CANNIBALISTIC BEHAVIOR IN ARMIGERES SUBALBATUS (DIPTERA: CULICIDAE)

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Abstract. Phenomenon of natural cannibalism was observed to be exhibited by late (III and IV) instar larvae of Armigeres subalbatus. Cannibalistic behavior in this species was studied in response to food and density. Cannibalism among late instars was found to occur even in the presence of an adequate quantity of food. The rate of cannibalism was enhanced when food was restricted to only the early stages. Even in the total absence of food early instars did not show any cannibalistic behavior. Density had no influence on the rate of cannibalism. Under forced cannibalism and predation fourth instar larvae could not successfully pupate but the duration was prolonged. Cannibalism was thus facultative without any value for the survival of larvae. It may help in maintaining a balance in immature density in their natural habitats.

INTRODUCTION

Cannibalism, defined as intraspecific predation, is not uncommon among larval forms of certain mosquito species. Larvae of Toxorhynchites spp. which are basically predators, feeding on the immatures of other mosquitoes are known to be cannibalistic (Furumizo and Rudnick, 1978; Stefan et al., 1980.) This behavioral trait has also been reported to be exhibited at the larval stages of certain other species of mosquitoes that are basically filter feeders or browsers which included Theobaldia longiareolata (Farghal, 1983); Anopheles pharoensis (Shoukry, 1980); An. stephensi (Roy, 1931; Reisen, 1975) and Culex tritaeniorhynchus (Mogi, 1978). Larvae of Armigeres subalbatus, a voracious biter have been reported to be predacious (Fletcher, 1917; Buddle, 1928) as well as cannibalistic (Iyengar, 1920), mainly based on casual observations and no information on the intricacies of this phenomenon is available. Therefore, a detailed study on Ar. subalbatus was conducted seeking to investigate its cannibalistic behavior in response to food and density, and its adaptive value for the survival of this species.

MATERIALS AND METHODS

Direct observation on cannibalistic behavior of Ar. subalbatus larvae was made in the larval rearing trays. As this was not possible in septic tanks which form their natural habitat, indirect observation was made by gut content analysis of the field collected larvae. Larval samples were collected from habitats breeding exclusively Ar. subalbatus to ensure that the larval remnants found in the gut were those of Ar. subalbatus.

Competition between individuals is primarily for the requirements of food and space. The influence of these two factors on cannibalism was studied in the laboratory using colony reared larvae. Experiments were conducted at 28 ± 2°C. A mixture of powdered dog biscuit and yeast in the ratio of 3:2 was provided as food. In all experiments the number of live larvae was recorded daily, so also the number of pupae until emergence was over. Larvae found dead without any injury were taken as natural mortality. The larvae that were found missing as well as those found injured were considered to be dead due to cannibalism.

The influence of food on cannibalism was studied with three different food regimens. This included:

- **Group A** - food provided *ad libitum*
- **Group B** - food given once at the beginning of the experiment
- **Group C** - subjected to starvation from the beginning

Experiments in duplicate were started with 100 freshly hatched first instar larvae released in trays of size 20 × 15 × 5 cm with one liter of water.
Another set of experiments (Group D) was conducted by depriving food to the larvae precisely from the third instar level, the stage from which they exhibited cannibalistic tendency. Larvae since hatching were reared on normal food until they moulted to third instar ($n = 50$ in replicates) after which food was withheld.

To determine the effect of density on cannibalism, 100, 200 and 400 freshly hatched first instar larvae were released in trays ($20 \times 15 \times 5$ cm) with 1 liter of water and food was provided ad libitum. A replicate was also run simultaneously.

The endurance of *Ar. subalbatus* to sustain itself through cannibalism (forced cannibalism - Group E) by withholding food at fourth instar level when cannibalism is observed to be pronounced was also studied. Larvae were reared on normal food up to the third instar and when they moulted to the fourth instar, 50 larvae were isolated individually in plastic containers. Normal food was withheld and 10 third instar larvae of *Ar. subalbatus* were added to each container as prey. The number consumed was recorded, the remaining larvae were removed and 10 fresh third instar larvae were added daily. The length of time each fourth instar survived and the number that pupated and emerged successfully were noted. A similar experiment was conducted by providing larvae of *Culex quinquefasciatus* as prey (group F - forced predation). Control (group G) was maintained on normal food.

**RESULTS AND DISCUSSION**

As many as 100 fourth instar larvae collected from natural habitats were subjected to gut content analysis. Remnants of larval parts were observed in 16 (16 %) larvae, confirming cannibalism as a natural phenomenon.

The effect of different food regimens is shown in Table 1. Out of 200 larvae reared with larval food ad libitum, 19 (9.5%) were found dead due to natural causes and 17 (8.5%) were eaten by their own kind. 164 larvae (82%) successfully pupated and 162 (81%) emerged into adults. When the larvae were deprived of food (Group B) the percentages dead (20.5%) and eaten (79%) were higher compared to that when food was given ad libitum. Only one had pupated but that too failed to emerge. In Group C where food was deprived from the time of hatching (total starvation), the proportions of larvae dead and eaten were 65% and 35% respectively and none pupated. When food was withdrawn at third instar (Group D) the proportions of larvae dead and eaten were 25% and 74% respectively and only one larva pupated and emerged successfully.

No instance of cannibalism was noticed among first and second instars in all these observations. Only third and fourth instars exhibited this behavior. Also, the early instars (I and II) and pupae were not preferred as prey. Only active and healthy larvae were seized and consumed while dead larvae were ignored. Nevertheless, larvae lying injured by bites were readily picked up by others and consumed. Congregational feeding was common where a single injured larva was held by a group feeding on it simultaneously.

Cannibalism was observed to be common even in the presence of adequate amounts of food. There was no preference for selection of site in seizing the prey and consumption was not in toto. Head capsule and the siphon were usually discarded. Unlike the first and second instars, the mandibles of the third and fourth instars are well developed with serrated margins. The cutting organ occupies the major part of the mandible and the mandibular hairs are short and simple, which facilitates seizure of the prey and cutting them into pieces. The maxillary brush is composed of apically serrated sharp spines. This may also aid in seizing the prey.

**Table 1**

<table>
<thead>
<tr>
<th>Group</th>
<th>Released</th>
<th>Dead</th>
<th>Eaten</th>
<th>Pupated</th>
<th>Emerged</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>200</td>
<td>19</td>
<td>17</td>
<td>164</td>
<td>162</td>
</tr>
<tr>
<td>B</td>
<td>200</td>
<td>41</td>
<td>158</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>C</td>
<td>200</td>
<td>130</td>
<td>70</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>D</td>
<td>100</td>
<td>25</td>
<td>74</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

A = Food ad libitum; B = Food at day 1 only; C = No food; D = Food withdrawn at third instar.

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To analyse the cannibalistic behavior in different groups, the cumulative values of the number dead as well as number eaten were plotted along with number surviving on different days, until all the larvae either pupated or died (Fig 1a-d). It was evident that the availability of adequate amount of food had not precluded cannibalism as observed in group A. Further, the pattern as well as the level of natural mortality and cannibalism was determined not merely by the presence or absence of food but by the time at which food was deprived. When food was available throughout (group A), natural mortality started on the third day while cannibalism was observed on the fourth day. Both natural mortality and cannibalism were at low level and almost equal (Fig 1a).

In group B natural mortality started on the third day and remained at a low level as seen in group A. However, cannibalism which started on fifth day gradually increased up to eight day after which there was a steep rise accounting for its high rate (Fig 1b). This shows that the availability of food at the initial stage had helped the larvae to attain the stage capable of devouring others when food was no more available. Only one larva had pupated but emergence was not successful.

Larvae were able to develop even in the total absence of food (group C). Natural mortality started on the third day as in the other groups but gradually increased up to the last day. Cannibalism started late (sixth day) and gradually escalated but did not surpass natural mortality (Fig 1c).
Absence of food had delayed development and resulted in higher mortality of larvae before they could attain the stage capable of devouring others. Thus the rate of cannibalism in this group was relatively lower (35%) compared to group B (79%).

The daily rate of cannibalism, when compared between group B and group C (Fig 2) showed that in both the groups cannibalism began late indicating that even in the absence of food cannibalism occurred only among the late instars. However, the progress in the rate of cannibalism differed considerably between the two groups. While starvation since beginning in group C resulted in wide fluctuation, the lack of food at later stages (group B) lead to pronounced cannibalism eventually producing a single peak.

The number of larvae surviving and cumulative natural mortality and cannibalism for different days in group D (Fig 1d) was comparable with that of group B (Fig 1b) confirming that the food provided on the first day in group B was only sufficient for the larvae to reach the stage capable of exhibiting pronounced cannibalism on lack of food.

Observations on the effect of density on cannibalism showed that there was cannibalism at all density levels, with 5.0%, 5.5% and 6.5% at 100, 200 and 400 larvae per unit volume respectively. The apparent difference in the degree of cannibalism was, however, not statistically significant (p = 0.74). The percentage of larvae pupated and emerged as adults was over 84.0% at all the density levels and it was not associated with density (p > 0.05) showing that limitation of space does not enhance cannibalism and the highly positive thigmotactic response exhibited by the larvae in the trays in the laboratory as well as in the natural habitats where the larvae tend to aggregate in large numbers at the corners, almost piling up on each other, is suggestive of the fact that space could never be a limiting factor influencing the cannibalistic behavior of the larvae.

The number of days that the fourth instar survived, the number of larvae consumed, the number pupated and emerged in the groups E, F and G are given in Table 2. The number of Ar. subalbatus larvae consumed in group E ranged from 1 to 30, with an average of $10.62 \pm 1.06$ per day. The duration of fourth instar was also prolonged, ranging from 4-20 days with a mean of $11.48 \pm 0.52$ days. When the fourth instar larvae of Ar. subalbatus were forced to feed on third instar of Cx. quinquefasciatus (Group F), the number consumed was relatively higher (range 1-147; mean $48.42 \pm 5.12$ per day). The length of days that the fourth instar survived was also longer and ranged from 5-56 days with a mean of $21.33 \pm 1.79$ days. In both the groups only 10% of the larvae pupated and emergence was 6% in group E and 7.5% in group F. In the control (Group G) all the larvae pupated (100%) and emerged (100%) within normal duration of 4-6 days and 3-4 days, respectively.

Though fourth instar larvae are capable of eating other larvae of their own kind as well as other species only very few larvae were able to survive and complete pupation and emergence, suggesting its facultative cannibalistic behavior. Thus, neither cannibalism nor predation is of advantage to this species for completing its immature development in the absence of food. However, this behavior may help in reducing the density under unfavorable conditions. It remains to be determined whether behavior is similar under natural field conditions.

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### Table 2
Predation, cannibalism and survival.

<table>
<thead>
<tr>
<th>Group</th>
<th>Number observed</th>
<th>Number of days survived</th>
<th>No. of larvae consumed</th>
<th>Number pupated</th>
<th>Pupal duration</th>
<th>Emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range     Mean ± SE</td>
<td></td>
<td>Range       Mean ± SE</td>
<td></td>
<td>Range        Mean ± SE</td>
<td>No.</td>
</tr>
<tr>
<td>E</td>
<td>50        4-20  11.5±0.5</td>
<td></td>
<td>1-30        10.6±1.1</td>
<td>5</td>
<td>3-4           3.7±0.1</td>
<td>3</td>
</tr>
<tr>
<td>F</td>
<td>40        5-56  21.3±1.8</td>
<td></td>
<td>1-147       48.4±5.1</td>
<td>4</td>
<td>3-4           3.3±0.1</td>
<td>3</td>
</tr>
<tr>
<td>G</td>
<td>20        4-6   5.1±0.1</td>
<td></td>
<td>-           -</td>
<td>20</td>
<td>3-4           3.7±0.1</td>
<td>20</td>
</tr>
</tbody>
</table>

E = Forced cannibalism; F = Forced predation; G = Control (Food ad libitum).

### REFERENCES


