

FORAGING IN LARVAE OF *AESHNA JUNCEA* (L.): PATCH USE AND LEARNING (ANISOPTERA: AESHNIDAE)

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Three laboratory experiments demonstrated that (1) larvae were able to detect patches of high prey density in small aquaria; — (2) an immobile foraging mode was adopted when prey were abundant, and an active mode when prey was absent and larvae were starved; and — (3) larvae learned to prey on dead *Chaoborus* larvae (Dipt.) after 2 days "training". Some larvae consumed dead *Chaoborus* larvae without previous training. — The observations indicate that *A. juncea* larvae are versatile predators, capable of modifying their foraging behaviour.

INTRODUCTION

According to optimal foraging theory, a predator has to face two main decisions when foraging; which type of food to eat and where to hunt for food (KREBS & DAVIES, 1984). These factors are crucial for the survival of the individual and the dynamics of predator prey interactions. To most predators potential prey are mostly unevenly distributed in space (BEGON et al., 1986). Thus it is important for predators to search in profitable areas to enhance their survival and fitness. Further, if predators aggregate in areas of high prey density this may promote stability in predator and prey populations (HASSELL, 1978).

Several authors have documented that some predators forage actively while others are immobile (e.g. CURIO, 1976; HUEY & PIANKA, 1981). Predators may sometimes shift between these two modes (CROWLEY, 1979). Depending on the characteristics of the prey, theoretical models have been proposed to describe when to use an active mode or an immobile one (e.g. NORBERG, 1977; ANDERSSON, 1981; JANETOS, 1982; CARACO & GILLESPIE, 1986).

Learning is a phenomenon with multiple manifestations, including acquisition of skills, improvement of sensory capabilities, etc. (KACELNIK & KREBS,

1985). It has been shown that predators can modify foraging in relation to prior experience (see references in BERGELSON, 1985). Thus "learning" could cause a change in prey value which may lead to switching and consequently promote predator-prey stability.

Odonate larvae are common predators in the littoral areas of lakes and ponds, and they mainly feed on aquatic invertebrates (CORBET, 1980). In odonate larvae, population densities can often be very high and values exceeding the standing stock of their prey by 2-3 times have been reported (BENKE, 1976). *Aeshna juncea* is one of the largest and most common odonate species in the northern Palearctic (D'AGUILAR et al., 1986). Thus the larval foraging of this species may have profound effects on the structure of aquatic invertebrate communities.

In this paper I ask three main questions about the foraging behaviour in *A. juncea* larvae. Can larvae detect patches of high prey density and adjust their foraging to these patches? Which foraging mode is used when prey is abundant or absent respectively, and which mode is used when the larvae are subjected to severe starvation? Finally I ask if prey learning can be important in prey detection.

MATERIAL AND METHODS

All *A. juncea* larvae (penultimate instar) and prey (*Chaoborus flavicans* Meig., Diptera) used in the experiments were collected from a bog pond in the vicinity of Umeå, northern Sweden. The experiments were conducted during spring and autumn, 1986-1989, under natural light regimens. All foraging trials were performed in small plastic aquaria (18x12, height 12 cm). The aquaria contained approximately 1.6 l tap water (about 17° C). In the bottom of each aquarium a styrelite plate was mounted, into which 40 wooden sticks were driven in a regular squarelike pattern, 2.0 cm apart.

In the first experiment I investigated if *A. juncea* larvae were able to distinguish between patches of high prey density and patches of low prey density. Each aquarium harboured only one larva, and 12 dragonflies were tested. Time spent in each half of the aquarium was measured when 12 *Chaoborus* larvae were placed in only one half. In the central part of each *Chaoborus* an insect pin was run from the side half way through. The living *Chaoborus* larvae were then carefully needed, approximately 3 cm down the wooden sticks, to represent non-mobile wriggling prey. These trials were run for two consecutive days. During the second day I registered the position of the *Aeshna* larvae every hour during an 8 hour period (09:00-17:00 h) as a measure of time spent in each half of the aquarium. The position of each larva was registered from the stick to which it was clinging. When not clinging to a stick (this happened quite frequently) the nearest stick was noted. Prey consumption was compensated for three times each 24 hours (8:00, 12:00 and 16:00 h). Mean number of prey consumed one hour after prey compensation was also noted to get a value of consumption rate.

When evaluating the effect of prey abundance and starvation on foraging mode the same aquarium arrangement as above was used. One *A. juncea* larva was placed in each aquarium 24 hours prior to the experiment. I then evaluated the foraging mode by noting the position of dragonfly larvae every hour during a 9 hour period. I performed this for four treatments; when free-swimming prey were abundant (24 *Chaoborus* larvae per aquarium, and consumption was compensated for as above), when prey was absent, and finally (also in the absence of prey) when dragonflies were starved for 12 and 25 days, respectively. I used 13 *Aeshna* larvae in each treatment.

Each larva was used only once except for the starvation treatment where each larva was used after both starvation periods. The changes of position were treated as number of movements per day and compared with a test by means of normal deviate z (SNEDECOR & COCHRAN, 1967). Because of comparing all combinations, a sequentially rejective multiple test procedure as described by HOLM (1979) was used.

In the "learning" experiments the same aquarium arrangement as above was used. This experiment consisted of two treatments and I used 18 dragonfly larvae in each. In the first treatment I needed 12 dead *Chaoborus* larvae in a regular manner to the wooden sticks in each of the aquaria. One *A. juncea* was placed in each aquarium, and the number of *Chaoborus* larvae eaten was noted three times over 24 hours (08:00, 12:00, 16:00 h) for four consecutive days. In the second treatment I used 12 living *Chaoborus*, carefully needed to the wooden sticks, to represent non-mobile prey during the first two days. These living prey larvae were then exchanged for dead ones during the following two days. Prey eaten were compensated for as above in both these treatments.

RESULTS

Of the 12 *Aeshna* larvae tested in the prey patch experiment three did not eat, and thus were excluded from further analyses. The larvae did differ with respect to time spent in good and poor foraging patches. There was a significant difference (Mann-Whitney U-test, $p < 0.05$) between the number of times dragonflies were situated in the halves of the aquaria containing *Chaoborus* ($\bar{x} = 5.7$, S.D. = 0.5) compared with the halves without prey larvae ($\bar{x} = 3.3$, S.D. = 0.5). Almost all prey were preyed upon during the first hour after prey compensation. Mean number of *Chaoborus* consumed within the first hour after prey compensation was 10.7 (S.D. = 1.5) and 9.6 (S.D. = 2.9) at 09:00 and 13:00 hour, respectively.

A. juncea larvae showed an immobile foraging mode when prey was abundant and the mean number of moves was 1.8 per day (S.D. = 1.2). An active foraging mode was observed in the absence of prey, and the mean number of moves was 4.4 per day (S.D. = 1.4). Starved larvae also showed an active foraging mode. The mean number of moves after 12 days was 4.9 per day (S.D. = 1.4), while the corresponding figure was 5.2 (S.D. = 1.3) after 25 days of starvation. The number of moves in the prey treatment differed significantly ($p < 0.001$) from all other treatments. No significant difference ($p > 0.05$) was found between the non-prey treatment and the two starvation treatments.

The "learning" experiment showed that *A. juncea* larvae were able to learn how to forage on dead *Chaoborus* larvae (Tab. I). More dead *Chaoborus* were eaten per day by those larvae that had been trained on living *Chaoborus* larvae during the previous two days. During the initial two days living *Chaoborus* larvae were significantly more often consumed compared to the dead ones (Mann-Whitney U-test, $p < 0.001$ and $p < 0.01$, respectively). A Mann-Whitney U-test showed a significant difference ($p < 0.05$ and $p < 0.01$, respectively) in the number of dead *Chaoborus* larvae eaten during the third and fourth experimental days between the two treatments. There was no difference in the number of *Chaoborus* eaten

Table 1

Mean number (N) of *Chaoborus* larvae eaten per *A. juncea* larva per day during four consecutive days. Two treatments are considered, one in which 18 *A. juncea* were fed dead *Chaoborus* for four days and one in which 18 *A. juncea* were fed living *Chaoborus* initially for two days and then dead *Chaoborus* during the two subsequent days. — [SD = standard deviation]

Dead <i>Chaoborus</i> for 4 days			Living <i>Chaoborus</i> for 2 days dead <i>Chaoborus</i> for 2 days		
	N	SD		N	SD
day 1	0.8	2.6	day 1	10.8	10.2
day 2	2.8	7.0	day 2	17.7	14.5
day 3	3.8	8.4	day 3	15.4	12.6
day 4	3.1	7.2	day 4	16.7	13.2

during the four consecutive days in either of the two experimental treatments (Kruskal Wallis test, $p > 0.05$) for both treatments.

DISCUSSION

The term "area restricted search" (HASSELL & MAY, 1974) predicts that a predator should spend more time in patches of high prey density than in patches of low prey density. *A. juncea* larvae responded to areas of high prey density in this experimental set up. Although aquatic invertebrates often have an aggregated distribution (SMYLY, 1957; ULFSTRAND, 1967; TOWNSEND & HILDREW, 1979; MINSHALL, 1984), not many invertebrate predators seem to search more intensively in areas of high prey density (PECKARSKY, 1984; BAKER, 1986). The absence of this behaviour could be due to lack of discrete persistent prey patches (BAKER, 1986), or mutual interference (PECKARSKY, 1984). However, in the laboratory, damselfly larvae have been shown to react to different prey densities (BAKER, 1980; McPEEK & CROWLEY, 1987). *A. juncea* larvae did not confine their foraging to the patches of high prey density. They did in fact spend some time in the low prey density area. I suggest that this could be due to too low density differences in prey during the latter part after prey compensation. The high predation rate during the first hour after prey compensation when the whole prey patch was almost annihilated supports this interpretation. Further, ROWE (1987) showed that larvae of *Hemianax papuensis* (Burm.) (Aeshnidae) larvae were very versatile aquatic predators, and they moved towards prey 5-10 cm away. Thus it may be that the two prey densities here offered were both judged as equal given the small aquaria used. The whole aquarium may have been regarded as one and the same patch. The change in foraging mode observed in my second experiment showed that *A. juncea* larvae used an active foraging mode when prey densities were low, whereas at high prey

densities they did not move. These data give additional support to the hypothesis that *A. juncea* larvae have the ability to assess prey density and detect high density patches.

According to a model proposed by JANETOS (1982), an active foraging mode should be favoured if the cost of moving is small and the difference between good and poor foraging sites is large. As aquatic prey often aggregate, good and poor foraging sites should differ markedly with respect to profitability. Thus, the foraging mode of *A. juncea* seems to be in accordance with the model. The foraging mode during starvation (active) observed in *A. juncea* is in accordance with observations on other dragonfly larvae (CROWLEY, 1979; HEADS, 1985). However, ETIENNE (1972) found that *Aeshna cyanea* (Müll.) decreased all movements and remained immobile when food deprived. It should be noted that Etienne's observation periods only lasted for 5 minutes.

Learning should bring more efficient exploitation of prey. The learning experiment performed showed that *A. juncea* larvae have a great capacity for learning. The results were in accordance with those on other aeshnids, where it has been shown that training affects the efficiency of prey capture (BERGELSON, 1985; BLOIS & CLOAREC, 1985). Learning can affect prey preference and switching, which in turn may have profound effects on the dynamics of the prey populations (HASSELL, 1978). Whether the ability of *A. juncea* to utilize dead prey was an effect of a specific search image (TINBERGEN, 1960), or an effect of searching in specific areas (near the top of the wooden sticks where the prey were situated) can not be evaluated in this experiment. PRITCHARD (1965) concluded that prey must move to elicit attacks in dragonfly larvae. My results indicate that under certain circumstances the shape of the prey may be a key stimulus eliciting an attack. However, it should be noted that without previous experience from living *Chaoborus* larvae, attack rates on dead prey were low. ROWE (1987) found that *H. papuensis* larvae preyed on dead snails and concluded that prey shape was important in recognizing a potential food item. Thus these results indicate that the ability to prey on dead items may be an effect of a specific search image. Also, these observations indicate that dead feigning (thanatosis) may be an inefficient antipredator behaviour to certain dragonfly larvae.

The high standard deviations in the treatment where *A. juncea* larvae received only dead *Chaoborus* larvae during four consecutive days (Tab. I) were due to some dragonflies that foraged on dead *Chaoborus* without previous "training" on living larvae. Out of 18 individuals three managed to forage on dead *Chaoborus* as fast as those that had been "trained" on living prey. PFAU (1967) noticed *Aeshna cyanea* (Müll) larvae feeding on spawn of the freshwater snail *Lymnaea stagnalis* (L.) without a previous training on this kind of "prey". These observations suggest high individual variability in foraging. Such a variation may have profound effects on predator fitness and survival. Versatile individuals could switch to more cryptic prey as the density of their prey usual declines. A positive

relationship between consumption rate and growth rate has been found in dragonfly larvae (LAWTON et al., 1980).

The optimal foraging theory has mostly focused on vertebrate predators (KREBS & DAVIES, 1984), and aquatic invertebrate predators are not usually considered (but see SIH, 1980). The versatility of Aeshnidae larvae indicates that these organisms are suitable for testing optimal foraging theories, and thus, enhance our knowledge of aquatic invertebrate predators.

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