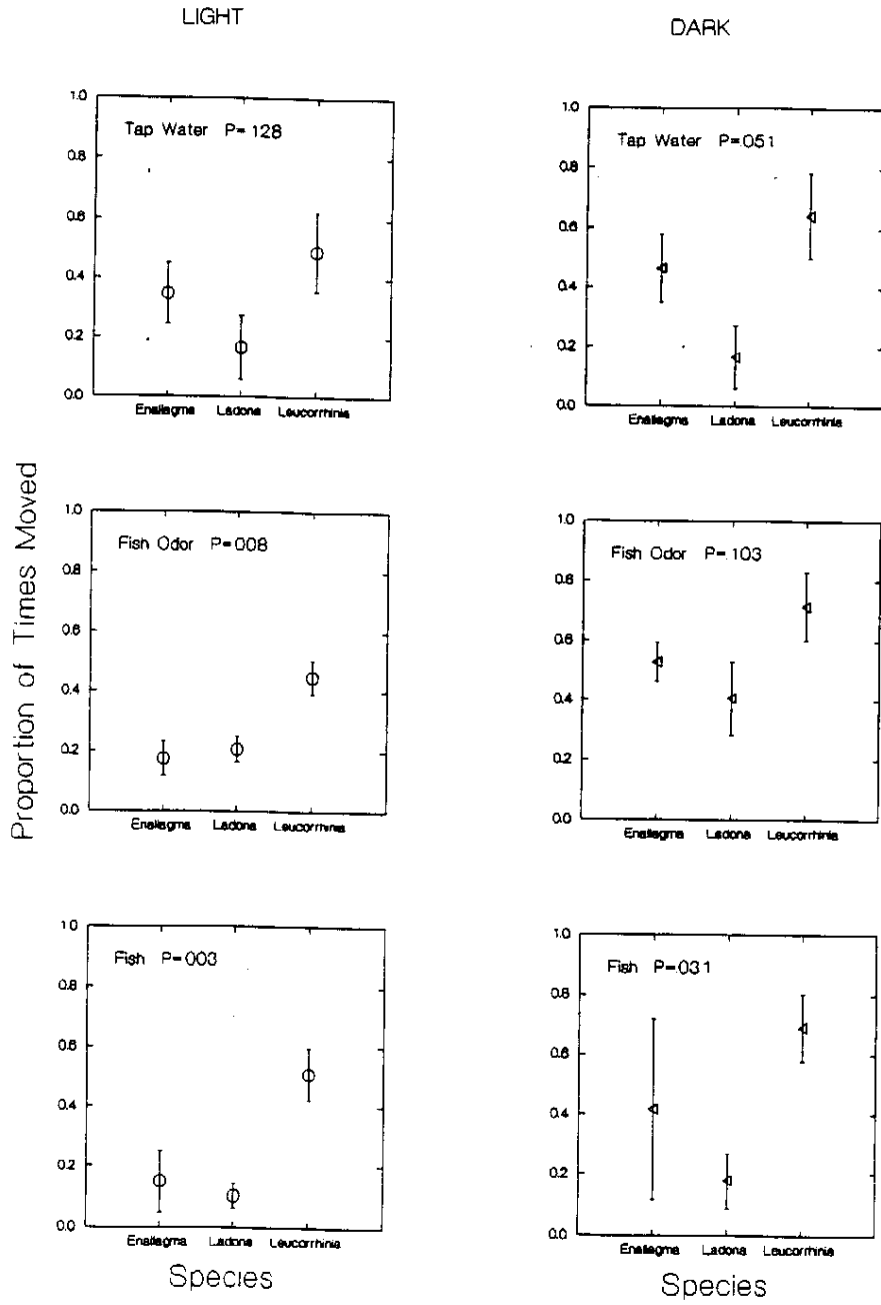
Behavior in Odonata

Variable	Category	Mean-Square	DF	F-Ratio	P
MOVE	SPP	17.484	2	35.456	<0.001
	TRTM	0.868	2	1.761	0.173
	LIGHT	9.724	1	19.719	<0.001
	SPP*TRTM	0.684	4	1.387	0.237
	SPP*LIGHT	0.584	2	1.185	0.306
	TRTM*LIGHT	1.107	2	2.244	0.107
	SPP*TRTM*LIGHT	0.055	4	0.112	0.978
	DIST	SPP	183.042	2	14.408
TRTM		0.114	2	0.009	0.991
LIGHT		117.138	1	9.220	0.003
SPP*TRTM		1.329	4	0.105	0.981
SPP*LIGHT		34.028	2	2.678	0.071
TRTM*LIGHT		5.825	2	0.458	0.633
SPP*TRTM*LIGHT		17.165	4	1.351	0.252

Table 2. Results obtained by performing a three-way ANOVA. Abbreviations in the table are: SPP=species (Enallagma, Ladona and Leucorrhinia), TRTM= treatment (tap water, fish odor or fish), DF= Degrees of Freedom, P=probability, Move=movement (frequency of) and DIST= distance (of movement).

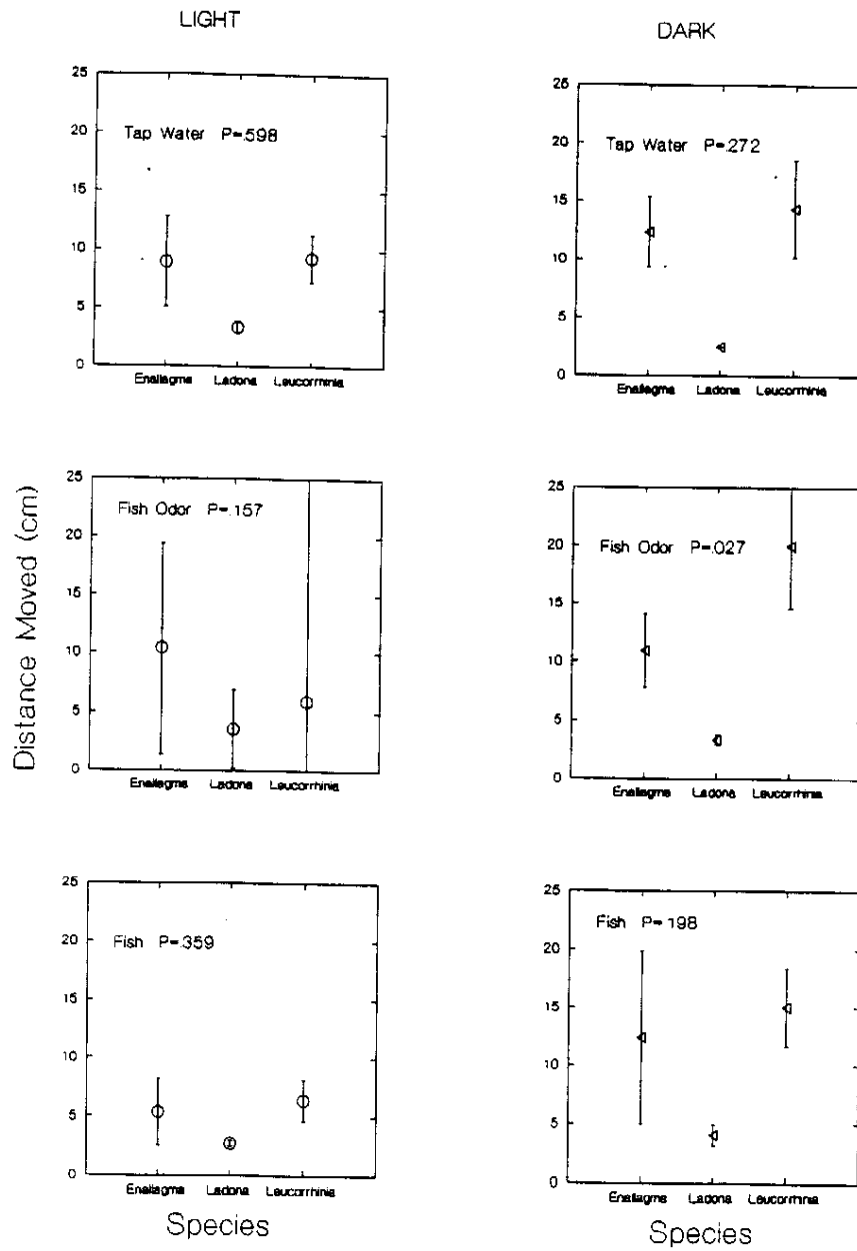
Behavior in Odonata

Figure 1. Proportion of Times Larvae Moved vs. Species. The error bars represent standard error and the P values indicate differences between species for the conditions within each graph (L:D-treatment combination).



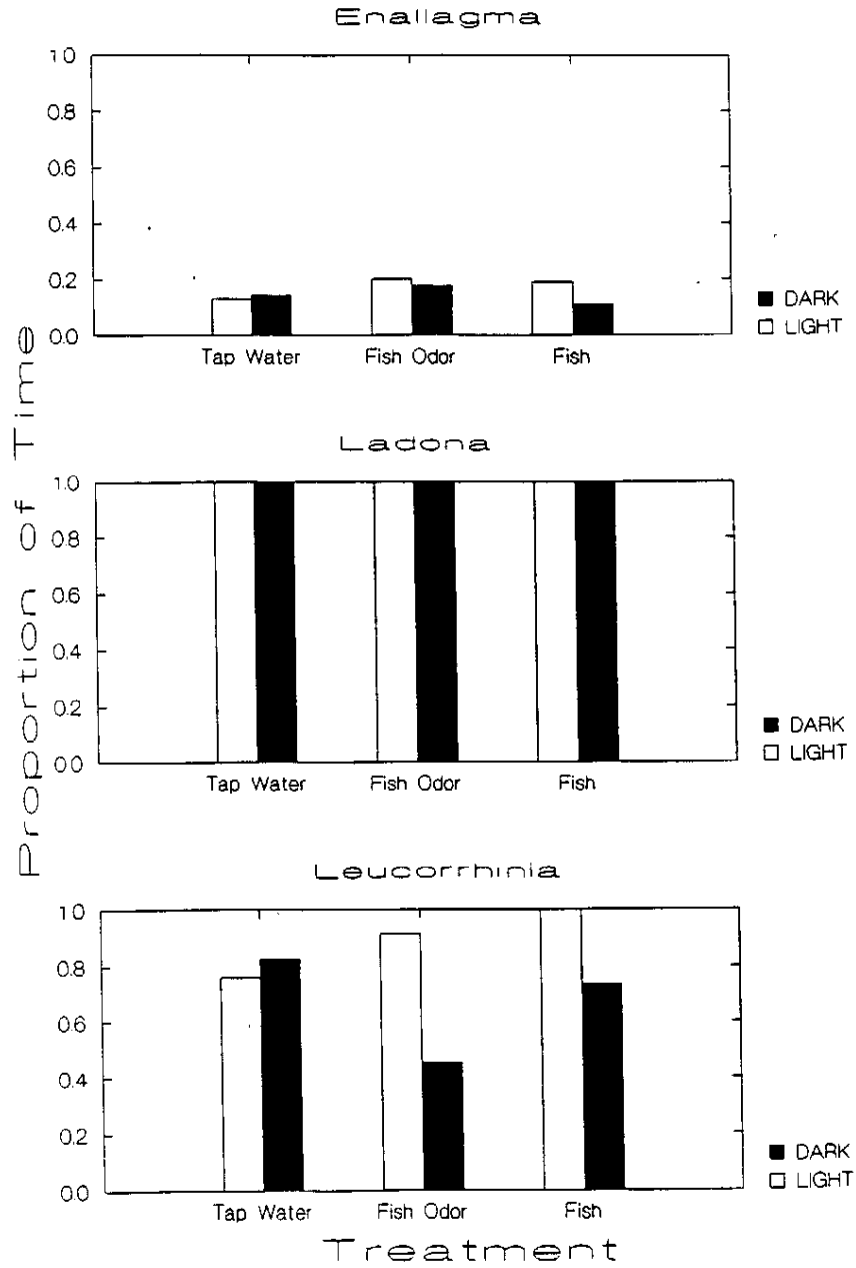
Behavior in Odonata

Figure 2. Distance Moved (cm) vs. Species.
 The error bars represent the standard error and the P values indicate differences between species for the conditions within each graph (L:D-treatment combinations).



Behavior in Odonata

Figure 3. Proportion of Time in Inconspicuous Position vs. Treatment.



Behavior in Odonata

Discussion

This experiment was designed to test the behavioral differences exhibited by different odonate genera and to determine which environmental cues cause behavioral changes. Possible environmental cues which could effect the behavior of the larvae include the presence of fish or fish odor and light conditions. The data obtained in this experiment indicate differences in behavior between genera, but do not attribute these differences to the experimental conditions (the presence of fish or fish odor were not shown to effect the frequency or distance of movement of the larvae). Nilsson (1981), Henrikson (1988) and McPeck (1990) obtained similar results, finding that species of larvae were unable to modify their behavior in the presence of predators.

Gilller and Sangrapub (1993), in their work with Limnephilid caddisflies, found a nocturnal pattern of feeding (increased activity in dark conditions) which they attributed predator activity (active predation under light conditions). Macchiusi and Baker (1992) tested the effects of fish odor on Chironomus tentans larvae. While they did observe decreased activity due to this stimulus during the day, it had no effect on larval behavior during dark conditions. These two experiments suggest a larval adaptation to visual predators. Larvae in this experiment also demonstrated an increase in activity under dark conditions. Furthermore, the genera Leucorrhinia exhibited a tendency to remain in inconspicuous positions under light conditions, moving to more conspicuous areas in the dark.

This lack of response to the experimental treatments (fish and fish odor), coupled with the response to light and dark conditions suggests that the larvae have evolutionarily adapted to the presence of visual predators, namely benthivorous fish. In order to coexist with fish, these larvae exhibit reduced and inconspicuous activity during those hours of the day when they are visible to predators.

Behavior in Odonata

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Behavior in Odonata

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